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Forest characteristics and population structure of *Glyptostrobus pensilis*, a globally endangered relict species of southeastern China

Cindy Q. Tang [a,*], Yongchuan Yang [b,**], Arata Momohara [c], Huan-Chong Wang [d], Hong Truong Luu [e], Shuaifeng Li [f], Kun Song [g], Shenhua Qian [b], Ben LePage [h,i], Yi-Fei Dong [a], Peng-Bin Han [a], Masahiko Ohsawa [j], Buu Thach Le [e], Huu Dang Tran [e], Minh Tri Dang [e], Ming-Chun Peng [a], Chong-Yun Wang [a]

[a] *Institute of Ecology and Geobotany, School of Ecology and Environmental Science, Yunnan University, Dongwaihuan South Road, University Town, Chenggong New District, Kunming, Yunnan 650504, China*
[b] *Key Laboratory of Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing 400045, China*
[c] *Graduate School of Horticulture, Chiba University, 648 Matsudo, Chiba 271-8510, Japan*
[d] *Institute of Botany, Yunnan University, Kunming, Yunnan 650091, China*
[e] *Southern Institute of Ecology, Vietnam Academy of Science and Technology, Ho Chi Minh City, Viet Nam*
[f] *Research Institute of Resource Insects, Chinese Academy of Forestry, Kunming, Yunnan 650224, China*
[g] *School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China*
[h] *Pacific Gas and Electric Company, 3401 Crow Canyon Road, San Ramon, CA 94583, USA*
[i] *The Academy of Natural Science, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA*
[j] *The Nature Conservancy Society of Japan, Mitoyo Bldg. 2F, 1-16-10 Shinkawa, Chuo-ku, Tokyo 104-0033, Japan*

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ABSTRACT

The Chinese water pine *Glyptostrobus pensilis* is the sole surviving species of the genus *Glyptostrobus*. It is endemic to southern China, central Vietnam, and eastern Laos, and today it is nearly extinct in the wild. Forest community characteristics and population structure of *G. pensilis* in China have remained unknown up to now. We investigated six swamp forest stands and analyzed their forest community characteristics (i.e. vertical stratification, species composition, and diversity) and population structure, including the frequency distribution of DBH (diameter at breast height) and age-classes as found in Fujian Province, southeastern China.

The vertical stratifications of all the forest stands were rather simple. The remaining wild specimens ranged from roughly 15 to some 357 years for an average of ca. 85 years, with only a few individuals less than 20 years old. Compared with the stands and populations of *G. pensilis* in Vietnam, the taxonomic compositions of the stands in the two regions were different, except for the dominant species-*G. pensilis*. The Shannon–Wiener index showed the overstory of each stand had much lower diversity (0.26 on average) in Fujian Province than that (1.97 on average) in Vietnam, whereas the diversity indices were about the same (around 2.41) for the understories in the two regions. Furthermore, we discovered 18 *G. pensilis* seedlings at the study sites in Fujian Province. This discovery demonstrates that *G. pensilis* regeneration is extremely poor and its populations are declining, although these populations are relatively healthier than those in Vietnam.

* Corresponding author.
** Corresponding author.
E-mail addresses: cindytang@ynu.edu.cn (C.Q. Tang), ycyang@cqu.edu.cn (Y. Yang), arata@faculty.chiba-u.jp (A. Momohara), 316731046@qq.com (H.-C. Wang), hongtruongluu@gmail.com (H.T. Luu), 12704391@qq.com (S. Li), ksong@des.ecnu.edu.cn (K. Song), qian@fastmail.com (S. Qian), balo@pge.com (B. LePage), dyf9981@qq.com (Y.-F. Dong), baqidehan@qq.com (P.-B. Han), masahiko.ohsawa@gmail.com (M. Ohsawa), thach73@yahoo.com.au (B.T. Le), tranhuudang@gmail.com (H.D. Tran), dangminhtri.nth@gmail.com (M.T. Dang), mchpeng@126.com (M.-C. Peng), cywang@ynu.edu.cn (C.-Y. Wang).

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1. Introduction

East Asia harbors an exceptional assemblage of monotypic genera of Paleogene-Neogene and even Cretaceous age relict plants (Qian, 2001; Manchester et al., 2009; Tang et al., 2018). Today, some of these genera are reduced to a single species with small wild populations occupying specific habitats in subtropical China, as exemplified by *Ginkgo biloba*, *Metasequoia glyptostroboides*, *Glyptostrobus pensilis*, *Cathaya argyrophylla*, *Taiwania cryptomerioides*, and *Davidia involucrata* (Tang and Ohsawa, 2002; Tang et al., 2011, 2012; Zheng et al., 2011; Tang, 2015; He et al., 2015; Qian et al., 2016). Habitat loss, degradation, and overexploitation have played significant and substantial roles in the decline of wild plants in China during the 20th and 21st centuries. At least 200 species have become extinct in the last 50 years (Chinese State Report on Biodiversity Editorial Committee, 1998), and about 5000 species are currently threatened or on the verge of extinction, leaving China to occupy one of the highest priorities for global biodiversity conservation (Volis, 2016). The survival of wild populations of such relict species strongly depends on their ability to regenerate in natural habitats (Tang, 2015). Detailed knowledge of relict plants' forest stands and demographic structure is often a pre-requisite to implementing effective conservation and management strategies for the species and habitats (e.g. Tang et al., 2011; Tang et al., 2012; He et al., 2015).

Glyptostrobus pensilis, commonly known as Chinese water pine or Chinese swamp cypress, is a deciduous, monoecious, wind-pollinated conifer of the Cupressaceae (previously Taxodiaceae). The fossil record of *Glyptostrobus* extends from the Cretaceous to the early Pleistocene (LePage, 2007). The genus was distributed widely in North America and Eurasia during the Eocene and Miocene epochs (Fig. 1A). Increasing global aridity and cooling, as well as landscape stabilization together with increasing competition for resources and habitat by representatives of the Pinaceae, seem to have forced the genus out of North America, Europe, and most of Asia during the Miocene and Pliocene (LePage, 2007). The youngest fossil record of the genus, is from the late early Pleistocene (ca. 1.2 Ma) of central Japan (Momohara, 2011). Today *G. pensilis* grows in swamps or on waterlogged soils along river banks, streams, floodplains, ponds, paddies, and low-lying wet areas in the subtropics of Fujian, Jiangxi, Guangdong, Hunan, Guangxi, and Yunnan Provinces in southern China, the tropics of central Vietnam and eastern Laos (Li and Xia, 2004; Farjon, 2005; Averyanov et al., 2009). The species resembles *Taxodium distichum*, which is common throughout the southeastern United States in general appearance, form, and habit, though the max. DBH (120 cm) and height (30 m) of *G. pensilis* are much smaller (300 cm DBH, 40 m tall for *T. distichum*) (Earle, 2018). When growing in water, *G. pensilis* produces knee-like aerial roots (pneumatophores) that are presumed to assist in bringing oxygen to the root system and/or providing stability to the trees growing in a soft substrate.

The plant fossil record indicates the genus was much more widespread from the Cretaceous to the Pliocene, with large areas covered with bottom-land *Glyptostrobus* forests. In southern China, *G. pensilis* roots were discovered in a peaty soil over large areas in Guangdong Province. The estimated age of some of these roots is 1000 years, indicating that *G. pensilis* trees once formed large forest stands (Xu and Li, 1959). Today *G. pensilis* exists only in small and isolated patches. In eastern Laos, *G. pensilis* trees are rare and less than 250 mature individuals are estimated to occur in small stands in Borikhamxai and Khammouan Provinces (Averyanov et al., 2014). In Vietnam, two populations are known, 18 trees in Trap K'sor and 140 trees in Ea Ral. In addition, four trees have been identified at three sites near Buon Ho Town and Ea Ho Commune.

In China, *G. pensilis* has suffered heavy losses from over-logging, drainage, and cultivation during the 21st century. Agricultural encroachment and excessive harvest of its decay-resistant wood, which is valuable for making coffins, boats, lifebuoys, bridges, buildings, furniture, and cork all contributed to the accelerated disappearance of this species. The genetic diversity of *G. pensilis* at both the species level and within populations is low (Li and Xia, 2005). It was once claimed that there were no *G. pensilis* remaining in the wild in China (Thomas et al., 2011). However, a recent Chinese national project "*Investigating Ancient and Big Trees*" has led to new discoveries of wild *G. pensilis* in the Chinese subtropics. These wild populations in Fujian, Jiangxi, Hunan, Guangdong, and Yunnan Provinces (Fig. 1B) are small and scattered, occur in rice paddies, secondary shrub land, planted forests, or human settlements and support the contention that *Glyptostrobus* is on the verge of extinction. It is listed as a first-grade protected species in the Catalog of the National Protected Key Wild Plants of 1999 and 2011 and, according to the IUCN evaluation criteria, it is categorized as "Critically endangered," with a decreasing number of individuals (Thomas et al., 2011).

Vertical stratifications of *G. pensilis* forest stands can provide information of the light condition in the understory for regeneration. Understanding species diversity of the fragmented forest stands is important for evaluation of the local threatened status because species in a community often interact and depend on each other. Clarification of forest stand characteristics, population sizes, and regeneration status provide valuable ecological indicators and inform future restoration activities. Unfortunately, understanding of the vertical stratification and species composition and species diversity of *G. pensilis* swamp forest stands, as well as the population status and age structure of this endangered species in China, are unavailable, though wild populations of *G. pensilis* have been discovered in Fujian Province, China (e.g. Zheng et al., 2011; Wu et al., 2008; Huang, 2013; Wu, 2016; Lei, 2017). The surviving *G. pensilis* populations and forest stands of Vietnam provide an opportunity to compare the status of this species of Fujian Province with that of Vietnam. The comparison would bring insights to evaluation of the current conservation measures. Therefore, the objectives of this paper are (1) to clarify the swamp community characteristics and population structure of wild *G. pensilis* in Fujian Province; and (2) to compare these Chinese data with those of wild forest stands and populations in Vietnam.

2. Methods

2.1. Study area

We investigated six natural *G. pensilis* stands in south-central and southeastern Fujian Province. The study sites are located at 26°03.687′N–27°8.7167′N, 118°19.637′–119°14.6167′E in Shangloucun, Lingfengcun, Lingfenglu in Pingnan County, Dongshancun and Shanlingcun in Youxi County, and Xianfengshan in Zhouning County (Fig. 1B, C). The elevational range of these populations extends from 1025 to 1300 m above sea level (asl) and is characteristic of the subtropical moist evergreen broad-leaved forest zone with a humid, warm climate. Within this zone, natural azonal forest communities of coniferous *G. pensilis* forest stands are found.

The study area is characterized by a subtropical, humid climate that is largely controlled by the East Asia monsoon. The mean annual temperature ranges from 11 to 19 °C with a warm month mean of 24–29 °C (July) and a cold month mean of 5–10 °C (January). The mean annual precipitation is 1600–1850 mm, of which about 80% falls between March and October. The monthly relative humidity is greater than 83%.

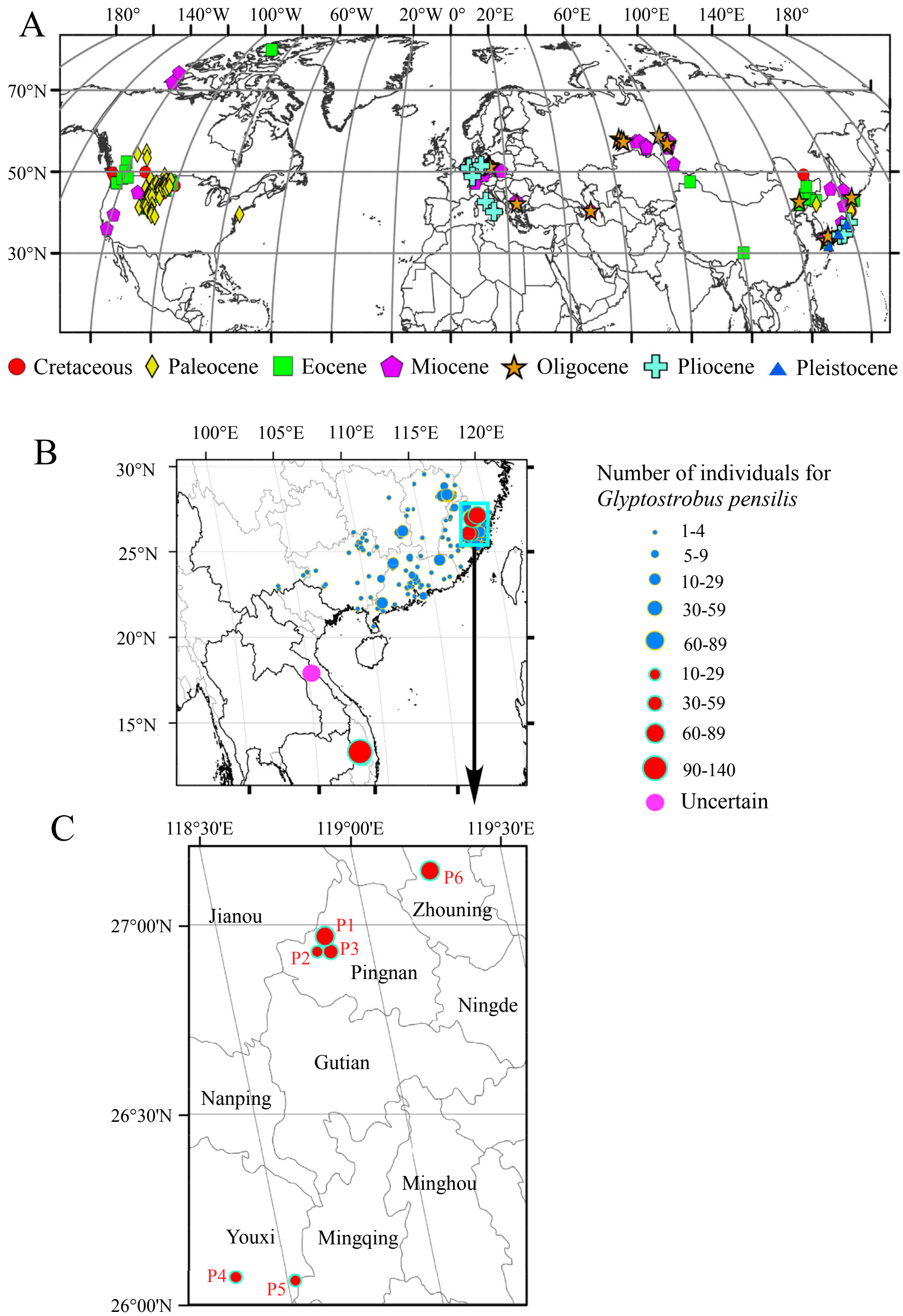

Fig. 1. Distribution of fossil *Glyptostrobus* and extant *Glyptostrobus pensilis*. (A) Fossil occurrences of *Glyptostrobus*. (B) Present-day distribution of *G. pensilis*. (C) The locations of six populations of *G. pensilis* in Fujian, China. Red circles are the wild populations in Fujian and Vietnam, presented in this study. A pink circle indicates the population size is uncertain. P=Population. Data sources for (A): Miki (1941); Miki (1948); Tanai (1961); Shimazu and Teraoka (1962); Tanai and Suzuki (1963); Matsuo (1967); Ishida (1970); Tanai (1970); Hayashi (1975); WGCPC, 1978; Guo and Li (1979); Tanai (1979); Chen et al. (1983); Fujita and Kasama (1983); Tanai and Uemura (1983); Hase (1988); Matthews and Ovenden (1990); Ina (1992); Momohara (1992); Liu et al. (1996); Jin and Sang (1998); Geng et al. (1999); Uemura et al. (1999); Martinetto (2001); Guo and Zhang (2002); Greenwood et al. (2005); Yamakawa et al. (2008); Bozukov and Tsenov (2012); Mathewes et al. (2016); PALEOBIDB (2017). Data sources for (B): Electronic Supplementary Information S1.

2.2. Data collection and analysis

In July 2015 and August 2016, we sought natural *G. pensilis* communities in Fujian Province. We found six natural swamp forests dominated by *G. pensilis* in Pingnan, Youxi, and Zhouning Counties. Local Forestry Bureau staff interviewed elderly residents of local villages and used village records to confirm estimates of the land areas for the six swamp forests and that these swamp forests have never been used. Among these forests, the swamp forest in Shanlingcun, Youxi (Plot 5), which is located in an extremely remote and isolated area, was only discovered by local villages recently, i.e., April, 2014. Experts at the Forestry Bureau of Youxi Country and Fujian Province confirmed the pristine natural conditions of this swamp forest (www.fjyx.gov.cn). In addition, our own field investigations have verified the natural status of these six swamp forests by comparing species composition and diversity of natural *G. pensilis* swamp forests and the habitats of planted *G. pensilis* populations. In contrast to the six natural *G. pensilis* swamp forests, forests of planted *G. pensilis* have only one tree species in the overstory, i.e., *G. pensilis*. In the understory of these planted forests, native species are very rare; in some cases, no plants are present in the understory, whereas in other forests, invasive species are present. We obtained 24 increment cores from the trunks of wild trees of varying DBHs. A core was taken from each trunk above ground level at 1.3 m, and the length of time from the position at 1.3 m in height to ground level was estimated to be 10 years (on average) as based on field observations made in past decades. Tree ages were determined using the software WinDENRO tree ring analysis system.

To include all individuals of *G. pensilis* in each study site, we established plots of various sizes (Plot 1: 4800 m^2 in Shangloucun; Plot 2: 1600 m^2 in Lingfengcun; and Plot 3: 800 m^2 in Lingfenglu, Pingnan County; Plot 4: 3200 m^2 in Dongshanchun; Plot 5: 10,000 m^2 in Shanlingcun, Youxi County; and Plot 6: 10,000 m^2 in Xianfengshan, Zhouning County, Fujian Province) in July–August of 2016 and 2017. The plots among Pingnan, Youxi and Zhouning are widely separated from each other; the geographic direct distance among them are from 50 km to 160 km. Though the first three plots are found within Pingnan, they are in fact isolated from each other because they are separated by mountains or valleys. Plots 1, 2 3 are located in different watersheds. In Youxi, Plots 4 and 5 are also in different watersheds and isolated by mountains. Therefore, we consider the six plots to be six populations. We used the relative basal area method (Ohsawa, 1984) for our vegetation sampling. In a community dominated by a single species, its relative dominance may be stated at 100%. If, however, two species share dominance, the relative dominance of each should ideally be 50%, or if there are three co-dominants, 33.3%, and so on. The number of dominant species is that which shows the least deviation between the actual relative dominance values and the expected percent share of the corresponding codominant-number model. The deviation (d) is calculated by the following equation:

$$d = 1/N\left\{ \sum (x_i - x')^2 + \sum x_j^2 \right\}$$

$$i \in T \quad j \in U$$

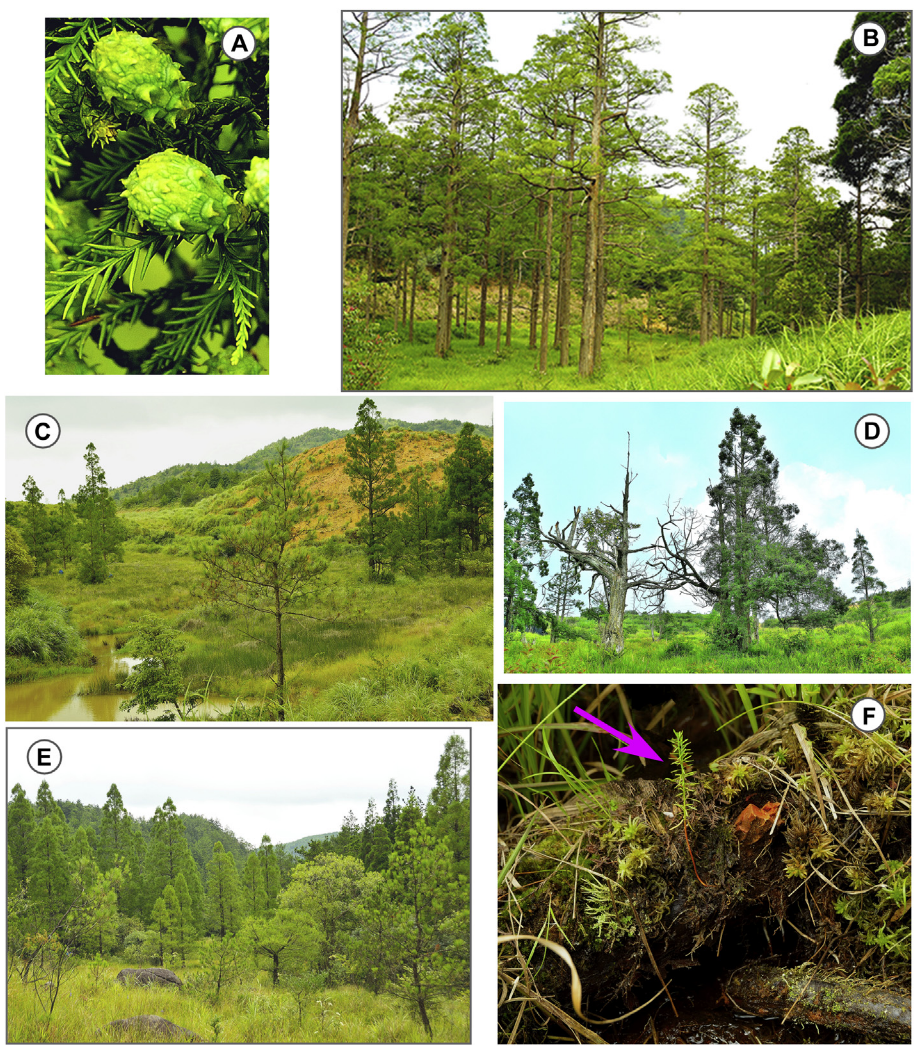

Fig. 2. ***Glyptostobus pensilis*** **forest stands in Fujian Province**. (A) Seed cones of *G. pensilis* in July. (B) A swamp forest stand of *G. pensilis* in Shangloucun, Pingnan. (C) A swamp forest stand of *G. pensilis* in Shanlingcun, Youxi. (D) A swamp forest stand of *G. pensilis* in Dongshancun, Youxi, showing some dead trees. (E) A swamp forest stand of *G. pensilis* in Xianfengshan, Zhouning. (F) A seedling of *G. pensilis* growing on a fallen log. Photographs by Cindy Q. Tang.

where x_i is the actual percent share (here relative basal area is adopted) of the top species (T), i.e., in the top dominant in the one-dominant model, or the two top dominants in the two-dominants model, and so on; x' is the ideal percent share based on the model as mentioned above, and x_j is the percent share of the remaining species (U). N is total number of species.

For the overstory, a species inventory was performed for all individuals at least 1.3 m in height in each plot. All were tagged, numbered, and identified to species level, whether healthy, unhealthy, or dead. We measured the DBH (diameter at breast height) and height of trees ≥ 1.3 m tall using a height-measuring pole. Tree stems were classified into three groups based on their vertical position, crown position, and height: canopy (at least 18 m tall); sub-canopy (8–18 m tall); and shrub layer (1.3 m and 8 m tall). The level of vitality was assessed by estimating the percent occupied by the living part of the tree canopy. Values ranged from 100% when all branches in the canopy were covered with normal healthy leaves to 0% when the canopy had no leaves (Averyanov et al., 2009). All woody species ranging in height from 5 cm to <50 cm tall for seedlings and 50 cm to <130 cm for saplings in the understory of each plot were identified, counted, and measured for height and percent cover. Each plot was divided into 10-m x 10-m subplots. In each subplot, we set up five 1-m x 1-m squares selected for investigation for the herbaceous species. Five 1-m x 1-m squares were respectively located in the four corners and the center of each subplot. Herb taxa were identified and the coverage and number of individuals of each species were recorded. In order to compare the populations of *Glyptostrobus* in Fujian Province and in Vietnam, in July 2018 we conducted fieldwork for the *G. pensilis* stands in Vietnam in addition to the work by Averyanov et al. (2009), using the same measurement criteria used in the Fujian Province forest stands.

Diversity was calculated for each forest stand using species richness (number of species), the reciprocal of the Berger–Parker index (1/d) (Magurran, 1988) and the Shannon–Wiener index (Pielou, 1969). The Sørensen's similarity index (beta diversity) was

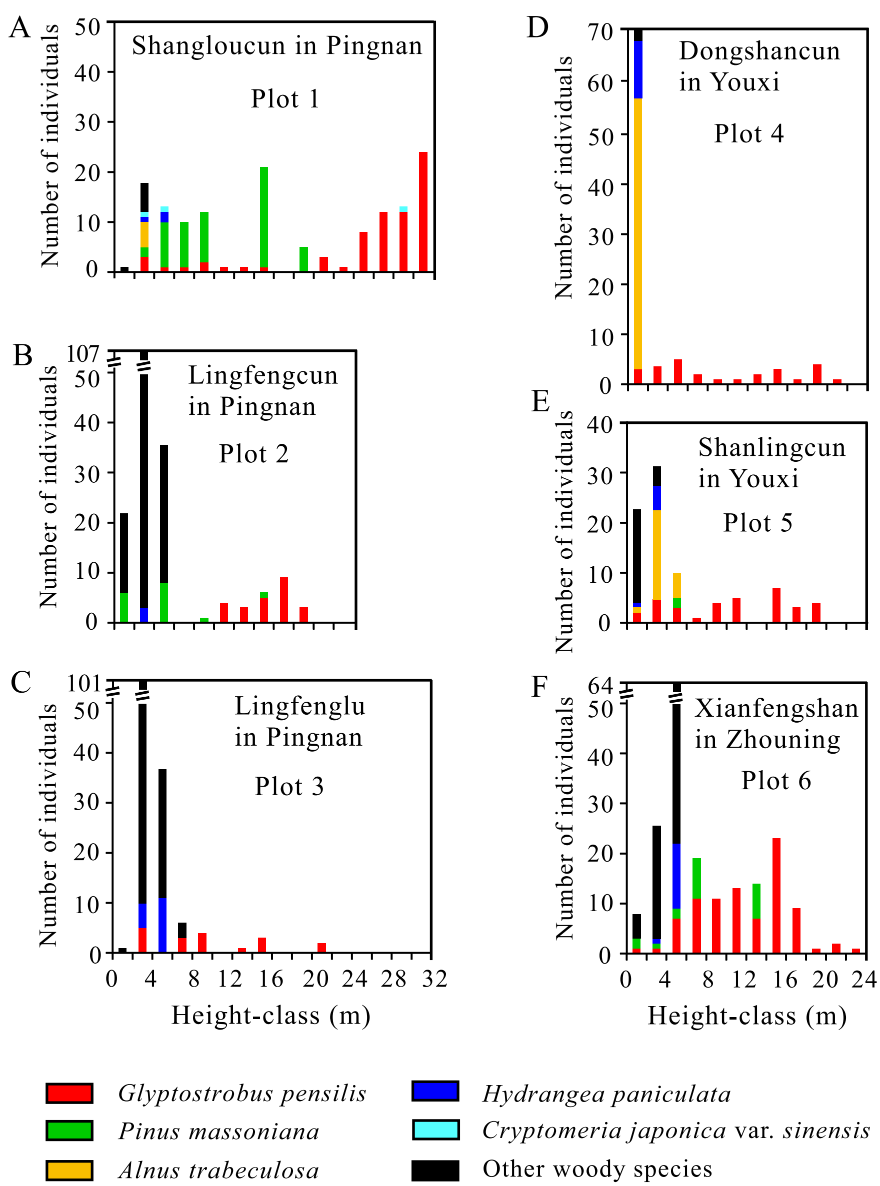

Fig. 3. Frequency distribution of woody species based on height (H ≥ 1.3 m) in the six swamp forest stands in Fujian (A)–(F).

used to compare the forest stands of Fujian Province, China with those of Vietnam (Sørensen, 1948).

3. Results

3.1. Community characteristics

Six forest stands dominated by *G. pensilis* are located in Pingnan (3 stands), Youxi (2 stands), and Zhouning (1 stand) Counties (Figs. 1C and 2). They typically grow in swamps with 15–60 cm of standing water being present throughout much of the year and at elevations that range from 1025 to 1300 m asl.

The vertical stratifications of the forest stands are shown in Fig. 3A–F. The maximum tree height was 31 m. All six plots were structurally simple and characterized by sparse (15–50%) canopy cover and once the trees reached approximately 8 m in height, the sub-canopies and canopies were dominated almost exclusively by *G. pensilis*. *Cryptomeria japonica* var. *sinensis* (naturally regenerated from planted *C. japonica* var. *sinensis* in the surrounding areas) (Plot 1, Fig. 3A) and/or *Pinus massoniana* (Plots 1, 2, 6, Fig. 3A, B, F) were occasionally present. In the shrubby layer, individuals of *Alnus trabeculosa*, *Hydrangia paniculata*, and *P. massoniana* were sparsely distributed, except *A. trabeculosa* was abundant in Plot 4 (Fig. 3D). In Pingnan, *G. pensilis* tree heights ranging from 4 to 8 m were rare. Other small tree and shrub elements that were identified in the 6 plots included *Nyssa sinensis*, *Ilex crenata*, *Ilex serrata*, *Viburnum luzonicum*, *Salix chienii*, *Lindera aggregata* (Table 1). In the herbaceous layer, *Molinia hui*, *Ischaemum anthephoroides*, *Isachne globosa*, *Osmundastrum cinnamomeum*, *Polygonum microcephalum* were generally dominant (Table 2). Few seedlings of *G. pensilis*, *C. japonica* var. *sinensis*, *Spiraea japonica*, or *Symplocos paniculata* were found on the forest floor. In these stands there were 43 woody species representing 32 genera and 22 families, and 83 herbaceous species representing 70 genera of 36 families (Tables 1 and 2).

Fig. 4A–C shows the overstory of each stand had very low values in species richness (4–13 species), Reciprocal of Berger–Parker index (1–1.2), and Shannon–Wiener index (0.05–0.65), whereas the understory of each stand had much higher values in species richness (18–62 species), Reciprocal of Berger–Parker Index (2.2–6.6), and Shannon Wiener-Index (1.6–3.9).

3.2. Population structure and regeneration

There is a positive correlation between *G. pensilis* age and DBH ($y = 0.0099x^2 + 1.4508x + 12.671$, Pearson's $r^2 = 0.89$, $p < 0.001$) (Fig. 5). The growth ring data indicate the growth rate or amount of wood added to the tree annually was relatively higher when the trees were under 60 years old, though the overall trend of the growth rate decreased with advancing age. The growth ring width varied from 7 mm for trees under 60 years old to 0.89 mm per year for trees older than 100 years.

The population structure in terms of the DBH and age distribution can provide an indication of the regeneration process of the population. Trees with DBHs between 1.5 and 127 cm ranged in ages from 15 to 357 years (Fig. 6A–L). The DBH and age distribution of each population was multimodal (a type with more than one peak in the size and age classes), indicating that recruitment varied by chance with regeneration depending on habitat and the availability of space. Few individuals with DBHs between 80 and 127 cm were observed and corresponded to ages of 192–357 years in Pingnan (Fig. 6A, C, G, I) and Youxi (Fig. 6D, E, J, K). There were very few *G. pensilis* trees with DBHs less than 10 cm, corresponding to ages <28 years, in Plots 1 and 3 in Pingnan (Fig. 6A, C, G, I), Plots 4

Table 1
Floristic composition of woody species (height ≥ 1.3 m) in the six plots in Fujian Province. RBA = relative basal area at the breast height.

Plot	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Plot area (m^2)	4800	1600	600	2500	15,000	5500
Elevation (m)	1249	1158	1180	1132	1025	1300
Plot site	Shangloucun in Pingnan	Lingfengcun in Pingnan	Lingfenglu in Pingnan	Dongshancun in Youxi	Shanlingcun in Youxi	Xianfengshan in Zhouning
Species	RBA (%)	RBA (%)	RBA (%)	RBA (%)	RBA (%)	RBA (%)
Glyptostrobus pensilis	86.5	96.2	96.3	99.96	99.3	97.6
Pinus massoniana	11.6	2.7			0.1	1.2
Cryptomeria japonica var. *sinensis*	1.9					
Toxicodendron succedaneum	0.02					
Sassafras tsumu	0.01					
Alnus trabeculosa	0.007			0.03	0.4	
Euscaphis japonica	0.004					
Hydrangea paniculata	0.001	0.02	0.1	0.008	0.09	0.08
Viburnum luzonicum		0.4				0.0005
Rhododendron simsii		0.2				0.3
Salix chienii		0.2	2.3			0.8
Lindera glauca		0.07			0.003	0.004
Litsea cubeba		0.07			0.004	
Rhododendron henryi		0.05	0.2			
Eurya chinensis		0.04				
Ilex serrata		0.04	0.06			0.05
Adinandra glischroloma		0.02				0.01
Dalbergia mimosoides		0.004				
Rosa laevigata		0.001		0.001	0.002	
Ilex crenata			0.8			0.001
Nyssa sinensis			0.3			
Lindera aggregata					0.01	
Rhamnus crenata					0.001	0.003
Rhaphiolepis indica					0.0003	
Glochidion puberum						0.004
Symplocos anotiiala						0.003
Eurya macartneyi						0.001

Table 2
Herbaceous species, dwarf woody species, and seedlings of woody species in the understory (height < 1.3 m). + = coverage less than 1%.

Plot	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Plot area (m^2)	4800	1600	600	2500	15,000	5500
Elevation (m)	1249	1158	1180	1132	1025	1300
Plot site	Shangloucun in Pingnan	Lingfengcun in Pingnan	Lingfenglu in Pingnan	Dongshancun in Youxi	Shanlingcun in Youxi	Xianfengshan in Zhouning
Species	Coverage (%)	Coverage (%)	Coverage (%)	Coverage (%)	Coverage (%)	Coverage (%)
Isachne globosa	25	8	+	31	+	6
Ischaemum anthephoroides	22	1	+	12	17	1
Molinia hui	20	45	+	1		15
Osmundastrum cinnamomeum	13	9	24	+	17	+
Cyperus haspan	3	3	+	1	1	+
Juncus bufonius	3	+		1		2
Carex dickinsii	2					+
Cryptomeria japonica var. *sinensis*	+					
Drosera rotundifolia	+	+		+		+
Eleocharis tetraquetra	+	+		7	+	+
Euphorbia esula	+					+
Glyptostrobus pensilis	+	+		+	+	
Hypericum japonicum	+	+		2	+	+
Ligularia japonica	+					15
Lobelia sessilifolia	+	10	+			2
Scirpus rosthornii	+	+	+			1
Viola verecunda	+	1	+	5	+	+
Hemerocallis fulva	+			+		
Miscanthus sacchariflorus		4	+	+	16	10
Ostericum grosseserratum		4	+		+	+
Scirpus juncoides		3				
Nymphaea tetragona		2				
Phragmites karka		2				
Aster ageratoides		1			+	+
Carex glossotigma		1	9	+		+
Cicuta virosa		1	+			+
Cirsium chinense		1		+	+	+
Juncus effusus		1		1	17	
Lysimachia fortunei		1		+	+	
Polygonum microcephalum		1	30	3		1
Calamagrostis epigeios		+	3	4		+
Eurya macartneyi		+				+
Cyclosorus parasiticus		+		+		
Habenaria schindleri		+		+		+
Osmunda japonica		+			+	+
Parathelypteris glanduligera		+		1	11	+
Pyrrosia lingua		+				+
Rabdosia amethystoides		+				
Rhamnus crenata		+		+	+	
Rhynchospora chinensis		+		3	1	19
Rosa laevigata		+				
Rosa lucidissima		+				
Rosa roxburghii		+		+		
Rubia cordifolia		+				
Smilax china		+			+	
Viburnum luzonicum		+			+	
Leersia hexandra			27			
Galium trifidum			+			+
Houttuynia cordata			+	+		
Lonicera japonica			+		+	
Lysimachia heterogenea			+			
Lythrum sp.			+			
Neanotis boerhaavioides			+			+
Sagittaria sagittifolia			+			
Triadenum breviflorum			+			
Eriocaulon faberi				17		3
Alnus trabeculosa				+	+	
Eriocaulon nipponicum				3		+
Oenanthe thomsonii subsp. *stenophylla*				2		
Haloragis micrantha				1	+	+
Isachne nipponensis				1	+	
Polygonum sp.				1		
Isodon sp.				1	+	+
Dryopteris peninsalae				+		
Emilia sonchifolia				+	+	
Kalimeris indica				+		
Lepisorus thunbergianus				+		

(*continued on next page*)

Table 2 (*continued*)

Plot	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Luzula sp.				+		
Osbeckia chinensis				+		+
Scleria biflora				+	+	1
Eriocaulon buergerianum					15	
Lindera erythrocarpa					+	
Adinandra glischroloma					+	+
Adinandra millettii					+	
Arundinella hirta					+	
Caldesia reniformis					+	
Cephalotaxus fortunei					+	
Dioscorea japonica					+	
Fordiophyton fordii					+	+
Ilex asprella					+	+
Lepisorus lewissi					+	
Ligustrum retusum					+	
Lindera glauca					+	
Rhaphiolepis indica					+	
Rubus corchorifolius					+	
Rubus impressinervius					+	
Scripus triqueter					+	
Vaccinium carlesii					+	+
Eleocharis congesta						8
Oplismenus undulatifolius						6
Arisaema sp.						+
Athyrium iseanum						+
Cerastium sp.						+
Dryopteris championii						+
Elaeagnus henryi						+
Gynura crepidioides						+
Ilex crenata						+
Sp. of Fabaceae						+
Lespedeza formosa						+
Melastoma dodecandrum						+
Paederia foetida						+
Parathelypteris nipponica						+
Pellionia brevifolia						+
Pseudocystopteris schizochlamys						+
Siraitia grosvenorii						+
Smilax sp.						+
Spiraea japonica						+
Symplocos paniculata						+
Sp. of Apiaceae						+

and 5 in Youxi (Fig. 6D, E, J, K) and Plot 6 in Zhouning (Fig. 6F, L). *G. pensilis* trees with DBHs less than 20 cm, i.e., less than 46 years old, were absent in Plot 2 in Pingnan (Fig. 6B, H). Seedlings between 5 cm and 50 cm in height and saplings between 50 cm and 130 cm in height were rare. Only 18 seedlings/samplings were found in all of our plots growing in better drained soil mounds that were located above the groundwater table and fallen logs where more sunlight reached them (Fig. 2F). Among the 18 seedlings/samplings, 14 were found in forest stand gaps without herbaceous coverage (Fig. 7). This suggests the establishment of *G. pensilis* seedlings require light, moderate disturbance for gap formation, and mesic (not saturated) soil conditions. Although the species is capable of reproducing vegetatively, reproduction is primarily through seeds.

Twenty-two withered *G. pensilis* trees with basal diameters of 26–90 cm and one standing dead tree with a DBH of 100 cm were identified in Plot 4 in Dongshancun in Youxi. The vitality of *G. pensilis* in the other plots (Plots 1, 2, 3, 5, and 6) was generally healthy.

3.3. *A comparison of diversity of taxa between Fujian Province and Vietnam*

The extant *G. pensilis* stands in Fujian Province and Vietnam were associated with different species assemblages. In Fujian Province, the forest stands were open, with *G. pensilis* trees covering 15–50% of the canopy and occasionally accompanied by scattered *P. massoniana*, and/or *C. japonica* var. *sinensis*. In the shrub layer, wet-loving *Hydrangea paniculata*, *A. trabeculosa*, and *S. chienii* were present. Species of *Viburnum*, *Ilex*, *Nyssa*, *Lindera*, *Rhododendron*, and *Adinandra* were components in the shrub layer of some of the swamps. In Vietnam, Averyanov et al. (2009) showed *G. pensilis* used to provide at least 65–70% coverage in the canopy a few decades ago and was associated with broad-leaved species such as *Sterculia pierrei* and *Litsea longipes*. The sub-canopy included *Elaeocarpus hygrophilus*, an evergreen broad-leaved tree. The shrub layer consisted mainly of *Ficus simplicissima*, *F. formosana*, *Syzygium formosum*, *Ilex cymosa*, and *Glochidion zeylanicum* var. *tomentosum*. On the forest floor, herbacous species and numerous wet-loving riparian and sub-aquatic grasses (Poaceae) and sedges (Cyperaceae) and a number of fern species were found in the two regions. Among the herbaceous flora, the dominant species in Fujian Province included *M. hui*, *I. anthephoroides*, *I. globosa*, *O. cinnamomeum*, and *P. microcephalum*, whereas in the Vietnamese stands, *Scleria sumatrensis*, *Leersia hexandra*, *Nephrolepis biserrata*, *Asplenium longissimum*, and *Colocasia esculenta* were dominants.

Fig. 8A shows that the number of families of the woody taxa for the forest stands as a whole was about the same (around 22) for Fujian Province and Vietnam, and the number of woody genera and species was higher in Fujian Province (32 genera and 42 species) than in Vietnam (25 genera and 32 species). The number of herbaceous families, genera, and species represented in the forest plots was greater in Fujian Province (36 families, 70 genera, 83 species)

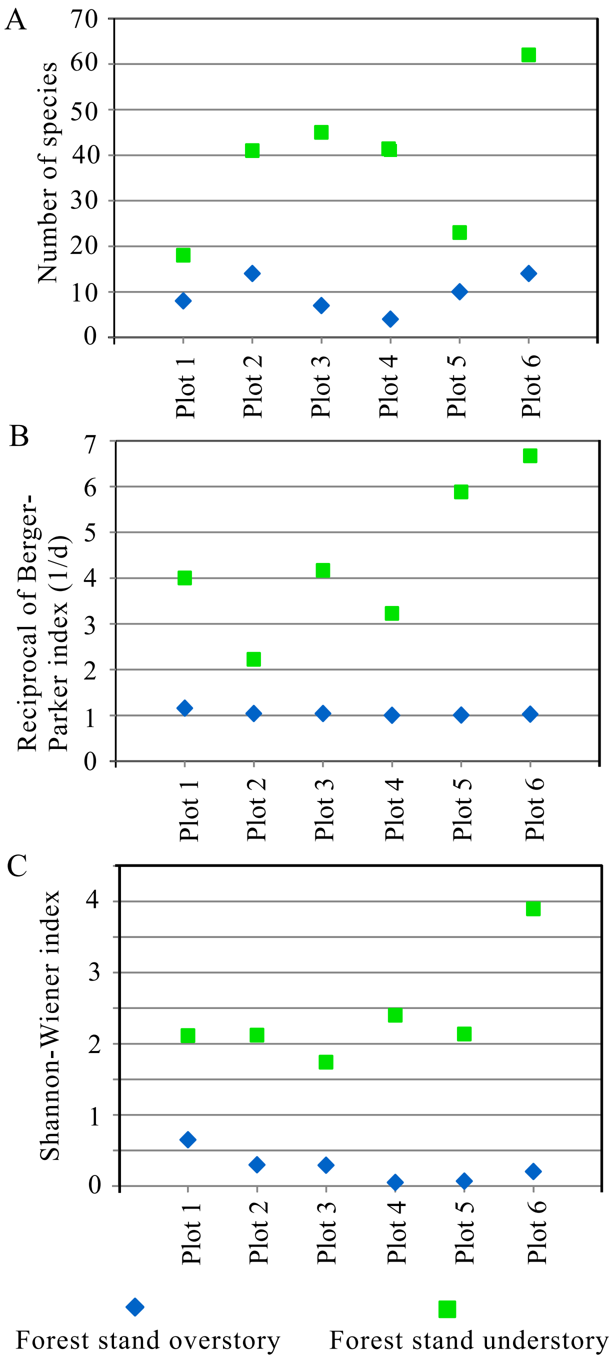

Fig. 4. Species diversity in the forest stand overstory and understory. (A) Number of species. (B) Reciprocal Berger–Parker Index (1/d). (C) Shannon–Wiener Index. Locations of each plot: Plot 1 at Shangloucun in Pingnan; Plot 2 at Lingfengcun in Pingnan; Plot 3 at Lingfenglu in Pingnan; Plot 4 in Dongshancun in Youxi; Plot 5 in Shanlingcun in Youxi; Plot 6 in Xianfengshan in Zhouning.

compared to those in Vietnam (21 families, 30 genera, 34 species). Fig. 8B indicates that Sørensen's similarity index (beta diversity) between the stands of the two regions was low (0.03–0.14 for woody taxa, 0.02–0.21 for herbaceous taxa) at all taxonomic levels for all classes of vegetation. This demonstrates the taxonomic compositions of the stands in the two regions were different, except that they shared the common dominant species-*G. pensilis*. The Shannon–Wiener index shows the overstory of each stand had much lower diversity (0.26 on average) in Fujian Province than that

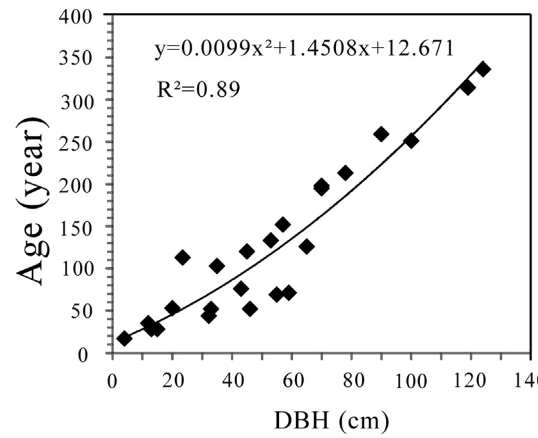

Fig. 5. Relationships between DBH and age for *G. pensilis*.

(1.97 on average) in Vietnam, whereas the diversity indices for the understories in the two regions were about the same (around 2.41) (Fig. 8C).

3.4. A comparison of population structure between Fujian Province and Vietnam

The population sizes of *G. pensilis* in Fujian Province (261 individuals in the six stands) and Vietnam (158 in the two stands) were small. The frequency distributions for height and DBH-classes in both Fujian Province and Vietnam populations show a multi-model type (Fig. 9A, B). In Fujian Province, the maximum height of *G. pensilis* was 31 m, whereas in Vietnam it was 25 m. The maximum DBH was 127 cm and 140 cm, with corresponding ages of 357 and 372 years in Fujian Province and Vietnam, respectively. In the Fujian Province populations, 9% of the trees were less than 4 m tall and 11% of the trees had DBHs less than 10 cm. In Vietnam, there were no trees less than 2 m tall and only 1% of the individuals had DBHs less than 10 cm. Regeneration of this species was poor (18 seedlings) in Fujian Province, while there was no natural regeneration occurring in Vietnam (Nguyen et al., 2013; our investigation in 2018).

The proportions of the number of individuals for both the high-vitality (100-80%) and the low-vitality (20-0%) for the Fujian Province populations were greater than those of Vietnam (Fig. 9C). The 22 withered *G. pensilis* trees in Dongshancun of Youxi, Fujian Province were caused by water loss and water pollution resulting from growing commercial mushrooms at the upper side of the habitat during 2012–2014. This demonstrates how human activities have impacted the habitat, dramatically threatening the survival of wild populations of *G. pensilis*.

4. Discussion

As far back as the Cretaceous (100 million years ago), and through to the late Pliocene (2.6 million years ago), ancient wetland forests were co-dominated by *Glyptostrobus* and *Metasequoia* (LePage et al., 2005; LePage, 2007; Yamakawa et al., 2017). Today, *G. pensilis* and *M. glyptostroboides* are not known to naturally coexist. However, *G. pensilis* found in the unstable swamp stands (with varied water levels throughout the year) shares ecological traits with many other Tertiary relict plant species, as exemplified by *M. glyptostroboides*, which is found on steep slopes and stream sides in deep valleys of Lichuan, Hubei (Tang et al., 2011); *G. biloba*,

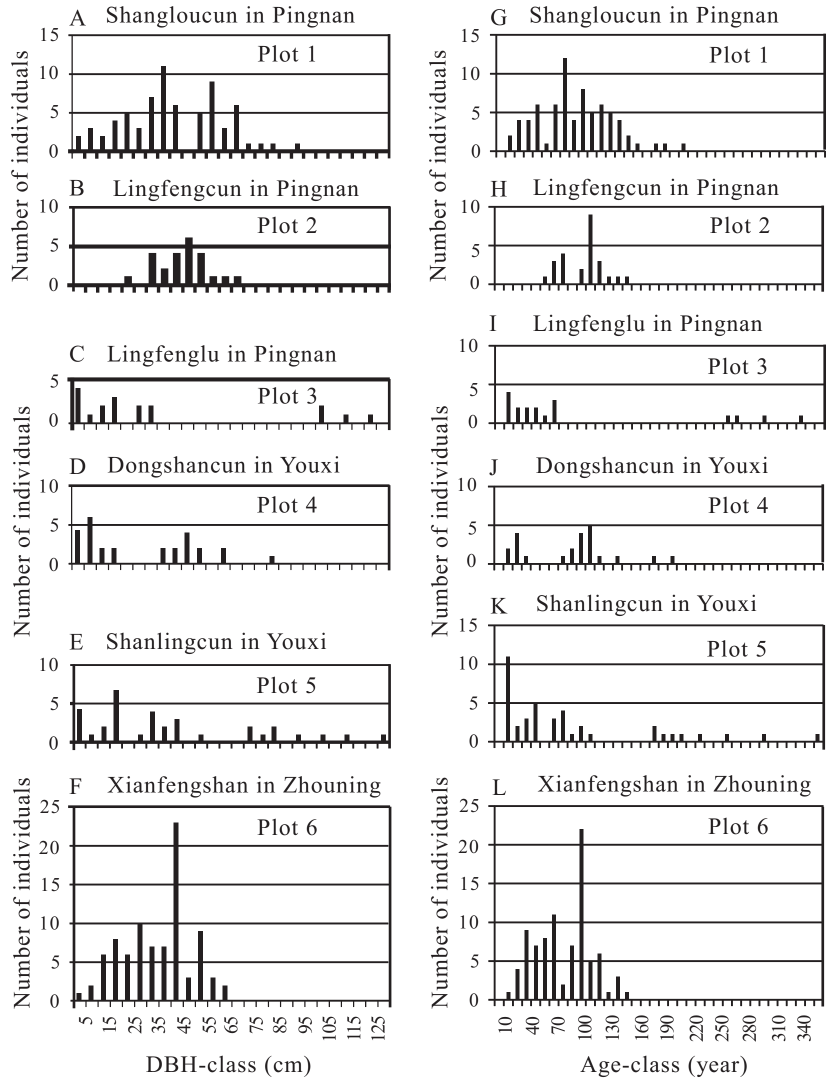

Fig. 6. Frequency distribution in DBH- and age-classes of *Glyptostrobus pensilis* in six swamp forest stands in Fujian. (A)–(F) Frequency distribution in DBH-classes; (G)–(L) Frequency distribution in age-classes.

which favors rock crevices in limestone habitats in the Dalou Mountains, Guizhou (Tang et al., 2012); *C. argyrophylla*, whichis found on steep slopes surrounded by cliffs on Mt. Jinfo, Chongqing (Qian et al., 2016); *Thuja sutchuenensis*, which is found on steep limestone slopes in the Daba Mountains, Chongqing (Tang et al., 2015); *T. cryptomerioides*, which is found on riverbanks in deep valleys, on steep slopes, and on cliffs in the Gaoligong mountains, Yunnan (He et al., 2015); *D. involucrata*, which is found in scree slops on the Mt. Emei, Sichuan (Tang and Ohsawa, 2002); *Tetracentron sinense*, which is found in deep ravines and on steep slopes in the Ailao Mountains, Yunnan (Tang et al., 2013). Recruitment of these species is restricted to local habitats that have moderate disturbance regimes where competition usually is less intense and the regeneration potential of non-relict species is lower.

G. pensilis is a heliophilous species that is highly drought sensitive, a poor competitor under dry conditions, and does not tolerate saline soil conditions (Xu and Li, 1959). In our study sites in Fujian Province, the dark red soil is deep, permeable, and has a pH that ranges from 6 to 7 (Zheng et al., 2008; NFGRP, 2018). The soil conditions appear to be suitable for the growth of *G. pensilis* in

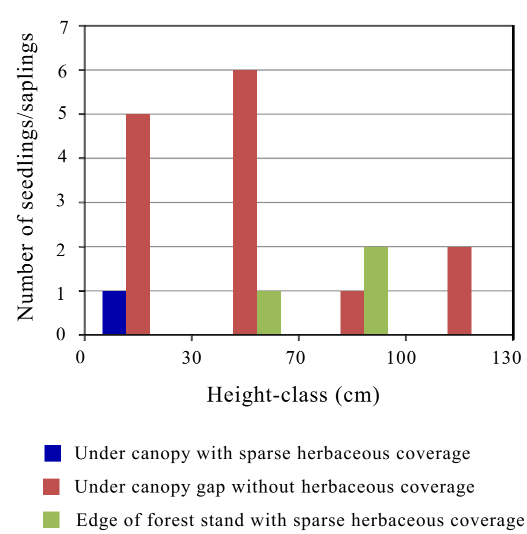

Fig. 7. *G. pensilis* seedlings/saplings emergence for swamp forest stands of Fujian, 2016.

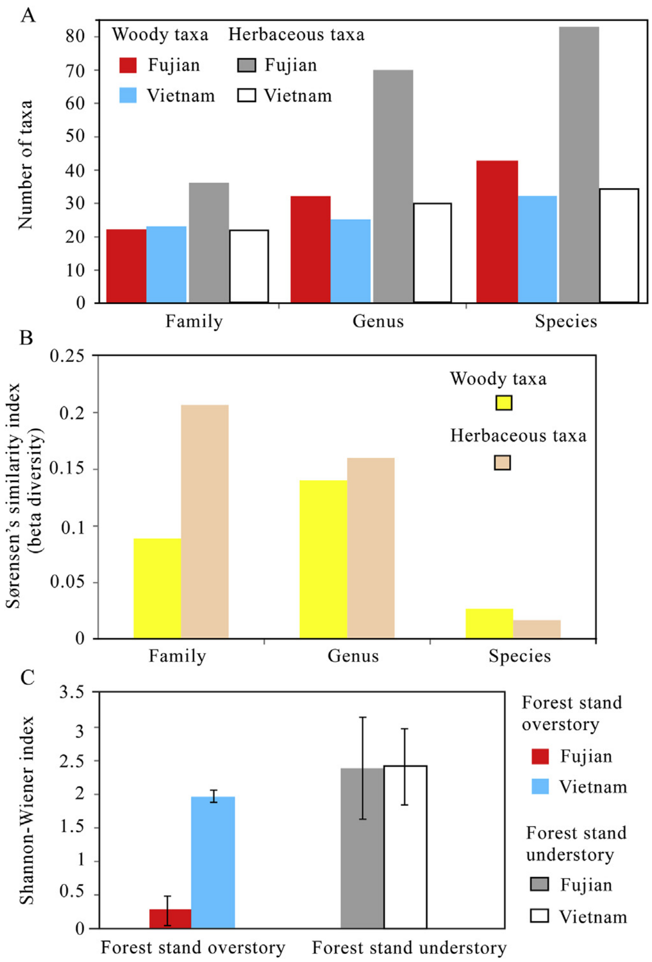

Fig. 8. A comparison of diversity of forest stands in Fujian and Vietnam. (A) The number of taxa respectively at the family, genus, and species levels for six stands in Fujian and two stands in Vietnam. (B) Sørensen's similarity index (beta diversity) at family, genus, and species levels between the forest stands in Fujian and Vietnam, respectively. (C) Shannon–Wiener index on average with standard deviation (SD) for the overstories and the understories of forest stands in Fujian and Vietnam.

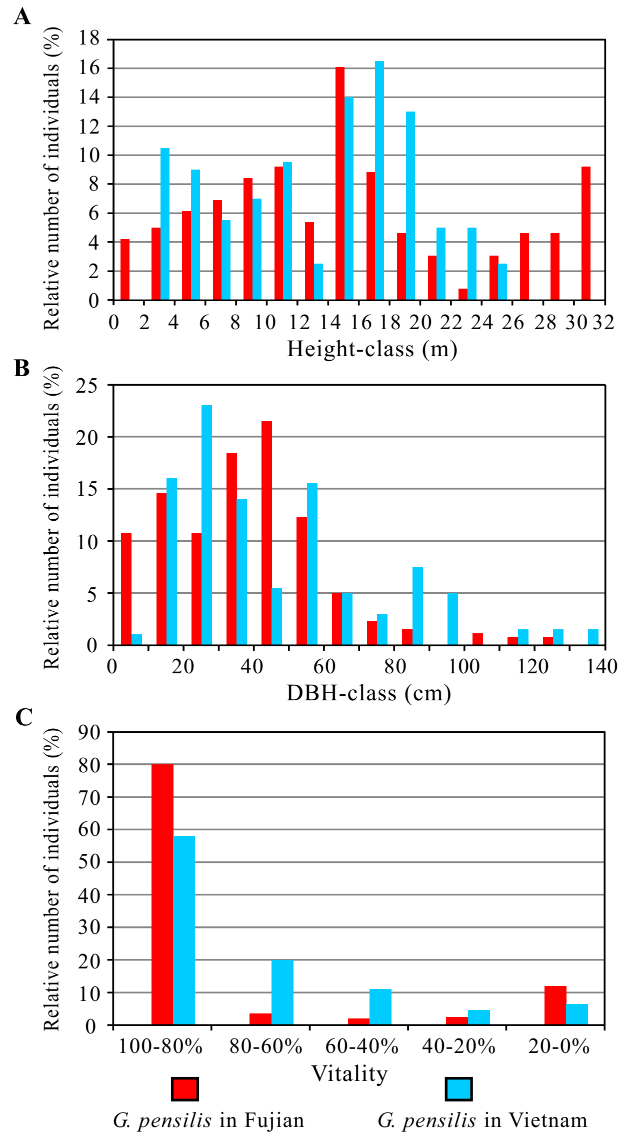

Fig. 9. A comparison of the population structures of *Glyptostrobus pensilis* in Fujian (the six stands) and Vietnam (combined the two stands in Trap K'sor and Ea Ral). (A) Frequency distribution of height. (B) Frequency distribution of DBH. (C) Frequency distribution of Vitality. Data for the Vietnamese stands are from Averyanov et al. (2009).

Fujian Province. However, the regeneration of this species is extremely poor. The micro-sites of the 18 seedlings found in Fujian Province suggest germination and establishment of *G. pensilis* requires light, wet but not saturated soil conditions. This observation agrees with experimental results that show germination and seedlings prefer wet sites, but not standing water (Xu and Li, 1959; Chen, 1977).

The population of *G. pensilis* is declining. The effective conservation and management of this endangered species requires several measures. Because the species shows weak recruitment, we recommend establishing *G. pensilis* seedling/sapling nurseries *in situ*. Tall, dense herbaceous vegetation covers most of the understories in Fujian Province forest stands. Thus, to provide well-lit sites for *G. pensilis* seedling survival, we recommend controlling herbaceous density in the understory. In the two stands in Shangloucun and Xianfengshan, water levels are very low, even intermittent. Thus, we suggest water levels be increased to maintain the present populations. Previous research reported that *G. pensilis* genetic diversity is low at both the species level and within populations, whereas the genetic differentiation among *G. pensilis* populations is high (Li and Xia, 2005). Although this study included only one of our six study sites, these findings indicate that it is critical to conserve genetic variability in *G. pensilis*. Thus, *ex situ* collections of *G. pensilis* should include representatives from all extant wild populations.

Conflict of interest

None.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2019.06.007.

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