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Species richness, forest types and regeneration of *Schima* in the subtropical forest ecosystem of Yunnan, southwestern China

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Abstract

Background: *Schima* genus of Theaceae is confined to subtropics and tropics of South, East and Southeast Asia. Thirteen species of *Schima* are distributed in subtropical China. Many of them appear as dominant canopy species in the subtropical forests. To date, *Schima* species richness distribution patterns of China have remained unknown. Meanwhile, there has been a longtime debate as to whether forests dominated by *Schima* species are early or late successional forests. We aim to clarify *Schima* species richness patterns and these species' roles in the forest succession and regeneration dynamics of the subtropical ecosystem in Yunnan Province, China.

Method: We mapped *Schima* species richness distribution patterns in China. Based on 71 vegetation plots, we analyzed forest characteristics, population structure, and regeneration dynamics of *Schima* species in Yunnan.

Results: Yunnan was found to harbor the greatest richness and the highest rarity-weighted richness of *Schima* species in the subtropical regions of China. We classified five primary and six secondary forest types containing *Schima* species as one of dominants. Yunnan had the high floristic diversity and varying stand structure of forests containing *Schima* species. The *Schima* species studied generally had a sporadic regeneration type and a long life-span. Four species (*Schima argentea*, *Schima villosa*, *Schima sinensis*, *Schima sericans*) were shade-intolerant. But three species (*Schima noronhae*, *Schima khasiana* and *Schima wallichii*) were considered as bi-modal type species having shade-intolerant and shade-tolerant traits. *Schima noronhae* was seen to be a top dominant in late successional forests, while *S. wallichii* was found as a top-dominant in early or middle or late successional forests. *S. khasiana*, *Schima villosa*, *Schima sinensis* usually appeared as a top dominant in early or middle successional secondary forests, though they also presented as a second dominant in late-successional forests. *Schima argentea* and *Schima sericans* dominated only in the early or middle/seral successional forests. *Schima* species' regeneration establishment depended mainly on forest canopy gap formation through moderate human and natural disturbances.

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Conclusions: Yunnan has high species richness and rarity-weighted richness of *Schima*. Both moderate human and natural disturbances have provided regeneration niches for *Schima* species. Some of the *Schima* species studied as a second dominant (rare as the top-dominant) present in the late-successional forests. Some of them are more often as the top-dominant in early or middle successional forests, where as time goes by the dominance of *Schima* species would be replaced by their associated dominant taxa such as *Castanopsis* species.

Keywords: Forest structure, Regeneration dynamics, *Schima*, Species richness, Forest succession, Yunnan

Background

Schima, a genus belonging to Theaceae, is widely distributed in the eastern Himalaya of Nepal, Bhutan, northeastern India, Bangladesh and northern Myanmar, Indochina (Thailand, Cambodia, Laos, and Vietnam), southern China, Japan (Ryukyu Archipelago and Ogasawara Islands), Malaysia, Indonesia and Brunei (Fig. 1a, Table 1). Fossil species of *Schima* have been found from the Miocene of Germany (Mai 1971), Yunnan of China (Li et al. 2013a), Japan (Choi et al. 2010), Styria of Austria (Kovar-Ender and Hably 2006) and the Oligocene of Guangxi of China (Shi et al. 2017). Recent molecular phylogenetic analysis showed *Schima* is closely related to *Gordonia* and *Franklinia*, forming the monophyletic tribe of *Gordoniae* (Prince and Parks 2001; Li et al. 2013b; Zhang et al. 2014). There has been an argument as to the number of species of *Schima* (Prince 2007). For example, Bloembergen (1952) recognized only one species, *Schima wallichii* with nine subspecies and three varieties. Airy Shaw (1985) mentioned that *Schima* has 15 species. Min and Bartholomew (2007) and Byng (2014) reported that there are about 20 species. We adapt Min and Bartholomew (2007) that 13 species present in China; among them 6 species are endemic to China. Most of the 13 species occur as one of dominants with some species of other genera in the subtropical evergreen broad-leaved forest ecosystem of China. The evergreen broad-leaved forests of China are generally found in large, discontinuous patches in the subtropical zone of China. However, due to human intensive activities on the subtropical ecosystem many primeval evergreen broad-leaved forests were replaced by secondary vegetation in China (Wu 1980; Tang 2015a, b).

Among the *Schima* species of China, *Schima superba* which widely distributed in the eastern subtropical regions of China, has been studied from aspects of its forest communities (e.g. Wang and Li 1999; Yang et al. 2006; Song 2007), population structure (e.g. Cai and Song 1997; Hu 2005; Li et al. 2008) and genetics (e.g. Zhang et al. 2006; Jin et al. 2007). In contrast, to date the knowledge on the other species of *Schima* is very scarce. It is critical to elucidate spatial patterns of species richness of the genus and ecological role of other *Schima* species in forest succession and regeneration dynamics of the subtropical ecosystem.

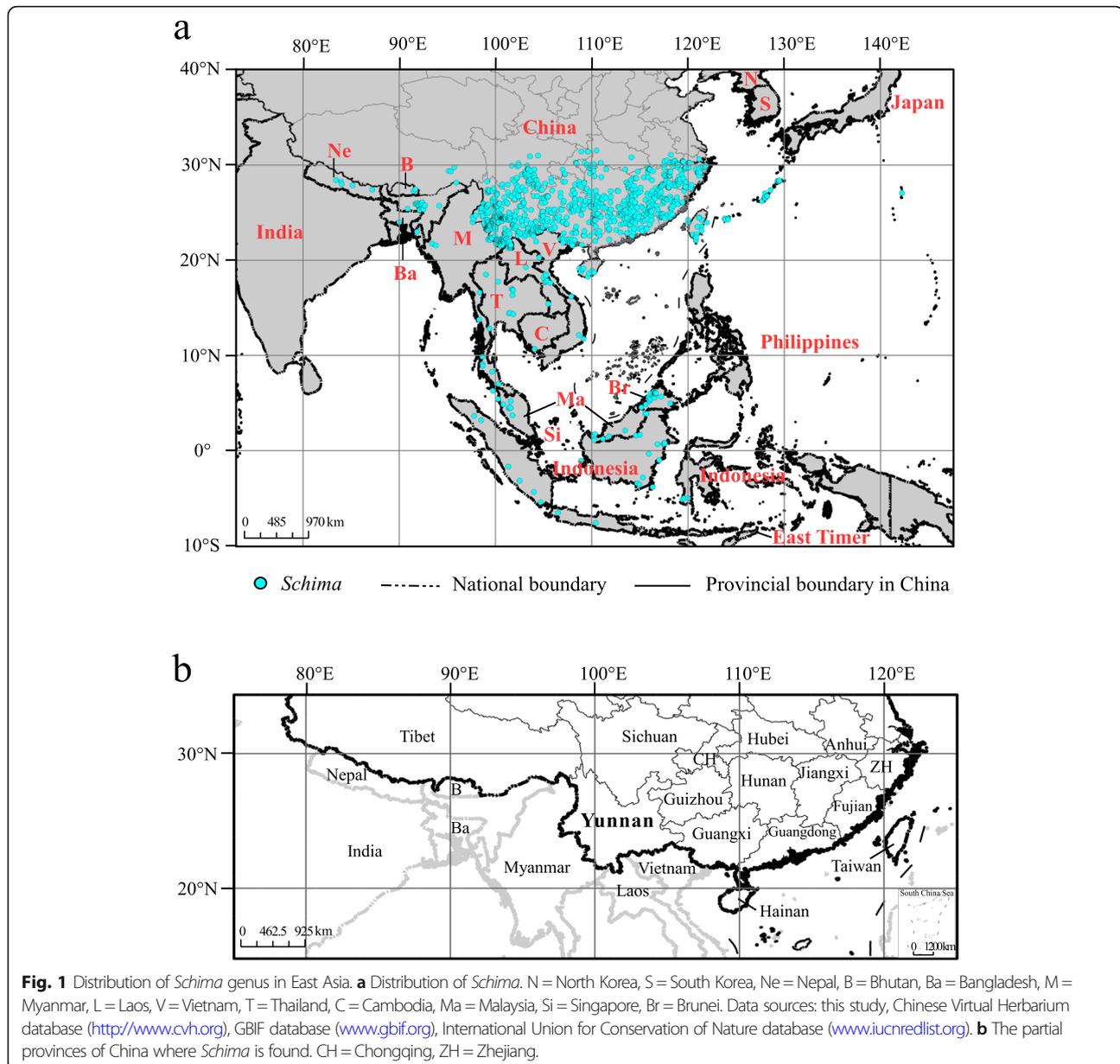
There has been a longtime debate as to whether forests dominated by *Schima* species are early or late

successional forests. Eight species of *Schima* are distributed in Yunnan, southwestern China. Yunnan affords us a unique opportunity to explore forests containing *Schima* species as one of the dominants in various landscape contexts. Understanding species richness patterns, forest types and regeneration characteristics of *Schima* are a prerequisite to understand the dynamics of the forests and provide a reference for forest reforestation and site restoration programs. We address the following questions: (1) How are the distribution patterns of species richness of *Schima* in Yunnan as compared with those in other regions of subtropical China? (2) What are the forest types and structure dominated by *Schima* species? (3) What are the regeneration dynamics of *Schima* species in Yunnan?

Methods

Study area

Yunnan is a highland province (21°08'–29°15' N, 97°31'–106°11' E) located in southwestern China, and having the greatest elevation difference on earth, from the northwest (6740 m a.s.l.) to the southeast (76 m a.s.l.). Set in the foothills of the Himalayas and Tibet, Yunnan's climate ranges from the icy highland climate of the northwestern frontier to the tropical lowland climate of the area bordering Myanmar and extending south and east toward Laos and Vietnam (Fig. 1b). The vegetation is from lowland tropical, to hilly/mid-elevation subtropical evergreen broad-leaved forests to alpine cold-temperate coniferous forests, scrubs, meadows and grasslands at the high altitudes. The Yunnan area is included in 'Indo-Burma' global hotspot of biodiversity (Myers et al. 2000). Most of the province falls into latitudes classified as middle subtropics (25°00'–29°15' N) and southern subtropics (22°30'–25°00' N). The small area between 21°08'–22°30' N is considered as northernmost tropics. The climate is monsoonal, with rainy summers. The monsoon, moving mainly from the Bay of Bengal, causes heavy rainfall on the southern aspect of the plateau, then it diminishes northward, creating a rainfall gradient. About 80% of the rain falls during rainy season-summer, and the most of the remainder falls in autumn and spring, leaving the winter cool and dry. The subtropical forests of Yunnan are remarkable for their



globally high plant diversity and extraordinary local endemism and diverse plant communities (Tang 2015a).

Study species

We made efforts to study species of *Schima* in the wild in Yunnan Province. Among the thirteen *Schima* species of China, eight occur in Yunnan (Table 1). Since one (*Schima brevipedicellata*) of the eight species does not appear as a dominant in the forests, we exclude it. Thus, our focal species in this paper are seven species, i.e. *Schima khasiana*, *Schima noronhae*, *Schima villosa*, *Schima sinensis*, *Schima wallichii*, *Schima sericans*, *Schima argentea*, each of which is found as one of the dominants in the primary or secondary subtropical

evergreen broad-leaved forests of Yunnan. Most of the seven species become quite tall (some can reach 45 m). They have showy, fragrant white flowers, with five petals and numerous yellow stamens. The leaves are alternate, spirally arranged, and entire or crenate or serrate. *Schima* flowers are hermaphrodite, axillary and solitary, or rarely three to five flowers are crowded along a short raceme. The fruit is a woody, globose or subglobose capsule, which splits for half its length into (four to) five (to six) segments; a stout, central column remains. The seeds are small and kidney-shaped, flat, with a narrow marginal wing. Representative characteristics of the *Schima* species and their forest communities are shown in Figs. 2a–l.

Table 1 *Schima* species of East Asia. Data Sources: this study, eFlora of China (<http://flora.huh.harvard.edu/china/>), Chinese Virtual Herbarium database (<http://www.cvh.org>), GBIF database (www.gbif.org) and International Union for Conservation of Nature (www.iucnredlist.org)

Species	Distribution region
<i>Schima khasiana</i>	Yunnan, SE Tibet of China; Bhutan; NE India; N Myanmar; N Vietnam
<i>Schima villosa</i>	Yunnan of China
<i>Schima sinensis</i>	NE Yunnan, N Guangxi, Guizhou, western Hubei, western Hunan, Sichuan of China
<i>Schima sericans</i>	NW Yunnan, SE Tibet of China
<i>Schima argentea</i>	Yunnan, S Guangxi, Jiangxi, SW Sichuan of China; Myanmar; Vietnam of China; Myanmar; Vietnam
<i>Schima noronhae</i>	S Yunnan of China; Indonesia; Laos; Malaysia; Myanmar; Thailand; Vietnam
<i>Schima wallichii</i>	S Yunnan, S Guangxi, S Guizhou, SE Tibet of China; Bhutan; NE India; Bangladesh; Laos; Myanmar; Nepal; Thailand; Vietnam; Japan (Ryukyu Islands); Indonesia; Brunei; Cambodia
<i>Schima brevipedicellata</i>	SE Yunnan, NW Guangdong, N Guangxi, Guizhou, Hunan, S Jiangxi, SE Sichuan of China; N Vietnam
<i>Schima multibracteata</i>	E & S Guangdong of China
<i>Schima crenata</i>	Hainan of China; Cambodia; Indonesia; Laos; Malaysia; Thailand; Vietnam
<i>Schima remotiserrata</i>	Fujian, Guangdong, E Guangxi, S Hunan, Jiangxi of China
<i>Schima parviflora</i>	N Guizhou, W Hubei, NW Hunan, E Sichuan of China
<i>Schima superba</i>	Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangxi, Taiwan, Zhejiang of China; Japan (Ryukyu Islands)
<i>Schima brevifolia</i> ^a	Malaysia
<i>Schima lobbii</i> ^a	Malaysia
<i>Schima monticola</i> ^a	Malaysia

^a: According to The Plant List database (www.theplantlist.org), the species name is unsolved, but it is used by local botanists

Data collection and analysis

The forests in the study area are subjected to a range of natural and anthropogenic factors such as elevation, topography, natural disturbances and human activities; thus, forests are structurally and floristically heterogeneous and the landscape pattern of vegetation takes the form of mosaic patches. We selected plots in each patch containing *Schima* species in the study area. During 2015–2019, we established 71 plots dominated by *Schima* species in Yunnan (Fig. 3). The plots were established in the locations where it was possible for us to access. The plot size varied between 20 m × 30 m to 30 m × 40 m where plot size depended on the size of a patch. Patch size was determined by species composition and topographic similarity.

For the species in each plot, all individuals at least 1.3 m in height were identified to species level, numbered and tagged, and their diameter at breast height (DBH) and height (H) were recorded. In addition, general information about each plot was noted, such as slope positions, altitude, slope exposure, slope inclination, as well as disturbance histories. Tree stems were classified into four types based on their vertical position, crown position, and height: emergent layer (greater than 28 m tall), canopy (20–28 m tall), subcanopy (8–20 m tall), and shrub layer (1.3–8 m tall). All understory woody species less than 130 cm tall, were divided into two classes: (1) 5–50 cm tall for seedlings and (2) 50–130 cm for saplings. Within these two classes, each individual was identified, counted, and measured for height and percent cover.

Based on tree sizes, ages of the forest stands, species composition and community structure, as well as degrees of naturalness or disturbance regime of the forests, we judged whether or not the forest stands were in early, middle, or late successional stages.

For all individuals greater than 1.3 m tall, DBH was used to calculate basal area and then basal area (BA) for each species found in a plot could be determined. In each plot, the relative importance value [RIV = (Relative density + Relative basal area)/2] of each species was used to measure the abundance of the species. Plant communities were classified using a floristic similarity dendrogram with Relative Sørensen and Group Average clustering [PCORD software (McCune and Mefford 1999)]. The communities were named according to dominant species. Diversity was calculated for each forest stand using species richness (number of species), the Shannon-Wiener's diversity index (Shannon-Wiener index, H' ; Pielou 1969) and Simpson's diversity index (Simpson index, D ; Lande 1996). Differences in species richness and diversity indices among habitats were analyzed by the non-parametric Kruskal–Wallis all-pairwise comparisons test, using Analyze-it software (United Kingdom).

Species richness (number of species) and the rarity-weighted richness (RWR) (each species is assigned a score—based on the inverse of the number of sites in which a species occurs) (Williams et al. 1996) are used to show the *Schima* species distribution patterns. A square of 1° latitude × 1° longitude (a cell per a grid size) was chosen as a geographic unit to show species richness and rarity-weighted richness at present on the map, using ArcGIS v. 10.5. The correlation of species richness and rarity-weighted richness was analyzed using Pearson's correlation coefficient.

Results

Schima species richness and rarity-weighted richness patterns

The patterns obtained for species richness and rarity-weighted richness (the latter representing concentrations



Fig. 2 Representative species, forests and habitats of *Schima* in Yunnan. **a** Leaves and flowers of *S. noronhae*; **b** A primary forest at late successional stage dominated by *S. noronhae* and *Castanopsis ceratocantha* in Wuliangshan, south-central Yunnan; **c** A tree of *S. noronhae* with 143 cm DBH and 40 m in height; **d** Leaves and flowers of *S. sericans*; **e** A secondary forest at mid-successional stage dominated by *S. sericans*, *Alnus nepalensis* and *Pinus yunnanensis* in Fengqing, SW Yunnan; **f** A mature tree of *S. sericans*; **g** Leaves and flowers of *S. argentea*; **h** A young secondary forest dominated by *S. argentea* in Yongde Daxueshan, SW Yunnan; **i** Leaves and fruits of *S. khasiana*; **j** Naturally regenerated *S. wallichii* trees growing around a farmland; **k** *S. wallichii* trees on the roadsides; **l** *S. wallichii* seedlings/saplings in a forest canopy gap in Shuangjing, SW Yunnan

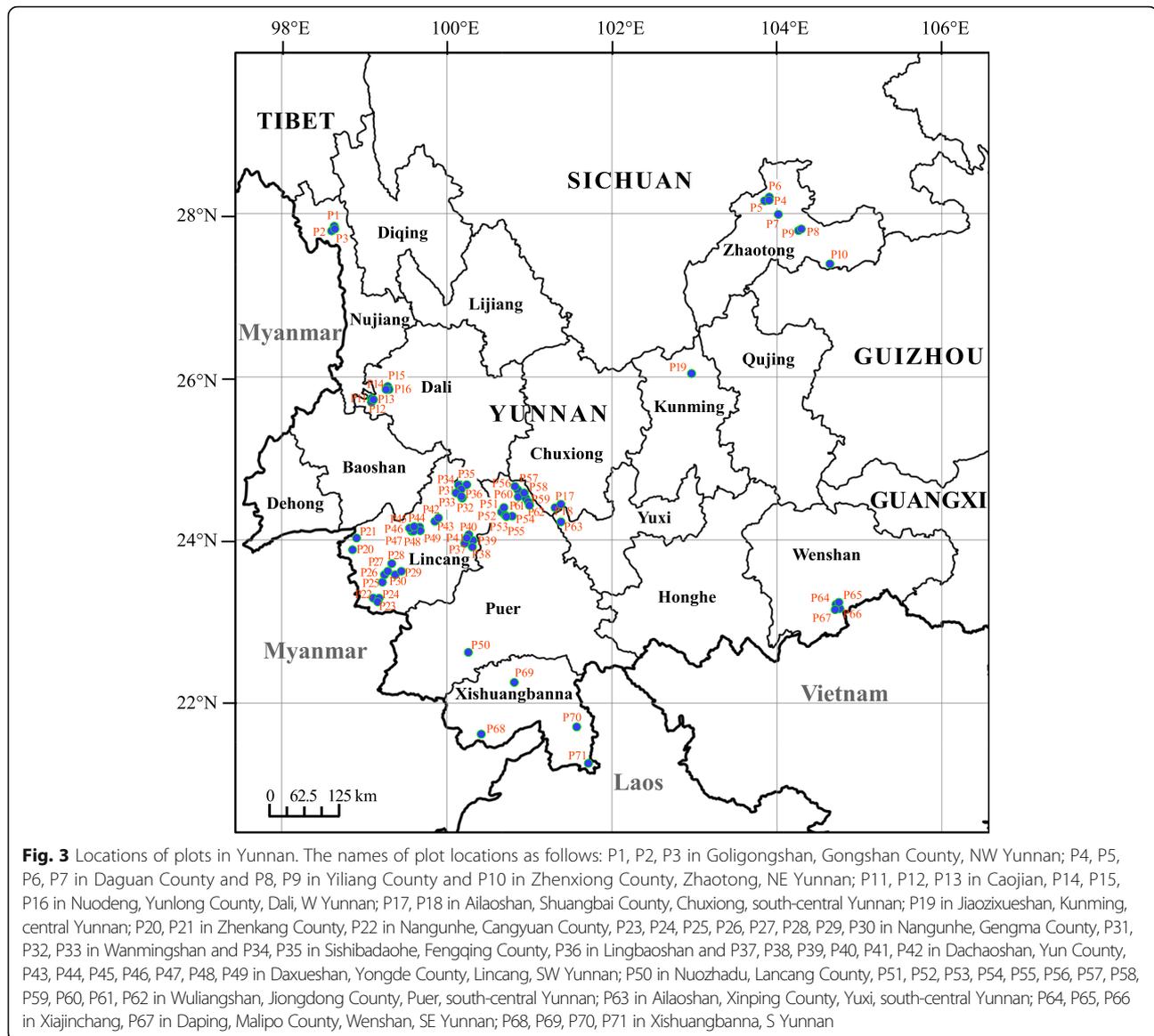
of limited-range species, as well as a high turnover of species between adjacent cells) show that the *Schima* species are confined to the subtropical and warm-temperate areas of China (Fig. 4a and b). Among 13 species found in China, 8 are distributed in Yunnan (Table 1). The areas of southeastern, south-central, southwestern and western Yunnan show the high species richness (4–7, yellow and red cells in Fig. 4a), while the other regions of China most often have 1–3 species (dark green, blue and light green cells) except for south-central China. The rarity-weighted richness (RWR) greater than 0.2 (yellow and red cells) was found in the areas of northwestern, southeastern, southern and south-central Yunnan, with two sites in Guangxi Province. The outstanding rarity weighted richness in northern Gaoligongshan, NW Yunnan is mostly contributed by *Schima*

sericans which has a very narrow distribution (endemic to NW Yunnan and SE Tibet), and *Schima khasiana* which is limited to western and southern Yunnan and SE Tibet (Fig. 4b). The distribution patterns of *Schima* species richness (Fig. 4a) and rarity-weighted richness (Fig. 4b) in the Yunnan area have linear relationships with significant positive correlations (Pearson's $r = 0.74$).

Forest types, stratification and species diversity

Primary forests

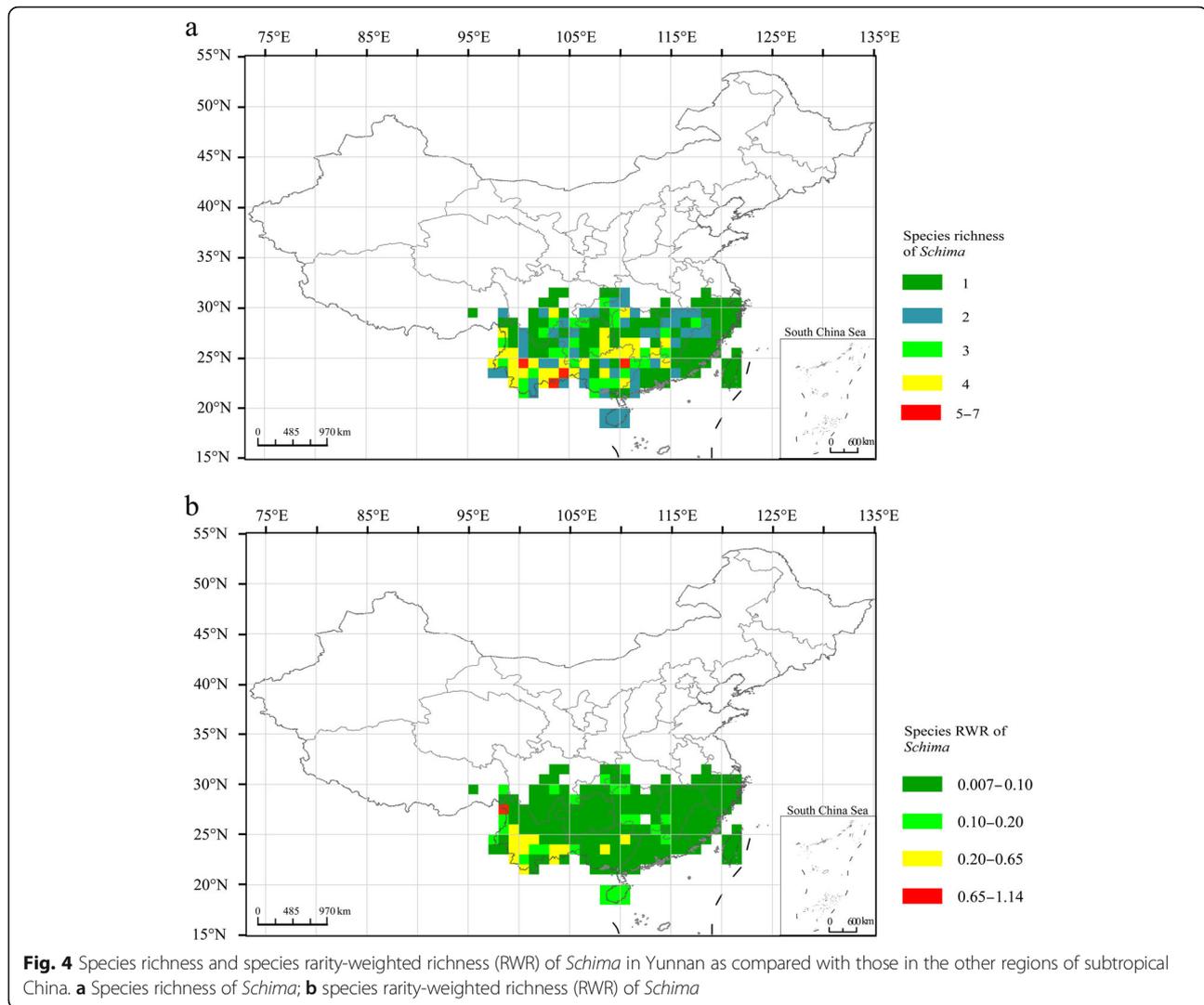
According to the similarity dendrogram, vegetation data of 22 plots in Yunnan were classified into five primary forest types (Fig. 5a): Type PF1, the *Schima noronhae*-*Castanopsis ceratocantha* evergreen broad-leaved forest on mountain slopes at elevations 1920–2480 m in Wuliangshan, south-central Yunnan; Type PF2, the



Castanopsis echidnocarpa-*Schima khasiana* evergreen broad-leaved forest at 2000–2710 m on mountain slopes in Wanmingshan, SW Yunnan; Type PF3, the *Tetracentron sinense*-*Schima villosa* deciduous and evergreen broad-leaved mixed forest on steep slopes and stream sides at 2450–2600 m in Zheonghoushan of the Ailao Mountains, south-central Yunnan; Type PF4, the *Castanopsis platyacantha*-*Schima sinensis* evergreen broad-leaved forest on mountain slopes at 1800–1950 m in Dagan, NE Yunnan; Type PF5, *Schima wallichii*-*Castanopsis hystrix* evergreen broad-leaved forest in valleys or on mountain slopes at 950–1380 m in Xishuangbanna, S Yunnan. No major anthropogenic disturbances have been found, though some natural disturbances including slight landslides, moderate wind-blow and occasional lightning strike occurred in the forests.

In each forest type, *Schima* and *Castanopsis* (*S. noronhae* and *C. ceratocantha* in Type PF1, *S. khasiana* and *C. echidnocarpa* in Type PF2, *S. sinensis* and *C. platyacantha* in Type PF4, *S. wallichii* and *C. hystrix* in Type PF5) dominated the canopy (18–28 m), except that Type PF3 was dominated by *Tetracentron sinense* and *S. villosa* (Fig. 5b). In Type PF1, PF2, PF3, PF5 forests, *Schima* also reached emergent layer (28–36 m). In the subcanopy (8–18 m), the shrub layer (3–8 m), and the understory (< 3 m) of the forest Types PF1, PF2, PF4, PF5, *Schima* was commonly found, while in Type PF3 it was absent in 8–12 m and infrequent in the shrub layer and the understory.

All the 22 plots of primary forests, taken together, contained 240 woody species, representing 147 genera in 72 families. Each forest type's species composition with



the relative importance value (RIV) is shown in Table 2. Type PF1 was dominated by *Schima noronhae* and *Castanopsis ceratocantha*. The other major components were *Lithocarpus truncatus*, *Machilus longipedicellata*, *Eurya yunnanensis*, etc. In the understory, a bamboo species-*Yushania polytricha*'s coverage reached 80%. Type PF2 was co-dominated by *Castanopsis echidnocarpa* and *Schima khasiana* along with *Lithocarpus xylocarpus*, *Cyclobalanopsis myrsinifolia*, *Ternstroemia gymnanthera* and *Craibiodendron stellatum*, etc. Type PF3 was co-dominated by *Tetracentron sinense* and *Schima villosa*, and the accompanying species were *Illicium simonsii*, *Ilex triflora*, *Symplocos sumuntia*, etc. Type PF4 was co-dominated by *Castanopsis platycantha* and *Schima sinensis* with *Acer oliverianum*, *Lindera thomsonii*, *Pittosporum tobira*, etc. Type PF5 was co-dominated by *Schima wallichii* and *Castanopsis hystrix*. The other components were *Castanopsis mekongensis*, *Lithocarpus truncates*, *Wendlandia tinctoria* and so on.

The Shannon-Wiener diversity index H' and the Simpson diversity index D ranged respectively from 2.364 to 3.076, and from 0.864 to 0.931 among the five forest types. The diversity indices were not significantly different among the various forest types (Table 2).

For per hectare basal area, forest Types PF2 and PF1 scored relatively high (111.35, 109.33 $\text{m}^2\cdot\text{ha}^{-1}$, respectively), followed by Types PF3 (75.25 $\text{m}^2\cdot\text{ha}^{-1}$) and PF4 (61.55 $\text{m}^2\cdot\text{ha}^{-1}$), and Type PF5 (40.37 $\text{m}^2\cdot\text{ha}^{-1}$) (Supplementary Table S1).

Secondary forests

According to the similarity dendrogram based on vegetation data of 49 plots of secondary forests, there are 6 forest types (Fig. 6a). Type SF1, the *Schima argentea* secondary evergreen broad-leaved forest was widely found on mountain slopes, in valleys, along roadsides or near farmland at elevations 1920–2650 m in Yongde daxueshan of SW Yunnan, Dachaoshan of SW Yunnan,

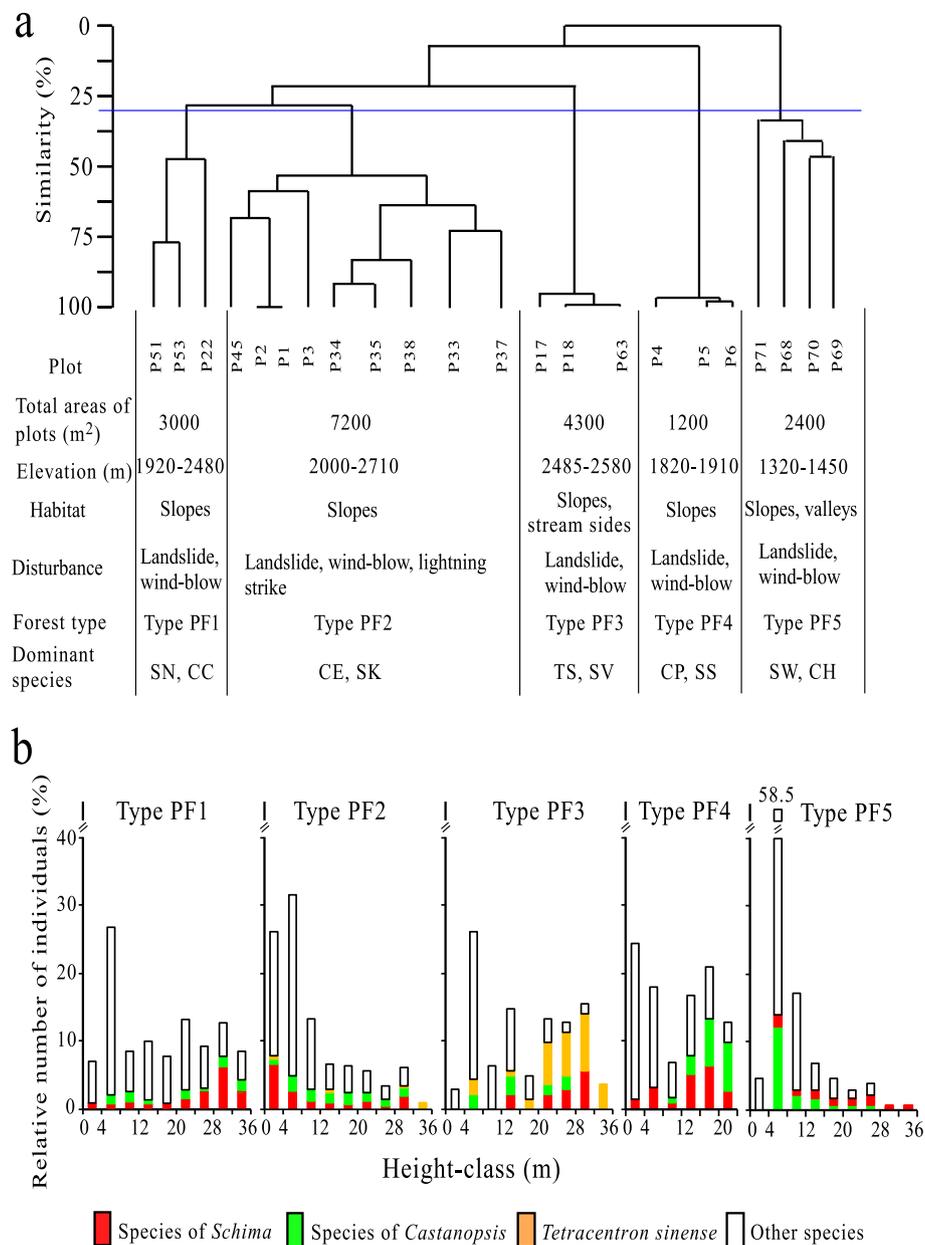


Fig. 5 Floristic dendrogram and stratification of primary forests. **a** Floristic similarity dendrogram; **b** Height-class frequency distribution of species (height ≥ 1.3 m). SN = *Schima noronhae*; CC = *Castanopsis ceratocantha*; CE = *Castanopsis echinocarpa*; SK = *Schima khasiana*; TS = *Tetracentron sinense*; SV = *Schima villosa*; CP = *Castanopsis platyacantha*; SS = *Schima sinensis*; SW = *Schima wallichii*; CH = *Castanopsis hystrix* for (**a**)

Wuliangshan of south-central Yunnan and Jiaozixueshan of central Yunnan; Type SF2, the *Schima khasiana-Dipentodon sinicus* secondary evergreen and deciduous broad-leaved mixed forest was found along roadsides or stream sides at 2390–2650 m in Chaojian, NW Yunnan; Type SF3, the *Schima wallichii* secondary evergreen broad-leaved forest was commonly found on mountain slopes, in valleys, along roadsides or near farmland at 950–2460 m in SW, NW and S Yunnan; Type SF4, the *Schima sericans-Castanopsis ceratocantha* secondary

evergreen broad-leaved forest was found on mountain slopes at 2040–2300 m in Yun County, SW Yunnan; Type SF5, *Schima villosa-Rhoiptelea chiliantha* secondary evergreen and deciduous broad-leaved mixed forest was found on mountain slopes at 1680–2100 m in Malipo County, SE Yunnan; Type SF6, the *Schima sinensis-Castanopsis platyacantha* secondary evergreen broad-leaved forest was found on mountain slopes at 1860–2110 m in Dagan County, Yiliang County and Zhenxiong County of Zhaotong, NE Yunnan. In the

Table 2 Floristic composition of woody species ($H \geq 1.3$ m) for primary forest types containing *Schima* species as one of the dominants. Only species with relative importance value (RIV) $\geq 1.5\%$ are shown. The same letter indicates no significant difference ($p > 0.05$) for average number of species and diversity indices among those forest types. SD = Standard deviation. RIV = relative importance value. Dominant species are indicated by boldface

Forest type	Type PF1	Type PF2	Type PF3	Type PF4	Type PF5
Elevation (m)	1920–2476	2000–2710	2485–2577	1820–1910	900–2100
Plots	P51, P53, P22	P45, P2, P1, P3, P34, P35, P38, P33, P37	P17, P18, P63	P4, P5, P6	P71, P68, P70, P69
Number of plots	3	9	3	3	4
Total areas of plots (m ²)	3000	7200	4300	1200	2400
Total number of species	85	85	30	39	48
Average number of species	32 ± 10.07 ^a	17 ± 5.84 ^a	15 ± 6.51 ^a	18 ± 3.46 ^a	32 ± 14.08 ^a
Shannon-Wiener $H' \pm SD$	3.076 ± 0.44 ^a	2.364 ± 0.50 ^a	2.392 ± 0.50 ^a	2.506 ± 0.14 ^a	2.477 ± 0.49 ^a
Simpson $D \pm SD$	0.931 ± 0.04 ^a	0.864 ± 0.09 ^a	0.87 ± 0.06 ^a	0.891 ± 0.01 ^a	0.869 ± 0.05 ^a
Species	RIV (%)	RIV (%)	RIV (%)	RIV (%)	RIV (%)
Evergreen broad-leaved					
<i>Schima noronhae</i>	16.32	–	–	–	–
<i>Castanopsis ceratocantha</i>	10.00	4.02	–	–	–
<i>Lithocarpus truncatus</i>	7.12	–	–	–	5.00
<i>Eurya yunnanensis</i>	3.68	–	–	–	–
<i>Phoebe puwenensis</i>	3.14	–	–	–	–
<i>Lithocarpus grandifolius</i>	3.01	–	–	–	–
<i>Machilus duthiei</i>	2.99	3.53	–	–	–
<i>Lindera supracostata</i>	2.61	–	–	–	–
<i>Lithocarpus hancei</i>	2.15	4.80	–	–	–
<i>Manglietia insignis</i>	2.00	1.65	9.55	–	–
<i>Michelia baillonii</i>	1.97	–	–	–	–
<i>Cinnamomum bejolghota</i>	1.91	–	–	–	–
<i>Castanopsis echinocarpa</i>	–	14.23	–	–	–
<i>Schima khasiana</i>	–	10.97	–	–	–
<i>Lithocarpus xylocarpus</i>	–	6.40	–	–	–
<i>Cyclobalanopsis myrsinifolia</i>	–	5.36	–	–	–
<i>Lithocarpus mairei</i>	–	3.89	–	–	–
<i>Cyclobalanopsis lamellosa</i>	–	2.75	–	–	–
<i>Myrsine semiserrata</i>	–	1.83	–	–	–
<i>Cinnamomum iners</i>	–	1.83	–	–	–
<i>Schima argentea</i>	–	1.77	–	–	–
<i>Rhododendron</i> sp.	–	1.55	–	–	–
<i>Schima villosa</i>	–	–	20.80	–	–
<i>Castanopsis wattii</i>	–	–	5.79	–	–
<i>Illicium simonsii</i>	–	–	2.90	–	–
<i>Ilex triflora</i>	–	–	2.82	–	–
<i>Symplocos sumuntia</i>	–	–	1.78	–	–
<i>Machilus salicina</i>	–	–	1.77	–	–
<i>Castanopsis platyacantha</i>	–	–	–	28.72	–
<i>Schima sinensis</i>	–	–	–	14.00	–

Table 2 Floristic composition of woody species ($H \geq 1.3$ m) for primary forest types containing *Schima* species as one of the dominants. Only species with relative importance value (RIV) $\geq 1.5\%$ are shown. The same letter indicates no significant difference ($p > 0.05$) for average number of species and diversity indices among those forest types. SD = Standard deviation. RIV = relative importance value. Dominant species are indicated by boldface (*Continued*)

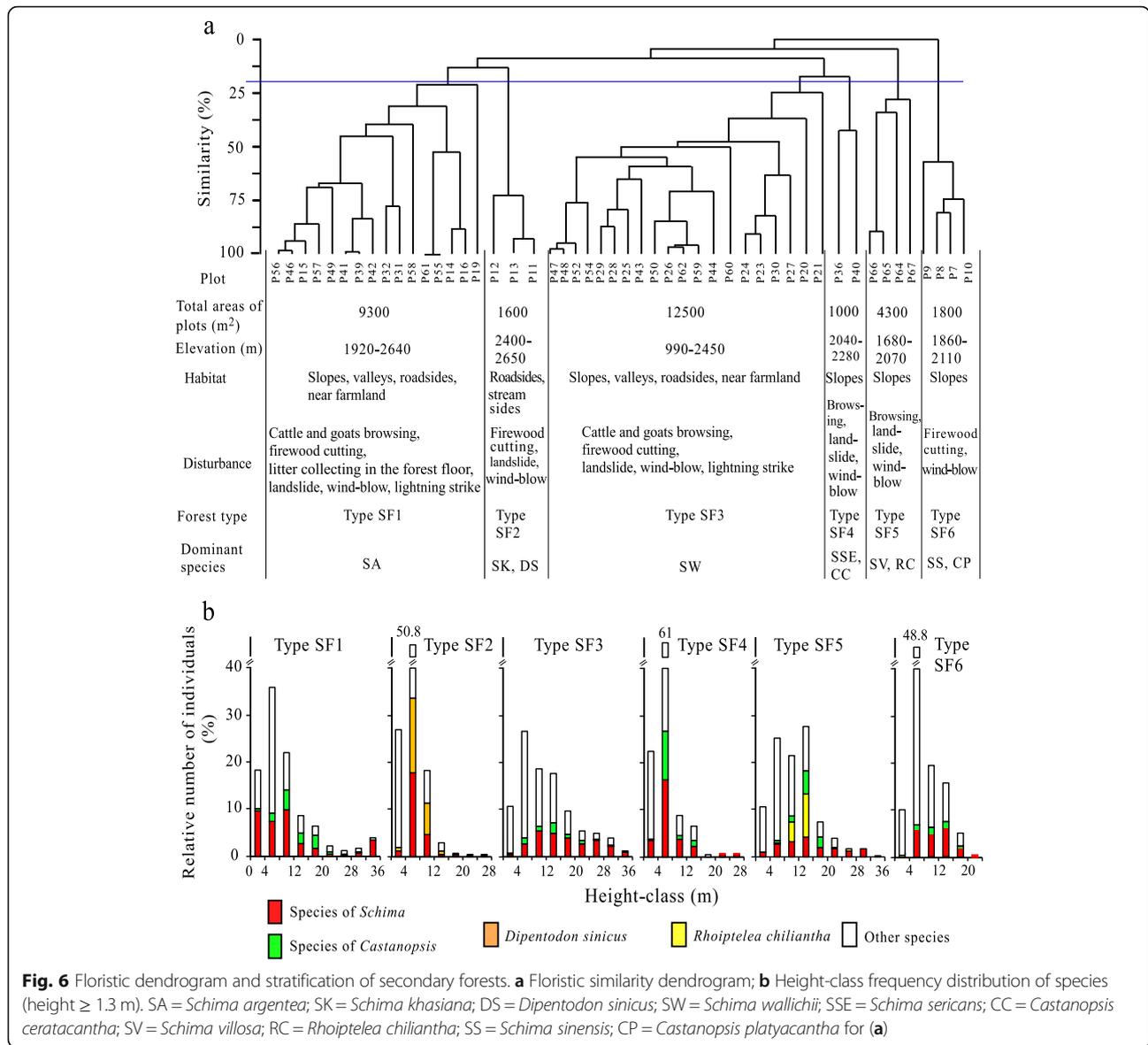
Forest type	Type PF1	Type PF2	Type PF3	Type PF4	Type PF5
<i>Lindera thomsonii</i>	–	–	–	5.92	–
<i>Symplocos anomala</i>	–	–	–	3.44	–
<i>Ilex subodorata</i>	–	–	–	2.77	–
<i>Pittosporum perryanum</i>	–	–	–	2.75	–
<i>Micheliacaloptila</i>	–	–	–	2.08	–
<i>Vaccinium mandarinorum</i>	–	–	–	1.74	–
<i>Schima wallichii</i>	–	–	–	–	16.74
<i>Castanopsis hystrix</i>	–	–	–	–	16.44
<i>Castanopsis mekongensis</i>	–	–	–	–	8.71
<i>Wendlandia tinctoria</i>	–	–	–	–	4.48
<i>Machilus rufipes</i>	–	–	–	–	3.35
<i>Anneslea fragrans</i>	–	–	–	–	3.25
<i>Syzygium cumini</i>	–	–	–	–	3.08
<i>Pertusadina metcalffii</i>	–	–	–	–	2.69
<i>Castanopsis calathiformis</i>	–	–	–	–	2.12
<i>Vaccinium bracteatum</i>	–	–	–	–	2.04
<i>Machilus tenuipilis</i>	–	–	–	–	1.74
<i>Litsea martabanica</i>	–	–	–	–	1.70
<i>Ilex godajam</i>	–	–	–	–	1.60
<i>Phoebe lanceolata</i>	–	–	–	–	1.54
Deciduous broad-leaved					
<i>Betula alnoides</i>	1.55	–	–	–	–
<i>Tetracentron sinense</i>	–	–	34.88	–	–
<i>Acer amplum</i>	–	–	1.67	–	–
<i>Acer oliverianum</i>	–	–	–	3.96	–
<i>Cornus controversa</i>	–	–	–	1.77	–
<i>Cerasus patentipila</i>	–	–	–	1.69	–
Coniferous					
<i>Tsuga dumosa</i>	–	3.19	–	–	–
<i>Taxus wallichiana</i> var. <i>chinensis</i>	–	–	2.99	–	–

secondary forests, there were evidences of anthropogenic disturbances such as occasional cattle and goats browsing or selective firewood cutting or collecting litters on the forest floor. Besides the moderate human activities, natural disturbances including landslides, wind-blow, and lightning strikes also occurred there. Especially in forest Types SF1 and SF3, there were many different types of disturbances.

In each secondary forest type, *Schima* species generally dominated the canopy (18–28 m) (Fig. 6b). In Type SF1, SF3, SF5 forests, *S. argentea*, *S. wallichii* and *S. villosa* reached the emergent layer (28–36 m). In the subcanopy (8–18 m), the shrub layer (3–8 m),

and the understory (< 3 m) of Types SF1, SF2, SF3, SF5, *Schima* was commonly found, while only few trees of *S. sericans* were in 8–28 m in Type SF4, *S. sinensis* was absent in 1.3–4 m in Type SF6. Except Type SF2, all the secondary forests had species of *Castanopsis* as a major component.

All the 49 plots of secondary forests, taken together, contained 370 woody species, representing 169 genera in 68 families. Species composition of each forest type with the relative importance value (RIV) is shown in Table 3. Type SF1, the *Schima argentea* secondary forest was dominated only by *S. argentea*. The other components were *Castanopsis orthacantha*, *Castanopsis echinocarpa*



and *Rhododendron delavayi*, etc. Type SF2, the *Schima khasiana*-*Dipentodon sinicus* secondary forest was co-dominated by *S. khasiana* and *Dipentodon sinicus*. The other components were *Illicium simonsii*, *Cyclobalanopsis augustinii* and so on. In the understory, many *Hypericum monogynum* invaded. Type SF3, the *Schima wallichii* secondary forest was dominated only by *S. wallichii*, and its components were *Castanopsis calathiformis*, *Lithocarpus xylocarpus*, *Betula alnoides*, *Alnus nepalensis*, *Pinus yunnanensis*, etc. Type SF4, the *Schima sericans*-*Castanopsis ceratacantha* secondary forest, was co-dominated by *S. sericans* and *C. ceratacantha*, along with other components including *Schima wallichii*, *Lynnia doyonensis*, *Ilex polyneura*, *Eurya nitida*, *Anneslea fragrans*, *Rhododendron vialii*, etc. Type SF5, *Schima*

villosa-*Rhoiptelea chiliantha* secondary forest was co-dominated by *S. villosa* and deciduous *R. chiliantha*. The companion species were *Castanopsis ceratacantha*, *Lithocarpus truncates*, *Eurya impressinervis*, *Craibiodendron stellatum*, etc. Type SF6, the *Schima sinensis*-*Castanopsis platyacantha* secondary forest was co-dominated by *S. sinensis* and *C. platyacantha* along with *Lithocarpus hancei*, *Camellia pitardii*, *Symplocos anomala* and so on. In the secondary forests, there were more pioneer deciduous broad-leaved species such as *Alnus nepalensis*, *Betula alnoides* and coniferous *Pinus yunnanensis* compared to the primary forests.

Among the 6 secondary forest Types SF1-SF6, the Shannon-Wiener diversity H' and the Simpson diversity D respectively ranged from 2.109 to 2.429 and 0.793–

Table 3 Floristic composition of woody species (Height ≥ 1.3 m) for secondary forest types containing *Schima* species as one of the dominants. Only species with relative importance values (RIV) $\geq 1.5\%$ are shown. The same letter indicates no significant difference ($p > 0.05$) for average number of species and diversity indices among those forest types. SD = Standard deviation. RIV = relative importance value. Dominant species are indicated by boldface

Forest type	Type SF1	Type SF2	Type SF3	Type SF4	Type SF5	Type SF6
Elevation (m)	1923–2640	2398–2636	990–2451	2043–2280	1680–2066	1860–2110
Plots	P56, P46, P15, P57, P49, P41, P39, P42, P32, P31, P58, P61, P65, P14, P16, P19	P12, P13, P11	P47, P48, P52, P54, P29, P28, P25, P43, P50, P26, P62, P59, P44, P60, P24, P23, P30, P27, P20, P21	P36, P40	P66, P65, P64, P67	P9, P8, P7, P10
Number of plots	16	3	20	2	4	4
Total areas of plots (m ²)	9300	1600	12,500	1000	4300	1800
Total number of species	122	49	189	35	47	53
Average number of species	17 \pm 4.50 ^a	26 \pm 1.53 ^a	16 \pm 4.91 ^a	23 \pm 8.50 ^a	17 \pm 5.94 ^a	17 \pm 4.79 ^a
Shannon-Wiener H' \pm SD	2.109 \pm 0.38 ^a	2.31 \pm 0.29 ^a	2.284 \pm 0.37 ^a	2.429 \pm 0.37 ^a	2.173 \pm 0.49 ^a	2.289 \pm 0.3 ^a
Simpson D \pm SD	0.793 \pm 0.11 ^a	0.833 \pm 0.05 ^a	0.95 \pm 0.07 ^a	0.909 \pm 0 ^a	0.801 \pm 0.13 ^a	0.846 \pm 0.05 ^a
Importance value	RIV (%)	RIV (%)	RIV (%)	RIV (%)	RIV (%)	RIV (%)
Species						
Evergreen broad-leaved						
<i>Schima argentea</i>	29.2	–	–	–	–	–
<i>Castanopsis orthacantha</i>	5.7	–	–	–	–	–
<i>Castanopsis echinocarpa</i>	4.5	–	–	–	–	–
<i>Myrica esculenta</i>	3.4	–	–	3.3	–	–
<i>Rhododendron delavayi</i>	3.4	–	–	–	–	–
<i>Lyonia ovalifolia</i>	2.3	–	–	2.3	–	–
<i>Schima khasiana</i>	2.2	21.9	–	–	–	–
<i>Lyonia ovalifolia</i> var. <i>lanceolata</i>	1.8	–	–	2.8	–	–
<i>Hypericum monogynum</i>	–	7.9	–	–	–	–
<i>Illicium simonsii</i>	–	6.6	–	–	4.1	–
<i>Vaccinium mandarinorum</i>	–	5.0	–	–	–	–
<i>Cyclobalanopsis augustinii</i>	–	3.8	–	–	–	–
<i>Lithocarpus confinis</i>	–	3.7	–	–	–	–
<i>Eurya nitida</i>	–	1.8	–	4.2	–	–
<i>Schima wallichii</i>	–	–	32.0	5.9	–	–
<i>Castanopsis calathiformis</i>	–	–	3.1	–	–	–
<i>Lithocarpus xylocarpus</i>	–	–	2.8	–	–	–
<i>Lithocarpus fenestratus</i>	–	–	2.1	–	–	–
<i>Litsea martabanica</i>	–	–	1.6	–	–	–
<i>Schima sericans</i>	–	–	–	21.2	–	–
<i>Castanopsis ceratocantha</i>	–	–	–	18.4	2.6	–
<i>Rhododendron vialii</i>	–	–	–	3.3	–	–
<i>Anneslea fragrans</i>	–	–	–	3.3	–	–
<i>Lithocarpus mianningensis</i>	–	–	–	3.1	–	–
<i>Manglietia hookeri</i>	–	–	–	2.8	–	–

Table 3 Floristic composition of woody species (Height ≥ 1.3 m) for secondary forest types containing *Schima* species as one of the dominants. Only species with relative importance values (RIV) $\geq 1.5\%$ are shown. The same letter indicates no significant difference ($p > 0.05$) for average number of species and diversity indices among those forest types. SD = Standard deviation. RIV = relative importance value. Dominant species are indicated by boldface (*Continued*)

Forest type	Type SF1	Type SF2	Type SF3	Type SF4	Type SF5	Type SF6
<i>Craibiodendron stellatum</i>	–	–	–	2.6	–	–
<i>Schima villosa</i>	–	–	–	–	22.4	–
<i>Castanopsis remotidenticulata</i>	–	–	–	–	12.9	–
<i>Lithocarpus truncatus</i>	–	–	–	–	7.0	–
<i>Eurya impressinervis</i>	–	–	–	–	6.0	–
<i>Lithocarpus megalophyllus</i>	–	–	–	–	2.1	2.5
<i>Elaeocarpus decipiens</i>	–	–	–	–	1.7	–
<i>Reevesia pubescens</i>	–	–	–	–	1.5	–
<i>Schima sinensis</i>	–	–	–	–	–	23.5
<i>Castanopsis platyacantha</i>	–	–	–	–	–	15.9
<i>Camellia pitardii</i>	–	–	–	–	–	6.2
<i>Lithocarpus hancei</i>	–	–	–	–	–	5.1
<i>Symplocos anomala</i>	–	–	–	–	–	4.3
<i>Symplocos lucida</i>	–	–	–	–	–	4.3
<i>Tetradium ruticarpum</i>	–	–	–	–	–	3.9
<i>Rhododendron coeloneurum</i>	–	–	–	–	–	2.6
<i>Rhododendron calostrotum</i>	–	–	–	–	–	2.0
Deciduous broad-leaved						
<i>Lyonia doyonensis</i>	3.2	–	–	8.6	–	–
<i>Alnus nepalensis</i>	2.5	–	3.1	–	2.0	–
<i>Ilex polyneura</i>	1.9	–	–	8.3	–	–
<i>Dipentodon sinicus</i>	–	20.2	–	–	–	2.7
<i>Sorbus folgneri</i>	–	2.8	–	–	–	–
<i>Padus brachypoda</i>	–	2.3	–	–	–	–
<i>Tetracentron sinense</i>	–	1.9	–	–	–	–
<i>Lindera obtusiloba</i>	–	1.7	–	–	–	–
<i>Litsea pungens</i>	–	1.7	–	–	–	–
<i>Salix matsudana</i>	–	1.5	–	–	–	–
<i>Betula alnoides</i>	–	–	4.4	–	–	–
<i>Rhoiptelea chiliantha</i>	–	–	–	–	17.4	–
<i>Quercus acutissima</i>	–	–	–	–	2.4	–
<i>Acer sterculiaceum</i>	–	–	–	–	–	2.2
<i>Rehderodendron macrocarpum</i>	–	–	–	–	–	2.1
<i>Enkianthus chinensis</i>	–	–	–	–	–	1.9
Coniferous						
<i>Pinus yunnanensis</i>	3.7	–	–	–	–	–
<i>Tsuga dumosa</i>	–	2.5	–	–	–	–

0.950. No significant difference among the diversity indices were found in all the secondary forest types. However, the Shannon-Wiener indices of the secondary forests were significantly lower than those of the primary forests ($p \leq 0.05$) (Table 3).

For per hectare basal area, all the six secondary forest Types SF1–SF6 scored relatively low (23.23–45.95 $\text{m}^2 \cdot \text{ha}^{-1}$, [Supplementary Table S2](#)). It is clear that the basal area per hectare of the secondary forests is much lower than that of the primary forests.

Along latitudinal, longitudinal and elevational gradients, the distribution pattern of forests containing *Schima* species as one of dominants in Yunnan is shown in Fig. 7. For both the primary forests and the secondary forests as a whole, *Schima* species were found at elevations between 990 and 2600 m. *S. noronhae* as a top dominant was only found in primary forests in Wuliangshan, while *S. wallichii* appeared in both primary and secondary forests in Xishuangbanna, Nangunhe and Yongde daxueshan. *S. khasiana* in Gaoligongshan, *Schima villosa* in Ailaoshan and Malipo, *S. sinensis* in Daguan as a second or third dominant appeared in primary forests. However, the four species, i.e. *S. wallichii*, *S. khasiana*, *Schima villosa*, and *S. sinensis*, were more often seen as a top dominant found in secondary forests, and *S. argentea* and *S. sericans* were only found as a top dominant in secondary forests.

Regeneration dynamics

The DBH-class frequency distribution of species can reveal their population structure and regeneration dynamics. In the primary forests, the DBH-class frequency distribution of each of the five *Schima* species i.e. *S. noronhae*, *S. khasiana*, *S. wallichii*, *Schima villosa*, *S. sinensis* shows a sporadic type with several peaks, indicating that recruitments varied by chance with the regeneration mainly depending on disturbances (e.g. canopy gap regeneration) (Fig. 8). *S. noronhae* had peaks at 25–30 and 45–50 cm DBH, with very few individuals less than 25 cm DBH. Some *S. noronhae* trees larger than 80 cm DBH were found, and its maximum DBH reached 145 cm (maybe ca. 280 years old based on our limited data of core samples). *S. khasiana* had a discontinued distribution between 5 and 155 cm DBH, and more individuals smaller than 10 cm DBH were found. *S. wallichii* had relatively more trees in 30–35 and 5–10 cm DBH, and reached 135 cm DBH (maybe ca. 152 years old based on our limited data of core samples) but was absent in 40–45, 55–60, 80–100, 105–130 cm DBH. *Schima villosa* only had 2 trees in the DBH-classes less than 50 cm, then it discontinuously distributed in 55–105 cm DBH. *Schima sinensis* had more trees in 10–25 cm DBH and reached 70 cm DBH, but was completely absent between 35 and 69 cm DBH. For all the *Schima* species except *S. khasiana*, it evidently shows the great lack of young trees and poor regeneration. The DBH-class frequency distribution of the major species of each primary forest type is provided in [Supplementary Table S1](#).

In the secondary forests, the DBH-class frequency distribution of each of the six *Schima* species, i.e. *S. argentea*, *S. khasiana*, *S. wallichii*, *S. villosa*, *S. sinensis* and *S. sericans* also generally shows a sporadic type with multi-peaks, indicating that recruitments varied by chance with the regeneration depending on disturbances (e.g. canopy

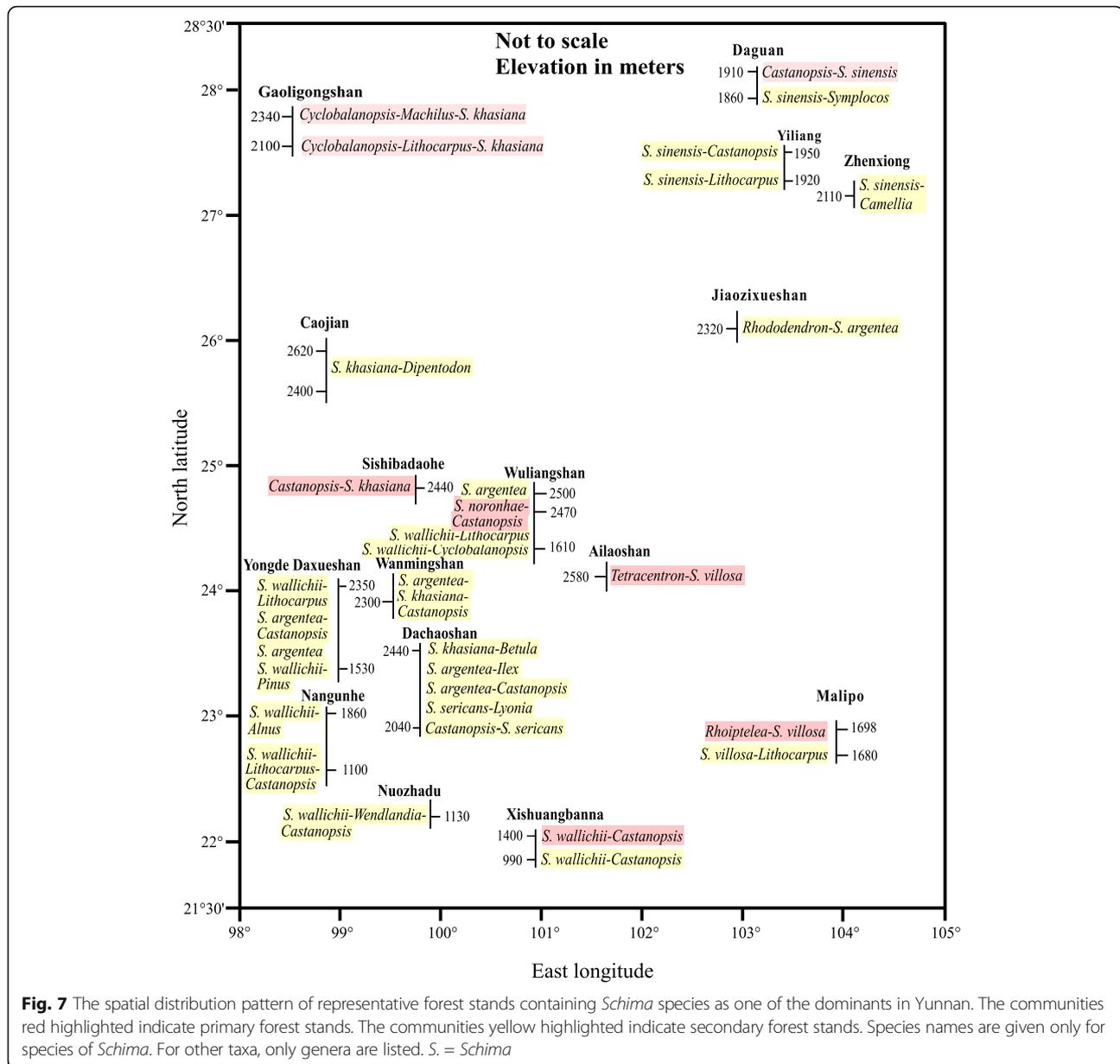
gap regeneration) (Fig. 8). Since moderate human activities or moderate natural disturbances in the secondary forests (Fig. 6a), many forest gaps formed, so abundant individuals of *S. argentea*, *S. khasiana*, *S. wallichii* in DBH-classes smaller than 30 cm, and overwhelmingly more young trees in 0–10 cm DBH (Fig. 8). *S. argentea* and *S. wallichii* respectively reached 75 cm DBH, while *S. khasiana*, *S. villosa*, *S. sinensis* and *S. sericans* reached 55 cm DBH, respectively. The DBH-class frequency distribution of the major species of each secondary forest type is provided in [Supplementary Table S2](#). Many small trees of non-*Schima* canopy species were also found in the secondary forests.

Seedlings/saplings of these seven *Schima* species were mainly found in well-lit sites including canopy gaps, forest edges and roadsides (Fig. 9). Canopy gaps contributed the most to the establishment of seedlings/saplings. However, *S. noronhae*, *S. khasiana* and *S. wallichii* had some established seedlings/saplings under canopies. The dense coverage (80%) of *Yushania polytricha* of bamboo in the understory of the forest Type PF1 impeded the regeneration of *S. noronhae*. Notably, abundant seedlings/saplings of *S. wallichii* and *S. argentea* were found, while the numbers of seedlings/sapling of *S. sinensis*, *S. villosa*, *S. sericans* were rather limited (Fig. 9). Since there were more canopy gaps in the secondary forests than the primary forests, the regeneration of these *Schima* species in the secondary forests had much better recruitments than those in the primary forests.

Discussion

Forest characteristics

Our study demonstrates that *Schima* is often co-dominated with or associated with various species of *Castanopsis* (e.g. *Castanopsis ceratacantha*, *C. echinocarpa*, *C. platyacantha* and *C. hystrix*) in the evergreen broad-leaved forests of Yunnan. In fact, it is also true in other regions of China and East Asia, as exemplified by *Schima superba* associated with *Castanopsis carlesii* in Tiantong, Zhejiang (Da et al. 2004; Yang et al. 2006; Song 2007), associated with *Castanopsis eyrei* in Gutianshan, Zhejiang (Zhu et al. 2008) and Wuyishan, Jiangxi (Cai and Song 1997), associated with *Castanopsis chinensis* on Mt. Dinghu, Guangdong (Huang et al. 2000), associated with *Castanopsis fabri* and *Castanopsis fargesii* in Wanmulin, Fujian (Huang et al. 1997), associated with *Castanopsis cuspidata* var. *carlesii* in Taiwan (Tang et al. 2013). *Schima argentea* associated with *Castanopsis carlesii* var. *spinulosa* in Jinyunshan, Chongqing (Zeng et al. 2010). *Schima sinensis* associated with *Castanopsis platyacantha* on Mt. Emei, Sichuan (Yang et al. 1994; Tang et al. 2007). *S. wallichii* associated with *Castanopsis sieboldii* in Okinawa, southwestern Japan (Xu et al. 2008). *S. wallichii* associated with *Castanopsis tribuloides* in Bhutan



Himalaya (Wangda and Ohsawa 2006), associated with *Castanopsis indica* in eastern Nepal Himalaya (Ohsawa 1986), and associated with *Castanopsis lanceifolia* in Meghalaya, NE India (Tripathi and Shankar 2014).

The Shannon-Wiener index H' of our studied primary forests and secondary forests is 2.563 ± 0.48 (average \pm SD) and 2.232 ± 0.36 , respectively. The indices of the forests in Yunnan are higher than those (1.768 for Dongbeishan, 1.566 for Fuzhou) of the *Schima superba*-*Pinus massoniana* forest in Dongbeishan, Zhejiang (Wang et al. 2015) and in the National Forest Park of Fuzhou, Fujian (Cheng 2006), and higher than those (1.255–1.886) of *Castanopsis platyacantha*-*Schima sinensis* forest in Wawushan, Sichuan (Bao et al. 2000), also higher than

that (1.72) of *Schima superba*-*Castanopsis sclerophylla* forest and that (2.19 ± 0.46) of *Schima superba* forest in Tiangtong, Zhejiang (He et al. 1998), while the indices in Yunnan are lower than that (2.76) of *Schima superba*-*Castanopsis carlesii* in Tiantong (He et al. 1998), Zhejiang and that (3.150) of *Castanopsis chinensis*-*Schima superba* in Dingfoshan, Guangdong (Huang et al. 2000). This is probably related to the different degrees of naturalness of the forests in the various study sites.

Ecological traits

The seven *Schima* species grow in a warm or mild climate with ample moisture and humidity in the study area. They mainly regenerate in canopy gaps formed

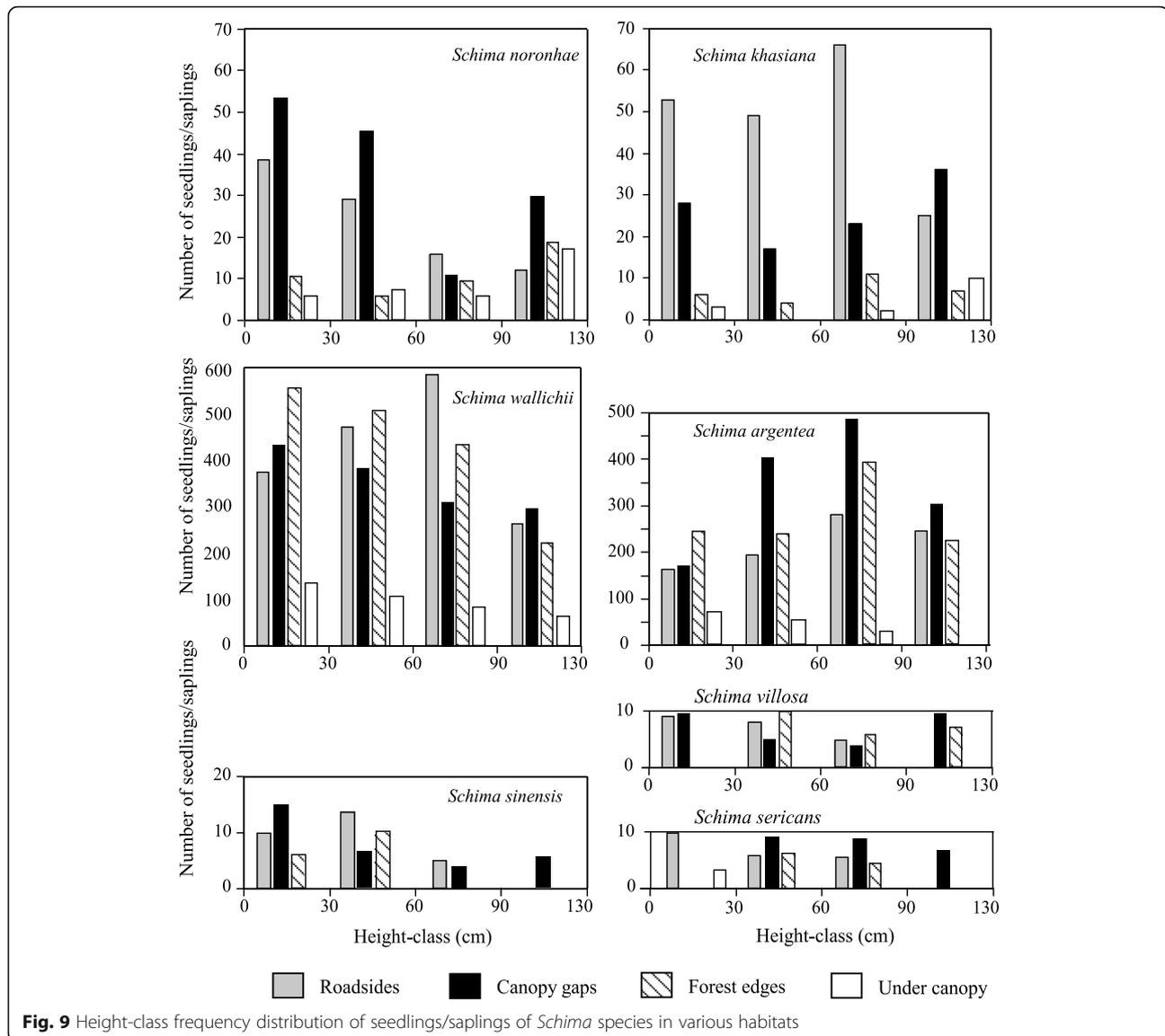


Fig. 9 Height-class frequency distribution of seedlings/saplings of *Schima* species in various habitats

The *Schima* species under this study, ecological traits are similar to those of *Schima superba* in eastern China, which is a fast-growing tree with a higher growth rate during its youth (Wei 2017) and has a growth plasticity and a certain shade-tolerance, meanwhile forest canopy gaps support its seed germination and seedling/sapling establishment (Song 2007). The *S. superba* forest in Guangxi is an earlier type of recovering evergreen broad-leaved forest resulting from serial communities following destruction of original evergreen broadleaved forest through progressive succession. It will be replaced by *Castanopsis* species (Wang and Li 1999). In our study area of Yunnan, *S. noronhae* is found in the primary forests at the late successional stage as the top dominant, and either *S. khasiana*, *S. wallichii*, *S. villosa* or *S.*

sinensis presents as one of the dominants in both late successional forests and early or middle-seral successional forests. However, *S. argentea* or *S. sericans* as one of dominants is only found in early or middle successional forests. As time goes by, the dominance of *S. argentea* and *S. sericans* would be replaced by their associated dominant taxa such as *Castanopsis* species (Supplementary Table S2).

In view of the potential effects of global climate warming on distribution, the *Schima* species under study may be forced to move to locations at higher latitudes or altitudes. *Schima* species in general have as strong dispersal capacity because of their lightweight and the fact that the seeds are wind-dispersed, so, they possibly can migrate to new sites. But they may not be able to evolve

needed new adaptations to new localities in the time projected for a rapid climate change. Especially, *Schima sericans* endemic to NW Yunnan and SE Tibet and *Schima villosa* endemic to Yunnan and having a narrow distribution range will be greatly vulnerable under rapid global climate change.

Conclusions

Yunnan is found to harbor a high species richness and rarity-weighted richness of *Schima*. Canopy gaps created by moderate human and natural disturbances have supported *Schima* species' regeneration establishment in forming a mosaic of forest stand structure across the landscape in the subtropical zone of Yunnan. Some of the *Schima* species studied as a second dominant (rare as the top-dominant) present in the late-successional forests. Some of them are more often found as the top-dominant in early or middle successional forests, where as time goes by the dominance of *Schima* species would be replaced by associated dominant taxa such as *Castanopsis* species. *Schima* species can be used for restoration projects to restore native forests as part of the subtropical evergreen broad-leaved forest ecosystem.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s40663-020-00244-1>.

Additional file 1. Supplementary Table S1. DBH-classes of species (IV $\geq 1.5\%$) of each primary forest type.

Additional file 2. Supplementary Table S2. DBH-classes of major species (RIV $\geq 1.5\%$) of each secondary forest type.

Abbreviations

DBH: Diameter at breast height; RIV: Relative importance value; SD: Standard deviation; H: Height

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Not applicable.

Authors' contributions

C.Q.T. designed the study, analyzed the data and wrote the manuscript. P.-B.H. organized and analyzed the data. S.L. identified the botanical specimens. C.Q.T., L.-Q.S., P.-B.H., D.-S.H., Y.-F.L., M.-C. P., C.-Y. W., X.-S. L., W. L. and Z.-Y.Z. conducted the fieldwork. All the authors contributed discussion to improve the manuscript.

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Availability of data and materials

The datasets generated and/or analyzed during the current study are not publicly available due limitation from the organization provided the research fund but are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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