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Biogeography of Shangri-la flora in southwestern China

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Abstract

Shangri-la region of southwestern China is within the Hengduan Mountains biodiversity hotspot and is exceptional in floral diversity. Based on intensive field investigations and herbarium specimens, 6807 species of native seed plants from 1297 genera and 166 families were recognized. The flora is dominated by families and genera with cosmopolitan and north temperate distributions, including Apiaceae, Asteraceae, Ericaceae, Fabaceae, Gentianaceae, Lamiaceae, and the genera *Pedicularis*, *Rhododendron*, and *Salix*, which contribute up to 73.15 % of the total number of species, but only make up a small portion of the total number of families and genera. Families and genera with fewer species more commonly have tropical distributions, while East Asian and Chinese endemic families and genera are mostly monotypic and oligotypic, and contribute little to the floristic diversity of the region. It is revealed that the flora of Shangri-la might have evolved through rapid speciation mainly from families and genera of cosmopolitan and north temperate distributions with the uplift of the Himalayas and climatic oscillations after the late Tertiary. The macroevolution of the flora in the Shangri-la region interpreted by floristic patterns is well supported by phylogeographic studies on plant taxa in Hengduan-Qinghai-Tibet Plateau regions.

Keywords: Biogeography; floristic composition; geographical elements; Shangri-la; southwestern China

Introduction

Shangri-la region is situated in the northwestern corner of China's Yunnan Province (27°10'–28°27' N and 98°53'–99°42' E) (Figure 1). It lies within the Hengduan Mountains (Li 1987), which is one of the world's biodiversity hotspots (Boufford & Dijk 2000; Le *et al.* 2007). Shangri-la is one of the most biodiverse regions in China and is of global conservation priority (Myers *et al.* 2000).

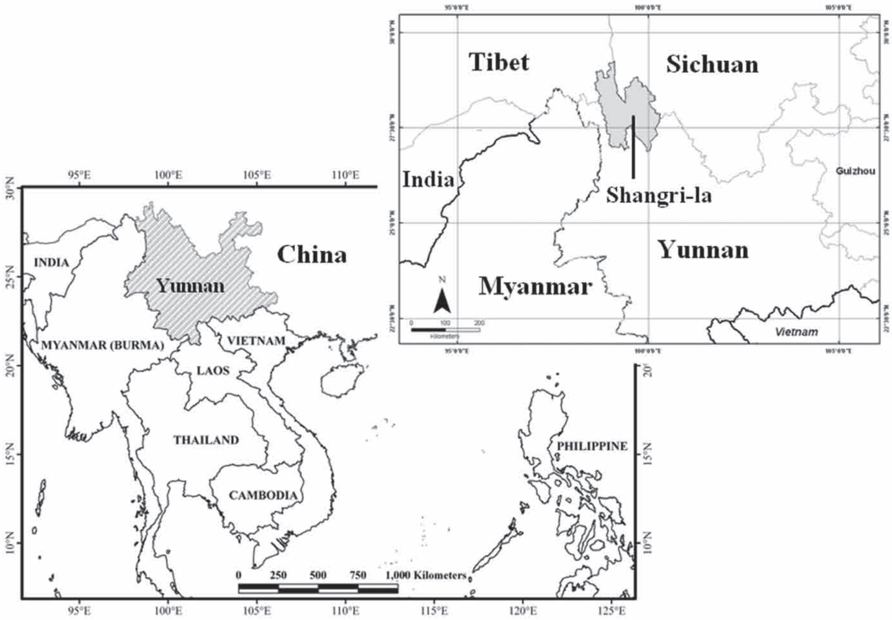

FIGURE 1. Map showing the study area, the Shangri-la region in SW China.

Shangri-la region has a very complex geology (Li 1987). The region was in a sutural zone between Gondwana and Laurasia (Jin 2002; Metcalfe 2006) and its topography shaped by the collision between the Indian and Eurasian plates and the uplift of the Himalayas (Office of Yunnan World Heritage management Committee 2002). The region underwent a more recent and rapid uplift with the Himalayas after the Pleistocene (Shi *et al.* 1999). Shangri-la region has an extremely diverse topography with altitudes from ca. 2000 m, at the bottoms of valleys, to 6740 m at the summit of the Meili Snow Mountain. Evidently, climatic variation in the region corresponds to altitude, with subtropical dry climates in valleys, and cold temperate climates in alpine areas.

Shangri-la region is extremely rich in biodiversity and is of great interest to botanists. The region holds more than 20% of the total sum of plant species in China, although it covers less than 0.2% of the country's territory. The region contains various habitats and vegetation types: subtropical evergreen broad-leaved forest, subtropical semi-humid evergreen broad-leaved forest, montane humid evergreen broad-leaved forest, sclerophyllous forest, warm temperate coniferous forest (such as *Pinus yunnanensis* forest), temperate deciduous broad-leaved forest, temperate coniferous forest (such as *Tsuga dumosa* forest and *Pinus densata* forest), cold temperate coniferous forest (such as *Picea* forest, *Abies* forest and *Larix* forest), microphyllous scrubs in warm and dry valleys, alpine meadows, and scrubs (Zhu 2009). Shangri-la is not only very rich in species diversity, but also in endemic species (Le *et al.* 2007). Understanding of the origin and evolution of the Shangri-la flora is extremely important for understanding the plant geography of Hengduan Mountains as a whole.

Shangri-la flora is composed largely of temperate elements and was suggested to have evolved with the uplift of the Himalayas (Zhu 2012). Studies on palaeobotany suggested that the region had a temperate and subtropical flora during the Tertiary (Mehrotra *et al.* 2005). Historic events such as the uplift of the Himalayas and climatic oscillations in the Quaternary period have affected the evolution of the flora of the Hengduan-Qinghai-Tibet Plateau. The divergence, radiation, evolution, and speciation of plants in these regions are considered to be correlated with the uplift of the Plateau (Chen *et al.* 2005; Liu *et al.* 2006; Yuan *et al*. 2008; Wang *et al*. 2009; Cun & Wang 2010; Zhang *et al.* 2011; Chen *et al.* 2012; Yang *et al.* 2012).

Phylogeographic studies revealed that divergence and speciation of plants in the Hengduan-Qinghai-Tibet Plateau are closely related to the uplift of Himalayas and many plants on these regions colonized from other areas or are recently derived endemic species (Liu *et al.* 2006; Ran *et al.* 2006; Yang *et al.* 2008). It is of interest to understand whether these phylogeographic patterns correspond to the macro-evolutionary patterns of regional flora. This paper aims to (i) analyze the floristic patterns and geographical elements of Shangri-la region; (ii) examine the origin and evolution of Shangri-la flora with the uplift of Himalayas; and, (iii) discuss the relationship between phylogeographic patterns and floristic evolution of the Hengduan Mountains.

Materials and Methods

Shangri-la region lies at the centre of the Hengduan Mountains and covers a total area of 23,870 km^2. During the years 2004–2009, the Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences conducted intensive plant inventories in the region. A complete list of native seed plant species was obtained based on inventory data, a recently completed Flora of Yunnan (Wu 1977–2006), a database of seed plants from KUN (herbarium of Kunming Institute of Botany, Chinese Academy of Sciences), and data from Wu and Ding (1999). The circumscriptions of families followed APG III (Chase & Reveal 2009; THE ANGIOSPERM PHYLOGENY GROUP 2009), and species followed the nomenclature of w^{3}TROPICOS (http://mobot.mobot.org/W3T/Search/vast.html). Patterns of seed plant distribution were quantified at the generic and the family levels following Wu (1991) and Wu *et al.* (2003, 2006). The biogeographical affinity of the flora is studied in view of geographical elements at family and generic levels. In order to discuss the relationship of the Shangri-la flora to floras of Southern and Southeast China, three representative regional floras from southern-west, southern-centre and Southeast China respectively at almost the same latitude as the Shangri-la region are selected to make comparison. The macro-evolution of the flora of the Shangri-la is discussed referring phylogeographical patterns of plants in the plateau.

Results

Floristic composition

A total of 6807 native seed plant species, including 270 subspecies and varieties, from 1297 genera and 166 families were recognized from the Shangri-la region. Families with the highest species richness include Asteraceae (518 species), Poaceae (395), Rosaceae (358), Orchidaceae (323), Fabaceae (299), Ericaceae (284), Ranunculaceae (238) and Lamiaceae (220) (Table 1). These families are also the most species rich families worldwide.

TABLE 1. Dominant families and genera in species richness with their distribution.

Family ranking by their species richness	No. of species in the flora	Distribution type*	Genera ranking by their species richness	No. of species in the flora	Distribution type*
Asteraceae	518	1	*Rhododendron* L.	183	4
Poaceae	395	1	*Pedicularis* L.	119	4
Rosaceae	358	1	*Salix* L.	105	4
Orchidaceae	323	1	*Carex* L.	93	1
Fabaceae	299	1	*Primula* L.	93	4
Ericaceae	284	1	*Gentiana* L.	90	4
Ranunculaceae	238	1	*Saxifraga* L.	86	4
Lamiaceae	220	1	*Saussurea* DC.	71	5
Apiaceae	198	1	*Polygonum* L.	65	1
Orobanchaceae	181	1	*Rubus* L.	64	1
Cyperaceae	176	1	*Corydalis* DC.	59	4
Primulaceae	146	1	*Aconitum* L.	56	4
Gentianaceae	145	1	*Berberis* L.	56	4
Saxifragaceae	124	1	*Acer* L.	54	4
Salicaceae	121	4	*Astragalus* L.	52	1
Liliaceae	113	4	*Ligularia* Cass.	50	5
Rubiaceae	111	1	*Ilex* L.	46	2
Caryophyllaceae	110	1	*Juncus* L.	43	1
Polygonaceae	99	1	*Poa* L.	41	1
Urticaceae	99	2	*Cotoneaster* Medik.	39	4
Brassicaceae	94	1	*Delphinium* L.	39	4
Caprifoliaceae	85	4	*Silene* L.	39	4
Papaveraceae	83	4	*Potentilla* L.	38	4
Campanulaceae	78	1	*Arenaria* L.	37	4
Araliaceae	71	3	*Arisaema* Mart.	37	4
Berberidaceae	69	4	*Aster* L.	36	4
Lauraceae	65	2	*Euonymus* L.	36	1
Crassulaceae	64	1	*Sorbus* L.	36	4
Gesneriaceae	61	3	*Clematis* L.	35	1
Sapindaceae	56	2	*Indigofera* L.	35	2

*Distribution type: 1: cosmopolitan, 2: pantropic, 3: tropical Asia and tropical America disjunct, 4: north temperate, 5: old world temperate.

Our inventory included 18 families with more than 100 species each, and 16 families with 50–99 species, most of which are also large species-rich families throughout the world. There were 55 families with 10–49 species, and 78 families with 1–9 species. However, the 34 families with 50 species or more (comprising a total of 4979 species), contribute up to 73.15 % of the total number of species, but only form ca. 20% of the total number of families.

There are 36 genera with more than 30 species, and these are also the most abundant genera: *Rhododendron* L.

(183 species), *Pedicularis* L. (119), *Salix* L. (105), *Carex* L. (93), *Primula* L. (93), *Gentiana* L. (90), *Saxifraga* L. (86), *Saussurea* DC. (71). There are 102 genera with 11–30 species and 147 genera with 6–10 species. There are 1013 genera with 1–5 species, which include 1907 species, contributing up to 27.9 % of the number of species, but forming 78% of the total number of genera. However, the 138 genera with more than 10 species include 3820 species, which is 56.02 % of the number of species, but only 10.63% of the number of genera in the flora.

Geographical elements

Eleven distribution types at family level are recognized from the flora of Shangri-la region: 1. Cosmopolitan; 2. Pantropic; 3. Tropical Asian and Tropical American disjunct; 4. Old World Tropic; 5. Tropical Asian to Tropical Australian; 6. Tropical Asian; 7. North Temperate; 8. East Asian and North American disjunct; 9. Old World Temperate; 10. East Asian and; 11. Chinese endemics.

Of the 166 families, tropical elements (types 2–6) in total are 75 families, contributing to 45.18% of the flora (Table 2). Among tropical elements, 57 families (or 34.34%) are pantropic distributions, including Acanthaceae, Anacardiaceae, Euphorbiaceae, Melastomataceae and Rutaceae; 11 families (6.63%) are tropical Asian and tropical American disjunct distributions, such as Actinidiaceae, Aquifoliaceae, Staphyleaceae. Families with cosmopolitan distributions make up 30.12% of the total number of families, and include Asteraceae, Apiaceae, Ericaceae, Fabaceae, Lamiaceae and Poaceae. Temperate elements (types 7–11) in total are 41 families, contributing to 24.69% of the flora. Among them, 24 families (14.46%) are north temperate distribution, including Betulaceae, Cornaceae, Coriariaceae, Geraniaceae and Hydrangeaceae; 9 families are East Asia and North America disjunct distributions, such as Magnoliaceae, Nyssaceae, Saururaceae, Schisandraceae, contributing to 5.42%.

TABLE 2. Geographical elements of seed plants at the family level in the flora of Shangri-la region.

Geographical elements at family level	Number of family	%*
1 **Cosmopolitan**	50	30.12
2 Pantropic	57	34.34
3 Tropical Asia and Tropical America disjunct	11	6.63
4 Old World Tropic	2	1.20
5 Tropical Asia to Tropical Australia	3	1.81
6 Tropical Asia	2	1.20
Tropical elements (types 2–6) in total	75	45.18
7 North Temperate	24	14.46
8 East Asia and North America disjunct	9	5.42
9 Old World Temperate	1	0.60
10 East Asia	6	3.61
11Endemic to China	1	0.60
Temperate elements (types 7–11) in total	41	24.69
Total number of families	166	100

*The number of families in each geographical element/ the number of families of all geographical elements times 100.

Fifteen distribution types at generic level are recognized from the flora (Table 3). Of the 1297 genera included in the inventory, temperate elements (types 8–15) contribute to 51.26%, and tropical elements (types 2–7) contribute to 42.87%. Among temperate genera, 16.19% have northern temperate distributions, and 14.26% have East Asian distributions. Other genera include those with old world temperate distributions (7.63 %), and East Asia and North American disjunct distributions (5.47 %). Among tropical genera, 14.80% have pantropic distributions, and 10.95% have tropical Asian distributions. There are 52 genera that are endemic or approximately endemic to China, including *Davidia* Baill. (which naturally occurs in Wei Xi county), *Dipelta* Maxim., *Ostryopsis* Decne., *Taiwania* Hayata.

Considering these geographical elements across families and genera, we might infer that families with high species richness (more than 50 species) predominantly have cosmopolitan and north temperate distributions, such as Apiaceae, Asteraceae, Ericaceae, Fabaceae and Lamiaceae, with a few having tropical distributions (Table1). However, families with 11–50 species all have pantropic distributions, such as Acanthaceae, Anacardiaceae, Asclepiadaceae, Theaceae. The families with 1–10 species are diverse in distribution, including 23 Pantropic families, 11 Northern temperate families, and 7 Tropical Asian and Tropical American disjunct distribution families, as well as 6 East Asian families, such as Cephalotaxaceae, Dipentodontaceae, Eupteleaceae, Stachyuraceae and Tetracentraceae (Wu *et al.* 2003).

TABLE 3 Geographical elements of seed plants at the generic level in the flora.

Geographical elements at generic level	Number of genera	%*
1 Cosmopolitan	**76**	**5.86**
2 Pantropic	192	14.80
3 Tropical Asia and Tropical America disjunct	31	2.39
4 Old World Tropic	81	6.25
5 Tropical Asia to Tropical Australia	64	4.93
6 Tropical Asia to Tropical Africa	46	3.55
7 Tropical Asia	142	10.95
Tropical elements (types 2–7) in total	**556**	**42.87**
8 North Temperate	210	16.19
9 East Asia and North America disjunct	71	5.47
10 Old World Temperate	99	7.63
11 Temperate Asia	18	1.39
12 Mediterranean, W Asia to C Asia	16	1.23
13 Center Asia	14	1.08
14 East Asia	185	14.26
15 Endemic to China	52	4.01
Temperate elements (types 8–15) in total	**665**	**51.26**
Total number of genera	1297	100.00

*The number of genera in each geographical element/ the number of genera of all geographical elements times 100.

Genera with high species richness (more than 30 species) predominantly have north temperate distributions (58.30 %), followed by cosmopolitan distributions (25.00 %) (Table 4). Among genera with 11–30 species, those with north temperate distributions still contribute the highest ratio (34.31%), followed by those with cosmopolitan (15.69%) and Pantropical distributions (14.71%). Genera with 1–5 species have very diverse distributions; those with East Asian distributions make up 15.5%, followed by pantropic (14.31%), tropical Asian (12.54%), and north temperate (12.04%) distributions. All 52 Chinese endemic genera included in the inventory are genera with 1–5 species (Table 4).

Comparison to regional floras at similar latitude in southern China

Three representative regional floras: Muchuan in southwestern China, Wulin Mts. in southern-centre China and Sanqingshan in southeastern China at almost the same latitude as the Shangri-la region are selected to make comparison (Figure 2). Muchuan is a county with a well-conserved national forest park. It has a record of 955 seed plant species of 127 families and 448 genera. Wulin Mts. is an important bio-diverse region and has a record of 3328 seed plant species of 174 families and 983 genera (Chen *et al.* 2002). Sanqingshan is a World Heritage site with well-conserved vegetation and biodiversity and has a record of 1772 seed plant species of 160 families and 785 genera (Peng *et al.* 2008).

The Shangri-la flora has similar compositions at the family (more than 89.94%) and the genera (more than 73%) levels, but differs at specific level to the three compared floras. The species similarities are low (32.51% and 29.23% respectively) between the flora of Shangri-la and those of Wulin Mts. and Sanqingshan (Table 5). The compositions of geographical elements at the family and generic levels reveal that all these compared floras are similar (Table 6, 7). The tropical elements make up 43.31%–48.26% at family level, 38.73%–42.87% at generic level, while the temperate elements contribute to 24.39%–28.36% at family level, 50.18%–52.87% at generic level.

The Shangri-la flora has similar dominant families except Ericaceae and Orobanchaceae, as those compared floras in southern China, while Pantropic Lauraceae and Urticaceae, and north temperate Caprifoliaceae and Fagaceae are among the dominant families in the floras of southern China (Table 8). The species-rich genera in the Shangri-la flora are mostly temperate and cosmopolitan, while many tropical genera are in the species-rich genera in the floras of southern China (Table 9).

TABLE 4 Geographical elements across genera in the flora.

Distribution type	No. of genera (more than 30 species)	%	No. of genera (11–30 species)	%	No. of genera (6–10 species)	%	No. of genera (1–5 species)	%
Cosmopolitan	9	25.00	16	15.69	8	5.44	43	4.24
Pantropic	3	8.33	15	14.71	29	19.73	145	14.31
Tropical Asia and Tropical America disjunct	0	0	3	2.94	5	3.40	23	2.27
Old World Tropic	0	0	1	0.98	9	6.12	71	7.01
Tropical Asia to Tropical Australia	0	0	5	4.90	5	3.40	54	5.33
Tropical Asia to Tropical Africa	1	2.78	1	0.98	4	2.72	40	3.95
Tropical Asia	0	0	4	3.92	11	7.48	127	12.54
North Temperate	21	58.30	35	34.31	33	22.45	122	12.04
East Asia and North America disjunct	0	0	6	5.88	10	6.80	55	5.43
Old World Temperate	2	5.56	8	7.84	9	6.12	80	7.90
Temperate Asia	0	0	1	0.98	2	1.36	15	1.48
Mediterranean, W Asia to C Asia	0	0	1	0.98	0	0.00	15	1.48
Center Asia	0	0	0	0.00	1	0.68	13	1.28
East Asia	0	0	6	5.88	21	14.29	157	15.50
Endemic to China	0	0	0	0.00	0	0.00	52	5.23
Total number of genera	36	100	102	100.00	147	100.00	1012	100.00

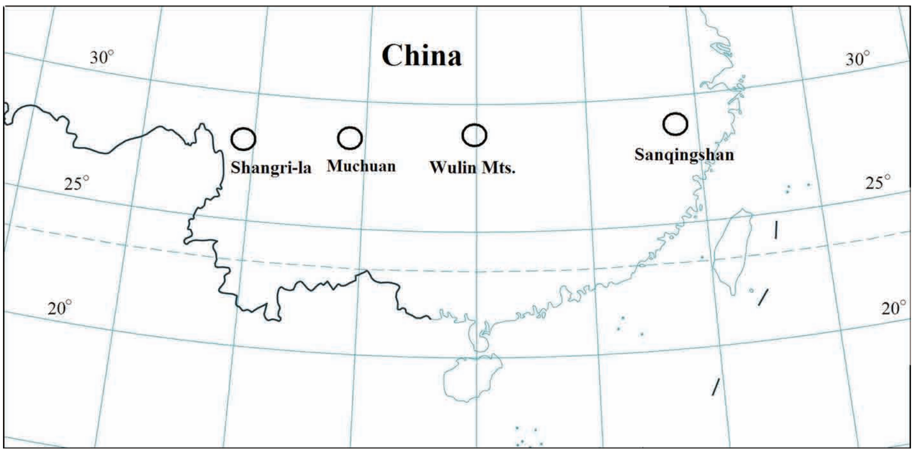

FIGURE 2. Map showing the locations of compared regional floras

TABLE 5. Comparison of floristic similarities at the family, generic and specific levels

Compared flora	Shangri-la 98°53'– 99°42' E, 27°10'– 28°27' N Similarity coefficient (%)	Muchuan 103°45′–103°59′E, 28°50′–29°5′N Similarity coefficient (%)	Wuling Mts. 107°02'–111°33'E, 27°28'– 33°05'N Similarity coefficient (%)	Sanqingshan 118°00'– 118°06E, 28°54'– 28°57'N Similarity coefficient (%)
Similarity coefficients at family level				
Shangri-la	100			
Muchuan	97.64			
Wuling Mts.	89.94	99.21	100	
Sanqingshan	90.63	94.49	97.5	100
Similarity coefficients at generic level				
Shangri-la	100			
Muchuan	88.33			
Wuling Mts.	77.01	91.75	100	
Sanqingshan	73.89	80.8	85.48	100
Similarity coefficients at specific level				
Shangri-la	100			
Muchuan	48.27			
Wuling Mts.	32.51	59.27	100	
Sanqingshan	29.23	36.86	59.88	100

*Similarity coefficient between A and B = the number of taxa shared by both A and B divided by the lowest number of taxa of A or B, multiplied by 100%

TABLE 6 Comparison of geographical elements of seed plants at the family level.

Compared regional floras	Shangri-la (166 families)	Muchuan (127 families)	Wuling Mts. (174 families)	Sanqingshan (160 families)
Geographical elements at family level	%*	%*	%*	%*
1 **Cosmopolitan**	30.12	**28.35**	**25.86**	27.5
2 Pantropic	34.34	31.5	34.47	35.01
3 Tropical Asia and Tropical America disjunct	6.63	7.09	7.47	6.88
4 Old World Tropic	1.20	2.36	2.3	1.88
5 Tropical Asia to Tropical Australia	1.81	1.57	2.3	2.5
6 Tropical Asia	1.20	0.79	1.72	1.89
Tropical elements (types 2–6) in total	**45.18**	**43.31**	**48.26**	**48.16**
7 North Temperate	14.46	18.91	15.5	15.01
8 East Asia and North America disjunct	5.42	3.94	5.17	5.63
9 Old World Temperate	0.60	0	0	0
10 East Asia	3.61	5.51	4.02	2.5
11Endemic to China	0.60	0	1.15	1.25
Temperate elements (types 7–11) in total	**24.69**	**28.36**	**25.84**	**24.39**
Total	100	100	100	100

*The number of family in each geographical element/ the number of family of all geographical elements times 100.

TABLE 7 Comparison of geographical elements of seed plants at the generic level.

Compared regional floras	Shangri-la (1297 genera)	Muchuan (488 genera)	Wuling Mts. (983 genera)	Sanqingshan (785 genera)
Geographical elements at generic level	%*	%*	%*	%*
1 Cosmopolitan	5.86	8.40	7.02	8.54
2 Pantropic	14.80	14.75	15.46	18.59
3 Tropical Asia and Tropical America disjunct	2.39	2.87	2.54	2.42
4 Old World Tropic	6.25	4.51	5.39	5.35
5 Tropical Asia to Tropical Australia	4.93	3.89	5.49	4.08
6 Tropical Asia to Tropical Africa	3.55	3.69	2.94	2.93
7 Tropical Asia	10.95	9.02	10.27	7.89
Tropical elements (types 2–7) in total	42.87	38.73	**42.09**	**41.26**
8 North Temperate	16.19	20.90	16.68	17.44
9 East Asia and North America disjunct	5.47	7.99	7.93	8.66
10 Old World Temperate	7.63	5.94	6.21	6.62
11 Temperate Asia	1.39	1.02	1.22	1.27
12 Mediterranean, W Asia to C Asia	1.23	0.41	0.72	0.77
13 Center Asia	1.08	0.00	0	0.13
14 East Asia	14.26	13.11	13.12	12.36
15 Endemic to China	4.01	3.48	4.98	2.93
Temperate elements (types 8–15) in total	**51.26**	**52.87**	**50.86**	**50.18**
Total	100.00	100.00	100.00	100.00

*The number of genera in each geographical element/ the number of genera of all geographical elements times 100.

TABLE 8 Dominant (top 10) families in these compared regional floras

Shangri-la flora	No. of species	DT*	Muchuan flora	No. of species	DT*	Wuling Mts. flora	No. of species	DT*	Sanqingshan flora	No. of species	DT*
Asteraceae	518	1	Asteraceae	56	1	Rosaceae	199	1	Poaceae	147	1
Poaceae	395	1	Rosaceae	43	1	Asteraceae	189	1	Asteraceae	104	1
Rosaceae	358	1	Lamiaceae	35	1	Fabaceae	148	1	Rosaceae	102	1
Orchidaceae	323	1	Poaceae	32	1	Poaceae	124	1	Fabaceae	83	1
Fabaceae	299	1	Fabaceae	29	1	Lamiaceae	121	1	Cyperaceae	75	1
Ericaceae	284	1	Caprifoliaceae	25	3	Orchidaceae	94	1	Lamiaceae	54	1
Ranunculaceae	238	1	Lauraceae	22	2	Lauraceae	82	2	Fagaceae	41	3
Lamiaceae	220	1	Ranunculaceae	22	1	Ranunculaceae	76	1	Lauraceae	40	2
Apiaceae	198	1	Orchidaceae	21	1	Caprifoliaceae	72	3	Brassicaceae	37	1
Orobanchaceae	181	1	Apiaceae	20	1	Urticaceae	60	2	Rubiaceae	37	1

*DT=Distribution type: 1: cosmopolitan, 2: pantropic, 3: north temperate.

TABLE 9 Species-rich genera in these compared regional floras

Shangri-la flora	No. of species	DT*	Muchuan flora	No. of species	DT*	Wuling Mts. flora	No. of species	DT*	Sanqingshan flora	No. of species	DT*
Rhododendron	183	temp	Rubus	11	cosm	Rubus	57	cosm	Carex	32	cosm
Pedicularis.	119	temp	Acer	9	temp	Ilex	47	trop	Rubus	28	cosm
Salix	105	temp	Lysimachia	9	cosm	Polygonum	41	cosm	Polygonum	26	cosm
Carex	93	cosm	Polygonum	9	cosm	Euonymus	32	cosm	Ilex	19	trop
Primula	93	temp	Rhododendron	8	temp	Acer	30	temp	Artemisia	18	cosm
Gentiana	90	temp	Symplocos	8	trop	Carex	29	cosm	Brassica	15	temp
Saxifraga	86	temp	Viburnum	7	temp	Viburnum	28	temp	Viola	15	cosm
Saussurea	71	temp	Ardisia	6	trop	Rhododendron	27	temp	Acer	12	temp
Polygonum	65	cosm	Hypericum	6	cosm	Smilax	27	trop	Euonymus	12	cosm
Rubus	64	cosm	Ilex	6	trop	Clematis	26	cosm	Eurya	12	trop
Corydalis	59	temp	Arisaema	5	temp	Symplocos	24	trop	Sedum	12	temp
Aconitum	56	temp	Cyclobalanopsis	5	trop:	Dioscorea	22	trop	Smilax	12	trop
Berberis	56	temp	Eurya	5	trop	Ficus	22	trop	Fimbristylis	11	trop
Acer	54	temp	Hydrangea	5	temp	Lysimachia	22	cosm	Lindera	11	temp
Astragalus	52	cosm	Lindera	5	temp	Zanthoxylum	22	trop	Lysimachia	11	cosm
Ligularia	50	temp	Lithocarpus	5	temp	Elatostema	21	temp	Castanopsis	10	trop
Ilex	46	trop	Litsea	5	trop	Rosa	19	temp	Clematis	10	cosm
Juncus	43	cosm	Lonicera	5	temp:	Artemisia	18	cosm	Ficus	10	trop
Poa	41	cosm	Magnolia	5	temp	Lindera	18	temp	Quercus	10	temp
Cotoneaster	39	temp	Primula	5	temp	Litsea	18	trop	Actinidia	9	temp

*DT=Distribution type: cosm= cosmopolitan, trop= tropical, temp= temperate; Generic name in bold are the dominant only in Shangri-la flora.

Discussion

Shangri-la region was included in the "Eastern Asiatic floristic region" delineated by Takhtajan (1978) in his floristic regionalization of the world. The large "Eastern Asiatic floristic region" is considered a major centre of higher plant evolution as it is especially rich in gymnosperms and primitive angiosperms (Wu & Wu 1996). However, East Asian and Chinese endemic families and genera make a minor contribution to the floristic richness of the Shangri-la flora, while large species-rich families and genera of cosmopolitan and north temperate distributions are well represented.

Comparisons of the Shangri-la flora and the other three representative regional floras at the same latitude in southern China reveal that they have high similarities at the family and genera levels, but low at specific level. The families Ericaceae and Orobanchaceae, which evolved mostly in mountain habitats, became dominant in the Shangri-la flora. Among the top 20 species-rich genera in the Shangri-la flora, 13 genera are the particular. All these compared floras should have originated from a common subtropical or temperate East Asian flora during the Tertiary. The uplift of the Himalayas since the late Tertiary caused a sudden uplift of the Shangri-la region and, resulted in the rapid speciation and diversification of plants.

Having undergone a rapid uplift with the Himalayas after the Pleistocene (Shi *et al.* 1999) Shangri-la region is evidently much younger in geological history than would be expected if the flora were of East Asian origin. Consequently, the flora is dominated by species-rich cosmopoltian and north temperate genera and families and is poor in primitive angiosperms. Therefore, the inclusion of the Shangri-la region in the "Eastern Asiatic floristic region" (Takhtajan 1978; Wu & Wu 1996) should be reconsidered.

Geographical elements of the Shangri-la flora at the specific level have not been documented. Of the 7000 species recorded from northwest Yunnan, 703 (13%) regional endemic species have been identified (Ma *et al.* 2007). Among large species-rich genera of cosmopolitan and north temperate distributions in the region, such as *Aconitum* L., *Gentiana, Pedicularis, Primula, Rhododendron, Saussurea* and *Saxifraga*, the regional endemic species contribute to more than 50%, as indicated by a study of selected taxa in the Hengduan Mountains (Zhang *et al*. 2009). This suggests that the dominant cosmopolitan and north temperate families and genera in Shangri-la region could have speciated rapidly. For example, *Solms-laubachia* Muschl. ex Diels, s.l. (Brassicaceae) is a genus of North Temperate distribution with 26 species in total, of which 11 species are endemic to the Hengduan Mountains region. A molecular phylogeny of *Solms-laubachia* s.l. suggested that the genus originated during the Pliocene in central Asia, and subsequently migrated eastward into the Hengduan Mountains, followed by rapid speciation in the region (Yue *et al*. 2009).

Phylogeographic studies have revealed that the uplift of the Himalayas resulted in divergence and speciation of a number of plant species. The *Ligularia* Cass.–*Cremanthodium* Benth.–*Parasenecio* W.W. Sm. and J. Small complex (Asteraceae) contains more than 200 species that are endemic to the Qinghai-Tibetan Plateau. The explosive radiation of the complex occurred mostly within the last 20 million years during the period of major uplift of the Qinghai-Tibetan Plateau (Liu *et al*. 2006). Significant increases in geological and ecological diversity that accompanied the uplift most likely promoted rapid and continuous allopatric speciation in small and isolated populations (Liu *et al*. 2006). For example, *Saussurea* (Asteraceae) is a species-rich genus that is mostly endemic to the Qinghai-Tibetan Plateau and species radiation was inferred to have occurred 14–7 Mya, during the period of major uplift of the Himalayas (Wang *et al.* 2009). Likewise, the genus *Incarvillea* Juss. (16 spp, Bignoniaceae) has a Himalayan to East Asia distribution (Chen *et al.* 2005), with genetic divergence associated with the uplift of the Himalayas (Chen *et al.* 2012). The genus *Dipentodon* Dunn (Dipentodontaceae) includes only two species in East Himalayan and Southwestern China, and species from the extremely uplifted (i.e., those at higher altitude) southeast Tibetan plateau contained more haplotype diversity than those of the much less uplifted region (i.e., lower altitude) (Yuan *et al.* 2008). Geographic isolation by the uplift of Himalayas and hybridization were suggested to be two important mechanisms responsible for population differentiation and speciation in *Meconopsis* Vig. (Papaveraceae), a species-rich genus in the Himalayas (Yang *et al.* 2012). The same suggestion was also given from *Tsuga* Carr. (Cun & Wang 2010). Geographical isolation caused by climatic oscillations also promoted plant diversification in the Hengduan-Qinghai-Tibet Plateau. For example, the Qinghai–Tibet Plateau developed during the largest glaciation of the early Quaternary, and mountainous isolation might have led to the deep intraspecific vicariance within the endemic species, *Cyananthus delavayi* Franch. (Campanulaceae) in the Hengduan Mountains (Li *et al.* 2012). The high species diversity of *Pedicularis* in the Hengduan-Qinghai-Tibet Plateau is thought to have originated through genetic isolation in the diverse habitats as a result of the rapid uplift of the Qinghai–Tibet Plateau (Axelrod *et al*. 1998). Additionally, as a consequence of further dispersal events of species responding to the Quaternary climatic change, recolonisation of some species to the Hengduan-Qinghai-Tibet Plateau from surrounding regions also resulted in the diversification of *Pedicularis* in these regions (Yang *et al*. 2008).

The Hengduan Mountains was also refugia for some north temperate genera during the last glacial cycle (Liu *et al.* 2006; Wang *et al.* 2008; Wang *et al*. 2009; Li *et al*. 2010; Sun *et al.* 2010; Zhang *et al.* 2010; Yang *et al.* 2012; Xue *et al.* 2012). For example, the genus *Angelica* L. (Apiaceae) consists of some 90–110 species distributed throughout north temperate regions, and 45 species in China, of which 32 are endemic to the Hengduan Mountains (She *et al.* 2005). A phylogeographic study revealed that Northeast Asia, Western Europe, and North America were ancestral areas of the genus, and the Hengduan Mountains was a refugia and a major diversification center for *Angelica* (Tu *et al.* 2009). Hengduan Mountains is also the centre of diversity for *Primula* (Hu 1994). It was found that Pleistocene climatic oscillations, combined with the complex local topography, were responsible for the phylogeographic pattern of *Primula ovalifolia* Franch., and that central and southwestern China were areas of important refugia for the survival, persistence, and further speciation of most East Asian flora, which has led to high species diversity in this region (Xie *et al*. 2012).

Evidently, the relatively quick uplift of the Himalayas and climatic oscillations after the late Tertiary have resulted in the rapid speciation and diversification of plants in the Hengduan Mountains. This is supported by both phylogeographic and floristic studies of the region that the dominant cosmopolitan and north temperate families and genera diversified rapidly in the region.

Conclusions

The flora of Shangri-la region is dominated by families and genera with cosmopolitan and north temperate distributions, while families and genera that are less species rich have diverse distributions, of which those with East Asian and Chinese endemic distributions are a minority. Among the species-rich families and genera of cosmopolitan and north temperate distributions, the regional endemic species contribute a conspicuously high percentage. The floristic patterns illustrate that the flora of Shangri-la could have evolved through rapid speciation mainly from families and genera of cosmopolitan and north temperate distributions, with the uplift of the Himalayas and climatic oscillations since the last glacial ages. The flora is obviously younger in evolutionary history than is usually supposed, and, therefore, not part of the age-old eastern Asian flora. The macroevolution of the flora in Shangri-la region is well corroborated by the phylogeographic implications of plant taxa in Hengduan-Qinghai-Tibet Plateau regions.

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