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Large-scale phytogeographical patterns in East Asia in relation to latitudinal and climatic gradients

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Abstract

Aim This paper aims at determining how different floristic elements (e.g. cosmopolitan, tropical, and temperate) change with latitude and major climate factors, and how latitude affects the floristic relationships between East Asia and the other parts of the world.

Location East Asia from the Arctic to tropical regions, an area crossing over 50° of latitudes and covering the eastern part of China, Korea, Japan and the eastern part of Russia.

Methods East Asia is divided into forty-five geographical regions. Based on the similarity of their world-wide distributional patterns, a total of 2808 indigenous genera of seed plants found in East Asia were grouped into fourteen geographical elements, belonging to three major categories (cosmopolitan, tropical and temperate). The 50°-long latitudinal gradient of East Asia was divided into five latitudinal zones, each of *c.* 10°. Phytogeographical relationships of East Asia to latitude and climatic variables were examined based on the forty-five regional floras.

Results Among all geographical and climatic variables considered, latitude showed the strongest relationship to phytogeographical composition. Tropical genera (with pantropical, amphi-Pacific tropical, palaeotropical, tropical Asia–tropical Australia, tropical Asia–tropical Africa and tropical Asia geographical elements combined) accounted for *c.* 80% of the total genera at latitude 20°N and for *c.* 0% at latitude 55–60°N. In contrast, temperate genera (including holarctic, eastern Asia–North America, temperate Eurasia, temperate Asia, Mediterranean, western Asia to central Asia, central Asia and eastern Asia geographical elements) accounted for 15.5% in the southernmost latitude and for 80% at 55–60°N, from where northward the percentage tended to level off. The proportion of cosmopolitan genera increased gradually with latitude from 5% at the southernmost latitude to 21% at 55–60°N, where it levelled off northward. In general, the genera present in a more northerly flora are a subset of the genera present in a more southerly flora.

Main conclusions The large-scale patterns of phytogeography in East Asia are strongly related to latitude, which covaries with several climatic variables such as temperature. Evolutionary processes such as the adaptation of plants to cold climates and current and past land connections are likely responsible for the observed latitudinal patterns.

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Biogeography, cold tolerance, East Asia, floristics, latitudinal gradient, regionalization, vascular plants.

INTRODUCTION

Discerning and understanding large-scale pattern is a fundamental aspect of ecology and biogeography. East Asia has long been a focus of attention of botanists and biogeographers in part because of its markedly high species diversity, relatively high proportion of Tertiary relicts of vascular plants, close floristic relationships with eastern North America, and a long, unbroken latitudinal gradient of forest vegetation. The southern part of East Asia, together with tropical Asia, is considered by many as the centre of origin and diversification of angiosperms (Takhtajan, 1969; Smith, 1970; Wolfe, 1975; Wu, 1980; Lidgard & Crane, 1990; but see Raven & Axelrod, 1974; Tiffney, 1985a,b). The earliest flower fossil record (a Jurassic angiosperm) was recently found in East Asia (Sun *et al.*, 1998). The unbroken latitudinal gradient of the forest vegetation in Asia, which extends from the treeline at the Arctic of Siberia southward to the tip of the Malay Peninsula (nearly at the Equator), is the longest latitudinal continuum (across nearly 60° latitude) of forest vegetation in the world. This vegetation continuum is connected with the Arctic tundra, which is the northernmost vegetation biome in the Northern Hemisphere. As it covers a variety of climate zones, this latitudinal vegetation gradient consists of a rich array of vegetation zones, including tropical forest, subtropical forest, warm temperate forest, temperate forest, boreal forest, subarctic dwarf forest and the Arctic tundra (Wu, 1980; Axelrod *et al.*, 1996). As a result, floristic turnover from south to north in East Asia is apparent (Wu, 1980). A latitudinal continuum of vegetation from the present-day tropical to the Arctic areas in East Asia existed even during the Pleistocene glaciations when organisms in much of the Northern Hemisphere such as Europe and North America were extirpated by thick ice sheets (Pielou, 1991). Thus, the latitudinal vegetation continuum in East Asia provides a unique opportunity to understand the origin and maintenance of many latitude-associated patterns in ecology and biogeography.

The latitudinal gradient of vegetation in East Asia arose primarily as a result of the late Tertiary climate cooling. During the early Tertiary, a relatively uniform, warm climate covered the Northern Hemisphere (Tiffney, 1985a). During this time, a relatively continuous, homogenous flora with many tropical and subtropical elements, called the 'boreotropical flora' (Wolfe, 1975), spanned most of the current Arctic area and covered almost the entire breadth of Eurasia and North America (Latham & Ricklefs, 1993). This boreotropical flora was gradually shaped into a mixed mesic forest and became fragmented as cooling climates in the middle and late Tertiary towards the Pleistocene forced the flora southward (Wolfe, 1975; Tiffney, 1985a). During the climate cooling, cold-intolerant taxa at higher latitudes either migrated to lower latitudes or went extinct, giving way to cool-adapted taxa selected from the boreotropical flora or evolved during the climate cooling (Leopold & MacGinitie, 1972; Wolfe, 1975; Tiffney, 1985a; Xiang & Soltis, 2001). Newly evolved taxa in the tropical climate regions might have extended northward into the temperate climate regions. However, this range extension was difficult because it required the evolution of frost tolerance (Latham & Ricklefs, 1993). Because of the tropical origin of flowering plants, and because of varied degrees of cold-tolerance in different plant lineages, a latitudinal gradient from the tropical to the Arctic exists in which the relative proportion of tropical elements decreases while the proportion of temperate elements increases. Furthermore, East Asia is part of the Eurasian landmass, which is connected with Africa, and was once connected with North America (through the Bering land bridge), which is in turn linked with South America; and South Africa, South America, and Australia all were part of the protocontinent Gondwana. These present and past land connections between different continents and between East Asia and the rest of the Eurasia at different latitudes have likely resulted in varying floristic relationships between regions at different latitudes in East Asia and the other parts of the world.

Despite the unique features of the latitudinal gradient of the East Asian vegetation and flora mentioned above, knowledge on how floristic composition changes along the world's longest unbroken latitudinal gradient of forest-predominated vegetation has been surprisingly lacking. The objectives of this study are to determine (1) how different floristic elements (e.g. cosmopolitan, tropical, and temperate) change with latitude and major climate factors, and (2) how latitude affects the floristic relationships between East Asia and the other parts of the world.

MATERIALS AND METHODS

In this study, we define East Asia to include the eastern part of China, Korea, Japan and the easternmost part of Russia (Fig. 1). This area encompasses 12×10^6 km^2 and ranges approximately from 18° to 73°N latitude and 97°E to 169°W longitude. The study area was divided into forty-five geographical regions as delineated in Fig. 1, largely based upon administrative divisions. The forty-five geographical regions were, depending on their midpoint latitudes, grouped into the following five latitudinal zones: $<30°$, 30–40°, 40–50°, 50–60° and $>60°$ (Table 1).

To document floristic data, we searched a large number of literature sources including journal articles, floras, checklists, monographs, and atlases pertinent to the floras of East Asia.

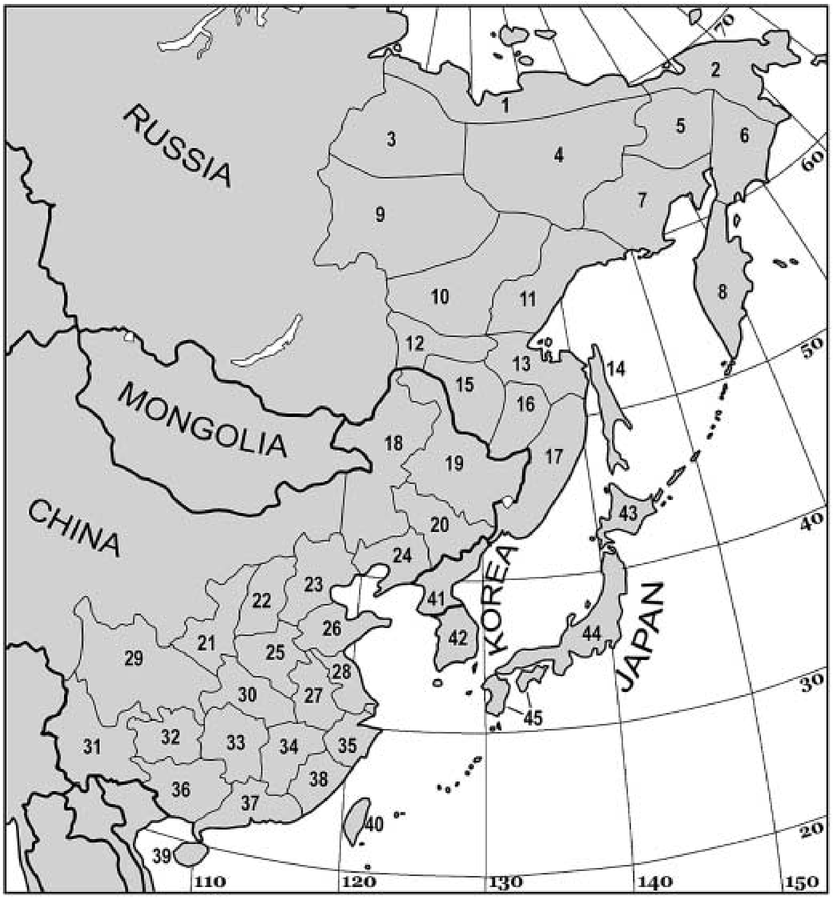

Figure 1 Map showing the overall study area and the forty-five regions used in the study. Codes for regions are as in Table 1.

The major sources for documenting China's plants were over 200 volumes of floristic books and a few electronic data bases. These include all published volumes of *Flora Republicae Popularis Sinicae* (Anonymous, 1959–98) and *Flora of China* (Wu & Raven; 1994–2000), *Seed Plants of China* (Wu & Ding, 1999), and all published volumes of regional and provincial floras such as *Clavis Plantarum Chinae Boreali-Orientalis* (Fu, 1995), *Flora of Taiwan* (Huang, 1993–2000) and *Flora of Xizangica* (Wu, 1983–87). The Russian floristic data were based on *Vascular Plants of Russia and Adjacent States* (Czerepanov, 1995), *Plantae Vasculares Orientis Extremi Sovietici* (Charkevicz, 1985–96, a set of eight volumes), and *Flora Sibiriae* (Krasnoborav *et al*., 1988–97, a set of fourteen volumes). Floristic data for Japan were largely based upon *Flora of Japan* (Iwatsuki *et al*., 1993–1999) and *New Flora of Japan* (spermatophyta, Ohwi & Kitagawa, 1992; pteridophyta, Nakaike, 1992). Korean floristic data were compiled according to *Illustrated Flora of Korea* (Lee, 1980), *Dictionary of Plant Names* (Ri & Hoang, 1984) and *Lineamenta Florae Koreae* (Lee, 1996).

The focus of this study is on the taxonomic level of seed plant genera. Standardization of generic nomenclature followed Brummitt (1992), Greuter *et al*. (1993), Wielgorskaya (1995) and Mabberley (1997). In general, a generic name was accepted if all these works adopted it. Generic names in the literature on the flora of East Asia that were absent from the above-mentioned works were treated carefully by consulting available taxonomic monographs and continental, national or regional floras. The world-wide distributional ranges of genera were documented based on a great bulk of the literature, including several familial and generic dictionaries on the world flora such as Wielgorskaya (1995) and Mabberley (1997). The genera found in the native flora of East Asia were first divided into three major groups: cosmopolitan, tropical and temperate. According to the similarity of their geographical distribution patterns, the tropical genera were divided into the following six groups (or geographical elements): pantropical, amphi-Pacific tropical, palaeotropical, tropical Asia–tropical Australia, tropical Asia–tropical Africa, and tropical Asia; and the temperate genera were divided into the following seven groups: holarctic, eastern Asia–North America, temperate Eurasia, temperate Asia, Mediterranean, western Asia to central Asia, central Asia, and eastern Asia, following Wu (1991) with the exception of the China's endemic genera,

Table 1 Geographical parameters for each of the forty-five regional floras of East Asia used in this study

Flora code	Flora	Country	Lat. zone	Area (km^2)	Lat. (°N)	Long. (°E)	Elev. (m)
1	Yakutia Arctic	Russia	> 60°	575,100	71.0	135.0	1584
2	Chukotka	Russia	> 60°	435,000	66.5	176.0	1775
3	Yakutia Lower Lena	Russia	> 60°	469,800	68.5	118.0	1511
4	Yakutia Yana and Kolyma	Russia	> 60°	842,400	66.0	144.0	3147
5	Anuj	Russia	> 60°	310,000	66.0	164.0	1797
6	Koriakia	Russia	> 60°	250,000	63.5	170.0	2562
7	Kolyma–Northern Okhotian	Russia	> 60°	485,000	63.0	155.0	2586
8	Kamchatka	Russia	50–60°	275,000	55.5	160.0	4750
9	Yakutia Viliuy	Russia	> 60°	882,900	63.0	120.0	2084
10	Yakutia Aldan	Russia	50–60°	558,900	59.5	130.0	2495
11	Aldan–Southern Okhotian	Russia	50–60°	350,000	58.5	140.0	2959
12	Upper Amur	Russia	50–60°	142,500	55.0	125.0	2412
13	Amgun	Russia	50–60°	217,500	53.5	135.5	2384
14	Sakhalin	Russia	40–50°	77,500	50.0	143.5	1609
15	Lower Zea	Russia	50–60°	225,000	52.0	129.0	1604
16	Bureja	Russia	50–60°	152,500	50.5	134.0	2640
17	Ussurian	Russia	40–50°	300,000	47.0	136.0	2077
18	Eastern Neimonggu	China	40–50°	473,000	46.0	120.0	2067
19	Heilongjiang	China	40–50°	463,600	47.0	127.5	1712
20	Jilin	China	40–50°	187,000	43.0	126.0	2691
21	Shaanxi	China	30–40°	195,800	36.0	108.0	3767
22	Shanxi	China	30–40°	157,100	37.5	112.0	3058
23	Hebei + Beijing + Tianjing	China	30–40°	219,800	39.0	117.0	2870
24	Liaoning	China	40–50°	151,000	42.0	122.0	1500
25	Henan	China	30–40°	167,000	34.5	114.0	2192
26	Shandong	China	30–40°	153,300	37.0	118.5	1546
27	Anhui	China	30–40°	139,900	31.5	117.5	1860
28	Jiangsu and Shanghai	China	30–40°	106,012	33.0	119.0	642
29	Sichuan	China	< 30°	569,000	30.0	105.0	7558
30	Hubei	China	30–40°	187,516	31.0	112.0	3105
31	Yunnan	China	< 30°	436,208	25.0	101.5	5596
32	Guizhou	China	< 30°	176,400	26.5	106.5	2900
33	Hunan	China	< 30°	210,490	27.5	112.0	2120
34	Jiangxi	China	< 30°	164,800	27.5	116.0	2120
35	Zhejiang	China	< 30°	101,787	29.0	120.5	1857
36	Guangxi	China	< 30°	236,000	23.0	107.5	2142
37	Guangdong	China	< 30°	198,400	23.0	113.5	1704
38	Fujian	China	< 30°	123,103	25.5	118.0	2158
39	Hainan	China	< 30°	33,000	19.0	110.0	1879
40	Taiwan	China	< 30°	35,760	23.5	121.0	3950
41	North Korea	N. Korea	40–50°	120,717	40.0	127.5	2744
42	South Korea	S. Korea	30–40°	98,477	36.5	128.0	1950
43	Hokkaido	Japan	40–50°	78,511	43.5	142.5	2290
44	Honshu	Japan	30–40°	223,377	37.0	139.0	3776
45	Shikoku + Kyushu	Japan	30–40°	60,736	32.5	131.5	1981

most of which were included in the eastern Asian element. Definitions for each of the fourteen geographical elements are described in Table 2.

We performed chi-square analysis (Zar, 1984; 400–401) to test whether the proportions of the genera for a given geographical element significantly differ among the five latitudinal zones. For each zone, the proportion of the genera for a given geographical element in a test was treated as one of the two categories of the test, and the proportion of the genera for the remaining thirteen geographical elements was treated as a second category. The null hypothesis was that the proportion of the genera for a given geographical element is the same across the five latitudinal zones.

Non-metric multi-dimensional scaling (NMDS) was used to extract floristic gradient. The data subjected to NMDS were the presence–absence matrix for each genus in each of the forty-five regions. NMDS was performed using Jaccard coefficient as a measure of dissimilarity. Correlation between floristic gradient extracted by NMDS and latitude was determined by Pearson's correlation coefficient. Correlation between generic composition and phytogeographical composition at the regional level was examined using canonical

Table 2 Description of geographical elements in the flora of East Asia

Cosmopolitan	Widely distributed across all or nearly all continents of the earth. In general, they do not have special distribution centres. Occasionally they have one or a few centres of high diversity but are distributed world-wide.
Pantropical	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.
Amphi-Pacific tropical	Distributed disjunctly between the two tropical sectors of America and Asia–Australia, but absent from tropical Africa–Madagascar. Some of them may be sporadically distributed on the islands of the Pacific, or may extend into temperate regions.
Palaeotropical	Also called 'Old World Tropics' in the literature. Distributed in the tropics of all three continents of the Old World: Asia, Australia and Africa (including Madagascar).
Tropical Asia–Tropical Australia	Restricted to Asia and Australia and are mainly distributed in the tropical regions of the two continents.
Tropical Asia–Tropical Africa	Restricted to Asia and Africa and are mainly distributed in the tropical regions of the two continents.
Tropical Asia	Mainly restricted to the tropical regions of Asia. Although some may extend northward into temperate regions, they do not reach the New World to the east, the African continent to the west and the Australian continent to the south.
Holarctic	Primarily distributed in extratropical regions of the Northern Hemisphere and present in 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 category has been frequently called 'North Temperate' (e.g. Wu & Wang, 1983; Wu, 1991; Ying *et al*., 1991), Eurasian–North American (e.g. Thorne, 1972), or Circumpolar *sensu lato*.
Eastern Asia–North America	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 Eurasia	Also termed 'Old World Temperate' (e.g. Wu, 1980, 1991). 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.
Temperate Asia	Restricted to temperate Asia. The distribution centres are mainly in temperate regions but they may occasionally occur in subtropical regions.
Mediterranean, western Asia to central Asia	Mainly distributed in the region including the Mediterranean, western Asia and central Asia. Some of the genera extend eastward into north-eastern Asia.
Central Asia	Mainly distributed in dry areas of central Asia.
Eastern Asia	Including all those listed under the heading of 'Eastern Asia' and most of the genera listed under the heading of 'Chinese endemic' in Wu (1991). They are mainly distributed in warm temperate to subtropical regions of East Asia.

correspondence analysis (CCA; ter Braak, 1986). CCA was also run on generic presence–absence data and proportional composition of geographical elements for the forty-five regions. A Monte Carlo permutation test was performed to evaluate whether the axes extracted by NMDS and the correlation determined by CCA between generic composition and phytogeographical composition were significantly different from random using 300 permutations. PC-ORD (version 3.0; McCune & Mefford, 1997) was used to perform NMDS, CCA and Monte Carlo permutations.

We also tabulated several climate variables for each of the forty-five regions using data in the International Institute of Applied System Analysis (IIASA) climatic data base (Leemans & Cramer, 1991), which has been widely used by other authors (e.g. Monserud *et al*., 1993; Tchebakova *et al*., 1993; Peng *et al*., 1995; Shao & Halpin, 1995). Five sites within each of the forty-five regions were selected for climate data: one at the midpoint of latitude and longitude and the other four each located on the eastern, western, southern and northern sides of the midpoint. The climatic variables examined were annual mean temperature, January mean temperature, annual precipitation, precipitation in June to September, and annual actual evapotranspiration (AET). AET was calculated following the approach developed by Cramer & Prentice (1988; see also Prentice *et al*., 1992, 1993). The average of each climatic variable in each region was also calculated based on the five climatic sites selected from the region. Latitudinal trends of the selected climate variables are summarized in Table 3.

RESULTS

A total of 2808 genera of native seed plants were compiled for East Asia. Some 91% (2555) of these genera were found in the latitudinal zone of < 30°N, and 1079 of them do not occur in latitudes north of 30° (Table 4). About 79% of the 394 genera present in latitudes north of 60°N also occurred in latitudes south of 30°N (Table 4). At a regional scale, a flora located in latitudes of > 60°N shared on average 53% of its genera with a flora located in latitudes of < 30°N (Table 5). Floristic similarity between different regions within the same latitudinal zone increased from the south to the north. For example, the Simpson coefficient was 0.75 ± 0.11 in the latitudinal zone of < 30°N and 0.85 ± 0.05 in the latitudinal zone of > 60°N (Table 5).

The stresses for the first, second and third dimensions of NMDS were 52.4, 4.8 and 2.7, respectively, which indicate that the first dimension had captured the great majority of

Table 3 Summarized data (mean ± standard deviation) for climatic and geographical variables of the forty-five regional floras according to latitudinal zone

	Latitudinal zone				
	< 30° (n = 11)	30–40° (n = 11)	40–50° (n = 8)	50–60° (n = 7)	> 60° (n = 8)
Climate					
Annual mean temperature	15.5 ± 4.4	11.4 ± 3.2	1.5 ± 2.7	−7.6 ± 2.8	−12.7 ± 2.5
January mean temperature	7.0 ± 5.1	−2.3 ± 4.9	−18.1 ± 4.3	−31.4 ± 6.5	−34.7 ± 8.3
Annual precipitation	1434.6 ± 214.9	939.2 ± 590.8	661.9 ± 212.4	507.0 ± 80.9	236.1 ± 84.9
Precipitation in June to September	775.4 ± 179.3	536.9 ± 246.5	425.4 ± 121.7	324.6 ± 72.8	131.3 ± 32.5
Annual AET	960.5 ± 149.0	686.2 ± 223.4	549.0 ± 106.8	408.4 ± 58.8	203.8 ± 57.2
Geography					
Area (×1000 km^2)	207.7 ± 162.8	153.8 ± 49.5	231.4 ± 162.5	274.5 ± 144.1	531.3 ± 228.5
Latitude (°N)	25.5 ± 3.2	35.0 ± 2.6	44.8 ± 3.2	54.9 ± 3.2	65.9 ± 2.8
Maximum elevation (×10 m)	308.9 ± 188.6	242.2 ± 97.6	209.4 ± 48.2	274.9 ± 97.3	213.1 ± 57.9

Table 4 Number of genera in each of the five latitudinal zones (diagonal) and number of genera shared between a pair of zones

Latitude zone	< 30°	30–40°	40–50°	50–60°	> 60°
< 30°	2555				
30–40°	1476	1664			
40–50°	732	852	891		
50–60°	471	526	546	572	
> 60°	313	351	365	373	394

the information about the floristic relationships among the forty-five geographical regions. The correlation between the first dimension of NMDS and latitude was extremely high ($r = 0.95$, $P < 0.001$; Fig. 2), indicating a strong pattern of generic turnover along a latitudinal gradient.

Figure 4 depicts the relationships between the relative frequencies of the cosmopolitan, tropical and temperate genera, and several geographical and climatic variables. Among all the variables considered, latitude showed the strongest relation with the relative frequencies of the three major groups. The proportion of tropical genera was *c.* 80% in the southernmost region around 20°N (i.e. Hainan), and decreased drastically northward to *c.* 40°N, and then continuously decreased to nearly 0% at the latitude of 55–60°N (Fig. 3a). In contrast, the proportion of temperate genera was 15.5% in the southernmost region, and increased rapidly northward up to *c.* 40°N and then increased slowly to 80% at 55–60°N, from where it tended to level off. The proportion of cosmopolitan genera increased gradually with latitude from 5% at the southernmost latitude to 21% at 55–60°N, where it levelled off northward. Trends in changes of the relative frequencies of the cosmopolitan, tropical and temperate genera along temperature, precipitation and AET gradients were more or less comparable with those along the latitudinal gradient as noted above (compare Fig. 3a with Fig. 3b–d). In particular, the trend of changes in relative frequencies of cosmopolitan, tropical and temperate genera along the temperature gradient primarily mirrored changes along the latitudinal gradient. For example, the sharp change between the tropical and temperate geographical elements at *c.* 40°N mirrored the change observed at *c.* 10 °C of the temperature gradient (compare Fig. 3a with Fig. 3b).

More details on the trend of changes in relative frequencies of tropical and temperate genera along the latitudinal gradient are shown in Table 6. Most of the fourteen geographical elements recognized in this study showed monotonic trends in their proportional compositions along the latitudinal gradient. All the six tropical elements showed a significant decrease in their percentages in a regional flora from the south to the north. The genera of pantropical, palaeotropical and tropical Asia accounted for *c.* 18, 10 and 14%, respectively, of the total regional flora at < 30°N, but these three geographical elements accounted for nearly 0% of the total of a flora at > 60° (Table 6). The eastern Asian endemic genera tended to follow the same trend as the tropical genera; however, it peaked at latitudes between 30° and 40°N, rather than < 30°N (Table 6). The proportion of

Table 5 Statistic summary for Simpson coefficient of similarity between all possible pairwise comparisons of the forty-five regional floras according to the five latitudinal zones

Latitude zone	n (mean ± SD)			
	< 30°	30–40°	40–50°	50–60°
30–40°	121 (0.75 ± 0.11)			
40–50°	88 (0.64 ± 0.11)	88 (0.74 ± 0.09)		
50–60°	77 (0.59 ± 0.12)	77 (0.71 ± 0.11)	56 (0.85 ± 0.06)	
> 60°	88 (0.53 ± 0.12)	88 (0.65 ± 0.11)	64 (0.81 ± 0.05)	56 (0.85 ± 0.05)

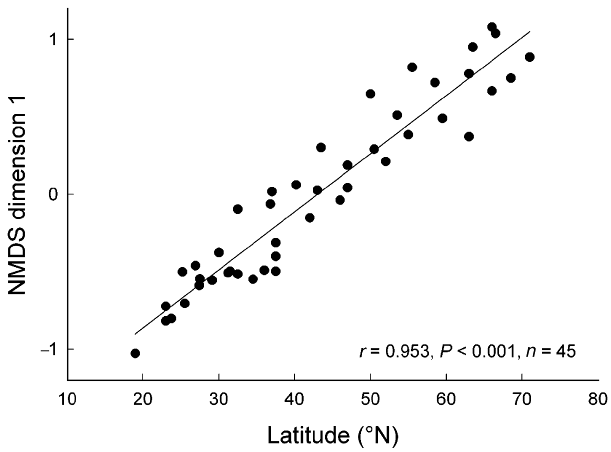

Figure 2 Correlation between latitude and NMDS dimension 1.

holarctic genera increased considerably (by 54%) from < 30°N to > 60°N. The geographical elements of eastern Asia–North America, temperate Eurasia and temperate Asia peaked around the mid-latitudes. Neither the central Asia element nor the Mediterranean, western to central Asia element showed significant patterns along the latitudinal gradient (Table 6).

Relationships between the set of the forty-five geographical regions and the set of the fourteen geographical elements were portrayed by a biplot of CCA using its first two ordination axes (Fig. 4). The eigenvalues of the first and second axes were 0.58 and 0.21, respectively. A Monte Carlo test with 300 permutations showed that the eigenvalues for both axes were significantly different from random ($P < 0.05$). It also showed that the generic composition–geographical element correlations for both axes were significant ($P < 0.01$). The six tropical geographical elements (i.e. pantropical, amphi-Pacific tropical, palaeotropical, tropical Asia–tropical Australia, tropical Asia–tropical Africa and tropical Asia) and the eastern Asia geographical element were strongly and positively correlated with the first CCA axis (Table 7), and were mainly associated with the regional floras which are located at latitudes primarily south of 30°N (Fig. 4). In contrast, the cosmopolitan and holarctic geographical elements were strongly and negatively correlated with the first

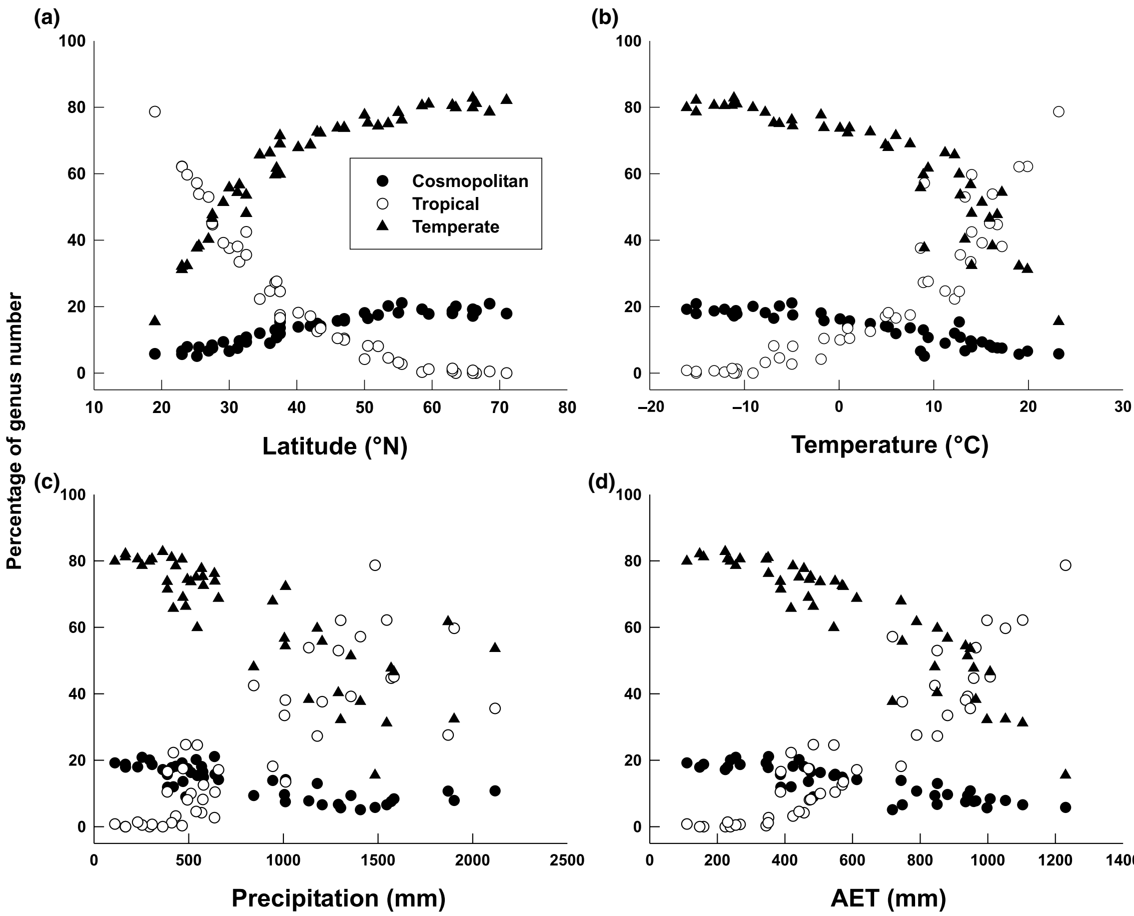

Figure 3 Relationships between the proportions of cosmopolitan, tropical and temperate genera of seed plants, and (a) latitude (b) temperature (c) precipitation and (d) AET.

Table 6 The proportion (%, mean ± standard deviation) of the genera across the fourteen geographical elements for each of the five latitudinal zones based on the forty-five regional floras used in this study

Geographical element	Latitudinal zone < 30° (n = 11)	30–40° (n = 11)	40–50° (n = 8)	50–60° (n = 7)	> 60° (n = 8)	Chi-square test
Cosmopolitan	7.1 ± 1.3	11.2 ± 2.3	15.4 ± 1.4	18.8 ± 1.5	18.7 ± 1.3	***
Pantropical	18.2 ± 2.9	14.2 ± 2.7	7.6 ± 2.9	2.2 ± 1.7	0.2 ± 0.3	***
Amphi-Pacific tropical	1.1 ± 0.1	0.8 ± 0.4	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	*
Palaeotropical	10.0 ± 2.3	5.1 ± 1.8	2.1 ± 0.9	0.7 ± 0.7	0.2 ± 0.3	***
Tropical Asia–tropical Australia	7.6 ± 2.5	3.4 ± 1.2	0.9 ± 0.4	0.3 ± 0.4	0.0 ± 0.0	***
Tropical Asia–tropical Africa	3.1 ± 0.9	1.2 ± 0.5	0.6 ± 0.1	0.1 ± 0.2	0.0 ± 0.0	***
Tropical Asia	14.0 ± 5.2	3.5 ± 2.4	0.7 ± 0.3	0.2 ± 0.2	0.0 ± 0.0	***
Holarctic	11.8 ± 3.3	24.1 ± 5.8	40.0 ± 5.8	55.6 ± 7.1	66.2 ± 5.9	***
Eastern Asia–North America	5.0 ± 1.5	6.9 ± 1.3	7.0 ± 1.5	4.0 ± 1.8	2.4 ± 0.9	*
Temperate Eurasia	5.3 ± 1.7	10.4 ± 2.4	13.4 ± 2.3	11.8 ± 2.3	8.3 ± 4.0	***
Temperate Asia	0.6 ± 0.2	1.5 ± 0.7	2.2 ± 0.9	2.7 ± 1.0	1.8 ± 0.5	**
Mediterranean and western to central Asia	0.2 ± 0.3	1.1 ± 1.1	0.9 ± 0.8	0.5 ± 0.7	1.3 ± 0.7	n.s.
Central Asia	0.3 ± 0.5	0.6 ± 0.5	0.7 ± 0.5	0.7 ± 0.2	0.8 ± 0.3	n.s.
Eastern Asia	15.9 ± 4.9	16.1 ± 3.5	8.4 ± 2.2	2.4 ± 2.0	0.1 ± 0.4	***

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, and n.s. = not significant ($P \geq 0.05$).

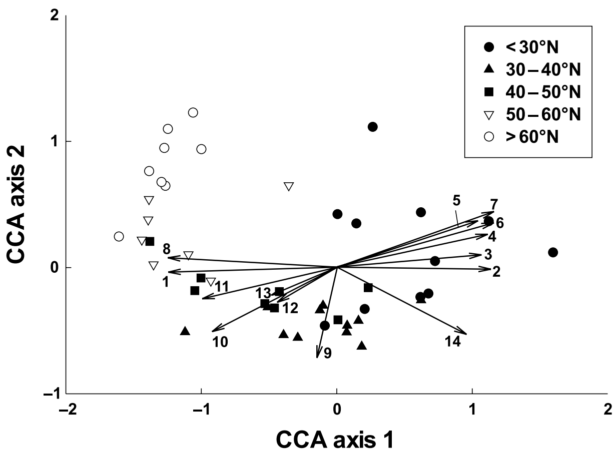

Figure 4 Biplot based on canonical correspondence analysis (CCA) of the forty-five regional floras of East Asia (differentiated by five latitudinal zones) in relation to the fourteen geographical elements (represented by arrows accompanied with numerical codes). Numerical codes are: 1 = cosmopolitan, 2 = pantropical, 3 = am-amphi-Pacific tropical, 4 = palaeotropical, 5 = tropical Asia–tropical Australia, 6 = tropical Asia–tropical Africa, 7 = tropical Asia, 8 = holarctic, 9 = eastern Asia–North America, 10 = temperate Eurasia, 11 = temperate Asia, 12 = Mediterranean and western to central Asia, 13 = central Asia, and 14 = eastern Asia.

CCA axis (the intraset correlations of both being 0.82; Table 7) and were mainly associated with the regional floras which are located at latitudes primarily north of 50°N (Fig. 4). The eastern Asia–North America geographical element, which was strongly and negatively correlated with the second CCA axis (Table 6), was primarily in favour of the regional floras located at latitudes between 30° and 40°N, and the geographical elements of temperate Eurasia and temperate Asia, which were negatively correlated with the first CCA axis (Table 7), were both mainly associated with the regional floras primarily located at latitudes between 40° and 50°N (Fig. 4). The geographical elements of central Asia and Mediterranean, western to central Asia were weakly in favour of the regional floras located at mid-latitudes (Fig. 4). The CCA results reinforced the conclusions on the latitudinal trends for most of the fourteen geographical elements as noted above (Table 6).

DISCUSSION

One of the major approaches used to characterize large-scale biogeographical patterns is to stratify all taxa found in a particular area into a number of geographical types or elements based on the nature, especially the affinities, of their distributions. For example, Thorne (1972) provides a world list of major disjunct distribution types of vascular plants, van Balgooy (1976) stratifies the native genera of New Guinea into fifteen geographical elements, and Qian (1999, 2001) stratifies the native genera of the North American vascular plants into ten geographical elements. The most comprehensive floristic study using such an approach in East Asia was conducted by Wu and colleagues (e.g. Wu, 1980; Wu & Wang, 1983). However, their work involved only the seed plant flora of China. They stratify the seed plants of China into fifteen geographical elements. Since the first edition of their scheme was published in the early 1980s, the scheme has been widely used in studying the phytogeography of China at regional, provincial and local levels (e.g. Liu & Qiu, 1986; Li & Walker, 1986; Qian, 1988; Ying et al., 1991; Xie & Wu, 1993; Fu et al., 1995a,b,c; Qi et al., 1995;

Table 7 Canonical correlations of geographical elements with the first two axes of canonical correspondence analysis (CCA) using the floristic data of the forty-five regions in East Asia

	Intraset correlation		Interset correlation	
Geographical element	Axis 1	Axis 2	Axis 1	Axis 2
Cosmopolitan	−0.818	−0.041	−0.974	−0.207
Pantropical	0.750	−0.016	0.903	0.098
Amphi-Pacific tropical	0.703	0.112	0.894	0.231
Palaeotropical	0.735	0.290	0.927	0.415
Tropical Asia–tropical Australia	0.687	0.408	0.902	0.538
Tropical Asia–tropical Africa	0.763	0.391	0.926	0.543
Tropical Asia	0.760	0.486	0.890	0.631
Holarctic	−0.820	0.084	−0.973	−0.075
Eastern Asia–North America	−0.096	−0.781	−0.110	−0.804
Temperate Eurasia	−0.603	−0.555	−0.740	−0.645
Temperate Asia	−0.652	−0.272	−0.769	−0.356
Mediterranean and western to central Asia	−0.294	−0.293	−0.397	−0.315
Central Asia	−0.318	−0.242	−0.441	−0.259
Eastern Asia	0.631	−0.581	0.685	−0.436

Table 8 Comparison of relative frequencies of five common geographical elements in East Asia (EA) and North America (NA) across four latitudinal zones [Zone 1 = 30–40°N zone in EA and LATS in NA, Zone 2 = 40–50°N in EA and LATMS in NA, Zone 3 = 50–60°N in EA and LATMN in NA, Zone 4 = > 60°N in EA and LATN in NA, data for NA from the Table 2 of Qian (2001)]

	Latitudinal zone				
Geographical element	Region	Zone 1	Zone 2	Zone 3	Zone 4
Cosmopolitan	EA	6.5	11.3	15.3	16.9
	NA	7.1	10.3	14.0	20.5
Pantropical	EA	13.8	10.1	4.7	1.0
	NA	13.8	11.6	7.6	1.7
Amphi-Pacific tropical	EA	0.7	0.4	0.0	0.0
	NA	2.0	2.1	1.7	1.0
Holarctic	EA	16.2	31.0	43.0	54.3
	NA	15.4	23.4	33.4	54.0
Eastern Asia–North America	EA	6.5	8.1	7.4	3.9
	NA	6.2	8.9	10.5	8.3
Other	EA	56.3	39.1	29.6	24.0
	NA	55.5	43.7	32.8	14.5

Wang *et al*., 1995). The present study is the first to apply their scheme, with a minor modification (see below), to the entire area of East Asia. Of the fifteen geographical elements defined in Wu's scheme, fourteen more or less reflect natural distributional patterns. Their last geographical element, 'Chinese endemic', is largely an artificial category because its geographical limitation is solely delineated by the national border of China. Most of the genera included in this category of their classification have similar geographical distributions with the eastern Asian geographical element except that the former does not extend eastward into Japan. In the present study, we included all genera endemic to China in the category of eastern Asia except for a few genera restricted to the north-western part of China, which were included in the category of central Asia.

East Asia shares the following five geographical elements with North America (Qian, 1999, 2001): cosmopolitan, pantropical, amphi-Pacific tropical, holarctic and eastern Asia–North America. The latitudinal zones of 30–40°N, 40–50°N, 50–60°N and > 60°N in East Asia are more or less comparable with the southern (LATS), south-middle (LATMS), north-middle (LATMN) and northern (LATN) latitudinal zones of North America, respectively, as defined in Qian (2001). Relative frequencies of the five shared geographical elements in the most southern zone of East Asia are about the same as in North America (Table 8). These five elements account for 44% of the total genera in this zone in both East Asia and North America. In the most northern zone, cosmopolitan genera account for 17% in East Asia and 20% in North America, and holarctic genera account for 54% in both continental regions (Table 8). The five shared elements together account for 76 and 85% of the total genera in the northernmost zone in East Asia and North America, respectively.

The more or less parallel patterns in the proportion of shared geographical elements in East Asia and North America along the latitudinal gradient presumably reflect the past connections between the two continental regions and similar histories in major evolutionary processes after they became separated. During the early Tertiary, an equable and warm climate, lasting for over 40 Myr (Latham & Ricklefs, 1993), spread widely across the Northern Hemisphere and resulted in the existence of a relatively stable, homogeneous subtropical flora – the boreotropical flora (*sensu* Wolfe, 1975) – in high latitudes of the Northern Hemisphere (Wolfe, 1975). As noted in the introduction, this flora spanned most of the present Arctic and covered almost the entire breadth of North America and Eurasia (Latham & Ricklefs, 1993). The early Eocene was the warmest interval in the Tertiary and it was in this period that megathermal rain forests reached their greatest poleward extent (Wolfe, 1985). The geological and palaeobotanical evidence shows that the northern parts of East Asia and North America were connected by the Bering land bridge throughout most of the Tertiary, permitting floristic interchange between the two continental regions (Tiffney, 1985a). The continuous boreotropical flora became gradually discontinuous as cooling climates in the middle and late Tertiary towards the Pleistocene forced the flora southward. After the separation of the East Asian and North American floras, the two floras may have responded similarly to evolutionary processes such as the development of cold tolerance. This may have resulted in the observed parallelism in the common geographical elements between East Asia and North America along the latitudinal gradient. Of the five shared geographical elements, the eastern Asia–North America element is the most frequently discussed (e.g. Li, 1952; Wu, 1983; Ricklefs & Latham, 1992; Hong, 1993; Wen, 1999; Guo & Ricklefs, 2000; Qian & Ricklefs, 2000; Mueller *et al.*, 2001). Approximately 120 genera of vascular plants belong to this element, and about sixty of them are restricted to eastern Asia and eastern North America, which have close floristic relationships and similar climates (Li, 1952; Qian, 2002). In both areas, the generic richness of the eastern Asia–eastern North America disjuncts peaks at latitudes of 30 ± 5°N, and the disjuncts primarily occur in mesic forests in both continental regions (Li, 1952). Furthermore, the latitudinal distributions of these genera are correlated between East Asia and North America (Ricklefs & Latham, 1992).

The present study clearly shows that the genera present in a more northerly flora are primarily a subset of the genera present in a more southerly flora. For example, more than 75% of the genera present in the northernmost latitudinal zone (> 60°N) are also present in the southernmost latitudinal zone (< 30°N). The striking latitudinal gradient in geographical element composition primarily is the result of the decreasing number of tropical genera from the south to the north. The rise of this pattern may be explained as follows. Flowering plants are thought to have originated in tropical regions (Takhtajan, 1969; Raven & Axelrod, 1974; Wu, 1980; Lidgard & Crane, 1990), and tropical and subtropical Asia is considered as one of the diversification centres for flowering plants (Takhtajan, 1969; Wu, 1980). From the earliest Tertiary to the early Eocene, the temperate global climates gave way to increasingly warmer climates (Latham & Ricklefs, 1993). Taxa that evolved in tropical regions at low latitudes spread poleward to higher latitudes, which may have created a latitudinal gradient along which tropical elements decreased from a donor latitude to a receiver latitude. Based on fossil data (Wolfe, 1977; Tiffney, 1985a; Spicer *et al.*, 1987; Taylor, 1990; Budantsev, 1992), the high-latitudinal Tertiary boreotropical flora (as discussed above) contained a large number of tropical taxa and showed strong affinities with modern low-latitudinal subtropical floras (Sharp, 1951; Latham & Ricklefs, 1993). In East Asia, megathermal evergreen plant communities occurred at high latitudes, including the southern edge of the Bering land bridge (Wolfe, 1985). Many genera of seed plants currently present in, or restricted to, the tropical to warm climate regions of East Asia were also elements of the boreotropical flora on the Bering land bridge during the Tertiary (e.g. *Alangium*, *Bauhinia*, *Castanea*, *Celtis*, *Cinnamomum*, *Celastrus*, *Cercidiphyllum*, *Corylopsis*, *Engelhardtia*, *Eucommia*, *Euodia*, *Glyptostrobus*, *Illicium*, *Juglans*, *Lindera*, *Liquidambar*, *Metasequoia*, *Persea*, *Platanus*, *Platycarya*, *Pterocarya*, *Rhamnus*, *Sassafras*, *Tilia* and *Zelkova*).

By the late early and early middle Eocene, a significant climate cooling occurred (Graham, 1999). The climates fluctuated between warm and cool in the later Oligocene and the Miocene, cooled further in the later Miocene and the Pliocene, and became extremely cold in the Pleistocene (Tiffney, 1985b). This climate cooling created an evolutionary barrier, frost tolerance, for most plant genera. As almost all tropical plants are highly frost-intolerant (Brown & Lomolino, 1998), and because the climatic tolerances of many angiosperm taxa could not be altered (Tiffney, 1985a), this climate cooling forced the evergreen and cold-intolerant plants of the boreotropical flora southward (Tiffney, 1985b). Where protected refugia were not available, or the climate changed more rapidly than the plants of the boreotropical flora could migrate into warmer refugia, local or global extinction of the early Tertiary floristic elements occurred (Tiffney, 1985b). As frost-influenced climates arose in the mid-Tertiary (Latham & Ricklefs, 1993), the history of the seed plants crossing the frost barrier was short relative to the entire evolutionary history of the seed plants. Some seed plant genera have crossed this barrier or can tolerate very cold climate, but a large number of seed plant genera remain restricted to tropical to subtropical regions. In general, the colder the climate, the fewer the genera that have crossed the cold barrier at that climate. This evolutionary process in cold adaptation leads to a decreasing proportion of tropical genera in a flora with increasing latitude.

One of the most striking patterns uncovered in this study is the abrupt change in the rate of decline of tropical genera at around 40°N from a steep decrease at lower latitudes to a more gradual decrease at higher latitudes (Fig. 3a). Latitude of 40°N more or less corresponds with the mean annual temperature of *c.* 10 °C in China (Domrös & Peng, 1988). This study also shows drastic changes in the rate of decrease of tropical genera and the rate of increase of temperate genera from the south to the north at the mean annual temperature (MAT) of *c.* 10 °C (Fig. 3b). This temperature may represent a particular biological threshold for plants to adapt cold climates and may have played a significant role in determining the latitudinal ranges of plant and biome distributions in East Asia. A remarkably large number of plant genera and species in East Asia are distributed in a wide range of latitudes south of 40°N but are barely distributed more northerly. Many of them (e.g. *Magnolia*, *Lindera*) have their northern range boundaries nearly congruent with this latitude. In addition, the northern boundary of the warm temperate broad-leaved deciduous forest more or less corresponds to the line of this temperature in North China (Wu, 1980). Most of the vegetation north of 40°N in East Asia is dominated by cool temperate and boreal forests, often called taiga forests; and most of the seed plant genera distributed in the taiga forests are generally specious and have rather wide geographical extents, both latitudinally and longitudinally. For example, many of tree genera of the taiga forests such as *Abies*, *Acer*, *Alnus*, *Betula*, *Larix*, *Picea*, *Pinus*, *Populus*, *Quercus* and *Salix* are distributed throughout the temperate regions from Europe to Asia and into North America. Previous authors (e.g. Stevens, 1989; Brown *et al.*, 1996) report that there is a latitudinal gradient of increasing latitudinal ranges of plant and animal species from low to high latitudes, a biogeographical pattern called Rapoport's rule (Stevens, 1989). It has been believed that selection for tolerance to marked seasonal variability in temperature (Stevens, 1989) and to temperature fluctuations during the Ice Ages (Rohde, 1996) resulted in the phenomenon that higher latitude plants have, in general, wider latitudinal ranges of distributions. To survive, living organisms at higher latitudes must be able to withstand greater variability in climatic conditions than those at lower latitudes (Stevens, 1989). This latitudinal pattern has been found in many groups of living organisms (e.g. North American trees, marine molluses with hard body parts, fresh water and coastal fishes; Stevens, 1989), particularly those distributed in the latitudes > 40–50°N (Rohde, 1996, 1999). The cause of the latitudinal pattern in distribution range of organisms described by Rapoport's rule is likely in part responsible for the lower rate of generic turnover between different latitudes north of 40°N than those south of that latitude in East Asia that we have documented in this study.

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