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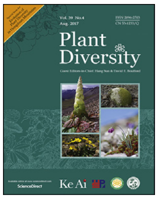

Editorial

Origins and evolution of plant diversity in the Hengduan Mountains, China

1. Introduction

The Hengduan Mountains region (HDM) in southwest China, one of the earth's 34 biodiversity hotspots, is characterized by its unique geology, dramatic topography, a climate where snow and below freezing temperatures can occur on any day of the year, by its location at elevations averaging between (1400–) 2000 and 4500 (–5300) meters above sea level (m a.s.l.), and by one of the richest floras in the temperate Northern Hemisphere. The formation and evolution of the plant diversity in the area and uplift of the Qinghai–Tibet Plateau (QTP) were synchronous (Sun, 2002; Sun and Li, 2003). During its geological history, as part of the QTP, the area was still below the Tethys Sea or on the coast of the Tethys in the late Cretaceous (Zhang, 2012). In the early Tertiary, the collision between the Indian plate and Eurasia led to the retreat of the Tethys Sea and the QTP entered an era of land evolution (Zheng, 2013). From the Eocene to the Oligocene, the Tethys gradually narrowed as the Indian plate continued its northward movement. By the end of the Oligocene, the sea had since dropped out and the main body of the QTP was transformed into a land environment (Zhang, 2012). The Hengduan Mountains (the eastern edge of the QTP) had formed as north–south asymmetric wavy creases and large intervening fault zones (gorges). The geological evolution of the HDM coincided with the uplift process and was synchronous with the evolution of the QTP (Zhang, 2012). Therefore, the flora of the HDM began its development and evolution with the retreat of the Tethys Sea and appearance of land in the early Paleogene. Along with the uplift of the QTP and the evolution of the geological environment, the flora underwent a change from a thermophilic flora in the early Paleogene to a xerophytic and temperate to alpine flora by the mid-to late Neogene (Sun, 2002). Additionally, many plant groups migrated into the region from various sources resulting in a very rich and complex flora, which the HDM has preserved in many ways to the present. After the Neogene, global temperatures decreased, resulting in the Quaternary glacial periods. Plant diversity and the flora of the Arctic-Tertiary in many parts of the Northern Hemisphere, such as in Europe and N America, suffered devastating destruction and a large number of species became extinct, resulting in the extant flora in these regions becoming poor and reduced to fragments of their former richness (Kubitzki and Krutzsch, 1996; Tiffney and Manchester, 2001). It is therefore difficult for us to study the origin, differentiation and formation mechanisms of plant diversity of the earth in those areas. The complex and diverse habitats in the HDM, however, were relatively little affected by climatic and geological processes. They therefore provided optimal conditions for evolution and diversification to take place while at the same time maintaining refugia where plants could ride out the glacial cycles. The synchronous evolution of plant diversity and geological events provide a relatively integrated framework for interpreting the evolutionary history of the flora. Not only are there some ancient remnants or relics, but also, more prominently, a large number of clades that experienced rapid radiations, forming relatively complete lineages and many young species and infraspecific taxa. The HDM is therefore not only a natural historical ‘museum’ that has preserved plant diversity since the Cenozoic era, but also a ‘cradle’ where many new species were born and flourished. The preservation of the old while giving rise to the new has resulted in the incredible plant diversity that has made the HDM the hotspot that it is today and the key area and natural laboratory for the study of the origins, evolution and dispersal of that diversity.

2. Plant diversity

The extent of the HDM hotspot as we define it is slightly larger than Li's definition (Li, 1989). The approximate geographical extent is similar to that of the Sino-Himalayan Subkingdom (Wu and Wu, 1996), an area of about 500 thousand square kilometers. Within the area, the most significant feature is the extreme species diversity, with estimates of 12,800 species accounting for about 42.5% of the total number of Chinese seed plants, belonging to at least 1767 genera (about 58.2% of all Chinese genera), 202 families (about 73.4% of all Chinese families), of which there are at least 3300 endemic species and 89 endemic genera. Of particular interest is the occurrence of one near endemic family, Circaeasteraceae (two genera, *Circaeaster* and *Kingdonia*) and the monotypic *Acanthochlamys*, which was at one time considered to be in its own family Acanthochlamydaceae (Wu, 1988), but is now considered to be a basal member of the predominantly Southern Hemisphere family Velloziaceae (Mello-Silva et al., 2011). Additionally, there are at least 16 genera with over 100 species, most of them formed in this region of dramatic differentiation. Xu et al. (2014a, b) calculated that the plant diversity in subnival (alpine) zone of the HDM numbers 942 species of seed plants in 168 genera and 48 families, which is two to three times the number of seed plant species than in any other known alpine belt region. Another notable feature is the complex diversity of the floristic elements. The west side of the region is adjacent to central Asia and a Mediterranean flora

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characterized mainly by a Mediterranean climate; the eastern part of the region is the Sino-Japanese Floristic Region characterized by a monsoon climate. To the north the flora links to the high latitude and arctic floras via the QTP and the high mountains of northern Asia. Southward through the valleys and lowlands the flora extends to the Indochina Peninsula and the Indo-Malaysian region.

3. Brief summary of surveys and progress in the study of plant diversity in the Hengduan Mountains

3.1. *A brief history of exploration on plant diversity*

The first western explorers, and essentially the first naturalists, in the area were French missionaries who traveled to the remotest regions of China with the main purpose of converting the locals to Christianity (Kilpatrick, 2014). Most, however, had also been trained in the natural sciences and were encouraged to collect and send back to Paris specimens of plants and animals. Among the most notable of these missionaries were Père Jean-Pierre-Armand David (1826–1900), the first westerner to send skins of the panda to Europe (in addition to many plant specimens), Père Jean Marie Delavay (1834–1895), who explored in western Yunnan and sent back thousands of plants specimens, Père Jean-Théodore Monbeig (1875–1914), who collected in southeast Xizang, and Jean André Soulie (1858–1905), who collected in western Sichuan and southeast Xizang. The rich and varied collections of so many unusual plants arriving in Paris, then distributed to other herbaria in Europe, eventually prompted the nurseries and scientific institutions of the day to send their own collectors to gather seeds and plants for the garden trade and for science (Kilpatrick, 2014).

Joseph Rock (1885–1969), George Forest (1873–1932), H. Handel-Mazzetti (1862–1940) and Ernest H. Wilson (1876–1930) visited parts of the area, and Kingdon-Ward (1885–1958) touched its southern and western edges (Bao et al., 1998). From the 1920s to the 1940s, several Chinese botanists, T. T. Yu (1908–1986), R. C. Ching (1898–1986), K. M. Feng (1917–2007), C. W. Wang (1913–1987), W. P. Fang (1899–1983), and H. T. Tsai (1901–1981), made extensive collections along the southern and eastern edges of the HDM region (Bao et al., 1998), but no comprehensive study of the entire region was undertaken until the Chinese Academy of Sciences organized a major multidisciplinary expedition to the area between 1973 and 1982. The findings from the expedition were to be published in 39 volumes and 48 monographs (Wang et al., 1993). The volumes of most interest to botanists are Vascular Plants of the Hengduan Mountains, volumes 1 and 2 (Wang et al., 1993, 1994). Those two volumes, unfortunately not widely available, provide detailed documentation of the plants collected in the area, not only those gathered on Chinese expeditions, but also specimens made by earlier Chinese and western collectors.

Recent comprehensive in-depth investigations and collections were carried out over a 15-year period in a joint Sino-US project to inventory the HDM region. Collections by David Boufford and Hang Sun and their colleagues, in collaboration with Chinese botanists and mycologists Shangwu Liu, Kaipu Yin, Yu Jia, Zhuliang Yang, collected around 30,000 numbers of specimens with about 150,000 duplicates. Details for these specimens, with complete collection data, GPS coordinates, vouchered photographs of many of the plants in their natural environment are available online at http://hengduan.huh.harvard.edu/fieldnotes.

The Kunming Institute of Botany – California Academy of Sciences expeditions, co-organized primarily by Heng Li, Peter Fritsch and Bruce Bartholomew, conducted over several years in the Gaoligong Shan and Dulong Jiang regions of western Yunnan, also resulted in thousands of additional specimens. These, too, are cited on the Hengduan Biodiversity website at http://hengduan.huh.harvard.edu/fieldnotes.

3.2. *Distribution and regionalization*

Wu and Wu (1996) and Sun (2013) divided the HDM into a Sino-Himalayan Subkingdom as a region, including most parts of the Yunnan-Xikang (Sikang) Province of Takhtajan (1986). As mentioned earlier, here we define a more extensive HDM, extending west to the eastern edge of Himalayan region (Sun, 2013) and including part of the Eastern Himalayan Region as defined by Takhtajan (1986). The scope is comparable to that of Li and Li (1993), who divided the HDM into three subregions, NW Yunnan–SW Sichuan Subregion, NW Sichuan–SW Gansu–SE Qinghai Subregion and SE Tibet Subregion. Sun (2013) further divided the HDM region into four subregions, the Three Rivers Gorges, South HDM, North HDM and the Taohe-Minshan Subregion.

Zhang et al. (2016) studied the floristic regionalization of the QTP using quantitative methods. They placed the HDM and the E Himalaya regions into a Sino-Himalayan Subkingdom, in which the HDM was further divided into southern HDM and northern HDM regions. In all of these divisions, the South HDM or NW Yunnan–SW Sichuan Subregion has the greatest number of endemic species.

Zhang et al. (2009a) analyzed species richness by latitude in the HDM. They found that the region south of 29° N latitude comprises only 40% of the total area of the HDM, but contains more than 83% of the species. Sixty percent of the endemic species and tree species have their distribution only in the southern area. Mao et al. (2013), who analyzed the abundance of vascular plants on the QTP, also pointed out that the highest species richness is concentrated in the southern and eastern parts of the plateau. Their scope was basically equivalent to that of Zhang et al. (2016). It is clear that the southern HDM forms the core area of plant diversity. On a vertical gradient, Zhang et al. (2009b) analyzed the 19 largest genera and the endemic genera in the HDM. The results showed those genera to be unimodal and to peak in diversity at similar elevations, with the highest species richness concentrated in the range between 3000 and 4000 m a.s.l. Li et al. (2014b), in analyzing variation in species phylogenetic diversity along an elevational gradient, found that the distribution of species mainly reflects competition at lower elevations, while the distribution of species at high altitude is mainly due to environmental filtering and rapid differentiation. They (Li et al., 2014b) also found that the phylogenetic structure tended towards overdispersal in the southern HDM and phylogenetic clustering in the northern HDM because of more favorable climatic conditions, such as higher mean annual temperature and greater mean annual rainfall, in the southern HDM (Li and Sun, 2017).

3.3. *Origins and evolution*

The history of the formation of plant diversity in the HDM has three main origins, Laurasia, Tethys and Gondwana (Li and Li, 1993). The greatest composition is derived from Laurasia. The vast subalpine coniferous forests and deciduous broadleaved forests in the HDM are descendants of the Arctic-Tertiary Geoflora, which appeared in the HDM mostly after the Miocene (Tao et al., 2000). Biogeographic studies of taxa such as *Saxifraga*, *Salix*, *Rhododendron*, *Deutzia*, *Maianthemum*, *Meehania*, *Astilbe*, *Diapensia* and many others also found that they migrated southward to the region during the global temperature declines in the Miocene (Chen et al., 2010; Deng et al., 2015; Ebersbach et al., 2017; Hou et al., 2016; Kim et al., 2015; Meng et al., 2008; Zhu et al., 2013).

Tethys elements are also significant. Some typical Tethyan elements, such as Mediterranean and western to central Asian groups, occur mainly in the arid areas, such as in Xinjiang, but about 10% of the taxa can be found in the HDM (Wu, 1988). There are still many Tethyan descendants or relics, such as *Eremurus*, *Colutea* and *Salweenia* in the dry valleys. Many groups such as *Helleborus* (Sun et al., 2001), *Pistacia* (Xie et al., 2014), Hyoscyameae and *Mandragora* (Tu et al., 2010) have a discontinuous distribution due to the uplift of the QTP. Some taxa such as *Solms-laubachia*, *Incarvillea*, *Myricaria* (although Zhang et al. (2014) suggested that the genus could have originated in the Himalaya) and the tribe Peracarpeae (Campanulaceae) (Chen et al., 2005; Wang et al., 2009b; Yue et al., 2009; Zhou et al., 2012) originated in the Tethys region, but formed differentiation centers or centers of endemism in the HDM.

The Gondwanan elements are few, but some genera are of significance. For instance, *Paliurus* perhaps originated in India in the late Cretaceous, evolved in the Northern Hemisphere and ultimately became disjunct between the Mediterranean and E Asia in the Miocene (Chen et al., 2017a). *Acanthochlamys* had a different Gondwanan origin. It is the basal group of Velloziaceae, a family distributed in the Southern Hemisphere (S America and Africa) (Wu, 1988; Mello-Silva et al., 2011). It was a member of the flora to the south of the Tethys or in northern Gondwana, but is now a relic in the valleys of the Jinsha Jiang and its tributaries. *Formania* (Asteraceae), also endemic to the dry valleys of the Three Rivers region, may also be Gondwanan in origin. Hyoscyameae are typical Tethyan elements, but their ancestor originated in South America, then supposedly dispersed over long distances to the Tethys region in the Miocene and further differentiated as elements of the Sino-Himalayan flora during the uplift of the QTP (Tu et al., 2010). Hyoscyameae appear to be Tethyan, but with Gondwanan affinities.

There are many groups, such as *Crawfurdia*, *Metagentiana*, *Tripterospermum* (Chen et al., 2005; Matuszak et al., 2015), *Lagotis* (Li et al., 2014a), *Rhodiola* (Zhang et al., 2014), *Stellera* (Zhang et al., 2010), *Leontopodium* (Blöch et al., 2010; Safer et al., 2011), *Androsace* (Wang et al., 2004), *Koenigia* (Fan et al., 2013a), *Anaphalis* (Nie et al., 2013b), *Gentiana* sect. *Cruciata* (Zhang et al., 2009c), *Soroseris*–*Stebbinsia*–*Syncalathium* (Zhang et al., 2011a), *Cyananthus* (Zhou et al., 2013), *Dolomiaea*, *Diplazoptilon* and *Xanthopappus* (Wang et al., 2007), *Gentiana* (Favre et al., 2016) and *Oxyria digyna* (Wang et al., 2016), that originated in situ or formed a modern center of distribution, such as in *Saxifraga*, *Rhododendron*, *Delphinium* and *Aconitum*, during the uplift of QTP (Ebersbach et al., 2017; Jabbour and Renner, 2012; Milne et al., 2010), then spread out from the plateau.

In addition, about 20% of the flora in the HDM comprises tropical elements, which occur mainly in the south and at the edge of low elevation areas (Wu, 1988) where subtropical evergreen broadleaved forests occur. They may be descendants of the thermophilic flora of the northern warm temperate belt of the Tethys in the early Paleogene and are a northern extension of the tropical and subtropical flora of Southeast Asia and Indo-Malaysia. Many tropical floristic elements extend to the hinterlands in the valleys, and even reach elevations up to 3000 m a.s.l., as in such genera as *Acacia*, *Terminalia* and *Paederia* (Nie et al., 2013a). Some alpine elements such as *Roscoea* (Zingiberaceae) formed differentiation centers from tropical ancestors during the QTP uplift and have typical tropical affinities (Zhao et al., 2016).

Liu et al. (2014) have suggested that most of the endemic genera have formed in situ while the endemic species and endemic clades rich in species mainly formed by radiation and differentiation and are associated with important geological events from the Miocene to the Pliocene. Wen et al. (2014) pointed out that allopatric differentiation by isolation, as well as plateau uplift and other geological events, were important factors in the formation of plant diversity in the region. In addition, climatic fluctuations since the Cenozoic, such as the formation of a monsoon climate and the Quaternary glaciations, as well as the unique north–south trending parallel mountain valleys and numerous, small, complex ecological niches, promote both speciation and north–south exchanges, but also strengthen east–west isolation. All of these factors are external driving forces that promote the rapid differentiation of species. Xing and Ree (2017) suggested that the rate of species differentiation in the Hengduan Mountains area increased significantly since 8 million years ago (Mya) to exceed the contribution from species migration to plant diversity in the HDM region. The rapid rate of species differentiation also coincides with the time of rapid uplift of the HDM and also supports the view that the rapid rise of the HDM in the Late Miocene (11.6–5.3 Mya) promoted the increase in biodiversity.

Hybridization may also have been an important mechanism for the formation of plant diversity in the region due to the frequent contact of recently diverged species and incomplete reproductive isolation, as in the complex of *Rhododendron delavayi*–*Rh. irroratum*, *Rh. decorum*, *Rh. cyanocarpum* (Ma et al., 2010a,b; Milne et al., 2010; Zha et al., 2010), *Buddleja crispa*–*B. officinalis* (Liao et al., 2015), *Primula beesiana*–*P. bulleyana* (Ma et al., 2014), *Ligularia* (Yu et al., 2014) and *Meconopsis* (Yang et al., 2012). It is generally believed that hybridization triggers speciation through both allopolyploid and homoploid speciation, but so far in the HDM there are no such reports. Confirmed hybrid speciation is still at the diploid level, as in *Pinus densata* (Wang and Szmidt, 2001), *Picea purpurea* (Sun et al., 2014), *Ostryopsis intermedia* (Lu et al., 2014), and *Hippophae goniocarpa* (Wang et al., 2008).

In recent years, phylogeographic studies, as well as investigations into the climate and environmental changes in the region, have provided a new perspective on the differentiation of lineages and the history of population changes (Qiu et al., 2011). Until now, studies on about 90 species in the HDM region can be summed up in three ways.

(1) The HDM region was an important refuge during the Quaternary glaciations.

Phylogeographic analysis of *Stellera chamaejasme* (Zhang et al., 2010), *Picea crassifolia* (Meng et al., 2007), *Metagentiana striata* (Chen et al., 2008), *Pedicularis longiflora* (Yang et al., 2008), *Tsuga dumosa* (Cun and Wang, 2015), eight closely related species of *Cupressus* (Xu et al., 2010) and *Sinopodophyllum hexandrum* (Li et al., 2011) showed that the HDM (the eastern margin of the QTP) was a refugium during glacial periods, after which the populations expanded their ranges beyond the refuge, or even beyond the HDM. In other situations, the populations remained in refugia during glacial periods without large-scale population expansion or shrinkage during inter- and postglacial periods. For instance *Eriophyton wallichii*, *Thalictrum squamiferum*, *Paraquilegia microphylla*, *Chionocharis hookeri* are endemic to the subnival habitat in the ‘sky island system’ of the HDM. Phylogeographic analyses indicate that these four subnival species show significant population genetic structure with most (cpDNA/nDNA) haplotypes being restricted to a single site or to neighboring populations. The studies also showed that most of these high elevation populations were likely stable and restricted to small mountain areas isolated from each other during glacial and postglacial periods. Such evidence demonstrates that the Quaternary glaciations had little or no influence on the survival and large scale geographic structure of alpine/subnival plants in the HDM (Luo et al., 2016), similar examples are also seen in other subnival species such as *Rhodiola alsia*, the alpine grassland species *Aconitum gymnandrum*, a coniferous species *Juniperus tibetica*, and in *Potentilla glabra*/*P. fruticosa* in forests and alpine scrub (Gao et al., 2012; Li et al., 2010; Opgenoorth et al., 2010; Shimono et al., 2010; Wang et al., 2009a).

(2) Molecular studies provide evidence for establishing floristic geographic boundaries within the HDM.

Evidence from phylogeographic studies of *Dysosma versipellis* (Qiu et al., 2009) and *Sophora davidii* have supported recognition of the 'Tanaka-Kaiyong Line' as the phytogeographic boundary between the Sino-Himalayan Subkingdom and Sino-Japanese Subkingdom. Such studies have provided new evidence for the division of the flora in the HDM region, with climatic oscillations and vegetation changes resulting from the last glaciation as the main external factors leading to the formation of the boundaries (Fan et al., 2013b). Phylogeographic analyses of *Sinopodophyllum hexandrum* (Li et al., 2011) and *Marmoritis complanatum* (Luo et al., unpublished data) demonstrated the 'Mekong-Salween Divide' to be a floristic boundary. Phylogeographic studies therefore have great potential for revealing floristic boundaries, regionalization and the finer details of the history of plant distributions.

(3) Confirmed changes in the physical environment, such as the evolution of drainage systems in the HDM.

Phylogeographic studies on characteristic taxa in the valleys reveal the reorganization of rivers and water systems by river separation and capture events. One example was found in *Terminalia franchetii*, a shrub or small tree endemic to the river valleys of the HDM. Its modern phylogeographic structure corresponds to the geography of past drainage systems in the region. Divergence times for the haplotype lineages in the modern river and water systems mostly dating to the mid-to late Pleistocene agree with previous time estimates of drainage rearrangements in the HDM (Zhang et al., 2011b; Zhang and Sun, 2011). The phylogeography of *Buddleja crispa* indicates that currently discontinuous drainage systems were historically linked. The population phylogeographic structure and genetic variation perfectly reflect the putative Paleo Red River drainage pattern (Yue et al., 2012).

In summary, whether in biogeography or phylogeography or other fields, studies of the diversity of plants in the HDM region have made good progress, so that we can gradually develop an in-depth understanding of the formation and evolution of plant diversity in the region. Comprehensive research in the region, however, is still rare. Multidisciplinary studies using multiple methods and multi-scale and meta-analysis should be encouraged (Favre et al., 2015).

4. A brief introduction to the present issue

Although the above review summarizes the progress in the study of plant diversity in the region, on the whole, it is far from complete. More taxa require study, and many further types of studies are needed. The present issue contains nine papers related to biogeography, pollination biology, hybridization, seed biology and cytology, species biology and climatic oscillations in the Quaternary.

Hauenschild et al. (2017) identified two independent processes to show how *Allium* became diverse in the QTP region and suggested that global climate oscillations in the Quaternary were major contributors to increased speciation rates in three clades of *Allium* and supported the 'mountain-geo-biodiversity hypothesis.'

Peng et al. (2017) first reported seed dormancy and germination traits in two species of *Rheum* and found that they shared similar seed dormancy types and germination patterns, indicating that they share the same germination strategy adapted to alpine environments. Soil water conditions appear to be the crucial factor in determining germination and seedling establishment, which may explain how these species have survived in dryish and wet habitats, respectively.

Niu et al. (2017) studied the function of staminate and hermaphroditic flowers and size-dependent gender diphasy in *Lloydia oxycarpa* (Liliaceae) and found sex expression to be related to bulb size and dry weight, with larger individuals producing hermaphroditic flowers and smaller individuals producing staminate flowers, suggesting that *L. oxycarpa* cannot be regarded as an androdioecious plant, but instead represents a rare case of size-dependent gender diphasy.

Zhang et al. (2017) examined natural selection of floral traits via female fitness in *Caltha scaposa*, an alpine perennial with a UV bullseye. They found statistically significant selection was for the size of the UV bullseye, size of the sepals and UV proportion in hand-pollinated flowers and interactions with pollinators related only to flower diameter, suggesting that floral traits subjected to selection might be driven by multiple selective agents, since *C. scaposa* is visited by different kinds of pollinators.

Ning et al. (2017) studied hybridization in *Ligularia* (Asteraceae) to further verify natural hybridization between *L. vellerea* and *L. subspicata*. They found that hybridization between *L. vellerea* and *L. subspicata* was bidirectional.

Li et al. (2017) investigated the ecology of *Fritillaria cirrhosa* under the influence of human disturbance, biotic species interactions and climatic conditions. They found that the abundance of *F. cirrhosa* and the depth of the underground bulbs showed significant linear increase with distance from main roads. The diameter/height of fruits and diameter/height of fruits/bulbs showed significantly different responses to human disturbance. The community associates, climate and spatial conditions can explain 58%, 22% and 27%, respectively, of the variance in the abundance of *F. cirrhosa*.

Chen et al. (2017b) summarized the reproductive strategies of alpine cushion species and discussed the importance for understanding the stability and maintenance of cushion communities in severe alpine environments and proposed directions for future work on the reproduction of cushion plants and their significance in alpine ecosystems.

Sun et al. (2017) reported on the chromosome numbers of 19 species (21 populations) of Asteraceae in the Hengduan Mountains. Among them, 14 species were investigated for the first time. Statistics on the chromosome number of 69 taxa in related genera from published reports found that ploidy levels and karyotype asymmetry index were not associated with the distribution of the species of Asteraceae in the region.

Xu et al. (2017) described and illustrated a new species, *Primula pengzhouensis* (Primulaceae), from the Hengduan Mountains (central Sichuan).

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