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Mountains of Southern China as "Plant Museums" and "Plant Cradles": Evolutionary and Conservation Insights

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The occurrence of areas or centers of endemism is commonly attributed to the existence of suitable refugia in which plant lineages survived while others evolved during the late Neogene and Quaternary global cooling. In China, several studies performed since the 1980s have identified the mountains of central and southern China as the main centers of endemism in the country. A recent work studied the patterns of endemism separately for palaeoendemics and neoendemics and found that these tend to be located in different mountain ranges. Whereas, young endemics are preferably located in the mountain ranges of the eastern fringe of the Tibetan Plateau ("plant cradles"), old endemics tend to occur in the mountains of central, south central, and southeastern China ("plant museums"), although there are some exceptions. This pattern seems to be related to the different geological history of the mountain ranges. The eastern fringe of the Tibetan Plateau clearly constitutes the "evolutionary front" of China, probably due to the uninterrupted uplift of the plateau from the late Neogene. In contrast, the relative tectonic stability in central and southern China during most of the Tertiary may have maximized the persistence of relict plant lineages. These results have significant implications in the conservation of the endemic flora, which are briefly discussed.

Keywords: *China; centers of endemism; conservation; neoendemics; palaeoendemics; species cradles; species museums.*

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Introduction

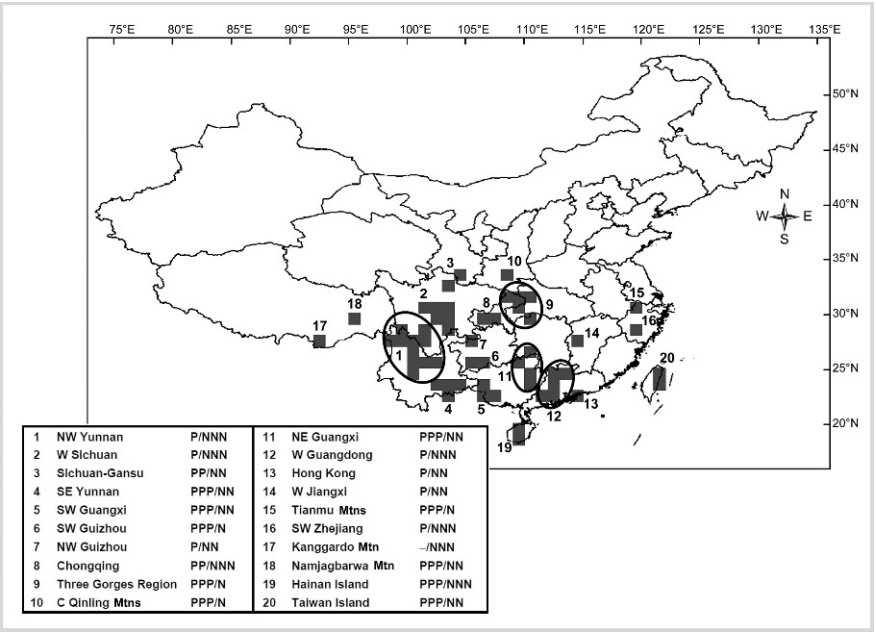
Mountains are often linked to high levels of plant diversity (Körner and Ohsawa 2005), and this is widely recognized to be a direct consequence of the geological history of mountainous regions (eg orogenic processes, past climatic changes) as well as of their climatic and topographic heterogeneity (Huber et al 2005; Médail and Diadema 2009). More contemporary events also explain why mountains usually harbor more plant diversity than lowlands, and these are mainly related to socioeconomic issues: mountains have often forcibly become the "last refuge" for wildlife because of dense human settlements and intensive agricultural practices in the lowlands. However, mountain biodiversity is at present at high risk because of intensification and changes of land use (departing from traditional management), global climate change (shrinkage of glaciers), or the introduction of non-native species (Huber et al 2005; Spehn et al 2010). Thus, mountains should be regarded as prime conservation targets.

China is not an exception to this close connection between mountains and plant diversity. Its mountainous areas, especially those located in the southern part of the country, harbor most of China's plants, both in terms of total species richness and endemism. According to Tang et al (2006), about 92% of the country's plant genera and 90.5% of endemic plant genera are located in just 10 areas, all of them in southern mountain regions. China has one of the highest percentages of mountainous lands in the world, with over 50% (Kohler et al 2010). These lands comprise the highest mountain range on Earth (the Himalaya), perhaps the most rugged one (the Hengduan Mountains, with altitudinal gradients of up to 5000 m), and also a wide array of mountainous types that range from cold and dry (eg Kunlun Mountains or the Tian Shan) to warm and humid ranges (eg Nanling or the Taiwanese Central Mountain Range). In addition, Chinese mountains also show a marked heterogeneity with respect to mountain formation: some are very old and highly eroded, and their origin can be traced back to the early Tertiary or before (Hsü 1983; Wang 1985), whereas others were not built until very recent times (eg Hengduan Mountains, probably uplifted during the last 3 million years; An et al 2001).

Mountains anywhere stand out for their levels of endemism, and this has been mostly attributed to the role played by them as refugia during the Neogene and Quaternary global cooling; their topographical diversity should have provided enough eco-environmental stability, buffering them against extreme climate fluctuations. Interestingly, these features not only allowed plants to persist but also propelled evolution and speciation (Fjeldså and Lovett 1997; Tzedakis et al 2002; Médail and Diadema 2009). Therefore, distributional patterns of endemism are a commonly used tool for inferring the location of glacial refugia (López-Pujol et al 2011 and

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FIGURE 1 The 20 centers of plant endemism in China (adapted from López-Pujol et al 2011); their delimitation has been done by using 1° × 1° latitude/longitude grid. The bottom left-hand box shows the geographical location of the centers together with the relative occurrence of palaeoendemics (P) and neoendemics (N): 3 letters, high occurrence; 2 letters, intermediate occurrence; 1 letter, low occurrence; –, no occurrence.



1	NW Yunnan	P/NNN	11	NE Guangxi	PPP/NN
2	W Sichuan	P/NNN	12	W Guangdong	P/NNN
3	Sichuan-Gansu	PP/NN	13	Hong Kong	P/NN
4	SE Yunnan	PPP/NN	14	W Jiangxi	P/NN
5	SW Guangxi	PPP/NN	15	Tianmu Mtns	PPP/N
6	SW Guizhou	PPP/N	16	SW Zhejiang	P/NNN
7	NW Guizhou	P/NN	17	Kanggardo Mtn	–/NNN
8	Chongqing	PP/NNN	18	Namjagbarwa Mtn	PPP/NN
9	Three Gorges Region	PPP/N	19	Hainan Island	PPP/NNN
10	C Qinling Mtns	PPP/N	20	Taiwan Island	PPP/NN

references therein). The strong endemic character of Chinese mountain flora has been stressed since the 1980s, and a big picture of the main areas of endemism (ie the hypothesized refugia) has been drawn in several studies (eg Ying and Zhang 1984; Ying et al 1993; Wang and Zhang 1994; Ying 2001; Tang et al 2006). Recently, López-Pujol et al (2011) went one step further and, in addition to delimiting the areas of endemism at species level (and not at genus level as in the above-mentioned works), they divided their endemic species database into relict endemics (palaeoendemics) and young endemics (neoendemics) to examine whether these areas are mainly places of plant survival ("plant museums") or areas from where differentiation and speciation occur ("plant cradles").

This article aims at summarizing the state of the art in research on patterns of plant endemism in Chinese mountains and their evolutionary aspects, that is, the role of mountains as "museums" and/or "cradles." Such information is of great value for setting up a conservation agenda for Chinese mountains.

Chinese mountains: places for both plant persistence and evolution

Centers of endemism as glacial refugia

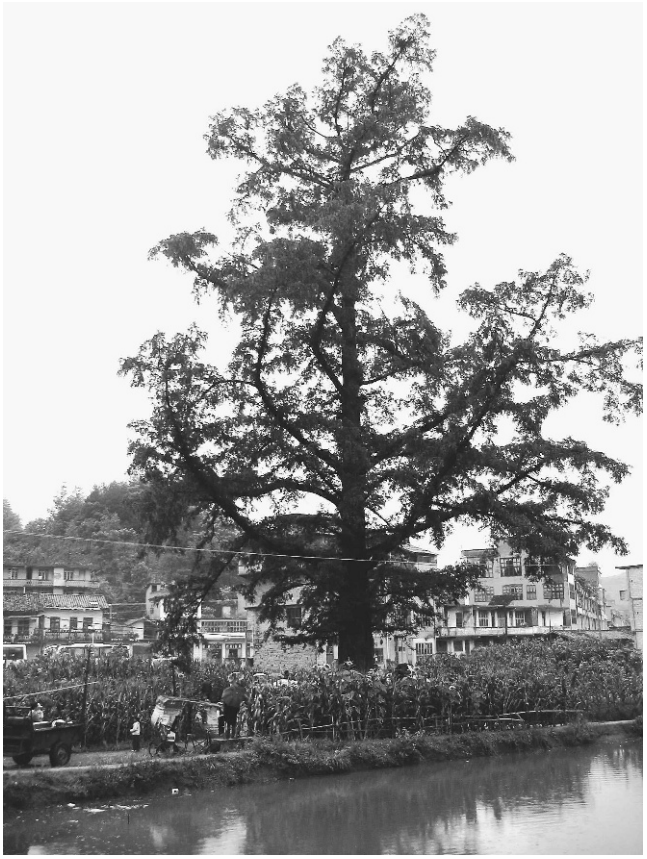
Up to 20 areas of endemism were delimited by López-Pujol et al (2011), all located in central and southern China, which coincide with the main mountain ranges of these regions (Figure 1), and broadly consistent with the above-mentioned earlier studies. Several lines of evidence indicate that southern Chinese mountains acted as "true" refugia.

First, it should be noted that China harbors more than 30,000 vascular species, much more than those found in Europe (about 11,500) and the United States (~18,000), territories with almost the same land area and a comparable floristic richness and composition up until the Middle Miocene (~14–15 million years ago [Ma]) (Axelrod et al 1996). Many lineages that were widely distributed along the Northern Hemisphere are today endemic to meridional Chinese mountains, thanks to a much lesser extinction rate experienced there. *Cathaya argyrophylla*, *Eucommia ulmoides*, *Ginkgo biloba*, *Glyptostrobus pensilis*, *Metasequoia glyptostroboides* (Figure 2), and *Taiwania cryptomerioides* are just the most conspicuous examples (indeed, they are regarded as "living fossils") of the Tertiary thermophilous flora that once spanned most of the Northern Hemisphere (the "boreotropical flora"; Kubitzki and Krutzsch 1996). The work of López-Pujol et al (2011) confirms the strong relictual character of the Chinese flora; 39.1% of their endemics database was classified as palaeoendemics and 60.9% as neoendemics; in the Mediterranean Basin, for instance, the percentage of relict endemics is much lower (~23%; Verlaque et al 1997). Other empirical data are also supportive of the antiquity of Chinese flora and show that China has a disproportionately large number of taxa that belong to the oldest plant taxonomic groups, that is, pteridophytes, gymnosperms, magnolids, and ranunculids (Qian and Ricklefs 1999; Qian 2001), that China has a significantly higher number of ancient endemic genera and families than the United States (Qian 2001), and, finally, that most of the endemic genera of spermatophytes of China (~240) are of ancient origin (Ying et al 1993; Wu et al 2007).

Second, almost all the centers of endemism (19 of 20; Figure 1) identified by López-Pujol et al (2011) contained both palaeoendemic and neoendemic taxa, as would be expected for glacial refuges; in fact, assemblages of relict and recently speciated taxa have been reported in other mountainous regions around the world, with a widely recognized role as refugia (eg the tropical Andes, the mountains of tropical Africa, South African Cape region, or the Mediterranean mountains; see references within López-Pujol et al 2011). However, the 2 classes of endemics are not evenly distributed within each center of endemism in southern China; a clear preponderance of neoendemics exists in the eastern section (ie the

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FIGURE 2 Type tree of *Metasequoia glyptostroboides* at Moudao Town (Hubei Province, Three Gorges Region). (Photo by Qin Leng)



Hengduan Mountains), although palaeoendemics are dominant in the areas to the east (Figure 1), which confirms the hypothesis raised by several Chinese botanists (Wu and Wu 1996; Li and Li 1997) and seems to be related to the different geological and tectonic history of the involved areas: the Tibetan Plateau is the most significant "evolutionary front" of China, probably due to its uninterrupted uplift from the late Neogene (Li and Fang 1999; An et al 2001), which enhanced differentiation. In contrast, the relative tectonic stability in central and southern China during most of the Tertiary (with a few exceptions, such as Hainan, Taiwan, or western Guangdong; Hsü 1983; Wang 1985; Liang and Li 2005) may have maximized the persistence of relict plant lineages. The Three Gorges Region, the northeastern corner of Guangxi, and the area formed by southeast Yunnan, southwest Guangxi, and southwest Guizhou are the most significant refugia for palaeoendemics in China (Figure 1).

Third, the existence of such southern refugia is consistent with the Quaternary vegetation reconstructions for China, which suggests the occurrence of extensive temperate and subtropical forests in these areas during the glacial periods (eg An et al 1990; Winkler and Wang 1993; Wang and Sun 1994; Harrison et al 2001; Ni et al 2010), quite a contrast to that which occurred in North America but especially in Europe (Adams and Faure 1997; Prentice et al 2000).

Fourth (and last), the glacial refugia identified through areas of endemism seem to coincide with those inferred from the still few but increasingly more frequently carried out molecular phylogeographic studies on Chinese plant species. In the excellent review by Qiu et al (2011), a general pattern of multiple refugia appears to emerge from the DNA-based data, and, interestingly, shows a broad congruence with the centers of endemism identified by López-Pujol et al (2011). A similar congruence is also evident in the Mediterranean Basin, where the areas of endemism (Médail and Quézel 1997) clearly match the phylogeographically defined refugia (Médail and Diadema 2009). The article by Qiu et al (2011) also depicts a very significant outcome: Chinese plant taxa tend to show a combination of high genetic diversity and strong divergence among populations, fairly compatible with a scenario of numerous and extensive Quaternary refugia in southern China.

To conclude, it can be stated that the numerous mountain ranges in the southern section of China, coupled with the limited ice coverage during the Quaternary glaciations (large ice caps were only present in the Tibetan Plateau; Shi 2002) and the lack of barriers to southward migration enabled the country to serve as a refuge for many Tertiary plant lineages as well as a region for plant evolution and speciation.

The Hengduan Mountains: a paradigmatic example of "species cradle"

The Hengduan Mountains *sensu lato* (that is, the Hengduan, Daxue, and Min Mountains) (Figure 3) are undoubtedly the richest area for plant diversity in China but also one of the most significant (if not the most significant) of the North Temperate Zone (it has gained international recognition as a world "biodiversity hotspot"). Spanning up to 5 different provinces (Yunnan, Tibet, Sichuan, Qinghai, Gansu), it harbors some 12,000 species, of which ~3500 are endemic (Myers et al 2000). Its varied and highly dissected topography (combining precipitous mountains, river valleys, and deep gorges) formed during the Pliocene and Pleistocene (An et al

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FIGURE 3 A view of Hengduan Mountains. The highest peak in the picture is Mount Gongga (7556 masl). Some deep gorges (of about only 1000 masl) can be found just a few km away. (Photo by Jordi López-Pujol)



2001), have greatly contributed to the appearance of many new species (mainly by allopatric and ecological speciation). Radiations are common here, even in primitive genera such as *Rhododendron* (276 of ~1000 of the world's species are present in the Hengduan Mountains, and 132 are strictly endemic; Zhang et al 2009). However, these mountains also allowed (although in a lower scale; Figure 1) the preservation of relict elements: *Taiwania cryptomerioides* and *Cunninghamia lanceolata*, 2 of the oldest lineages of spermatophytes (>100 Ma; LePage 2009; Ran et al 2010), found in the Hengduan Mountains a suitable refugia. Despite their inaccessibility, these mountains have been severely logged and overgrazed, and numerous dams have been planned or are already in place (CI 2007; Morell 2008).

Three Gorges Region: a paradigmatic example of "species museum"

The Three Gorges Region (which is also known as the central China Mountains, namely Daba and Wu Mountains) is also one of the richest areas in plant diversity in China, with ~6400 plant species (López-Pujol and Ren 2009). This region, in contrast to the Hengduan Mountains, contains more relict than recently evolved taxa (López-Pujol et al 2011). One of the most interesting areas within this hotspot is the so-called metasequoia area, a region of about 800 km^2 in the juncture of Hubei and Chongqing (ie the Fangdou Mountains), where there are still natural populations of *Metasequoia glyptostroboides* (Figure 2). In this very small land extension, at least 550 species of vascular plants occur, including many "living fossils" in addition to *M. glyptostroboides*, for example, *Cunninghamia lanceolata*, *Eucommia ulmoides*, *Keteleeria davidiana*, *Pseudolarix amabilis*, *Taiwania cryptomerioides*, *Tapiscia sinensis*, and *Tetracentron sinense* (Hu 1980), all of them with fossil records dating back to the early Tertiary or even before (Manchester et al 2009). Not within the metasequoia area but nearby are occurrences of other very ancient plants, such as *Cathaya argyrophylla*, and some truly wild populations of *Ginkgo biloba*. Unfortunately, human activities such as hydroelectric development and farming represent growing challenges for the conservation of the Three Gorges Region relict flora (López-Pujol and Ren 2009).

Conservation of Chinese mountainous flora: challenges and recommendations

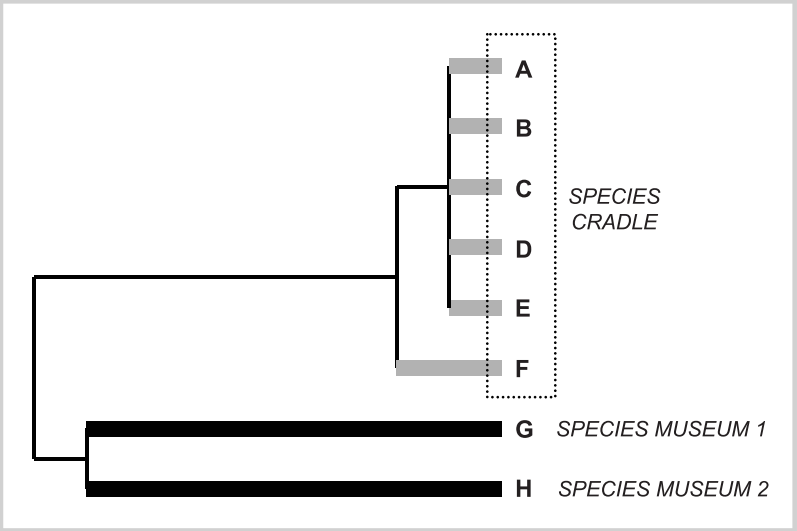
Protecting biodiversity and natural ecosystems is a necessary prerequisite to guarantee (and is also a consequence of) sustainable development in mountain regions. Local mountain communities have always relied on their natural resources; both their agricultural practices and their overall social organization have generally been respectful of mountain biodiversity and mountain environments (Xu et al 2005; Ramakrishnan 2007). Thus, the design of conservation strategies for mountain biodiversity needs to take into account sustainable development. The mountains of southern China, as discussed in the former paragraphs, support very rich and heterogeneous plant diversity from the point of view of evolution. At the same time, however, these mountains have become subject to increasingly intense human pressures; intensification of agriculture, hydroelectric development, and other industrial activities (eg mining), and the rise of tourism activities have all gone well beyond the limits of sustainable development.

Conservation considerations under an evolutionary framework

The need to protect the ecological and evolutionary processes that create and maintain biodiversity (eg preserving those areas characterized by topographic, climatic, and environmental heterogeneity and those providing migratory corridors and landscape connectivity) and not exclusively the current patterns of this biodiversity (eg simply preserving those species included in a Red List) has become a more important consideration when designing conservation strategies (Cowling and Pressey 2001; Mace et al 2003; Davis et al 2008). Because the processes that trigger species diversification and those that promote their maintenance may not always completely coincide, distribution patterns for relict and newly generated taxa can differ to some extent (Fjeldså 1994; Silva and Bates 2002), as also revealed in China in the study of López-Pujol et al (2011). In this context, a debate is

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FIGURE 4 Hypothetical phylogram of 8 plant species (A–H). Species with the gray branches are probably the result of a recent radiation and then share most of their evolutionary history; thus, extinction of one of them would not be very serious. In contrast, species with black branches (G and H) are relict lineages which share very little phylogenetic history. The loss of any of them will be very serious based on criteria of irreplaceability.



growing about whether priority should be given to areas of active speciation ("species cradles") or, on the contrary, to those acting mainly as a repository of ancestral taxa ("species museums") (Erwin 1991; Fjeldså 1994; Crozier 1997; Cowling and Pressey 2001). One may be especially interested in preserving the "evolutionary fronts" or the "species pumps," that is, those places that contribute most to the growth of the Tree of Life, but one may also focus on areas with assemblages of isolated lineages that carry unique gene combinations and biological characters (Erwin 1991; Mace et al 2003).

When focusing on China, we should have in mind 2 important evolutionary considerations. On one hand, and as discussed above, China maintains a very rich sample of relict lineages, generally consisting of unique, very deep evolutionary lineages, in some cases that represent entire families or even higher taxonomic levels (eg Ginkgoales or Trochodendrales). On the other hand, China harbors probably the largest "evolutionary front" of the world's North Temperate Zone, the Hengduan Mountains, which are still active because the Tibetan Plateau is uplifting (Zhang et al 2000) and which have experienced extensive explosive radiations in the last million years (Liu and Tian 2007). The extirpation of relict taxa would imply the loss of unique, irreplaceable evolutionary history (or "phylogenetic diversity"; Faith 1992) (Figure 4). For instance, their potential economic uses could be definitively lost because these taxa generally do not have close living relatives. In radiating areas, in contrast, floras tend to be phylogenetically clustered, that is plant taxa usually have many close relatives (Cowling and Pressey 2001). Thus, the extinction of a given taxon will not involve a significant loss of evolutionary history because of the presence of its congeners (Mace et al 2003) (Figure 4). However, evolutionary fronts are regarded as very important for assuring the maximum levels of both present and future biodiversity (Erwin 1991), because biodiversity is rapidly replaced after any extinction event (Crozier 1997).

Leaving aside this evolutionary debate (which today still remains as an open question in conservation biology; Mace et al 2003; Isaac et al 2007), the protection of both palaeoendemic and neoendemic plant taxa in China represents a great challenge in terms of practical conservation. Regarding neoendemics, their centers of abundance are much more defined compared with palaeoendemics: young taxa are mostly concentrated in the eastern fringe of the Tibetan Plateau (most of the 1° latitude × 1° longitude cells richest in neoendemics are located there; López-Pujol et al 2011). These features may confer significant advantages concerning conservation purposes. For example, protecting relatively few areas might ensure the conservation of a considerable portion of the neoendemic taxa. In addition, the Tibetan Plateau is one of the regions in China with less population density and also one of the most inaccessible, which limits the a priori potential impact of human activities. However, the astonishing rise of domestic tourism in China (which has tripled in just 15 years; NBSC 2009) is bringing visitors even to the most remote places, including the Hengduan Mountains; for example, the new airport of Jiuzhaigou-Huanglong, opened in 2003, has contributed to the increase in the number of visitors in Jiuzhaigou Nature Reserve, from only 32,000 in 1984 to more than 2 million at present (Hendrickson 2009), with pervasive effects on the reserve's biodiversity (eg Zhu et al. 2006; Morell 2008). Also, intensive logging during the second half of the 20th century destroyed large areas of Hengduan's primary forests (Morell 2008). Other areas rich in young endemics (Guangdong) are among the most populated regions of China, which makes their preservation a very difficult task.

Areas rich in palaeondemics, in contrast, seem to be more dispersed throughout the country according to the distribution maps specific for palaeoendemics and neoendemics provided in the article of López-Pujol et al (2011), and this might be because old endemics showed significantly wider distribution ranges (more than double) as reported by the same researchers. Whatever the reason, this feature, which was also reported in South America and sub-Saharan Africa

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(Fjeldså 1994; Fjeldså and Lovett 1997), confers some "degree of protection" from human perturbations (but, ironically, not from the evolutionary forces; Erwin 1991). Despite the fact that some palaeoendemic centers are located in relatively remote sites (eg Shennongjia), most of the mountains where they can be found are generally close to the densely populated and cultivated areas of southern China. Anthropogenic habitat destruction caused, for example, the local extinction of the relict *Euryodendron excelsum* (a species that belongs to a monotypic genus endemic to China) from Guangxi and the shrinkage of the Guangdong populations (Shen et al 2009).

Recommendations for conservation

Because the refugia of the past are the areas best suited to being the refugia of the future, and this is especially significant in the context of global climate change (Bhagwat and Willis 2008; Médail and Diadema 2009), it is urgent that a conservation agenda is launched, which should ensure: (1) the conservation of the taxonomic entities that inhabit the mountain centers of endemism; (2) the preservation of their landscape features, keeping them as intact as possible to conserve those processes that maintain and generate biodiversity; and (3) development of mountain regions in an ecologically sustainable manner.

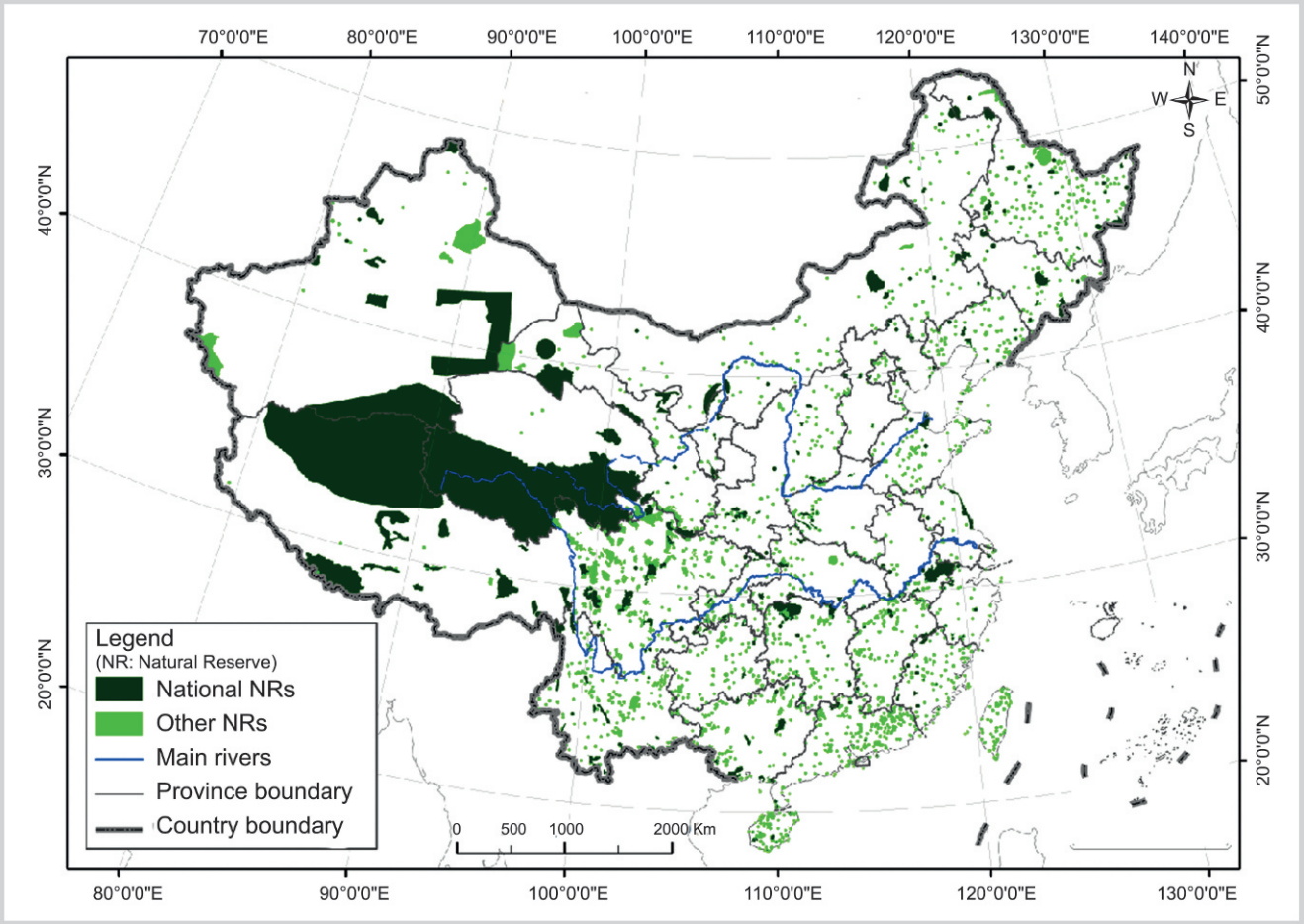
Achieving a deeper scientific knowledge: Despite the recent efforts to study mountain plant diversity in China, there are still significant gaps, especially in the remote western ranges (Li et al 2011); botanical exploration in this region was scarce until the 1980s, and comprehensive inventories had to wait another 2 decades (eg Kelley 2001). Thus, the available studies on endemism or taxonomic richness (eg Ying et al 1993; Tang et al 2006) were performed at genus level to avoid the biases caused by regional differences in the level of investigation; only the recent work of Huang et al (2011) uses the species level, although the scale of the operational geographic units (provincial) invalidates its use for identifying areas of endemism. However, because botanical exploration has grown significantly in recent years (mainly because of the rise of funding and scientific personnel at Chinese universities and research institutes), and molecular studies are expanding at an even faster pace, it can be anticipated that we will soon be able to obtain a reasonably precise location of glacial refugia and to decipher the evolutionary patterns of the Chinese flora. The localization of refugia would also benefit from obtaining more palaeoecological data, which are at present still scarce especially in latitudes between 25° and 30°N (Ni et al 2010) where most of the hypothetical refugia were located (Figure 1).

Improving both in situ and ex situ conservation: Irrespective of the type of endemics, and even though commendable progress has been made in recent decades, the current in situ and ex situ measures implemented by the Chinese governmental agencies in charge of biodiversity conservation are still insufficient. Despite being well above the average for developing countries, the current network of protected areas (PA), which covers 18% of the country's total land area (MacKinnon and Xie 2008), has 3 major deficiencies: (1) lack of budget; (2) PAs are too small, which is especially true in eastern China (eg the 20% of the total number of PAs account for just 0.13% of the total area, which means an average of less than 4 km^2 per PA; MacKinnon and Xie 2008); and (3) plant hotspots coverage is inadequate (Figure 5). Although more than 80% of the network protects mountainous areas (Tang et al 2006) and thus one can be satisfied with this situation, a large part of these protected areas is found in the northern part of the Tibetan Plateau, in western China (Figure 5). Hence, it is mandatory to enlarge the PAs within or around the centers of endemism as well as to ensure their connectivity through biological corridors. It is also desirable that their funding be increased to avoid departures from their intended purpose (Yu 2010). The current ex situ strategies also fall short in their protection of the endemic, evolutionarily significant flora: very few botanical gardens (BG) in China are located in the southwest (Huang 2010), where some of the major areas of endemism are found (Figure 1), although the network is adequate in southeastern China. The threatened flora of China (to which most of the endemic species belong) is still poorly represented in the BGs (for example, fewer than 40% of the taxa included in the *China Species Red List* are cultivated; Huang 2010). Another weakness is the size of the collections, which usually are too small to be representative of the species' genetic diversity; for example, the only ex situ collection of *Picea neoveitchii* (a narrow endemic species of Qinling Mountains) consists of just 2 individuals cultivated in Xi'an Botanical Garden (Zhang 2007).

Involving the local people and raising environmental awareness: For various reasons, in China, there is a strong correlation between mountains and indigenous people (the *shaoshu minzu* or China's minority nationalities), especially in the southwest (Xu et al 2005). These cultures have been stewards of the land for centuries or even millennia and are used to managing it in a sustainable way. Indeed, there is a traceable link between biodiversity conservation and ethnic minorities in China. The conservation of Holy Places, Holy Mountains, and Holy Trees by several ethnic minorities is well known (Yang et al 2004; Xu et al 2005): for example, in the Tibetan "sacred mountains," such the Khawa Karpo in northwest Yunnan, the biodiversity is better conserved than in the

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FIGURE 5 A map of nature reserves in China at the end of 2008. Elaborated by Lu Zhang, Research Center for Eco-Environmental Sciences, Beijing, as requested by the authors.



nonsacred mountains (Salick et al 2007). The establishment of modern conservation measures (mainly setting PAs) often creates conflict with the local population (eg by denying access to territory and environmental services, or even their resettlement); moreover, corruption among local officials may result in the failure of compensation schemes, whereas new opportunities, such as the benefits from non-timber forests products and cultural (ethnic) tourism, often enrich outsiders (Xu et al 2005; Xu and Melick 2007). Therefore, it not only is essential to engage local people in conservation activities as well as in the planning and management of the PAs but also to grant them an active role in the local economies. The strengthening of environmental awareness at all levels (high-rank cadres, local officials, the public in general) is also crucial, but this should be particularly geared toward the indigenous and local communities, which are in direct contact with the plant diversity. One example of how to proceed is the case of *Acer yangbiense*, the rarest maple of the world (with only 4 individuals remaining in the southwest corner of the Hengduan Mountains): the local communities of the mountain where the trees are located were not only promptly informed but also invited to take part in their management (BGCI 2008).

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