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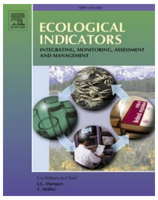

Late Pleistocene glacial expansion of a low-latitude species *Magnolia insignis*: Megafossil evidence and species distribution modeling

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ABSTRACT

The Pleistocene Epoch, marked by significant climatic fluctuations and glaciations, profoundly impacted plant populations. However, our understanding of the influences of last glaciations on tropical-subtropical flora and vegetation remains limited due to insufficient data. Here, we present mummified wood of *Magnolia insignis* (Wall.) Bl. from the Upper Pleistocene (33–30 ka cal. BP) of Maoming, South China, providing direct evidence of a broader historical range for this species during the period prior to the LGM in the last glaciation. Combining these findings with results from MaxEnt modeling, we demonstrate an expanded range of *M. insignis* into lower latitudes during last glaciation with subsequent interglacial contraction. This represents the second documented case of such a scenario for a cold-tolerant high-elevation plant species at low latitudes. The results of MaxEnt modeling and a comparison of climatic data across different time periods indicate that the contraction of *M. insignis* from the Maoming and other low latitude regions of East Asia was driven by the increase in summer temperatures during Holocene. This study not only sheds light on the responses of cold-adapted mountainous species at low latitudes of East Asia to last glaciation, but also justifies the importance of their protection in the view of nowadays and future climate changes.

1. Introduction

The Pleistocene, extending from 2.58 million years ago (Ma) to 11.7 thousand years ago (ka) (Gibbard & Head, 2020), featured rapid and intense climatic oscillations, including glacial-interglacial cycles (Westerhold et al., 2020). Climate fluctuations have deeply affected the flora since the Late Pleistocene (127.2–11.7 ka BP, Litt & Gibbard, 2008), in particular throughout the last glacial and interglacial cycles (Hewitt, 2000; Prentice et al., 2000; Huang et al., 2001). Understanding the influence of the last glaciation on plant diversity is crucial for reconstructing past biotas and conserving the diversity of plants in face of climate changes in the present and future. Although its influence on the plant diversity and distribution in high-mid latitudes is relatively well explored, the responses of the low-latitude species to the last glaciation remain poorly understood.

The Asian summer monsoon influence widely varied across the region and weaker monsoons during the glacial interval caused the range reduction and even extinctions of various species in the Northern Hemisphere (Rodríguez-Sánchez & Arroyo, 2008; Hofreiter & Stewart, 2009; Stojak & Jędrzejewska, 2022), especially during the Middle Pleistocene Transition (1.25–0.7 Ma, Clark et al., 2006), Mid-Bruhnes Events (0.43 Ma) and Last Glacial Maximum (LGM, 29–19 ka BP, Hughes, 2022). However, many cold-tolerant species underwent range expansion during cold periods, a process known as glacial expansion. Although this phenomenon has been widely documented for several species at high and middle latitudes based on fossils and molecular evidence (Tremblay & Schoen, 1999; Birks, 2008; Alsos et al., 2009), glacial expansion for plant species at low latitudes was hardly confirmed by evidences other than molecular phylogeographic studies for plant species of *Pinus kwangtungensis* (Tian et al., 2010), *P. armandii* (Liu et al.,

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2014, 2022), *Emmenopterys henryi* (Zhang et al., 2016), etc.. Up to date, megafossil evidence is known only for *Pinus armandii* (Huang et al., 2023a).

Fossil evidence and species distribution modeling (SDM) provide valuable insights on plant responses to climate fluctuations. SDM is a statistical or mechanistic approach for assessing and predicting species distributions at spatial and/or temporal scales (Gavin et al., 2014). The maximum entropy (MaxEnt) modeling (a widely used SDM method) employing a maximum entropy approach to estimate species distribution based on environmental variables, displays an excellent predictive performance even with limited data and sampling (Pearson et al., 2007; Phillips & Dudík, 2008; Elith et al., 2010).

Magnolia insignis (Wall.) Bl. is an endangered precious cold-tolerant montane species distributed in southwestern Hunan, Guizhou, southwestern Sichuan, Guangxi, Yunnan and southeastern Xizang of China, as well as in Nepal, northwestern Thailand, northeastern India and northern Myanmar (Dong, 2017) (Fig. 1A). This tree thrives in evergreen broad-leaved forests across a range of 1700–2500 m above sea level affected by seasonal frosts (see Table S1 for its climatic ranges). According to the IUCN Red List of Threatened Species, *M. insignis* is now classified as “Least Concern” (Khela, 2014) due to the seriously decline of the wild plants caused by its low rate of seed-germination (Lu et al., 1999) and global climate changes etc.. The environmental factors (including climatic and topographic) affecting the distribution of extant *M. insignis* had been analyzed using MaxEnt modeling under different spatial scales, i.e. for the region of Three Parallel Rivers in Yunnan, for the whole Yunnan Province in China, and for the whole country of China (Zhuang et al., 2018). However, the spatial scales of *M. insignis* for modeling were confined to China and there was no species distribution modeling for temporal scales in Zhuang’s et al. (2018) work. Thus, more

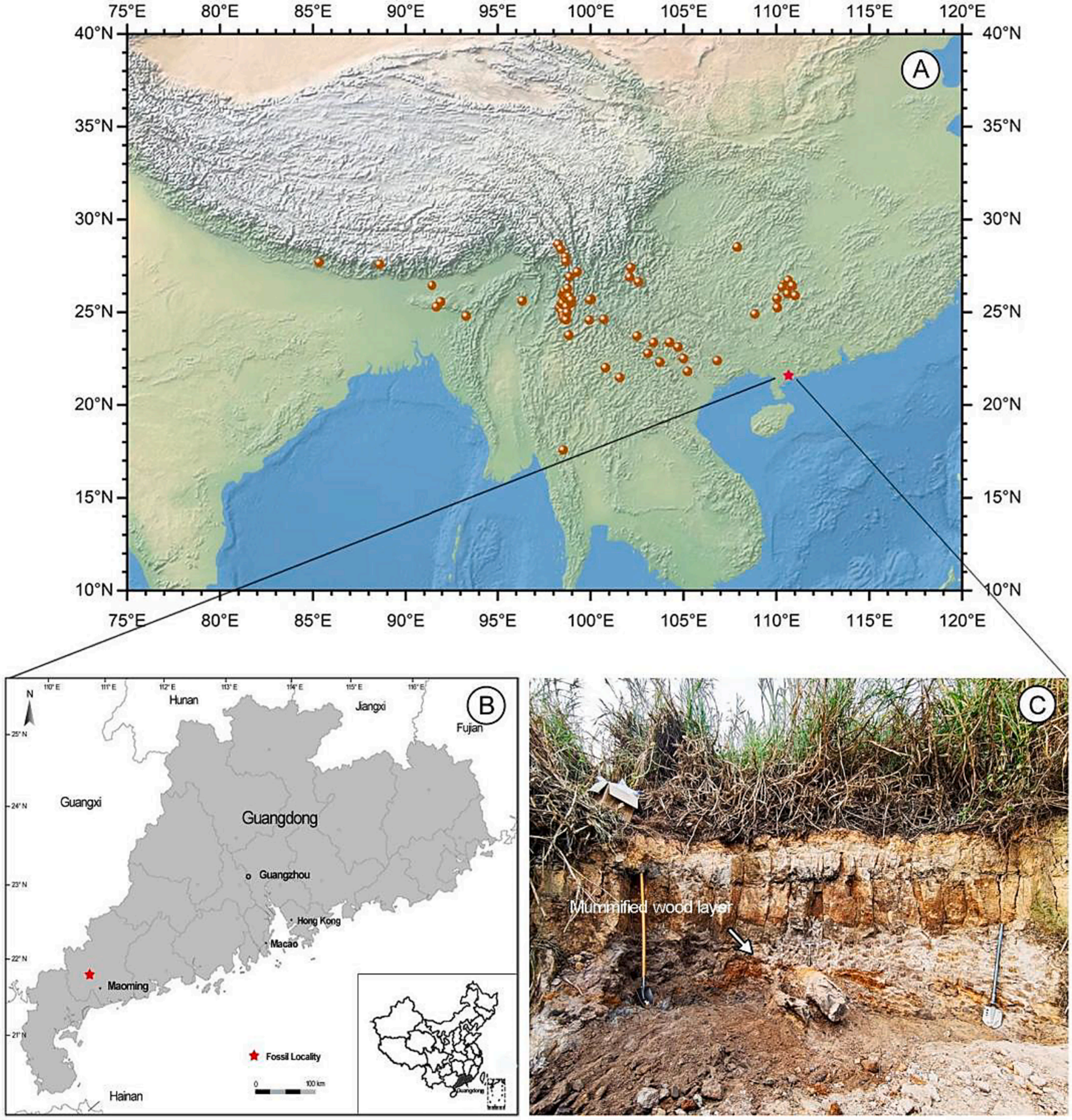

Fig. 1. The locality of extant (brown dots) and fossil wood (red star) of *Magnolia insignis*. **A** Current distribution of *M. insignis* based on the occurrence records and locality of fossils site. **B** Fossil wood location (the map was modified from d-maps: https://d-maps.com). **C** Strata profile of the sediments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fossil evidences and species distribution modeling at temporal scales for *M. insignis* are vital for understanding how this cold-tolerant species respond to the climate changes since Pleistocene glaciations.

In this study, we describe mummified fossil wood *Magnolia* Linn. from the Upper Pleistocene of the Maoming in Guangdong of South China (Fig. 1). The geological age of the fossil woods is 33–30 ka cal. BP, the period prior to the LGM in the last glaciation. South China is known as one of the centers of plant endemism and hotspots for biodiversity in East Asia (Myers et al., 2000). A detailed comparison with the wood anatomical data for this genus convincingly suggest the most similarity of this megafossil is to the extant species *M. insignis* (Wall.) Bl. (see Supplementary File). The fossil wood material provides direct evidence of a broader historical range of *M. insignis* during the period prior to the LGM, in the last glaciation. Additionally, we also used the MaxEnt modeling, conducted at a global scale, to clarify the history of this plant species since the last glaciation of the Late Pleistocene, which strongly support the glacial expansion in range in recent biogeographic history. Our study adds to the existing megafossil proof of glacial expansion for plants at low latitudes, complementing previous fossil data from the Maoming Basin (Huang et al., 2023a, 2023b), and elucidate the responses of cold-adapted species at low latitudes of East Asia to the last glaciation.

2. Material and methods

2.1. Studied materials

Three fragments of fossil woods examined in the present study were discovered from a Quaternary deposit in Maoming Basin, located in Maoming City (Guangdong Province, South China) (21.87°N; 110.67°E; Fig. 1), an area characterized by a subtropical–tropical monsoon humid climate. The deposit is primarily composed of yellow, gray, and black mudstones, grayish yellow and grayish-white fine sandstones, with conglomerate. The mummified fossil woods under study, with rough and uneven surface and irregularly shape, were found in the layers of gray mudstones. Numerous other mummified woods, fruits and seeds have been discovered from this deposit (Huang et al., 2021a, 2021b; Bazhenova et al., 2022; Huang et al., 2023a, 2023b; Xiang et al., 2022, 2023). These fossils irregularly occur in the same stratum, which probably means there is no sedimentary sorting between them, indicating these fossils might be *in situ* buried. The ^{14}C dating of some of those fossil plants estimated their geological age as 33–30 ka cal. BP (29–27 ka BP), i.e., as the period prior to the LGM in the last glaciation of the Late Pleistocene (Huang et al., 2021a). In present study, the taxonomic position of fossil woods is determined by careful comparative work with similar modern and fossil wood structures (see Supplementary File), which is based on our re-examination for modern wood slices and reference materials, such as the computerized InsideWood database (InsideWood, 2004–onwards). Then, the species distribution modeling (SDM) was applied for projecting the modern and past suitable habitat for the identified species, including at 30 ka BP (the present fossil record), 20 ka BP (Last Glacial Maximum, LGM), 6 ka BP (Northgrippian).

2.2. Species distribution modeling

2.2.1. Species occurrence and climatic data collection

We collected the data from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), the Flora Reipublicae Ropularis Sinicae (FRPS, http://www.iplant.cn/frps), for species occurrence. Before the model-building, duplicate records and occurrences outside of known species' natural ranges, without georeferencing, or recorded as preserved specimen and artificial planted occurrences were excluded from the analyses. We used ArcMap 10.1 (ESRI: Redlands, CA) to plot points for further inspecting the data (Fig. 1A).

Using the Raster package (Hijmans & Etten, 2012) in R, we obtained the average, minimum and maximum values of 19 bioclimatic parameters for the species occurrence of *Magnolia insignis* (Wall.) Bl. (Table S1) from WorldClim dataset (version1.4, http://www.worldclim.org/) with 2.5 arc-min resolution (Hijmans et al., 2005).

The 19 environmental variables for present (for the period 1950 ~ 2000 CE) and 6 ka BP (Northgrippian) for fossil sites with the spatial resolution of 5 arc-min were extracted from the WorldClim database. 19 environmental variables at 20 ka BP and 30 ka BP for fossil sites were extracted from the Oscillayers dataset with resolution of 2.5 arc-min (Gamisch, 2019). In addition, the paleoclimate data of the fossil site (30 ka BP) was also reconstructed by Coexistence Approach (CA, Utescher et al., (2014)) according to Maoming fossil data (Huang et al., 2023a).

2.2.2. Bioclimatic variable processing

To address multicollinearity among the 19 bioclimatic variables, we followed a rigorous approach (Dormann et al., 2013). These variables were input into the MaxEnt model repeated 15 times to gain the contribution values for each bioclimatic variable. We carried out the Pearson's rank correlation analysis by the "laverStats" function which is from the package "spatialEco" in R for different climate variables. The variables with a Pearson correlation value greater than 0.9 were excluded; the importance of each variable was also taking into consideration empirical knowledge. Finally, there were 9 variables left for simulating the distribution of *M. insignis* after above filtering procedure: BIO2 (mean diurnal range, ℃), BIO3 (isothermality), BIO7 (temperature annual range, ℃), BIO9 (mean temperature of driest quarter, ℃), BIO12 (annual precipitation, mm), BIO14 (precipitation of driest month, mm), BIO15 (precipitation seasonality), BIO18 (precipitation of warmest quarter, mm), BIO19 (precipitation of coldest quarter, mm).

By selecting these variables, we aimed to capture the key climatic variables which have great influence on the distribution of *M. insignis*. This careful selection process ensures that the model incorporates relevant and non-redundant climate variables, improving its performance and interpretability.

2.2.3. Model establishment, evaluation, statistical processing

In modeling, we applied MaxEnt software (version 3.4.3) to model the potential distribution of *Magnolia insignis* in different geological periods and at the present time with the default settings, with the exception of using the 15 replications, and setting 20 % for the random test percentage (80 % of the sample for training dataset and 20 % for test dataset). To evaluate the model performance measures, AUC (area under the receiver-operator-curve) was used as an indicator. The AUC ranges from 0.5 to 1, with values greater than 0.9 indicating excellent model results (Elith et al., 2006). To evaluate the relative importance of each variable, the jackknife test was used (Phillips, 2005).

The suitability index which varies from 0 to 1, was used to quantitatively assess probability distribution sites for species, and derived from the MaxEnt model. The MaxEnt model learns from known species distribution data to construct a probability distribution function. This function represents the likelihood of finding a species across the study area in relation to the environmental conditions. In other words, the function provides a probabilistic framework allowing us to predict the probability of species occurrence at unknown locations based on the learned patterns from the known occurrences (Phillips et al., 2004). The value of suitability index was calculated by the function, higher value represents a higher probability to occur the species in the given locality (Phillips et al., 2004).

To quantify the range shift of suitable habitats of *Magnolia insignis* in terms of longitude and latitude, raster cells with suitability index greater than 0.5 at each latitude or longitude were counted and scaled by dividing by the total number of raster cells. The range shifts at different periods were then plotted and smoothed using a loess (locally weighted regression) algorithm in OriginPro for visualization.

3. Results

3.1. Maoming climatic data for 30 ka BP and 20 ka BP in the Late Pleistocene, 6 ka BP in middle Holocene and present

The values of 19 bioclimatic variables in modern and 6 ka BP (Northgrippian) for fossil locality and current distribution of *Magnolia insignis* were downloaded from the WorldClim dataset (see Tables S1 and S2). The values in 30 ka BP and 20 ka BP in last glaciation of the Late Pleistocene of these bioclimatic variables at the locality near fossil site (22.50°N, 112.50°E) were extracted from the Oscillayers datasets; as for the Late Pleistocene (33–30 ka cal. BP) of Maoming, their ranges were estimated by Coexistence Approach (CA) (Huang et al., 2023a). All climatic data are organized in Table S2. Based on the comparison of different paleoclimatic proxies, we suggest that Maoming in the 33–30 ka cal. BP of Late Pleistocene was cooler and drier compared to the modern climate of the region. All estimated variables for the climate of the Late Pleistocene are among the modern ranges of corresponding variables in the distribution area of *Magnolia insignis*. Nevertheless, the maximum values of some variables (BIO5 (maximum temperature of warmest month), BIO8 (mean temperature of wettest quarter) and BIO10 (mean temperature of warmest quarter), BIO14 (precipitation of driest month) and BIO17 (precipitation of driest quarter)) reconstructed by the CA for 33–30 ka cal. BP are close to the modern maximum values for *M. insignis.* These data suggest that the summer temperature and winter (=dry season) precipitation are the crucial bioclimatic variables affecting the distribution of *M. insignis* in the Maoming Basin during the period prior to the LGM in last glaciation of the Late Pleistocene. The climatic conditions of the LGM (20 ka BP), in this region were also favorable for this species. Warming occurred from 6 ka (Northgrippian) to present leading to a drop in mean diurnal range (BIO2) as well as to the increase of mean temperatures of the wettest quarter (BIO8) and the warmest quarter (BIO10) above and beyond their limiting values for *M. insignis*. Probably, the summer seasons in South China became too hot for this species during the Holocene.

3.2. Model evaluation, contribution and response curves of bioclimatic variables

The AUC value for the MaxEnt was 0.945 (Fig. 2), indicating the modeling performance was excellent.

The contributions in percentage of BIO14 (Precipitation of driest month, mm), BIO9 (Mean temperature of driest quarter, ℃), BIO3 (Isotermality), BIO18 (Precipitation of warmest quarter, mm), BIO7 (Temperature annual range, ℃), BIO12 (Annual precipitation, mm), BIO15 (Precipitation seasonality), BIO19 (Precipitation of coldest quarter, mm), and BIO2 (Mean diurnal range, ℃) for the current distribution of *Magnolia insignis* were 30.4 %, 23.2 %, 17.5 %, 17 %, 6.4 %, 1.9 %, 1.7 %, 1.4 %, and 0.4 %, respectively (Fig. 3).

As the curves of nine variables for *M. insignis* from MaxEnt shown (Fig. 4), the possible suitable ranges of BIO9 are −70 to 120 with the threshold of 0.6. For BIO12, the suitable was range from 1000 to 2000 if the threshold was 0.6. If BIO14 is more than 6, habitat suitability will increase rapidly with threshold of 0.6. The habitat suitability was negative related to BIO3, BIO7, BIO15 and BIO19; but positive related to BIO2, and BIO18.

3.3. Predicted climatically suitable habitats of Magnolia insignis at present and past

As the results for the predicted suitable habitats of modern *Magnolia insignis* shown (Fig. 5A), the potentially climatically suitable habitats (suitability index > 0.25) were mostly limited to the mountains of central and southwestern China, northeastern India and Nepal, which matches well with the actual distribution, although the former was smaller (Fig. 5A).

The suitable habitats for 6 ka BP (Northgrippian) of *M. insignis* shows almost the same potentially suitable habitats as the modern, with the exception that there was a loss of suitable habitats in central China, i.e. Hunan (Fig. 5B).

The projected climatically suitable habitats for *M. insignis* during last glacial intervals (20 ka BP and 30 ka BP) (Fig. 5C–E), indicated the suitable habitats not only expanded within the modern distribution area, but even extended southeast to Guangdong (including the fossil locality under study) and Hainan.

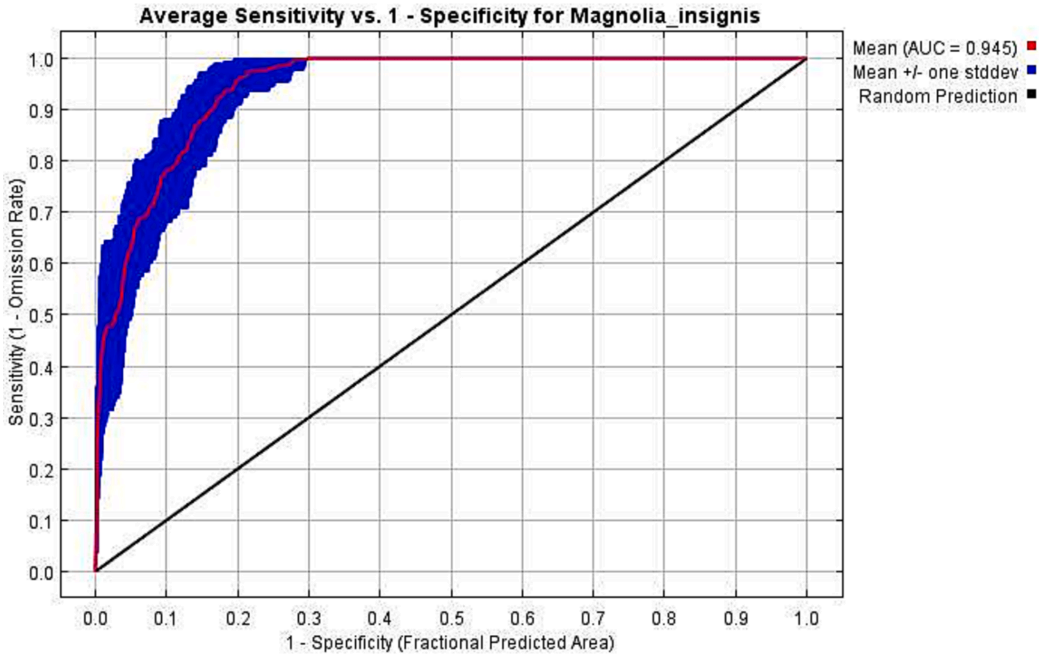

Fig. 2. The receiver operating characteristic (ROC) curve averaged over the replicate runs. The average test AUC is 0.945, the standard deviation is 0.019.

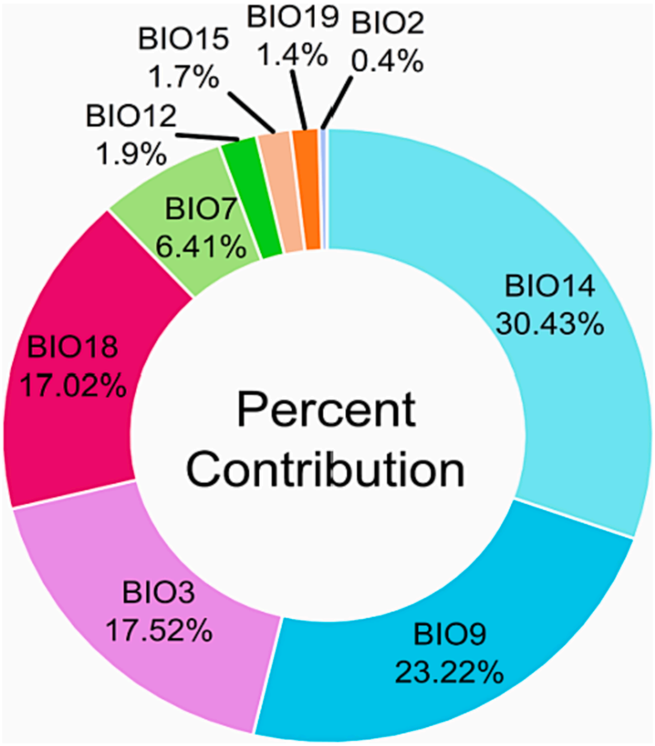

Fig. 3. The percentage contribution of nine important climate variables for the modern distribution of *Magnolia insignis*.

4. Discussion

4.1. Range fluctuations of Magnolia insignis from the Late Pleistocene to present

The *Magnolia insignis* mummified wood from the Upper Pleistocene of Maoming strongly confirms the occurrence of this species in South China, i.e. far beyond its modern range, during the period prior to the LGM. Such expansions in last glaciation of the Late Pleistocene (Gao et al., 2015; Shao et al., 2022) have been evidenced by molecular phylogeographic studies for low latitudes plant species from eastern Asia (Tian et al., 2010; Liu et al., 2014, 2022; Gao et al., 2015; Zhang et al., 2016), but actual fossil evidences are necessary to confirm such hypotheses. The presence of fossil wood of *Pinus armandii* from the Maoming Basin (Huang et al., 2023a) was previously the only paleontological evidence supporting this expansion model for low latitudes. The discovery of *Magnolia insignis* fossil wood now adds to this evidence and further confirms the glacial expansion for cold-tolerant species at low latitudes during last glaciation. This finding is significant as it further supports the idea of cold-adapted species at low latitudes experienced range expansions during last glacial periods.

This scenario is also supported by our results of the MaxEnt modeling showing that the climatically suitable habitats for *M. insignis* were spread over a wider area (including South China) during the most recent episodes of last glaciation, i.e. 30 ka BP and 20 ka BP, than 6 ka (Northgrippian) and present (Fig. 5). This indicates that the species had wide distributions since the period prior to the LGM. However, over time, its distribution area contracted and it is currently restricted to mountainous interglacial refugia which was in central and southwest regions of China (*sensu* Bennet & Provan, 2008). In the absence of other fossils of *M. insignis*, our suggestions about the range fluctuations of this species could be tested by a phylogeographical study, i.e., analysing the genetic diversity in the populations of this species.

4.2. The climatic factors influencing the distribution of M. insignis

According to Zhuang et al. (2018), the environmental factors affecting the distribution of extant *M. insignis* vary based on the different spatial scales used for modeling. Topographic factors (including altitude, aspect, slope) are the main environmental factors on the scale of the Three Parallel Rivers region, which is an area of high relief mountains. At the scale of Yunnan Province overall, however, the annual precipitation (BIO12) and temperature seasonality (BIO4) are the leading factors, while at the country scale, the mean diurnal range (BIO2), the temperature annual range (BIO7) and the precipitation of warmest quarter (BIO18) are the leading factors. Our MaxEnt modeling results showed that the top four important bioclimatic variables

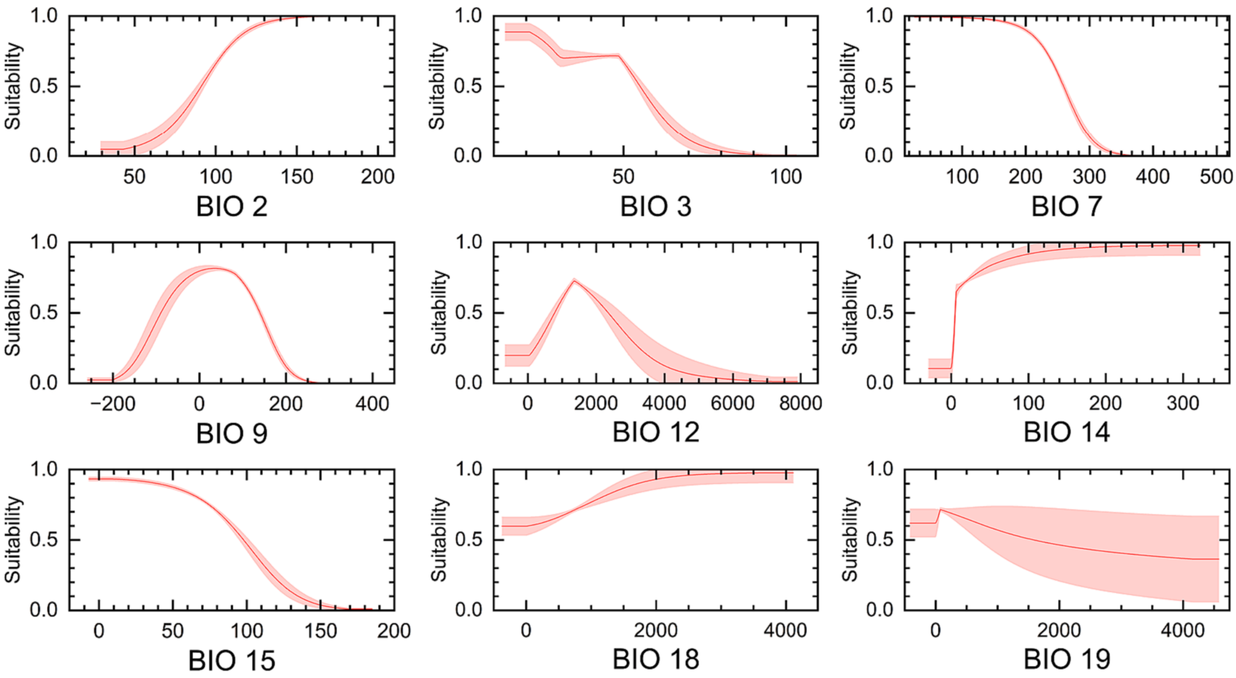

Fig. 4. Response curves for the nine important bioclimatic variables.

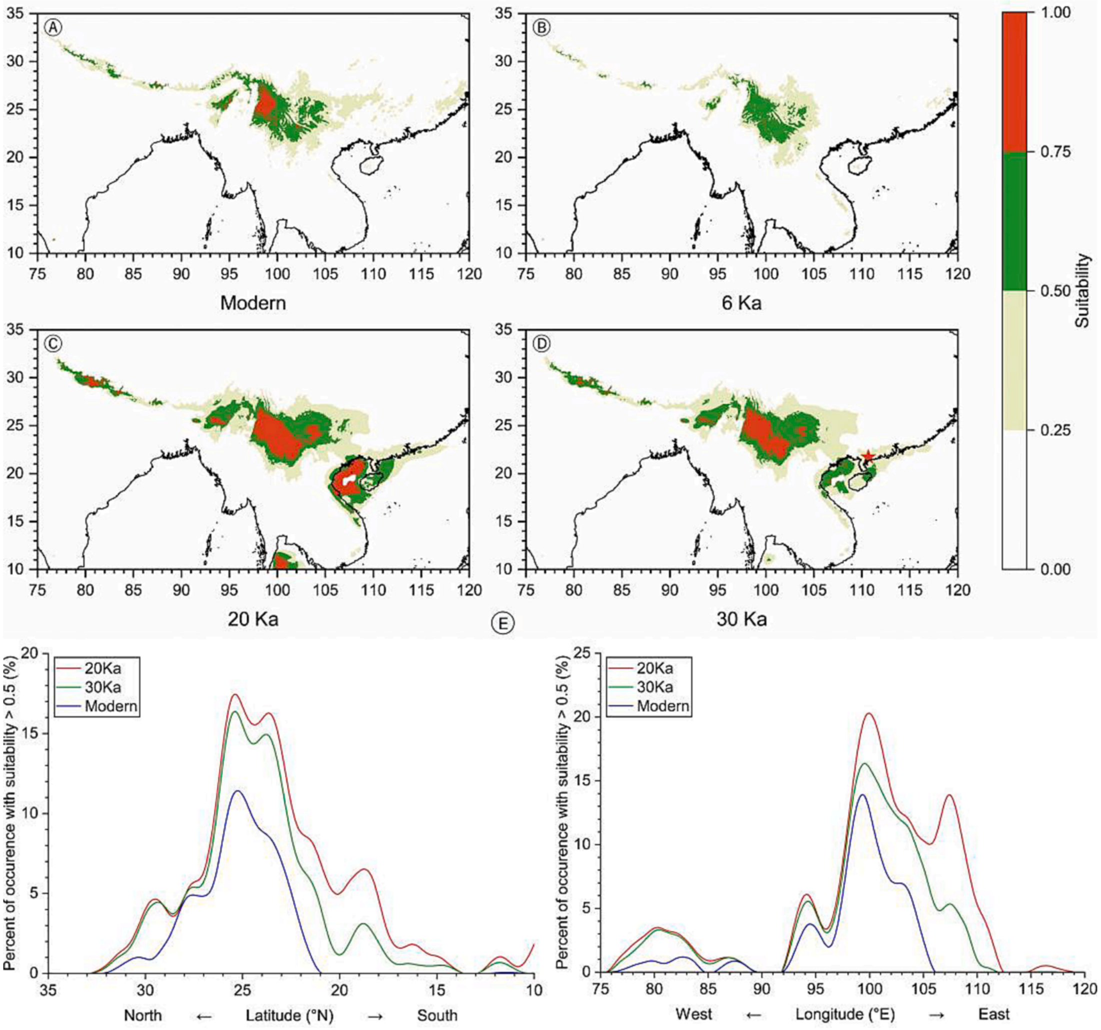

Fig. 5. Projected climatically suitable habitats for *Magnolia insignis* at different times. **A** Projections of suitable habitats for present. **B** Projections of suitable habitats at 6 ka BP. **C** Projections of suitable habitats at 20 ka BP. **D** Projections of suitable habitats at 30 ka BP. The fossil locality was indicated by the red star. **E** The latitudinal and longitudinal change of high suitable habitats (suitability index > 0.5) of *M. insignis* at different times. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

determining the distribution of extant *M. insignis* are precipitation of the driest month (BIO14), mean temperature of the driest quarter (BIO9), isothermality (BIO3, =BIO2/BIO7, *100), and precipitation of warmest quarter (BIO18), which suggest BIO14 and BIO9 are the main climatic factors that determine the current distribution of *M. insignis* on a global scale compared to that at the scale of China (BIO2, BIO7, BIO18), indicating the extreme precipitation and mean temperature in winter play critical roles in shaping the current global distribution of this species.

Table S2 shows that all values of bioclimatic variables for Maoming, South China at 30 ka BP and 20 ka BP by different paleoclimatic proxies are among the ranges of that for modern distribution area of *Magnolia insignis.* However, maximum values of BIO5 (Max. Temperature of Warmest Month), BIO8 (Mean Temperature of Wettest Quarter), BIO10 (Mean Temperature of Warmest Quarter), BIO14 (Precipitation of Driest Month), BIO17 (Precipitation of Driest Quarter) for the Maoming climate at 30 ka BP reconstructed by CA are close to their modern maximum values for *M. insignis*. The present climate in Maoming has higher values of BIO2 (Mean Diurnal Range), BIO8 and BIO10 than that in the modern distribution area of *M. insignis*. We speculated that, based on the above data, BIO8 and BIO10, i.e., warmer summers, are the crucial climatic factors leading to the retreat of *M. insignis* from the Maoming Basin in Holocene.

4.3. *Conservation implications*

Global warming is impacting organisms in diverse ways, such as driving shifts in geographic ranges and change in extinction rate (Dillon et al., 2010). To address the accelerating warming climate crisis, conservationists are turning to trace possible climate refugia for the living populations, especially for vulnerable ones of the cold-adapted plants in low-latitude which has already inhabited “interglacial refugia” (Meng et al., 2019). Molecular phylogeography and species distribution modeling had indicated that mountains regions with high elevations are the important climate refugia in present and future, particularly for cold tolerant plants at low latitudes (Quiroga & Premoli, 2007; Opgenoorth et al., 2010; Meng et al., 2019). However, the importance of mountains at low latitudes is less know than that in mid-high regions as climate refugia.

Our study highlights the influence of past climate changes on the range dynamics of the endangered montane species *Magnolia insignis*. The range of this cold-tolerant tree showed prominent expansion during the most recent glacial interval, followed by its retreat to mountain refugia in Holocene. Our results based on paleoecological evidences indicate that with global warming, the survival of many cold-tolerant montane organisms from tropical and subtropical regions might face significant threat and undergo marked range contraction to mountains, even go extinct. The protection of these species is urgently required in the face of future warming climate. The paleoecological data for *Magnolia insignis* and other low-latitude cold-tolerant species can be taken into consideration for organization of protective areas with climatically suitable habitats, like those that existed at the last glacial interval, where large sized and widely distributed populations may be maintained by cultivation.

5. Conclusions

Mummified wood from the Upper Pleistocene of the low latitudes in South China, was investigated. Detailed comparison with data on fossil and extant wood confirmed its greatest similarity to the endangered cold-tolerant montane species of *Magnolia insignis* (Wall.) Bl.

This fossil provides compelling evidence for a broader historical range of *M. insignis* than present during the period prior to the LGM, indicating a glacial expansion in its recent biogeographic history. MaxEnt modeling of the distribution range of this species confirms this scenario. These findings contribute additional evidence of glacial expansion model for other cold-tolerant montane species at low latitudes in last glaciation.

At a global scale, extreme precipitation and mean temperature in winter emerge as the key bioclimatic variables influencing the present distribution of *M. insignis*. The contraction of *M. insignis* from Maoming and other low latitude regions of East Asia was driven by an increase of summer temperatures during the Holocene.

In summary, these findings provide valuable insights into the biogeographic history of *Magnolia insignis*, highlighting the impact of past climate changes on its range dynamics and emphasizing the distinctive responses of cold-tolerant species to last glacial-interglacial cycles in low latitude regions, shedding light on the plant diversity conservation under the climate changes in present and future.

CRediT authorship contribution statement

Luliang Huang: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Shufeng Li:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Weiye Huang:** Writing – review & editing, Software, Methodology, Investigation. **Jianhua Jin:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Alexei A. Oskolski:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization.

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.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111519.

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