



Ecological niche modeling applied to the conservation of the East Asian relict endemism *Glyptostrobus pensilis* (Cupressaceae)

Paula Pueyo-Herrera¹ · Cindy Q. Tang² · Tetsuya Matsui^{3,4} · Haruka Ohashi³ · Shenhua Qian⁵ · Yongchuan Yang⁵ · Sonia Herrando-Moraira^{1,6} · Neus Nualart¹ · Jordi López-Pujol^{1,7}

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Abstract

Glyptostrobus pensilis (Cupressaceae) is the only surviving species of the genus *Glyptostrobus*. Although the species is widely cultivated throughout China, in the wild it only occurs as small stands in southeastern China, central Laos, and southern Vietnam. However, its low genetic variability, lack of recruitment, and the progressive destruction of its habitat caused by humans, have meant that the populations are showing a clear declining trend and the species as a whole is threatened. Ecological niche modeling is used here to study the present potential distribution, as well as in the future (2061–2080) using several global circulation models under two of the shared socioeconomic pathways (SSP 126 and SSP 585) that are being used to produce the IPCC Sixth Assessment Report. The current potential area of *G. pensilis* is of 1,452,481 km² with the areas of greatest probability of presence located in southeastern China. This potential area is reduced for the future according to most models, with greater losses for the SSP 585 scenario. Between 6.9 and 31.3% of all wild populations of *G. pensilis* would be outside potential areas (including the Lao populations, which harbor the highest levels of genetic variability). Conservation measures include the expansion of the current network of protected areas (since over 90% of wild populations do not occur within them), the development of propagation techniques, and the carrying out of translocation activities that should require international collaboration among the countries in which the species is found. With the current knowledge, we have reassessed the threat status of the species under the IUCN criteria, downgrading it from CR to EN both for China and at global level.

Keywords Climate change · Conservation · East Asia · *Glyptostrobus* · Management · Niche modeling

✉ Cindy Q. Tang
cindytang@ynu.edu.cn

✉ Jordi López-Pujol
jlopez@ibb.csic.es

Introduction

East Asia has an unusual concentration of relict lineages whose distribution was often much larger in the past (Tang et al. 2018). The fossil record shows that many relict lineages were distributed throughout Europe, North America and other areas of Asia until the Neogene, when they disappeared as a result of global cooling (Latham and Ricklefs 1993; Manchester et al. 2009). Current relict taxa are generally survivors of previously much more widespread lineages, whose close relatives have become extinct. Furthermore, in some cases they have remained unchanged for millions of years, being thus considered true “living fossils” (López-Pujol and Ren 2011). Recent studies based on ecological niche modeling have shown the existence of long-term climatically stable refugia (mainly located in central and southwestern China and adjacent areas of Indochina), where climatic fluctuations would have been reduced to a minimum compared to other places in the Northern Hemisphere (Tang et al. 2018).

Glyptostrobus pensilis (Staunton ex D. Don) K. Koch (Cupressaceae), commonly known as water pine (*shuǐ sōng*) or Chinese swamp cypress, is the only surviving species of the genus *Glyptostrobus* and it is considered a living fossil. It is one of the oldest conifers of the world, as its fossil record dates back to at least 100 million years (LePage 2007). Nowadays, the species survives in flooded or in waterlogged places such as river banks, swamps, ponds, floodplains and deltas (Fu et al. 1999; Tang et al. 2019; Missouri Botanical Garden 2021). The fossil records indicate that the genus *Glyptostrobus* was widely distributed throughout the Northern Hemisphere from early Cretaceous to early Pleistocene (Tang et al. 2019, and references therein). However, at present its distribution has been reduced to southern China, southern Vietnam and central Laos where isolated populations are found (Averyanov et al. 2009; Tang et al. 2019). This reduction in range would have occurred due to increased aridity, cooling, and probably greater competition for the space and resources (LePage 2007). The species would have been extremely common in present-day Guangdong Province in the mid/late Holocene, but also extending to Fujian and even southern Zhejiang (Peng et al. 2015; Ma et al. 2016; Zheng et al. 2021), and it is believed that it still formed extensive forests in this region until just 1000 years ago (Tang et al. 2019), which is consistent with some sources in Chinese historiography (see Thomas and LePage 2011). The development of intensive rice-based agriculture in East Asia from approximately 2000 years ago transformed many of the lowlands and wetlands, habitats where *G. pensilis* had persisted, leading to a reduction in both area and abundance and the fragmentation of wild populations, which are now restricted to remote and inaccessible areas (Li and Xia 2005; Averyanov et al. 2009, 2014; Thomas and LePage 2011; Zheng et al. 2021).

In southeastern China, *G. pensilis* is widely cultivated along rice paddies, in temples and villages. As a result of its extensive cultivation, its current natural range is difficult to determine (Li and Xia 2005; Wu et al. 2020), but recent field studies have made it possible to obtain primary data of the origin (wild/cultivated) of the populations. The project “Investigating Ancient and Big Trees”, carried out by government organizations in China (such as the forestry offices of each county), in addition to the several years of field work by our group has allowed, within the framework of this work, to obtain tentative distribution maps of wild and cultivated populations (Fig. 1). Natural and cultivated populations overlap in areas close to the coast while the latter reach areas further north, where there are no natural populations. As can be seen in Fig. 1, this species has wild occurrences in a total of six Chinese provinces (Fujian, Guangdong, Guangxi,

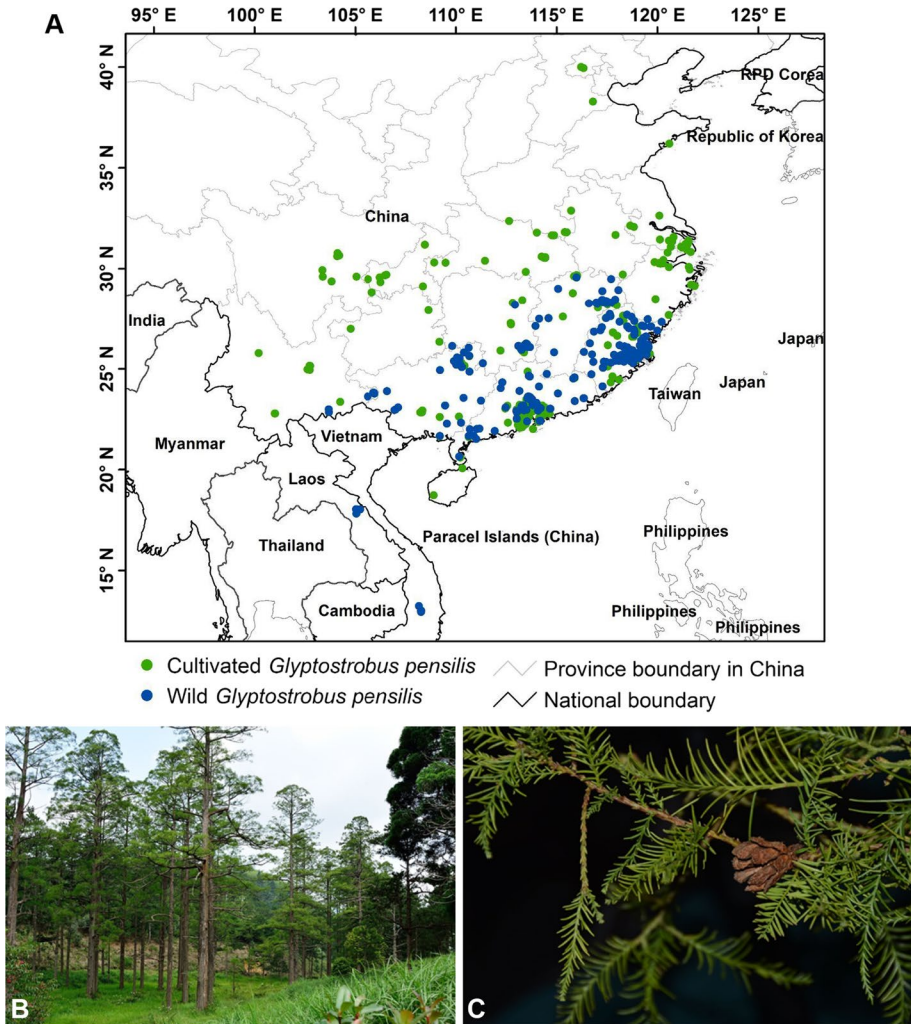


Fig. 1 Current distribution map of *Glyptostrobus pensilis* (wild populations and cultivated populations in the study area) (A); *Glyptostrobus pensilis* swamp forest in Shangloucun, Pingnan, Fujian Province (B); Detail of a mature seed cone and leaves of *Glyptostrobus pensilis* (C). Photographs by Cindy Q. Tang

Hunan, Jiangxi and Yunnan) as well as in the Hong Kong Special Autonomous Region. In Vietnam, natural populations are restricted to a few small localities in Dak Lak Province (Averyanov et al. 2009). The total number of mature trees in Vietnam is less than 300 and these are mainly concentrated around two small protected areas. The discovery of *G. pensilis* populations in Laos is more recent, with several occurrences located in the Nakai plateau, between southern Borikhamxai Province and northern Khammouan Province, with a few hundred individuals in total (Thomas and LePage 2011; Averyanov et al. 2014; Coffman 2021).

Recent demographic studies show that wild populations of *G. pensilis* are in decline. According to Tang et al. (2019) the number of seedlings produced is very low or even

null in some populations of China, indicating that the regeneration of the species is poor. Lack of regeneration is also common in populations of Laos and Vietnam (Thomas and LePage 2011; Averyanov et al. 2009, 2014). Another problem, apart from recruitment, is the loss of vigor of some trees, due to the reduction of the quantity and quality of water, as a result of the drying up of land for crop cultivation, or the construction of reservoirs (Averyanov et al. 2009, 2014; Tang et al. 2019). This shows how human activities have impacted—and are continuing to do so—on the habitat, drastically threatening the survival of *G. pensilis* (Tang et al. 2019). This loss of water quality does not only affect the survival of adult specimens, but also prevents seed germination (Xu and Li 1959). In addition to the loss of habitat quality, the species has also suffered in recent times the direct destruction of its habitat, mainly due to dam building; the recent construction of the Nam Thien 2 dam led to the disappearance of the population discovered in 2007 in Laos (Thomas 2019), while 200 of the 600 trees discovered in 2015 were illegally cut shortly thereafter (Coffman 2021). For all these reasons, *G. pensilis* is listed under the highest category of threat, “Critically Endangered” (CR), at global level (Thomas et al. 2020) and also in China (Qin et al. 2017) and in Vietnam (Nguyen et al. 2007). Although Laos does not have a red list of plant species at the moment, *G. pensilis* most likely meets the criteria to be categorized also as CR (Averyanov et al. 2014).

Regarding population genetics, various studies using nuclear and plastidial molecular markers indicate that genetic variability within populations is low (though genetic divergence between populations is high; Li and Xia 2005; Wu et al. 2011, 2012, 2020), which represents a potential threat to the conservation of *G. pensilis* in the long term. These genetic patterns may likely reflect the effects of population fragmentation, which could be the result of old events (e.g. Pleistocene climatic deterioration) or more recent ones (e.g. Bronze Age rise of rice agriculture). The low within-population genetic diversity (which translates into the loss of evolutionary potential; Frankham et al. 2002), together with the very poor regeneration capacity, make this species very sensitive to climatic changes (LePage 2007). The species seems to have survived only in those areas where its ancestral ecological niche preferences are preserved; these areas would have been characterized, among other environmental traits, by humid and warm climates (as also suggested for many other relict species; Tang et al. 2019). As a consequence of climate change, a significant reduction is expected in humid regions and an expansion in arid zones in Asia (Wang and Zhang 2020), which could further reduce the distribution of this relict tree.

Ecological niche modeling (ENM) is widely used for mapping species’ distributions across space and time, which in turn can inform conservation plans for many endemic and threatened taxa (e.g. Qu et al. 2018; Draper et al. 2019). Though recent studies on reconsideration of the native range (Zhang and Fischer 2021) and the impact of climate change on the potential habitat area of *G. pensilis* in East Asia (Ye et al. 2022) were conducted, they have serious limitations and/or did not address important aspects. For example, both studies only used climatic variables, only one explored potential distribution under future climatic change (but using a small occurrences dataset, and a single—and outdated—general circulation model), and they do not deal with conservation specific aspects. Our aims are: (1) to predict the potential distribution of *G. pensilis* for the present time employing a combined set of climatic, edaphic, and topographic variables, (2) to explore the impact of the most updated climate change scenarios into the distribution of the species, (3) to check whether wild and cultivated stands occur within ecologically suitable areas in present and in future, (4) to see whether the current network of nature reserves is effective in protecting current populations and current and future suitable areas, and (5) to reassess its IUCN

threat category (both for China and for the entire world) and to suggest appropriate conservation measures.

Materials and methods

Study species

Glyptostrobus pensilis has an average height of about 15 m, although specimens of up to 30 m have been found (Fig. 1B). Its bark is grayish-brown or white, cracked into long and irregular strips, and its needle-shaped leaves (Fig. 1C) are deciduous (Fu et al. 1999; Missouri Botanical Garden 2021). It is also characterized by having pneumatophores around the base, which allow it to obtain oxygen in the flooded soils where it grows (Missouri Botanical Garden 2021). Although the species, monoecious, is able to reproduce clonally, its reproduction is mainly through seeds and the pollination, as in most conifers, is by wind (Tang et al. 2019). It is a very useful species for humans; its roots are used to make life jackets or cork stoppers due to their great buoyancy, while tannins are extracted from the scales of its bark and are used to tan fishing nets; furthermore, it is often planted in damp places to control erosion, as protection against the wind and for beliefs related to good luck (Fu et al. 1999).

Study area

For the present study, all known occurrences of *G. pensilis*, both natural and cultivated, were gathered. Sources included our own field investigations, but also data from the Chinese national project “Investigating Ancient and Big Trees” (see above), the Chinese Virtual Herbarium (CVH; <https://www.cvh.ac.cn/>), and numerous literature sources (that are listed in Tang et al. 2019). In total, 249 natural populations were compiled, of which the vast majority (240) are from China. The number of cultivated populations accounted for 298, all of them distributed in China (Fig. 1A).

In order to unravel the potential distribution in the future, the ENM study area (0–54° N and 80–155° E) has a considerably greater extension than the species current range. Although this scheme may produce a somewhat less precise potential distribution of the species (Anderson and Raza 2010), having a large geographical background allows the detection of potential areas far away from the present occurrences (e.g. Japan).

Ecological variables and ecological niche modeling (ENM)

The starting point of ENM was compiling a set of 26 ecological variables, including the 19 bioclimatic variables of WorldClim v. 2.1 for the period 1970–2000 (www.worldclim.org), three topographic variables (elevation, slope and terrain roughness) from EarthEnv (www.earthenv.org), soil pH from ISRIC (www.isric.org/), maximum soil moisture (of two types, available and readily available) from GeoNetwork (geonetwork-opensource.org), and distance to freshwater bodies calculated from World Linear Water and World Water Bodies layer packages (www.arcgis.com). All variables had a cell resolution of 2.5×2.5 arc-min (ca. 5×5 km). In total, after removing duplicate records within each cell, 201 wild occurrences of *G. pensilis* were used for the ENM.

For modeling the potential distribution, the maximum entropy algorithm implemented in MaxEnt v. 3.3.3 was used (Phillips et al. 2006). The method used as resampling strategy was subsampling, with 25% of the localities randomly selected to test the model. For the exploratory models, a total of 20 replicates were made, while for the definitive models the total was 100. Although the probability of occurrence ranges from 0 to 1, only those cells with values higher than the Maximum Training Sensitivity Plus Specificity Cloglog Threshold (MSS) were regarded as suitable for the species (Liu et al. 2016). To reduce the number of variables, a correlation analysis was carried out in R v. 4.0.3 (R Development Core Team 2010) using the Rstudio platform (Racine 2012). Therefore, a Pearson correlation matrix was obtained from 10,000 random points and transformed to a dendrogram (Supplementary Fig. S1) with the *randomPoints* function of the *dismo* package v. 1.3–3 (Hijmans et al. 2020) and *cor* and *hclusts* functions from *stats* package v. 3.6.2 (R Core Team 2021). Based on the ecological knowledge of the species, but also on the response curves and the weight of the variables (percentage of contribution, permutation importance, and jackknife test; Supplementary Figs. S2–S4 and Table S1) in the exploratory model, a single variable was chosen from each of the different groupings of correlated variables ($r \geq 0.3$). The variables selected to run the definitive models were the following: bio2 (mean diurnal range of temperature), bio3 (isothermality), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio12 (annual precipitation), bio15 (precipitation seasonality), bio 19 (precipitation of coldest quarter), distance to freshwater bodies, soil pH, and slope.

For future scenarios, the models proposed by the Sixth Coupled Model Intercomparison Project (CMIP6) for the period 2061–2080 were taken into account with a bias correction and scale reduction carried out by WorldClim v. 2.1 (www.worldclim.org/). CMIP6 models were used instead of CMIP5 ones because the former are based on new, updated emission pathways driven by different socioeconomic assumptions (the ‘Shared Socioeconomic Pathways’, SSPs), in addition to providing greater sensitivity (Hausfather 2019). The Shared Socioeconomic Pathways (SSP) chosen here were SSP 126 and SSP 585, which are the most optimistic and pessimistic scenarios and can be understood as updates of the CMIP5 scenarios RCP 2.6 and RCP 8.5, respectively. Preliminary ENMs using the eight general circulation models available in WorldClim v. 2.1 that had data on the bioclimatic variables for all possible SSPs (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6 and MRI-ESM2-0) were run. The rest of variables (distance to freshwater bodies, soil pH, and slope) were considered constant, as no significant changes are expected in the near future. The visual inspection of these preliminary ENMs allowed us to identify the combination of models that offered the greatest variability of climatic scenarios. So, for the final ENMs the BCC-CSM2-MR of the Beijing Climate Center (Wu et al. 2019), the CanESM5 of the Canadian Center for Climate Modeling and Analysis (Swart et al. 2019) and the MIROC-ES2L of the Meteorological Research Institute Earth System Model (Hajima et al. 2020) were employed. Another reason for choosing the BCC-CSM2-MR model was that it is considered one of the models that performs better for the study region (Xin et al. 2020).

To estimate the gains or losses of suitable areas (or unchanged areas) for future scenarios with respect to the present, binary maps were obtained with the *reclassify* function of the *raster* package v. 3.4–13 (Hijmans 2021). The binary maps were subsequently overlapped using the *gIntersection* function of the *rgeos* package v. 0.5–5 (Bivand and Rundel 2020) to obtain the overlapped areas, the lost areas (present areas minus overlapped areas) and the gained areas (future areas minus overlapped areas); the *area* function of this

package was also used to estimate suitable areas (in km²). All maps were drawn with ArcGIS v. 10.6 (Esri Inc., Redmond, WA, USA).

Protected areas

To see whether the current network of protected areas (PAs) is effectively protecting *G. pensilis*, the digitized map of PAs of China, Laos and Vietnam (the three countries where the species occurs in the wild) was overlapped with the species' wild occurrences and with binary maps of present and future scenarios. Data from Protected Planet (<https://www.protectedplanet.net>) for Vietnam and Laos has been used to complete our digitized map of PAs. The intersect tool of ArcGIS was used to estimate the number of occurrences of *G. pensilis* located within PAs, while *shapefile* and *area* function of the *raster* package v. 3.5–11, and *Intersection* of the *rgeos* v. 0.5–9 package were used to estimate the fraction of potential area (present and future) that is covered by the current network of PAs.

IUCN threat categories

Distribution and population size data are key when assessing species under IUCN Red List standards, as their knowledge is a prerequisite to applying most criteria and subcriteria (IUCN Standards and Petitions Committee 2019). For reassessing the threat status of *G. pensilis*, we have used all the gathered data on all wild known occurrences location (for details, see above) to estimate the distribution range through (1) extent of occurrence (EOO) and (2) area of occupancy (AOO). The EOO has been estimated using the *eo* function of the *red* package v. 1.5.0 (Cardoso 2020), which calculates the EOO as the minimum convex polygon covering all records of presence as suggested by the recommendations of the IUCN Standards and Petitions Committee (2019). The AOO has also been calculated with the *ao* function of the same package, with a resolution of 2×2 km following the IUCN recommendations. Both calculations have been carried out specifically for China, taking into account only the occurrences of that country, and at global level, thus adding the occurrences of Laos and Vietnam to the Chinese ones. Using our own field data but also using data from others (see above and also Tang et al. 2019) we have classified all known populations of China of *G. pensilis* into several size classes: 1–4 individuals, 5–9, 10–29, 30–59, 60–89, and 90–220 except those populations from Laos and Vietnam, for which we have adopted the data from Averyanov et al. (2009) and Coffman (2021).

Results

Current and future potential distribution of *G. pensilis*

The potential distribution of *G. pensilis* for the present time is shown in Fig. 2, expressed as probability of presence. The model showed a very high predictive capacity, since the AUC values were close to 1, thus indicating a near perfect fit (AUC = 0.975 ± 0.003). The bio19 variable was the one with the highest percentage of contribution to the model (48.9%), followed by bio3 (15.8%), bio12 (13.6%), bio9 (13%) and bio15 (4.2%). The rest of the variables had an individual contribution of less than 2% (Supplementary Table S1). Regarding permutation importance, bio9 showed the highest value (54%; Supplementary Table S1). According to the jackknife test, the ecological variable with

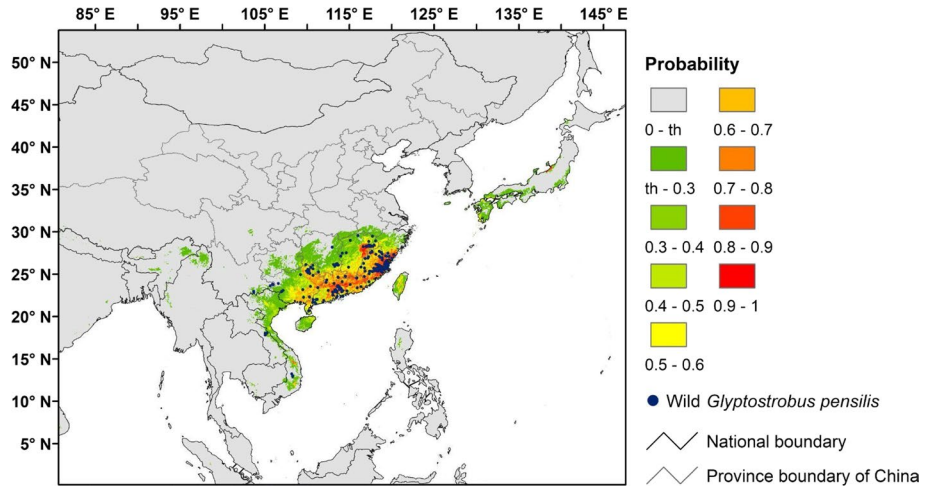


Fig. 2 Presence records (dark circles) and potential distribution map for the present climatic conditions (in colour scale) of *Glyptostrobos pensilis*

the highest gain when used in isolation was also bio19, but the variable that decreased the gain the most when it was omitted was bio9 (Supplementary Fig. S2). Most of the presence records of the species (96.7%) were within the potential areas under current climate conditions (Fig. 2), i.e., sensitivity was very high. The total area of potential distribution above the MSS threshold value (0.0853) was 1,452,481 km² (Table 1), with SE China showing the highest probability of presence (most of Fujian and Guangdong provinces, and parts of Guangxi and Jiangxi). The potential areas of *G. pensilis* in Vietnam and Laos showed a low probability (values of 0.3–0.5), as occurred for certain areas of China such as Hainan or parts of Guizhou, Hunan and Zhejiang. Potential

Table 1 Potential areas for *Glyptostrobos pensilis* for each future climate model employed and comparison with the current climate model

Model	Predicted area (km ²)	Difference respect to present (%)	Overlap with present (%)	Lost area in the future (%)	Gained area in the future (%)
Present	1,452,481	–	–	–	–
BCC-CSM2-MR 126 2061–2080	1,322,037	– 8.98	81.64	18.36	9.38
BCC-CSM2-MR 585 2061–2080	1,144,166	– 21.23	70.11	29.89	8.66
CanESM5 126 2061–2080	1,221,238	– 15.92	76.12	23.88	7.96
CanESM5 585 2061–2080	809,013	– 44.30	46.31	53.69	9.39
MIROC-ES2L 126 2061–2080	1,528,321	+ 5.22	86.24	13.76	18.98
MIROC-ES2L 585 2061–2080	1,300,229	– 10.48	79.05	20.95	10.47

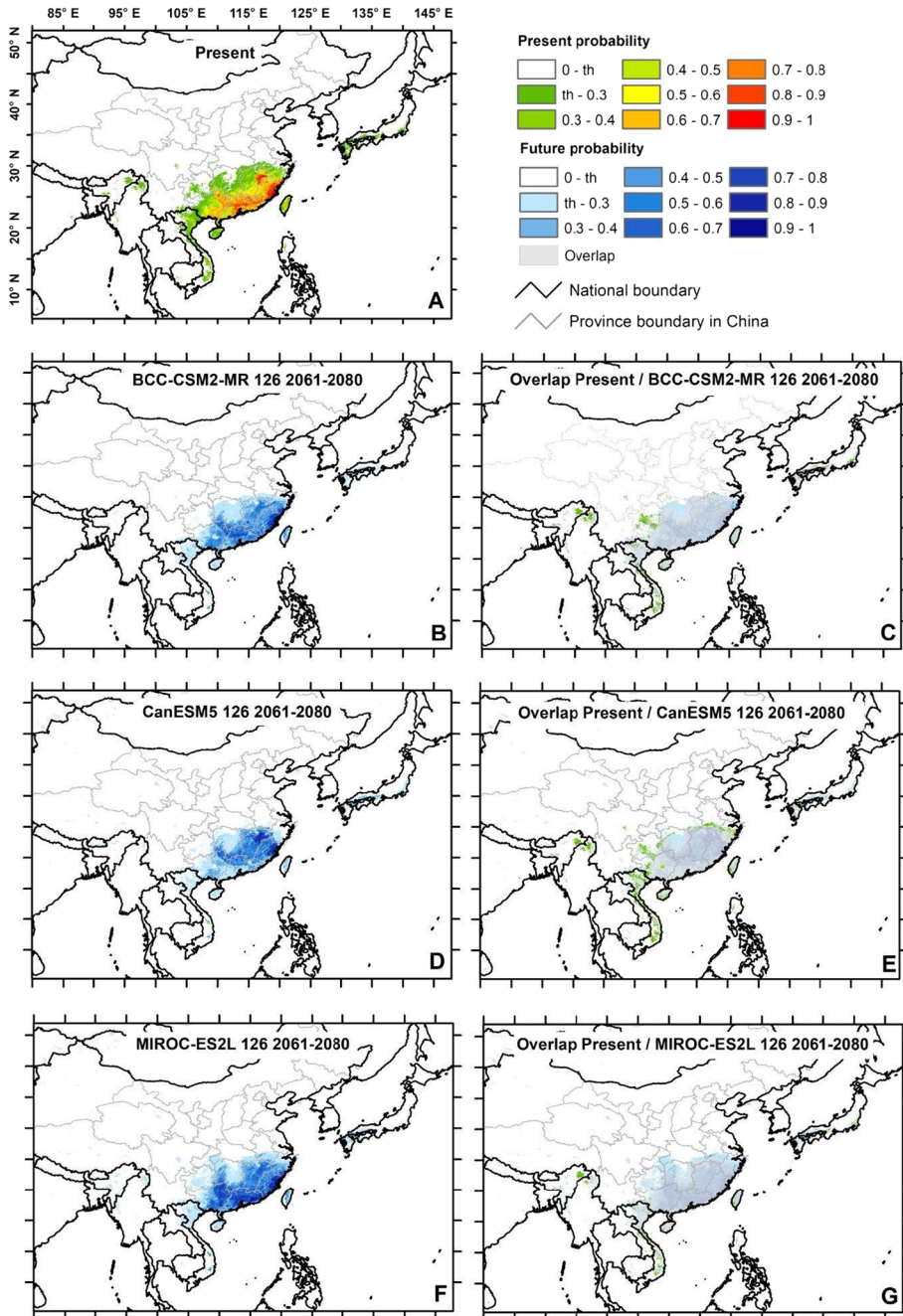


Fig. 3 Comparison of potential habitats for *Glyptostrobos pensilis* under the current climate (A) and three scenarios of future climate change (2061–2080) for SSP 126: BCC-CSM2-MR (B), CanESM5 (D) and MIROC-ES2L (F); overlapping areas of the present and future scenarios are in grey: BCC-CSM2-MR (C), CanESM5, (E) and MIROC-ES2L (G)

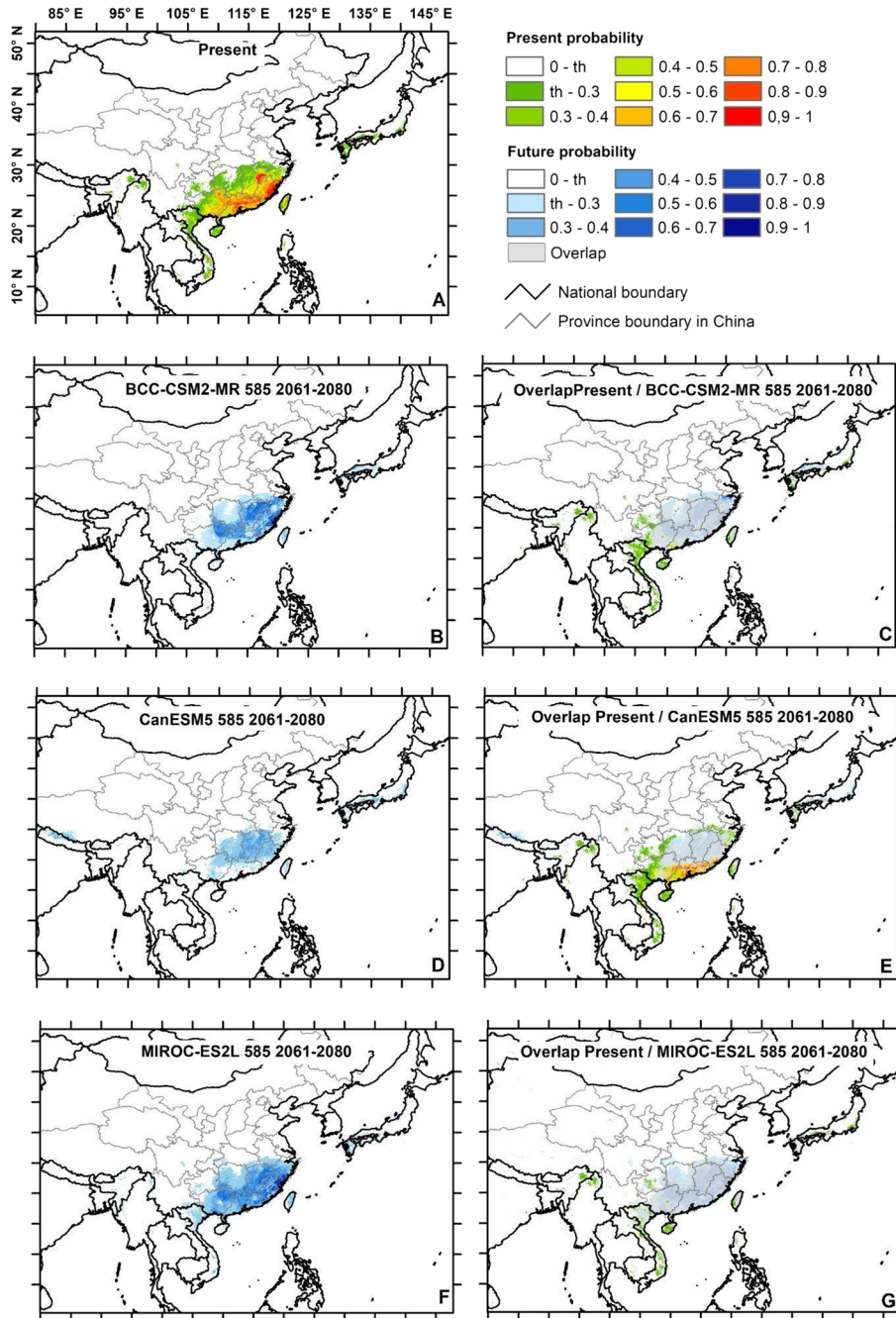


Fig. 4 Comparison of potential habitats for *Glyptostrobos pensilis* under the current climate (A) and three future climate change scenarios (2061–2080) for SSP 585: BCC-CSM2-MR (B), CanESM5 (D), and MIROC-ES2L (F); overlapping areas of the present and future scenarios are in grey: BCC-CSM2-MR (C), CanESM5 (E), and MIROC-ES2L (G)

habitats with high probability appeared in Taiwan and the SW part of Japan; however, *G. pensilis* is not found there at present (Fig. 2).

The potential distribution of *G. pensilis* under various climate change scenarios for the period 2061–2080 are shown in Figs. 3 (SSP 126) and 4 (SSP 585). For SSP 126, the potential area of *G. pensilis* was slightly reduced (−8.98% and −15.92%) for BCC-CSM2-MR and CanESM5 models, respectively, while it increased for MIROC-ES2L model (+5.22%) (Table 1). Regarding lost areas with respect to the present, the largest corresponded to CanESM5 model (23.88%), followed by BCC-CSM2-MR (18.36%) and MIROC-ES2L (13.76%) models. Thus, overlap with the present was relatively high (over 75% for all models; Table 1). Regarding area gainings, the largest occurred under the prediction of MIROC-ES2L model (18.98%), followed by BCC-CSM2-MR (9.38%) and the CanESM5 (7.96%) models.

For SSP 585, the potential distribution areas of *G. pensilis* were further reduced (−21.23%, −44.30% and −10.48% for the BCC-CSM2-MR, CanESM5 and MIROC-ES2L models, respectively) in comparison with the present model (Table 1). Currently suitable areas where wild populations are found such as Vietnam and Laos almost completely disappeared for the period 2061–2080. Overlap areas, indeed, were only found in mainland China (Fig. 4), with overlap percentages much reduced when compared to SSP 126 (particularly for CanESM model, with only 46.31% of overlap; Table 1). Area losses for CanESM, in addition to including Indochina, also affected the entire southern strip of Guangdong Province. Gained areas showed similar percentages with respect to SSP 126 models, with the relative exception of MIROC-ES2L (gain of 10.47% vs. 18.98% for SSP 126).

To know whether the current wild populations of *G. pensilis* will be located within potential areas for the period 2061–2080, the three models under SSP 126 were overlapped (as well as those for SSP 585). For the first of the scenarios (SSP 126) 6.9% of wild *G. pensilis* populations would be outside potential areas; these populations included those located further north (Jiangxi and Hunan provinces), in western Guangxi, and in southern and eastern Yunnan, as well as those from Vietnam and Laos (Fig. 5A). The percentage of populations that would be outside potential areas increased considerably with SSP 585, reaching 31.3% of all wild populations; in addition to the regions listed above, most of the populations located south of Guangdong fell outside the species' potential range for 2061–2080 (Fig. 5B). As for cultivated populations, 28.8% were outside the current potential area. This percentage increased slightly for the prediction of SSP 126 scenario (34.8% of lost populations), but escalated to 75.8% for SSP 585, leaving out of the potential area all those cultivated populations located beyond the northern limit of the wild ones (and, for the specific case of SSP 585, also those from Hainan Island and southern Guangdong; Fig. 5).

Conservation aspects of *G. pensilis*

Only 10.04% of the wild *Glyptostrobus pensilis* populations were located within protected areas (Fig. 6). The areas where current potential and protected areas overlap (Fig. 6) accounted for 96,125.41 km², that is, only 6.62% of the potential area under current climatic conditions is covered by the network of PAs. This area contained most of the wild populations mentioned above, as only two populations were in protected but not potential areas, which means that 9.23% of the total wild populations of *G. pensilis* occur in both protected and suitable areas. However, these percentages decrease for future scenarios. Under the prediction of the SSP 126 scenario, the overlap of protected and potential

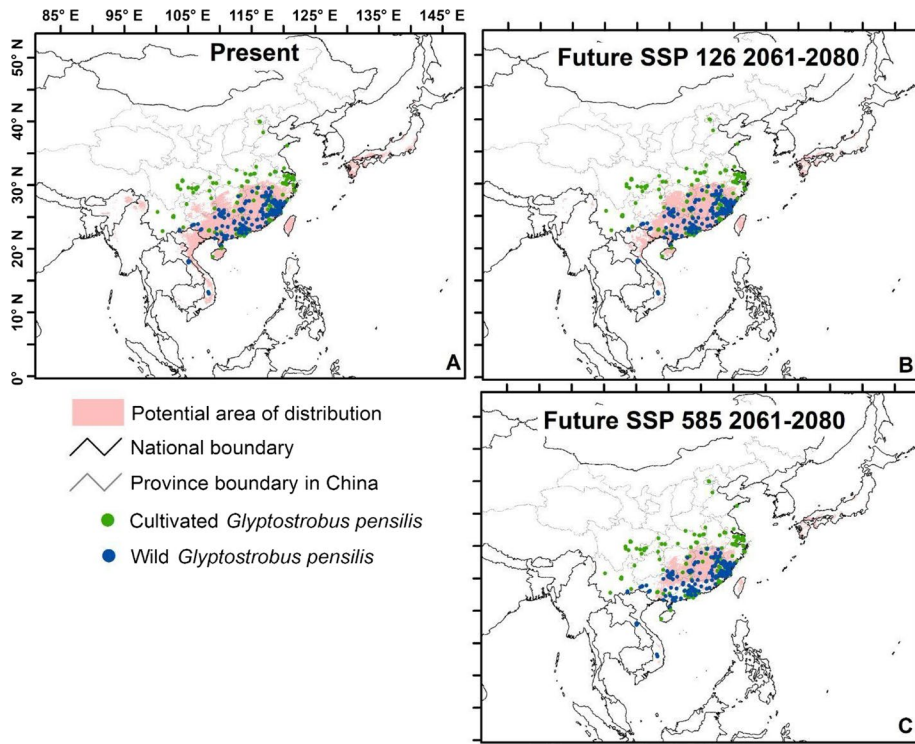


Fig. 5 Maps of present (A) and future (B, C) potential distribution of *Glyptostrobos pensilis*, with the location of both cultivated and wild populations. Consensus potential distribution area for the period 2061–2080 was estimated by overlapping BCC-CSM2-MR, CanESM5 and MIROC-ES2 models, both under SSP 126 (B) and SSP 585 (C)

areas would be 67,388.54 km² (i.e., 4.64 and 6.07% of the potential area for the present time and for the period 2061–2080, respectively), while these overlap areas would just include 8.43% of wild populations of *G. pensilis*. Under SSP 585, the both protected and potential areas would occupy 38,640.04 km² (2.66 and 5.88% of the potential area for the present time and for the period 2061–2080, respectively) and would contain 7.6% of wild populations.

The extent of presence (EOO) of *G. pensilis* for China accounted for 824,709 km², while globally it rose to 1,499,032 km². Regarding the occupancy area (AOO), the values were 904 km² for China and 936 km² globally. Regarding the total population size, for China it ranged from about 700–1900 individuals, but reached 1500–2700 individuals when adding the (approximate) censuses from Laos and Vietnam.

Discussion

Modeling of ecological niche and current potential area of *G. pensilis*

The great importance of precipitation of the coldest quarter (bio19) and temperature of the driest quarter (bio9) for the potential distribution model of *G. pensilis* could be due

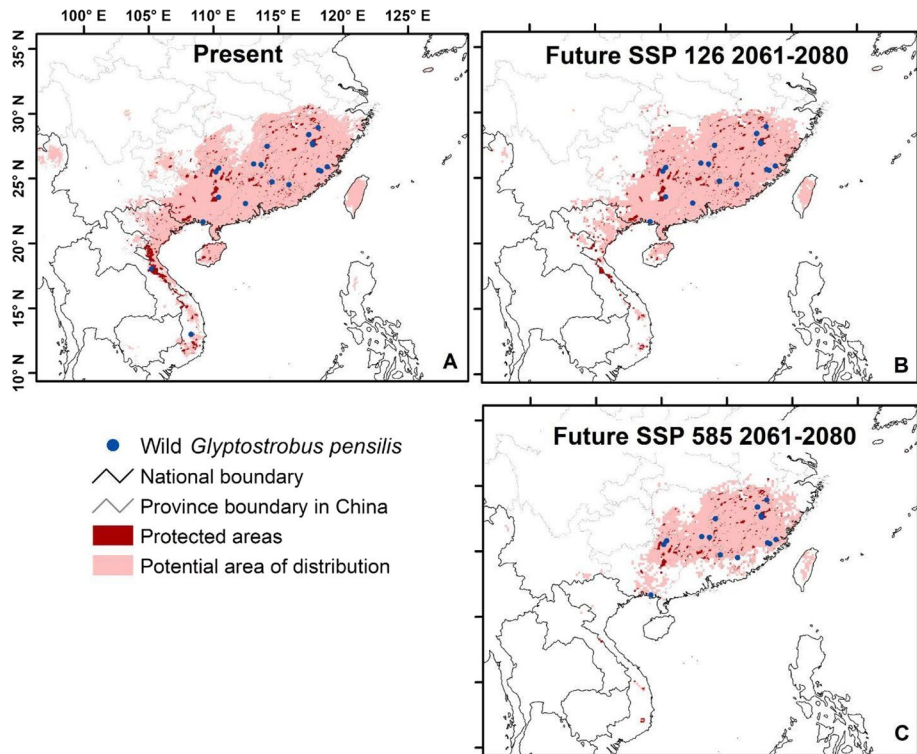


Fig. 6 Map of the overlap of potential and protected areas of *Glyptostrobus pensilis* at the present (**A**), and future (**B**, **C**). In blue, wild occurrences of *G. pensilis* that are located within both potential and protected areas. Consensus potential distribution area for the period 2061–2080 was estimated by overlapping BCC-CSM2-MR, CanESM5 and MIROC-ES2 models, under both SSP 126 (**B**) and SSP 585 (**C**)

to an adaptation of this species to the monsoons and to its occurrence in climatic refugia, respectively. East Asian monsoons are characterized by summer heavy rains, while in winter the climate becomes drier—but not totally dry (as, for example, it does occur in northern China). It seems that *G. pensilis* needs some amount of rainfall in the coldest season (the coldest quarter corresponds to the driest quarter within the species distribution area, usually between December–February), but not in excess (of approximately between 100 and 300 mm; Supplementary Figs. S3 and S4). The paramount importance of bio19 (or bio17: precipitation of the driest quarter) has also been reported when modeling other subtropical/northern tropical species of East Asia, including both gymnosperms and angiosperms; examples include *Taxus chinensis* var. *mairei* (Li et al. 2021), some Gentianaceae (in particular, *Sinogentiana* and *Metagentiana*; Matuszak et al. 2016) or, *Blumea balsamifera* (Guan et al. 2022), *Impatiens hainanensis* (Ning et al. 2018), and *Zelkova schneideriana* (Sun et al. 2020). Winter precipitation is important to balance soil moisture during the early growing season. This is of particular importance in tree physiology, as enough precipitation in winter (the dry season) has been reported to be decisive for radial growth in subtropical trees (Sigdel et al. 2018); in a water-loving tree such as *G. pensilis*, enough rainfall to maintain appropriate soil moisture in winter is thus, beyond discussion. Some studies, however, pointed out that winter temperatures are more important than winter

precipitations in southeastern China (Chen et al. 2015, and references therein) for tree growth. Too low winter temperatures could produce freezing injuries (e.g. bud damage and frost desiccation), and these are even more serious than expected in subtropical latitudes because—unlike at higher latitudes—trees may not be completely dormant in winter (Chen et al. 2015). This can be linked to the equally important bio9 variable in our model (in southern China, the driest quarter is the coldest one). Indeed, a large part of the distribution area of *G. pensilis* occurs within areas with a moderate role as “long-term climatic refugia”. These sort of refuges, which enabled the persistence of many relict species in East Asia, are characterized by mild winters, and where temperatures have rarely dropped below 0 °C at any time since the LGM (Tang et al. 2018). *G. pensilis* has a temperature tolerance of approximately 0–27 °C during winters, but the optimum is around 12–20 °C (Supplementary Fig. S3). It seems that the parameters related to precipitation and temperature were crucial for the survival many of the relict genera in China (Huang et al. 2015; Tang et al. 2018), with edaphic and topographic variables—as exemplified by *G. pensilis*—having played a minor role.

Although MaxEnt generally produces very robust predictions, particularly for endemic species (e.g. Cobben et al. 2015), it does not take into account biological phenomena such as competition or the dispersal capacity of the species. So, it is not surprising that our models are showing some potential habitats where the species is not actually found (i.e. empty habitats). Some of these habitats for *G. pensilis* are located in Japan or Taiwan (Fig. 2), where the species has either not managed to disperse or has not been able to establish viable populations there (perhaps because its niche is occupied by other species). There is fossil evidence that the genus *Glyptostrobus* was distributed in Japan during the late Miocene (when there was a land bridge between Japan and China), and it seems that it remained there until the Pleistocene (LePage 2007). While such terrestrial connection is no longer present, the dispersal mechanism of *G. pensilis* (anemochory; Givnish 1980) only allows seeds to be dispersed over short distances. Therefore, it is very unlikely that seeds can reach Taiwan or Japan naturally, since they would have to be moved through a distance of more than 120 km over the sea for the first case (which corresponds to the distance between the current populations of Fujian and Taiwan) or more than 1000 km to Japan. Furthermore, in the hypothetical case that some seeds reach these areas, the very poor recruitment capacity of the species (Tang et al. 2019) would make the establishment and viability of new populations unlikely.

The whole eastern coast of Indochina also appears as suitable habitat for *G. pensilis* (Fig. 2), however, only a few populations can be found at present, which could be due to the loss of its suitable habitats during the most recent decades, either by cropland conversion or by direct destruction during the Vietnam War (Lang 2001). The United States Army used different chemical compounds on the rainforest of Vietnam (and bordering areas of Laos and Cambodia), mostly south of 17th parallel, during the period 1961–1971; furthermore, napalm bombs were sometimes thrown to supplement the destructive effect of defoliant and herbicides. Defoliant agents such as Agent Orange and other herbicides are estimated to have removed about 14% of the forest cover in Vietnam (Hanson et al. 2009). River banks, which are among the preferred habitats of *G. pensilis*, were often targeted by the Americans. So, many of the species’ habitats would have been deeply modified, affecting existing *G. pensilis* populations (if any). Notably, many potential areas in central and southern Indochina overlap with areas sprayed with these chemicals (Stellman et al. 2003); in contrast, the small region that harbors the current populations of *G. pensilis* south of 17° N (the central part of Dak Lak Province) was never subject to the action of defoliant according to the map provided by Stellman et al. (2003).

Effects of climate change on the potential future (2061–2080) distribution of *G. pensilis*

Despite the loss of potential habitats expected for the period 2061–2080 (which is higher for the SSP 585 scenario compared to the SSP 126 one; Table 1), it can be generally stated that the future potential areas would remain more or less the same as the present ones, at least for China. A similar pattern has been observed in other relict species that are dwelling in southwestern, central and southeastern China (e.g. *Dipentodon sinicus*, Tang et al. 2020; or *Taiwania cryptomerioides*, Zhao et al. 2020), where there are stable climatic refugia. In these refugia, suitable conditions for pre-Quaternary thermophilic elements (of the boreotropical flora) would have been maintained over millions of years (average annual temperatures of between 10 and 20 °C with very little or no frost, annual rainfall between 1000 and 2000 mm, and moderate seasonality; Tang et al. 2018). Despite ongoing global warming, these conditions will not change drastically in the coming decades over many mountainous areas in central and southern China, as shown by Tang et al. (2018) but also in global assessments of future climate (e.g. Beck et al. 2018; Herrando-Moraira et al. 2022). In agreement with this, it is expected that the current extension of the subtropical vegetation in China will be maintained in the coming decades (Yang et al. 2019a). In contrast, the whole northern China, as well as northwestern China, would suffer from dramatic climate changes, which would be translated into large changes in their vegetation belts (Yang et al. 2019a). Thus, it is not surprising that the ENM for other East Asian species not located within Chinese climatic refugia are predicting potential areas for them further north and/or important latitudinal/longitudinal migrations (e.g. Bai et al. 2018; Lv and Li 2021; Zhao et al. 2021).

Although most of the current populations of *G. pensilis* would remain in potentially suitable areas, between 7 and 31% (for SSP 126 and SSP 585 respectively) of these could be lost because they are outside future potential areas (Fig. 5). Although these percentages may seem relatively low, we should bear in mind that the germination rates for the species are very low (Thomas 2019) and, as mentioned above, regeneration is extremely poor (very few seedlings are produced), with many populations showing a declining trend (Tang et al. 2019); these bad demographic data would, thus, increase the percentage of wild *G. pensilis* populations that would be potentially lost. Among the candidate populations to remain outside potential habitats for the period 2061–2080 are those of Laos which, regrettably, are the genetically most diverse among all populations (and carry unique alleles/haplotypes; Wu et al. 2020). Urgent conservation measures are, thus, badly needed to ensure the mid- and long-term viability of this species, which are discussed in the following section.

Conservation issues of *G. pensilis*: threat category reassessment, protected areas, and suggestions

The current IUCN evaluation of the threat status of *G. pensilis* at global level (“Critically Endangered”, CR) was based on the belief that there are no natural populations in China (Thomas et al. 2020). However, we have documented at least 240 wild populations in China which, together with the known populations of Laos and Vietnam, are making a total of 249 natural populations. With a very conservative application of the IUCN criteria, the threat category of *G. pensilis* would be downgraded to “Vulnerable” (VU) under the following criteria: B2ab(iii,iv,v) and C2a(i). It meets criterion B2 because the area of

occupation (AOO) is below 2000 km² (936 km²) and criterion C because the total population size of the species is below 10,000 mature individuals. However, taking the lower bound of the census range (1500–2700 individuals), and considering that not all trees are mature (i.e., to be capable of reproduction), the species is better categorized as “Endangered” (EN) based on criterion C (less than 2500 mature individuals). Given that populations are currently declining and no population contains more than 250 mature individuals, then the full assessment would be EN C2a(i). For the specific case of China, *G. pensilis* is currently categorized as CR in the last version of the national red list (Qin et al. 2017). According to the criteria used in this assessment [B1ab(iii)], the species would have an estimated EOO of less than 100 km² (criterion B1). This categorization is probably based on the assumption that the majority of populations in China are cultivated. With wild populations extending from Yunnan to Fujian, both the EOO and AOO values of *G. pensilis* (824,709 and 904 km²) does not allow it to be classified as CR or EN. However, it meets criteria for EN under C2a(i); the total number of individuals per population varies between 1 and 220 individuals in China (though most stands are composed of 1–4 trees; Tang et al. 2019).

The coverage of *G. pensilis* wild populations by the current network of PAs is absolutely insufficient (just about 10%, which drops to 9% when potential areas and PAs are overlapped). Some authors argue that even though some populations are found within PAs, their size is too small, which makes them susceptible to fires and changes in water levels produced by agricultural activities (Thomas and LePage 2011). In addition, some PAs would not effectively protect the species because of poor management; for example, deforestation is still common within and surrounding Chinese PAs, with half of the PAs having a high deforestation rate (> 1%) between 2000 and 2015 (Yang et al. 2019b). Indeed, about 200 of the 600 trees discovered in 2015 within the Nakai–Nam Theun National Park were illegally logged (Coffman 2021). This unfortunate event could be worse than anticipated, as Lao populations are the most variable genetically (Wu et al. 2020); so part of the original species’ genetic variability would have been lost. While the role of PAs should be strengthened to avoid them becoming “paper parks”, the current network of PAs should be expanded to cover a larger fraction of the wild populations of *G. pensilis*. Priority should be given to populations occurring on areas of potential habitat overlap under present and future conditions.

Regarding the ex situ conservation measures, it is desirable to conserve as much as genetic variability as possible of *G. pensilis*. Given the high genetic differentiation between existing populations ($F_{ST}=0.452$; Wu et al. 2020), it would be necessary to collect seeds from a large number of populations (Chung et al. 2020). However, if it is not possible, those populations with greater genetic diversity/singularity should be prioritized (as established by the population genetics canons), particularly when they occur outside future suitable areas for the species (as these populations will face extinction). Based on these criteria, ex situ actions should focus on Lao populations. Already from seeds collected from the remaining stands in Laos, successful propagation trials have been carried out, obtaining almost 2000 seedlings; in 2019, trial plantations were started on the Nakai Plateau (Coffman 2021). However, although the areas of Laos with *G. pensilis* stands are eco-climatically suitable in the present, our results show it might not be the case in the future. A proper strategy could include population reinforcements of the most genetically impoverished populations (both those from Vietnam and some from China; Wu et al. 2020) with genetic material from Laos. Although care should be taken (as mixing genetically divergent stocks could lead to outbreeding depression; Frankham et al. 2011), the benefits of mixing material from diverse populations are probably exceeding their potential risks (Godefroid

et al. 2011; Frankham 2015). In China, seeds (over 2000) from several populations are stored in gardens and nurseries, but ex situ sampling in Vietnamese populations remains a challenge as no viable seeds have been observed yet (Averyanov et al. 2009; Linsky 2018).

The more than 200,000 individuals of *G. pensilis* known in cultivation (Thomas et al. 2020)—there is a single population planted in 24 hm² (probably more than 70,000 trees) at Zhuzhoutou Village in Baijiao Town, Doumen, Zhuhai, Guangdong (Zhou et al. 2014)—are, in addition, a great ex situ resource. The adequacy of these cultivated stands for translocation activities should be, nevertheless, evaluated, given some of the risks associated with ex situ cultivation. The values of genetic diversity of cultivated populations of *G. pensilis* are considerably lower than those of the natural populations (Wu et al. 2011), which may reflect either a poorly-designed strategy of ex situ collection in terms of genetic representation or genetic erosion during cultivation (Ensslin et al. 2015). Another risk that can reduce the suitability of cultivated populations as a source for reintroductions is their adaptation to the ex situ environment (but the loss of adaptation to the natural one; Ensslin et al. 2015); we believe that this is a real risk given that nearly 30% of the cultivated populations are outside the current potential area, and that this percentage will escalate to over 75% under the SSP 585 scenario.

Finally, since *G. pensilis* populations are found in three different countries, the collaboration of the respective governments is absolutely necessary to carry out comprehensive conservation efforts. Because some areas will no longer be suitable in the future, assisted migrations, even between different countries, seem necessary to guarantee the mid and long-term survival of some populations in the wild. In any case, the carrying out of propagation (including vegetative propagation as in some areas trees do not produce seeds, e.g. Vietnam) and reintroduction tests for the elaboration of detailed and successful protocols is essential, with some efforts having been done in recent times (Linsky 2018).

Conclusions

The areas with the highest probability of occurrence of the relict East Asian species *G. pensilis* are in SE China (mostly Fujian and Guangdong provinces). Regardless of the model used, as socioeconomic trajectories worsen, habitat loss increases, leaving some wild populations out of potential areas (approximately between 7 and 31%). Among these populations that would become extinct are those of Laos, which is worrying because they are the populations with the highest levels of genetic diversity and genetic uniqueness. As most (about 90%) wild populations of *G. pensilis* do not occur within PAs, the current network of PAs should be expanded to cover a larger percentage of them, with priority given to populations occurring on areas of potential habitat overlap under present and future conditions. International collaboration among the countries that harbor *G. pensilis* populations is indispensable for carrying out comprehensive translocation projects.

With the current knowledge, we have reassessed the threat status of the species under IUCN criteria, as former assessments considered all Chinese populations as cultivated. The reporting of numerous wild populations in China (though fragmented and of very small size) in recent times suggest downgrading *G. pensilis* from CR to EN, both for China but also at global level. The (also relatively recent) discovery of populations in Laos also adds some hope for a possible increase in the number of known populations in remote areas. ENM can be of great help in searching for new populations of threatened species, with numerous examples of success being described around the world (e.g. Menon et al. 2010;

Fois et al. 2015). Botanical field explorations are recommended in the regions of potential habitat for the *G. pensilis* with no current presence of the species, such as occurs in large stretches of the eastern coast of Indochina.

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Data availability Almost all data generated or analyzed during this study are included in this published article [and its supplementary information files]. If other data than those included here are required, they are available from the corresponding authors on request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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Authors and Affiliations

Paula Pueyo-Herrera¹  · Cindy Q. Tang²  · Tetsuya Matsui^{3,4}  · Haruka Ohashi³  · Shenhua Qian⁵  · Yongchuan Yang⁵  · Sonia Herrando-Moraira^{1,6} · Neus Nualart¹  · Jordi López-Pujol^{1,7} 

¹ Botanic Institute of Barcelona (IBB, CSIC-Ajuntament de Barcelona), Passeig del Migdia s/n, 08038 Barcelona, Catalonia, Spain

² Institute of Ecology and Geobotany, College of Ecology and Environmental Science, Yunnan University, Building Shixun, Chenggong Campus, Dongwaihuan South Road, University Town, Chenggong New District, Kunming 650504, Yunnan, China

³ Forestry and Forest Products Research Institute, Forest Research and Management Organization, Matsunosato 1, Tsukuba-shi, Ibaraki-ken 305-8687, Japan

⁴ Faculty of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki 305-8572, Japan

⁵ Key Laboratory of Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing 400045, China

⁶ Servei de Fauna i Flora, Generalitat de Catalunya, Provença 204, 08036 Barcelona, Catalonia, Spain

⁷ Escuela de Ciencias Ambientales, Universidad Espíritu Santo (UEES), 091650 Samborondón, Ecuador