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Forest and population characteristics of vulnerable relict *Pseudotsuga sinensis* in southwestern China

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ABSTRACT: *Pseudotsuga sinensis*, a vulnerable relict coniferous tree species, faces threats from overexploitation and habitat loss. Despite its status, the forest types, community structure, and population characteristics of this species in China have remained largely unknown. In our study, we conducted analyses of 69 vegetation plots where *P. sinensis* was the dominant species in southwestern China. We identified five forest types, i.e., Type 1: *Pseudotsuga sinensis* evergreen coniferous forest; Type 2: *Pseudotsuga sinensis* - *Pinus yunnanensis* evergreen coniferous forest; Type 3: *Pseudotsuga sinensis* - *Cyclobalanopsis glaucoides* evergreen coniferous and broad-leaved mixed forest; Type 4: *Pseudotsuga sinensis* - *Platycarya strobilacea* evergreen coniferous and deciduous broad-leaved mixed forest; Type 5: *Pseudotsuga sinensis* - *Calocedrus macrolepis* evergreen coniferous forest. These forests exhibited a multilayered vertical structure. The Simpson diversity index ranged between 0.58-0.86, while the Shannon-Wiener diversity index ranged from 1.24 to 2.3. *P. sinensis* trees' average growth rate of ring width decreased from 5.86 to 0.33 mm/year as increasing ages. Observed maximum age of *P. sinensis* was 115 years with 78 cm diameter at the breast height. Age frequency distribution of *P. sinensis* was multimodal. There was a great lack of individuals at 0-20 years old. Forests with moderate disturbance showed a significantly higher number of *P. sinensis* individuals younger than 30 years compared to areas with no, slight, or severe disturbance. *P. sinensis*' regeneration depends on moderate disturbance. We recommended delineating buffer zones in the protected areas at certain sites and in such zones can be allowed to sustainable firewood cutting by selectively marked species other than *P. sinensis*.

KEY WORDS: Age structure, forest characteristics, growth patterns, *Pseudotsuga sinensis*, regeneration, species diversity.

INTRODUCTION

In East Asia, numerous subtropical/warm temperate coniferous species are relict plants (Tang *et al*., 2018). Many relict tree species face the threat of human-induced overexploitation, resulting in a continuous decline in their populations. The survival of these relict plant species in the wild strongly depends on their ability to regenerate in natural habitats (Tang, 2015). Forest and population structure of tree species can indicate regeneration characteristics and future stability, as well as influence forest biodiversity (Singh *et al*., 1986; Tang, 2015; Seidler, 2017). Many relict coniferous tree species have specific regeneration strategies, and the persistence of populations is maintained by unstable micro-habitats (e.g., Yamamoto, 1992; Tang *et al*., 2015; Qian *et al*., 2015; Tang *et al*., 2023). Comprehensive knowledge on forest stands, habitats, population structure and regeneration of vulnerable relict tree species is critical to effective conservation management.

Fossil records suggest that the genus *Pseudotsuga* was widely distributed in the Northern Hemisphere (e.g., Schorn, 1994; Denk, *et al*. 2005; Palamarev *et al*., 2005; Gugger *et al*., 2010; Yabe, 2011). In warmer climates during the Eocene, *Pseudotsuga* expanded its range as far north as 70° latitude and possibly attained a Holarctic distribution, along with many other temperate floras (Hermann, 1985). The number of extant species of *Pseudotsuga* has long been debated, but it is generally recognized that *Pseudotsuga* contains seven species, two of which occur in western North America (*P. menziesii*, *P. macrocarpa*) and five in eastern Asia (*P. sinensis*, *P. forrestii*, and *P. brevifolia* in mainland China, *P. wilsoniana* in Taiwan, *P. japonica* in Japan). *P. wilsoniana*

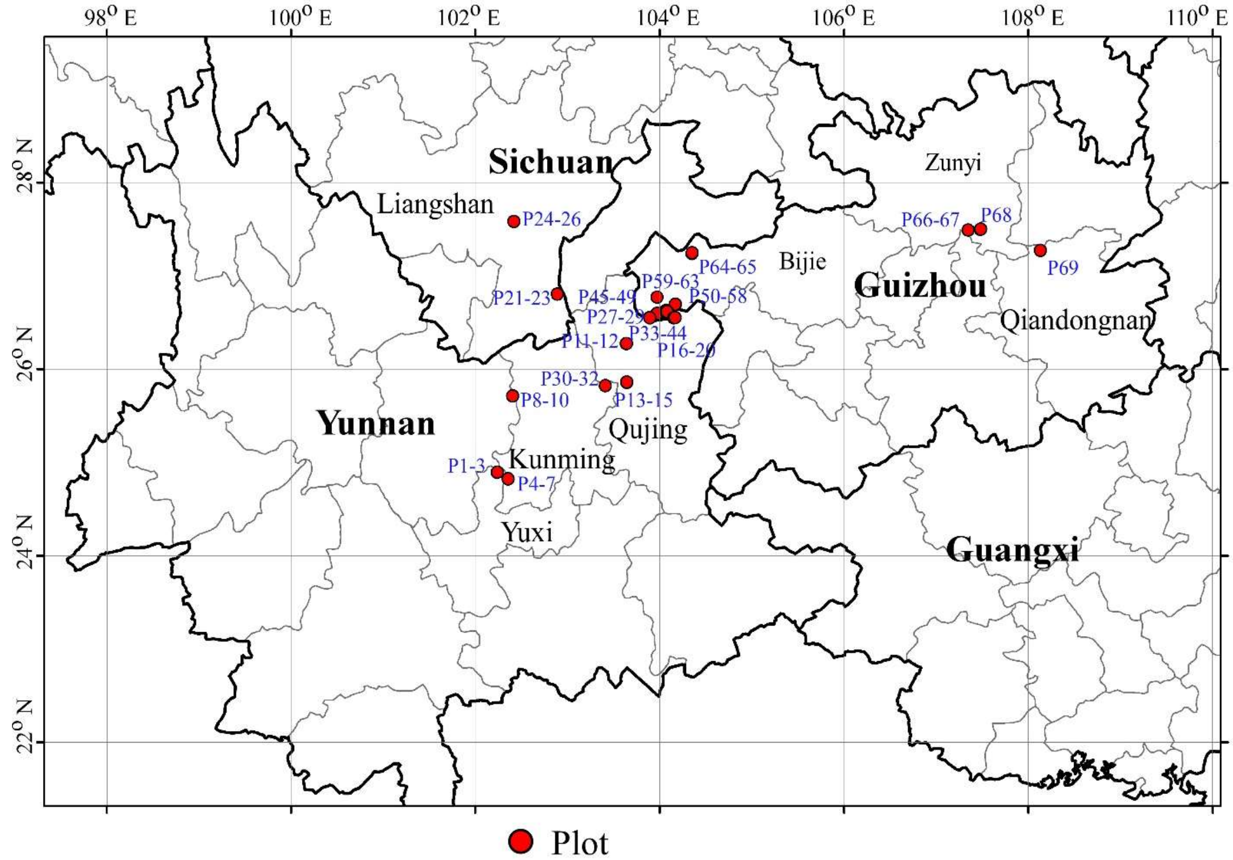

Fig. 1. The distribution of plots of forest stands containing ***Pseudotsuga sinensis*** as the most dominant.

in Taiwan is treated as *P. sinensis* var. *wilsoniana* in Flora of China (FOC, 2022). In this paper we follow Flora of Taiwan (Huang, 2003), we use *P. wilsoniana* as an independent species. According to fossil records and molecular phylogeny, *Pseudotsuga* originated in North America in the Eocene and migrated to Asia through the Bering land bridge during the early Miocene, and diversified into Chinese and Japanese lineages c. 25–20 Mya (Wei *et al*., 2010). The genus is characterized by seed cones bearing trilobed bract scales that exerted far beyond the seed scales. While the American species yield nonreflexed bract scales and acutely or bluntly pointed leaves, the Asian species possess reflexed bract scales and emarginated leaf apices (Yabe, 2011).

Pseudotsuga sinensis is sporadically distributed in southeastern and southwestern China. In northern Vietnam *P. sinensis* is the most common conifer in the karst areas stretching from Ha Giang to Cao Bang and Lang Son (Bac Son). These subpopulations are sometimes identified as *P. sinensis* var. *brevifolia* (Thomas and Yang, 2019). The timber is used for construction, bridge building, furniture and wood fiber (Thomas and Yang, 2019; FOC, 2022). This species is ecologically and economically valuable.

Previous research has conducted preliminary studies on *P. sinensis* communities at several subtropical Chinese sites by various researchers (Zuo, 1995; Chen *et al*., 2001; Guo *et al*., 2007; Meng *et al*., 2008, Xu and Yu, 2010; Li and Xie, 2015; Xiong *et al*., 2017). Nevertheless, a systematic examination of the growth patterns and population structures of *P. sinensis* in forests predominantly dominated by this species has been lacking. Our objectives are to (1) analyze forest types and community structure, (2) elucidate growth patterns, population structure and regeneration characteristics of *P. sinensis* in southwestern China, and (3) propose conservation strategies for this relict species.

MATERIAL AND METHODS

Study areas

We searched forests containing *P. sinensis* as one of the dominants in its distribution range in southwestern China. We established 69 plots located in 12 counties and 1 County-level city (Anning) of Kunming, Yuxi, Qujing Cities in Yunnan Province, Bijie and Zunyi Cities, Qiandongnan Prefecture in Guizhou Province, Liangshan Prefecture in Sichuan Province, southwestern China (Fig. 1; Table S1).

Kunming and Yuxi Cities are situated in central Yunnan-Guizhou Plateau. Qujing is located in eastern Yunnan Province, on the boundaries between Yunnan, Guizhou and Guangxi Provinces.

Bijie City is located in northwestern Guizhou Province, on the boundaries between Yunnan, Guizhou and Sichuan Provinces; its southern boundary is next to Qujing City, Yunnan. Qiandongnan Prefecture is located in southeastern Guizhou, on the boundaries between Guizhou and Hunan Provinces; it is a transition from the Yunnan-Guizhou Plateau to Hunan-Guangxi Hilly Basin. Zunyi City is located in northern Guizhou, on the boundaries between Chongqing Municipality, Guizhou, and Sichuan Provinces; it is a transitional slope zone from Yunnan-Guizhou Plateau to the Hunan hills and the Sichuan Basin. Liangshan Prefecture is located in southwestern Sichuan Province, on the boundaries between the Sichuan Basin and the central plateau of Yunnan Province.

Elevations of the study plots ranged from 800 to 2300 m a.s.l and the soil types are generally red soil and yellow-brown soil. Information on environmental characteristics of plots is shown in Table S1.

The climate of study areas is largely controlled in summer by the Indian Ocean monsoon. For the plots sites, the annual mean temperature is 9.8–16.1˚C. The mean temperature of the warmest month, July, is 16.3–26.1˚C and of the coldest month, January, is 1.1–7.1˚C. The annual mean precipitation is 856–1129 mm, and the evapotranspiration is 602–843 mm. The moisture index is 0.9–1. These data on the plot sites were extrapolated from the observed data during 50 years (1950–2000) of local climatological stations.

Species

Pseudotsuga sinensis, specifically referring to *P. sinensis* var. *sinensis i*n this paper, is an evergreen coniferous canopy tree species. Trees reach 50 m tall and 100 cm DBH (diameter at the breast height (1.3 m tall)). The bark exhibits a gray to dark gray coloration, appearing irregularly and thickly scaly with a corky texture. Its leaves are pectinately arranged, linear, with two whitish bands of stomata beneath. Seed cones are pale purple, glaucous, eventually maturing to a purplish brown hue, with shapes varying from ovoid to ellipsoid or conical-ovoid. The bracts are reflexed, with a narrowly triangular cusp and an obtuse apex (FOC, 2022).

Data collection and analyses

We established 69 plots to include various types of *P. sinensis*-dominated plant communities in southwestern China including Yunnan, Guizhou and Sichuan Provinces. The plot size is 400 m^2 based on the smallest area for the maximum number of species. We divided each plot into subplots. The size of each subplot was 10 m × 10 m. For the species in each plot, all individuals at least 1.3 m tall were identified to species level, numbered and tagged, and their diameter at breast height (DBH) and height were recorded. In addition, general information about each plot was noted, such as slope position, altitude, slope exposure, slope inclination, as well as human disturbance history. Woody stems (≥ 1.3 m tall) in the overstory were classified into two categories based on their vertical position and height: arborous layer (height ≥ 5 m) and shrub layer (1.3 m ≤ height < 5 m tall). The arborous layer included emergent (height > 25 m), canopy (10 m ≤ height ≤ 25 m), subcanopy (5 m ≤ height < 10 m) sublayers. All woody species less than 1.3 m tall in the understory, each individual was identified to species level, counted, and measured for height and percent cover. Based on the classification on forest vertical layers, we elucidated forest stratification using the frequency distribution in height-classes of woody species (height ≥ 1.3 m).

We specifically noted microhabitats of *P. sinensis* seedlings. In each plot, we set up five 1 m × 1 m squares selected for investigation for the herbaceous taxa in the understory. Five 1 m × 1 m squares were respectively located in the four corners and the center of each subplot. Herb taxa in the understory were identified and the coverage and number of individuals of each species were recorded.

We obtained 45 increment cores from *P. sinensis* trees of varying DBHs in the study plots (the plot area in total: 27,600 m^2). For each tree trunk, a single increment core was taken from at 1.3 m above ground level. The length of time from the position at 1.3 m in height to ground level was estimated to be seven years based on the tree rings in the stem base of saplings with a height ≤ 1.3 m. The seven years was added to the data of ages we obtained from each increment core. In addition, we obtained five *P. sinensis* saplings with a DBH ≤ 5 cm and cut the stem at the positon at 1.3 m above the ground level for each sapling to obtain its cross section for age based on tree rings, because it is difficult to use increment borers to get increment cores from trees with DBHs ≤ 5 cm. Tree age was determined using the software WinDENRO tree ring analysis system (Regent Instruments Inc., Canada). We used the data on ages and DBHs of the 50 tree samples to obtain a formula on correlation of ages and DBHs. Then we used the formula to calculate ages of *P. sinensis* trees according to the measured DBHs of *P. sinensis* trees in the study plots. From the tree ring analysis, we were also able to determine ring widths and to calculate basal area increments (BAI). The following formula was used to calculate BAI: T-Y, where T is the basal area at year X (last year of growth) and Y is the basal area of the tree measured up to the year previous to X. BAI is used in forest growth studies because it accurately quantifies wood production based on the ever-increasing diameter of a growing tree (Rubino and McCarthy, 2000).

For all woody individuals ≥ 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. To measure the abundance of species, we used relative importance value (RIV) = (Relative density + Relative basal area)/2 for species in the overstory, and RIV = (Relative density + Relative coverage)/2) for species in the understory (Tang *et al.*, 2022). Plant communities were classified using a floristic similarity dendrogram with Sørensen and Ward's Method (McCune and Mefford, 2016). The communities were named by dominant/indicator species of the overstory. Diversity was calculated for each forest stand using species richness (number of species), Simpson's diversity index D (Lande, 1996), Shannon-Wiener's diversity index H′ (Pielou, 1969).

To compare the status of regeneration and population structure among sites with varying levels of disturbances, we assessed the intensity of disturbances in each plot using specific criteria. These criteria indicated the degree of disturbances, which included logging or frequent harvesting for fuel wood, cultivating medicinal herbs or vegetable crops in the forest understory, cattle and sheep entering the forest, selective cutting within the last 30 years, and the presence of steep slopes prone to landslides. As a result, we categorized the intensity of disturbances into three groups:

(1) Low intensity: Characterized by no distinctive interventions, being untouched or nearly untouched, and the absence of natural disturbance such as the presence of steep slopes.

(2) Moderate intensity: This category included one of the last two disturbances, namely selective cutting or the presence of steep slopes.

(3) Severe intensity: involving two or more of the mentioned interventions above.

Differences in species richness and diversity indices among habitats, also differences among number of young trees of *P. sinensis* in forests with various intensities of human disturbances were analyzed by the nonparametric Kruskal–Wallis all-pairwise comparisons test, using Analyse-it (version 5.11.3, Analyse-it Software, Ltd., 2019).

RESULTS

Forest types and stratification

Based on 69 vegetation plots, five distinct forest types (at the 55% floristic similarity threshold) were classified according to the floristic similarity cluster analysis (Fig. 2A). The five forest types were as follows: Type 1 — *Pseudotsuga sinensis* evergreen coniferous forest; Type 2 — *Pseudotsuga sinensis* - *Pinus yunnanensis* evergreen coniferous forest; Type 3 — *Pseudotsuga sinensis* - *Cyclobalanopsis glaucoides* evergreen coniferous and broad-leaved mixed forest; Type 4 — *Pseudotsuga sinensis* - *Platycarya strobilacea* evergreen coniferous and deciduous broad-leaved mixed forest; Type 5 — *Pseudotsuga sinensis* - *Calocedrus macrolepis evergreen* coniferous forest.

Type 1: *Pseudotsuga sinensis* evergreen coniferous forest at elevations of 1920-2300 m in Anning City, Xundian, Zhanyi, Luquan, Xuanwei Counties of Yunnan, and Weining, Hezhang Counties of Guizhou, Puge County of Sichuan. The habitats are steep slopes or along road sides (Fig. 2A; Table S1). *P. sinensis* reached 37 m tall in the emergent sublayer (height > 25 m), and absolutely dominated the canopy (10 m ≤ height ≤ 25 m), subcanopy (5 m ≤ height < 10 m) and shrub layer (1.3 ≤ height < 5 m) (Fig. 2B). The accompanying species were *Alnus nepalensis*, *Ternstroemia gymnanthera*, *Pinus yunnanensis*, *Pinus armandii*, *Quercus spinose*, etc. In the shrub layer, major species were *Rhododendron spinuliferum*, *Corylus yunnanensis*, *Cotoneaster franchetii*, etc. In the understory, herbaceous species were mainly *Pteris cretic, Ainsliaea latifolia, Oplismenus undulatifolius*, etc.

Type 2: *Pseudotsuga sinensis* - *Pinus yunnanensis* evergreen coniferous forest at elevations of 1910-2270 m in Xundian, Zhanyi and Huize Counties of Yunnan, Weining and Hezhang Counties of Guizhou, Huidong County of Sichuan. The habitats are mostly steep slopes or along road sides (Fig. 2A; Table S1). *P. sinensis* and *Pinus yunnanensis* respectively reached 27 m and 36 m tall in the emergent sublayer (Fig. 2B). In the canopy, *P. sinensis* and *Pinus yunanensis* were co-dominants, and accompanying species were *Schima argentea, Acer davidii*, *Cyclobalanopsis glaucoides*, etc. In the subcanopy, it was mainly occupied by *P. sinensis* along with *Keteleeria evelyniana, Pinus yunnanensis, Juglans regia*, etc. In the shrub layer, *Rhododendron* spp., *Myrica nana, Pyracantha fortuneana, Campylotropis macrocarpa*, etc. were present. In the understory, herbaceous species were mainly *Ainsliaea latifolia, Athyrium dissitifolium, Oplismenus undulatifolius*, etc.

Type 3: *Pseudotsuga sinensis* - *Cyclobalanopsis glaucoides* evergreen coniferous and broad-leaved mixed forest at elevations of 1910-2180 m in Anning City, Luquan and Weining Counties of Guizhou, Huidong County of Sichuan. This forest type is mainly distributed in slope sides of gullies (Fig. 2A; Table S1). *P. sinensis* reached 27 m tall in the emergent sublayer. *P. sinensis* mainly occupied the canopy, but *P. sinensis* and *Cyclobalanopsis glaucoides* co-dominated the subcanopy (Fig. 2B). Accompanying species were *Pinus armandii*, *Keteleeria evelyniana, Pinus yunnanensis, Photinia glomerata,* etc. In the shrub layer, there were mainly *Viburnum foetidum* var. *ceanothoides, Rhododendron* spp., *Lyonia macrocalyx, Berberis pruinosa* and some saplings of canopy species. In the understory, herbaceous species were abundant, including *Athyrium biserrulatum, Ophiopogon bodinieri, Ageratina adenophora*, etc.

Type 4: *Pseudotsuga sinensis* - *Platycarya strobilacea* evergreen coniferous and deciduous broad-leaved mixed forest at elevations of 815–1030 m in Shibing, Meitan Counties of Guizhou. It is found on steep slopes and ridges in the limestone area (Fig. 2A; Table S1).

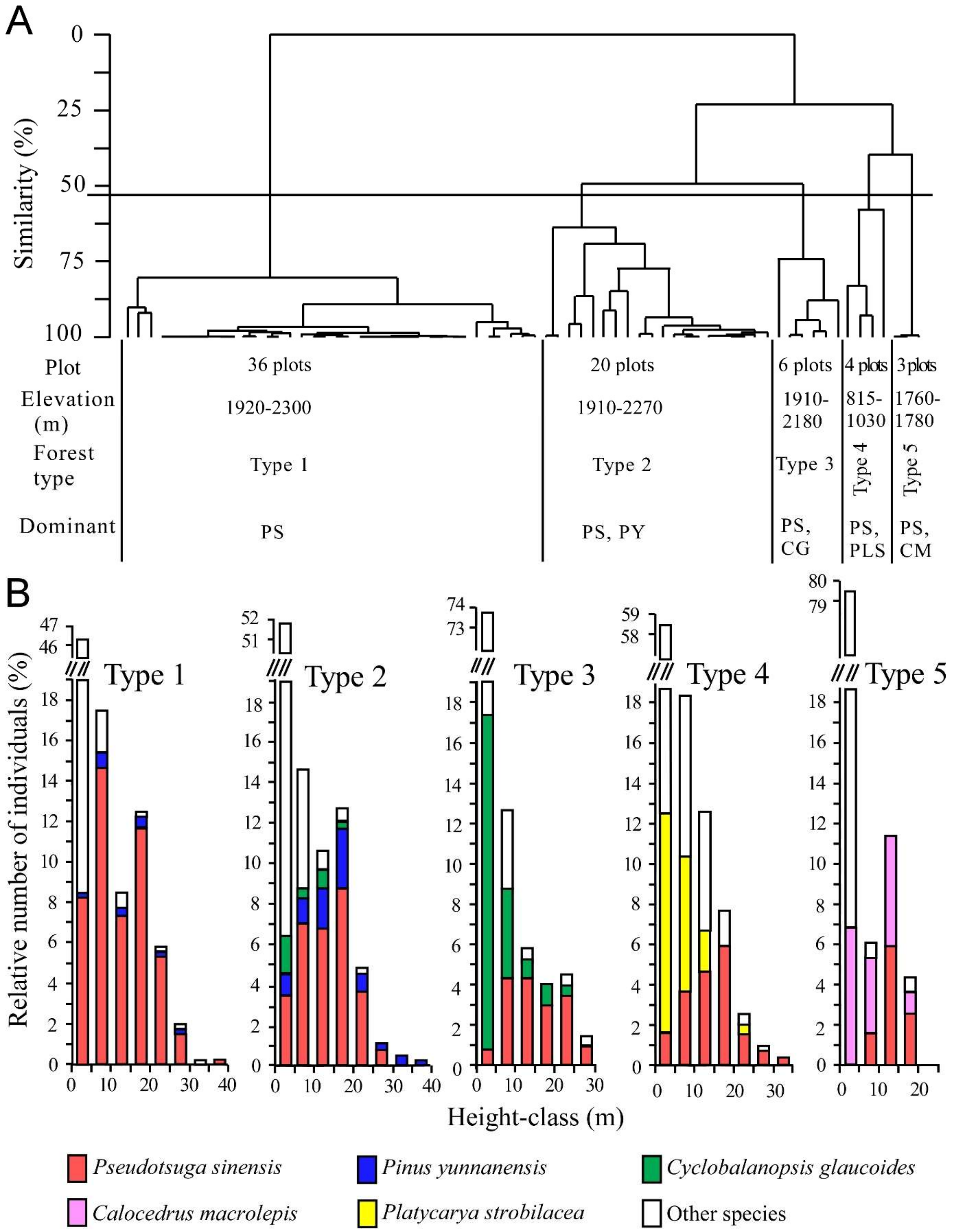

Fig. 2. Floristic similarity dendrogram for the 69 plots (**A**) and frequency distribution in height-classes of woody species (height ≥ 1.3 m) of each forest type (**B**). ***Type 1***: *Pseudotsuga sinensis* evergreen coniferous forest; ***Type 2***: *Pseudotsuga sinensis - Pinus yunnanensis* evergreen coniferous forest; ***Type 3***: *Pseudotsuga sinensis - Cyclobalanopsis glaucoides* evergreen coniferous and broad-leaved mixed forest; ***Type 4***: *Pseudotsuga sinensis - Platycarya strobilacea* evergreen coniferous and deciduous broad-leaved mixed forest; ***Type 5***: *Pseudotsuga sinensis - Calocedrus macrolepis evergreen* coniferous forest. PS = *Pseudotsuga sinensis*, PY = *Pinus yunnanensis*, CG = *Cyclobalanopsis glaucoides*, PLS = *Platycarya strobilacea*, CM = *Calocedrus macrolepis*.

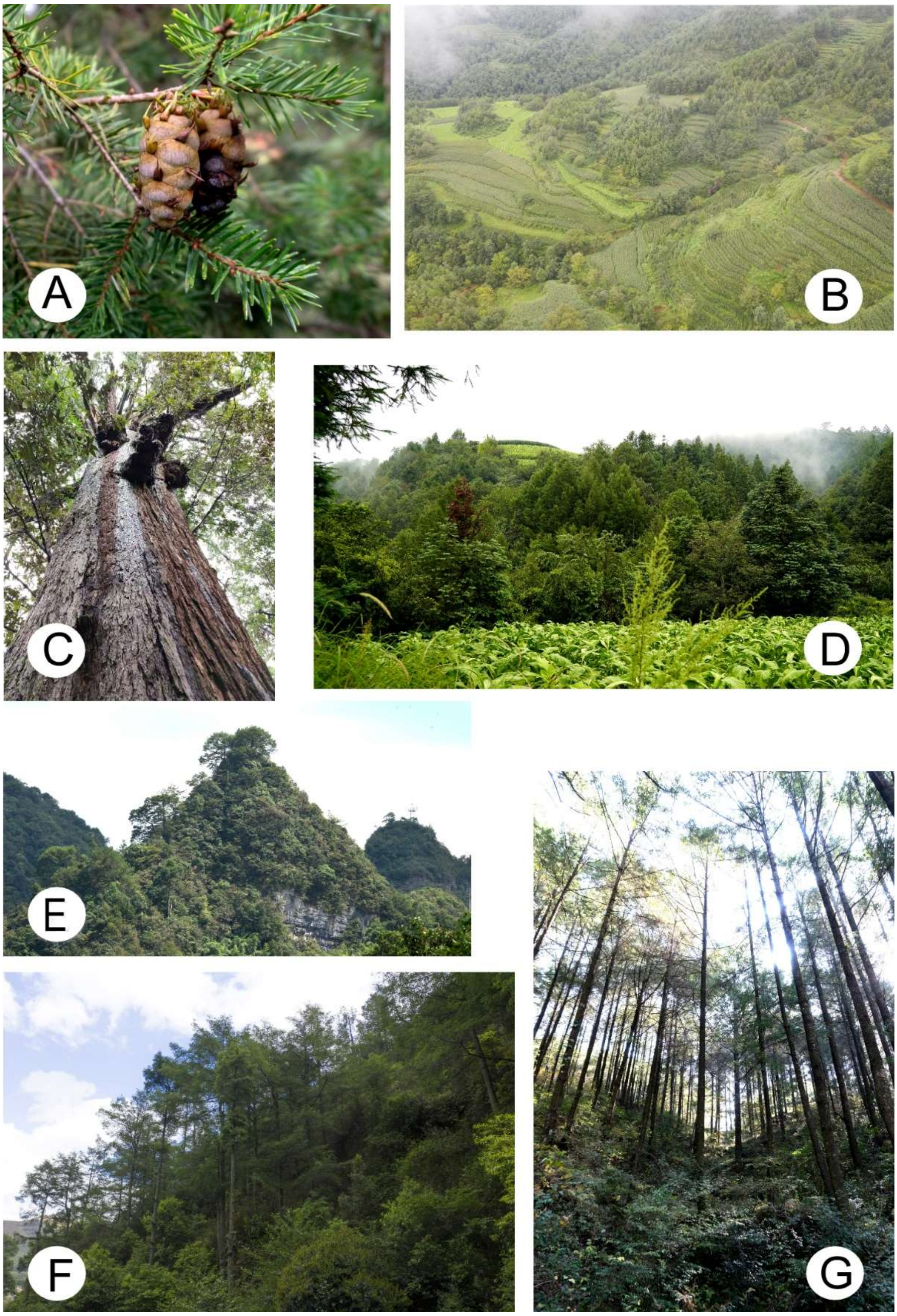

Fig. 3. *Pseudotsuga sinensis* and its representative forest stands and habitats in southwestern China. **A.** Seed corns of *P. sinensis*; **B.** A *P. sinensis* forest was fragmented by the conversion of forest land to agriculture field at ca. 2200 m a.s.l. in Zhaxiang, Weining County, Guizhou; **C.** A *P. sinensis* tree with 137 cm DBH and 28 m tall at ca. 2110 m a.s.l. in Maoshan Zhen, Luquan, Yunnan; **D.** A fragmented forest stand of *P. sinensis* by a crop field at ca. 2060 m a.s.l. in Sijiacun, Dachong Zhen, Huidong County, Sichuan; **E.** *P. sinensis* trees grow on a limestone ridge at ca. 1030 m a.s.l. in Daxigou, Xinnan Zhen, Beitan County, Guizhou; **F.** A *P. sinensis* forest at ca. 1990 m a.s.l. in Yuanlianghoushan, Anning City, Yunnan; **G.** A *P. sinensis* forest at ca. 2040 m a.s.l. in Changtang Zhen, Xuanwei City, Yunnan Photographs: Jian-Ran Wen for (A)-(C), (E)-(G), Min-Rui Du for (D).

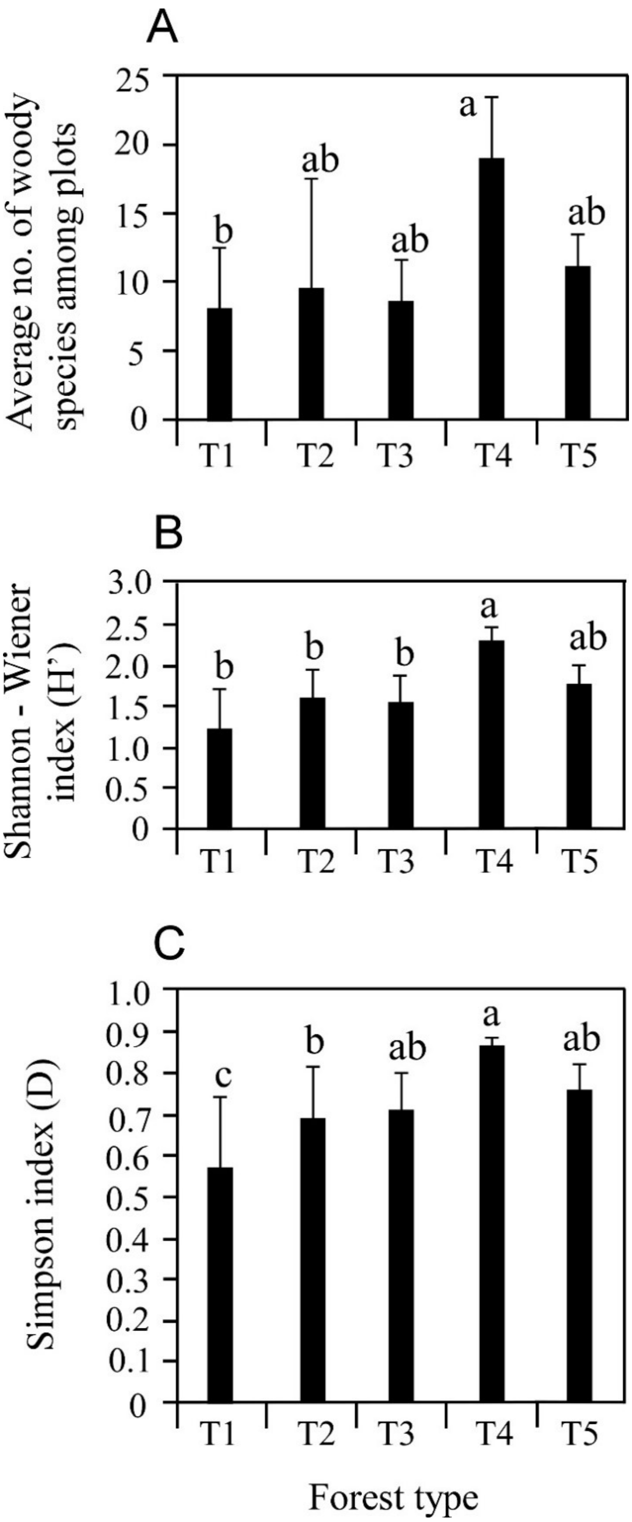

Fig. 4. Woody species (height ≥ 1.3 m) diversity of each forest type. T1 = Type 1; T2 = Type 2; T3 = Type 3; T4 = Type 4; T5 = Type 5. In (A)-(C), forest sharing the different letters differ significantly; sharing the same letters do not differ significantly by the non-parametric Kruskal-Wallis all-pairwise comparisons test ($p < 0.05$). Bar: Standard deviation.

P. sinensis reached 32 m tall in the emergent sublayer. *P. sinensis* mainly occupied the canopy, but *P. sinensis* and *Platycarya strobilace* co-dominated the subcanopy (Fig. 2B). Accompanying species were *Pinus massoniana*, *Liquidambar formosana, Cyclobalanopsis myrsinifolia*, etc. In the shrub layer, there were *Rhamnus virgate, Eurya loquaiana, Myrsine Africana, Metapanax davidii*, etc. In the understory, herbaceous *Cyperus rotundus*, *Pyrrosia lingua, Ainsliaea latifolia,* etc. were present.

Type 5: *Pseudotsuga sinensis - Calocedrus macrolep* is evergreen coniferous forest at elevations of 1760-1780 m in Yimen County of Yunnan. This type of forest is found on both gentle and steep slopes nearby villages (Fig. 2A; Table S1). *P. sinensis* and *Calocedrus macrolepis* co-dominated the canopy and subcanopy (Fig. 2B). Accompanying species were *Pinus armandii, Cyclobalanopsis myrsinifolia*, etc. In the shrub layer, mainly were saplings of some canopy species, along with shrubs *Spatholobus suberectus*, *Rubus Irenaeus*, *Rhamnus leptophylla*, etc. In the understory, herbaceous *Ophiopogon intermedius*, *Ageratina adenophora, Dryopteris fuscipes, Solanum violaceum*, etc. were present.

Pseudotsuga sinensis and its representative forest stands and habitats are shown in Fig. 3.

Forest species diversity

We recorded a total of 381 plant species in 98 families and 237 genera. Among all the taxa, 10 species in 3 families and 8 genera were gymnosperms, 343 species in 86 families and 210 genera were angiosperms, 28 species in 9 families and 19 genera were ferns. According to (Wu, 1991, 1993), among seed plants, tropical and temperate elements were respectively 40.6% and 29.7% for families, and respectively 16.3% and 26.1% for genera; tropical and subtropical East Asia and South Tropical America disjunctive distribution elements were 10.9% and 1.1% for families and genera, respectively; tropical Asia elements were 1.6% and 12% for families and genera, respectively. Other elements are shown in Supporting Information Table S2. Thus the floristic features of the forests were warm-temperate/subtropical (the transition from tropical to temperate) affinities.

The species composition of the arborous layer, shrub layer and understory for each forest type is shown in Tables S3-S5, respectively.

Species richness and diversity indices for each forest type are shown in Fig. 4. Average number of woody species among plots of each forest type ranged from 8 to18, and significantly differed between Type 1 (8 species) and Type 4 (18 species) ($p < 0.05$) (Fig. 4A). Shannon-Wiener diversity index ranged from 1.24–2.3. Types 1, 2 and 3 had significantly lower values than that of Type 4 , and Type 5 showed no significant difference from the other four forest types ($p < 0.05$) (Fig. 4B). Simpson diversity index ranged from 0.58 to 0.86. Type 1 had significantly lower value (0.58) than those of the other four forest types ($p < 0.05$) (Fig. 4C).

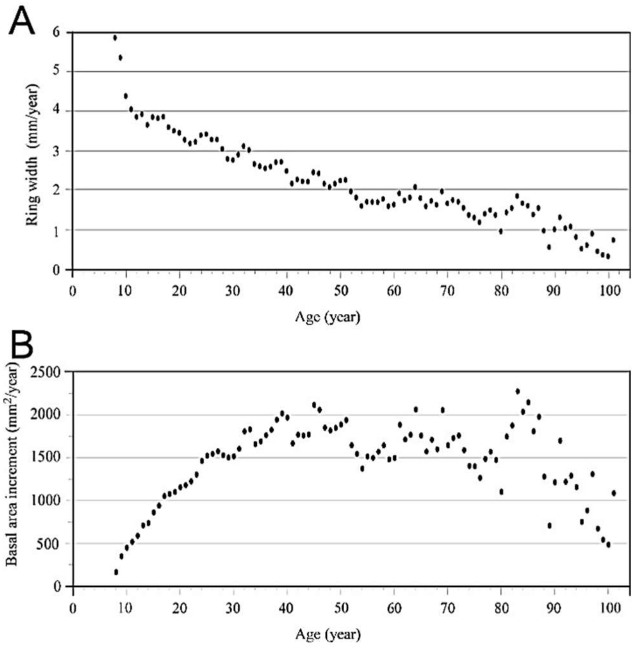

Fig. 5. Growth trends of *Pseudotsuga sinensis*. **A.** The ring width for trees (height ≥ 1.3 m) at various ages; **B.** The basal area at the breast height (1.3 m tall) increment for trees at various ages. Each dot represents the mean value of the tree core samples at a given age.

Population characteristics

Growth patterns

The relationship between DBH and the age of *P. sinensis* is shown in Fig. S1, demonstrating a strong positive correlation ($y = 1.37x + 11.708$, $R^2 = 0.635$, $n = 50$). The correlation was found to be statistically significant ($p < 0.05$).

Among the 45 tree core samples, *P. sinensis* trees' ring width and basal area increments exhibited high variability (Fig. 5, Table S6). The average growth rate of *P. sinensis* trees' radius (ring width) decreased from 5.86 to 0.33 mm/year as the trees aged (Fig. 5A, Table S6). The basal area increments (BAI) of *P. sinensis* trees initially increased for the first 39 years, reaching 2015 mm^2/year at the end of this period. Subsequently, there was a decrease, albeit with fluctuations between years (Fig. 5B, Table S6).

Age structure and regeneration

The estimated age-class frequency distribution of individuals of *P. sinensis* in each forest type was multimodal (Fig. 6). The observed maximum age of *P. sinensis* was 115 years in forest Type 1, while it was respectively 95, 85, 80 and 75 in forest Types 2, 3, 4 and 5. In general, *P. sinensis* trees were continuously distributed between 20–75 years old. There was a great lack of individuals with ages at 0–20 years. Number of trees older than 75 years was very limited. The age structure had a similar pattern to that of the frequency distribution in DBH-classes of individuals of *P. sinensis* (Fig. S2).

The number of *P. sinensis* individuals younger than 30 years old was significantly higher in forest stands experiencing a moderate intensity of disturbance compared to those subjected to low or severe intensity of disturbance. However, there wasn't a significant difference in the numbers between areas with low intensity of disturbance and those with severe intensity of disturbance ($p < 0.05$) (Fig. 7). Moderate disturbance includes occasionally selective cutting within the recent 30 years or habitats located alongside roads or on steep slopes prone to landslides. Severe disturbance encompasses logging or cultivating vegetable crops in the forest understory or frequent entry of cattle and sheep into the forests.

Pseudotsuga sinensis seedlings were shade intolerant and number of seedlings under canopy was rather limited, especially when the height of seedlings reached 60 cm. Established seedlings/saplings at last remained in quite open microhabitats including canopy gaps, forest edges and roadsides, where moderate disturbances occurred (Fig. S3).

DISCUSSION

Forests and regeneration

The comparison between *P. sinensis* and its forests and other species of *Pseudotsuga*, along with their respective forests in mainland China and Taiwan, is detailed in Table 1. In southwestern mainland China, *P. sinensis* as the most dominant species is found in highly fragmented or patchy forests at 800-2300 m a.s.l. on steep or gentle slopes or limestone areas. *P. sinensis* is found in mountain slopes and hills at 800–1600 m a.s.l in southeastern subtropical mainland China. However, its major associated canopy species in the two regions are different. There are *Pinus yunnanensis*, *Cyclobalanopsis glaucoides, Platycarya strobilacea*, *Calocedrus macrolepis* in southwestern mainland China, while there are *Castanopsis eyrei*, *Pinus masoniana*, *Pinus taiwanensis*, *Quercus phillyreoides* in eastern mainland China (Guo *et al*., 2007; Xu and Yu, 2010; Xiong *et al*., 2017). *P. forrestii* was found on steep slopes along rivers in gorgers at ca. 2400 m–3300 m a.s.l. Its associates are mainly *Quercus guyaviolia, Acer davidii, Pinus yunnanensis, Abies georgei* var. *smithii, Tsuga dumosa* (Tang *et al*., 2023). *P. wilsoniana* scattered in Taiwan at elevations between (800) 1000–2200 (2500) m a.s.l (Su, 1980; TaiBIF, 2022). It occurs in broad-leaved forests (Su, 1980), or coexists with *Tsuga chinensis* var. *formosana*, *Calocedrus macrolepis* var. *formosana*, *Pinus taiwanensis*,*Ternstroemia gymnanthera*, *Elaeocarpus japonicas*, *Elaeocarpus sylvestris* in mixed coniferous and broad-leaved forests in Taiwan (Ou, 2004). *P. wilsoniana* grows on slopes of river valleys or rocky cliffs and steep mountain slopes and its maximum DBH was about 85 cm in the Da-siao-jian region of Shei-pa National Park (Ou,

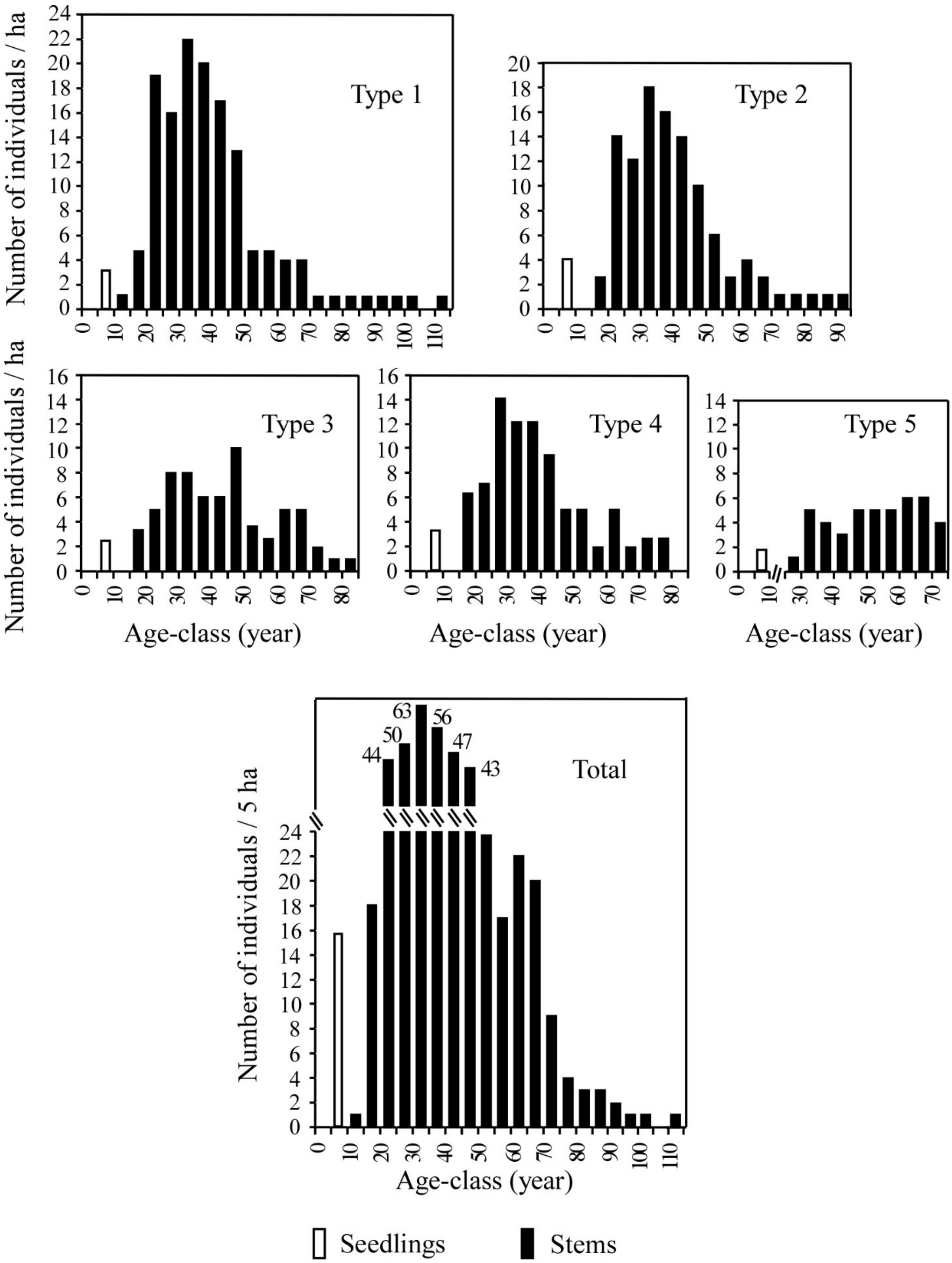

Fig. 6. The estimated age structure of *Pseudotsuga sinensis* (height ≥ 1.3 m) of each forest type.

Table 1. Comparison of *Pseudotsuga sinensis* and its forests with other *Pseudotsuga* species and their respective forests in mainland China and Taiwan.

Species	Distribution region	Major habitats & elevations	Height (m)	DBH (cm)	Age (year)	Major associated species	Source
P. sinensis	SW mianland China	Slopes in hills and mountains or Karst limestone mountain slopes at 800-2300 m a.s.l.	5-27 (37)	10-50 (78)	20-75 (115)	*Pinus yunnanensis, Cyclobalanopsis glaucoides, Platycarya strobilacea, Calocedrus macrolepis, Quercus spinose,* etc.	This study
	SE mainland China	Mountain slopes and hills at 800-1600 m a.s.l.	20-35	15-60	NA	*Castanopsis eyrei, Pinus masoniana, Pinus taiwanensis, Quercus phillyreoides*	Zuo, 1995; Chen et al., 2001; Guo et al., 2007; Xu and Yu, 2010; Li and Xie, 2015; Xiong et al., 2017; Thomas, 2019
P. forrestii	SW mainland China	Steep slopes along rivers in gorgers at ca. 2400 m-3300 m a.s.l.	15-28 (44)	22-70 (145)	53-220 (570)	*Quercus guyaviolia, Acer davidii, Pinus yunnanensis, Abies georgei* var. *smithii, Tsuga dumosa*, etc.	Tang *et al.*, 2023
P. wilsoniana	Taiwan	River valleys, rocky cliffs and steep slopes at (800) 1000-2200 (2500) m a.s.l.	25 (50)	25-85 (200)	NA	*Tsuga chinensis* var. *formosana, Calocedrus macrolepis* var. *formosana, Pinus taiwanensis,Ternstroemia gymnanthera, Elaeocarpus japonicas, Elaeocarpus sylvestris*, etc.	Li, 1975; Su, 1980; Huang, 1994; Ou, 2004; TaiBIF, 2022

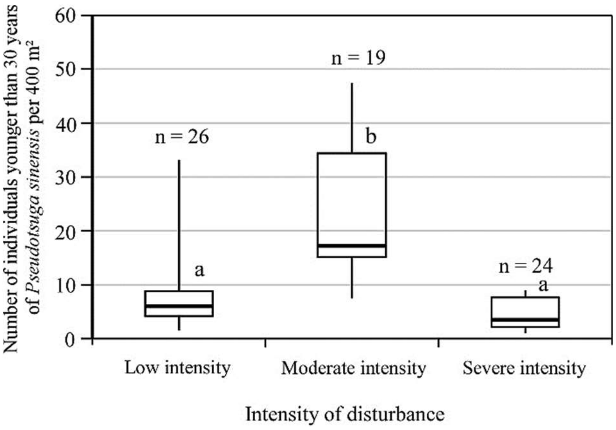

Fig. 7. Number of individuals younger than 30 years old of *Pseudotsuga sinensis* under various intensities of disturbances.

2004). In summary, *P. sinensis* has a wider range and more diverse habitats than those of *P. forrestii* and *P. wilsoniana*. Their associated common genera of canopy trees were only a few such as *Pinus* and *Quercus*. *P. sinensis* forests were patchily distributed in the subtropical evergreen broad-leaved forest zone in southwestern and southeastern China, while *P. forrestii* forests are scattered in the altitudinal coniferous forest zone in northwestern Yunnan and southeastern Tibet. *P. wilsoniana* is not a dominant in its forest communities in Taiwan.

Pseudotsuga sinensis' regeneration is poor and there is a great lack of individuals during recent 20 years. Based on our statistical analysis, *P. sinensis* trees younger than 30 years old are significantly more in the forest stands under moderate disturbance than those in the stands without or slight, or severe disturbance ($p < 0.05$). It demonstrates that *P. sinensis* regeneration depends on moderate disturbance. Moreover, this species' dispersal has limited distance by wind, and seedlings are shade intolerant. Established seedlings/saplings are found in canopy gaps, forest edges and roadsides where moderate disturbances occur, by avoiding competition with other species. Such ecological traits are similar to other relict coniferous species exemplified by *Pseudotsuga japonica* (Yamamoto, 1992), *Pseudotsuga forrestii* (Tang *et al*., 2023), *Thuja sutchuenensis* (Tang *et al*., 2015), *Taiwania cryptomerioides* (He *et al*., 2015), *Cathaya argyrophylla* (Qin *et al*., 2016) and *Pseudolarix amabilis* (Zhou *et al*., 2022).

Conservation strategies: recommendations

P. sinensis forests face persistent threats due to unsustainable human activities. In the study areas, major pressures include recurrent firewood cutting, extensive livestock grazing, and cultivation of crops for economic purposes within the forest understory. In China, conflicts between nature reserves and surrounding villages usually exist (Zhang *et al*., 2020). We recommend delineating buffer zones in the protected areas at the sites of Yushicun, Heishizhen in Weining County, and Meileba, ShilianXiang, Meitan County, Guizhou Province, Shaoshangcun, Gongshanxiang in Xundian County, and Jizongqing, Liujiexiang in Yimen County, Yunnan Province. In the protected areas cultivating crops such as medicinal herbs and vegetables for cash gain in the forest understory and heavy grazing by livestock should be prohibited. However, in designated buffer zones, sustainable firewood cutting could be permitted by selectively marked species (e.g., *Pinus yunnanensis*, *Cyclobalanopsis glaucoides*, *Rhammus virgate*) other than *P. sinensis*. This approach aims to create additional space, sunlight, and nutrients, fostering a conducive environment for the regeneration of *P. sinensis*.

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