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Centres of plant endemism in China: places for survival or for speciation?

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ABSTRACT

Aim This study aimed to identify the 'centres of endemism' of the Chinese spermatophyte flora in order to indirectly detect the locations of past glacial refugia. The role of these areas as places for plant survival ('plant museums') and/ or areas for plant evolution and speciation ('plant cradles') was also assessed.

Location China.

Methods Distribution patterns of 555 plant endemic taxa, taken as a representative sample of the Chinese endemic flora, were mapped on a $1° \times 1°$ latitude/longitude grid. For each grid cell, species richness (total count of species) and weighted richness (down-weighting each species by the inverse of its range) were calculated. Grid cells within the top 5% of highest values of weighted richness were considered centres of endemism. Based on available information, all plant taxa included in this study were classified into palaeoendemics and neoendemics, and their distributional patterns were represented separately.

Results Twenty areas of endemism were identified in central and southern China, roughly corresponding to mountain ranges, including the Hengduan and Daxue Mountains, the Yungui Plateau, central China Mountains, the Nanling Mountains, eastern China Mountains, and Hainan and Taiwan. Although almost all centres of endemism contained both palaeoendemic and neoendemic taxa, considerable differences in their respective numbers were recorded, with the majority of neoendemics on the eastern fringe of the Tibetan Plateau (Hengduan Mountains *sensu lato*) but more palaeoendemics towards the east.

Main conclusions Owing to their varied topography, the mountainous regions of central and southern China have provided long-term stable habitats, which allowed palaeoendemics to persist and facilitated the process of speciation. Contrasting patterns between the palaeoendemics and neoendemics within refugia might be attributable to the geological and tectonic history of specific areas. The eastern fringe of the Tibetan Plateau clearly constitutes the 'evolutionary front' of China, probably as a result of the uninterrupted uplift of the plateau since the late Neogene. In contrast, the tectonic stability of central and southern China during the Tertiary may have facilitated the persistence of relict plant lineages.

Keywords

Centres of endemism, China, conservation, environmental stability, glacial refugia, mountains, neoendemics, palaeoendemics, plant diversity patterns, Quaternary.

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INTRODUCTION

Centres of endemism have attracted the attention of biologists and biogeographers since the 19th century. Although the concepts surrounding centres of endemism are the subject of controversy, identifying and explaining their distribution has important historical, evolutionary and conservation implications (Jetz *et al.*, 2004; Mittermeier *et al.*, 2005). Their occurrence is generally attributed to historical processes, such as the existence of Pleistocene refugia or the occurrence of major geological events. These historical processes are in contrast to present ecological and environmental factors, which are normally considered to be the main determinants of patterns of overall species richness (Jetz *et al.*, 2004; Orme *et al.*, 2005).

The term 'refugia' is commonly used in biology to designate the sites where a wide array of both animal and plant species lived during the Quaternary full-glacial periods. During glacial maxima (the 'ice ages'), when the climate became significantly colder and drier, the distribution of plant species changed significantly and resulted in the range contraction and/or range displacement of plants towards sites of suitable ecological conditions (Davis & Shaw, 2001; Hu *et al.*, 2009). There is general agreement that refugial areas, regardless of their latitude, would have occurred in stable habitats with high topographic diversity, in locations that experienced limited changes in environmental conditions. Together, these characteristics allowed plants to persist, differentiate and ultimately speciate (Tzedakis *et al.*, 2002; Jetz *et al.*, 2004; Thompson, 2005). Thus, it can be anticipated that Quaternary refugia, often located in mountainous areas, probably played the dual role of preserving Tertiary lineages ('species museums') and promoting the evolution of new taxa ('species cradles') (Tzedakis *et al.*, 2002).

Once climatic conditions improved (e.g. in the Holocene), not all species were able to migrate out of refugia and colonize formerly glaciated or inhospitable areas. Instead, a significant proportion of the refugial species (those with narrow environmental tolerances) remained restricted to these pockets, leaving a traceable imprint in modern distributional patterns (Crisp *et al.*, 2001; Linder, 2001; Tribsch, 2004). The existence of a close relationship between areas of endemism and glacial refugia is widely recognized in biology (e.g. Tribsch & Schönswetter, 2003; Carnaval & Moritz, 2008; Médail & Diadema, 2009), and the distributional patterns of endemic species have been extensively used to infer the locations of refugia in many parts of the world (e.g. Toledo, 1982; Crisp *et al.*, 2001; Linder, 2001; Tribsch, 2004).
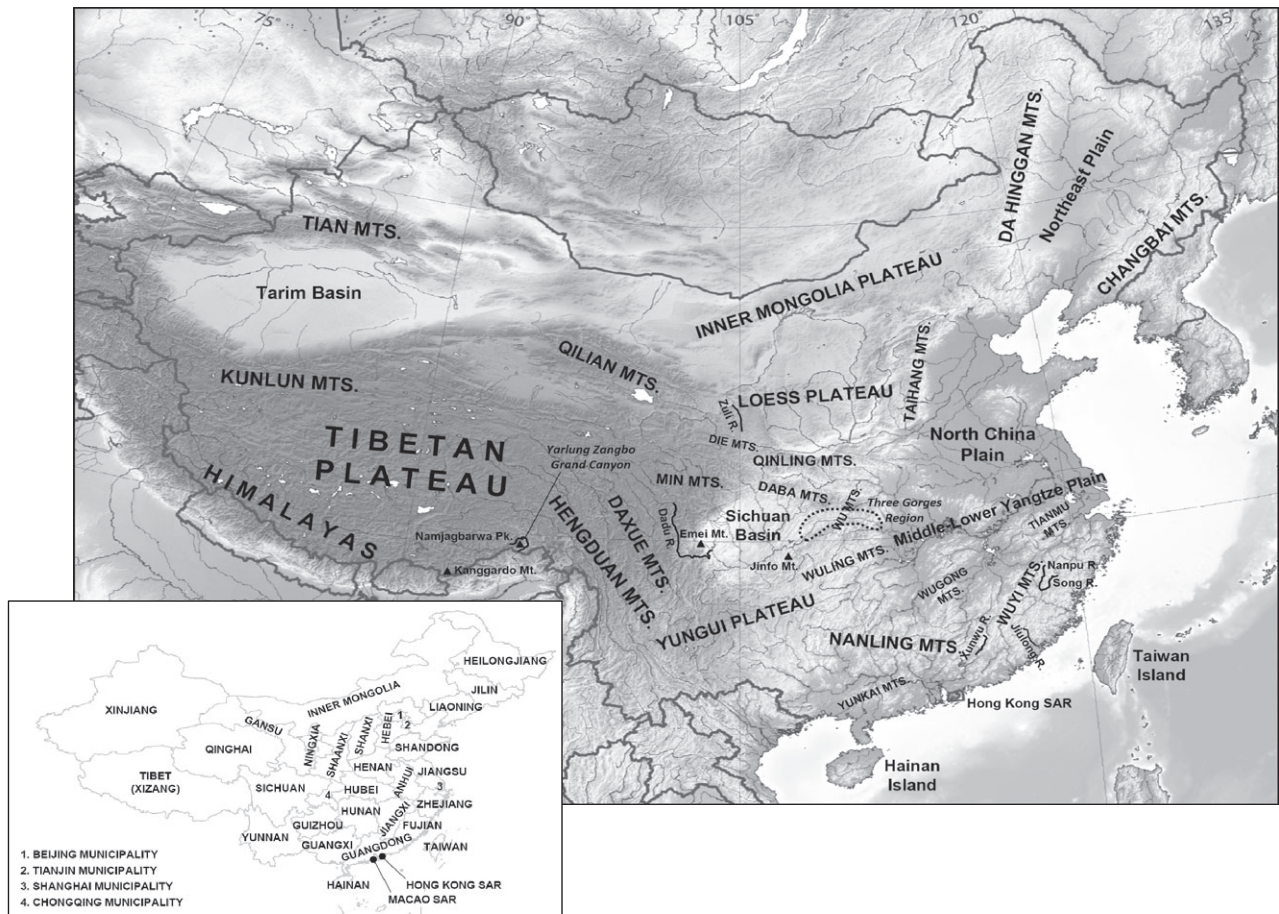
Figure 1 Topographic map of China, with the locations of major mountain ranges, plateaux, basins and plains. All the geographical features quoted in the text are also indicated.

China ['China' is used here as the geographical entity including the lands currently under the jurisdiction of the People's Republic of China (PRC) according to the United Nations criterion, which includes Taiwan within the PRC] has one of the world's richest floras with at least 30,000 vascular plants, of which a remarkable 50–60% (up to 18,000) are endemic (López-Pujol *et al.*, 2006). This wealth of species diversity and endemism is attributable to a series of factors including: (1) a large continental area (about 9.6 million km^2); (2) an unbroken connectivity between tropical, subtropical, temperate and boreal forests; (3) a large proportion of tropical and subtropical habitats; (4) the close connection of China to tropical regions of Southeast Asia; (5) a highly rugged and dissected topography (especially in southern China; Fig. 1); and (6) reduced extinction rates during the late Cenozoic global cooling (Axelrod *et al.*, 1996; Qian & Ricklefs, 1999; Qian, 2002).

Despite the impressive size of China's endemic flora, the number, locations and evolutionary patterns of endemic areas remain poorly understood. To date, areas of endemism have been surveyed exclusively at high taxonomical levels (at generic and family levels; Ying *et al.*, 1993; Wang & Zhang, 1994; Tang *et al.*, 2006) or at coarse geographical scales (Mittermeier *et al.*, 2005). These preliminary studies indicate that endemic taxa are concentrated mainly in the central and southern regions, but these rough patterns have yet to be verified with species-level data. As a result, a comprehensive investigation based on country-wide data is required to enable a better understanding of the patterns of the centres of endemism in Chinese plant taxa.

The present study examines the distributional patterns of a representative set of Chinese endemic seed plant taxa at finer geographic and taxonomic (species-level) scales. By dividing our data set into two categories, palaeoendemics and neoendemics, we aim to discern the number and locations of the centres of endemism in China, as well as to examine whether these areas acted primarily as places for plant survival ('plant museums') or as places that played a significant role in speciation and evolution ('plant cradles'), or as both. Our conclusions will shed light both on the age of the current Chinese flora and on its recent (Neogene–Quaternary) evolutionary history, and will also provide new insights into the biotic richness of this region. In addition, such information has significant implications for conservation practices; at present, controversies exist over whether 'museums' or 'cradles' should be given priority status (Fjeldså, 1994; Mace *et al.*, 2003).

MATERIALS AND METHODS

Selected taxa

A set of 555 Chinese endemic (or nearly endemic) seed plant taxa were used to (1) delimit the centres of endemism and (2) obtain the centres of palaeoendemism and neoendemism separately (see Appendix S1 in the Supporting Information). These taxa are the species (and, for a few cases, entities of lower rank such as subspecies and varieties) belonging to the 243

Chinese endemic genera recognized by Ying *et al.* (1993). Although this is a very small fraction of the total Chinese flora, the 'flagship' status of these select taxa provides several advantages. First, knowledge of their distribution is accurate and reliable (see below), and is not subject to large regional differences in chorological investigation (i.e. different sampling efforts for different areas). This is a common problem for the floras of vast territories and can lead to significant biases in biogeographic studies (La Ferla *et al.*, 2002; Morawetz & Raedig, 2007). Second, a significant fraction of these taxa (see below) have been well studied in terms of systematics and evolution (e.g. complete phylogenies are available), which was of assistance when classifying the species into palaeoendemics and neoendemics (Appendix S1).

This sample of 555 taxa constitutes a highly heterogeneous group, in which all the life forms (annual or perennial herbs, shrubs, lianas and both deciduous and evergreen trees), habitats, ecosystems (from desert to alpine plants) and phytogeographical elements present in China are represented. The 72–78 families to which these taxa belong account for nearly a quarter of the total number of seed plant families in China, covering the main groups (i.e. gymnosperms, magnoliids, monocots, commelinids, eudicots, core eudicots, rosids, fabids, malvids, asterids, lamiids and campanulids, following the APG III classification system; Angiosperm Phylogeny Group, 2009) and orders.

Operational geographic units (OGUs)

The distributional data for the 555 taxa were provided by one of the authors of this study (T.-S. Ying) and were based on both the revision of herbarium specimens and exhaustive field surveys. Infraspecific taxa were treated as equivalent to species for ease of analysis. Squares of 1° latitude × 1° longitude (i.e. from 68 × 110 km in north-east China to 106 × 110 km in Hainan Island) were chosen as operational geographic units (OGUs), a grid size that has previously provided optimal results in detecting the major areas of endemism in territories of a comparable study area (e.g. Australia; Crisp *et al.*, 2001). This spatial resolution has also been useful for detecting centres of endemism in both larger (e.g. sub-Saharan Africa or the Neotropics; La Ferla *et al.*, 2002; Morawetz & Raedig, 2007) and much smaller (e.g. Mexico; Contreras-Medina & Luna-Vega, 2007) territories, but is too coarse to reveal patterns of endemism at the regional scale (e.g. to detect finer-scale variations within major centres of endemism). However, this grid size has the advantage of reducing the effect of sampling artefacts, such as the occurrence of artificially empty grid squares and mapping errors (see Linder, 2001 for a more detailed discussion).

Palaeoendemics versus neoendemics: the theoretical framework

In the wider scientific literature, endemic species can be classified as either palaeoendemics ('relictual' endemics) or

neoendemics ('young' endemics) according to biogeographic and systematic criteria. In general, palaeoendemics are defined as those taxa that were formally more widespread, having suffered a severe range contraction as a result of Neogene and Quaternary climatic changes, and that are currently surviving in a small part of their original distribution area (i.e. 'biogeographic relicts'). It is thought that these species were unable to recover their original range once the climatic conditions became more favourable as a result of the constriction of their specialized habitats and the loss of genetic variability (Stebbins & Major, 1965; Kruckeberg & Rabinowitz, 1985). Moreover, many palaeoendemics show disjunct distributions (Kruckeberg, 2002), because of their persistence in distinct isolated refugia during the late Cenozoic cooling or older geological events. Taxonomically, palaeoendemics are mostly isolated (i.e. 'phylogenetic' or 'taxonomic' relicts) owing to the extinction of their sister lineages and/or very long divergence (Stebbins & Major, 1965); thus, they usually belong to monotypic or oligotypic genera and even to monotypic families.

In contrast, neoendemics are defined as taxa that have recently evolved from their parental entities, and that have not yet spread significantly beyond their region of origin. Neo-endemics are usually linked with geologically youthful habitats (Verlaque *et al.*, 1997), and they may experience further expansion before their potential distribution areas are reached (Kruckeberg & Rabinowitz, 1985). From a phylogenetic perspective, neoendemics represent an almost opposite situation to palaeoendemics in that they usually belong to polytypic genera, even forming species complexes with no clear taxonomic boundaries. As a result of their recent *in situ* formation, closely related neoendemics are usually found in the same area or in adjacent regions, often constituting groups of vicarious taxa (Cowling & Holmes, 1992; Kruckeberg, 2002).

Analytical methods

The distributional data of all taxa were converted into a presence/absence matrix for each of the grid squares (1111 in total). To detect the centres of endemism, two widely used parameters, species richness and weighted richness, were computed (Crisp *et al.*, 2001; Linder, 2001; Tribsch, 2004). Species richness was measured as the total number of species endemic to China present in each grid cell independent of their degree of range restriction. For the weighted richness, each species was down-weighted by the number of grid squares in which it occurred (i.e. by the inverse of its range size). Thus, a species restricted to a single square had a maximum weight of 1; a species found in two squares had a weight of 0.5; a species occurring in three squares had a weight of 0.333, and so on. The weighted richness score for a given square was obtained by summing the weights of all the species found in that square (Linder, 2001).

Both parameters (species richness and weighted richness) were represented in the 1° × 1° grid matrix covering the total

area of China. The patterns obtained were examined to detect cells, or concentrations of cells, with high values of richness; these were interpreted as centres of endemism or 'hotspots' (Prendergast *et al.*, 1993; Crisp *et al.*, 2001; Orme *et al.*, 2005). The grid cells with the highest scores for the richness parameters (applying the widely used threshold of the top 5% of cell grids; Prendergast *et al.*, 1993; La Ferla *et al.*, 2002) were considered centres of endemism. When a centre of endemism was composed of a single cell, or of two cells with no contiguous cells harbouring high values of richness, it was considered a 'minor' or 'discrete' area of endemism. In contrast, clusters of high-richness cells (≥ 3 cells) were regarded as 'major' centres of endemism. Finally, specific maps for palaeoendemics and neoendemics were constructed, to determine whether the detected areas of endemism were assemblages primarily of the former or the latter. Linear correlations were used to test the relationships between species richness and weighted richness for the total set of plant taxa, as well as between weighted palaeoendemism and weighted neoendemism. In addition, species range sizes of the two categories of endemics were compared by means of a Kruskal–Wallis test. Statistical analyses were carried out using the STATGRAPHICS PLUS 5.1 software (http://www.statgraphics.com/statgraphics_plus.htm).

Although no standard threshold has been established to differentiate between palaeoendemics and neoendemics in biology, some authors consider that palaeoendemics are Tertiary lineages or older (>2.6 Ma), whereas neoendemics are the result of recent speciation processes mostly as a consequence of the glacial/interglacial cycles during the Quaternary (e.g. da Silva & Bates, 2002). Other workers, however, situate the boundary between palaeoendemics and neoendemics earlier, in the Miocene/Pliocene transition (i.e. 5–6 Ma; e.g. Fjeldså & Lovett, 1997). We follow the latter criterion, because the major uplift of the whole Tibetan Plateau probably started in the Pliocene (Li & Fang, 1999; Zheng *et al.*, 2000), an event that has been linked to the intensification of the Asian monsoons (An *et al.*, 2001). Such large orogenic and climatic events probably made the Pliocene a turning point for the floristic composition and evolution of Chinese flora. We have divided the 555 selected taxa into these two categories using the following data obtained from the scientific literature: (1) fossil remains, (2) dated molecular phylogenies, (3) non-dated molecular phylogenies, (4) morphological phylogenies, (5) other evidence (morphological, chemical and cytological data), and (6) systematic and biogeographic data (Appendix S1).

Fossils are one of the most precise methods for estimating the minimum age of plant lineages. However, these are rarely available for extant plant species, and in many cases (especially for fossilized pollen grains, or wood and leaves in the case of macrofossils) they cannot be identified at low taxonomical levels (Hu *et al.*, 2009). Molecular phylogenies can also be extremely useful for estimating the age of taxa when dating methods such as chronograms are employed. However, fossil remains and/or dated molecular phylogenies (i.e. those criteria that provide us with a relative high a priori confidence) were

available for only a very small proportion of plant taxa (43 species out of 555; see Appendix S1). Consequently, we were forced to invoke other criteria to categorize taxa into palaeoendemics or neoendemics. Data such as non-dated molecular phylogenies, morphological phylogenies, and other morphological, chemical or cytological data (e.g. the presence of 'primitive' versus 'advanced' characters) can also provide useful information for inferring the age of plant lineages. These were available for a much larger proportion of taxa from our database (about 30%) but are considerably less precise than fossils and dated molecular phylogenies. In addition, personal communications from experts, when supported by data, were also used, whereas unsupported statements and vague opinions were not considered even if published.

Systematic and biogeographic criteria have the important advantage that they can be easily applied for the 555 taxa used in this study. Systematic criteria have included, for example, comparing monotypy with polytypy at the genus or family level, as well as comparing clearly defined taxa with ambiguous ones, whilst biogeographic criteria have involved distinguishing between disjunction and geographic clustering of closely related taxa. While the geographic distributions of the taxa were mapped in detail by Ying *et al.* (1993), their systematic positions were obtained either from Ying *et al.* or from other major taxonomic works, such as *Flora Reipublicae Popularis Sinicae* (Editorial Committee of FRPS, 1959–2004) or from the updated but still incomplete *Flora of China* (http://hua.huh.harvard.edu/china/). Remarkably, these data served as accurate markers for assigning the plant taxa included in our data set to palaeoendemics or neoendemics. In the cases in which fossils or dated molecular phylogenies were also available (43 taxa), the categorization between palaeoendemics and neoendemics coincided for the two approaches. In general, the other forms of data (e.g. non-dated molecular and morphological phylogenies) were also in agreement with the systematic and biogeographic classification scheme, and clear disagreements occurred within only a dozen taxa. However, it should be noted that the present classification between palaeoendemics and neoendemics is open to modifications as new phylogenetic reconstructions, fossils, or other high-resolution data become available.

RESULTS

Delimitation of the centres of endemism in China

The patterns obtained for species richness and weighted richness (Fig. 2) were very similar ($r^2 = 0.75$; $P < 0.000$). This
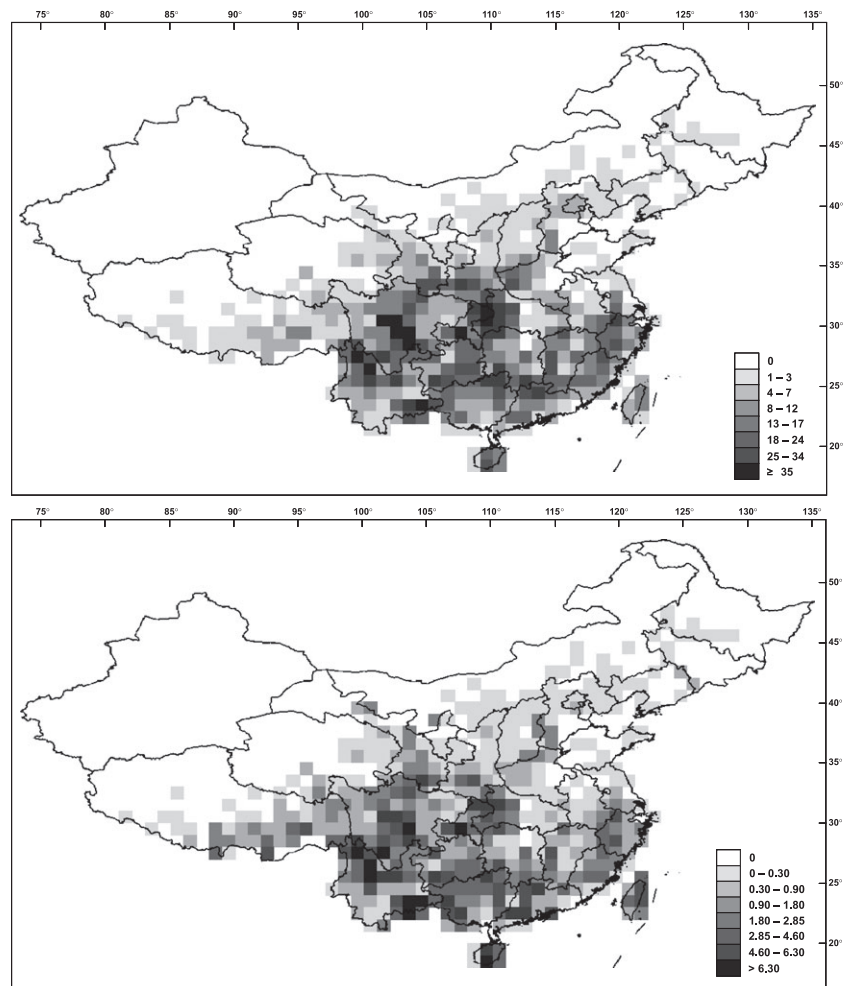
Figure 2 Species richness (above) and weighted richness (below) mapped in $1° \times 1°$ grid cells for the total set of plant taxa in China. Darker shading indicates higher values. Cells with the three darkest colours are those scoring within the top 5% highest values.

result was expected, because the vast majority of the species analysed in this study demonstrated a very limited geographical range, with approximately three-quarters of the taxa (416) found in only one to six grid cells (i.e. in less than 0.6% of the total number of grid squares computed in this study). The weighted richness method used to compute centres of endemism (Figs 2 & 3) should be considered as the most appropriate statistic for inferring sites of glacial refugia, because the effect of the few (relatively) widespread species included in our analysis is minimized.

All the major areas of (weighted) endemism were located in central and southern China (Figs 2 & 3, and Table 1). Perhaps the most significant of these areas was that situated in north-west Yunnan (no. 1 in Fig. 3 and Table 1), which corresponds roughly to the Hengduan Mountains and the north-western tip of the Yungui (Yunnan-Guizhou) Plateau and contains some of the cells with the highest weighted richness coefficient (Table 2). Next (although partly connected to the former), we found a second major centre (no. 2) in western Sichuan, corresponding approximately to the area covered by the Daxue Mountains and the lower reaches of Dadu River. The third highest scoring cell for weighted richness (which was also the cell with the maximum number of endemic

species recorded in China; Table 2) was located in centre number 2 (Emei Mountain). A minor area of endemism was located further to the north of this region and was confined to the Sichuan–Gansu border (i.e. the Min Mountains; no. 3). Two geographically proximate areas of endemism were found in the region bordering Vietnam: one was confined to the south-eastern corner of Yunnan (no. 4) and the other was situated in south-west Guangxi (no. 5). Centre number 4 contained the cell scoring highest for weighted richness, as well as two cells among the 'top ten' (Table 2). To the north of these two centres, a small area of endemism was located in south-west Guizhou (south-eastern tip of the Yungui Plateau, no. 6) and another minor centre comprised a single cell in north-west Guizhou (north-eastern edge of the Yungui Plateau; no. 7). In the central region of China, three areas of endemism were identified. The first was a small area in Chongqing (including Jinfo Mountain, no. 8); next was a large centre located in the Three Gorges region of the Yangtze River, at the confluence of three Chinese provinces (Chongqing, Hubei and Hunan) dominated by three mountain ranges (Daba, Wu and partially Wuling; no. 9). Finally, a minor centre of endemism was found in the central Qinling Mountains (no. 10).

Table 1 Centres of plant endemism in China according to weighted richness.

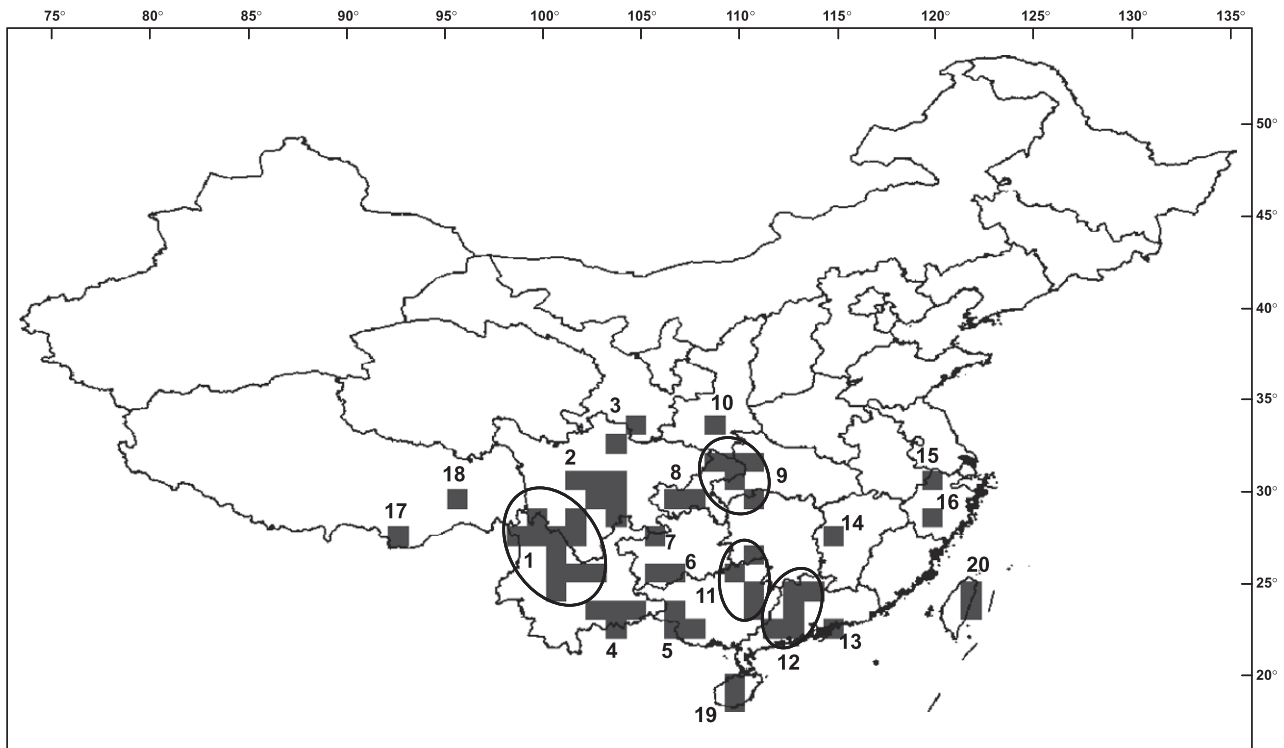| Code number*	Centre of endemism	Status†	Province‡	Occurrence of palaeo-/ neoendemics
1	NW Yunnan	M	Yunnan/Sichuan/(Tibet)	+/+++
2	W Sichuan	M	Sichuan/(Yunnan)	+/+++
3	Sichuan-Gansu	m	Sichuan/Gansu	++/++
4	SE Yunnan	M	Yunnan	+++/++
5	SW Guangxi	M	Guangxi	+++/++
6	SW Guizhou	m	Guizhou/(Guangxi)	+++/+
7	NW Guizhou	m	Guizhou/(Sichuan)/(Yunnan)	+/++
8	Chongqing	m	Chongqing/(Guizhou)	++/+++
9	Three Gorges region	M	Chongqing/Hubei/Hunan/ (Shaanxi)/(Sichuan)	+++/+
10	C Qinling Mountains	m	Shaanxi	+++/+
11	NE Guangxi	M	Guangxi/Hunan/(Guizhou)	+++/++
12	W Guangdong	M	Guangdong/(Guangxi)/ (Hunan)	+/+++
13	Hong Kong	m	Hong Kong/Guangdong	+/++
14	W Jiangxi	m	Jiangxi	+/++
15	Tianmu Mountains	m	Zhejiang/Anhui	+++/+
16	SW Zhejiang	m	Zhejiang	+/+++
17	Kanggardo Mountain	m	Tibet	−/+++
18	Namjagbarwa Mountain	m	Tibet	+++/++
19	Hainan Island	m	Hainan	+++/+++
20	Taiwan Island	m	Taiwan	+++/++

*The code numbers for the centres of endemism correspond to those in Fig. 3.

†M, major centre of endemism; m, minor centre of endemism.

‡The text in parentheses represents provinces harbouring only the edges of the centres of endemism.

Symbols used for describing the occurrence of palaeo-/neoendemics: +++, high occurrence; ++, intermediate occurrence; +, low occurrence; −, no occurrence.

Figure 3 The 20 centres of plant endemism in China. The shaded cells are those scoring within the top 5% highest values for weighted richness. The code numbers for the centres of endemism correspond to those in Table 1.

Table 2 Top ten 1° × 1° grid cells with the highest score of weighted richness for the endemic plant species in China.

Rank	Geographic coordinates	Province	Weighted richness score	Species richness	Centre of endemism
1	23–24° N, 104–105° E	Yunnan	11.72	47	SE Yunnan
2	18–19° N, 109–110° E	Hainan	11.64	22	Hainan Island
3	29–30° N, 103–104° E	Sichuan	10.64	52	W Sichuan
4	26–27° N, 100–101° E	Yunnan	9.66	39	NW Yunnan
5	27–28° N, 99–100° E	Yunnan	7.83	36	NW Yunnan
6	23–24° N, 103–104° E	Yunnan	7.65	25	SE Yunnan
7	25–26° N, 100–101° E	Yunnan	7.12	29	NW Yunnan
8	27–28° N, 101–102° E	Sichuan/Yunnan	6.74	28	NW Yunnan
9	22–23° N, 103–104° E	Yunnan	6.49	23	SE Yunnan
10	29–30° N, 107–108° E	Chongqing/Guizhou	6.35	39	Chongqing

South-central China harboured two major and two minor centres of endemism. One of the major centres included north-east Guangxi and a small region in south-west Hunan (i.e. the western section of Nanling Mountains; no. 11), and the other was located in the western part of Guangdong Province, namely the Yunkai Mountains and the eastern section of the Nanling Mountains (no. 12). The two minor centres of endemism were in Hong Kong (no. 13) and in the Wugong Mountains in western Jiangxi (no. 14). Eastern China had two discrete areas of endemism, namely one cell shared between Zhejiang and Anhui (Tianmu Mountains; no. 15) and another in south-west Zhejiang (no. 16). The westernmost areas of endemism of China were located in the eastern Himalayas (south-east Tibet), where two cells scoring high values for weighted richness were found: one corresponded to the Kanggardo Mountain and the deep river valleys facing India (no. 17), and the other quadrat comprised the Namjagbarwa Peak and the Yarlung Zangbo (Brahmaputra) River U-shaped canyon (no. 18). The two large islands of China, Hainan and Taiwan, also constituted centres of endemism (no. 19 and no. 20, respectively).

Patterns of palaeoendemism and neoendemism

Of the 555 taxa, 221 were classified as palaeoendemics (belonging to 163 genera) and 334 as neoendemics (belonging
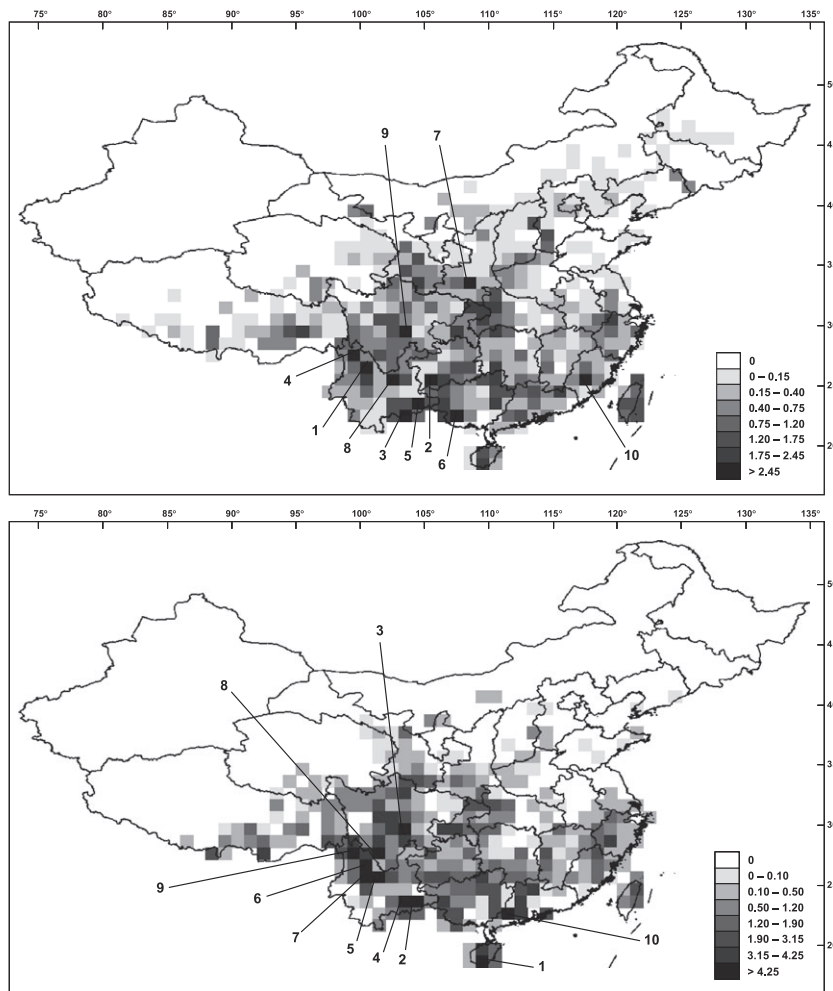
Figure 4 Weighted plant species richness mapped in 1° × 1° grid cells for palaeoendemics (above) and neoendemics (below) in China. Darker shading indicates higher values. Cells with the three darkest colours are those scoring within the top 5% highest values. The code numbers are the top ten 1° × 1° grid cells and correspond to the rank number of Table 3 (palaeoendemics) and Table 4 (neoendemics).

to 83 genera). Despite their lower number, old endemics were present in more grid cells of China than neoendemics (their grid occurrences were 432 and 304 cells, respectively; Fig. 4), probably because the former showed significantly wider ranges at the taxon level (the median was five and two grid cells for palaeoendemics and neoendemics, respectively; Kruskal–Wallis test, $P < 0.001$). Although almost all the areas of endemism in China exhibited the presence of both palaeoendemics and neoendemics (Table 1), considerable differences in their respective numbers for both the major and the minor centres of endemism were evident when the patterns of weighted richness were represented separately (Fig. 4). However, the patterns of weighted richness for palaeoendemics and neoendemics showed a low but significant correlation ($r^2 = 0.44$; $P < 0.000$), which can be largely attributed to the fact that for the two types of endemics, approximately the same areas of China remained blank (or with a low density of species). When a linear regression was performed considering only the cells within the 20 detected centres of endemism (i.e. the 56 cells shaded in Fig. 3), no correlation was observed, indicating significant differences in their distributions ($r^2 = 0.005$; $P = 0.606$).

Palaeoendemics were mainly concentrated in the central (Three Gorges region) and southern regions of China adjacent to Vietnam (Fig. 4). Three distinct areas (south-east Yunnan, south-west Guangxi and south-west Guizhou) in Fig. 2 appeared as a continuous, very large centre consisting of *c.* 12–13 grid cells in the map of palaeoendemics (Fig. 4). Indeed, four of these were among the top-scoring cells for weighted (palaeo)endemism (see Table 3). The large centre of endemism detected in north-east Guangxi was also a rich area for palaeoendemics. In contrast, palaeoendemic taxa were less important in the major centre close to this region (western Guangdong), which was also the case for the two major areas of endemism in south-western China, namely north-west Yunnan and western Sichuan. However, it should be noted that some of the grids located in these two centres were among the 'top ten' cells for palaeoendemics (Table 3).

The main centres of endemism in south-western China (i.e. north-west Yunnan and western Sichuan) were generally composed of neoendemic taxa (Fig. 4), because most of the top-scoring cells for weighted (neo)endemism (six out of ten; Table 4) were located in these regions. Neoendemics were also observed in the Three Gorges region and in the southern centres of endemism, but these were of secondary importance with respect to neoendemic richness. A notable exception was western Guangdong, which emerged as the third largest area for neoendemism in China (Fig. 4).

Table 3 Top ten 1° × 1° grid cells with the highest score of weighted plant species richness for the palaeoendemics in China.

Rank	Geographic coordinates	Province	Weighted richness score	Species richness	Centre of endemism
1	26–27° N, 100–101° E	Yunnan	4.19	18	NW Yunnan
2	25–26° N, 105–106° E	Guizhou	3.85	22	SW Guizhou
3	22–23° N, 103–104° E	Yunnan	3.85	15	SE Yunnan
4	27–28° N, 99–100° E	Yunnan	3.00	20	NW Yunnan
5	23–24° N, 104–105° E	Yunnan	3.00	23	SE Yunnan
6	22–23° N, 107–108° E	Guangxi	2.87	10	SW Guangxi
7	33–34° N, 108–109° E	Shaanxi	2.82	19	C Qinling Mountains
8	25–26° N, 102–103° E	Yunnan	2.78	17	NW Yunnan
9	29–30° N, 103–104° E	Sichuan	2.76	26	W Sichuan
10	25–26° N, 117–118° E	Fujian	2.62	10	Not detected

'Not detected' means that the cell does not belong to any centre of endemism inferred using the set of 555 taxa.

Table 4 Top ten 1° × 1° grid cells with the highest score of weighted plant species richness for the neoendemics in China.

Rank	Geographic coordinates	Province	Weighted richness score	Species richness	Centre of endemism
1	18–19° N, 109–110° E	Hainan	9.20	14	Hainan Island
2	23–24° N, 104–105° E	Yunnan	8.72	24	SE Yunnan
3	29–30° N, 103–104° E	Sichuan	7.87	26	W Sichuan
4	23–24° N, 103–104° E	Yunnan	6.09	12	SE Yunnan
5	25–26° N, 101–102° E	Yunnan	5.68	12	NW Yunnan
6	26–27° N, 100–101° E	Yunnan	5.46	21	NW Yunnan
7	25–26° N, 100–101° E	Yunnan	5.36	15	NW Yunnan
8	27–28° N, 101–102° E	Sichuan/ Yunnan	5.28	16	NW Yunnan
9	27–28° N, 99–100° E	Yunnan	4.83	16	NW Yunnan
10	22–23° N, 111–112° E	Guangxi/ Guangdong	4.56	7	W Guangdong

Differences concerning minor centres of endemism were also significant (Fig. 4 and Table 1). Furthermore, several areas not included in the general centres of endemism (those detected with the total set of species) gained significance when both classes of endemics were represented separately. The Die Mountains and the upper reaches of Zuli River (south Gansu), the Taihang Mountains (Shanxi/Hebei), the upper reaches of Jiulong and Min Rivers in western Fujian (i.e. the southeastern section of Wuyi Mountains) and the Xunwu River valley (north-east Guangdong/south Jiangxi) were high in palaeoendemic richness, whereas the Nanpu and Song River valleys (including the north-eastern section of Wuyi Mountains, north Fujian) and the Tibetan region immediately adjacent to the Indian state of Sikkim were noteworthy for the occurrence of neoendemics (Fig. 4).

DISCUSSION

Location of Chinese glacial refugia

China has a vascular flora of more than 30,000 species, which is much larger than those of Europe (c. 11,500 species) and the United States (c. 18,000 species). These territories are of almost the same land area and experienced comparable floristic richness and composition up until the Middle Miocene, c. 14–15 Ma (Tiffney, 1985; Axelrod et al., 1996). Among other factors related to biogeography, tectonics and geological history, it has been suggested that the differences in taxonomic richness in these regions are a result of the higher rate of plant extinctions during the late Cenozoic (e.g. Tiffney, 1985; Axelrod et al., 1996; Qian & Ricklefs, 1999). The progressive Cenozoic global cooling that was accentuated from the middle Miocene and extended into the Pliocene and Pleistocene periods (Zachos et al., 2001) produced numerous extinctions of plant lineages (Tiffney, 1985; Axelrod et al., 1996; Qian & Ricklefs, 2000). These extinctions were centred mainly on the thermophilic elements of the boreotropical flora (Tiffney, 1985; Latham & Ricklefs, 1993). However, a large fraction of this thermophilous flora can still be found in several mountainous enclaves in central and southern China (Axelrod et al., 1996; Qian, 2001), including *Eucommia*, *Ginkgo*, *Glyptostrobus* and *Metasequoia*, which were widespread in many parts of the Northern Hemisphere until the Pliocene (Manchester et al., 2009). Thus, extensive refugial areas must have existed in these

regions, which helped to prevent many Neogene and Quaternary extinctions (Axelrod *et al.*, 1996; Qian & Ricklefs, 2000).

This study identified 20 centres of endemism located in the central and southern part of the country below latitudes of 35° N (the majority being below 32° N). These sites are hypothesized to be areas of former glacial refugia, and our findings are generally consistent with former preliminary surveys (Ying *et al.*, 1993; Wang & Zhang, 1994; Tang *et al.*, 2006). Chinese centres of plant endemism show a marked mountainous character, falling almost entirely within the main mountain ranges and highlands of the central and southern regions of the country (Fig. 1), including: the Hengduan Mountains *sensu lato* (including Daxue and Min ranges); the Yungui Plateau; the central China ranges (mainly Qinling and Daba Mountains); the southern China ranges (Nanling and Yunkai Mountains); and the eastern China Mountains (e.g. Tianmu). Areas of endemism located outside these mountainous ranges include the two small Himalayan centres, and Hong Kong and its north-east surroundings. Hong Kong was the first botanical region of China to be heavily explored (the *Flora Hongkongensis* of G. Bentham dates from 1861 and contains almost 1000 newly described species; Cox, 1986), which may, in addition to its rugged topography, account for the high richness of range-restricted species in this area (i.e. a sampling effort bias; La Ferla *et al.*, 2002; Morawetz & Raedig, 2007). In contrast to mountainous areas, the large flat areas in the central region below 35° N of latitude, such as the Sichuan Basin, the Middle-Lower Yangtze Plain and the southern part of the North China Plain, have a very low density of endemic species.

Interestingly, most of the centres of endemism identified here coincide with those obtained for several groups of animals, for example birds (Lei *et al.*, 2003), mammals (Tang *et al.*, 2006), amphibians (Chen & Bi, 2007) and insects such as grasshoppers (Xu, 2005) and aphids (Huang *et al.*, 2008). This congruence among taxonomic groups suggests that these mountainous areas probably enjoyed relatively stable environmental conditions during the Quaternary, allowing them to sustain large assemblages of a variety of living forms throughout glacial/interglacial cycles. The relative eco-climatic stability generally attributed to the Pleistocene glacial refugia might arise from the varied topography in mountainous areas, which provided a wide array of sheltered habitats with milder and moister conditions for plant species (Fjeldså & Lovett, 1997; Hewitt, 2000; Tzedakis *et al.*, 2002; Médail & Diadema, 2009). The mountains also allowed elevational shifts of plant species to track warm interglacials/cold glacials and thus maximized their persistence (Hewitt, 2000; Davis & Shaw, 2001; Hu *et al.*, 2009). Furthermore, the highly heterogeneous topography of the mountains favoured the emergence of new lineages, which are generally thought to have evolved as a result of microallopatric speciation (Hewitt, 2000; Tzedakis *et al.*, 2002). In contrast to mountains, lowland habitats rarely form suitable refugia (at least in temperate latitudes) because of their much harsher and less stable eco-climatic conditions (Tribsch & Schönswetter, 2003; Tribsch, 2004; Médail & Diadema, 2009).

In addition, it should be noted that lowland areas in China have been severely transformed by humans (because of cultivation and human settlements), especially those areas north of the Yangtze River. Southern China remained relatively natural until the beginning of the 20th century, but at present its lowlands are intensively cultivated and densely populated (Ellis *et al.*, 2010). Thus, mountainous areas have become a kind of 'refuge from humans' (Tang *et al.*, 2006; Hou *et al.*, 2010).

The existence of refugia in southern China based on the identification of centres of endemism is also supported by Quaternary vegetation reconstructions, which indicate the occurrence of extensive temperate and subtropical forests in these areas, even during glacial periods (An *et al.*, 1990; Winkler & Wang, 1993; Wang & Sun, 1994; Adams & Faure, 1997; Yu *et al.*, 2000; Harrison *et al.*, 2001). Compared with present conditions, the cooler, drier climates during the Last Glacial Maximum (Yu *et al.*, 2000; An *et al.*, 2001) produced a considerable southward displacement (of up to *c.* 1000 km) of the temperate and warm vegetation, roughly confined to the modern limits of the subtropical and tropical vegetation, that is, to central and southern China. Throughout the rest of China a very poor desert, steppe, or tundra vegetation was dominant (extensively reviewed in An *et al.*, 1990; Winkler & Wang, 1993; Wang & Sun, 1994; Yu *et al.*, 2000; Harrison *et al.*, 2001).

The occurrence of large refugial areas for temperate and warm vegetation in Pleistocene China was possible also because of the lack of major geographic barriers for dispersal. Latitudinal plant migrations were able to track climatic oscillations well below 20° N, through Hainan and the exposed continental shelf of the South China Sea, which enabled the establishment of floral refugia in more favourable southern latitudes. In contrast, southward displacements in other parts of the Northern Hemisphere were more limited. In North America, the Gulf of Mexico and Mexican deserts (which at this time were much less extensive than today; Metcalfe, 2006) partially blocked migrations below 30° N, whilst in Europe, the large east–west-oriented mountains, the Mediterranean Sea and the Sahara Desert constituted insurmountable obstacles (Latham & Ricklefs, 1993; Axelrod *et al.*, 1996). Consequently, refugia were limited to small, mountainous enclaves scattered within the southern regions (Adams & Faure, 1997).

Glacial refugia in China: places for both survival and speciation

There is a growing consensus that environmental stability, in the context of changing climate, is not only a pre-requisite for the preservation of relict lineages but also the driver for the emergence of novel taxa (e.g. Fjeldså, 1995; Jansson, 2003; Jetz *et al.*, 2004). Glacial refugia, often associated with varied topography, provided this stability by buffering the extreme Pleistocene fluctuations (Hewitt, 2000; Tzedakis *et al.*, 2002). Thus, it is not surprising that assemblages of palaeoendemics and neoendemics are present in a number of regions charac-

terized by a rugged topography and well recognized as refugia, such as California (Stebbins & Major, 1965), the Mediterranean Basin (Verlaque *et al.*, 1997), the tropical Andes (Fjeldså, 1995), the South African Cape region (Verboom *et al.*, 2009) and tropical Africa (Fjeldså & Lovett, 1997), as well as southern China, as revealed here.

Almost all the areas of endemism detected in China acted as refugia for both palaeoendemics ('plant museums') and neoendemics ('plant cradles'). However, substantial differences occur between the two types of endemics for most centres, suggesting that other processes, in addition to environmental stability, could have had a differential impact on the rates of plant persistence/cladogenesis within the different refugia. Mountain-building processes and other tectonic movements are well-known speciation drivers for the late Neogene and Quaternary; in South America, for example, the recent phases of the Northern Andes uplift (from the Pliocene onwards) are correlated with many speciation events (Fjeldså, 1994; Richardson *et al.*, 2001). The significance of tectonics as a powerful engine for speciation is also evident in the Mediterranean Basin, where the larger proportion of neoendemics in its eastern section has been attributed to its relative geological youth compared to the west (Verlaque *et al.*, 1997).

The clear trend of the preponderance of neoendemics in the eastern fringe of the Tibetan Plateau (Hengduan Mountains *sensu lato*) and the higher density of palaeoendemics in the areas to the east (despite some exceptions, e.g. western Guangdong; Fig. 4) confirm the hypothesis of several Chinese scholars (e.g. Ying *et al.*, 1993; Wu & Wu, 1996; Li & Li, 1997) and appear to be directly related to the fact that the current mountain ranges harbouring the Chinese areas of plant endemism formed at different times. The uplift of the ranges east of the Tibetan Plateau is generally much older than that of the plateau itself (Wang, 1985; Fan, 1997). For example, the formation of the Qinling Mountains and the Nanling orogeny began during the Triassic and the Cretaceous, respectively. Other highlands east of the Tibetan Plateau, such as the Yunnan–Guizhou Plateau and the mountain ranges in south-eastern China, started to uplift in the early Cenozoic (Hsü, 1983; Wang, 1985). In contrast, the major uplift of the Tibetan Plateau took place much more recently, either during (Li & Fang, 1999; Zhang *et al.*, 2000; Zheng *et al.*, 2000) or immediately before (Harrison *et al.*, 1992; An *et al.*, 2001) the Pliocene and Pleistocene. Its eastern edge (i.e. Hengduan, Daxue and Min Mountains) was the last sector uplifted (An *et al.*, 2001). The Tibetan Plateau orogeny, which is still active, created a vast array of new habitats across wide elevational ranges (up to 5000 m in the Hengduan Mountains, which are perhaps the largest 'evolutionary front' of the world's temperate zone) and stimulated allopatric and habitat differentiation, thus ultimately giving rise to adaptive radiations (Liu & Tian, 2007). A suitable example is *Nannoglottis*, a relict genus that probably arrived on the Tibetan Plateau no later than Oligocene and underwent a rapid re-diversification during the Pliocene–Pleistocene (Liu *et al.*, 2002).

Central, south-central as well as south-eastern China (with the exception of the two large islands, Hainan and Taiwan) have generally enjoyed relative tectonic stability since the late Tertiary (Hsü, 1983). In Hainan, the formation of the Qiongzhou Strait in the late Tertiary broke its longstanding connection with the continent and became an island (Wang, 1985), whereas Taiwan did not emerge from the sea until the late Miocene (Sibuet & Hsu, 2004). These islands were periodically connected to the continent by the marine regressions that occurred during the several Quaternary glacial periods (Ferguson, 1993; Wang & Sun, 1994). Moreover, volcanism was frequent in Hainan during the Pleistocene (Wang, 1985). Combined, these events provided plants with many opportunities for speciation and for the migration of palaeoendemics between the mainland and the islands (Ferguson, 1993), explaining the high concentrations of both types of endemics in Hainan and Taiwan. Peaks of neoendemics on other mountain ranges of southern China could be related to their orogenic reactivation in recent times (e.g. the Yunkai Mountains in western Guangdong, one of the areas with more recent endemics of southern China, were reactivated during the late Miocene; Liang & Li, 2005).

The high percentages obtained for the two classes of endemics at the country level (39.1% for palaeoendemics and 60.9% for neoendemics) suggest that central and southern China played a significant role both as a centre of survival and as a centre of differentiation and evolution for seed plants during Neogene and Quaternary global cooling. The relatively high proportion of palaeoendemics from our data set (in the Mediterranean Basin these represent only *c.* 25% of the total; Verlaque *et al.*, 1997; Thompson, 2005) is in agreement with other lines of evidence suggestive of the persistence of a very significant fraction of Cenozoic or older elements in China. Such evidence includes the following: (1) many palaeoendemic lineages that are still present in China once existed in Europe and/or North America (including some 'living fossils'), but were extirpated at some point of the Cenozoic (Latham & Ricklefs, 1993; Manchester *et al.*, 2009) – from a conservation point of view, the extinction of these palaeoendemics would imply the loss of unique, irreplaceable evolutionary history; and (2) China harbours more ancient endemic genera and families than North America (Qian & Ricklefs, 1999; Qian, 2001).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Classification between palaeoendemics and neoendemics of the 555 recorded Chinese endemic plant taxa.

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BIOSKETCHES

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