Plant Syst Evol (2017) 303:689–698
DOI 10.1007/s00606-017-1401-3

ORIGINAL ARTICLE

Phytogeographical patterns of genera of endemic flora in relation to latitudinal and climatic gradients in China

Jihong Huang[1,2] · Keping Ma[3] · Jianhua Huang[4]

Received: 29 July 2016 / Accepted: 3 March 2017 / Published online: 28 March 2017
© Springer-Verlag Wien 2017

Abstract This paper aims at detecting the relationships between phytogeographical patterns of genera of Chinese endemic seed plants and latitude or climatic factors. The landmass of China was divided into four latitudinal zones, each of c. 8°. Based on a total of 1664 indigenous genera of Chinese endemic seed plants which were grouped into fifteen geographical elements, belonging to three major categories (cosmopolitan, tropical and temperate) and which were absent or present in 28 provinces in China, we analyzed the phytogeographical patterns of genera of Chinese endemic seed plants and detected the relationships between them and main climatic factors. Our results showed that the proportion of tropical genera decreases with the increase in latitude; the proportion of temperate genera increases with the increase in latitude; and the proportion of cosmopolitan genera increased gradually increased gradually with latitude. There are a slow decrease in the proportion of tropical genera and slow increase in the proportion of temperate genera at latitudes 35°–40°. Alternatively, the tropical genera and the temperate genera have the same proportion at latitude c. 25°. These changes and issues about the different genera also appeared in main climate factors. In general, the genera present in a more northerly flora are a subset of the genera present in a more southerly flora. In summary, the large-scale patterns of phytogeography of endemic flora in China are strongly related to latitude, which covary with several climatic variables such as temperature.

Keywords Biogeography · China flora · Endemic flora · Latitudinal gradients · Seed plants

Handling editor: Yunpeng Zhao.

Electronic supplementary material The online version of this article (doi:10.1007/s00606-017-1401-3) contains supplementary material, which is available to authorized users.

✉ Keping Ma
kpma@ibcas.ac.cn

Jihong Huang
northalluvion@163.com

Jianhua Huang
jh996996@sina.com

1 Key Laboratory of Forest Ecology and Environment, the State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China

2 Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China

3 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Science, Beijing 100093, China

4 School of Economics, Minzu University of China, Beijing 100081, China

Introduction

China flora has long been attracted an attention of botanists and biogeographers, not only because it has markedly high species diversity, significant endemism, and relatively high proportion of Tertiary relicts of plants, but also because it owns a long, continuous latitudinal gradient of forest vegetation (Axelrod et al. 1996; Du et al. 2015; Feng et al. 2016; Huang et al. 2011, 2012, 2014; Lopez-Pujol et al. 2011; Qian et al. 2016; Qiu et al. 2011; Raven and Axelrod 1974; Wang et al. 2011; Wu et al. 2011). The southern part of East Asia, especially the southwest of China, is considered as the center of origin and diversification of angiosperms (Lidgard and Crane 1990; Raven and Axelrod

1974; Smith 1970; Takhtajan 1969; Tiffney 1985a, b; Wolfe 1975; Wu 1980). The earliest flower fossil record (an Upper Jurassic angiosperm) was recently found at Beipiao in west Liaoning of China (Sun et al. 1998). Patterns of endemism in China flora have also long attracted interest. At the genus level, three centers of endemism were found (Ying and Zhang 1994), which was interpreted by results from markedly heterogenetic landform and distinctly different climate. Recently decades, some studies have shown that the centers of endemism could be in the places where the climatic are stable over longer periods (Fjeldsā and Lovett 1997; Lovett and Friis 1996).

Diversity of endemic plant species has become one of both key criterions to identify global biodiversity hotspots (Myers et al. 2000). The China seed plant flora is highly endemic (Fu et al. 1993; Huang et al. 2011; Wang and Zhang 1994; Ying and Zhang 1994). At genus level, the early summaries endemic genera richness by province (Wang 1992) already revealed that southwest China, such as Yunnan province, with some 180 plant genera, is much richer than center China and east China, while the endemic flora of Northwest China and Northeast China are the poorest. At species level, endemic rate of seed plant is 52.1% (Huang et al. 2011). Hotspots of Chinese endemic seed plants are located in mountainous areas mainly within the road area-the Qinling Mountainous and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau (Huang et al. 2014).

China is unique country with the longest latitudinal continuum of forest vegetation in the world (across above 35° latitude). This latitudinal forest vegetation gradient is composed of a various array of vegetation zone, such as boreal forest, temperate forest, warm temperate forest, subtropical forest, and tropical forest (Axelrod et al. 1996; Wu 1980). The continuous latitudinal gradient of the forest vegetation covers a variety of climate zones and fills in the eastern China monsoon region and extends from the latitude 53°31′N to 18°23′N, and thus, floristic turnover from north to south in China is apparent (Wu 1980). The latitudinal continuum of vegetation, as a result of the late Tertiary climate cooling (Qian et al. 2003), has existed during the Pleistocene glaciations when organisms most in the Northern Hemisphere, especially Europe and North America, were covered with thick ice sheets (Pielou 1991). During the early Tertiary, a relatively uniform, warm climate covered the Northern Hemisphere (Tiffney 1985b) and a relatively continuous, homogenous flora called the "boreotropical flora" (Wolfe 1975), composing of many tropical and subtropical elements, occurred in most of the current Arctic, the entire Eurasia and north America (Latham and Ricklefs 1993). During the climate cooling, this boreotropical flora was gradually shaped into a mixed mesicforest and forced the flora southward (Tiffney 1985a; Wolfe 1975).

Therefore, to comprehensively understand the origin and maintenance of many latitude-associated patterns in ecology and biogeography, the latitudinal vegetation continuum in China provides an uncommon and unique opportunity (Qian et al. 2003, 2006; Zhu et al. 2007). The study on distribution patterns of geographical elements of Chinese flora with palaeoecological studies together demonstrate the northward shifts of tropical and subtropical broad-leaved evergreen forest in eastern China during the mid-Holocene (Zhu 2013). However, we have no idea about the distribution patterns of Chinese endemic flora along this latitudinal continuum. In this study, based on a list of Chinese endemic seed plants and their distribution database, We will analyze the distributional characters of genera of Chinese endemic seed plants, detected distribution patterns of different geographical elements (e.g., cosmopolitan, tropical, and temperate) of Chinese endemic seed plants change with latitude and major climate factors. Moreover, we will discuss commons and differences in distribution patterns of Chinese flora and Chinese endemic flora and discuss their possible causes.

Materials and methods

In this study, we define the land of China include all part of land China, which encompasses c. 960×10^4 km^2 and ranges approximately from 18°23′ to 53°31′N latitude and 74°40′E to 135°5′E longitude (Fig. 1). The study area was divided into 28 geographical regions as delineated in Fig. 1, totally based upon administrative divisions. The 28 geographical regions were grouped into the following five latitudinal zones: <24°, 24°–32°, 32°–40°, and >40° (Table 1), according to their midpoint latitudes.

To comprehensively collect floristic data, we compiled the distribution data from a large number of literature, including journal articles, floras, checklists, monographs, and atlases pertinent to the floras of China. 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 of China* (Wu et al. 1994–2012), and *Flora Republicae Popularis Sinicae* (Editorial-Committee-of-Flora-Reipublicae-Popularis-Sinicae 1959–2004), *Seed plants of China* (Wu and Ding 1999), and all published volumes of regional and provincial floras such as *Flora of Tibet* (Wu 1983–1987), *Flora of Yunnanica* (Editorial Committee of Flora of Yunnannica 1977–2006), *Flora of Sichuanica* (Editorial Committee of Flora of Sichuanica 1981–1999), and compilation of type specimen of higher plant of China (Jin 1994, 1999) and all journals of botanic taxonomy or flora,

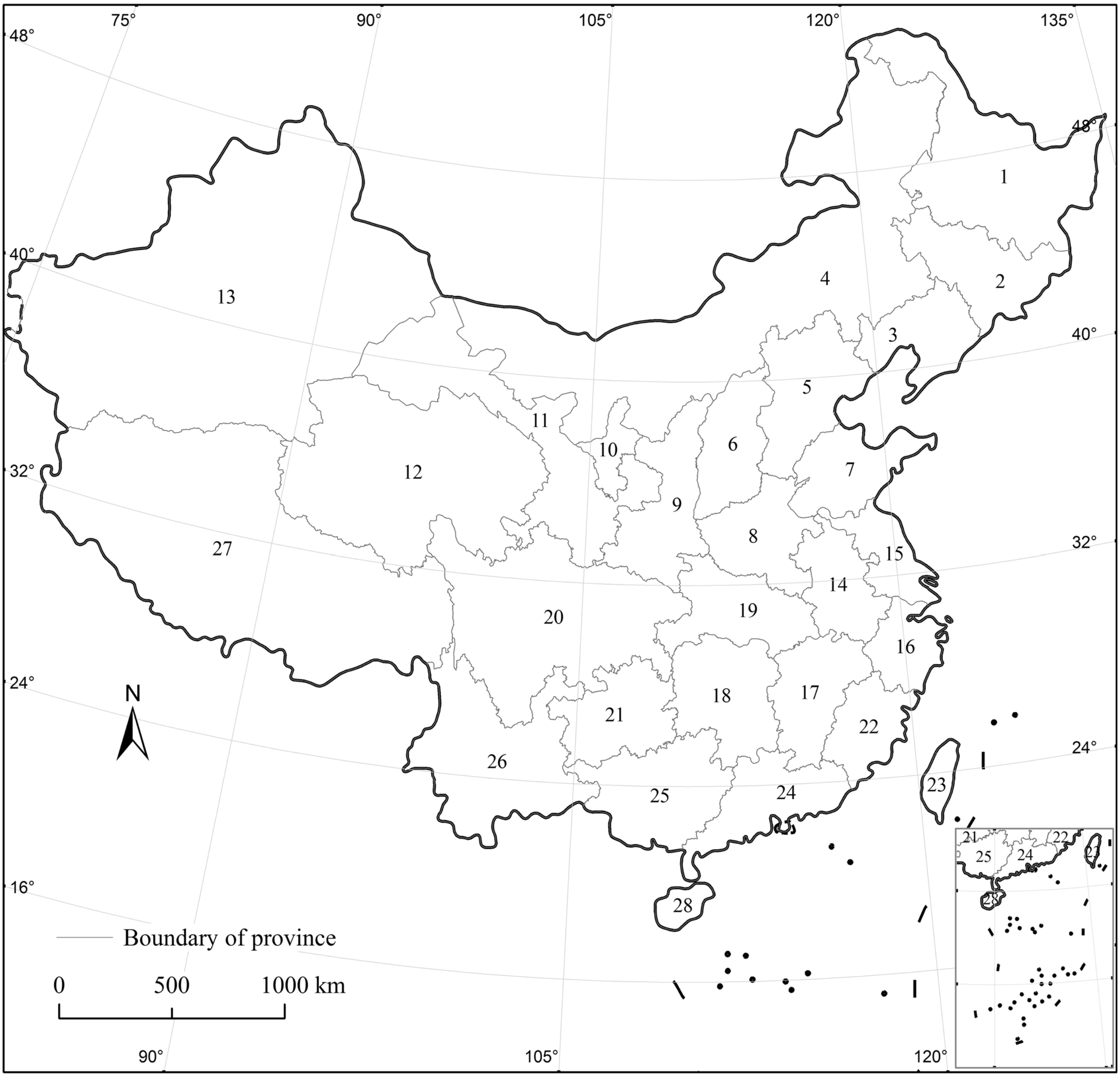

Fig. 1 Map showing the overall study area and the 28 regions used in the study. Codes for regions are as in Table 1

such as *Acta Phytotaxonomica Sinica*, *Acta Botanica Yunnanica*, *Journal of Wuhan Botanical Research*, and *Bulletin of Botanical Research*. List of all references is provided in Online Resource 1. Ultimately, 1664 indigenous genera of Chinese endemic seed plants (including subspecies and varieties) were collected.

The geographical elements of genera were documented based on Areal-types of Seed Plants and Their Origin and Differentiation (Wu et al. 2006). The genera found in the endemic seed plants flora of China 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 (geographical elements): the Pantropical, the Amphi-Pacific tropical, the Palaeotropical, the tropical Asia-tropical Australia, the tropical Asia-tropical Africa, and tropical Asia. The temperate genera were divided into eight groups, including the Holarctic, the eastern Asia–North America, the temperate Eurasia, the temperate Asia, the Mediterranean, western Asia to central Asia, the central Asia, the eastern Asia, and China's endemic genera. Definitions for each of the fifteen geographical elements are updated and described in recent study (Wu et al. 2006).

Table 1 Geographical parameters for each of the 28 regional floras of China in this study

Flora code	Flora	Lat. zone	Area (km^2)	Lat. (°N)	Long. (°E)	Elev. (m)
1	Heilongjiang	>40°N	53,690	48.48	128.14	1617
2	Jilin	>40°N	20,910	43.06	126.47	2565
3	Liaoning	>40°N	15,140	41.11	122.31	1244
4	Neimenggu	>40°N	128,180	45.37	111.62	3304
5	Hebei	32–40°N	22,290	39.33	116.65	2711
6	Shanxi	32–40°N	15,810	37.66	112.39	2983
7	Shandong	32–40°N	14,920	36.40	118.75	1378
8	Henan	32–40°N	15,940	33.88	113.50	2268
9	Shaanxi	32–40°N	20,150	35.65	108.37	3594
10	Ningxia	32–40°N	5150	37.31	105.97	3430
11	Gansu	32–40°N	41,030	37.69	100.74	5709
12	Qinghai	32–40°N	70,980	35.44	96.24	6619
13	Xinjiang	>40°N	174,400	41.76	84.94	7822
14	Anhui	32–40°N	13,180	32.03	117.26	1680
15	Jiangsu	32–40°N	9860	32.90	119.13	535
16	Zhejiang	24–32°N	8910	29.12	120.49	1784
17	Jiangxi	24–32°N	15,100	27.28	116.03	2040
18	Hunan	24–32°N	19,180	27.38	111.52	1976
19	Hubei	24–32°N	17,340	31.16	112.25	2962
20	Sichuan	24–32°N	52,840	30.18	103.77	7213
21	Guizhou	24–32°N	15,770	26.92	106.59	2600
22	Fujian	24–32°N	10,480	25.94	118.28	1993
23	Taiwan	<24°N	2990	23.85	121.95	3743
24	Guangdong	<24°N	14,830	22.87	113.48	1723
25	Guangxi	<24°N	20,570	23.64	108.27	1971
26	Yunnan	24–32°N	33,690	25.20	101.86	5956
27	Xizang	24–32°N	113,300	31.67	88.75	8191
28	Hainan	<24°N	2710	20.18	109.82	1721

We executed Chi-square analysis (Zar 1984) to test whether the proportions of the genera for a given geographical element significantly differ among the four 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 fourteen 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 four latitudinal zones. We used model predictions and fitting linear models to fit curve (Legendre and Legendre 1998). We have calculated inflection points by using a proper Taylor regression procedure (Demetris 2014) in Package RootsExtremaInflections of R (Online Resource 2).

Based on generic presence/absence data and proportional composition of geographical elements for the 28 regions, correlation between generic composition and phytogeographical composition at the regional level was examined using canonical correspondence analysis (CCA) (Terbraak 1986). A Monte Carlo permutation test (Legendre and Legendre 1998) was performed to evaluate whether the correlation determined by CCA between generic composition and phytogeographical composition were significantly different from random using 1000 permutations. R software was used to perform CCA and Monte Carlo permutations (R Core Team 2016).

In addition, we tabulated several climate variables for each of the 28 regions from data in Chinese Ecosystem Research Network dataset for the period 1971–2000 (Yu et al. 2004). ArcGIS 9.0 (ESRI 2008) was used to calculate the climate variables for each of 28 regions by performing zonal statistics to the administrative divisions of China layer and all various climate layers. We examined six climate variables, including mean annual temperatures, mean January temperatures, mean July temperatures, mean annual precipitation, mean warmest quarter precipitation, and annual total radiation. Topographic data (i.e., elevation) downloaded from the USGS's Hydro-1K dataset (http://edcdaac.usgs.gov/gtopo30/hydro/). By the above same zonal statistics in ArcGIS, we got the range of elevation (or max elevation) for each of 28 regions. Trends of

Table 2 Summarized data (mean ± SD) for climatic and geographical variables of the 28 regional floras according to latitudinal zone

	Latitudinal zone			
	<24°N (n = 4)	24–32°N (n = 10)	32–40°N (n = 9)	>40°N (n = 5)
Climate				
Annual mean temperature	19.6 ± 4.1	13.2 ± 5.8	9.5 ± 5.3	4.3 ± 2.3
January mean temperature	13.3 ± 3.3	2.8 ± 6.2	−4.9 ± 5.6	−15.5 ± 4.0
July mean temperature	24.6 ± 5.6	22.7 ± 5.9	22.3 ± 5.5	21.3 ± 1.5
Annual precipitation	1676.9 ± 141.8	1279.8 ± 399.4	655.0 ± 322.3	466.8 ± 242.9
Precipitation in June to September	2077.5 ± 349.1	1481.6 ± 330.8	1048.0 ± 347.5	871.8 ± 469.0
Annual radiation	5154.0 ± 571.9	4743.9 ± 697.6	5381.1 ± 418.8	5251.6 ± 479.7
Geography				
Area (×1000 km^2)	10.3 ± 8.9	31.8 ± 33.5	62.9 ± 19.4	78.5 ± 70.0
Latitude (°N)	22.6 ± 1.7	28.3 ± 2.3	22.9 ± 2.3	44.0 ± 3.0
Maximum elevation (×10 m)	402.2 ± 278.1	1316.9 ± 1481.6	35.8 ± 1250.1	778.1 ± 715.7

Table 3 Number of genera in each of the four latitudinal zones (diagonal) and number of genera shared between a pair of zones

Latitude zone	<24°N	24–32°N	32–40°N	40°N
<24°N	1046			
24–32°N	835	1364		
32–40°N	447	662	722	
>40°N	145	229	255	307

the selected climate variables along latitudinal gradients are summarized in Table 2.

Results

A total of 1664 genera of endemic seed plants were compiled for China. 63% (1046) of these genera were found in the latitudinal zone of <24°N, and 211 of them do not occur in latitudes north of 24°N (Table 3). About 47% of the 307 genera present in latitudes north of 40°N also occurred in latitudes south of 24°N (Table 3).

The relationships between the proportion of the cosmopolitan, tropical and temperate genera, and latitude and climatic variables were depicted in Fig. 2. Among those, latitude represented the strongest relation with the proportion of the three major groups. The proportion of tropical genera was c. 75% in the southernmost region around 20°N (i.e., Hainan), and decreased to nearly 0% at the latitude of 45–50°N (Fig. 2a). In contrast, the proportion of temperate genera was 20% in the southernmost region, and increased rapidly northward up to c. 35°N to 80%, and then it tended to level off. The proportion of cosmopolitan genera increases with increasing latitude from 5% at the southernmost latitude to c. 21% at 50°N. Tropical genera occur predominantly in southern China <25°N latitude and decreased with increasing latitude (Fig. 2a). The value of the estimated inflection points for percentages of three geographic elements along with latitude is ca. 35°N (Fig. S1). Trends in changes of the relative frequencies of the cosmopolitan, tropical and temperate genera along temperature, and precipitation and radiation gradients were more or less comparable with those along the latitudinal gradient as noted above (Fig. 2). 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. 35–40°N mirrored the change observed at c. 10 °C of the temperature gradient (compare Fig. 2a with b).

More detail on the trend of changes in relative frequencies of tropical and temperate genera along the latitudinal gradient is shown in Table 4. Most of the 15 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. 16, 9, and 20%, respectively, of the total regional flora at <24°N, but these three geographical elements accounted for nearly 0% of the total of a flora at >40°N (Table 4). The proportion of holarctic genera increased considerably (by 31%) from <24°N to >40°N. The geographical elements of eastern Asia–North America, temperate Eurasia, and temperate Asia peaked around the mid-latitudes. The Chinese endemic genera trended to follow the same trend as the tropical genera. They peaked at latitudes between 24 and 32°N, rather than <24°N (Table 4). Neither the central Asia element nor the Mediterranean, western to central Asia element showed significant patterns along the latitudinal gradient (Table 4).

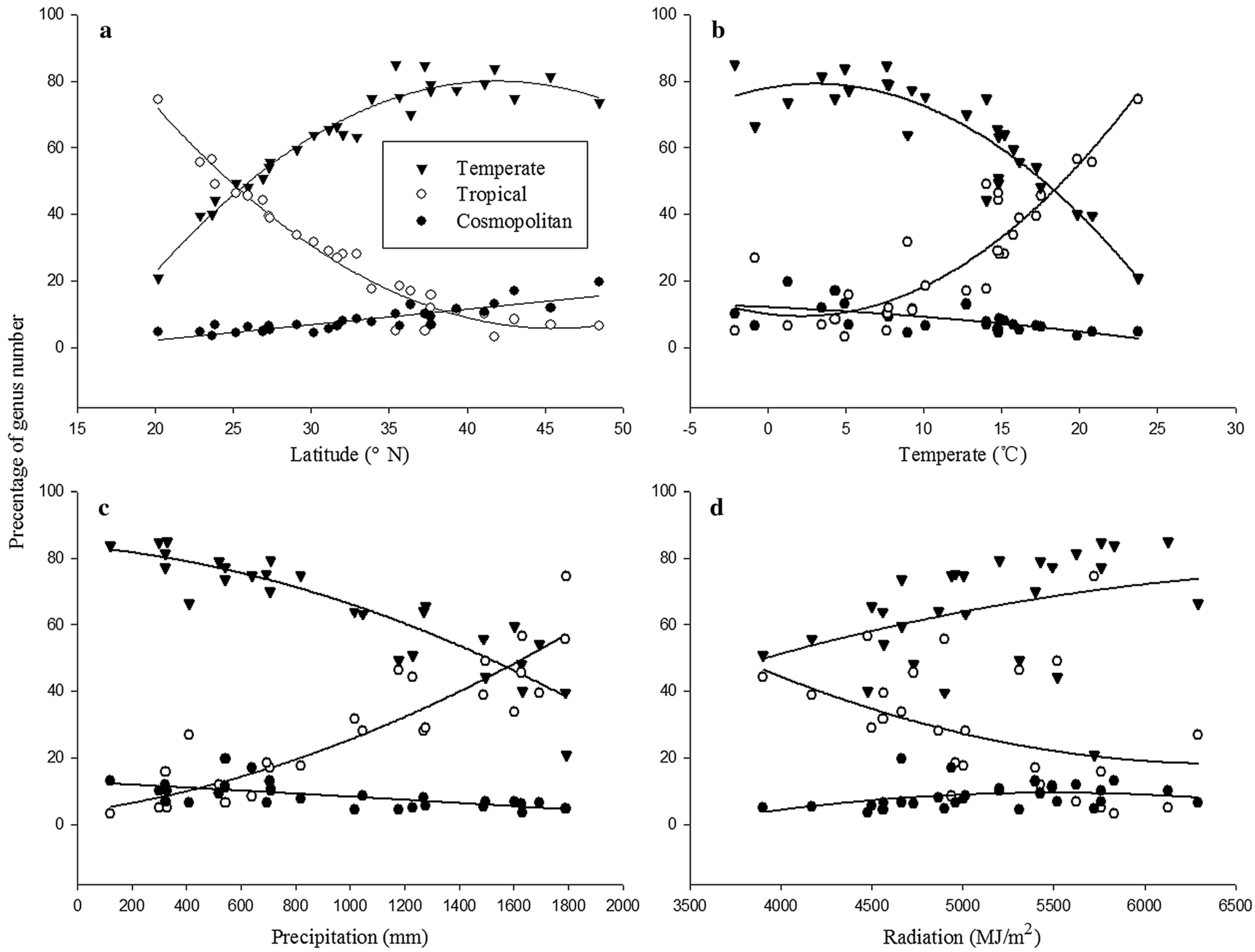

Fig. 2 Relationships between the proportions of cosmopolitan, tropical, and temperate genera of endemic seed plants, and **a** latitude, **b** temperature, **c** precipitation and **d** radiation. All *black lines* are curve fitted for scatterplots for distribution patterns of proportions of three geographic elements along with geographic and climatic gradients

Relationships between the set of the 28 geographical regions and the set of the 15 geographical elements were portrayed by a biplot of CCA using its first two ordination axes (Fig. 3). The eigenvalues of the first and second axes were 0.41 and 0.25, respectively. A Monte Carlo test with 999 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 the first CCA axis ($P < 0.05$). The six tropical geographical elements (i.e., pantropical, amphi-Pacific tropical, palaeotropical, tropical Asia-tropical Australia, tropical Asia-tropical Africa, and tropical Asia) were strongly and positively correlated with the first CCA axia (Table 5), and were mainly associated with the regions floras which are located at latitudes south of 32°N (Fig. 3). In contrast, the cosmopolitan and Holarctic geographical elements were strongly and negatively correlated with the first CCA axis (the intraset correlations of both being 0.80 and 0.97, Table 5) and were mainly associated with the regional floras which are located at latitudes primarily north of 40°N (Fig. 3). The geographical elements of temperate Eurasia, temperate Asia, Mediterranean and western to central Asia and Central Asia were which were positively correlated with the first CCA axis (Table 5), were mainly associated with the regional floras primarily located at latitudes between 32°N and 40°N (Fig. 3). The geographical elements of eastern Asia–North America, Eastern Asia, and Chinese endemic were weakly correlated with both CCA axes (Table 5). The CCA results reinforced the conclusions on the latitudinal trends for most of the fifteen geographical elements as noted in Table 4.

Discussion

At present, to characterize large-scale biogeographical patterns, one of the popular approaches is to stratify all taxa found in a particular area into many of geographical

Table 4 Proportion (%, mean ± SD) of the genera across the 15 geographical elements for each of the four latitudinal zones based on the 28 regional floras used in this study

Geographical element	Latitudinal zone				
	<24°N ($n = 4$)	24–32°N ($n = 10$)	32–40°N ($n = 9$)	>40°N ($n = 5$)	Chi-square test
Cosmopolitan	4.9 ± 1.4	5.8 ± 1.5	9.2 ± 2.1	14.5 ± 3.6	n. s.
Pantropical	16.3 ± 3.2	11.3 ± 3.9	5.3 ± 2.6	2.7 ± 1.2	**
Amphi–Pacific tropical	2.7 ± 0.5	2.4 ± 0.6	1.3 ± 0.8	0.3 ± 0.5	n. s.
Palaeotropical	8.5 ± 2.3	4.6 ± 2.4	1.9 ± 1.2	0.8 ± 0.5	**
Tropical Asia–tropical Australia	9.0 ± 1.2	4.5 ± 2.6	2.0 ± 0.8	2.0 ± 1.0	n. s.
Tropical Asia–tropical Africa	2.5 ± 0.6	2.1 ± 0.6	1.4 ± 0.3	1.7 ± 0.5	n. s.
Tropical Asia	19.9 ± 5.7	11.5 ± 5.7	2.5 ± 2.4	0.0 ± 0.0	**
Holarctic	11.3 ± 5.7	19.0 ± 5.8	32.5 ± 4.9	42.1 ± 3.5	***
Eastern Asia–North America	5.1 ± 1.4	6.9 ± 2.0	5.8 ± 2.0	2.9 ± 0.9	n. s.
Temperate Eurasia	3.5 ± 1.6	7.2 ± 2.6	15.2 ± 2.8	16.1 ± 1.7	**
Temperate Asia	0.4 ± 0.3	1.2 ± 0.7	3.2 ± 0.8	4.2 ± 0.9	n. s.
Mediterranean and western to central Asia	0.2 ± 0.0	0.2 ± 0.2	2.0 ± 2.1	3.6 ± 4.2	n. s.
Central Asia	0.0 ± 0.0	0.6 ± 0.9	1.8 ± 2.1	3.2 ± 3.7	n. s.
Eastern Asia	9.3 ± 2.1	14.2 ± 3.7	10.2 ± 2.6	4.0 ± 1.5	n. s.
Chinese endemic	6.5 ± 2.7	8.5 ± 2.5	5.6 ± 2.1	1.8 ± 1.8	n. s.

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

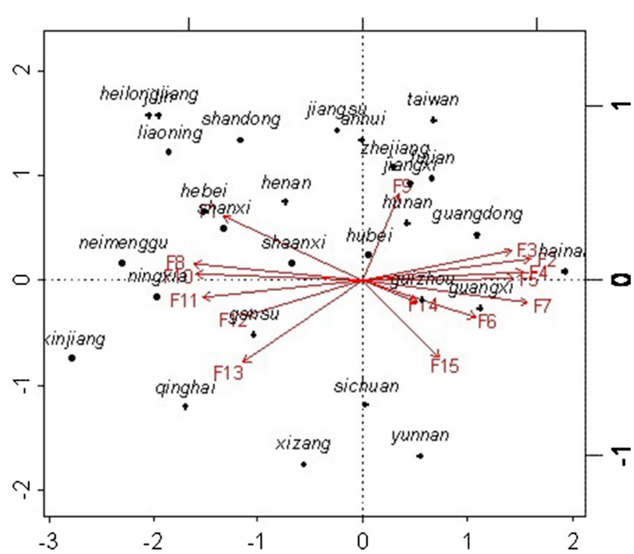

Fig. 3 Biplot based on canonical correspondence analysis (CCA) of the 28 regional floras of China in relation to the fourteen geographical elements (represented by *red line* accompanied with numerical codes). Numerical codes are: *F1* Cosmopolitan, *F2* Pantropical, *F3* Trop. and Subtr. E. Asia and (S.) Trop. Amer. Disjuncted, *F4* Old World Tropics, *F5* Trop. Asia to Trop. Australasia Oceania, *F6* Trop. Asia to Trop. Africa, *F7* Trop. Asia, *F8* N. Temp, *F9* E. Asia and N. Amer. disjuncted, *F10* Old World Temp, *F11* Temp. Asia, *F12* Medit., W. to C. Asia, *F13* C. Asia, *F14* E. Asia and *F15* Endemic to China

elements considering the nature, especially the affinities, of their distribution. Our study is the first to apply the geographical elements defined by Wu et al. (2006) to stratify the genera of the endemic seed plants into fifteen geographical elements.

The main conclusions from our study are similar to the results found by Qian et al. (2003) and Zhu et al. (2007), although we found that the value of tropical genera occur predominantly and the value of abrupt change in the rate of decline of tropical genera were further south by 5° latitude. This difference in our results might confirm that the main body of Chinese endemic seed flora distributes further south than that of Chinese seed flora, and that temperate genera are dormant in Chinese endemic seed flora.

Our study distinctly shows that the genera of the endemic seed plants in China exhibit a clear gradient distribution from the north to the south. We get the similar distribution pattern with the genera of all seed plant in China (Qian et al. 2006; Zhu et al. 2007), and that in East Asia (Qian et al. 2003). The significant latitudinal gradient in geographical element composition primarily comes from the increasing number of tropical genera from the north to the south. Tropical regions are thought as the spot of origin of angiosperm (Lidgard and Crane 1990; Raven and Axelrod 1974; Takhtajan 1969; Wu 1980), and tropical and subtropical Asia, China chiefly, is figured as one of the diversification centers for angiosperm (Takhtajan 1969; Wu 1980). Since the global climates gradually became warmer from the earliest Tertiary to the early Eocene, and taxa, evolved in tropical regions, spread from low latitudes to higher latitudes, a clear decreasing latitudinal gradient along tropical elements may have been created (Qian et al. 2003). From our result, the higher taxa, genera, of endemic

Table 5 Canonical correlations of geographical elements with the first two axes of canonical correspondence analysis (CCA) using the floristic data of the 28 regions in China

Geographical element	Intraset correlation		Interset correlation	
	Axis1	Axis2	Axis1	Axis2
Cosmopolitan	0.802	0.402	0.802	0.401
Pantropical	−0.953	0.081	−0.952	0.081
Amphi–Pacific tropical	−0.749	0.2	−0.748	0.2
Palaeotropical	−0.911	0.073	−0.91	0.073
Tropical Asia–tropical Australia	−0.852	0.041	−0.851	0.041
Tropical Asia–tropical Africa	−0.675	−0.246	−0.674	−0.245
Tropical Asia	−0.948	−0.089	−0.947	−0.089
Holarctic	0.973	0.122	0.972	0.122
Eastern Asia–North America	−0.212	0.464	−0.212	0.463
Temperate Eurasia	0.958	0.061	0.957	0.061
Temperate Asia	0.916	−0.04	0.915	−0.04
Mediterranean and western to central Asia	0.694	−0.152	0.694	−0.151
Central Asia	0.677	−0.416	0.676	−0.415
Eastern Asia	−0.332	−0.241	−0.332	−0.24
Chinese endemic	−0.427	−0.473	−0.426	−0.471

seed plants exhibit a very consistent rule with the angiosperm along the latitudinal gradients. The research from the fossil data have testified that the Tertiary boreotropical flora in high latitude contained a large number of tropical taxa (Qian et al. 2003) and showed close affinities with modern subtropical floras in low latitude (Latham and Ricklefs 1993). In China, many genera of endemic seed plants, which currently occurred at, or restricted to the tropical to temperate zones, were also elements of boreotropical flora in high latitude during the Tertiary (e.g., *Alangium*, *Castanea*, *Celastrus*, *Juglans*, *Lindera*, *Metasequoia*, *Sassafras*, *Tilia* and *Zelkova*) (Qian et al. 2003).

A significant climate cooling occurred (Graham 1999) by the late early and early middle Eocene. For most plants, this climate changing created an evolutionary barrier, that is, frozen tolerance. As almost all tropical plants are greatly frost-intolerant (Brown and Lomolino 1998), and the climatic tolerances of many flowering plant taxa could not be altered (Tiffney 1985a), the evergreen and cold-intolerant plants of the boreotropical flora were forced southward by this climate cooling in north hemisphere (Tiffney 1985b). It is reasonable that this evolutionary process for cold adaptation results in a descending proportion of tropical genera in a flora along increasing latitude (Qian et al. 2003).

One of the most striking patterns in this study in the abrupt change in the rate of decline of tropical genera for Chinese endemic seed flora at around 35°N from a steep crease at lower latitudes to a more gradual decrease at higher latitudes (Fig. 2a). The latitude 35°N more or less corresponds with the mean annual temperature of c. 14 °C in China from the map of the mean annual temperature of China (Liu 1998). Our study also shows drastic changes in the rate of decrease in tropical genera of Chinese endemic flora and the rate of increase in temperate genera of Chinese endemic flora from the south to the north at the mean annual temperature of c. 14 °C (Fig. 2b). This temperature may indicate a special biological threshold for plants to adapt upheaval climates, mainly in cold climate, and may have played an important role in determining the latitudinal ranges of plant and biome distributions in China. A greatly large number of plant genera and species in China are distributed southern more. Many of them (e.g., *Magnolia*, *Lindera*) have their northern range boundaries nearly congruent with this latitude in East Monsoon Area. Likewise, we can see that the trends of change of tropical and temperate genera at mean annual precipitation are similar with that of at mean annual temperature, with the sudden changes in the rate of two group genera at mean annual precipitation of c. 700 mm. For the annual all radiation, there is a trend of changes in the rate of two group genera. We also can find outstanding changes with two rates, which lie in the cross of the scatter spot of the rate of the tropical and cosmopolitan genera, at the annual total radiation c. 5000 MJ/m^2. Comparing with the above latitude and the three climatic variables, we find they have common in location at latitude c. 35°N. Topographically, the natural watershed of the south and the north in China—Mt. Qinling lies at latitude near 35°N. The northern boundary of the subtropical evergreen broad-leaved forest more or less corresponds to the line of latitude 35°N (Wu 1980).

Acknowledgements We are grateful to the many people who have contributed to this study, especially Prof. Runguo Zang, Dr. Yi Ding and Dr. Xinghui Lu in the Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry for their assistance in the formation of idea in the article. We are appreciating the constructive comments from the two anonymous referees, which have greatly improved the manuscript. This study was funded by the National Nonprofit Institute Research Grant of the Chinese Academy of Forestry (CAFYBB2014MA005), National Natural Science Foundation of China (41471048), and National Nonprofit Institute Research Grant of the Institute of Forest Ecology, Environmental and Protection, Chinese Academy of Forestry (CAFIFEEP2015B02).

Author contributions Jihong Huang, Keping Ma and Jianhua Huang designed the study. Jihong Huang collected data. Jihong Huang and Jianhua Huang carried out the data analysis. Jihong Huang, Keping Ma and Jianhua Huang wrote and reviewed the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animals rights The research doesn't involve human participants and animals.

Information on Electronic Supplementary Material

Online Resource 1. Reference list that we have consulted to collect distribution information of Chinese seed plants.
Online Resource 2. Inflection points by using a proper Taylor regression procedure in Package RootsExtremaInflections of R. The value of the measured inflection point is 33.879, while the value of the estimated inflection point is 35.441.

References

Axelrod DI, Al-Shehbaz I, Raven PH (1996) History of the modern flora of China. In: Zhang AL, Wu SG (eds) Floristic characteristics and diversity of east Asian plants. China Higher Education Press, Beijing, pp 43–55

Brown JH, Lomolino MV (1998) Biogeography, 2nd edn. Sinauer Associates, Sunderland

Demetris TC (2014) Roots, extrema and inflection points by using a proper Taylor regression procedure. ResearchGate publications. Available at: https://www.researchgate.net/publication/261562841

Du Y, Mao L, Queenborough SA, Freckleton RP, Chen B, Ma K (2015) Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. Global Ecol Biogeogr 24:928–938. doi:10.1111/geb.12303

Editorial Committee of Flora of Sichuanica (1981–1999) Flora of Sichuanica. Sichuan Science and Technology Press, Chengdu

Editorial Committee of Flora of Yunnannica (1977–2006) Flora of Yunnannica. Science Press, Beijing

Editorial Committee of Flora Reipublicae Popularis Sinicae (1959–2004) Flora Reipublicae Popularis Sinicae. Science Press, Beijing

ESRI (2008) ArcGIS 9.3. ESRI Press, New York

Feng G, Mao L, Sandel B, Swenson NG, Svenning J-C (2016) High plant endemism in China is partially linked to reduced glacial–interglacial climate change. J Biogeogr 43:145–154. doi:10.1111/jbi.12613

Fjeldså J, Lovett JC (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. Biodivers Conservation 6:325–346. doi:10.1023/A:1018356506390

Fu L, Feng Z, Zhuang J, Ying J (1993) Species Diversity. In: Chen L, Wang X, Wang S (eds) Biodiversity in China: status and conservation strategy. Science Press, Beijing, pp 31–99

Graham A (1999) Late Cretaceous and Cenozoic history of North American vegetation north of Mexico. Oxford University Press, New York

Huang JH, Chen JH, Ying JS, Ma KP (2011) Features and distribution patterns of Chinese endemic seed plant species. J Syst Evol 49:81–94. doi:10.1111/j.1759-6831.2011.00119.x

Huang J, Chen B, Liu C, Lai J, Zhang J, Ma K (2012) Identifying hotspots of endemic woody seed plant diversity in China. Diversity Distrib 18:673–688. doi:10.1111/j.1472-4642.2011.00845.x

Huang J, Ma K, Chen B (2014) Diversity and geographic distribution of endemic species of seed plants in China. Higher Education Press, Beijing

Jin S (1994) Compilation of type specimen of higher plant of China. Science Press, Beijing

Jin S (1999) Supplements of compilation of type specimen of higher plant of China. Chinese Forestry Press, Beijing

Latham RE, Ricklefs RE (1993) Continental comparisons of temperate-zone tree species diversity. In: Ricklefs RE, Schluter D (eds) Species Diversity in Ecological Communities: historical and geographical perspectives. University of Chicago Press, Chicago, pp 294–314

Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science, Amsterdam

Lidgard S, Crane PR (1990) Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. Paleobiology 16:77–93. doi:10.1017/S009483730000974X

Liu MG (1998) The atlas of the physical geography of China, 2nd edn. SinoMaps Press, Beijing

Lopez-Pujol J, Zhang FM, Sun HQ, Ying TS, Ge S (2011) Centres of plant endemism in China: places for survival or for speciation? J Biogeogr 38:1267–1280. doi:10.1111/j.1365-2699.2011.02504.x

Lovett JC, Friis I (1996) Patterns of endemism in the woody flora of north-east and east Africa. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM (eds) The biodiversity of African plants. Kluwer Academic Publisher, Dordrecht, pp 582–601

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi:10.1038/35002501

Pielou EC (1991) After the ice age. University of Chicago Press, Chicago

Qian H, Song JS, Krestov P, Guo QF, Wu ZM, Shen XS, Guo XS (2003) Large-scale phytogeographical patterns in East Asia in relation to latitudinal and climatic gradients. J Biogeogr 30:129–141. doi:10.1046/j.1365-2699.2003.00807.x

Qian H, Wang S, He J, Zhang J, Wang L, Wang X, Guo K (2006) Phytogeographical analysis of seed plant genera in China. Ann Bot (Oxford) 98:1073–1084. doi:10.1093/Aob/Mcl192

Qian H, Field R, Zhang J-L, Zhang J, Chen S (2016) Phylogenetic structure and ecological and evolutionary determinants of species richness for angiosperm trees in forest communities in China. J Biogeogr 43:603–615. doi:10.1111/jbi.12639

Qiu YX, Fu CX, Comes HP (2011) Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of quaternary climate and environmental change in the world's most diverse temperate flora. Molec Phylogen Evol 59:225–244. doi:10.1016/j.ympev.2011.01.012

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movements. Ann Missouri Bot Gard 61:539–673. doi:10.2307/2395021

Smith AC (1970) The Pacific as a key to flowering plant history. In: Harold L (ed) Lyon Arboretum Lecture. Hawaii University of Hawaii, Hawaii, pp 1–26

Sun G, Dilcher DL, Zheng S, Zhou Z (1998) In search of the first flower: a Jurassic angiosperm, Archaefructus, from northeast China. Science 282:1692–1695. doi:10.1126/science.282.5394.1692

Takhtajan AL (1969) Flowering plants: origin and dispersal. Oliver & Boyd, Edinburgh

Terbraak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179. doi:10.2307/1938672

Tiffney BH (1985a) The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. Arnold Arboretum 66:243–273. doi:10.5962/bhl.part.13183

Tiffney BH (1985b) Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. Arnold Arboretum 66:73–94. doi:10.5962/bhl.part.13179

Wang H (1992) Floristic plant geography. Science Press, Beijing

Wang H, Zhang Y (1994) The biodiversity and characters of spermatophytic genera endemic to China. Acta Bot Yunnanica 16:209–220

Wang ZH, Fang JY, Tang ZY, Lin X (2011) Patterns, determinants and models of woody plant diversity in China. Proc Roy Soc Ser B Biol Sci 278:2122–2132. doi:10.1098/rspb.2010.1897

Wolfe JA (1975) Some aspects of plant geography of the northern Hemisphere during the Late Cretaceous and Tertiary. Ann Missouri Bot Gard 62:264–279. doi:10.2307/2395198

Wu Z (1980) The vegetation of China. Science Press, Beijing

Wu ZY (1983–1987) Flora of Tibet. Science Press, Beijing

Wu ZY, Ding TY (1999) Seed plants of China. Yunnan Science and Technology Press, Kunming

Wu Z, Raven PH, Hong D (1994–2012) Flora of China. Science Press, Beijing

Wu Z, Zhou Z, Sun H, Li D, Peng H (2006) Areal-types of seed plants and their origin and differentiation. Yunnan Science and Technology Press, Kunming

Wu Z, Sun H, Zhou Z, Li D, Peng H (2011) Floristics of seed plants from China. Science Press, Beijing

Ying J, Zhang Y (1994) The endemic genera of seed plants of China. Science Press, Beijing

Yu G, He H, Liu X, Niu D, Wang Q, Ren C, Li Z (2004) China spatial information of terrestrial ecosystem research Atlas—climate division. China Meteorological Press, Beijing

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice Hall Inc, New Jersey

Zhu H (2013) Geographical elements of seed plants suggest the boundary of the tropical zone in China. Palaeogeogr Palaeoclimatol Palaeoecol 386:16–22. doi:10.1016/j.palaeo.2013.04.007

Zhu H, Ma Y, Yan L, Hu H (2007) The relationship between geography and climate in the generic-level patterns of Chinese seed plants. Acta Phytotaxon Sin 45:134–166. doi:10.1360/aps06118