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BIODIVERSITY RESEARCH

Identifying hotspots of endemic woody seed plant diversity in China

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ABSTRACT

Aim This study aimed to detect distribution patterns and identify diversity hotspots for Chinese endemic woody seed plant species (CEWSPS).

Location China.

Methods Presence of 6885 CEWSPS throughout China was mapped by taking the Chinese administrative county as the basic spatial analysis unit. The diversity was measured with five indices: endemic richness (ER), weighted endemism (WE), phylogenetic diversity (PD), phylogenetic endemism (PE) and biogeographically weighted evolutionary distinctiveness (BED). Three levels of area (i.e. 1, 5 and 10% of China's total land area) were used to identify hotspots, but the 5% level was preferred when both the total area of the hotspots identified and the diversity of CEWSPS reached by the hotspots were considered.

Results Distribution patterns of CEWSPS calculated with the five indices are consistent with each other over the national extent. However, the hotspots do not show a high degree of consistency among the results derived from the five indices. Those identified with ER and PD are very similar, and so are those with WE and BED. In total, 20 hotspots covering 7.9% of China's total land area were identified, among which 11 were identified with all the five indices, including the Hengduan Mountains, Xishuangbanna Region, Hainan Island, and eight mountainous areas located in east Chongqing and west Hubei, in east Yunnan and west Guangxi, in north Guangxi, south-east Guizhou and south-west Hunan, in north Guangdong and south Hunan, in south-east Tibet, and in south-east Hubei and north-west Jiangxi. Taiwan Island was also identified as a major hotspot with WE, PE and BED.

Main conclusions Hotspots of CEWSPS were identified with five indices considering both distributional and phylogenetic information. They cover most of the key areas of biodiversity defined by previous researchers using other approaches. This further verifies the importance of these areas for China's biodiversity conservation.

Keywords

Biodiversity conservation, endemism, evolutionary distinctiveness, phylogenetic diversity, range size, weighted endemism.

INTRODUCTION

Biodiversity loss resulting from human activities has been more rapid in the past 50 years than at any other time in human history (Millennium Ecosystem Assessment, 2005). Biodiversity conservation has therefore attracted considerable attention from biologists, ecologists and biogeographers (Reid, 1998; Myers *et al.*, 2000; Brooks *et al.*, 2006). The importance of the flora of China to planning global conservation of biodiversity has frequently been emphasized (Raven & Axelrod, 1974; Wu, 1980; Axelrod *et al.*, 1996; Liu *et al.*, 2003; Qian *et al.*, 2006; Tang *et al.*, 2006). Endemic seed plant species richness is extremely high in China and accounts for more than half of the total seed flora of China (Fu *et al.*, 1993). Endemic species are more vulnerable to extinction than more widespread species because of their limited geographic ranges and

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thus have become one of the most effective surrogates for identifying conservation priorities or hotspots (Myers *et al.*, 2000). Therefore, some researchers have stated that the detection of areas with high plant endemism is crucial for Chinese conservation (Ying & Zhang, 1994; Axelrod *et al.*, 1996; Yang & Zuo, 1998; Ying, 2001). Unfortunately, China's natural habitats, particularly forests, have suffered severe degradation because of increasingly intensive human activities (Liu *et al.*, 2003; Cyranoski, 2008).

When conservation resources are limited, identifying priority areas or hotspots where biodiversity is most threatened is critical (Olson & Dinerstein, 1998; Myers *et al.*, 2000; Brummitt & Lughadha, 2003). Biodiversity hotspots defined by Norman Myers (1988) are characterized by exceptional concentrations of endemic species experiencing relatively high rates of habitat loss (Prendergast *et al.*, 1999; Myers *et al.*, 2000). This approach to defining hotspots has been used in many studies (Mittermeier *et al.*, 2005). To define a hotspot adequately, it is necessary to delineate its boundary. A predefined proportion of areas with high values of both endemic species richness and habitat loss are taken as hotspots (Prendergast *et al.*, 1993; Orme *et al.*, 2005; Tang *et al.*, 2006). In recent years, the definition of the term 'hotspot' of biodiversity has been generalized. In addition to number of endemic species and loss of habitat, other aspects, including total number of species, number of threatened species, as well as evolutionary history, have been proposed to identify hotspots (Spathelf & Waite, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010).

In past decades, researchers have paid much attention to species diversity, which is the most prominent and readily recognizable form of biodiversity and includes species richness and number of endemic, rare or threatened species (Reid, 1998; Brummitt & Lughadha, 2003; Orme *et al.*, 2005). However, in recent years, much attention has been focused on the evolutionary process (Vane-Wright *et al.*, 1991; Faith, 1992; Sechrest *et al.*, 2002; Redding & Mooers, 2006; Forest *et al.*, 2007; Isaac *et al.*, 2007). Phylogenies – evolutionary trees – have become increasingly important in identifying biodiversity hotspots (Faith, 1992; Spathelf & Waite, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010; Cadotte *et al.*, 2010). Phylogenetic diversity is often favoured because it is assumed that it captures feature diversity (Vane-Wright *et al.*, 1991; Faith, 1992), shows relationships between extant species and provides more information about evolution over a long time-scale (Omland *et al.*, 2008). A number of measures combining phylogenies and geographic distributions of taxa have been proposed (Faith, 1992; Spathelf & Waite, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010; Cadotte *et al.*, 2010). Some of these measures focus on the phylogenetic diversity (PD) (Faith, 1992; Forest *et al.*, 2007) or taxonomic distinctiveness (May, 1990; Vane-Wright *et al.*, 1991; Redding & Mooers, 2006). Others combine phylogenetic features and geographic ranges (Isaac *et al.*, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010), for example phylogenetic endemism (PE) (Rosauer *et al.*, 2009) and biogeographically weighted evolutionary distinctiveness (BED) (Cadotte & Davies, 2010). Where conservation resources are limited, PE and BED are useful means for understanding biogeographic patterns and subsequent setting of biodiversity conservation priorities (Rosauer *et al.*, 2009; Cadotte & Davies, 2010).

Several studies have identified critical regions or hotspots for China's biodiversity, especially plant diversity. Wang *et al.* (1993), based on individual studies and estimations, proposed roughly 14 terrestrial key areas for the conservation of China's biodiversity using one of the three criteria: (1) extraordinary species diversity, (2) high richness of endemic or threatened species and (3) high genetic diversity. Ying (2001) defined three biodiversity centres using species richness based on published floristic data. Ying & Zhang (1994) identified three centres of endemism according to richness of Chinese endemic seed plant genera based on herbarium specimens. Zhang & Ma (2008) proposed eight hotspots of China's biodiversity in view of the threatened plant species. Tang *et al.* (2006) identified ten hotspot ecoregions in China based on investigated or collected genus richness and endangered species richness of seed plants, species richness and endemic species of terrestrial mammals, and species richness of endangered vertebrates. Chen (1998), using estimated species richness and number of endemic species, also defined 11 terrestrial key areas for the conservation of China's biodiversity. In addition, globally, the WWF's Global 200 also included 12 most critical and endangered terrestrial ecoregions located in or partly within China (Olson & Dinerstein, 1998). Among the 34 global biodiversity hotspots identified by Conservation International, four either intersect with or are located in China (Mittermeier *et al.*, 2005).

However, it is clear that previous studies on China's biodiversity are limited, and they are also difficult to compare directly. They are characterized by at least one of the three limitations: (1) different taxonomic levels used in different studies [e.g. genus used in Ying & Zhang (1994) and species in Ying (2001)], even in the same study (e.g. Wang *et al.*, 1993; Tang *et al.*, 2006), (2) limitations of data sources: the data used in most studies were compiled from literature and not herbarium records except the studies on endemic genera (Ying & Zhang, 1994) and native threatened plants (Zhang & Ma, 2008), and (3) simple diversity measurement used: all studies only focused on species richness and ignored the important roles of geographic range and phylogeny in the identification of biodiversity priority areas or hotspots. Thus, in this study, based on a comprehensive data set of Chinese endemic woody seed plant species (CEWSPS) compiled from literature and herbarium specimens, we analyse the spatial patterns of the diversity of CEWSPS systematically over the whole landmass of China using five diversity indices, into which ecological and/or evolutionary information is incorporated in different ways. We then identify hotspots of CEWSPS, which would be useful for China's conservation planning. We also discuss the potential causes of the patterns revealed in this study.

METHODS

Data set

A list of Chinese endemic seed plants was compiled based on an extensive literature review (see Appendix S1 in Supporting Information) and experts' scrutiny. Woody plants were selected from this list (see Appendix S2). Information on their distribution was collated by consulting references and checking herbarium specimens.

Thus, distribution records from references or floristic point records such as those found in Flora of China (Wu *et al.*, 1994–2006) and Flora Yunnanica (Editorial Committee of Flora Yunnanica, 1977–2006) are almost always reported as originating from an administrative unit. In the present paper, we take county as the basic spatial analysis unit. There are 2377 counties with areas ranging from 22.4 to 208,134 km^2, of which only 162 (accounting for 6.8% of the total) are over 10,000 km^2.

Endemism is inherently scale dependent. It is sensitive to the delineation of boundaries (Good, 1974; Crisp *et al.*, 2001; Lomolino *et al.*, 2006). Ideally, endemic taxa are those whose distributions are delimited using natural and geographic boundaries. However, it is difficult to define the Chinese endemic taxa with these natural boundaries (rather than using administrative boundary) because of the absence of data at the correct level of detail. Therefore, despite these issues, we still use administrative boundary to delimit Chinese endemic plants and refer to endemic taxa as those only occurring within China's borders. This allows us to address our aim of elucidating the distributional patterns of all CEWSPS.

The information for the presence of 6885 CEWSPS (including intraspecific taxa) was documented for each of the 1958 counties, in which at least one CEWSPS occurs; no record of CEWSPS was found for the remaining 419 counties, and therefore, CEWSPS was considered absent from these counties. The data for all administrative units at both county and province levels (Fig. S1), and main rivers (Fig. 1) were downloaded from the National Fundamental Geographic Information System of China (http://nfgis.nsdi.gov.cn/nfgis/chinese/c_xz.htm). The data for the main mountains (Fig. 1) were derived from a digital elevation model (DEM, http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/GTOPO30) according to the criteria described in the Editorial Committee of China's Physical Geography (1985).

Pattern analysis

Measures of diversity

The most straightforward and universal measurement of biodiversity is species richness because species is the basic taxonomic unit for biological classification. In this article, species richness of CEWSPS is called endemic richness (ER). ER is measured simply as the total count of CEWSPS within a spatial unit.

Biodiversity conservation is intimately associated with species distribution and biogeography. As the geographic ranges of species are not equal, those confined to a limited area are vulnerable to risk of extinction. Another popular approach is to use range weighting in the identification of biodiversity priority areas (Dony & Denholm, 1985; Williams & Humphries, 1994; Williams *et al.*, 1994; Crisp *et al.*, 2001; Linder, 2001). This measure is termed inverse weighted endemism (WE) (Linder, 2001): $\mathrm{WE} = \sum_{i=1}^{n} W_i$, where n is the number of taxa (i.e. CEWSPS in this study) in a spatial unit, and W_i is the weighting of taxon i, which is the inverse of its range. Here, we take the Chinese county as a spatial unit. Thus, the range of a species in our study is the sum of the areas of counties in which the focal species is recorded. Ten thousand-kilometer square is taken as the unit of area in our calculation.

Some researchers argue that phylogenetic or evolutionary diversity may play a more important role in identifying areas for biodiversity conservation because it reflects the evolutionary history and potential that might hold the information for the survival and development of a taxon both in the past and future (Vane-Wright *et al.*, 1991; Faith, 1992). A series of measures, using phylogenetic information or both phylogenetic and geographic range information, have recently been emphasized (Faith, 1992; Sechrest *et al.*, 2002; Forest *et al.*, 2007; Isaac *et al.*, 2007; Spathelf & Waite, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010; Cadotte *et al.*, 2010), especially after the publication of APG II (Bremer *et al.*, 2003). The PD index proposed by Faith (1992) is equal to the sum of the lengths of all branches that are members of the corresponding minimum spanning path and is a simple measure of evolutionary diversity, i.e. $\mathrm{PD} = \sum_{\{c \in C\}} L_c$, where C is the set of branches in the minimum spanning path joining the taxa to the root of the tree (constructed by a set of taxa found in a given area), c is a branch in the spanning path and L_c is the length of branch c.

Faith's PD focuses on phylogenetic features and ignores the spatial distribution of taxa. Recently, a number of new indices have been developed that combine both evolutionary and spatial features to elucidate the distribution patterns of biodiversity and identify hotspots (Soutullo *et al.*, 2005; Isaac *et al.*, 2007; Rosauer *et al.*, 2009; Cadotte & Davies, 2010; Cadotte *et al.*, 2010). Among them, PE (Rosauer *et al.*, 2009) and BED (Cadotte & Davies, 2010) are the two most representative indices. PE is calculated by combining PD and WE based on the length and geographic range size for each branch on a phylogeny (Rosauer *et al.*, 2009). $\mathrm{PE} = \sum_{\{c \in C\}} L_c / R_c$, where C, c and L_c are the same as in PD, R_c is the clade range, which is defined as the union of the ranges of the taxa descended on the phylogeny from branch c and occurring in the focal spatial unit, such that overlapping areas are considered only once. In contrast, BED combines species evolutionary distinctiveness and species spatial extent. Species evolutionary distinctiveness is the 'weighted sum' of ancestral branch lengths (Isaac *et al.*, 2007). Cadotte and his colleagues combined species evolutionary distinctiveness and spatial extent to help inform conservation prioritization

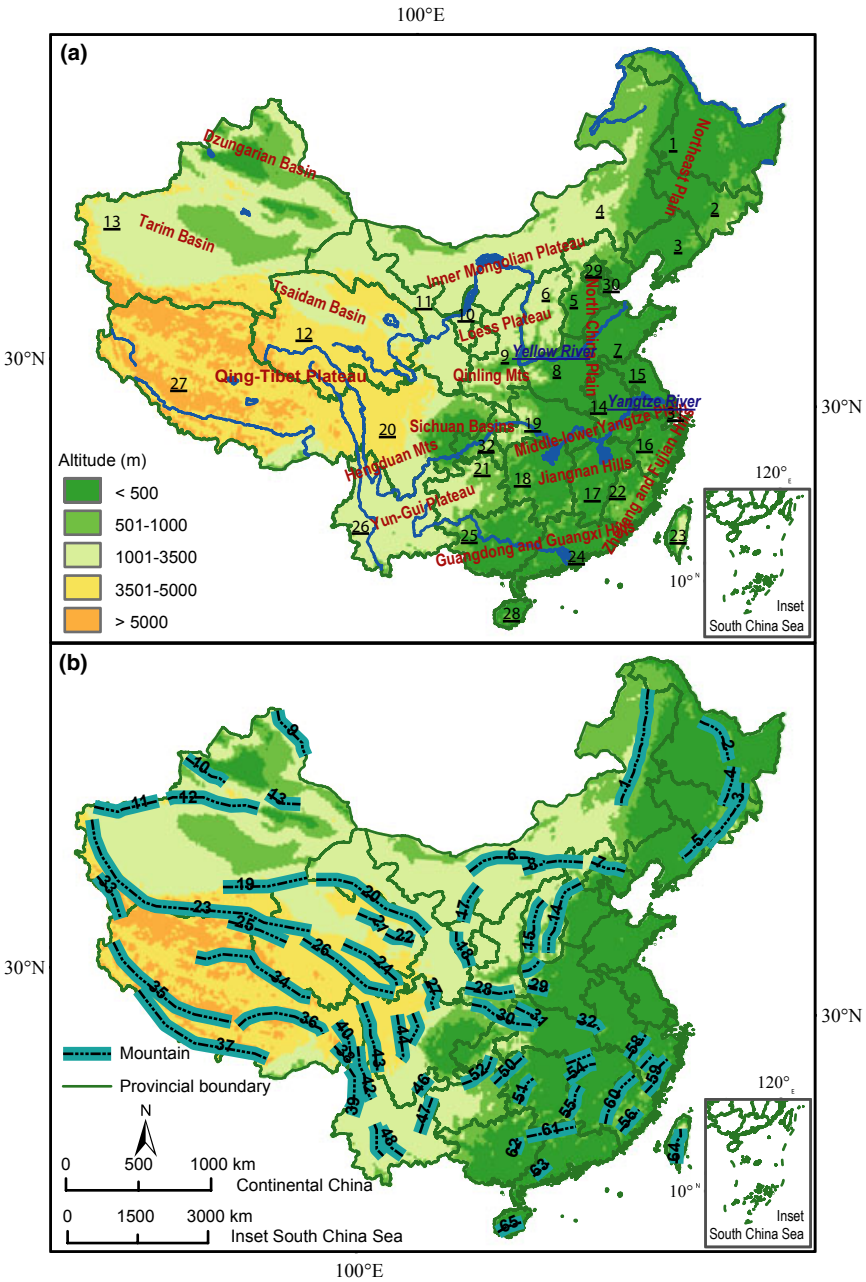

Figure 1 Maps of administrative provinces, macrotopography and major mountain ranges in China. (a) Locations of administrative province and major morphostructures (Scarlet text). Black number with underline identifies administrative province: 1 Heilongjiang, 2 Jilin, 3 Liaoning, 4 Inner Mongolia, 5 Hebei, 6 Shanxi, 7 Shandong, 8 Henan, 9 Shaanxi, 10 Ningxia, 11 Gansu, 12 Qinghai, 13 Xinjiang, 14 Anhui, 15 Jiangsu, 16 Zhejiang, 17 Jiangxi, 18 Hunan, 19 Hubei, 20 Sichuan, 21 Guizhou, 22 Fujian, 23 Taiwan, 24 Guangdong, 25 Guangxi, 26 Yunnan, 27 Tibet, 28 Hainan, 29 Beijing 30, Tianjin, 31 Shanghai, 32 Chongqing. According to Chinese physical geography (Editorial Committee of China's Physical Geography, 1985), the macrotopography is shown as five types, including plains (elevation < 500 m), low mountains (elevation of 500–1000 m), middle mountains (elevation of 1000–3500 m), high mountains (elevation of 3500–5000 m) and very high mountains (elevation > 5000 m). (b), Black number indicates main mountain ranges (Wang *et al.*, 2004) (codes are consistent with Table S1). The terrain of China from west to east forms a flight of three steps, commonly called 'Three Steps'. The First Step mainly includes Qinghai-Tibetan Plateau, north to Kunlun, Aerjin, and Qilian Mountains and east to Min, Qionglai, Daxue and Hengduan Mountains. The Second Step lies between the Hengduan Mountains to the west and Daxing'anling, Taihang, Funiu, and Xuefeng Mountains to the east, including mainly inner Mongolian Plateau, Loess Plateau, Qinling Mountains, Sichan Basin, and Yun-Gui Plateau. The Third Step scans all remaining regions, which covers North-east Plain, North China Plain, Middle-lower Yangtze Plain, Jiangnan Hills, Guangdong and Guangxi Hills, Zhejiang and Fujian Hills as well as Taiwan and Hainan islands. The inset in the right bottom of the figure shows the south boundary of China, including all islands in the South China Sea. Albers projection.

(Cadotte & Davies, 2010; Cadotte *et al.*, 2010) and termed it as BED: $\mathrm{BED} = \sum_{i=1}^{n}\sum_{j=1}^{m} L_j/N_j \Big/ R_i$, where n is the number of taxa, m is the number of branches, L_j is the length of branch j, N_j is the number of terminal taxa descended from branch j and R_i is the range of species i.

Constructing the phylogenetic tree

A phylogenetic supertree was constructed by inputting the woody endemic seed plants into the plant phylogeny database Phylomatic (Webb & Donoghue, 2005). A Nexus file obtained from Phylomatic was imported into the community phylogenetic software Phylocom (version 4.1, available online: http://phylodiversity.net/phylocom/). The Angiosperm Phylogeny Group classification system (Bremer *et al.*, 2003) was taken as the backbone of the supertree. Branch lengths of the phylogenetic tree were adjusted by using the BLADJ algorithm (Webb *et al.*, 2008) inside Phylocom with known molecular and fossil dates (Wikstrom *et al.*, 2001). The 'known' molecular and fossil dates used to calibrate the supertree are estimates, but they improve the robustness of phylogenetic analyses of endemism in comparison with the alternative, which is to use nodal distances (Webb, 2000). The phylogenetic tree constructed for CEWSPS in this study is provided in Appendix S3.

Detecting patterns of diversity and identifying hotspots

All the five diversity indices were calculated for each spatial unit using two R packages, Ape (Paradis, 2006) and Picante (Kembel *et al.*, 2010), in R 2.10.0 (R Development Core Team 2009), and the resultant maps were generated using ArcGIS 9.0 (ESRI, Redlands, CA, USA). The consistency between the patterns of diversity characterized with different indices was analysed using Spearman's correlation coefficient for each pair of indices. The related P-value was corrected for spatial autocorrelation with Dutilleul's (1993) method and implemented with Legendre's Fortran program modttest (http://www.bio.umontreal.ca/casgrain/en/labo/mod_t_test.html).

Five sets of priority counties were determined with the top scores for each index. Three thresholds (1, 5 and 10% of the land area of China) were used in the determination process. This procedure is called local maximization method (LMM) in our study.

It is widely recognized that species diversity is strongly dependent on sample size. To correct this effect on hotspot identification, a power function $\mathrm{D} = bA^{c}$ was fitted with nonlinear regression, where D is a diversity index and A is the area of the county for which the diversity is calculated. The reason that this function was chosen is that a statistically significant linear relationship exists between $\ln D$ and $\ln A$ (Fig. S2). Then, the residuals from the above power function for each index were used in the same way as the original index in the identification of hotspots with the LMM.

In a given area, the complementarity method (CM) might include more species (Vane-Wright *et al.*, 1991). In our study, this method was implemented by starting from the county with the highest value of the diversity index and adding another county so that the value of the diversity index of the pooled area (i.e. the union of the counties selected during the previous steps and the county added in this step) is higher than that by adding any other individual county, until a specified total area is reached. ER and WE were calculated with this method, which are denoted as ER_CM and WE_CM, respectively. The above three levels of land area (1, 5 and 10%) were also used to specify the total area of hotspots.

The hotspots identified for each index/method/area proportion combination as a whole is called a hotspot complex. After a hotspot complex was identified, the five diversity indices were also calculated at the hotspot complex level so that diversity can be compared at this level. The similarity between two hotspot complexes was calculated using Sørensen similarity coefficient (Sørensen, 1948): $S = 2c/(a + b)$, where a and b are the numbers of species occurring in the two hotspot complexes respectively, and c is the number of common species between the two complexes. This indicates the similarity of the two complexes in species composition. Similarly, area was also used to calculate the similarity to show the consistency of the two complexes in spatial occupancy. In this case, a and b are the areas of the two complexes, respectively, and c is the overlapping area of the two complexes.

RESULTS

Distribution patterns of diversity

Chinese endemic woody seed plant species are mainly distributed in the Qinling Mountains and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau, and more than 80% of the total CEWSPS occur in these regions. The five diversity indices calculated for each county over the country are highly significantly correlated with each other (Table 1). After the area effect is accounted for, i.e.

Table 1 Spearman's correlation coefficient ρ (with spatial autocorrelation-corrected P-value) between a pair of diversity indices.

Index 1	Index 2	Spearman's ρ	P-value
ER	WE	0.9352	0
ER	PE	0.9136	0
ER	PD	0.9982	0
ER	BED	0.9212	0
WE	PE	0.9572	0
WE	PD	0.9349	0
WE	BED	0.9977	0
PE	PD	0.9130	0
PE	BED	0.9554	0
PD	BED	0.9234	0

BED, biogeographically weighted evolutionary distinctiveness; ER, endemic richness; PD. phylogenetic diversity; PE, phylogenetic endemism; WE, weighted endemism.

each diversity index is regressed on the corresponding county area according to the power function, the residual from this function is still highly significantly correlated with the original corresponding diversity index (Table 2). That is, whether to account for the area effect or not, the five diversity indices show similar trend across the country (Figs. 2 and S3).

Distribution patterns of hotspots

In our study, the observed pattern of CEWSPS is not affected by the difference between the areas of the basic spatial units, i.e. counties. We therefore calculated all metrics based on the raw data without accounting for the area effect. Hotspots are identified at three levels of area (i.e. 1, 5 and 10% of China's total land area), with each of the five diversity indices using LMM (Figs. 3 and S4). The hotspot complexes identified with LMM at the three levels of area contain 27–69%, 78–90% and 92–95% of total CEWSPS, respectively. The hotspot complexes identified with CM at the three levels of area (Fig. S5) contain 62–71%, 87–92% and 96–98% of total CEWSPS, respectively. The species composition is very similar among the hotspot complexes identified in the above at 5% and 10% levels of area (Tables 3 and S2). In comparison, the similarity in both species composition and spatial occupancy is very high between the hotspot complexes identified with ER and PD, between those identified with WE and BED, between those identified with WE and WE_CM and between those identified with BED and WE_CM, especially the first two pairs. All the five diversity indices calculated for each hotspot complex identified in the above are shown in Fig. 4. Considering all the five diversity indices at the hotspot complex level, ER_CM is not as good as WE and BED although it is better than the other three indices using LMM, whereas WE_CM is better than any other metric. However, the definition of CM determines that none of the five diversity indices are guaranteed to reach the highest level of diversity at the individual county level. Therefore, CM will not be further discussed. It can also be seen from Fig. 4 that, for all the five hotspot complexes using LMM, the hotspot complexes identified with WE and BED have the highest values for almost all the five diversity indices at all the three levels of area. The hotspots identified using the residuals from the regression of each index on the county area with power function are similar to those from its original index (Table 4). Considering the total area a hotspot complex occupies and the values of the five diversity indices it attains, especially the total number of CEWSPS it contains, 5% is a reasonable level of area. Detailed results from the five diversity indices using LMM at this level of area will be given in the following paragraphs.

Table 2 Spearman's correlation coefficient ρ (with spatial autocorrelation-corrected *P*-value) between a diversity index and the residual from a nonlinear regression in which the index is a power function of the county area.

Index	Spearman's ρ	*P*-value
ER	0.9489	0
WE	0.8731	0
PE	0.8426	0
PD	0.9633	0
BED	0.8649	0

BED, biogeographically weighted evolutionary distinctiveness; ER, endemic richness; PD, phylogenetic diversity; PE, phylogenetic endemism; WE, weighted endemism.

The hotspots identified with ER are mainly distributed in 14 distinct centres (Fig. 3): (1) Hengduan Mountains, (2) the mountainous areas of east Chongqing and west Hubei, (3) the mountainous areas of east Yunnan and west Guangxi, (4) the mountainous areas of north Guangxi, south-east Guizhou and south-west Hunan, (5) the mountainous areas of north Guangdong and south Hunan, (6) the mountainous areas of south-east Tibet, (7) Xishuangbanna region, (8) the mountainous areas of south-east Anhui and north-west Zhejiang, (9) the mountainous areas of south Zhejiang, north-west Fujian and south-east Jiangxi, (10) Qinling Mountain, (11) the mountainous area of west Henan, (12) Hainan Island, (13) the mountainous areas of south-east Hubei and north-west Jiangxi and (14) the mountainous areas of west Jiangxi and east Hunan.

To facilitate the subsequent comparisons and discussions, we use two terms: major centre and minor centre. While a major centre is a geographic region covering a large area, usually with many counties that have been selected as a hotspot, a minor centre only covers a small area, usually with a few counties that have been selected as a hotspot. Among the 14 hotspot centres, seven are major centres (Fig. 3, Centres 1 through 7). The hotspots identified with WE are mainly located in 16 areas (Fig. 3): 13 of the above 14 centres (i.e. all except 11), and three more centres: (15) the mountainous areas of central and west Guangdong, (16) Taiwan Island and (17) the mountainous areas of south Fujian and north Guangdong. Centres 1 through 7, 12 and 16 are major ones. Those identified with PD have the same centres as ER plus Centre 15 (Fig. 3), and they have the same major centres as ER. The hotspots identified with PE include 17 centres (Fig. 3): 14 of the above 17 centres (i.e. Centres 1 through 16 except 10 and 13), and three more centres: (18) Changbai Mountain, (19) Nielamu region and (20) Yadong region. Six (i.e. Centres 1, 2, 4, 6, 12 and 16) out of the 17 centres are major ones. Those identified with BED have the same centres as WE but lack Centre 10 (Fig. 3), and they have the same major centres as WE.

It is evident in Fig. 3 and Table 5 that geographic distributions of the hotspots identified with ER and PD are very similar, so are those identified with WE and BED. There are some differences between the geographic distributions of the hotspots identified with ER, PD, WE and BED. The most prominent difference can be seen in the two centres: Centre 12 and Centre 16. Centre 12 is apparently highlighted by WE and BED. Centre 16 is a major centre in the hotspots identified with WE and BED, but missed using ER. It is evident that in Centres 12 and 16, many more counties have high WE and

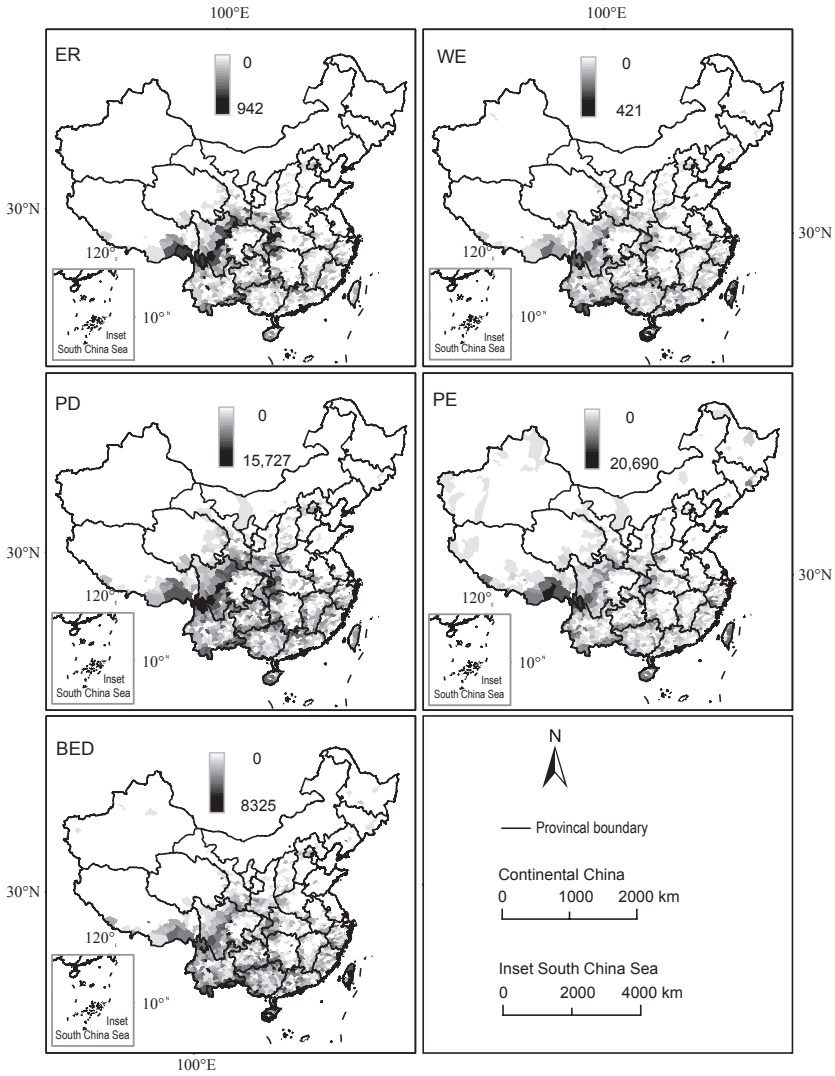

Figure 2 Geographic distribution of Chinese endemic woody seed plant species (CEWSPS) with five diversity indices: endemic richness (ER), weighted endemism (WE), phylogenetic diversity (PD), phylogenetic endemism (PE), and biogeographically weighted evolutionary distinctiveness (BED). Albers projection.

BED values, but more counties have low ER and PD values (Fig. 2). Another centre, Centre 17, is recognized using WE and BED, but missed using ER and PD. Conversely, one centre, Centre 11, is ignored using WE and BED. The hotspots identified with PE are the least similar to those identified with any other indices. The most conspicuous difference can be seen in three centres: Centres 3, 5 and 7. All these three centres are identified as the major centres with four indices: ER, WE, PD and BED. However, it is evident in Fig. 3 that they are all small in size. Another difference between hotspots identified with PE and the other four indices is the three small centres that are only identified with PE. They are Centres 18, 19 and 20. Comparing with WE and BED, PE also favours the identification of Centres 12 and 16 as the major centres, even though the highest values of PE are not shown in these two centres (Fig. 2).

A total of 20 hotspot centres (Table 5) are identified with at least one of the five diversity indices using LMM. They cover an area of about 0.76 million km^2, or 7.91% of China's total land area, and contain 6400 CEWSPS, or 92.96% of total CEWSPS. We take these 20 centres as the hotspots for CEWSPS. Eleven of the 20 centres, including Centres 1–9, 12 and 14, are commonly identified with all the five indices. They cover an area of about 0.25 million km^2, accounting for 2.60% of China's total land area, and harbour 5241 CEWSPS, accounting for 76.12% of the total CEWSPS.

DISCUSSION

Detecting hotspot centres of CEWSPS with diversity indices

While it was considered arbitrary to choose the top 5% areas as hotspots (e.g. Prendergast *et al.*, 1993), this level of area has been widely used in previous studies (Prendergast *et al.*, 1993; La Ferla *et al.*, 2002; Tang *et al.*, 2006), including the identification of the diversity centres of gymnosperms in China (Li *et al.*, 2009). To alleviate this arbitrariness, we tried three levels of fixed proportion of area (which are 1, 5 and 10%) in this study to identify hotspots. It seems that 5% level

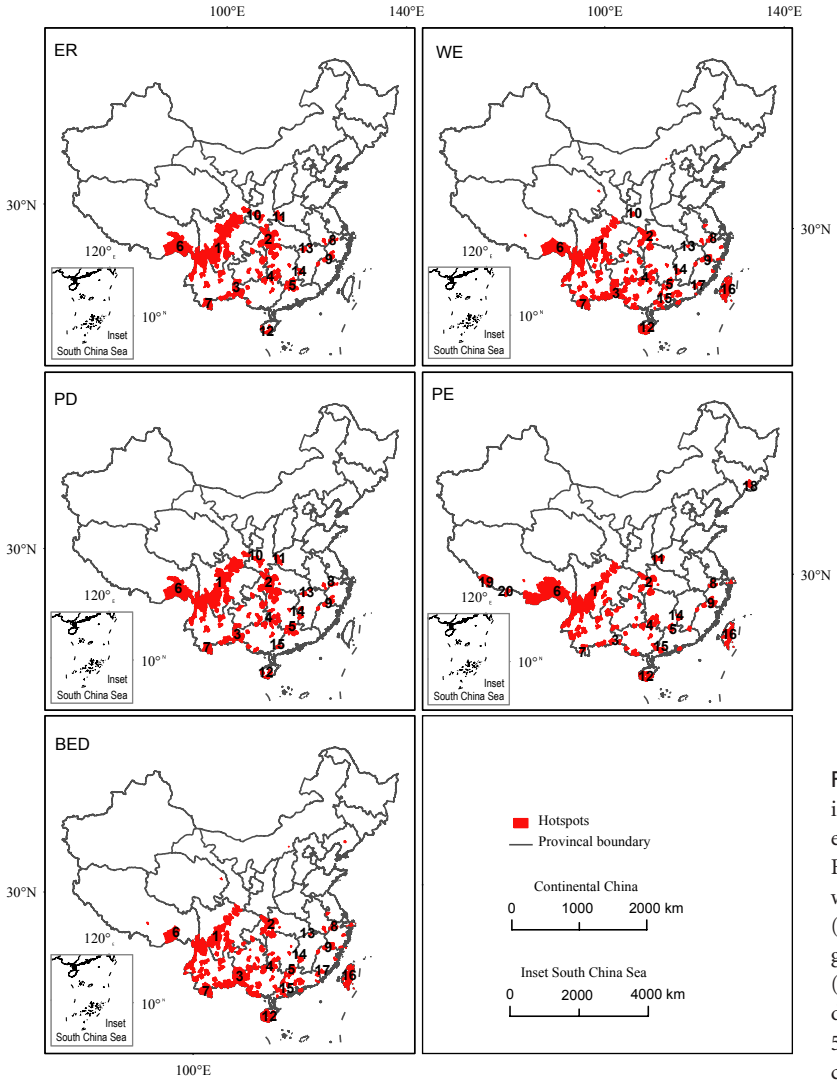

Figure 3 Geographic distribution of hotspots identified with five diversity indices for Chinese endemic woody seed plant species (CEWSPS). Five indices include endemic richness (ER), weighted endemism (WE), phylogenetic diversity (PD), phylogenetic endemism (PE), and biogeographically weighted evolutionary distinctiveness (BED). For each diversity index, hotspots are defined with local maximization method at the 5% level of area. Albers projection. Hotspot centre codes are consistent with Table 5.

is reasonable because a very high level of diversity (e.g. about 80% of CEWSPS) is reached in a relatively small percentage of area.

Although the hotspot complex identified with ER_CM and WE_CM at the 5% level of area contains few more endemic taxa than those with LMM at the same level of area, a high level of diversity at county level is not guaranteed with ER_CM and WE_CM. That is to say, for any single county all metrics from LMM are always higher than those from CM. At the hotspot complex level, with CM, WE is better than ER, and with LMM, WE and BED are better than the others.

The 20 hotspots identified in this study cover most of the previously defined key areas for biodiversity conservation in China. They include all the terrestrial key areas or critical regions for conservation of China's biodiversity defined by Wang *et al.* (1993) and Chen (1998) except one typical alpine grassland in Qinghai-Tibetan Plateau and a grassland in the mountainous areas of north Hebei. They also cover all the hotspot ecoregions of China's biodiversity delineated by Tang *et al.* (2006), all the hotspots of China's threatened plants identified by Zhang & Ma (2008), all the centres of Chinese flora characterized by Ying (2001) and all the centres of endemic genera of China recognized by Ying & Zhang (1994).

This indicates that CEWSPS are a valuable indicator group for the identification of hotspots or priority areas for China's biodiversity conservation. Endemic genera or threatened plants are not enough to reflect the hotspots of plant diversity at the species level. It is the best if all the species in a given area can be protected, but this is usually impossible because of the limitation of available resources. Therefore, for any given area, it is worthwhile to protect hotspots of unique species within that area, and we suggest that a comprehensive data set for the endemic species such as that used in this study should be incorporated in the identification of hotspots for biodiversity conservation.

Importance of geographic range and phylogeny for conservation

The intersections of the hotspots from all five indices are important for identifying hotspots of biodiversity conservation because all five indices are maximized in these areas. However,

Table 3 Comparison of the number of Chinese woody seed plant species (CEWSPS) and area between the hotspots identified with a pair of diversity indices at the 5% level of area. SC stands for similarity coefficient.

Index 1(I1)	Index 2 (I2)	Number of CEWSPS with I1	Number of CEWSPS with I2	Number of common CEWSPS	SC according to CEWSPS	SC according to spatial occupancy
ER	WE	5573	6201	5483	0.9314	0.7071
ER	PE	5573	5930	5367	0.9332	0.6501
ER	PD	5573	5660	5573	0.9923	0.9775
ER	BED	5573	6182	5425	0.9230	0.6461
ER	ER_CM	5573	5995	5350	0.9250	0.5026
ER	WE_CM	5573	6302	5414	0.9118	0.5334
WE	PE	6201	5930	5804	0.9569	0.6877
WE	PD	6201	5660	5562	0.9379	0.7157
WE	BED	6201	6182	6142	0.9920	0.9331
WE	ER_CM	6201	5995	5854	0.9600	0.6034
WE	WE_CM	6201	6302	6099	0.9756	0.7651
PD	PE	5660	5930	5447	0.9400	0.6620
PD	BED	5660	6182	5511	0.9308	0.6619
PD	ER_CM	5660	5995	5432	0.9321	0.5165
PD	WE_CM	5660	6302	5500	0.9196	0.5508
PE	BED	5930	6182	5776	0.9538	0.6556
PE	ER_CM	5930	5995	5714	0.9583	0.6268
PE	WE_CM	5930	6302	5781	0.9452	0.6145
BED	ER_CM	6182	5995	5806	0.9536	0.5484
BED	WE_CM	6182	6302	6100	0.9773	0.7841
ER_CM	WE_CM	5995	6302	5844	0.9505	0.5629

BED, biogeographically weighted evolutionary distinctiveness; ER, endemic richness; ER_CM, endemic richness used with complementarity method (CM); PD, phylogenetic diversity; PE, phylogenetic endemism; WE, weighted endemism; WE_CM, weighted endemism used with complementarity method (CM).

hotspots that are only identified by some indices are also important because different indices emphasize different aspects, including species richness, geographic range and phylogeny. These distinctive hotspots are more likely to be overlooked if we pay attention only to one aspect in the identification of hotspots. For example, compared with the hotspots identified with ER, those identified with WE include one more major centre, Taiwan Island. Meanwhile, the centre in Hainan Island is also enhanced. Similar results occur when comparing those identified with PD and BED. The importance of centres identified with both indices has been repeatedly highlighted by other researchers (Wang *et al.*, 1993; Xing *et al.*, 1995; Ying & Hsu, 2002; Tang *et al.*, 2006). This suggests that those measures incorporating geographic range are important in selecting those regions that have low species richness but have relatively more species with limited geographic ranges because both indices WE and BED incorporate information of the geographic range of species. Thus, it is clear from this study that geographic range of plant species is important in the identification of hotspots.

Our study finds that across the whole country, the distributional patterns of plant diversity characterized with different indices are very consistent. Endemic plant richness and PD are also highly consistent at the hotspot level. The similarity between the hotspots identified with the five diversity indices is very high in terms of species composition, rather than their spatial similarity. Although PD and BED mainly involve evolutionary history, and ER and WE primarily signal species richness, it is clear that the similarity between the hotspots identified with BED and WE reflects their greater emphasis on range-restricted endemic plants.

However, these conclusions are only tentative, because data are not ideal to fully estimate various metrics accurately for the following reasons. First, all the PD indices assume that the phylogeny is completely resolved, but the phylogeny is unresolved below genus in our study. PD and BED are likely to be overestimated, because terminal branches will be stretched out for sharing internal branches. Second, BED and WE assume that species range size is known, but in our study, it is simply calculated as the total area of the counties in which the focal species is recorded. Range size is therefore likely to be sensitive to data quality, which is likely to be highly variable. Although we have proved that county area does not have significant effect on the results, we cannot ensure that we have obtained complete distribution data at county level for every species. Nonetheless, all such large-scale data sets are rife with similar data quality issues, and we have used what information we can obtain. Therefore, these may more or less affect the results of each index, resulting in dependence of phylogeny on species richness or an over-emphasis on spatial distribution in the combined indices. Furthermore, in the case of the identification of centre of endemism, it is possible that there

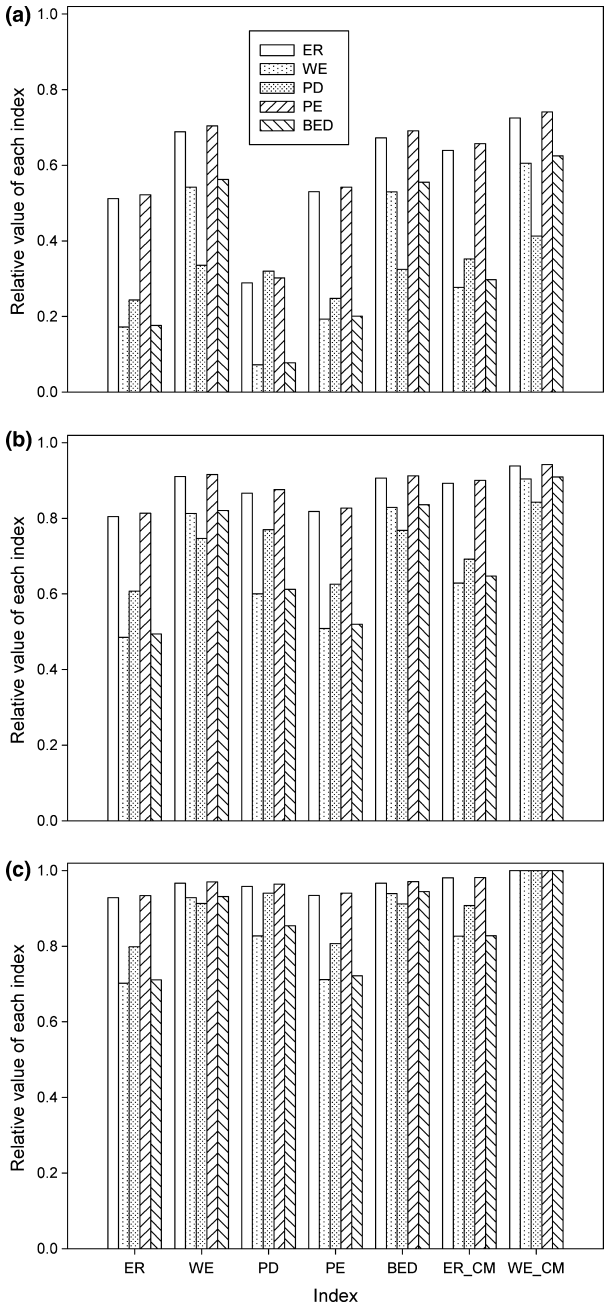

Figure 4 Comparisons of relative values of the five diversity indices at the whole hotspot complex level for each of the six index/method combinations at each of the three levels of area: 1% (a), 5% (b) and 10% (c) of China's total land area. ER_CM and WE_CM stand for the endemic richness and weighted endemism of the hotspots for Chinese endemic woody seed plant species (CEWSPS) identified with complementarity method (CM).

are centres of endemism that have not been identified owing to narrow-range endemics being found in both China and neighbouring countries and thus being excluded from these analyses focussed on Chinese endemic plant species.

Consequently, it is still inconclusive whether the distribution pattern of species richness can represent that of PD or not.

Table 4 Similarity coefficient (SC) between the hotspots for Chinese endemic woody seed plant species (CEWSPS) identified with a diversity index and the residual from a nonlinear regression, in which the index is a power function of the county area, using local maximization method at three levels of area (i.e. 1, 5 and 10% of China's total land area).

Index	Level of area (%)	Number of common CEWSPS	Percentage of common CEWSPS (%)	SC according to CEWSPS	SC according to spatial occupancy
ER	1	3634	52.78	1	1
WE	1	4757	69.09	1	1
PE	1	2222	32.27	1	1
PD	1	3682	53.48	0.9913	0.9906
BED	1	4611	66.97	1	1
ER	5	5554	80.67	0.9961	0.9880
WE	5	6171	89.63	0.9970	0.9898
PE	5	5926	86.07	0.9981	0.9952
PD	5	5650	82.06	0.9988	0.9800
BED	5	6126	88.98	0.9926	0.9463
ER	10	6373	92.56	0.9976	0.9919
WE	10	6537	94.95	0.9983	0.9730
PE	10	6510	94.55	0.9974	0.9713
PD	10	6376	92.61	0.9988	0.9933
BED	10	6558	95.25	0.9992	0.9851

BED, biogeographically weighted evolutionary distinctiveness; ER, endemic richness; PD, phylogenetic diversity; PE, phylogenetic endemism; WE, weighted endemism.

Some studies have concluded that taxa richness is a good surrogate for PD, making it an effective means for identifying conservation priorities (Rodrigues & Gaston, 2002; Torres & Diniz, 2004; Brooks *et al.*, 2006). Other studies have found that taxa richness is not completely consistent with PD (Forest *et al.*, 2007). We agree that phylogenies provide new ways to measure biodiversity, to identify hotspots or to assess conservation priorities, because they quantify the evolutionary history in any set of species (Mace *et al.*, 2003). We suggest that further studies on phylogenies in biodiversity conservation should pay more attention to methodological improvement and comprehensiveness of data, because these problems have so far hampered the use of phylogenies in biodiversity conservation.

The hotspots in major mountain ranges and their potential causes

Chinese endemic woody seed plant species are unevenly distributed across the country. All the hotspots are located in mountainous areas mainly within the broad area – the Qinling Mountains and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau. Geographically, this area corresponds approximately to the subtropical evergreen broad-leaved forest and tropical monsoon forest and rain forest vegetational regions (Wu, 1980). Almost every hotspot embraces several high mountains

Table 5 Hotspot centres for Chinese endemic woody seed plant species (CEWSPS) found in the present study and their main ranges, and for comparison, the critical regions of biodiversity in China recognized by Wang *et al.* (1993). Centre codes follow Fig. 3.

		Present study					
Centre	Main ranges (Summit (m asl))*	Endemic richness	Weighted endemism	Phylogenetic diversity	Phylogenetic endemism	Biogeographically weighted evolutionary distinctiveness	Wang *et al.* (1993) key biodiversity regions†
1. Hengduan Mountains	Gaoligong Mountains (3374), Yunling Mountains, Shaluli Mountains (Que'ershan, 6168), Nu Mountains (Biluoxueshan, 4379), Meilixueshan (6740), Yulongxueshan (5596), Daxue Mountains (Gonggashan, 7556), Qionglai Mountains (Siguliangshan, 6250), Min Mountains (Xuebaoding, 5588)	++	++	++	++	++	+
2. Mountainous areas of east Chongqing and west Hubei	Daba Mountains (Shennongding, 3105), Wudang Mountains (1612)	++	++	++	++	++	+
3. Mountainous areas of east Yunnan and west Guangxi	Transition areas of vegetation, Yun-Gui Plateau and Guangdong and Guangxi Basin	++	++	++	+	++	+
4. Mountainous areas of north Guangxi, south-east Guizhou and south-west Hunan	Transition areas of vegetation, Yun-Gui Plateau, Guangdong and Guangxi Hills and Jiangnan Hills, Leigong Mountains (2178), Jiuwanda Mountsins, Xuefeng Mountains (1934)	++	++	++	++	++	–
5. Mountainous areas of north Guangdong and south Hunan	Nanling Mountains (1902)	++	++	++	+	++	+
6. Mountainous areas of south-east Tibet	Edge of Qing-Tibet Plateau	++	++	++	++	++	+
7. Xishuangbanna Region	Valleys of Lancangjiang River	++	++	++	+	++	+
8. Mountainous areas of south-east Anhui and north-west Zhejiang	Tianmu Mountains (1787), Huang Mountains (1873)	+	+	+	+	+	–
9. Mountainous areas of south Zhejiang, north-west Fujian, and south-east Jiangxi	E-China Mountains, Xianxialing Mountains (1621), Wuyi Mountains (2157),	+	+	+	+	+	+
10. Qinling Mountain	Qinling Mountains (3767)	+	+	+	–	–	+
11. Mountainous area of west Henan	Funiu Mountians (2212), Zhongtiao Mountains	+	–	+	+	–	–
12. Hainan island	Wuzhi Mountains (1867)	+	++	+	++	++	+
13. Mountainous areas of south-east Hubei and north-west Jiangxi	Jiuling Mountains (1794), Mufu Mountains (1543)	+	+	+	–	+	–
14. Mountainous areas of west Jiangxi and east Hunan	Luoxiao Mountains (1918)	+	+	+	+	+	–

Table 5 Continued.

Centre	Main ranges (Summit (m asl))*	Present study					Wang *et al.* (1993) key biodiversity regions†
		Endemic richness	Weighted endemism	Phylogenetic diversity	Phylogenetic endemism	Biogeographically weighted evolutionary distinctiveness	
15. Mountainous areas of central and west Guangdong	Yunwu Mountains (1703), Yunkaida Mountains	–	+	+	+	+	–
16. Taiwan island	Yushan Mountains (3952)	–	++	–	++	++	+
17. Mountainous areas of south Fujian and north Guangdong	Hills of south Fujian and north Guangdong (1559)	–	+	–	–	+	–
18. Changbai Mountain	Changbai Mountains (2681)	–	–	–	+	–	+
19. Nielamu region	South edge of Himalayas	–	–	–	+	–	–
20. Yadong region	South edge of Himalayas	–	–	–	+	–	–

++: major centre; +: minor centre (major or minor centres have not been distinguished in study of Wang *et al.* (1993).); –: no centre.
†Fourteen critical regions were proposed by Wang *et al.* (1993). Apart from the 11 regions shown in this table, there are three critical regions, i.e. the mountainous areas of north Hebei, the HOh Xil in Qinghai, the mountainous areas of Sichuan and the mountainous areas of Yunnan (these two critical regions were covered by one hotspot, Hengduan-Min Mountains, in our study).
*Readers can refer to Wang *et al.* (2004) and Liu (1998) for names of main ranges and to Liu (1998) for summits.

(Table 5). For example, the prominent hotspot – Hengduan Mountains (Centre 1) – spans Gaoligong, Yunling, Shaluli, Daxue, Qionglai and Min Mountains, which has various summits from 3374 to 7556m. Some hotspots stand in the junction of major morphostructures or edges of huge mountains. For instance, the mountainous areas of east Yunnan and west Guangxi (Centre 3) and the mountainous areas of north Guangxi, south-east Guizhou and south-west Hunan (Centre 4) lie in the area between Yun-Gui Plateau and Guangdong and Guangxi Basin, and in the area between Yun-Gui Plateau, Guangdong and Guangxi Hills and Jiangnan Hills, respectively (Figs 1a and 3). The smallest hotspots, Nielamu region (Centre 19) and Yadong region (Centre 20), are in the south edge of Himalayas (Figs 1b and 3).

All these hotspots correspond to those regions that contribute greatly to the survival, speciation and evolution of vascular plants in China (Axelrod *et al.*, 1996; Qian, 2002). It is widely recognized that many endemic and relic genera of vascular plants, including *Metasequoia*, *Cathaya*, *Pseudolarix* and *Pseudotaxus*, can only be found in these regions (Wu & Wang, 1983; Ying & Zhang, 1994; Axelrod *et al.*, 1996). The best-known example is *Metasequoia glyptostroboides*. This species is a typical relic species of the Cretaceous and Cenozoic, during which time the genus was widely distributed in the ancient continent Laurasia (Hu & Zheng 1948). The modern distribution of this species is confined to east Chongqing, west Hubei and north-west Hunan (Hu, 1980; Ying & Zhang, 1994). Additionally, many original and isolated taxa are also found in these areas, such as *Tsoongiodendron*, *Cyclocarya*, *Cercidiphyllum*, *Tetracentron* and *Liriodendron* (Ying & Zhang, 1984).

Mountainous areas are important to the distribution of CEWSPS, which could be understood as follows. Firstly, the area – the Qinling Mountains and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau – has high level of heterogeneity in physiognomy and is older and more complex than the other areas in China (Editorial Committee of China's Physical Geography, 1985), which offers a diversity of environments and thus has promoted great species diversity and high degree of endemism (Qian & Ricklefs, 1999). Secondly, both Qinling Mountains and Hengduan Mountains are two natural physical barriers that restrict north–south and east–west plant migration and interchange, forming a geographically isolated area (Wu & Wang, 1983), thereby facilitating the speciation and differentiation of endemics. Meanwhile, these natural physical barriers also change the movement of atmosphere and cause changes in precipitation and temperature within the Qinling Mountains and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau. Qinling Mountains and Hengduan Mountains prevent the monsoon winds from passing from south and east China to north and west China, thus maintaining a wet climate and adequate moisture in summer. These mountains also prevent Siberian cold air masses from reaching south China, thus maintaining the warm climate in winter (Hsu, 1984). These favourable conditions maintain greater variety of habitats within the

subtropical evergreen broad-leaved forest and tropical monsoon forest and rain forest vegetational regions and thus probably accelerate the speciation, differentiation and preservation for the species living in these regions because species diversity increases with habitat variation (Latham & Ricklefs, 1993; Rosenzweig, 1995). Thirdly, the absence of severe continental glaciations during the Plio-Pleistocene periods has contributed to the maintenance of exceptional plant species richness in subtropical and tropical forest in China (Wu & Wang, 1983; Hsu, 1984; Latham & Ricklefs, 1993). Many Chinese endemic genera were once distributed broadly in Laurasia during the Tertiary or even earlier, but now they are extant only in China (Ying & Zhang, 1994; Axelrod *et al.*, 1996; Qian & Ricklefs, 1999).

There are other factors that may not play decisive but do play prominent roles in some local regions. For example, some transition areas of vegetation in China are identified as the main distribution centres and origins of East Asia flora, and even one of the centres of the origin of angiosperms (Wu, 1980; Wu & Wang, 1983; Axelrod *et al.*, 1996), and provide refugia for many relict and ancient genera (Raven & Axelrod, 1974; Axelrod *et al.*, 1996). In addition, Hainan and Taiwan Islands have high endemism, which may result from their isolation from the continental part of China, resulting in dispersal barriers and accelerated speciation and differentiation (Lomolino *et al.*, 2006).

Consequently, the concentration of CEWSPS in the Qinling Mountains and farther south and in the eastern portion of the Qinghai-Tibetan Plateau and to the east of that plateau is the result of the combined effects of the heterogeneous terrain, geological history and contemporary environments in this region. Compared with Europe and the United States, these combined effects are highly pronounced in China, which results in the ratio of species of vascular plants in China, the United States and Europe as 3 to 2 to 1 (Axelrod *et al.*, 1996). This is similar to the conclusions for Australia and tropical Afria. The modern pattern of endemism in Australia is ascribed to adaption and selective extinction of endemic species, driven by extreme climate conditions during the Pleistocene glacial maxima (Crisp *et al.*, 2001). Tropical Africa is known to be floristically poorer than south-east Asia, and this has been ascribed to extinctions caused by glacial aridity or palaeoclimatic fluctuations (Axelrod & Raven, 1978; Linder, 2001). China has a huge area; thus, the diversity of CEWSPS is intimately linked with the diversity of total native seed plants of China. Therefore, mountains are also likely to explain variation in total species richness and are hence critical for protecting China's biodiversity.

CONCLUSIONS

The administrative county is appropriate to use as the basic spatial unit to analyse distribution patterns and identify hotspots of the diversity of CEWSPS. We found that different diversity indices produced similar distribution patterns of plant diversity at the national extent. It was demonstrated that the 5% of total land area is a reasonable threshold in comparison with 1 and 10% in the identification of the hotspots, because a high level of diversity is reached in such a small proportion of area. For the LMM, the hotspots identified with WE and BED have higher levels of diversity than those identified with the other indices, because they put more weight on the range-restricted species; hence, there is likely to be lower species overlap. A total of 20 hotspots were identified with at least one of the five diversity indices, which should serve to direct conservation priorities in China. All of these hotspots are located in the mountainous areas, and most of them have been proposed as key areas for protecting China's biodiversity in previous studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Map of administrative provinces and counties in China.

Figure S2 Relationships between county area (A) and diversity of Chinese endemic woody seed plant species (CEWSPS).

Figure S3 Geographic distribution of the residuals from the power function $D = bA^c$.

Figure S4 Geographic distribution of the hotspots for Chinese endemic woody seed plant species (CEWSPS) identified with local maximization method at the three levels of area (1, 5 and 10%) using five diversity indices.

Figure S5 Geographic distribution of the hotspots for Chinese endemic woody seed plant species (CEWSPS) identified with complementarity methods (CM) for two diversity indices [Endemic richness (ER) and Weighted endemism (WE)] at three levels of area.

Table S1 List of China's major mountain ranges.

Table S2 Similarity coefficients between the hotspots for Chinese endemic woody seed plant species (CEWSPS) identified with a pair of diversity indices at the level of the 1 and 10% of China's total land area in terms of the number of endemic taxa contained in the hotspots and the area occupied by the hotspots.

Appendix S1 Literature list that we have consulted to establish the Chinese seed plant species inventory and to collect their distribution information.

Appendix S2 The list of Chinese endemic woody seed plant species (CEWSPS) and range of each species.

Appendix S3 The phylogenetic tree of Chinese endemic woody seed plant species (CEWSPS).

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BIOSKETCH

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