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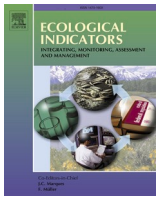

Influence of climate factors on the global dynamic distribution of *Tsuga* (Pinaceae)

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ABSTRACT

Throughout the Quaternary period, climate change has significantly influenced plant distribution, particularly affecting species within the genus *Tsuga* (Endl.) Carrière. This climatic impact ultimately led to the extinction of all *Tsuga* species in Europe. Today, there are ten recognized species of *Tsuga* worldwide, one of listed as a vulnerable species and four as near-threatened species. The genus *Tsuga* exhibits a disjunctive distribution in East Asia (EA), eastern North America (ENA), and western North America (WNA). It is crucial to comprehend the mechanisms underlying these distributional changes and to identify key climate variables to develop effective conservation strategies for *Tsuga* under future climate scenarios. In this study, we applied the maximum entropy (MaxEnt) model by combining distribution data for *Tsuga* with abundant pollen fossil data. Our objective was to investigate the climate factors that shape the distribution of *Tsuga*, identify climate thresholds, and elucidate distribution dynamics in the context of significant climate changes over the past 1070 thousand years (ka). Our findings highlight the pivotal role of precipitation as the key climate factor affecting the distribution of *Tsuga*. Specifically, in EA, summer precipitation was the key driver, while in North America (NA), winter precipitation exerted greater importance. Moreover, we observed similarities in climatic requirements between *Tsuga* species in Europe and EA, and declines in summer precipitation and winter temperature were major factors contributing to the extinction of *Tsuga* species in Europe. Quaternary glacial and interglacial fluctuations exerted substantial impacts on *Tsuga* distribution dynamics. The disappearance of *Tsuga* species in the Korean Peninsula may have occurred during the LGM (Last Glacial Maximum). The potential suitable area for *Tsuga* species in EA expanded during the cold periods, while in NA, it contracted. In the future, climate change may result *Tsuga* distribution area contraction in both the EA and NA. Our study has identified distinct response patterns of *Tsuga* in various geographic regions to Quaternary climate change and offers corresponding suggestions for *Tsuga* conservation. In the future, it will be imperative to prioritize the conservation of natural *Tsuga* distributions in EA and NA, with a focus on the impacts of precipitation fluctuation on the dynamic distribution of this genus.

1. Introduction

The Quaternary climate experienced repeated temperature fluctuations (Hewitt, 2003), mainly manifested in the periodic growth and retreat of continental glaciers in the Northern Hemisphere (Hansel and McKay III, 2010; Willeit et al., 2019). The severe climate changes had profound impacts on the migration, diffusion, differentiation, and even extinction of species (Van Andel and Tzedakis, 1996; Sandel et al., 2011), leading to dramatic biodiversity changes (Davis, 1983; Hewitt, 2000) and the development of a fragmented distribution pattern among certain species in the Northern Hemisphere (Hong et al., 2018). Compared to other geological periods, the Quaternary was more closely related to the modern era and therefore had a significant impact on current Northern Hemisphere biodiversity (Zhou et al., 2017). Understanding climate change and species response mechanisms in the Quaternary is of great significance for gaining a deeper understanding of

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global climate change and ecosystem relationships (Fordham et al., 2020), as well as for predicting the impact of future climate change on species distributions and the preservation of threatened species (Fordham et al., 2014, 2016; Bhattacharyya et al., 2023).

Tsuga (Endl.) Carrière, in the family Pinaceae, plays a significant role in subalpine and lowland moist coniferous forests as well as broad–leaved forests (Lepage, 2003). *Tsuga* have been greatly affected by Quaternary climate change (Magri and Palombo, 2013), leading to its disappearance in Europe (Davis, 1983; Magri et al., 2017). Currently, *Tsuga* have a fragmented distribution pattern in East Asia (EA) and North America (NA) (Li, 1995; Lepage, 2003; Qiao et al., 2007; Holman et al., 2017). The widely accepted classification contains nine extant species, including *T. chinensis* (Franch.) Pritz., *T. forrestii* Downie and *T. dumosa* (D. Don) Eichler distributed in China and other countries around the Himalayas. *T. diversifolia* (Maxim.) Mast. and *T. sieboldii* Carrière are endemic in Japan, *T. canadensis* (L.) Carrière, *T. caroliniana* Engelm., *T. heterophylla* (Raf.) Sarg. and *T. mertensiana* (Bong.) Carrière are distributed in NA (Farjon, 2017). In addition, a new species, *T. ulleungensis* G. P. Holman et al., has recently been reported and distributed on Ulleungdo Island, Korea (Holman et al., 2017; Feng et al., 2021). Among them, *T. forrestii* is listed as vulnerable species (Yang and Luscombe, 2013, Yang et al., 2017), and some others are listed as near-threatened species including *T. sieboldii* (Katsuki and Luscombe, 2013), *T. canadensis* (Farjon, 2013a), *T. caroliniana* (Farjon, 2013b), *T. chinensis* var. *robusta* and *T. mertensiana* (Yang et al., 2017). Therefore, assessing the distribution status of *Tsuga* has important significance for the conservation of *Tsuga*, especially considering in the future climate scenarios.

This genus thrives in shaded and humid environments and is sensitive to prolonged droughts, it is usually considered an excellent indicator of humid environment in the geological time (Lepage, 2003; Yang et al., 2009; Lacourse, 2012; Xing et al., 2013; Ding et al., 2021). The macrofossil occurrence of *Tsuga* is frequently used to indicate warm and humid climate in the geological time, such as the Miocene climate in Weichang, Hebei Province, North China (Li et al., 2023); the late Paleogene climate in Markam, southeastern margin of the Qinghai–Tibetan Plateau (Wu et al., 2020); the Miocene climate in Xundian County, Yunnan Province, southwestern China (Wang et al., 2015). The above research indicates that *Tsuga* is a good indicator of climate change and has received wide attention. However, the most important climate variables driving the distribution of *Tsuga* are not yet clearly identified. Therefore, conducting research on the distribution dynamic of *Tsuga* has important environmental inductive significance.

Tsuga is commonly found in fossil records (Lepage, 2003; Magri et al., 2017), particularly in the form of pollen grains. Its abundant Quaternary pollen fossils make it an exceptional conifer plants for exploring the impact of Quaternary climate change on its species distribution. Magri et al. (2017) observed the disappearing pattern of *Tsuga* in southern Europe during the Quaternary, and Davis et al. (1986) suggested an expansion route of *Tsuga* in the USA around 7 thousand years (ka). In addition, Bertini (2000) found that extinction of *Tsuga* in Europe was associated with global drought events during the middle Pleistocene, and Prentice et al. (1991) indicated that a cool and humid climate promoted the expansion of *T. mertensiana* during 12–9 ka. Although previous palynology studies have revealed the distribution pattern and key climate variables of *Tsuga* during the Quaternary, they just contained part of the region and species. In this regard, species distribution modeling in palaeoecology is a valuable approach for predicting past species distributions in large spatial scale and continuous time series (Svenning et al., 2011; Varela et al., 2011) and examining the relationship between climate change and suitable species habitats (Elith et al., 2011). However, previous research using models to simulate the distribution of *Tsuga* are constrained in some areas such as Japan (Tsuyama et al., 2014), southwestern China (Dakhil et al., 2019), Maine, U.S.A (Dunckel et al., 2017), and limited species. There is still lack of integrative research on its Quaternary distribution dynamic of all species in *Tsuga*, the specific climate factors that contributed to the extinction of *Tsuga* in Europe is not yet fully understand.

The MaxEnt model, also known as the maximum entropy model, is based on the principle of maximum entropy theory (Phillips and Dudík, 2008). It uses existing species distribution and environmental data (Phillips et al., 2006; Elith et al., 2011) to estimate a species distribution by identifying the distribution that exhibits maximum entropy constrained by the environmental conditions observed at recorded locations (Phillips et al., 2006, 2017). Compared with other models, MaxEnt offers notable advantages such as high simulation accuracy and satisfactory modeling results, even with relatively small sample sizes (Guo et al., 2020). Consequently, it has been widely applied across various ecological research fields (Phillips et al., 2017; Liu et al., 2019; Xiao et al., 2022).

According to Magri et al. (2017), the distribution pattern of *Tsuga* in Southern Europe changed dramatically after 1070 ka. Therefore, this study used MaxEnt to simulate the global distribution change of *Tsuga* from 1070 ka into the future and analyze critical bioclimate variables. Additionally, pollen fossil data were collected from previous publications and compared with the modeling outputs to facilitate mutual validation and comprehensive analyses. This study aimed to address three key scientific questions: 1) What was the impact of Quaternary climate change on the distribution of *Tsuga*; 2) What were the underlying climatic factors for the extinction of *Tsuga* in Europe; and 3) What are potential distribution regions of *Tsuga* under future climate change. We hypothesize that precipitation and temperature in different seasons may affect the distribution and extinction of *Tsuga* in various regions.

2. Materials and methods

2.1. Study regions

This study used data on the global natural distribution of *Tsuga*, which exhibits a fragmented pattern in EA, eastern North America (ENA), and western North America (WNA, Fig. 1). In EA, *Tsuga* are mainly distributed in the Asian monsoonal regions of Japan, China, and other countries around the Himalaya (Yang et al., 2009). In ENA, *Tsuga* are distributed in the eastern United States and Canada, characterized by a humid and cold climate with sufficient water throughout the year (Hough, 1960). In WNA, *Tsuga* thrive in cool to cold marine climates characterized by mild to cold winters, short and warm to cool growing seasons, and moderate to heavy precipitation (Berntsen, 1958; Means, 1990). Due to the distinct differences in climatic and environmental conditions in these three regions, the impacts of Quaternary climate change on *Tsuga* were significantly varied different (Eiserhardt et al., 2015). Therefore, this study conducted separate simulations individually for these three regions.

2.2. Species data collection and processing

The extant distribution data of *Tsuga* came from online sources, namely the Chinese Virtual Herbarium (https://www.cvh.ac.cn/) and the Global Biodiversity Information Facility (https://www.gbif.org/; GBIF.org, 2022). A total of 46,185 modern distribution records were collected. To ensure data quality, a rigorous cleaning process was conducted, which excluded missing location information, duplicate entries, and cultivated occurrences. After data cleaning, 36,842 records remained. To avoid spatial bias, the remaining records were randomly gridded using the 'grid Sample' function from the 'dismo' package in the software R. Only one occurrence per $20' \times 20'$ area was retained, resulting in a final dataset of 2,425 standard records used for distribution modeling (Fig. 1).

In addition to the modern distribution data, a collection of pollen fossil records was compiled. A total of 268 pollen fossil records were collected from various sources (Table S1), including studies by the relevant references (McLachlan and Brubaker, 1995; Jacques et al., 2000; Toney et al., 2003; Hayashi, 2010; Xu et al., 2010; Tarasov et al.,

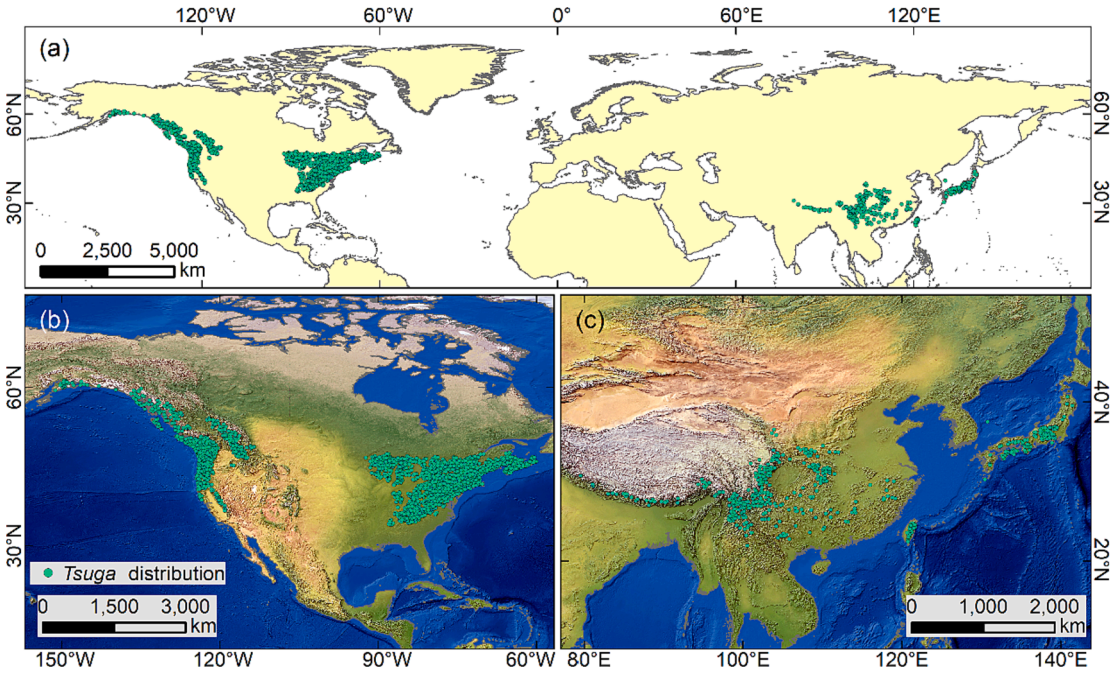

Fig. 1. Modern distribution of *Tsuga* at the global scale (a), NA (b) and EA (c).

2011; Corrado and Magri, 2011; Sun and Feng, 2015; Donders et al., 2021; Liu and Yuan, 2022 etc.), and two pollen databases, Neotoma Explorer (https://apps.neotomadb.org/explorer/) and Paleobiology Database (https://palaeobiodb.org/).

2.3. Bioclimate variables and selection

Climate data were primarily obtained from the World Climate Database (https://www.worldclim.org) with a spatial resolution of 2.5 arc minutes (~5 km) and encompassing 19 bioclimate variables (Table S2). The climate data cover multiple periods, including the Last Glacial Maximum (LGM, ca. 22 ka BP, CCSM4), the mid-Holocene (MH, ca. 6 ka BP, CCSM4), the present period (average for 1970–2000), and the future (2021–2040 and 2041–2060). Future climate data were derived from two shared socioeconomic pathways (SSP245 and SSP585) of five models (ACCESS–CM2, CMCC-ESM2, EC-Earth3-Veg, MRI-ESM2-0, UKESM1-0-LL) from the Coupled Model Intercomparison Project Phase 6 (CMIP6). The Quaternary climate data preceding the LGM were derived from Oscillayers (https://doi.org/10.5061/dryad.27f8s90, Gamisch, 2019). These data were chosen based on the global mean surface temperature (Gamisch, 2019, refer to Fig. S1) and the consideration of the dynamic changes in pollen fossil data. The selected Quaternary climate data included periods of 1,070 ka, 880 ka, 780 ka, 440 ka, LGM and MH. Of these, 1,070 ka, 780 ka, and MH represented warm periods, while 880 ka, 440 ka, and LGM represented cold periods.

To reduce the impact of overfitting due to climate variable multicollinearity, we used the "laverStats" function from the package "spatialEco" in R to analyze Pearson's correlation coefficient of bioclimate variables. Bioclimate variables with high contributions and low correlations (<0.8) were selected (Table S3, S4). Consequently, in EA, we selected bio6 (min temperature of coldest month/°C), bio7 (temperature annual range/°C), bio9 (mean temperature of driest quarter/°C), bio10 (mean temperature of warmest quarter/°C), bio11 (mean temperature of coldest quarter/°C), bio15 [precipitation seasonality (coefficient of variation)], bio18 (precipitation of warmest quarter/mm) and bio19 (precipitation of coldest quarter/mm). In ENA, we selected bio7, bio9, bio10, bio11, bio12 (annual precipitation/mm), bio15, bio17 (precipitation of driest quarter/mm) and bio18 as relevant variables. In WNA, we selected bio3 [isothermally (bio2/bio7) (×100)], bio4 (temperature seasonality), bio8 (mean temperature of wettest quarter/°C), bio10, bio11, bio15, bio18 and bio19.

2.4. Species distribution model building

We used the species distribution model MaxEnt (version 3.4.3, https://biodiversityinformatics.amnh.org/open_source/MaxEnt/) to simulate the potential distribution of *Tsuga* in the EA, ENA, and WNA regions under different climate scenarios. MaxEnt is efficient when handling presence-only data and species-environment relationships (Elith et al., 2011; Phillips et al., 2006). Setting up the model involved randomly selecting 75 % of the distribution data to be used as training data, while the remaining 25 % was treated as testing data. This process was repeated 10 times using a cross–validation procedure. The area under the receiver operating characteristic curve (AUC value) was used to evaluate model performance. AUC values range from 0.5 to 1.0, where AUC > 0.9 indicates better model performance (Phillips and Dudík, 2008). We conducted a jackknife test to assess the relative importance of all variables.

The MaxEnt predictions were converted into raster data. We then classified the raster data using a reclassification method proposed by Cao et al. (2022), in which the potential adaptability of *Tsuga* was divided into four suitability ranges: unsuitable (0.0–0.1), low suitability (0.1–0.3), medium suitability (0.3–0.5), and high suitability (0.5–1.0). These classifications provided insights into the changes to potentially suitable regions for *Tsuga* in response to different climate scenarios. Then we use subtraction tools to calculate changes in climate scenarios and potential distribution regions.

3. Results

3.1. Model performance, variable contributions, and response curves

The model simulation results showed that AUC values for EA (0.977), ENA (0.948), and WNA (0.973) were all greater than 0.9 (Fig. S2). These high AUC values indicated that the simulations obtained in this study were highly reliable, demonstrating the robustness of our approach. The contribution rates of the eight main bioclimatic variables in the three regions are shown in Fig. 2. Overall, precipitation was identified as the

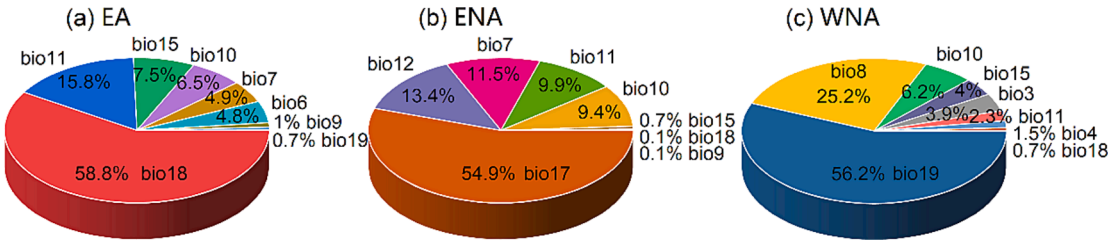

Fig. 2. The contribution rates of several important climate variables to the modern distribution of *Tsuga* in the EA (a), ENA (b), and WNA (c) regions.

crucial climate variable influencing the distribution of *Tsuga* in all regions. However, the influence of specific precipitation variables varied across regions. In EA, the precipitation of the warmest quarter (bio18) in summer had a significant effect on the distribution of *Tsuga*. In ENA, the precipitation of the driest quarter (bio17) in winter played an important role in species survival. Similarly, in WNA, the precipitation of the coldest quarter (bio19) during winter had a notable impact on the distribution of *Tsuga*. Because the driest quarter in ENA and the coldest quarter in WNA both occurred during winter, it was inferred that winter precipitation played a critical role in the survival and distribution of *Tsuga* in NA. In conclusion, summer precipitation had a crucial influence on the distribution of *Tsuga* in EA, while winter precipitation played a significant role in NA. Additionally, annual precipitation (bio12) impacted the distribution of *Tsuga* in the ENA, and precipitation seasonality (bio15) and annual temperature range (bio7) affected the two regions. Both winter and summer temperatures had important effects on the survival and distribution of *Tsuga* in all regions.

The response curves provide valuable insights into species ecological niches and suitable bioclimatic variable ranges for its habitat (Liu et al., 2021). Fig. 3 showed the response curves of *Tsuga* in EA, ENA, and WNA for important climates. The high suitability area was defined within a range of 0.5–0.1. The area with a response curve greater than 0.5 was considered to fall within the threshold range of climate variables suitable for *Tsuga* survival. In EA, the response curves showed that *Tsuga* had the strongest response to precipitation during the warmest season, particularly when it exceeded 500 mm. Additionally, the mean temperature of the coldest quarter ranging from 0 to 10 °C had a significant influence on *Tsuga* habitat suitability. Similarly, in ENA, annual precipitation (900–1400 mm) and annual temperature range (34–41 °C) produced strong impact on *Tsuga* distribution. These climatic variables played a crucial role in determining the suitability of habitats for *Tsuga* in the ENA region. In WNA, the important variables included precipitation of the coldest quarter (440–1750 mm), mean temperature of the wettest quarter (-6–6 °C), and mean temperature of the warmest quarter (12–17 °C), which had a strong influence on the distribution and viability of *Tsuga*.

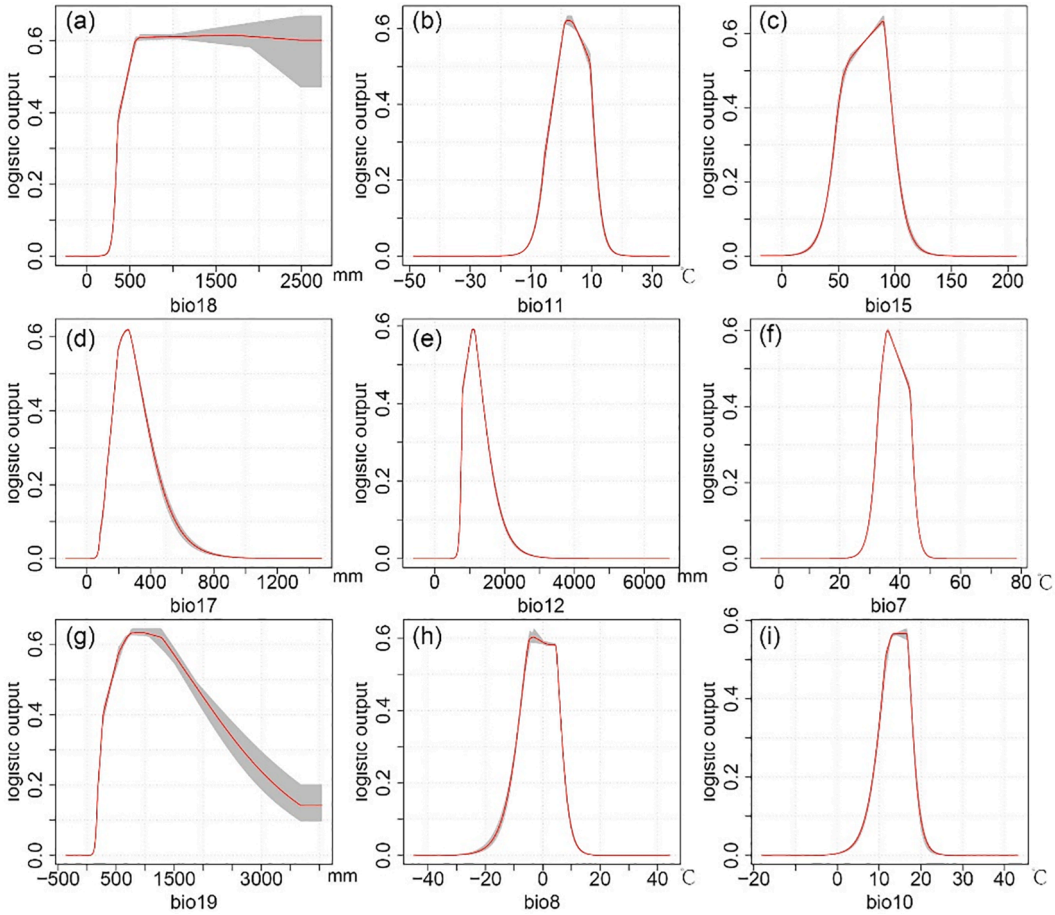

Fig. 3. Response curves of *Tsuga* to important climate variables in EA (a–c), ENA (d–f), and WNA (g–i).

3.2. Comparison of the predicted and actual Tsuga distribution regions

The simulated model results from this study closely matched the natural distribution sites of *Tsuga*. In EA, the potential suitable area was basically consistent with the natural distribution regions, including the surrounding regions of the Sichuan Basin, Qinling Mountains, Hengduan Mountains, Himalaya, Hills in Southeast China, Central Mountain Range on the island of Taiwan, and Honshu, Shikoku, and Kyushu in Japan (Fig. 4a–b). The estimated potential high suitable areas in EA covered 2.85 million km^2 (Fig. S3a). Interestingly, there were small regions of potential high suitable outside the natural distribution regions, such as the Taebaek Mountains and southeastern Korean Peninsula, and parts of Jeju Island and the European Alps (Fig. 4b). In ENA, the species was primarily distributed in the Appalachian Mountains, the Great Lakes region (Fig. 4c–d). The estimated potential high suitable areas in ENA spanned 3.93 million km^2 (Fig. S4a). In WNA, the main distribution regions for *Tsuga* included the Coast Mountains, the Rocky Mountains, and other coastal regions (40–55 °N, Fig. 4e–f), with a potential high suitable area of 2.63 million km^2 (Fig. S5a). Notably, some areas had potential medium suitable for the fragmented distribution of *Tsuga* in Europe (Fig. 4f). In conclusion, the potential suitable regions for modern *Tsuga* based on the natural distribution areas in EA and ENA were generally consistent with the modern natural distribution. Additionally, the study suggested there may be some potential suitable areas for *Tsuga* in Europe beyond its current distribution range (Fig. 4).

3.3. The potential suitable regions of Tsuga in the past

The study simulated the past potential distribution regions of *Tsuga* in EA, ENA, and WNA and compared them with collected pollen fossil data (Fig. 5–Fig. 7). The pollen fossil data were mainly concentrated in the LGM and MH periods, and they were found within or surrounded the regions of potential high suitable (Fig. 5e–f, Fig. 6e–f, Fig. 7e–f). Compared with previous pollen research results by Magri et al. (2017), this study found that the distribution of pollen sites in Europe was generally consistent with the simulation results of *Tsuga* in EA, with *Tsuga* disappearing in Europe after 780 ka (Fig. S6–S8). Consequently, pollen sites in Europe were added to the simulated map of the potential distribution of *Tsuga* in EA (Fig. 5A). Overall, the distribution of pollen sites corresponded well with the potential suitable regions, suggesting that the simulation results effectively represented the dynamic distribution change of *Tsuga* during geological periods.

In EA, the area of potential suitable for *Tsuga* during warm periods was significantly smaller than that during cold periods (Fig. 5a–f). The LGM exhibited the largest distribution area of potential suitable regions for *Tsuga* (Fig. 5e). The periods from 1,070 to 880 ka and from 780 to 440 ka showed the most significant increase in potential suitable regions for *Tsuga*, with the area of potential high and medium suitable expanding by 86.56 %, 60.14 %, 28.17 %, and 37.88 %, respectively (Fig. S3a–b). The expansion areas were primarily located in the Himalaya, southern Hengduan Mountains, Hills in Southeast China, Central Mountain Range on the island of Taiwan, and southern Japan, while the contraction areas were mainly concentrated in middle and northern Japan (Fig. 5a–d). The potential distribution areas for *Tsuga* disappeared in the Korean Peninsula during the LGM (Fig. 5e). The spatial distribution of potential suitable regions shifted notably to lower latitudes and elevations (Fig. 5e). The most obvious reduction in the potential suitable area of *Tsuga* occurred during 880–780 ka and from the LGM to MH. The potential high and medium suitable area decreased by 30.43 % and 54.23 % and by 18.36 % and 14.65 %, respectively (Fig. S3a–b). The contracting regions were primarily located in the Himalayas, southern Hengduan Mountains, Hills in Southeast China, Central Mountain Range on the island of Taiwan, and southern Japan. The spatial distribution of potential suitable regions moved significantly to higher latitude and elevation areas (Fig. 5b–c, e–f). The expanding regions were mainly distributed in the central area of Honshu Island, the southern Ōu Mountains in Japan, and the Korean Peninsula (Fig. 5b–c, e–f). In summary, throughout geological periods, the potential habitat of *Tsuga* experienced both expansions and contractions in response to climate change. The regions where the potential habitat of *Tsuga* contracted were largely congruent with the regions where it expanded, indicating that *Tsuga* populations in these regions were highly sensitive to climate change.

In ENA, the potential suitable area for *Tsuga* was considerably larger during relatively warm periods than during relatively cold periods (Fig. 6). The smallest potential suitable area for *Tsuga* were observed during the LGM. The most pronounced contractions in the potential suitable area for *Tsuga* occurred during 1,070–880 ka and 780–440 ka, with areas of potential high and medium suitable decreasing by 40.38 %, and 48.27 %, 51.8 % and 46.52 %, respectively (Fig. S4a–b). Reductions in regions were primarily distributed in the Great Lakes, central and northeastern Appalachian Mountains, and northern Newfoundland (Fig. 6a–d). On the other hand, the most significant expansions in potential suitable area for *Tsuga* were observed during 880–780 ka, LGM–MH, and MH–Present, with areas of potential high suitable expanding by 53.82 %, 81.31 %, and 39.46 %, respectively (Fig. 4a). The potential medium suitable areas expanded by 38.65 % (880–780 ka) and 177.12 % (LGM–MH) (Fig. S4b). The expanded regions were mainly distributed in the Great Lakes, central Appalachian Mountains, with potential suitable noticeably shifting to higher latitudes and elevations (Fig. 6b–c, e–f).

In WNA, the potential suitable area for *Tsuga* was larger during warm periods than during cold periods (Fig. 7). The significant contractions in areas of potential high suitable mainly occurred during 1,070–880 ka and 780–440 ka, with reductions of 36.72 % and 27.23 %, respectively (Fig. S5a). The potential high suitable area retreated southwards along the Coast Mountains and Rocky Mountains, extending even to regions south of 45.5 °N (Fig. 7a–d). Some of the regions classified as high suitable regions transformed into medium and low suitable regions. On the other hand, the significant expansion periods of potential high suitable area for *Tsuga* occurred mainly in 880–780 ka, LGM–MH, and MH–Present, with expansions of 48.17 %, 20.58 %, and 60.55 %, respectively (Fig. S5a). The potential high suitable area expanded northwards and eastwards along the Coast Mountains and Rocky Mountains, extending further to 58 °N (Fig. 7b–c, e–f). Parts of the medium and low suitable regions were transformed into high suitable regions that expanded inland and into higher latitudes.

3.4. Analysis of changes in Europe based on important climate variables

Palynological studies have found that there was a substantial contraction of *Tsuga* populations in Europe during the late early Pleistocene, followed by a gradual disappearance in the middle Pleistocene (Biltekin et al., 2015; Magri et al., 2017). The decline and eventual disappearance of *Tsuga* populations in Europe during the middle Pleistocene may have been associated with intensified drought and decreased temperatures during glacial periods (Bertini, 2000). This study considered the important climate variables affecting the survival and distribution of *Tsuga* in EA (summer precipitation and winter temperature) and NA (precipitation of coldest quarter and annual precipitation), and further examined the changes to these climate variables in Europe (Fig. 8). The changes in the most influential climatic factors in EA were consistent with distribution shifts of *Tsuga* pollen in Europe, while NA was different (Fig. S6–S8). Specifically, there was a transition from a relatively warm period to a cold period, the percentage of *Tsuga* pollen in Europe decreased, and the corresponding climate variables (summer precipitation and winter temperature) significantly decreased (Fig. 8a1, a3–a4; c1, c3–c4). However, the critical climate variables for the distribution of *Tsuga* in NA did not correspond to the distribution changes in Europe. These findings suggest that *Tsuga* in Europe may have had more similar climate requirements to those in EA, and reductions to summer precipitation and winter temperatures may have caused its

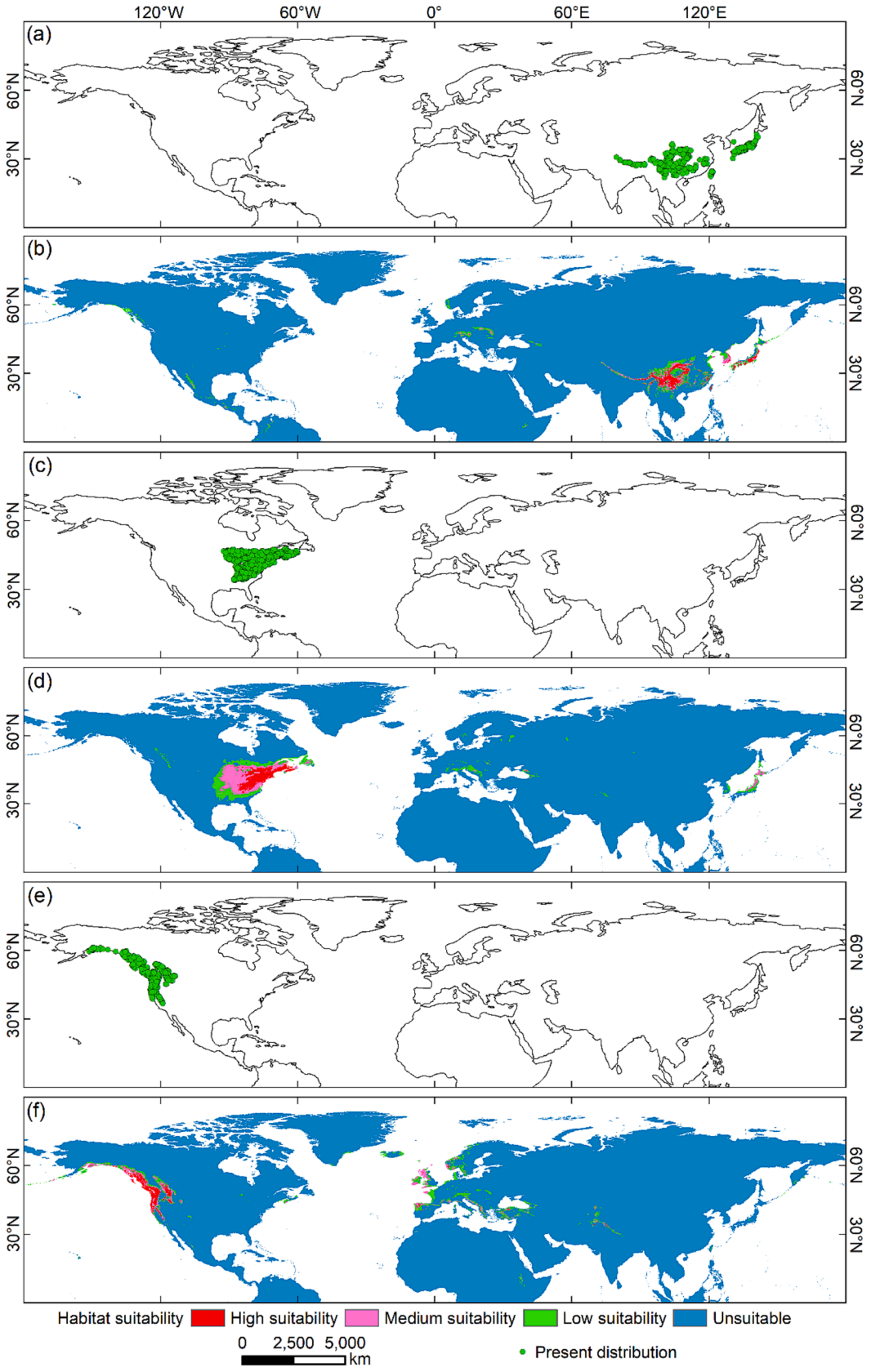

Fig. 4. Comparing modern natural and potential distribution regions of *Tsuga* in EA (a–b), ENA (c–d) and WNA (e–f).

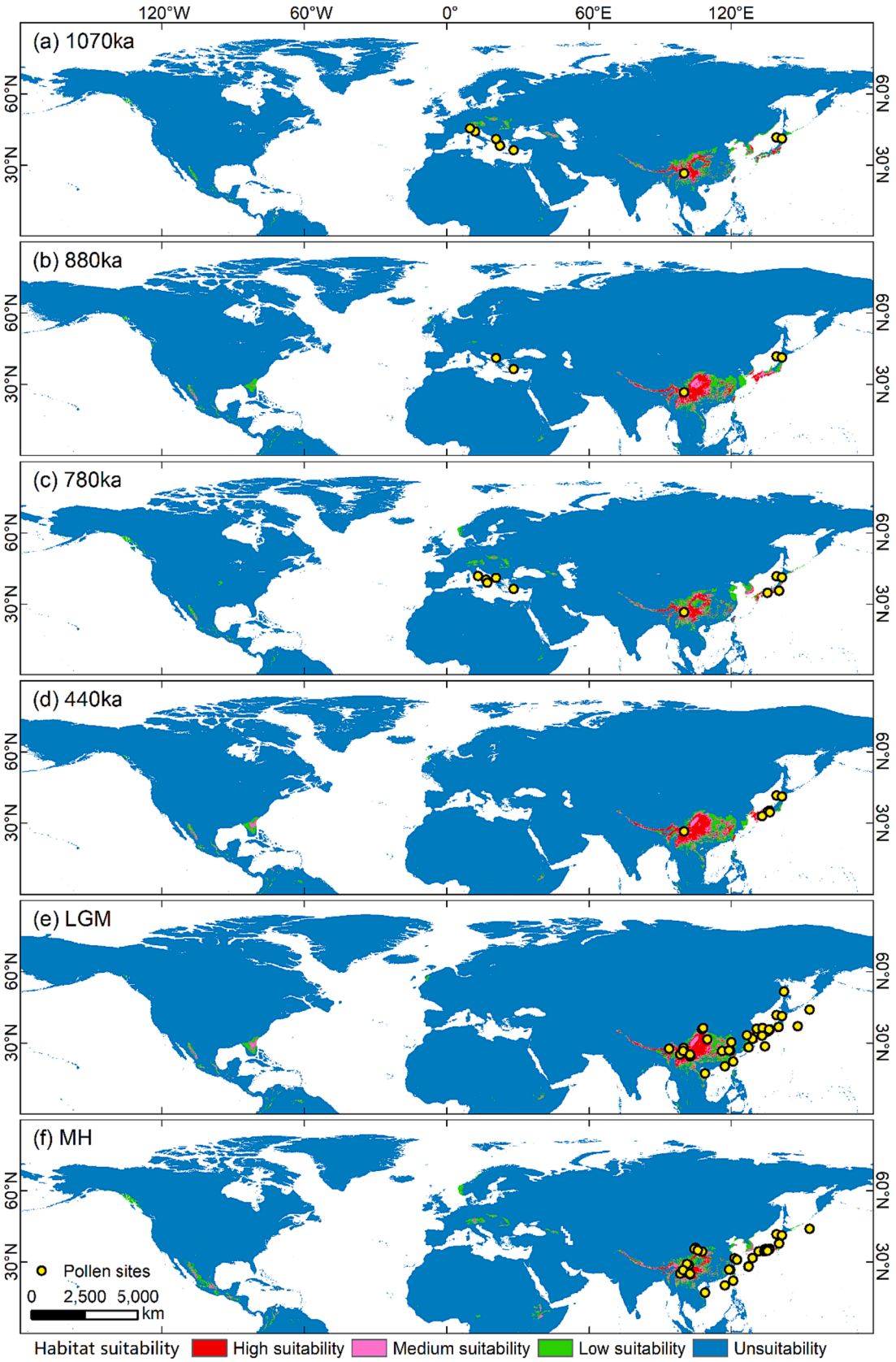

Fig. 5. Predict past potential distribution regions of *Tsuga* in EA.

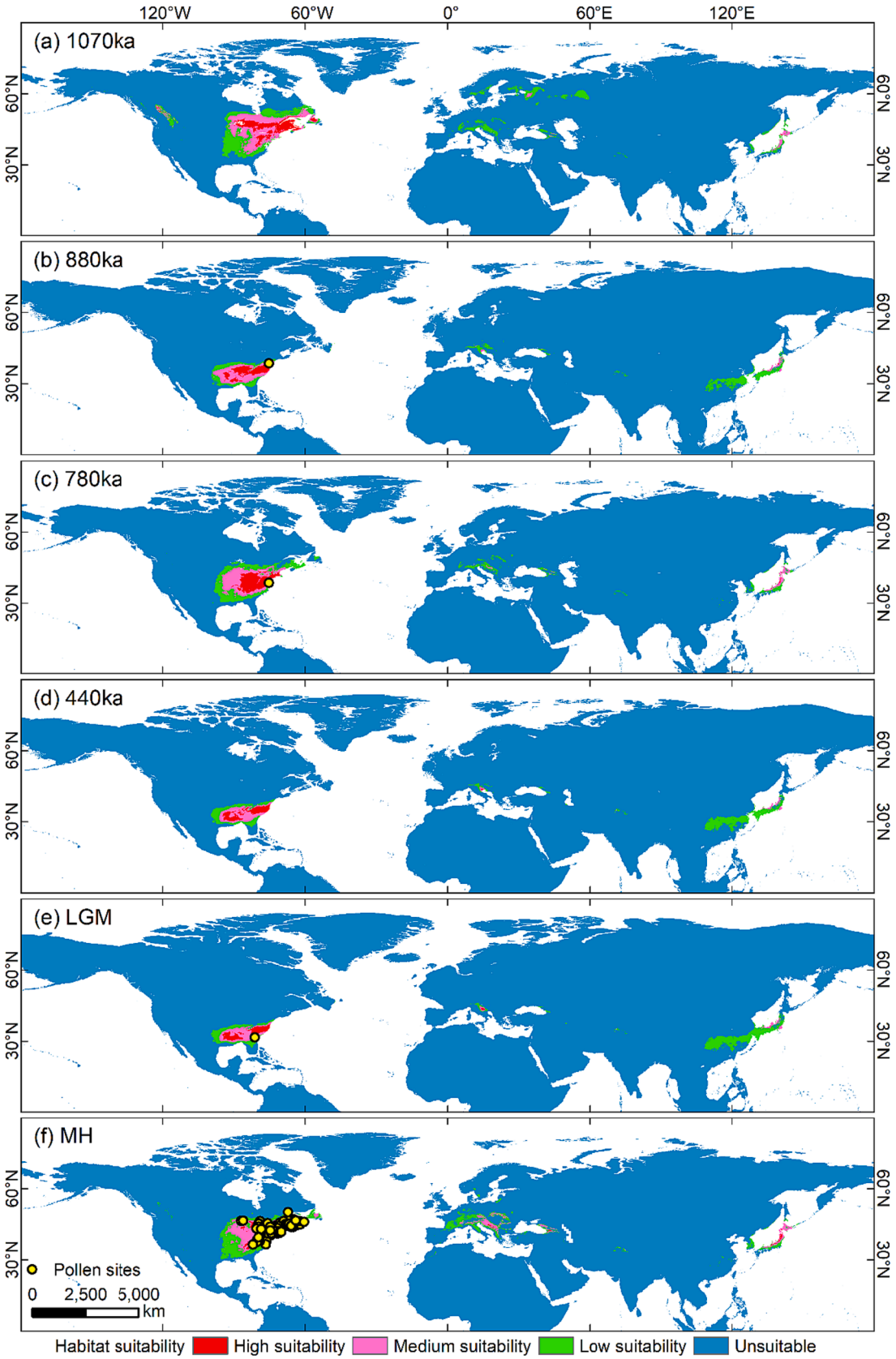

Fig. 6. Predict past potential distribution regions of *Tsuga* in ENA.

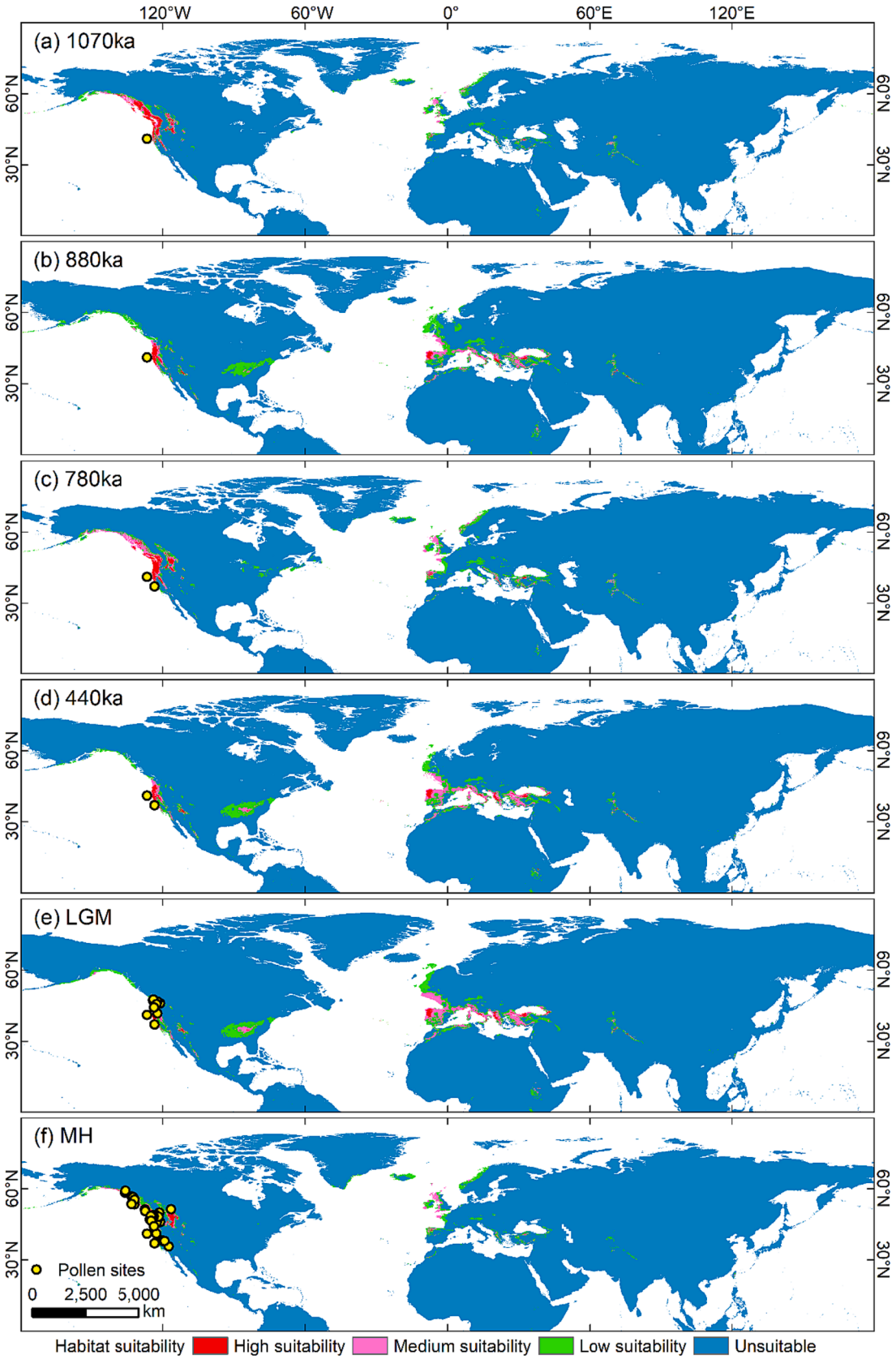

Fig. 7. Predict past potential distribution regions of *Tsuga* in ENA.

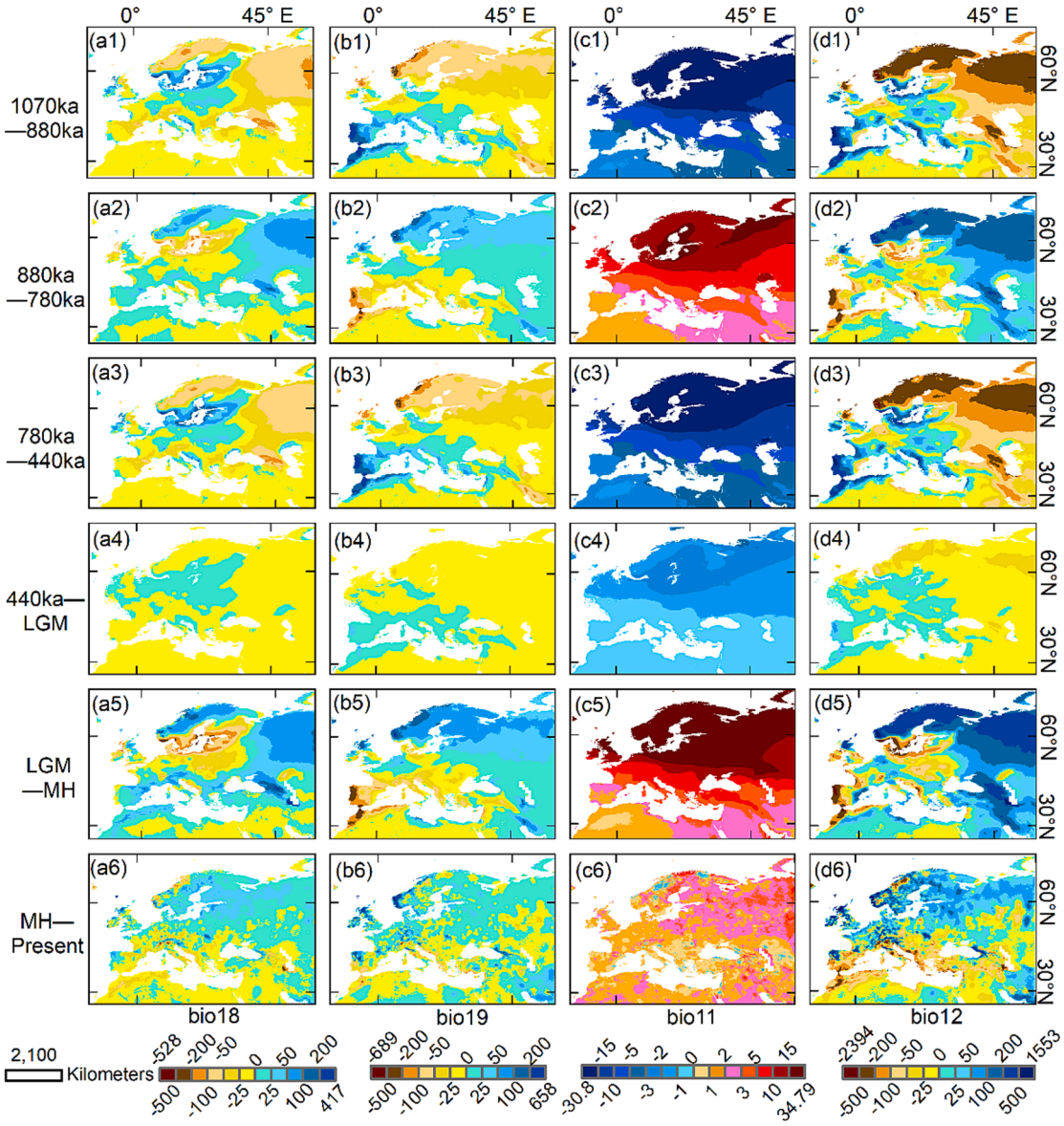

Fig. 8. The variations in four important climate variables in Europe. Note: these four climate variables were found to be the most important climate variables affecting the survival and distribution of *Tsuga* in EA (bio18 and bio11) and NA (bio19 and bio12).

disappearance.

3.5. Potential suitable regions for future Tsuga

In EA, the areas of future potential suitability for *Tsuga* were projected to contract even further, with a shift towards higher latitude and elevation regions. In particular, under the higher carbon emission scenarios (SSP585), the potential suitable area decreased significantly (Fig. S3a–b) and moved towards higher elevations in regions like those in the surrounding Himalaya, southwestern Qinling Mountains, Hengduan Mountains, and the Kyushu and Shikoku Islands in Japan (Fig. S9b, d). In ENA, the potential suitable area for *Tsuga* was projected to decrease in the future, especially under SSP585 (2041–2060), with a noticeable reduction in the distribution area (Fig. S4a). The decreased areas were projected to be mainly distributed in the southwest Appalachian Mountains, while expansions were predicted to occur in the areas north of the Great Lakes in NA and Labrador Plateau. (Fig. S10d). In general, under the high carbon emissions scenario, the potential suitable area for *Tsuga* noticeably expanded to higher latitudes and altitudes. In WNA, the potential suitable area for *Tsuga* in the future was expected to generally decrease compared to present conditions (Fig. S5, Fig. S11). Under future climate scenarios, the potential suitable area significantly contracted, especially in SSP585(2021–2040) and SSP585 (2041–2060) climate scenarios, with high suitable area decreasing by 26.37 % and 35.03 %, respectively (Fig. S5a). These areas were predominantly located in the Coast Mountains (45–48 °N) and the southern Rocky Mountains (Fig. S11b, d).

4. Discussion

4.1. Key bioclimatic variables influencing Tsuga distribution

This study highlighted the significant impact of climate change on the distribution of *Tsuga* (Fig. 3, Fig. S12). Precipitation was the most crucial climate variable affecting *Tsuga* distribution, with different regions showing sensitivity to either summer or winter precipitation. Previous research has shown that *Tsuga* prefer humid climates and exhibit limited drought tolerance (Lepage, 2003; Yang et al., 2009). Dry climatic conditions in the geological past have been linked with the disappearance of *Tsuga* various regions of EA and NA (Lepage, 2003),

such as in Markam, the southeast margin of the Qinghai–Tibetan Plateau (Wu et al., 2020); Xianfeng Basin, central Yunnan Wang et al. (2015); Hokkaido, Japan (Tsukada, 1985); and interior Alaska, WNA (Ager et al., 1994). Specifically, in EA, *Tsuga* needs high levels of precipitation for survival, especially in summer (Yang et al., 2009; Tsuyama et al., 2014; Ni et al., 2019). In NA, the *Tsuga* distribution area needs high annual and winter precipitation. Research has found that 90 % of the *Tsuga* population in NA is distributed in areas where the annual precipitation exceeds 800 mm (Thompson et al., 1999). Increased precipitation in the geological past has expanded the distribution range of *Tsuga* (Calcote, 2003; Williams et al., 2004; Munoz et al., 2010). Adequate water availability in winter is crucial for the seed germination and seedling growth of *Tsuga* (Godman and Lancaster, 1990; Means, 1990), and drought conditions can lead to seed mortality (Berntsen, 1958). Our research showed that *Tsuga* had distinctive seasonal precipitation demands in different regions.

Furthermore, the survival of *Tsuga* was strongly influenced by winter and summer temperatures (Fig. 3, Fig. S12). The annual temperature range and precipitation seasonality impacted the survival and distribution of *Tsuga* in EA and ENA (Fig. 3, Fig. S12). Previous studies have indicated that vernalization, a process requiring exposure to cold temperatures, is necessary for seed germination of *Tsuga* spp. (Vasiliauskas, 1996). In EA, *Tsuga* are naturally distributed in the monsoon region (Yang et al., 2009). It is sensitive to winter and annual temperature ranges (An et al., 2011). In NA, *Tsuga* growth necessitates approximately 10 weeks of vernalization at temperatures slightly below or around the freezing point to achieve the highest germination rate (Godman and Lancaster, 1990). In its natural distribution range, the average temperature is -8 °C in January, while it reaches 21 °C in July (Oswald and Foster, 2012). A decrease in average January temperatures leads to a contraction in the distribution range of *Tsuga* (Calcote, 2003), while warm and humid summers facilitate its expansion (Graumlich et al., 1989; Whitlock and Bartlein, 1997). This study further confirmed that winter temperatures are conducive to *Tsuga* survival and that summer and annual temperatures also impact *Tsuga* distribution.

4.2. The extinction of Tsuga in Europe

This study conducted simulations of the current distribution of *Tsuga* in EA, ENA, and WNA, revealing potential regions of *Tsuga* in Europe. Wagner et al.(2017) and Fanal et al.(2021) suggested that *Tsuga*, particularly *T. heterophylla*, has been extensively planted in Europe as an alien species. This indicates that the current climate in Europe may be suitable for the survival of *Tsuga*. The disappearance of *Tsuga* in Europe may have been related to summer precipitation and winter temperature declines during the extremely cold period (440 ka and the LGM).

The potential distribution area of *Tsuga* in the past is aligned with previous palynology research records (Bertini, 2010; Corrado and Magri, 2011; Santangelo et al., 2012; Magri et al., 2017). This alignment suggests that the climate adaptation mechanism of *Tsuga* in Europe may have been similar to that in EA. Arid climatic conditions affected the survival and distribution of *Tsuga*, leading to its disappearance in central Italy in the early Brunon period (700 ka, Bertini, 2000). Summer drought in particular has had a significant impact on the survival of *Tsuga* in Italy (Ravazzi et al., 2005). In addition, the extinction of *Tsuga* in Europe was related to continuous cooling in the early Miocene and rapid and severe cooling during the Pleistocene, forming a fragmented distribution in EA and NA (Farjon and Filer, 2013). The fossil evidence, particularly the Oligocene fossils *T. moenana* Kirchheimer and *T. plicata* (Geinitz) Mai reported in Germany, exhibits strong morphological similarities to the extant Chinese *Tsuga* species *T. chinensis* and *T. dumosa* (Mai and Walther, 1991, 1978). This morphological similarity suggests that *Tsuga* in Europe may have similar climatic requirements to *Tsuga* in EA. Therefore, summer precipitation and winter temperature decline during the extremely cold periods (440 ka and the LGM) may have led to *Tsuga* disappearance in Europe.

This study utilized species distribution modeling, and pollen data provided important results regarding the factors contributing to the disappearance of *Tsuga*. Future research should incorporate fossil morphology data, molecular phylogeny, and physiological experiments to further explore the factors contributing to its disappearance from Europe during the Quaternary.

4.3. Distribution changes of potential suitable Tsuga regions during the past

The results of this study indicated that most of the distribution region of *Tsuga* expanded to lower elevations and latitudes during warm to cold periods due to decreased winter temperatures (Fig. S13a1–d1, a3–d4). Similar cold expansion patterns have also been found in other taxa of Pinaceae. *Pinus armandii* Franch. (Huang et al., 2023), temperate coniferous forests, are one example (Dakhil et al., 2019), *Picea likiangensis* (Franch) Pritz, *P. purpurea* Mast. and *P. wilsonii* Mast. (Zhang et al., 2018). Climate deterioration led to an increase in the percentage of *Tsuga* pollen during the last glacial period (28.3–17.6 ka, Chen et al., 2017). The contracting regions have mainly been located in high latitude and elevation regions, characterized by reduced summer precipitation and extreme decreases in winter temperature (Fig. S13a1–d1, a3–d4). *Tsuga* pollen existed in the Korean Peninsula until the middle Pleistocene, and none existed in the Holocene (Kong, 2000). The disappearance of *Tsuga* in the Korean Peninsula may caused by decreases in winter temperatures (Fig. S13c1, c3–c4). Tsuyama et al. (2014) suggested that *T. seiboldii* is distributed in temperate regions with warm climates, while *T. diversifolia* is distributed in colder winter temperature regions, and the increase in summer drought before or during the LGM in the Quaternary glacial periods caused the extinction of *T. diversifolia* on Hokkaido Island. That is why the *Tsuga* distribution pattern differs between northern and southern Japan, and the reduction in summer precipitation caused *Tsuga* to disappear in part of Japan. During the transition from a relatively cold climate to a warm climate, the potentially suitable area of *Tsuga* in the lower latitudes also contracted (Fig. S13a2–d2, a5–d6). This study found that *Tsuga* in EA had different response dynamics to climate change during glacial and interglacial periods at different latitudes.

In ENA, the distribution area of *Tsuga* shifted to lower latitudes and elevations from warm to cold periods due to precipitation and temperature decreases (Fig. S14a1–d1, a3–d4). This finding was in agreement with the observations of Prentice et al. (1991) and Williams (2009) who proposed that the potential distribution of *Tsuga* was limited to the southern Appalachian Mountains in the LGM. Conversely, during the transition from a relatively cold period to a warm period, accompanied by increases in precipitation and temperature, *Tsuga* expanded towards high latitudes (Fig. S14a2–d2, a5–d6). This phenomenon has also been confirmed by pollen research; for example, Davis et al. (1986) demonstrated the rapid expansion of *Tsuga* in the eastern half of upper Michigan at approximately 6–5.5 ka, Jacobson et al. (1987) described expansion routes to the northeast, north, and west, and Prentice et al. (1991) suggested that *Tsuga* expanded in response to rising winter and summer temperatures and increasing precipitation. Compared with previous studies, this study represented the distribution pattern of *Tsuga* and the corresponding relationship with important climate changes, revealed Quaternary climate change caused the migration of *Tsuga* in the latitudes and elevation distribution pattern.

In WNA, *Tsuga* exhibited a similar movement pattern to ENA, transitioning from warm to cold periods and corresponding with decreased winter precipitation and temperatures to move to higher latitudes (Fig. S15a1–d1, a3–d4). For example, *Tsuga* in WNA contracted towards lower latitudes during the LGM (Williams, 2009). Gedalof and Smith (2001) found that *T. mertensiana* is sensitive to summer temperatures in WNA, while it is susceptible to winter precipitation in southern Alaska. Our results showed that in addition to summer temperatures and winter precipitation, winter temperatures also impacted *Tsuga* distribution

pattern in WNA. When the climate changed from cold to warm, *Tsuga*expanded and migrated to higher latitudes (Fig. S15a2–d2, a5–d5). The warm climate promoted the northward migration of *Tsuga* during postglacial periods, and humid and cool climate conditions further promoted the expansion of *Tsuga* (Rosenberg et al., 2003). Brown (2000) and Lacourse (2012) also stated that the expansion of *Tsuga* were driven by a humid climate environment. This study revealed that the distribution dynamics of *Tsuga* in the WNA were mainly driven by changes in winter precipitation during glacial and interglacial periods, followed by changes in winter and summer temperatures.

4.4. Potential distribution in the future and conservation advice

The results of this study indicated that a projected shift in the potentially suitable area for *Tsuga* towards higher latitudes and elevations in the future, with contraction in EA and NA (Fig. S16–S18). This study corroborate previous findings suggesting that *T. canadensis* is expected to expand towards higher latitudes in the northwest region (Dunckel et al., 2017), and *T. mertensiana* is expected to decrease and migrate to higher elevations (Means, 1990). More importantly, our research predicted the distribution pattern based on the responses of different taxa distributed in different regions, providing valuable guidance for future *Tsuga* conservation efforts. Tsuyama et al. (2014) suggested that *T. diversifolia* extinct in Hokkaido in Japan during a certain ice age in the Pleistocene, but was unable to migrate back to Hokkadio Island when the climate was suitable due to the barrier of lowlands and the Tsugaru Straight.

Based on the findings presented above, it is imperative to implement relevant actions to protect *Tsuga* populations in their natural habitats. The study proposes the following strategies:

1) Focused monitoring and reserve adjustments: Give special attention on monitoring the natural growth status of *Tsuga* populations in southwestern China, around the Himalaya, and southern Japan in EA; the southwest Appalachian Mountains in ENA; the Coast Mountains and Rocky Mountains in WNA; and adjust nature reserves or protected regions to better protect *Tsuga* populations.

2) Customized conservation approaches: In areas where the potential distribution of *Tsuga* is threatened, consider implementing *ex-situ* conservation measures. In regions where *Tsuga* populations are expected to increase, explore options for artificial introduction and cultivation. For stable regions, prioritize an *in-situ* conservation strategy, designating these areas as refuges for *Tsuga* and intensifying protective efforts.

3) Prioritizing preservation and mitigation: It is crucial to prioritize assessing the impacts of precipitation changes on the distribution of *Tsuga*. This may contribute to decisions on conservation strategies and help to mitigate potential threats to *Tsuga* populations. Implementing these strategies could contribute to the preservation and safeguarding of *Tsuga* populations, ensuring their long–term survival under changing environmental conditions.

5. Conclusions

This study employed climate data and modern distribution data for *Tsuga* to assess the present, past, and future potential distribution regions of the species in EA, ENA, and WNA. The findings highlighted the significant influence of precipitation as well as temperature on the survival and distribution of *Tsuga*. More importantly, our research shows that the seasonal precipitation demand of *Tsuga* varies in different regions. In EA, summer precipitation and winter temperatures exhibited a strong impact on *Tsuga* distribution, while winter precipitation, annual precipitation, and winter temperatures played key roles in NA, ENA, and WNA, respectively. Our result indicated that the decreases in summer precipitation and winter temperatures may have led to the extinction of *Tsuga* in Europe. In EA, the potentially suitable area for *Tsuga* was larger during relatively cold periods. In NA, the potentially suitable area expanded during relatively warm periods. Under future climate scenarios, the overall distribution area of *Tsuga* is projected to significantly decrease in EA and NA. These findings emphasize the importance of considering precipitation changes in future conservation efforts for *Tsuga* populations. It is crucial to vigilantly monitor and protect *Tsuga* populations in EA and NA. We propose strategies for *ex-situ* protection, artificial introduction, and *in-situ* cultivation protection tailored to potential distribution areas with varying changes. Through simulating the historical distribution patterns of *Tsuga*, our research reveals the possible reasons for the disappearance patterns of *Tsuga* in Europe and the Korean Peninsula. Furthermore, we suggest that the disappearance time of *Tsuga* in the Korean Peninsula may occurred in LGM. However, it's worth acknowledging that our study has certain constraints. We concentrated primary on the implications of climate change for species distribution and offer pertinent recommendations. The potential effects of human activities, including alterations in land use, logging, and natural events such as wildfires, could exert effect on the persistence and distribution of *Tsuga*. Despite these constraints, our results underscore that climate remains the predominant factor influencing the distribution of *Tsuga*, as evident from our findings. Further research on integrating climate data, distribution models, and conservation strategies is crucial for effectively protecting *Tsuga* populations and helping them better respond to climate change.

CRediT authorship contribution statement

Shumei Xiao: Conceptualization, Data curation, Formal analysis, Methodology, Software, Supervision, Writing – original draft, Writing – review & editing. **Shufeng Li:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Jian Huang:** Conceptualization, Writing – review & editing. **Xiaojun Wang:** Conceptualization, Writing – review & editing. **Mengxiao Wu:** Conceptualization, Writing – review & editing. **Rizwan Karim:** Writing – review & editing. **Weiyudong Deng:** Data curation, Writing – review & editing. **Tao Su:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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

Share data at appendix

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Appendix A. Supplementary data

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