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Zhanhui Xu
Chinese Academy of Sciences

Hai Ren
Chinese Academy of Sciences

Xiao Wei
Guangxi Institute of Botany

Kangting Ouyang
Chinese Academy of Sciences

Dongxing Li
Guangxi Institute of Botany

See next page for additional authors

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Authors
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Original Research Article

Distribution and conservation status of *Camellia longzhouensis* (Theaceae), a critically endangered plant species endemic to southern China

Zhanhui Xu[a,b], Hai Ren[a,b,*], Xiao Wei[c,d], Kangting Ouyang[a,b], Dongxing Li[c,d], Yili Guo[c,d], Shujun Wen[c,d], Jifeng Long[d,e], Jun Wang[a], Dafeng Hui[f]

[a] *Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*
[b] *University of Chinese Academy of Sciences, Beijing 100049, China*
[c] *Guangxi Key Laboratory of Funetional Phytochemicals Research and Utilization, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China*
[d] *Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China*
[e] *Nonggang National Nature Reserve Administration of Guangxi, Longzhou, Guangxi 532400, China*
[f] *Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA*

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ABSTRACT

Camellia longzhouensis (Theaceae) is an endemic evergreen shrub or small tree with a distribution restricted to South China. It is listed as Grade-II in the National Key Protected Wild Plants List. In this study, we surveyed its distribution, examined its population structure, identified factors affecting its survival, and reassessed its extinction risk. We found that *C. longzhouensis* was only distributed in the Nonggang National Nature Reserve and the surrounding area. Its individuals only grew under the secondary forest canopy in the karst mountain. A total of 58 individuals of *C. longzhouensis* in three sub-populations were found. Soil fertility and understory light availability were the main habitat factors influencing the survival of *C. longzhouensis*. Anthropogenic disturbances and reproductive obstacles have caused a low seed-setting rate, poor seedling survival, and a lack of adult plants of *C. longzhouensis* in the natural habitat. The population structure of *C. longzhouensis* is spindle-shaped, indicating poor natural regeneration and inhibited seedling recruitment. *Cleistanthus petelotii* had a significant positive interspecific interaction with *C. longzhouensis* in the community. Based on the information obtained here and IUCN criterion C2ai, we recommend that *C. longzhouensis* be categorized in the International Union for Conservation of Nature (IUCN) Red List as Critically Endangered. We also developed a comprehensive protection strategy, consisting of in situ conservation, *ex situ* conservation, reintroduction, and commercial utilization. This strategy can be readily applied to protect other endangered plants with economic value in karst poor regions.

* Corresponding author at: Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China.
E-mail address: renhai@scib.ac.cn (H. Ren).

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1. Introduction

Global biodiversity losses are occurring at an unprecedented rate. According to the State of the World's Plants and Fungi Report by Kew Garden (Lughadha et al., 2020), 39.4% of all vascular plant species are threatened with extinction. In China, the proportion of higher plants threatened is estimated to be 15–20% (Qin and Zhao, 2017). The causes include habitat loss and fragmentation, overexploitation, invasion of alien species, environmental pollution, global climate change, and reproductive disorders. The conservation of rare and endangered plants has therefore become a major global concern. The conservation, restoration, and sustainable utilization of rare and endangered plants requires an understanding of their distribution ranges, population structures, and factors threatening their survival.

Camellia longzhouensis J.Y. Luo is an evergreen shrub or small tree in the family Theaceae and the sect. Chrysanthaare Chang (Fig. 1) (Chang and Ren, 1998; KBI-CAS, 2020). Species of sect. *Chrysanthaare* Chang are commonly named Golden Camellia. Golden Camellia is known as "the Queen of Camellias" and "the Giant panda of the plant kingdom". It is also celebrated as one of the top ten traditional flowers in China (Liang, 1993). As an appealing plant with attractive golden flowers, *C. longzhouensis* has excellent horticultural and economic value. It also contains chemicals with pharmaceutical value.

All species of *Camellia* sect. *Chrysantha* Chang are included in the Key Protected Wild Plants List in Guangxi Province in 2012. They are also listed as Grade-II National Key Protected Wild Plants in China. *C. longzhouensis* was first reported in Guihaia by Luo (1983), and was subsequently added to the *World Checklist of Seed Plants* (Govaerts, 1999). In China, the species is listed as a synonym of *Camellia chrysanthoides* in the *Flora of China* (Ming, 2000). However, Chang and Ren (1998) indicated that it should be a separate species due to the presence of a tomentum on its terminal buds and ovaries. Genetic analysis also suggests that *C. longzhouensis* and *C. chrysanthoides* are different species (Xiao et al., 2014). Therefore, the International Union for Conservation of Nature separated this species from *C. chrysanthoides* and assessed it as Endangered B1ab(iii) (IUCN, 2015).

To date, only a few studies have been conducted on C. *longzhouensis*. Researchers have found that the total flavone content in *C. longzhouensis* leaves is lower than in other plants in *C.* sect. *Chrysanthaare* (Huang et al., 2011), and that the flavonoid content in the whole plant is also low (Li et al., 2019). Wang et al. (1994) found a difference in karyotypes between C. *longzhouensis* and other plants in *C.* sect. *Chrysanthaare.* Tang et al. (2004) and Xiao et al. (2014) reported that the genetic relationship between *C. longzhouensis* and other *C.* sect. *Chrysanthaare* species is not strong, which was consistent with its classification as a separate species.

Here, we studied the distribution range of *C. longzhouensis*, its population structure, habitat characteristics, and threats. We also developed a comprehensive strategy for *C. longzhouensis* conservation. We attempted to answer the following questions: (1) Is the population of *C. longzhouensis* declining and endangered? (2) Does *C. longzhouensis* share an ecological niche with any other species in the community where it grows? (3) Which environmental factors are associated with the abundance of wild *C. longzhouensis?* The results of this study will provide a reference for the protection and utilization of *C. longzhouensis* and other rare plant species in the karst poor region.

2. Methods

2.1. Study area

The study was conducted in Longzhou County, Chongzuo City, Guangxi Province, China (106°42′28′−107°04′54′E , 22°13′56′−22°33′09′N), which is the area with both the historical and current distribution of *C. longzhouensis*. The typical vegetation in the region is karst seasonal rain forest of the northern tropics with abundant karst endemic tree species (Su et al., 1988; Su, 1994). The

Fig. 1. Flowers (a), buds (b), fruits (c), and individuals (d) of *Camellia longzhouensis.*

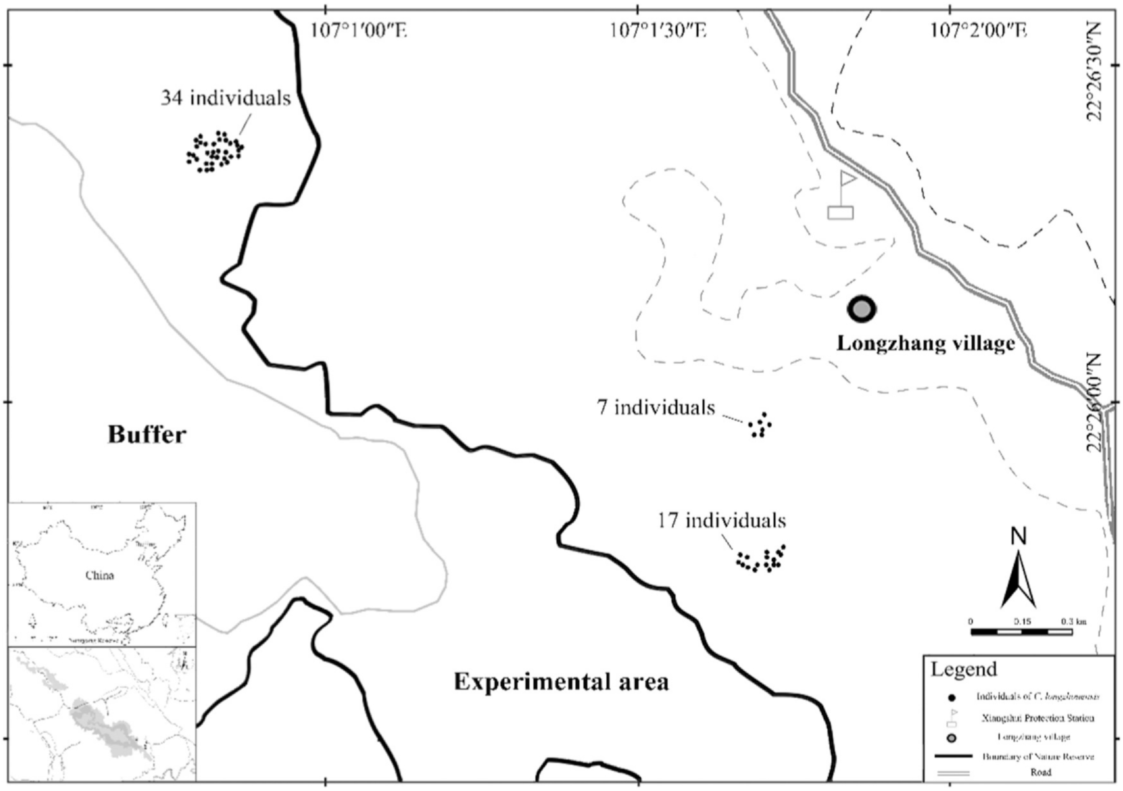

Fig. 2. The distribution of *Camellia longzhouensis* in 2020. Dot represents the area that contains one plant community.

region has a tropical monsoon climate with tropical monsoon with an annual mean temperature of 22 °C and annual rainfall of 1200–1500 mm (ca. 76% of which falls in May to July). The soil is laterite. The geomorphological type is "peak-cluster deeply incised round depression (valley)", which is composed of a plurality of mountain peaks and depressions (Wang et al., 2014).

2.2. Examination of specimens and wild populations

We examined all five preserved *C. longzhouensis* specimens at the National Plant Specimen Resource Center (NPSRC); these specimens were collected in the wild by the Guangxi Institute of Botany, Guangxi Province, and the Chinese Academy of Science in 1980, 1982, 1985, 1991, and 1998. In addition, we reviewed the *Flora of China* (Flora of China Editorial Committee, 2007) and the *Flora of Guangxi* (Li and Liang, 1984) for the description of *C. longzhouensis*. We also extensively interviewed taxonomists, forest rangers, and local farmers within the range of the *C. longzhouensis* distribution to establish the historical distribution of *C. longzhouensis*. After reassessing the populations based on data collected during 1980–2020, we confirmed that *C. longzhouensis* specimens are still located in Longzhou County.

2.3. Vegetation survey

In June 2020, we conducted a vegetation survey in Longzhou County. We assumed that all individuals detected (see Fig. 2.) belonged to one community. In the *C. longzhouensis* community, we established 12 plots (10 × 10 m^2 each) to survey the species in tree layer. Within 12 tree plots, five tree plots were selected and one 5 × 5 m^2 subplot was established in each of them to investigate the shrubs. Within five shrub subplots, three subplots were selected, and one 1 × 1 m^2 quadrat was set up in the center of each of them to investigate the herbaceous plants. In each plot, the species name, height (H), and diameter at breast height (DBH) were recorded for all trees (H > 1.3 m). In each subplot and quadrat, the height, crown width or coverage of shrubs (H = 0.5–1.3 m), herbs (H < 0.5 m), and vines were also measured.

2.4. Population structure

In June and September 2020, we conducted a field survey and located all living individuals of *C. longzhouensis* in the wild and recorded the location, elevation, slope, and numbers of individual of each subpopulation of *C. longzhouensis*. To investigate the population structure of *C. longzhouensis*, we measured the height, DBH, and crown area of all individuals. All individuals were grouped into 12 size categories based on the H of younger individuals and the DBH of older individuals. Younger individuals (DBH < 1 cm) were divided into three grades: grade I with H ≤ 33 cm; grade II with 33 ≤ H ≤ 100 cm; and grade III with H > 100 cm. For older individuals (DBH ≥1 cm, of any height), each additional 1 cm was assigned one grade, i.e., grade IV with 1 ≤DBH < 2 cm, grade V with 2 ≤ DBH < 3 cm, and so on. The static life table, the fecundity schedule, and the Leslie matrix model (Leslie, 1945) were applied to explore the dynamics and the age structure of the population.

2.5. Soil physical and chemical properties

In June 2020, we collected soil samples to a depth of 10 cm from five points randomly selected in each of the six tree plots using a 5-cm-diameter soil corer. After mixing the soil from the five points, we used a 0.5-kg subsample/plot for analysis. The six subsamples were air-dried and passed through a 2-mm sieve for determination of soil chemical properties. The pH (1:2.5 soil water extracts), soil organic matter (SOM, determined by the potassium dichromate method), total soil nitrogen (TN, determined by the semi-micro Macro Kjeldahl method); total phosphorus and available phosphorus (TP and AP, determined by Mo-Sb Anti-spectrophotometry), total potassium and available potassium (TK and AK, extracted with HF-$HClO_4$ and analyzed by atomic absorption spectrophotometry) were assessed according to *Methods in National Standards of China* (Liu, 1996). The contents of soil water (g of water per 100 g of fresh soil), ammonium nitrogen (determined by the UV spectrophotometric method), and nitrate nitrogen (determined by the indophenol blue spectrophotometric method) were assessed as described by Dong (1996).

2.6. Standing litter crop

We randomly designated five 1 × 1 m^2 quadrats in the *C. longzhouensis* community to collect and quantify the mass of the standing litter crop. After the litter was weighed before and after drying to constant weight at 65 °C, we calculated the water content of the sample. The five dried samples were ground and passed through a 0.85-mm sieve for determination of total carbon (determined by the potassium dichromate method), total nitrogen (determined by the Kjeldahl method), and total phosphorus (determined by the Mo-Sb Anti-spectrophotometry method) (Dong, 1996).

2.7. Light environment measurement

At the *C. longzhouensis* community, leaf area index (LAI) and diffuse non-interceptance (DIFN) (Machado and Reich, 1999) were measured at 10 points using a Plant Canopy Analyzer (LAI-2200C, LI-COR Inc., Lincoln, NE, USA). Light availability was measured at 10 points using a Li-190R quantum sensor (LI-COR Inc., Lincoln, NE, USA). These measurements were conducted from 9:00–12:00 on sunny days in June and August 2020.

2.8. Data analysis

We calculated the importance values (IV) of species in the community (Peng, 1996). The 25 species with the highest IV in the community were selected for further analyses.

IV was calculated as follows:

$$IV = \frac{RD + RA + RF}{3} \tag{1}$$

where RD is relative dominance, RA is relative abundance, and RF is relative frequency.

Levins niche breadth (B_i) was also calculated (Levins, 1968).

Bi was calculated as follows:

$$B_i = 1 / \sum_{j=1}^{r} P_{ij}^2,\ P_{ij} = \frac{n_{ij}}{N_i},\ N_i = \sum_{j=1}^{t} n_{ij} \tag{2}$$

where Bi is the niche breadth of species i, j is quadrat number, r is the number of quadrats and P_{ij} is the proportion of the importance value of species i in j quadrat to the total importance values in all quadrats, n_{ij} is the importance value of species i in the j quadrat, and N_i is the sum of the importance values of species i in all quadrats.

To compare *C. longzhouensis* with selected species, we also calculated the Pianka niche overlap coefficients (Pianka, 1973), χ^2 test (Grizzle, 1964; Peng et al., 1999), association coefficient (AC), and Ochiai index (OI) (Wang and Peng, 1985). The Pianka niche overlap coefficient was calculated as follows:

$$O_{ik} = \frac{\sum_{j=1}^{r} N_{ij} N_{kj}}{\sqrt{\left(\sum_{j=1}^{r} N_{ij}\right)^2 \left(\sum_{j=1}^{r} N_{kj}\right)^2}} \tag{3}$$

where O_{ik} is the niche overlap coefficients of species i and k, N_{ij} is the importance value of species i in the j quadrat, N_{kj} is importance value of species k in the j quadrat, and r is the number of quadrats.

χ^2 was calculate as follows:

$$\chi^2_{Yates'} = \frac{(|ad - bc| - 0.5n)^2 n}{(a + b)(a + c)(b + d)(c + d)} \quad (4)$$

For AC calculation,
if ad ≥ bc:

$$AC = \frac{ad - bc}{(a + b)(b + d)} \quad (5)$$

if bc > ad, d≥a:

$$AC = \frac{ad - bc}{(a + b)(a + c)} \quad (6)$$

if bc > ad, d < a:

$$AC = \frac{ad - bc}{(b + d)(d + c)} \quad (7)$$

The OI was calculated as follows:

$$OI = \frac{a}{\sqrt{(a + b)(a + c)}} \quad (8)$$

where a is the number of quadrats shared by species A and B, b is the number of quadrats where only species A appears, c is the number of quadrats where only species B appears, d is the number of quadrats where neither species A nor species B appear, and n is the total number of quadrats (n = a + b + c + d).

Four species diversity indices (i.e., the Margalef's index, the Shannon-wiener index (Magurran, 1988), the Simpson index (Simpson, 1949), and Pielou's index (Qian and Ma, 1994)) were calculated using the following formula:

Margalef's index,

$$d_{ma} = \frac{s - 1}{InN} \quad (9)$$

Shannon-wiener index,

$$H' = -\sum_{i=1}^{S} P_i \ln P_i, P_i = \frac{n_i}{N} \quad (10)$$

Simpson index,

$$\mathbf{D = 1} - \sum_{i=1}^{S} P_i^2 \quad (11)$$

and Pielou's index,

$$J = \frac{H'}{H_{max}} = \frac{H'}{\ln S} \quad (12)$$

where $_{Pi}$ is relative dominance of species i in the quadrat, S is the number of species, N is the number of individuals, and n_i is the number of individuals of species i.

We used the Leslie matrix model to predict the age distribution of the population over the next 20 years. The population was divided into n + 1 equal age groups, i.e., group 0, 1, 2, 3,..., n. The model was then presented by the following matric equation:

$$\begin{pmatrix} f_0 & f_1 & f_2 & \cdots & f_{n-1} & f_n \\ p_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{n-1} & 0 \end{pmatrix} \times \begin{pmatrix} n_{1,0} \\ n_{6,1} \\ n_{i,2} \\ \vdots \\ n_{2,n} \end{pmatrix} = \begin{pmatrix} n_{1+1,0} \\ n_{1+1,1} \\ n_{t+1,2} \\ \vdots \\ n_{i+1,n} \end{pmatrix} \quad (13)$$

The number of organisms in the various age classes at time t + 1 was obtained by multiplying the numbers of individuals in these age classes at time t by a matrix, which expressed the fecundity and survival rates for each age class. f_1, f_2 ...f_n gave the reproduction in the i^{th} age group and P_0, P_1, P_2, P_3, P_4 ... P_n represented the probability that an organism in the i^{th} age group would still be alive after promotion to that group.

Based on the experience of *ex situ* conservation at the Guangxi Institute of Botany, Guangxi Province and the Chinese Academy of Science, the basal diameter of *C. longzhouensis* requires about 2 years to increase by 1 cm. The individuals of *C.*

longzhouensis in 12 size categories were divided into 6 age classes with a gradient of 4 years, and the maximum tabulated age class was 20 years.

Spearman's rank correlation coefficient analysis was used to determine the relationships between the main habitat properties and *C. longzhouensis* abundance. A principle component analysis (PCA) of the environmental variables was conducted using SPSS 24.0 (IBM Inc., Chicago, USA). The "spaa" package of R language was used to calculate the niche overlap value and association coefficients. A map of the study area was made with ArcGIS 10.2. Origin R 3.6.3 and Excel 2013 were also used for related calculations and chart construction.

3. Results

3.1. Species distribution

Based on the specimens collected from 1980 to 1998, *C. longzhouensis* plants were found in the Wuming District of Nanning City; Ningming County, Fusui County, and Longzhou County of Chongzuo City, Guangxi, China (Flora of China Editorial Committee, 2007; IB-CAS, 2020). A previously reported field survey that was conducted in 2014 found that the species was mainly located in Longzhou County and Fusui County, and the extent of occurrence was calculated as 2217 km^2 (Wheeler, 2015). However, the field survey conducted up to 2020 in the current study showed that the distribution of *C. longzhouensis* was limited to about 7 km^2 in the Nonggang section and its edge of Nonggang National Nature Reserve in Longzhou County, Guangxi (Fig. 2). We found only 58 individuals at three sub-populations in the wild.

3.2. Population structure

We grouped the 58 individuals into 12 size categories and found that the size structure had a spindle-shaped frequency distribution (Fig. 3). There was a lack of seedlings and large-DBH adult plants in the population, and individuals were concentrated in the medium-DBH category, i.e., plants with 3 ≤ DBH < 4 cm were the most common and accounted for 31% of the total. The proportions of death (q_x) of 2a and 4a individuals were negative, and the killed power (K_x) of 12a individuals was high. The net reproduction rate (R_0), the intrinsic increase rate (r_m), and the finite increase rate (λ) of *C. longzhouensis* populations were all very low, and the average age of reproductive-stage individuals of *C. longzhouensis* was 12.45 years ($R_0 = 0.057$, $R_0 < 1$; $r_m = -0.230$, $r_m < 0$; $T = 12.45$; $\lambda = 0.795$, $\lambda < 1$) (Tables A1–3). The Leslie matrix model predicted that the number of individuals of each age class and the total number in the population would continuously decline over the next 20 years (Table 1).

3.3. Habitat

3.3.1. Plant community of the Camellia longzhouensis population

In the sampling plots in the plant community with *C. longzhouensis*, a total of 85 species and 511 individuals of vascular plants were recorded; these individuals belonged to 69 genera and 36 families (Table A4–6). The dominant families were

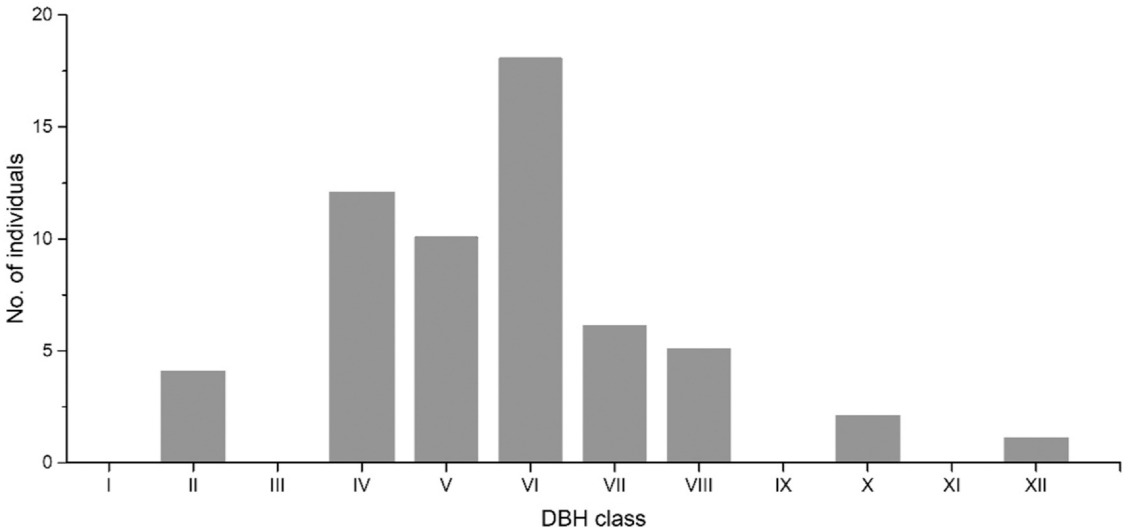

Fig. 3. Frequency distribution of *Camellia longzhouensis* size categories (in cm). Note: I: DBH < 1, H < 33; II: DBH < 1, 33 ≤H < 100; III: DBH < 1, H ≥ 100; IV: 1 ≤ DBH < 2; V: 2 ≤ DBH < 3; VI: 3 ≤ DBH < 4; VII: 4 ≤ DBH < 5; VIII: 5 ≤ DBH < 6; IX: 6 ≤ DBH < 7; X: 7 ≤ DBH < 8; XI: 8 ≤ DBH < 9; XII: 9 ≤ DBH < 10. DBH: diameter at breast height.

Table 1
Numerical dynamics of the *Camellia longzhouensis* population in the next 20 years as predicted by the Leslie matrix model.

Age class	N_0	N_1	N_2	N_3	N_4	N_5
2	4	2	1	1	0	0
4	12	10	4	4	2	1
8	28	12	10	4	3	2
12	11	9	4	3	1	1
16	2	3	2	1	1	0
20	1	1	1	1	0	0
Total	58	36	22	13	8	5

N_0: current survival number; N_1–N_5: predicted number of surviving individuals in the next 20 years at 4-year intervals.

Euphorbiaceae (16 species belonging to 13 genera), Annonaceae (4 species belonging to 4 genera), Poaceae (4 species belonging to 3 genera), and Moraceae (4 species belonging to 2 genera).

According to the classification of areal-type of Chinese seed plant (Wu, 1991; Wu et al., 2003), in the *C. longzhouensis* community, 23 families and 61 genera had a tropical distributions and accounted for 65.7% of the total families and 89.7% of the total genera (Table A7). Two genera whose species had high importance values were *Cephalomappa* and *Camellia*. The tree density in the community was 0.3 individuals per m^2, and the shrub density was 0.9 individuals per m^2. The community height was low (average tree height was 5.82 ± 5.96 m), and the canopy layer structure was relatively simple. The average DBH of trees was 5.83 ± 3.24 cm, and the number of small-diameter individuals (DBH < 10 cm) was significantly greater than number of large-diameter individuals (DBH ≥ 10 cm). In our survey area, 25 species had IV greater than 1.0% (Table 2). Among them, *Bambusa sinospinosa* had the highest IV, followed by *C. longzhouensis* and *Streblus tonkinensis*.

Niche width was highest for *Cleistanthus petelotii* and was only slightly lower for *C. longzhouensis* and *Antidesma japonicum* (Table 2). The species with the largest niche overlap with *C. longzhouensis* were *Cephalomappa sinensis*, *Caryota obtusa*, *Hydnocarpus hainanensis*, *Lirianthe fistulosa*, *Cleistanthus petelotii*, and *Antidesma bunius* (Table 2).

Cleistanthus petelotii, *Cephalomappa sinensis,* and *Caryota obtusa* were all canopy tree species, while *Hydnocarpus hainanensis*, *Lirianthe fistulosa* and *Antidesma bunius* were small trees or shrubs similar to *C. longzhouensis*.

The χ^2 test showed that there was a close association between *Cleistanthus petelotii* and *C. longzhouensis* ($\chi^2 = 5.185$, $P < 0.05$). The species with higher AC values with *C. longzhouensis* were *C. petelotii* (0.70), *A. bunius* (0.66), *Streblus tonkinensis* (−0.57), and *H. hainanensis* (−0.40). The species with higher Ochiai index values with *C. longzhouensis* were *C. petelotii* (0.89), *A. bunius* (0.8), *C. obtusa* (0.48), *C. sinensis* (0.45), *C. chinensis* (0.45), and *Zenia insignis* (0.45). The Margalef index, Shannon Weiner index, Simpson dominance index, and Pielou evenness index of this community was 4.81 ± 1.72, 2.29 ± 0.21, 0.82 ± 0.05, and 0.73 ± 0.05, respectively.

Table 2
Importance values, niche breadths, niche overlaps, and association coefficients of the top 25 species (based on importance values) in the plant community.

Number	Name of species	Importance value (%)	Niche width	Niche overlap (to *Camellia longzhouensis*)	Association coefficients (to *Camellia longzhouensis*)
1	*Bambusa sinospinosa*	10.47	1.22	0.13	-0.40
2	*Camellia longzhouensis*	7.86	1.94	1.00	1.00
3	*Streblus tonkinensis*	6.56	1.47	0.18	-0.57
4	*Cephalomappa sinensis*	6.23	1.00	0.92	0.13
5	*Cleistanthus petelotii*	4.66	1.95	0.85	0.70
6	*Bambusa tuldoides*	4.26	1.00	0.09	-0.20
7	*Cryptocarya lyoniifolia*	4.21	1.00	0.09	-1.00
8	*Glochidion lanceolarium*	3.63	1.00	0.39	0.04
9	*Caryota obtusa*	3.49	1.00	0.92	0.13
10	*Antidesma bunius*	3.19	1.48	0.61	0.66
11	*Celtis timorensis*	2.66	1.18	0.40	-1.00
12	*Hydnocarpus hainanensis*	2.48	1.58	0.90	-0.40
13	*Cryptocarya chinensis*	2.40	1.00	0.39	0.13
14	*Catunaregam spinosa*	2.33	1.00	0.39	0.04
15	*Antidesma japonicum*	2.28	1.94	0.37	-0.52
16	*Vitex kwangsiensis*	1.98	1.00	0.09	-1.00
17	*Zenia insignis*	1.51	1.00	0.09	0.13
18	*Cipadessa baccifera*	1.48	1.00	0.09	-1.00
19	*Phyllanthus reticulatus*	1.40	1.55	0.40	0.04
20	*Lirianthe fistulosa*	1.37	1.62	0.89	0.04
21	*Ficus hispida*	1.34	1.00	0.09	-1.00
22	*Dracaena cochinchinensis*	1.31	1.00	0.09	0.04
23	*Clausena dunniana*	1.27	1.00	0.09	-1.00
24	*Strophioblachia fimbricalyx*	1.18	1.00	0.09	0.20
25	*Pterospermum truncatolobatum*	1.04	1.00	0.09	-1.00

Table 3
Habitat properties of the *Camellia longzhouensis* community.

Property	Mean ± SD
Soil pH	6.71 ± 0.11
Soil water content (SWC, %)	14.74 ± 1.14
Soil organic matter content (SOM, g/kg)	113.67 ± 19.43
Soil total nitrogen content (STN, g/kg)	9.27 ± 1.26
Soil ammonium nitrogen content (NH_4^+ N, mg/kg)	3.75 ± 0.84
Soil nitrate nitrogen content (NO_3^- N, mg/kg)	5.59 ± 2.83
Soil total phosphorus content (STP, g/kg)	1.45 ± 0.58
Soil available phosphorus content (SAP, mg/kg)	8.66 ± 5.62
Soil total potassium content (STK, g/kg)	1.21 ± 0.55
Soil available potassium content (SAK, mg/kg)	0.13 ± 0.02
Standing litter crop (LT, kg/m^2)	0.34 ± 0.08
Water content of litter (LWC, %)	57.30 ± 3.30
Litter organic carbon content (LTC, g/kg)	86.10 ± 0.17
Litter nitrogen content (LTN, g/kg)	16.51 ± 1.37
Litter phosphorus content (LTP, g/kg)	0.84 ± 0.13
Leaf area index (LAI)	3.63 ± 0.86
Diffuse noninterceptance (DIFN, %)	11.87 ± 5.47
Ambient light intensity (LI, μmol m^{-2} s^{-1})	2.11 ± 0.74

3.3.2. Soil properties, standing litter crop, and light environment

C. longzhouensis was distributed in the northern tropical karst seasonal rain forest, where the geomorphologyical type was "peak-cluster deeply incised round depression (valley)". *C. longzhouensis* grew on the middle and lower slope or valley bottom of the “peak-cluster” landform, and about 80% of the bedrock on the middle slope was exposed. Other habitat properties are presented in Table 3.

3.3.3. Correlations between C. longzhouensis abundance and habitat properties

C. longzhouensis abundance was positively correlated with soil water content ($P < 0.01$) and soil available potassium content ($P < 0.05$), and was negatively correlated with environmental light intensity ($P < 0.05$) and soil ammonium nitrogen ($P < 0.01$) (Table 4).

Result of PCA indicated that the main habitat properties associated with C. longzhouensis abundance were soil nitrate nitrogen, soil total phosphorus, soil total potassium and soil ammonium nitrogen, followed by soil pH, diffuse noninterceptance, and environmental light intensity (Table A8, Fig. 4).

The PCA results differed slightly from the correlation analysis results. This may be due to their different principles. Principal component analysis recombines the initial variables with certain correlation into a group of unrelated indicators, while rank correlation analysis only focuses on the relationship between a single variable and abundance. Generally, some data information will be lost in the process of PCA, which may lead to some small differences in the analysis results. For example, in Spearman rank correlation analysis, soil water content and soil available potassium content, which were positively correlated with the number of individuals in *C. longzhouensis* population (0.804, $P < 0.01$; 0.965, $P < 0.05$), did not have large enough factor loading in the PC1 of PCA (0.720; 0.801). However, some variables that were not significant in correlation analysis had larger factor loading in PC1 and PC2 of PCA. This may be because there is usually a correlation between variables describing the same aspect of the problem, and it is reflected in the factor loading of the common factor.

Table 4
Correlations between *Camellia longzhouensis* abundance and habitat properties; coefficients with one or two asterisks are significant at $P < 0.05$ or < 0.01, respectively.

Soil property		Element content of litter or light	
Property	Correlation coefficient	Property	Correlation coefficient
pH	0.754	LTC	-0.536
SOM	0.316	LTN	0.268
STP	0.643	LTP	-0.482
SAP	0.482	LWC	-0.482
STN	0.482	LT	-0.482
SNH4N	-0.965**	LAI	-0.158
SNO3N	0.482	LI	-0.733*
STK	0.482	DIFN	-0.580
SAK	0.965*		
SWC	0.804**		

Note: pH- Soil pH, SOM- Soil organic matter, STP- Soil total phosphorus, SAP- Soil available phosphorus, STN- Soil total nitrogen, SNH4N- Soil ammonium nitrogen, SNO3N- Soil nitrate nitrogen, STK- Soil total potassium, SAK- Soil available potassium, SWC- Soil water content, LTC-Litter total carbon, LTN-Litter total nitrogen, LTP- Litter total phosphorus, LWC- Litter moisture content, LT- Standing litter crop, LAI- Leaf area index, LI- Ambient light intensity, DIFN- diffuse noninterceptance.

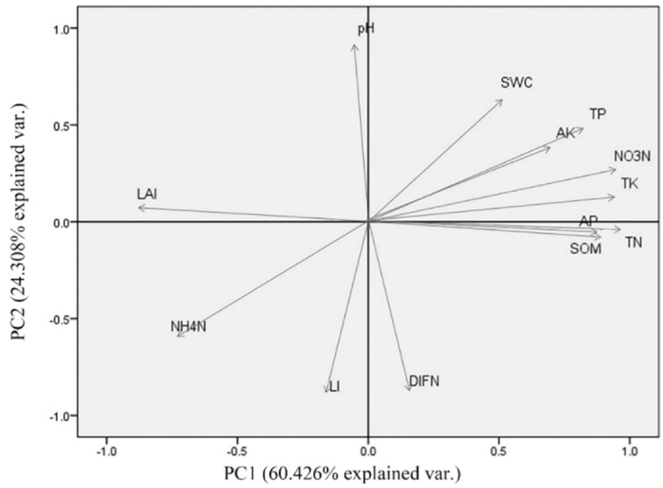

Fig. 4. Principal component analysis (PCA) of the habitat properties of *Camellia longzhouensis* community. Note: pH- Soil pH, SOM- Soil organic matter, STP- Soil total phosphorus, SAP- Soil available phosphorus, STN- Soil total nitrogen, SNH4N- Soil ammonium nitrogen, SNO3N- Soil nitrate nitrogen, STK- Soil total potassium, SAK- Soil available potassium, SWC- Soil water content, LAI- Leaf area index, LI- Ambient light intensity, DIFN- diffuse noninterceptance.

4. Discussion

4.1. Habitat of Camellia longzhouensis

Camellia longzhouensis grew in the northern tropical karst seasonal rain forest in South China. The community was rich in species and showed obvious tropical characteristics at the family and genus levels. The structure of the associated community was relatively simple and resembled that of a secondary forest, i.e., the community had a medium height and more individuals of large than of small diameter classes. In order to protect plant species and natural environments, the Nonggang National Nature Reserve was established in 1979, at which time logging was prohibited in the reserve. But almost all of the tall trees outside the reserve were cut by villagers for firewood, and this destructive activity only stopped 10 years ago. Because of the hot and humid environment, the remaining secondary monsoon forest is luxuriant (Nong, 2015). Compared to the 15 hm^2 karst seasonal rain forest plot in Nonggang (Huang et al., 2016), the *C. longzhouensis* community in the current study had slightly lower Shannon-Weiner index values but similar values for the Simpson index and Pielou index. The original habitat of *C. longzhouensis* was located in the limestone area, where the ecosystem was extremely fragile due to the rocky mountain soil structure. As a result, soil stability was poor. Once that stability is destroyed, it causes soil erosion and leads to rocky desertification, a condition that is difficult to correct.

After the farmers stopped logging, the original habitat outside the reserve had experienced ecological succession. After 10 years of natural succession, the original habitat of *C. longzhouensis* became species rich and relatively complex, but it was quite different from the climax community in the north tropical monsoon forest, and it still had obvious characteristics of a secondary forest. We found that the niche breadth value of *C. longzhouensis* was large, indicating that *C. longzhouensis* has strong adaptability. *C. longzhouensis* had more than 80% niche overlap with some canopy tree species (*C. obtusa*, *C. sinensis*, and *C. petelotii*) and small tree species (*H. hainanensis* and L. *fistulosa*). *C. longzhouensis* and these tree species grew in limestone mountain or valley forests, and they preferred a humid environment and fertile, acidic soil. Among the three parameters of interspecific association, *C. petelotii* showed a significant positive correlation with *C. longzhouensis* ($\chi 2$ test results were significant, AC = 0.70, OI = 0.89), indicating that *C. petelotii* is a companion species of *C. longzhouensis*. The importance value and niche width of *C. petelotii* were large. *C. petelotii* was usually 7–18 m high and often appeared above *C. longzhouensis*. It can be considered a highly competitive species that can effectively use resources in the community. The ambient light in the *C. longzhouensis* habitat was weak. Because of the strong competitiveness and large average crown width, *C. petelotii* helped shade *C. longzhouensis*. Although no significant results were obtained in the χ^2 test, competitive relationships between *C. longzhouensis* and *H. hainanensis* and *S. tonkinensis*, and a complimentary association between *C. longzhouensis* and *A. bunius* were suggested by AC and OI values. *C. longzhouensis* apparently relies on the shade created by *C. petelotii* and other plants, and might compete with *H. hainanensis* and *S. tonkinensis.*

Correlation analysis and PCA indicated that the main factors associated with *C. longzhouensis* abundance were soil factors (pH and the contents of N, P, K, and water) and light intensity. In the karst area, P has been leached by rain in the upper and middle parts of the peak cluster, and has accumulated in the depression and the middle and lower parts of the peak cluster. The high temperature and drought conditions in the upper and middle parts of the peak cluster lead to the slow decomposition of soil organic matter and therefore to a high soil organic matter content (Guo et al., 2017). Because *C. longzhouensis* grew in the middle and lower part of the peak cluster, it grew in soil enriched with P as well as with C and N decomposed from SOM and litter. Based on the nutrient grading standard of the second national soil survey of China, the soil C, N, and P contents of the companion communities of *C. longzhouensis* all reached the first-class standard (C: > 40 g/kg, N: > 2 g/kg, P: > 1 g/kg). However, the contents of total potassium (1.21 ± 0.55 g/kg) and available potassium (0.13 ± 0.02 mg/kg) were much lower than the average values (5.7 g/kg; 41 mg/kg) in other areas with the same geological conditions. The N content in the litter on the soil surface was higher in the *C. longzhouensis* community than in the subtropical evergreen-deciduous broadleaved mixed forest of the karst area in northwest Guangxi (12.7 g/kg) and of the subtropical evergreen broad-leaved forest of Dinghu mountain in Guangdong (14.2 g/kg), but was lower than China's average (18.6 g/kg). The P content in the litter in the *C. longzhouensis* community was higher than in the subtropical evergreen broad-leaved forest in Dinghu mountain (0.4 g/kg), was equivalent to the P content in the litter of the karst evergreen deciduous broad-leaved mixed forest in northwest Guangxi (P: 0.9 g/kg), but was lower than China's average (P: 1.2 g/kg) (Han et al., 2005; Kang et al., 2010; Zeng et al., 2015).

Overall, soil N was abundant while soil K was scarce in the *C. longzhouensis* habitat. The high contents of N and P in litter ensured the return of N and P to the soil. Because of the topography, plants in karst areas often suffer periodic drought or flooding. Water is of course required for plant growth, and water and temperature greatly affect the rate at which SOM decomposes. Soil water content is therefore closely related to *C. longzhouensis* survival. There was also a negative correlation between light intensity and *C. longzhouensis* abundance. We infer that this species cannot tolerate strong light, and that *C. petelotii* in particular might provide the required shade. Studies on plant functional traits of *C. longzhouensis* as affected by conservation translocation showed that the species may be adapted to some habitat conditions by rapidly altering their morphological, anatomical, and eco-physiological traits (Unpublished data).

4.2. Camellia longzhouensis – A critically endangered species

Based on IUCN Red List Categories and Criteria Version 3.1 and the information of the Chinese Virtual Herbarium, *Camellia longzhouensis* had been distributed in the Wuming District of Nanning City and Ningming County, Longzhou County, and Fusui County of Chongzuo City. The extent of occurrence was previously estimated as 2217 km^2, and it is was considered likely to be found in fewer than five locations (Wheeler, 2015). When IUCN assessed the species in 2015, there was a lack of habitat and population information, and the population was thought to be declining due to the habitat deforestation resulting from the establishment of plantations of economic plants. The flat lands among the hills in Fusui have been planted with crops such as peanut, green bean, sesame, sugarcane, and jute. In this area, local farmers are allowed to cut trees for firewood. The construction of a railway and other human activities in these areas have fragmented the landscape. The abundance of *C. longzhouensis* and quality of its habitat are declining due to these threats. In the IUCN Red List Categories and Criteria Version 3.1, *C. longzhouensis* was assessed as Endangered B1ab(iii) in 2015.

Based on our field survey of 2020, *C. longzhouensis* is only distributed in the Nonggang National Nature Reserve and along its edge, i.e., in an area of about 7 km^2. The distribution in 2020 involves a total of 58 plants belonging to three subpopulations. Its distribution range was narrower in 2020 than 5 years ago, and its abundance in 2020 was extremely small. In addition to being influenced by habitat properties, the abundance of *C. longzhouensis* was also directly reduced by human activities including poaching (*personal observations*). In recent years, there were organized poaching activities in the local area, mainly in the form of acquisition by outsiders, and theft by both locals and outsiders. In 2017, there were a lot of poaching of *C. longzhouensis*, and we found 15 poaching pits outside the reserve.

At present, the largest *C. longzhouensis* individual in the reserve had a DBH of 5.9 cm and a height of 4 m, and it could bear fruit. However, individuals outside the reserve were all adult plants that regrew after being cut down, and they were scattered and fruitless. In addition, the surviving *C. longzhouensis* plants had reproductive disorders. The numbers of flowers and initial fruits were large, but few fruits remained until the final maturity, which was the reason for the small number of seedlings. In this survey, we found fewer than 50 fruits, and almost no seedlings. The proportions of death (q_x) of 2a and 4a individuals were negative, indicating that younger individuals could not survive to the next age stage, and that the number of young individuals was seriously insufficient. At the age classes of 8a and 12a, the mortality rate and population killed power (K_x) were high, indicating that the maintenance of the population mainly depended on the middle age individuals, and that the individuals in the population were affected by the environment during this period. Except for the low content of soil P, the soil fertility of the *C. longzhouensis* habitat was relatively rich and probably sufficient to meet the survival requirements of this species. At the same time, *C. petelotii* companion plants could ensure the weak light environment required by *C. longzhouensis*. However, poaching has reduced the number of adult plants in the wild, and the low fecundity and poor stability of the population have led to a serious shortage of seedlings.

Therefore, the structure of the *C. longzhouensis* population was extremely poor. The net reproduction rate (R_0), the intrinsic increase rate (r_m), and the finite increase rate (λ) of *C. longzhouensis* population were all very low, indicating that the population of *C. longzhouensis* would decline and could not complete self-renewal. The Leslie population matrix model predicted that the number of individuals in each age class and the total number of individuals would be in a continuous decline for the next 20 years. The model was based on the fecundity and survival rates calculated in the static life table. If the fecundity and survival remain low, the population will continue to decrease.

The current situation of *C. longzhouensis* is consistent with IUCN Red List Criterion C2ai: the number of mature individuals is fewer than 250(C); the population is experiencing a continuing decline (2); the number of mature individuals in each subpopulation is fewer than 50(i); and at least 90% of the mature individuals are in one subpopulation(ii). We therefore recommend that *C. longzhouensis* be recategorized as Critically Endangered C2a(i,ii).

4.3. Strategies to protect Camellia longzhouensis

The small number of wild individuals of *C. longzhouensis* found in our survey was apparently the remnants of habitat destruction, and protective measures should be taken as soon as possible. We suggest that following strategies for the protection of *C. longzhouensis*:

(a) Locate all wild individuals, expand the range of the reserve, and conduct regular inspections
First, because the existing individuals of *C. longzhouensis* are rare, each wild individual should be located, and the areas with individuals at the edge of the reserve should be incorporated into the reserve. The condition of the individuals should be assessed every 2–3 months. At the same time, the habitat supported the wild individuals and their community should be well protected. Because *C. longzhouensis* is not adapted to strong light, its survival depends on other tree species that create weak light environments. Moreover, the original habitat of *C. longzhouensis* is difficult to restore after being destroyed. Attention should be paid to maintaining the most suitable environment for *C. longzhouensis* survival and natural reproduction in order to achieve effective in situ conservation.
(b) Conduct *ex situ* conservation and reintroduction
In 2005, the Guangxi Institute of Botany carried out *ex situ* conservation on 80 individuals of *C. longzhouensis*. To date, about 2600 seedlings have been obtained from those individuals, mainly propagated by cuttage. In 2019, 70 individuals of *C. longzhouensis* were planted at South China Botanical Garden.
We suggest the establishment of a habitat in the nursery at the Nonggang National Nature Reserve for *ex situ* conservation. This nursery would be established by collecting as many branches of individuals in the field as possible without causing lethal damage, and establish a full genetic diversity nursery to protect genetic resources. These branches would be grafted to existing plants in the nursery to prevent inbreeding depression and to protect the genetic resources of the species during *ex situ* conservation (Ren et al., 2016). *C. longzhouensis* seedlings from various sources could be used to increase the numbers of seedlings and adult plants in the native populations. At the same time, the population dynamics should be continuously monitored. The success of the *ex situ* conservation and reintroduction should be maximized by applying the latest information and technology concerning material reproduction, cryobiotechnology, habitat restoration, horticultural measures, and interspecific interactions (Ren et al., 2014; Pence et al., 2020).
(c) Promote commercial production

In the early years, local farmers excavated *C. longzhouensis* plants without regard to the maintenance of local populations (Fig. A1). Traditional agricultural planting in the karst area not only produces low yields, but also causes soil erosion and aggravates rocky desertification, especially on land with slopes >15°. Although *C. longzhouensis* has both ecological and economic value, it has not been commercialized. We suggest the establishment of a bank for germplasm conservation and propagation with the goal of protecting *C. longzhouensis*. The commercial production of the species should be encouraged to reduce illegal excavation and to increase sustainable development.

Until recently, Longzhou County was considered to be poverty-stricken. It was only relieved from the poverty in August 2018 because of China's poverty alleviation actions. It is the first county among the 33 key counties that benefitted from the poverty alleviation and development work in Guangxi. With the economic development, local farmers may no longer need to make a living by poaching wild plants but they can sustainably use the local plant resources.

5. Conclusions

Camellia longzhouensis is a narrowly distributed species that only grows in the natural secondary forest with fertile soil in the karst area of southeastern China. As of 2020, there were only 58 plants in the wild, with few young plants and poor population structure. Threats to the species include biological factors such as competition from several species with similar niches and environmental factors such as soil N and P contents and light intensity. In addition, illegal excavation and natural reproduction obstacles have contributed to the decline of the population size. We recommend that *C. longzhouensis* be categorized in the IUCN Red List as Critically Endangered based on criterion C2ai. Several protective measures are proposed, including expanding the area of the Nonggang National Nature Reserve to include all individuals of *C. longzhouensis*, marking all wild individuals and inspecting them regularly to achieve effective on-site protection, and collecting the branches of all individuals in the wild for grafting to established nursery plants or to establish new plants from cuttings; the goal is to establish a *C. longzhouensis* nursery with full genetic diversity and to use that nursery for the establishment of new populations in the wild via reintroduction. The findings of this study and the recommended conservation approach should be useful for developing integrated conservation strategies for other economically valuable endangered plants in the karst areas.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01585.

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