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Phytogeographical Analysis of Seed Plant Genera in China

HONG QIAN[1,2,*], SILONG WANG[2], JIN-SHENG HE[3], JUNLI ZHANG[4], LISONG WANG[5], XIANLI WANG[6] and KE GUO[7]

[1]Research and Collections Center, Illinois State Museum, 1011 East Ash Street, Springfield, IL 62703, USA, [2]Center for Forest Ecology and Forestry Eco-engineering, Institute of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang, Liaoning 110016, China, [3]Department of Ecology, College of Environmental Sciences, Peking University, Beijing 100871, China, [4]School of Life Sciences, Sun Yatsen University, Guangzhou 510275, China, [5]Research Center of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China, [6]Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1, Canada and [7]Research Center of Plant Ecology and Biodiversity Conservation, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

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• *Background and Aims* A central goal of biogeography and ecology is to uncover and understand distributional patterns of organisms. China has long been a focus of attention because of its rich biota, especially with respect to plants. Using 290 floras from across China, this paper quantitatively characterizes the composition of floristic elements at multiple scales (i.e. national, provincial and local), and explores the extent to which climatic and geographical factors associated with each flora can jointly and independently explain the variation in floristic elements in local floras.
• *Methods* A study was made of 261 local floras, 28 province-level floras and one national-level flora across China. Genera of seed plants in each flora were assigned to 14 floristic elements according to their worldwide geographical distributions. The composition of floristic elements was related to climatic and geographical factors.
• *Key Results and Conclusions* Variations in percentages of cosmopolitan, tropical and temperate genera among local floras tend to be greater at higher latitudes than at lower latitudes. Latitude is strongly correlated with the proportions of 13 of the 14 floristic elements. Correlations of the proportions of floristic elements with longitude are much weaker than those with latitude. Climate represented by the first principal component of a principal component analysis was strongly correlated with the proportions of floristic elements in local floras ($|r| = 0{\cdot}75 \pm 0{\cdot}18$). Geographical coordinates independently explained about four times as much variation in floristic elements as did climate. Further research is necessary to examine the roles of water–energy dynamics, geology, soils, biotic interactions, and historical factors such as land connections between continents in the past and at present in creating observed floristic patterns.

Key words: Biogeography, climate, floristics, latitudinal gradient, regionalization, seed plants.

INTRODUCTION

A central goal of biogeography and ecology is to uncover and understand distributional patterns of organisms. China has long been a focus of attention because of its rich biota, especially with respect to plants (Wu, 1991; Axelrod *et al.*, 1998). The composition of the flora of China has been well documented through the compilation of the *Flora Reipublicae Popularis Sinicae* (an 80-volume set of 125 books, all having been published during 1959–2004), the *Flora of China* (Wu and Raven, 1994 to present; 11 volumes having been published), and many regional, provincial and local floras. Although China is nearly identical in size and of similar latitudinal breadth to the United States (9·6 vs. 9·4 million km^2), the vascular plant flora of China is richer than that of the USA by a factor of 1·6 (Qian and Ricklefs, 1999). Of the world's estimated 260 140 species of vascular plants (Mabberley, 1997), approximately 30 000 (or 11·5 %) occur in China. The earliest (at least 124·6 million years old) angiosperm megafossil known to date, from the Archaefructaceae, is found in China (Sun *et al.*, 2002). China is also the only country in the world that supports vegetational continuity from tropical, subtropical, temperate to boreal forests (Axelrod *et al.*, 1998). This unbroken latitudinal gradient of forest vegetation, together with many north–south-orientated, highly rugged mountain ranges in south-western China, presumably reduced rates of extinction when advances and retreats of Pleistocene glaciations forced plant species to migrate southward and northward in response to climate change. Furthermore, the collision of the Indian subcontinent with the Asian continent commencing about 50 million years ago (Ma) created highly dissected and elevated landscapes in China, which made the region not only an important centre of survival (i.e. a 'living museum' or 'refugia'), but also an important centre of speciation and evolution (i.e. a 'cradle') for vascular plants (Axelrod *et al.*, 1998; Qian, 2002). Many genera and families of vascular plants can be found nowhere else (Ying *et al.*, 1993). The flora of China is considered to be a mixture of Laurasian, Gondwanan and Tethyan

* For correspondence. E-mail hqian@museum.state.il.us

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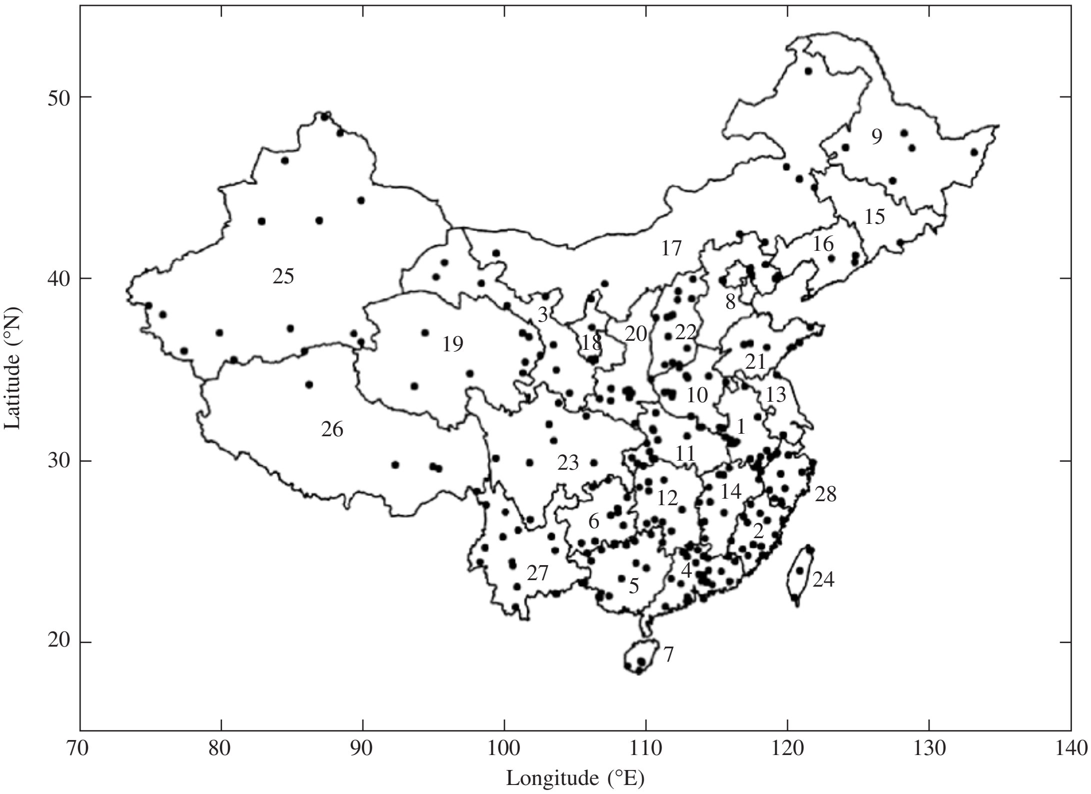

FIG. 1. Map showing the locations of the 261 local floras (dots) and 28 province-level floras (numerical codes) used in this study. Numerical codes for the provinces are: 1 = Anhui, 2 = Fujian, 3 = Gansu, 4 = Guangdong (including Hong Kong, Shenzhen and Macau), 5 = Guangxi, 6 = Guizhou, 7 = Hainan, 8 = Hebei (including Beijing and Tianjin), 9 = Heilongjiang, 10 = Henan, 11 = Hubei, 12 = Hunan, 13 = Jiangsu, 14 = Jiangxi, 15 = Jilin, 16 = Liaoning, 17 = Neimenggu, 18 = Ningxia, 19 = Qinghai, 20 = Shaanxi, 21= Shandong, 22 = Shanxi, 23 = Sichuan (including Chongqing), 24 = Taiwan, 25 = Xinjiang, 26 = Xizang, 27 = Yunnan, and 28 = Zhejiang (including Shanghai).

elements (Wu, 1988), thus providing unique opportunities for addressing numerous important issues concerning global biogeography.

A major approach used to characterize a flora or fauna and to determine its biogeographical relationships with other regions is to group the taxa that comprise the flora or fauna of a given geographical area into geographical elements or types, defined according to the geographical range of taxa (Stott, 1981). Zhengyi Wu (C. Y. Wu) used this approach to characterize the flora of China at the generic level, based on floristic relationships between China and the rest of the world. He grouped the genera of Chinese seed plants into 15 areal types (floristic or phytogeographical elements), based on their worldwide distributions, and the results of his studies were reported in several publications (e.g. Wu, 1980, 1991; Wu and Wang, 1983). Following his classification, several hundred regional, provincial and local floras in China have been analysed. Each analysis tabulated the number of genera in each of the 15 areal types. However, none has analysed multiple floras except for a few studies that focused on a particular region (e.g. Shen and Zhang 2000). Little is known about how floristic patterns are related to climatic conditions and geographical factors.

The objectives of this study were to characterize quantitatively the composition of floristic elements in floras across China at multiple scales and to explore the extent to which geographical variables (e.g. latitude, longitude, area, elevation) and climatic variables (e.g. temperature and precipitation) can jointly as well as independently explain the variation in each of the different floristic elements in local floras. In addition, the present paper updates tabulations of genera in each of Wu's floristic elements for all of China and each of its provinces.

MATERIALS AND METHODS

Data sets

A database was compiled that included all genera of seed plants known in China primarily based upon the *Flora Reipublicae Popularis Sinicae*, *Flora of China*, regional and provincial floras, and journal articles pertinent to the flora of China. Electronic data from the *Flora of China Checklist* (http://mobot.mobot.org/W3T/Search/FOC/projsfoc.html) and the electronic version of the *Flora of China* included in eFlora (http://www.efloras.org/) were frequently accessed during this compilation. The information for the presence/absence and native/exotic status of each Chinese seed plant genus was documented for each of the 28 Chinese provinces and autonomous regions (all provinces and autonomous regions are referred to as provinces hereafter for convenience of discussion; Fig. 1).

TABLE 1. *Definitions of floristic elements*

Cosmopolitan (FE1)	Widely distributed across all or nearly all continents. In general, they do not have special distribution centres. Occasionally they have one or a few centres of high diversity but are distributed worldwide.
Pantropical (FE2)	Occurring in all three sectors of the tropical zone (i.e. America, Africa–Madagascar and Asia–Australia). Some of the genera in this category may have species extending into temperate regions.
Tropical Asian–tropical American (FE3)	Disjunct between tropical Asia and tropical America. Some of them may be sporadically distributed on the islands of the Pacific, or may extend into temperate regions.
Palaeotropical (FE4)	Distributed in the tropics of the Old World: Asia, Australia and Africa (including Madagascar). This floristic element is also called the 'Old World Tropics' in the literature.
Tropical Asian–Tropical Australian (FE5)	Restricted to Asia and Australia and mainly distributed in the tropical regions of these two continents.
Tropical Asian–Tropical African (FE6)	Restricted to Asia and Africa and mainly distributed in the tropical regions of these two continents.
Tropical Asian (FE7)	Mainly restricted to tropical Southeast Asia, although some may extend northward into temperate regions.
Holarctic (FE8)	Primarily distributed in extratropical regions of all three continents in the Northern Hemisphere (Europe, Asia and North America), although a few extend their distributions to high elevations of tropical mountains or further south. This floristic element is referred to as 'North Temperate' in Wu (1980, 1991), and also called 'Eurasian–North American' and 'circumpolar' in the literature.
Eastern Asian–North American (FE9)	Having disjunct distributions between the temperate–subtropical regions of eastern Asia and North America, with a few extending into tropical regions of their respective continents.
Temperate Eurasian (FE10)	Widely distributed across the temperate zone of Europe and Asia. Some of them may extend into the northernmost part of Africa, but they do not occur in the New World. This floristic element is referred to as 'Old World Temperate' in Wu (1980, 1991).
Temperate Asian (FE11)	Restricted to temperate Asia. The distribution centres are mainly in temperate regions but they may occasionally occur in subtropical regions.
Mediterranean, western to central Asian (FE12)	Distributed mainly in the region across the Mediterranean, western Asia and central Asia. Some of the genera extend eastward into eastern Asia.
Central Asian (FE13)	Mainly distributed in dry areas of central Asia.
Eastern Asian (FE14)	Distributed mainly in warm temperate to subtropical regions of eastern Asia. This floristic element includes all genera in the categories 'eastern Asian' and 'Chinese endemic' of Wu (1991, 1993).

Following Wu (1991, 1993), each genus of the Chinese seed plants was assigned to one of the following floristic elements based on the native distributions of each genus: cosmopolitan, pantropical, tropical Asian–tropical American, palaeotropical, tropical Asian–tropical Australian, tropical Asian–tropical African, tropical Asian, holarctic, eastern Asian–North American, temperate Eurasian, temperate Asian, Mediterranean, western to central Asian, central Asian, eastern Asian, and Chinese endemic (Table 1). Because the geographical limit of Chinese endemics was set by the national border of China and because the nature of this floristic element is by and large shared with the eastern Asian floristic element, as discussed in Qian *et al*. (2003), the Chinese endemics were combined with the eastern Asian floristic element in data analyses. Geographical delineations of the 14 floristic elements are described in Table 1. The proportions (in percentages) of genera for each of the 14 floristic elements in China as a whole and in each of 28 provinces were tabulated.

Data of floristic element composition in local floras were collected primarily from literature that was exclusively published in Chinese. The literature to 2003 was searched, including floras, books, monographs, proceedings, theses and journal articles. Data were found on the floristic elements defined by Wu for over 300 local floras. The following were excluded: those floras that were atypical to a region (e.g. floras from dry-hot valleys in south-west China, small limestone areas, wetlands), that applied to a particular type of vegetation (e.g. evergreen plant communities, alpine tundra), that did not include all seed plant genera in a flora (e.g. only for woody plants or halophytes), or that did not provide geographical coordinates. As a result, 232 local floras were selected. In addition, there are 29 floras for which the number of genera for each of Wu's floristic elements is not available in the original literature, and for these seed plant genera were tabulated in each of Wu's 15 floristic elements. As a result, a total of 261 local floras were included in the present study. These floras sampled every province and the full geographical range of China (Fig. 1). Most characterized vegetation in nature reserves. Chinese endemic genera were combined with eastern Asian genera in data analyses as discussed above.

For each flora, latitude and longitude (°) of the geographical midpoint and, if available, area (km^2), maximum elevation (m) and topographic relief (elevation range; m) were recorded. Of the 261 local floras, 215 have area size data, and 151 have area size data plus maximum elevation and topographic relief. The mean area of the 215 floras is 15 327 km^2, which is equivalent to a circle with a diameter of approximately 140 km. Several climatic variables were also obtained for the latitude–longitude half-degree grid point closest to the geographical midpoint of each flora using data in the International Institute of Applied System Analysis (IIASA) climatic database

(Leemans and Cramer, 1991). This database provides values for each 0·5° of latitude and longitude. The climatic variables were mean annual temperature (°C), mean January temperature (°C), difference between mean January temperature and mean July temperature (°C), annual precipitation (mm) and summer (May to August) precipitation (mm). Two derived climatic indices were included: actual evapotranspiration (AET, mm) and potential evapotranspiration (PET, mm), which is proportional to the drying power of the environment, primarily a function of temperature. AET and PET were calculated following the approach developed by Cramer and Prentice (Cramer and Prentice, 1988; Prentice *et al*., 1992, 1993). These variables are often considered the most important climatic factors generating large-scale biotic patterns (e.g. Turner *et al*., 1988; O'Brien, 1998; O'Brien *et al*., 1998; Qian, 1998; Badgley and Fox, 2000; Rahbek and Graves, 2001; Diniz-Filho *et al*., 2003; Hawkins and Porter, 2003; Qian and Ricklefs, 2004; Ricklefs *et al*., 2004).

Data analyses

To minimize the effect of area size on analytical results, the percentage contribution of each floristic element to a flora was used to compare the compositions of floristic elements between floras. The total number of seed plant genera and the proportions (%) of genera for each floristic element were tabulated for the flora of China as a whole and for each province. The proportion of genera for each of the 14 floristic elements in the 261 local floras was summarized for their mean and standard deviation (s.d.) for each of the 28 provinces in China.

Spearman's rank correlations were used to determine correlations between proportions of floristic elements and latitudes and longitudes using the 261 local floras. To examine the relationships between floristic element compositions and climatic conditions, multivariate analyses were first performed to extract fewer synthetic variables for each data set and these resulting variables were then related to each of the original variables of the two data sets. A principal component analysis (PCA) was performed on the climatic data set based on a correlation matrix. The statistical significance of principal components was evaluated using the broken-stick model of Jackson (1993). A global non-metric multidimensional scaling (NMDS; Minchin, 1987) was used to extract highly informative dimensions from the data set of floristic elements. NMDS was chosen because it is well suited to floristic data (McCune and Mefford, 1999) and because it makes no assumptions about the data and provides a robust solution. The NMDS used Sørensen's index as a measure of distance with the maximum number of iterations set at 200. Significance of extracted dimensions was evaluated by a Monte Carlo test (30 runs with randomized data).

Using the 261 local floras, partial regressions were performed to determine the variation in floristic elements explained by geographical coordinates and climate. In each partial regression, three coefficients of determination were obtained using three general linear models: one combining both geographical coordinates and climate, one including only geographical coordinates, and the other including only climate. By comparing the three coefficients of determination, the proportions of the variance explained (1) by geographical coordinates independently, (2) by climate independently and (3) by the two jointly can be determined (Legendre and Legendre, 1998). The procedure of Borcard *et al*. (1992; see also Legendre, 1993) was followed by including all terms in a third-order polynomial of geographical coordinates (e.g. x, y, x^2, xy, y^2, x^3, x^2y, xy^2, y^3, where x and y represent latitude and longitude, respectively). This ensures not only linear relationships but also more complex (e.g. quadratic and cubic) relationships between floristic elements and geographical coordinates (Borcard *et al*., 1992). Bivariate plots of the relationships of the proportions of floristic elements and the seven climatic variables used in this study were examined to determine the relationships between these variables; no evidence for non-linear relationships was found.

Because area and elevation vary among the local floras used, which may have effects on the proportional composition of floristic elements in local floras, it is necessary to examine the amount of variation in floristic elements that can be explained by these two geographical variables in addition to the variation explained by latitude and longitude. The same partial regression models mentioned above were used except that climatic variables were replaced with $\log_{10}$-transformed area, maximum elevation and topographic relief.

SYSTAT version 7 (Wilkinson *et al.*, 1992) was used for statistical summaries, correlation analyses and partial regression analyses, and PC-ORD version 4 (McCune and Mefford, 1999) was used for multivariate analyses (i.e. PCA and NMDS).

RESULTS

According to the data, China has 3143 genera of native seed plants. Of these, 105 (3·3 %) are cosmopolitan, 1512 (48·1 %) are tropical in nature (FE2–FE7 in Table 2) and 1526 (48·6 %) are primarily temperate (FE8–FE14 in Table 2). In total, 590 (18·8 %) genera are restricted to eastern Asia, of which 270 are endemic to China. The total number of seed plant genera and the percentages of genera for each floristic element in each of the 28 provinces are shown in Table 2. The proportion of genera for each of the 14 floristic elements for the 261 local floras was summarized according to province (Table 3).

Latitude strongly and positively correlates with the proportions of genera of the cosmopolitan, holarctic, temperate Eurasian, temperate Asian, Mediterranean, western to central Asian, and central Asian floristic elements, and it strongly and negatively correlates with the proportions of genera in all six tropical floristic elements and negatively correlates with eastern Asian genera weakly but significantly (Table 4). Correlations of floristic elements with longitude are much weaker than those with latitude (Table 4). The strongest correlation is with the proportion of the eastern Asian–eastern North American

TABLE 2. *Total number and proportion (%) of seed plant genera in each of the 14 floristic elements (FE1–FE14) in China as a whole and in the 28 Chinese provinces*

Flora	No. of genera	FE1	FE2	FE3	FE4	FE5	FE6	FE7	FE8	FE9	FE10	FE11	FE12	FE13	FE14
China	3143	3·3	11·2	1·2	6·1	4·8	4·5	20·3	9·6	3·8	5·2	1·8	5·3	3·9	18·8 (8·6)
Province															
Anhui	886	8·5	15·8	1·2	5·0	3·4	2·5	6·0	18·1	8·8	7·8	1·6	0·6	0·2	20·7 (4·3)
Fujian	1195	6·9	18·8	1·8	8·5	5·7	4·1	15·1	11·5	5·8	4·9	0·9	0·6	0·1	15·2 (3·4)
Gansu	753	9·7	8·0	0·8	2·1	1·1	1·5	1·9	28·4	5·8	10·6	3·3	6·8	3·9	16·2 (4·0)
Guangdong	1460	5·8	19·0	1·8	9·8	7·2	5·5	19·0	9·0	4·3	3·6	0·8	0·5	0·1	13·6 (4·2)
Guangxi	1693	5·0	16·2	1·7	8·3	6·6	5·7	24·0	9·1	4·1	3·8	0·5	0·3	0·1	14·6 (4·9)
Guizhou	1249	5·9	16·7	1·5	7·5	4·6	4·6	18·8	12·4	5·1	3·8	1·0	0·2	0·1	17·7 (6·2)
Hainan	1317	5·1	22·4	2·1	11·8	9·2	6·8	26·1	5·2	2·7	2·1	0·2	0·2	0·1	6·1 (1·7)
Hebei	719	11·8	11·1	0·3	2·5	1·9	1·3	1·3	30·9	6·8	11·7	4·3	4·0	1·4	10·7 (2·8)
Heilongjiang	559	14·7	7·7	0·0	1·8	0·5	0·7	0·5	39·0	7·7	12·5	5·2	2·0	0·7	7·0 (0·4)
Henan	505	11·1	10·1	1·4	3·4	2·6	1·2	3·4	27·5	7·9	8·9	3·0	1·6	0·6	17·4 (4·6)
Hubei	1264	6·5	14·5	1·2	5·9	3·6	3·1	10·0	16·7	7·3	7·4	1·8	1·0	0·2	20·9 (6·3)
Hunan	1156	6·5	16·2	1·3	6·7	4·2	3·8	13·1	14·4	7·0	5·8	1·1	0·3	0·1	19·6 (5·6)
Jiangsu	950	8·2	17·5	1·3	6·5	4·1	3·6	9·3	15·9	6·8	7·1	1·5	0·7	0·3	17·3 (3·2)
Jiangxi	1086	7·4	16·7	1·3	6·7	4·1	4·1	12·3	14·3	7·2	6·0	1·0	0·4	0·3	18·2 (4·1)
Jilin	585	13·5	7·7	0·0	1·5	1·0	0·9	1·0	38·3	8·7	12·3	4·1	1·5	0·7	8·7 (0·7)
Liaoning	708	12·1	10·7	0·1	2·5	1·4	1·4	1·3	31·5	7·9	11·4	3·7	2·7	1·1	12·0 (2·5)
Neimenggu	647	12·2	6·6	0·0	1·5	0·8	0·9	0·5	34·9	5·1	13·0	5·7	7·4	4·3	7·0 (1·7)
Ningxia	413	14·0	6·1	0·2	1·2	0·2	0·5	0·5	35·6	5·1	13·3	3·6	7·0	4·1	8·5 (2·7)
Qinghai	581	11·9	5·7	0·2	1·0	0·0	0·5	0·7	33·2	3·4	13·4	4·1	6·4	5·9	13·6 (4·5)
Shaanxi	1014	7·7	11·4	0·9	3·7	1·9	2·5	4·3	22·7	8·0	9·9	2·9	3·2	1·4	19·6 (5·1)
Shandong	586	13·3	14·0	0·5	4·1	2·4	1·7	2·4	27·0	7·3	10·6	2·7	1·9	0·7	11·4 (2·4)
Shanxi	678	10·6	9·6	0·6	1·8	1·9	1·2	1·6	32·0	6·0	11·8	4·1	3·4	1·2	14·2 (3·5)
Sichuan	1384	5·6	13·9	1·3	5·5	3·0	3·9	10·2	17·2	5·7	6·7	1·7	1·2	1·6	22·6 (6·7)
Taiwan	1206	7·0	21·8	2·0	9·9	7·3	4·2	15·1	12·4	5·1	4·2	0·6	0·2	0·1	10·1 (1·3)
Xinjiang	758	10·3	5·8	0·1	0·7	0·1	0·8	0·3	29·6	1·8	13·9	3·4	19·1	11·1	3·0 (0·9)
Xizang	1395	5·8	14·0	1·4	5·9	3·8	4·3	14·7	16·1	4·5	5·9	1·6	3·1	2·3	16·6 (2·7)
Yunnan	2069	4·5	14·2	1·3	7·0	5·2	5·7	24·1	11·2	4·0	4·3	0·9	0·6	0·6	16·4 (5·1)
Zhejiang	1038	8·2	16·0	1·1	6·3	3·9	3·4	8·6	16·3	7·7	7·1	1·2	0·4	0·2	19·7 (4·3)

Values in parentheses under FE14 are the proportions of the Chinese endemic genera. Codes for floristic elements are the same as in Table 1.

genera (r_s = 0·44), which is followed by the correlations with the proportions of the central Asian genera (r_s = – 0·37) and Mediterranean, western to central Asian genera (r_s = –0·35) (Table 4).

The first and second principal components of the PCA had eigenvalues of 5·404 and 0·965, and explained 77·2 and 13·8 % of the variation in the climatic data set, respectively. A broken-stick test indicated that only the first principal component (PC1) was significant. This principal component is highly correlated with all the seven climatic variables ($|r|$ = 0·82 ± 0·07; Table 5), and is correlated highly to moderately with the floristic elements ($|r|$ = 0·75 ± 0·18). The autopilot mode of an NMDS analysis running on the data set of floristic elements recommended a one-dimensional solution, and this dimension (NMDS1) is statistically significant (Monte Carlo test: P < 0·05, n = 30). Correlations between NMDS1 and the seven climatic variables and 14 floristic elements are all significant (P < 0·05), albeit weak in some cases (Table 5). The correlation between PC1 and NMDS1 is high (r = –0·89, P < 0·001), indicating strong relationships between climate variables and floristic elements. Both PC1 and NMDS1 are highly correlated with latitude (r = 0·902 for PC1, r = –0·871 for NMDS1). When the 261 local floras were ordinated by PC1 and NMDS1, the floras south of 30 °N tended to be completely separated from the floras north of it, and the floras north of 40 °N tended to intermingle with those located between 30 ° and 40 °N (Fig. 2).

The geographical coordinates of local floras explained, on average, 79·6 % of the variation in floristic elements (fractions [a] + [b] in Table 6). When climatic variables were added to the models, the two sets of variables together explained, on average, 82·9 % of the variation in floristic elements (Table 6). Partial regressions indicated that large amounts (66 % on average) of the variation in floristic elements were explained by both geographical coordinates and climatic variables (fraction [b] in Table 6). In other words, approximately four-fifths (or 80 %) of the explained variation was shared by the two sets of the explanatory variables. Of 16·9 % of the variance to which independent effects could be attributed, geographical coordinates accounted for 4·1 times as much as did climatic variables (the average of fraction [a] vs. the average of fraction [c] in Table 6, i.e. 13·6 vs. 3·3 %). When individual floristic elements were examined separately, geographical coordinates explained more variation than did climatic variables for 13 of the 14 floristic elements (compare fractions [a] with [b] in Table 6; binomial test: variation explained by geographical coordinates > variation explained by climatic variables, 13 of 14, P < 0·001). For the holarctic genera, the amounts of variation explained independently by geographical coordinates and by climatic variables were nearly equal (4·0 vs. 4·4 %; Table 6).

When using a smaller data set with 151 local floras that have both area size and elevational data (see Materials and methods for details), geographical coordinates explained

TABLE 3. *Mean and standard deviation (s.d.) of the proportion (%) of seed plant genera for each of the 14 elements (FE1–FE14) in local floras according to provinces in China*

Province	Statistics	FE1	FE2	FE3	FE4	FE5	FE6	FE7	FE8	FE9	FE10	FE11	FE12	FE13	FE14
Anhui (16)	Mean	9·7	16·2	1·9	4·2	2·8	2·5	5·2	21·8	8·5	6·9	1·6	0·8	<0·1	18·0 (2·7)
	s.d.	2·3	2·6	0·7	0·9	0·8	0·6	1·7	3·5	1·1	1·5	0·5	0·7	<0·1	3·4 (0·7)
Fujian (12)	Mean	9·4	24·3	3·4	7·1	4·8	4·3	12·3	12·4	5·7	3·2	0·8	0·4	0·1	11·9 (1·5)
	s.d.	1·1	2·9	1·5	1·4	0·7	0·8	2·2	2·7	1·0	0·8	0·7	0·5	0·4	2·9 (0·6)
Gansu (9)	Mean	14·9	6·7	0·3	0·8	0·2	0·4	0·3	35·1	2·3	13·0	4·7	10·6	4·7	5·9 (1·7)
	s.d.	3·9	2·6	0·4	0·5	0·3	0·4	0·3	5·5	1·5	3·1	0·8	7·2	3·2	3·9 (1·0)
Guangdong (25)	Mean	7·8	25·4	3·8	9·6	6·6	5·1	15·6	8·9	4·6	2·7	0·3	0·2	<0·1	9·3 (1·6)
	s.d.	1·0	3·1	1·6	2·0	1·4	0·9	2·0	3·0	1·2	1·0	0·2	0·2	<0·1	3·3 (0·9)
Guangxi (14)	Mean	7·2	20·9	2·6	8·9	5·9	5·2	19·3	9·6	4·7	3·1	0·6	0·2	<0·1	11·9 (2·7)
	s.d.	2·4	2·8	0·6	1·7	1·3	1·4	5·0	2·4	1·6	0·7	0·3	0·2	0·1	3·7 (1·4)
Guizhou (8)	Mean	8·5	17·4	2·6	6·8	4·0	4·3	13·2	15·3	6·7	4·1	0·7	0·5	0·1	15·9 (3·4)
	s.d.	2·8	1·0	0·6	1·9	1·3	1·7	4·7	5·4	2·1	1·3	0·2	0·4	0·2	2·2 (0·9)
Hainan (4)	Mean	4·5	26·9	2·8	12·1	10·5	7·0	26·4	2·8	2·2	0·8	0·1	0·3	<0·1	3·7 (1·2)
	s.d.	0·4	1·9	1·1	1·6	1·1	0·9	1·8	0·6	0·6	0·4	0·1	0·2	<0·1	1·3 (0·5)
Hebei (7)	Mean	13·5	11·9	0·3	2·0	1·4	2·0	1·0	36·2	5·9	11·8	3·7	1·1	0·8	8·6 (1·4)
	s.d.	1·1	2·3	0·3	0·6	0·6	0·8	0·4	3·0	0·4	1·4	1·0	0·5	0·4	1·5 (0·6)
Heilongjiang (5)	Mean	19·1	6·2	0·1	1·5	0·1	0·9	0·5	43·0	5·9	12·6	3·2	0·8	0·6	5·5 (0·1)
	s.d.	3·9	1·5	0·2	0·3	0·2	0·5	0·3	5·8	2·3	1·2	0·9	0·6	0·8	0·8 (0·1)
Henan (14)	Mean	11·0	14·8	1·4	2·7	2·5	2·4	2·7	25·9	6·9	10·1	2·6	1·9	0·7	14·4 (2·6)
	s.d.	1·7	2·4	0·9	0·8	0·4	0·5	1·2	3·2	1·0	1·1	0·6	1·4	0·5	2·7 (1·2)
Hubei (11)	Mean	9·0	13·7	1·7	3·8	2·8	2·5	6·1	23·1	9·1	7·0	1·4	0·2	0·3	19·3 (3·8)
	s.d.	1·3	1·9	0·4	0·7	0·6	0·5	1·3	3·0	1·3	1·5	0·5	0·2	0·3	2·2 (1·0)
Hunan (13)	Mean	8·3	18·1	2·2	5·7	3·7	3·0	9·5	16·9	8·1	5·7	0·7	0·2	<0·1	18·0 (3·6)
	s.d.	1·1	1·4	1·0	0·7	0·7	0·8	1·8	1·4	0·7	0·7	0·4	0·2	0·1	1·9 (1·3)
Jiangsu (3)	Mean	11·8	17·2	1·4	4·3	3·1	2·1	3·7	22·6	8·1	8·5	1·7	0·7	0·2	14·5 (2·3)
	s.d.	1·1	0·7	0·5	1·0	0·4	0·6	0·5	2·4	0·8	0·7	0·1	0·5	0·2	1·7 (0·3)
Jiangxi (11)	Mean	8·1	17·3	2·8	6·1	3·7	3·4	9·7	15·7	7·4	5·3	1·2	0·7	0·3	18·4 (2·7)
	s.d.	2·3	3·2	1·1	0·9	1·4	1·4	2·6	2·9	1·7	1·3	0·8	0·6	0·8	2·5 (0·6)
Jilin (1)	Mean	14·1	5·9	0·2	0·8	0·6	1·4	0·6	41·8	9·2	12·0	5·1	0·6	0·2	7·5 (0·0)
	s.d.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Liaoning (3)	Mean	13·0	9·6	0·3	1·7	0·8	1·9	1·1	35·1	9·2	14·2	2·7	1·5	0·6	8·4 (1·1)
	s.d.	0·9	2·0	0·3	0·5	0·5	0·4	0·3	4·2	0·3	0·7	0·3	0·7	0·1	1·2 (1·0)
Neimenggu (8)	Mean	17·9	6·0	0·3	0·7	0·1	0·6	0·3	40·7	2·7	11·8	5·5	7·0	3·1	3·1 (0·8)
	s.d.	3·0	2·7	0·2	0·3	0·1	0·6	0·3	9·6	1·7	2·3	1·0	6·6	2·9	1·6 (0·6)
Ningxia (3)	Mean	14·1	6·0	0·1	0·5	0·5	0·7	0·9	41·5	3·1	14·6	4·6	6·0	2·5	5·1 (1·6)
	s.d.	3·0	1·0	0·2	0·6	0·5	0·7	0·5	5·2	2·6	1·6	1·7	3·2	1·4	2·1 (0·2)
Qinghai (8)	Mean	14·2	3·1	0·1	0·5	0·0	0·1	0·3	44·4	2·3	12·2	4·6	4·7	4·6	8·9 (2·2)
	s.d.	2·7	1·7	0·3	0·4	0·1	0·2	0·3	3·3	2·0	1·4	1·2	2·4	1·3	3·1 (0·8)
Shaanxi (8)	Mean	9·5	12·2	1·7	2·9	2·0	2·7	3·4	27·0	8·0	9·7	2·3	1·4	0·6	16·7 (3·8)
	s.d.	1·2	1·8	0·7	0·8	0·7	0·8	1·3	4·6	1·1	1·3	0·5	1·1	0·3	1·5 (0·7)
Shandong (6)	Mean	13·9	16·2	0·6	2·7	2·3	2·0	1·8	28·4	6·4	11·4	2·8	1·4	0·9	9·3 (1·2)
	s.d.	1·5	0·9	0·4	0·6	0·3	0·3	0·5	1·3	1·4	0·9	0·4	0·3	0·2	2·2 (0·9)
Shanxi (13)	Mean	12·5	9·3	1·9	1·2	1·2	1·7	1·0	36·3	5·4	13·2	3·8	3·1	1·4	8·0 (1·8)
	s.d.	1·7	2·5	1·3	0·7	0·4	0·8	0·6	5·6	1·2	1·4	0·9	1·0	0·7	2·6 (0·7)
Sichuan (10)	Mean	8·9	15·4	2·5	3·9	2·8	3·5	6·2	23·9	6·5	7·3	1·7	1·1	0·6	16·0 (3·8)
	s.d.	2·2	4·9	1·8	1·6	1·1	1·6	2·9	8·6	1·1	1·5	0·6	0·6	0·7	3·3 (1·5)
Taiwan (3)	Mean	8·7	25·0	2·8	10·0	6·9	4·7	13·2	11·2	5·0	3·1	0·4	0·1	<0·1	9·0 (1·2)
	s.d.	0·8	3·7	0·2	3·5	1·8	0·8	1·4	4·5	1·0	1·1	0·4	0·1	<0·1	3·0 (0·5)
Xinjiang (15)	Mean	15·2	3·3	0·0	0·3	0·0	0·0	0·1	41·4	0·9	12·2	4·6	11·8	6·8	3·5 (0·5)
	s.d.	2·3	1·8	0·0	0·4	0·0	0·1	0·2	8·1	0·6	3·8	2·0	7·5	1·3	2·4 (0·6)
Xizang (4)	Mean	11·3	10·0	1·6	3·3	2·7	3·0	7·9	28·5	3·9	8·0	2·7	1·8	2·4	13·0 (2·1)
	s.d.	4·9	7·2	1·2	3·5	3·0	2·9	9·2	14·0	1·4	4·5	2·5	1·2	3·0	1·7 (0·9)
Yunnan (14)	Mean	7·0	18·1	2·4	6·6	4·2	5·9	17·0	15·3	4·9	4·6	1·0	0·7	0·2	12·3 (2·2)
	s.d.	2·3	2·8	1·0	1·8	1·5	1·2	10·7	6·6	1·3	2·5	0·6	0·6	0·3	3·4 (0·8)
Zhejiang (13)	Mean	9·5	18·4	1·9	5·4	3·5	2·9	7·1	18·5	8·1	5·7	1·5	0·5	0·1	17·1 (2·4)
	s.d.	1·6	1·8	0·9	0·9	0·7	0·7	1·5	2·4	1·6	0·7	0·9	0·4	0·3	1·9 (0·6)

The value in parentheses after a province name is the number of local floras used for that province. Values (%) in parentheses under category FE14 are for Chinese endemic genera. Codes for floristic elements are the same as in Table 1.

approximately the same amount of the variation in floristic elements as they did in the full data set with 261 local floras (80·9 ± 11·2 vs. 79·6 ± 9·3 %, $P = 0·808$). When the proportion of a floristic element was regressed on the geographical coordinates (including all terms in a third-order polynomial) plus $\log_{10}$area, maximum elevation and topographic relief, they together explained, on average, 83·4 % of the variation in floristic elements (Table 7). The largest amount of the explained variation (95·4 %) is with the model for the holarctic genera (Table 7). The amount of the variation in floristic elements explained by geographical coordinates independent of area and elevation variables

TABLE 4. *Spearman rank correlation coefficients between the percentages of each of the 14 floristic elements in local floras (*n = 261*) and latitude or longitude*

Floristic element	Latitude	Longitude
Cosmopolitan	0·81***	0·08^{ns}
Pantropical	–0·87***	0·29***
Tropical Asian–tropical American	–0·80***	0·13*
Palaeotropics	–0·93***	0·18**
Tropical Asian–tropical Australian	–0·91***	0·18**
Tropical Asian–tropical African	–0·87***	0·06^{ns}
Tropical Asian	–0·94***	0·08^{ns}
Holarctic	0·93***	–0·13*
Eastern Asian–North American	–0·05^{ns}	0·44***
Temperate Eurasian	0·93***	–0·06^{ns}
Temperate Asian	0·88***	–0·11^{ns}
Mediterranean, western to central Asian	0·71***	–0·35***
Central Asian	0·74***	–0·37***
Eastern Asian	–0·29***	0·15*

Significance of statistics: *$P < 0·05$, **$P < 0·01$, ***$P < 0·001$, ns = not significant ($P > 0·05$).

TABLE 5. *Pearson correlation coefficients between each of the climatic variables and floristic elements and the first principal component of the PCA and dimension 1 of the non-metric multidimensional scaling (NMDS)*

	Correlation coefficient (*r*)	
Variable	PC1	NMSD1
Climate		
Mean annual temperature (°C)	–0·884***	0·763***
Mean January temperature (°C)	–0·954***	0·846***
Difference in temperature between January and July (°C)	0·837***	–0·792***
Annual precipitation (mm)	–0·870***	0·767***
Summer (May–August) precipitation (mm)	–0·797***	0·684***
Annual actual evapotranspiration (mm)	–0·925***	0·830***
Annual potential evapotranspiration (mm)	–0·875***	0·762***
Floristic element		
Cosmopolitan	0·771***	–0·783***
Pantropical	–0·905***	0·882***
Tropical Asian–tropical American	–0·709***	0·723***
Palaeotropics	–0·888***	0·906***
Tropical Asian–tropical Australian	–0·861***	0·895***
Tropical Asian–tropical African	–0·822***	0·866***
Tropical Asian	–0·789***	0·856***
Holarctic	0·913***	–0·908***
Eastern Asian–North American	–0·346***	0·222***
Temperate Eurasian	0·856***	–0·863*
Temperate Asian	0·857***	–0·827***
Mediterranean, western to central Asian	0·593***	–0·560***
Central Asian	0·717***	–0·638***
Eastern Asian	–0·422***	0·314***

Significance of statistics: ***$P < 0·001$, *$P < 0·05$.

is much larger, by a factor of 18·3, than that explained by area and elevation variables independent of geographical coordinates (compare fractions [a] and [c] in Table 7; 51·2 ± 11·9 vs. 2·8 ± 2·0 %; ANOVA: $F_{1,26} = 224$, $P < 0·001$). Approximately 29 % of the variation in floristic elements is explained jointly by geographical coordinates and by $\log_{10}$area, maximum elevation and topographic relief (fraction [b] in Table 7).

When all tropical and temperate genera were pooled from each of the 261 local floras, the equilibrium latitude between tropical and temperate genera is approximately 27·5 °N (Fig. 3). The proportion of tropical genera decreases drastically and almost linearly from the southernmost latitude (approx. 18 °N) northward to approx. 35–37 °N, from where it decreases slowly and tended to level off. The proportion of temperate genera primarily mirrors, but inversely, the pattern for the tropical genera (Fig. 3). Variation in the percentage of the three major floristic groups (i.e. cosmopolitan, tropical and temperate genera) among local floras tended to be greater at higher latitudes than at lower latitudes (Fig. 3).

DISCUSSION

A major objective of floristic analysis is to identify floristic patterns among the distributions of taxa (Stott, 1981; McLaughlin, 1989). A traditional approach of identifying distribution affinities among the taxa of a flora involves the recognition of floristic elements (phytogeographical elements or areal types) based upon the native worldwide distributional ranges of the taxa. Although floristic elements may be defined in different ways and the assignment of taxa to floristic elements may be more confident for some taxa than others, the floristic element approach has been used widely. For example, Weber (1965) used a hierarchical system of floristic elements to describe the flora of the southern Rocky Mountains; van Balgooy (1976) recognized 15 elements in a study of the phytogeography of New Guinea; Thorne (1972) recognized 16 elements that included all major disjunct distributions; Lausi and Nimis (1985) classified plant species from the Yukon Territory (north-west Canada) into eight elements; Qian (1999, 2001) recognized ten floristic elements in the native flora of North America north of Mexico; and Wu and Wang (1983; Wu, 1991) segregated indigenous Chinese seed plant genera into 15 elements, which they refer to as areal types. Wu's approach has been used in studies of over 400 regional, provincial and local floras across China. Following Wu's approach, except that Chinese endemic and eastern Asian elements were combined, Qian *et al*. (2003) analysed the phytogeography of East Asia that includes the eastern forested part of China, the Korean peninsula, Japan and the Russian Far East. The latitudes of the study area ranged from the southernmost land area of China (at about 18 °N) northward to 73 °N. The floras used in Qian *et al.* (2003) were at the provincial level or equivalent. Thus, the present study extended this by analysing local-scale floras distributed across the entire ranges of latitudes and longitudes in China.

The present study shows that the majority of the variation in floristic elements explained by climatic variables can also be explained by geographical coordinates, and vice versa. However, the amount of the variation uniquely explained by geographical positions is more than that uniquely explained by climatic variables, by a factor of 4·2 on average (Table 6). This suggests that geographical position, represented by latitude and longitude, of a flora

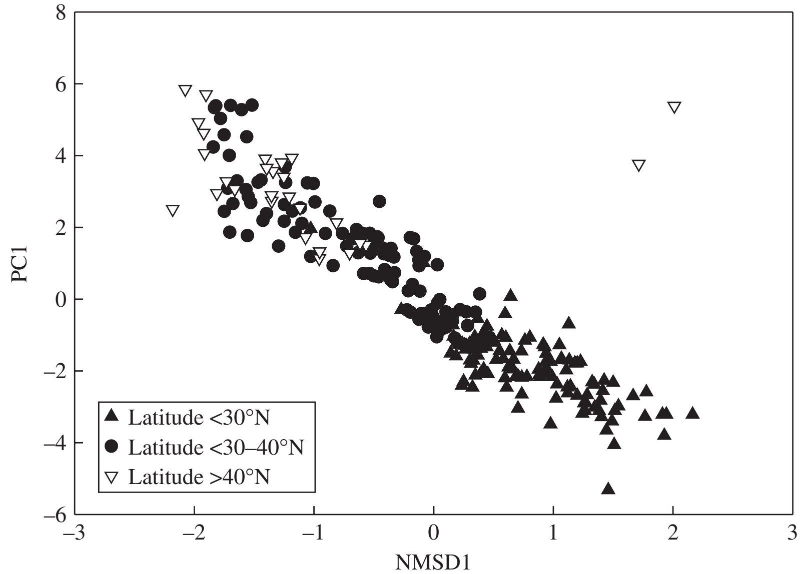

FIG. 2. Diagram showing locations of the 261 local floras in the ordination space of PC1 vs. NMSD1 (see text for details). Floras located in different latitudinal zones are differentiated by symbol.

TABLE 6. *Partial regression analyses of floristic elements on geographical coordinates and climate variables*

	Model (n = 261)			Fraction of R^2		
Floristic element	SS	$F_{16,244}$	R^2	[a]	[b]	[c]
Cosmopolitan	3646	48·4	0·761	0·103	0·636	0·022
Pantropical	13211	115·3	0·883	0·044	0·810	0·029
Tropical Asian–tropical American	565	21·4	0·584	0·056	0·509	0·019
Palaeotropics	2889	157·5	0·912	0·100	0·792	0·020
Tropical Asian–tropical Australian	1515	113·8	0·882	0·089	0·784	0·009
Tropical Asian–tropical African	1025	75·8	0·832	0·097	0·716	0·019
Tropical Asian	14035	121·4	0·888	0·182	0·692	0·014
Holarctic	39607	142·7	0·903	0·040	0·819	0·044
Eastern Asian–North American	1751	46·4	0·752	0·333	0·386	0·033
Temperate Eurasian	4556	100·8	0·869	0·074	0·782	0·013
Temperate Asian	803	73·1	0·827	0·067	0·732	0·028
Mediterranean, western to central Asian	4478	61·8	0·802	0·224	0·458	0·120
Central Asian	1138	100·9	0·869	0·212	0·643	0·014
Eastern Asian	8051	81·7	0·843	0·286	0·481	0·076

[a] = variance explained independently by geographical coordinates, [b] = variance explained jointly by geographical coordinates and climatic variables, and [c] = variance explained independently by climatic variables. All models are significant (P < 0·001). SS = total sum of squares.

has played a more important role in determining the composition of floristic elements than climate. This may be in part because floristic elements are defined by their geographical, rather than ecological, distributions. For example, the genera of the Mediterranean, western to central Asian element and the central Asian element are both centred in the areas west of China. As a result, the proportion of genera belonging to these two elements in a flora decreases from west to east. By contrast, the proportion of genera belonging to the eastern Asian–North American and tropical Asian–tropical American elements increases from west to east.

Variation in the proportional contribution of each of the floristic elements to a flora increases with latitude (Fig. 2). Floras north of 40 °N tend to intermingle with those located between 30 ° and 40 °N (Fig. 3). One possible explanation for this pattern may be that the penetration of some tropical genera into northern floras is determined more by the availability of particular suitable habitats in northern floras than by latitude, which is highly correlated with temperature (MacArthur, 1972). Some more northern localities may hold suitable habitats for certain tropical genera, and these habitats may be absent from some less northern localities. Variation in the proportion of genera belonging to tropical elements ultimately results in variation in the proportion of genera belonging to temperate elements. Testing this hypothesis requires additional data that include information about both plant distributions and local habitats.

The flora of China is strongly linked to the rest of the world. Of the 3143 seed plant genera in China, 1733 (55·1 %) are distributed in two or more of the world's

TABLE 7. *Partial regression analyses of floristic elements on geographical coordinates as one set of explanatory variables and area and elevation as a second set of explanatory variables*

	Model (n = 151)			Fraction of R^2		
Floristic element	SS	$F_{12,138}$	R^2	[a]	[b]	[c]
Cosmopolitan	1568	45·0	0·796	0·439	0·287	0·070
Pantropical	7879	97·9	0·895	0·443	0·422	0·030
Tropical Asian–tropical American	285	13·7	0·543	0·291	0·215	0·037
Palaeotropics	1719	109·1	0·905	0·597	0·299	0·009
Tropical Asian–tropical Australian	887	103·1	0·900	0·584	0·306	0·010
Tropical Asian–tropical African	571	65·0	0·850	0·575	0·257	0·018
Tropical Asian	8426	100·0	0·897	0·662	0·220	0·015
Holarctic	23770	238·7	0·954	0·564	0·353	0·037
Eastern Asian–North American	953	31·0	0·729	0·498	0·207	0·024
Temperate Eurasian	2409	101·4	0·898	0·610	0·283	0·005
Temperate Asian	373	76·9	0·870	0·437	0·408	0·025
Mediterranean, western to central Asian	1241	42·3	0·786	0·471	0·245	0·070
Central Asian	462	57·5	0·833	0·318	0·500	0·015
Eastern Asian	4728	53·0	0·822	0·684	0·105	0·033

[a] = variance explained independently by geographical coordinates, [b] = variance explained jointly by geographical coordinates and climatic variables, and [c] = variance explained independently by climatic variables. All models are significant (P < 0·001). SS = total sum of squares.

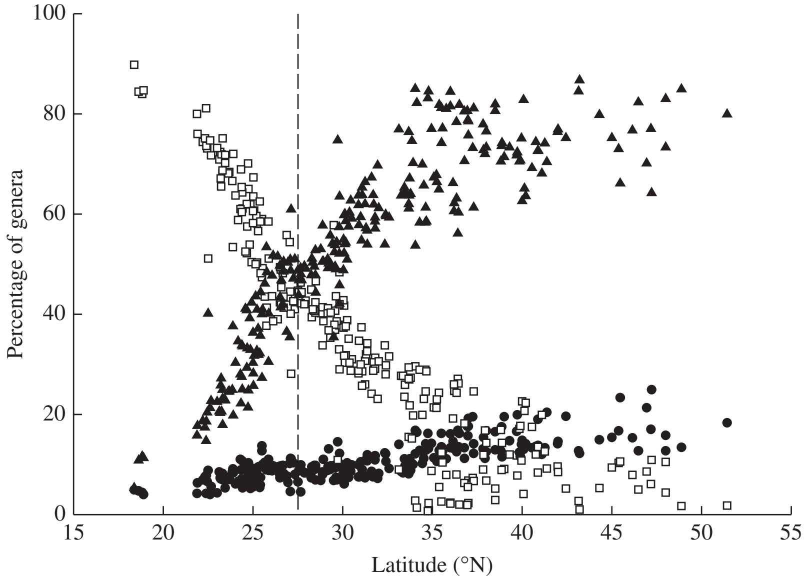

FIG. 3. Latitudinal gradients in the proportions (%) of the cosmopolitan (circles), tropical (squares) and temperate (triangles) genera in the 261 local floras. Tropical genera include those belonging to floristic elements FE2–FE7, and temperate genera include those in FE8–FE14 (see Table 1). The vertical, dashed line indicates the equilibrium latitude (approx. 27·5 °N) between tropical and temperate genera.

continents (i.e. all those genera other than in the floristic elements FE7, FE11, FE13 and FE14 in Table 2). Although counts of genera shared between China and other continents are not available, we may make reasonable estimates based on the number of genera in each of the 14 floristic elements. China shares about 740 genera of seed plants with Europe (i.e. all genera in the floristic elements FE1, FE8, FE10 and FE12 in Table 2), shares no fewer than 650 genera with Africa (i.e. all genera in FE1, FE2 and FE4, and some genera in FE12), shares about 770 genera with Australia (i.e. all genera in FE1, FE4 and FE5 plus those genera in FE2 that reach the Australian continent), shares about 790 genera with North America (i.e. all genera in FE1, FE8 and FE9, and about 260 genera in FE2 and FE3), and shares about 500 genera with Central and South America (i.e. genera in FE1, FE2 and FE3). The floristic relationships between China and other regions of the world may be traced back to a time when all the major landmasses were united in the single supercontinent, Pangaea. About 180 Ma (McLoughlin, 2001), Pangaea broke into Gondwana, which became Australia, Antarctica, India, South America and South Africa, and Laurasia, which consisted of the present-day continents of Asia, Europe and North America (including Greenland). Asia and Europe have been on the same landmass since the breakup of Pangaea, although the floras of the two continents were once separated by the Eurasian north–south epicontinental seaway, the Turgai Strait, in western

Siberia and eastern Europe before the end of the Eocene (approx. 35 Ma) (Wolfe, 1997). North America was connected to Europe until at least the early Eocene (50 Ma) through the North Atlantic Land Bridge (Tiffney, 1985, 2000), and was connected to Asia by land between Alaska and eastern Siberia in the mid Cretaceous (100 Ma) (Sanmartín *et al*., 2001). The connection between Asia and North America persisted via the Bering Land Bridge until the Pliocene. Because of the breakup of Pangaea, the terrestrial connection between North and South America was broken in the early Cretaceous (Emery and Uchupi, 1984) but the two continents were reunited during the Pliocene (3·7–3·0 Ma) via the Isthmus of Panama, the Panamanian Land Bridge (Hallam, 1994; Coates, 1996). All these land connections have undoubtedly contributed to the current floristic relationships between China and the rest of the world, through providing passages for plant migration between continents. According to palaeobotanical data, the Bering Land Bridge was open to migration of deciduous taxa throughout most of the Tertiary and was possibly open to evergreen taxa in the early Eocene; the North Atlantic Land Bridge, which lay at a lower latitude (with the southern tip of Greenland perhaps extending south to 45 °N; Smith *et al.*, 1981; Tiffney and Manchester, 2001) in the early Tertiary, was open to both deciduous and evergreen taxa in the early Eocene (Tiffney, 2000). The floristic relationship between China and Africa was established in part because of the current terrestrial connection between Africa and Eurasia and in part because India brought the Gondwanan elements with it when it broke away from Gondwana, to which both India and Africa belonged, and then collided with Asia in the early Tertiary. Although India underwent remarkable latitudinal, and hence climatic and vegetational, changes (McLoughlin, 2001) after it rifted from Madagascar about 90 Ma and extensive volcanism, approximately 65 Ma, erased many taxa from central western India (Officer *et al.*, 1987; Conti *et al*., 2002), fossil and molecular data demonstrate that some of the current elements in the Asian flora and fauna were brought by India from Gondwana (Conti *et al*., 2002).

Based upon the above estimated numbers of genera shared between China and other continents, China shares more genera with North America than with Europe, despite the fact that China and Europe are on the same Eurasian landmass. This pattern is concordant with the pattern reported by Qian (1999): of the 908 genera shared between North America (north of Mexico) and Eurasia, 93·6 % occurred in Asia and 81·7 % in Europe. This pattern could have arisen for several reasons. First, North America is geographically closer to Asia than to Europe. Although Asia and Europe are connected, they were separated by the Turgai Strait during the early Tertiary as mentioned above. This epicontinental seaway—which extended from the Arctic Ocean to the Tethys Seaway, was closed at its northern end in the Palaeocene and retreated in the late Oligocene (Tiffney and Manchester, 2001)—is believed to have acted as a barrier for floristic interchanges between the two continents. Second, the Bering Land Bridge persisted for much longer than the North Atlantic Land Bridge (Tiffney, 2000). The Bering Land Bridge was open to terrestrial migrations from at least the early Palaeogene until the opening of the Bering Strait between about 7·4 and 4·8 Ma (Marinkovich and Gladenkov, 1999; Tiffney and Manchester, 2001). During Pleistocene glaciations, terrestrial connections between Asia and North America were re-established (Sanmartín *et al*., 2001). By contrast, the southern (Thulean) route of the North Atlantic Land Bridge was broken in the early Eocene (50 Ma) and the northern (De Geer) route of the bridge was broken in the late Eocene (39 Ma) (Sanmartín *et al*., 2001). Third, fossil evidence demonstrates that more genera of seed plants went extinct in Europe than in Asia and North America during late Tertiary climate cooling and Pleistocene glaciations. For example, *Aralia*, *Carya*, *Castanopsis*, *Catalpa*, *Hamamelis*, *Illicium*, *Lindera*, *Liriodendron*, *Liquidambar*, *Lithocarpus*, *Magnolia*, *Nyssa*, *Sassafras*, *Stewartia*, *Thuja* and *Torreya* are all well-known eastern Asian–North American disjuncts; they occurred in Europe during the Tertiary (Latham and Ricklefs, 1993). Their extinction from Europe but persistence in both Asia and North America contributes to the closer floristic relationship of eastern Asia with North America than either with Europe.

Of the 1410 genera in China that are restricted to Asia (i.e. all genera belonging to floristic elements FE7, FE11, FE13 and FE14 in Table 2), many, if not most, are Tertiary relicts and hence palaeoendemics (Ying *et al*., 1993). Some were once distributed in one or more of the other continents, usually Europe and/or North America, based on fossil evidence. These Tertiary relicts include all endemic gymnosperm genera such as *Cathaya*, *Cephalotaxus*, *Cunninghamia*, *Ginkgo*, *Glyptostrobus*, *Keteleeria*, *Metasequoia* and *Pseudolarix*, and many angiosperm genera such as *Cercidiphyllum*, *Cyclocarya*, *Emmenopterys*, *Engelhardtia*, *Eucommia*, *Euptelea*, *Fortunearia*, *Hemiptelea*, *Paulownia*, *Phellodendron*, *Platycarya*, *Pteroceltis*, *Sargentodoxa*, *Sinowilsonia* and *Tapiscia* (Benton, 1993; Latham and Ricklefs, 1993, and references therein; Manchester, 1999). These once widely distributed but now narrowly restricted eastern Asian endemic genera provide links between the modern flora of eastern Asia and the Tertiary floras of other continents. Neoendemic genera probably account for a very small proportion of the total number of the eastern Asian endemics (Ying *et al*., 1993). These genera include *Ajania*, *Anemoclema*, *Diplazoptilon*, *Dipoma*, *Formania*, *Isometrum*, *Metanemone*, *Sinadoxa*, *Skapanthus* and *Smithorchis* (Wu, 1988; Ying *et al*., 1993). Some may have evolved probably as a result of the Himalayan–Tibetan uplift. One such example is *Ajaniopsis*, which is a close relative of *Ajania* and is distributed between 4600 and 5000 m in elevation in Xizang (Tibet) (Ying *et al*., 1993); another example is *Sinadoxa* distributed between 3900 and 4800 m in Qinghai (Wu, 1988; Liang and Wu, 1995). A low level of divergence in the internal transcribed spacer of the nuclear ribosomal DNA sequence of *Sinadoxa* from its progenitor *Adoxa* suggests a recent origin of this genus (Liu *et al*., 1999, 2000).

In conclusion, floristic patterns are strongly associated with geographical (particularly latitudinal) factors in

local floras across China. Climate alone explains a small proportion of the variance in the composition of floristic elements. Further research is necessary to examine the roles of water–energy dynamics, geology, soils, biotic interactions, and historical factors such as land connections between continents in the past and present in creating observed floristic patterns.

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