

How a fungal order *Hymenochaetales* diversified in China inferred from its spatiotemporal pattern

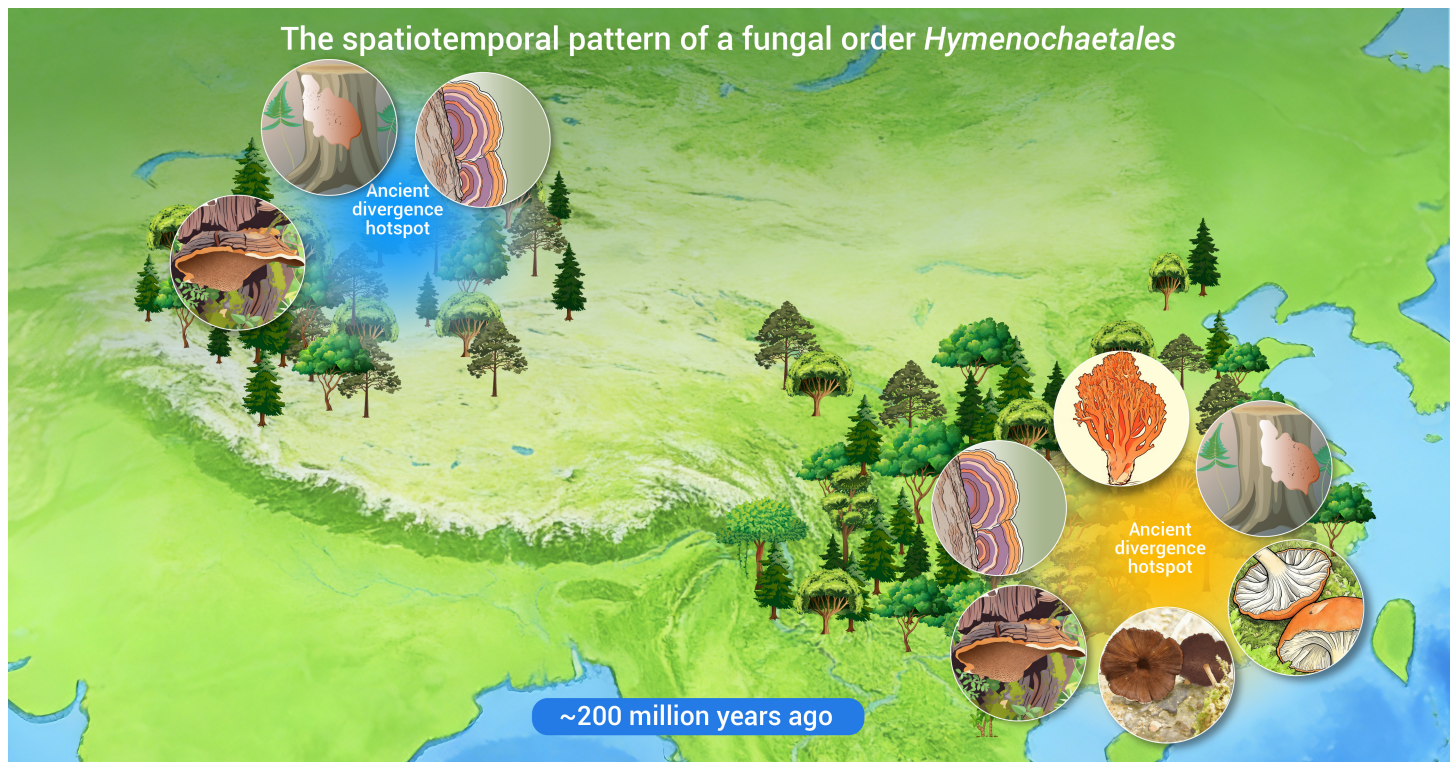
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- The diversity indices of *Hymenochaetales* were generally higher in southern China with lower latitudes.
- The lineages in highly suitable habitats concentrated in the central to southern China were oldest.
- The Chinese ancestor was evaluated to originate 201.63 million years ago.
- The two ancient divergence hotspots of *Hymenochaetales* underwent different diversification scenarios.
- The differentiated diversification scenarios were correlated with local temperature and host plant density.

How a fungal order *Hymenochaetales* diversified in China inferred from its spatiotemporal pattern

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Spatiotemporal pattern of biodiversity is an indicator of evolutionary history, and provides crucial information for recognizing evolutionary process of life on the Earth over time and space. Here, we for the first time comprehensively analyze macrofungal spatiotemporal pattern in China at the order level taking *Hymenochaetales* as the exemplar. A total of 3950 occurrence records from all 490 known species in China are included, and the results indicate that species richness, weighted species endemism, phylogenetic diversity and phylogenetic endemism of *Hymenochaetales* were generally higher in southern China with lower latitudes. Accordingly, the predicted current highly suitable habitats for *Hymenochaetales* concentrated in the central to southern China, where the lineages of *Hymenochaetales* were older than those in habitats with other suitability levels. The Chinese ancestor of *Hymenochaetales* was evaluated to originate 201.63 million years ago with two ancient divergence hotspots. Since the origination, *Hymenochaetales* in southeastern China intensively diversified, while the other ancient divergence hotspot near Tianshan Mountains in the northwest of northwestern China underwent much less diversification. The differentiated fate of *Hymenochaetales* between these two ancient divergence hotspots was correlated with local temperature and host plant density. In summary, the current study revealed the diversification scenario of *Hymenochaetales* in China, and provided a leading demonstration for macrofungal macroevolution.

INTRODUCTION

Biodiversity is the biotic part of ecosystem and also plays a pivotal role in sustaining the balance and stability of ecosystem. The recognition of biodiversity and their composition is crucial for conservation and utilization of bioresources. Species composition within a region results from a series of historical processes, including speciation, extinction, migration, and ongoing ecological interactions.¹ All of these historical process contributes to spatiotemporal patterns of biodiversity, and the extent of contribution by each historical process depends mainly on various natural ecological landscape and also on human landscape. Therefore, biodiversity can be considered to be irreplaceable strategic biological resource on the national scale.² This opinion is also recognized by the Nagoya Protocol.

Currently, biodiversity, evolutionary history and spatiotemporal patterns of various animal and plant groups have been widely recognized on different regional scales. For example, Lu et al.³ comprehensively analyzed the spatiotemporal patterns and evolutionary history of angiosperms in China. The results indicated that eastern China serves as a museum and western China acts as a cradle for herbaceous plants, while for woody plants eastern China serves as both museum and cradle.³ Via a combination of phylogenomic and ecological analyses, Jin et al.⁴ revealed the spatiotemporal patterns of *Pinus* species all over the world, which showed that mid-latitude regions serve as a museum for *Pinus* and topography plays a crucial role in the diversification process. In terms of insects, Fan et al.⁵ discovered that southeastern and southwestern China are the museums, while northwestern China serves as a cradle. Xu et al.⁶ identified ten biodiversity hotspots for amphibians in China with six new hotspots located in the southeastern mountainous regions, and most of them are threatened by human activities. Furthermore, the evolutionary histories of different organisms shaping their spatiotemporal patterns within certain regions may be influenced by their niche specialization and shifts. For instance, it has been found that temperature drives lizard diversification,⁷ while the evolution of angiosperms in China

correlates with the amount of annual precipitation.³ Therefore, current spatiotemporal patterns and corresponding evolutionary theories predominantly derived from animal and plant groups cannot be directly applied to other life forms. In this case, to comprehensively recognize the diversification scenarios of life on the Earth, it is time to reveal spatiotemporal patterns of various biological groups, including macrofungi that occupy a significant proportion of biodiversity.

Previous research preliminarily resolved the spatiotemporal pattern of the macrofungal genus *Phylloporia* in *Hymenochaetales* and accordingly inferred its evolutionary process in China.⁸ This is the first attempt for macrofungi; however, from the relatively small taxonomic scale and corresponding limited data, the concluded pattern needs to be tested by more comprehensive macrofungal occurrence records, like the entire order of *Hymenochaetales*. *Hymenochaetales* is one of the fungal orders being mainly composed of wood-inhabiting macrofungi within *Agaricomycetes*, *Basidiomycota*.⁹ Species in *Hymenochaetales* could be found on a wide range of substrates, habitats and ecological conditions in forest ecosystems.⁹⁻¹⁵ Therefore, the evolutionary process of this macrofungal order is supposed to be related to their host plants. Many species in this order are economically important with pharmacologically relevant fungi from the genera *Sanghuangporus* and *Phylloporia* as representatives.¹⁶⁻¹⁹ In addition, *Hymenochaetales* includes many notorious forest pathogens, especially those from the genera *Coniferiporia*.²⁰⁻²² Therefore, the species diversity of *Hymenochaetales* has been extremely explored with enthusiasm,²² and accordingly the taxonomic framework of the entire order has been clarified.^{9,23} In brief, 15 families, containing 84 genera and ca. 1500 species, are accepted in *Hymenochaetales*.^{9,23} Apart from high species diversity, the morpho-ecological traits of species in this macrofungal order are also various. The evolutionary history of these biological traits has been recently explored in association with environmental factors, which indicated that the divergence of parasitic species, the expansion of host plants and the increase of paleotemperature may drive the diversification of *Hymenochaetales*.²⁴ Moreover, the geographical distribution of *Hymenochaetales* in China has been documented in detail, typically represented by two volumes of *Flora fungorum sinicorum*.²⁵⁻²⁶ Given above, *Hymenochaetales* is an ideal exemplar of exploring fungal diversification process from the perspective of spatiotemporal patterns.

In this study, the diversity and geographical distribution of *Hymenochaetales* in China are first explored. Accordingly, the spatiotemporal pattern of this fungal order is inferred. In association with bioclimatic variables, the diversification process of *Hymenochaetales* in China is eventually concluded.

MATERIALS AND METHODS

Distribution and occurrence records of *Hymenochaetales*

The geographical distribution in China of known species in *Hymenochaetales* was mainly collected from the “*Flora fungorum sinicorum*—volumes 29 & 57”.²⁵⁻²⁶ Meanwhile, the occurrence records from the articles officially published in the past 15 years were supplemented.²⁷⁻³⁰ The unpublished fungarium records were not included due to the potential unreliability of species identification. It is reasonable to postulate that some undescribed species and also certain geographical distribution of known species were omitted here. However, we may never completely recognize any fungal group at the current annual rate of species description.³¹ Moreover, as an important macrofungal order, *Hymenochaetales* has received wide and intensive attentions from the perspective of species diversity all over the

world,^{22,32–35} which results in a large amount of solid distribution data in China for the spatiotemporal pattern analysis.

The map of China was divided into 100 km × 100 km grid cells to minimize the sampling bias of unequal sampling areas, and grid cells on the border that cover less than 50% of the area of a grid cell (that is, 5000 km²) were excluded. Map of China used in this study was adapted from the standard map released by the National Administration of Surveying, Mapping and Geoinformation of China (<http://bzdt.ch.mnr.gov.cn/>; review drawing number: GS(2019)1822). If no accurate coordinate is available for a fungal occurrence record from its collection information, its distribution data will be accurate down to the county with an average area of approximately 4000 km². The coordinate of each fungal occurrence record is represented by the center point of the county, where the species is located. Regarding the occurrence record in a specific nature reserve or scenic spot, its coordinate will be represented by the center point of the corresponding location.

Phylogeny reconstruction

A total of 17 species in *Hymenochaetales* and 14 species from other orders within *Basidiomycota* as ingroup taxa, and *Neurospora crassa* and *Sordaria humana* from *Ascomycota* as outgroup taxa were included to construct a phylogenomic backbone tree. Their whole genome sequences were downloaded from JGI-Mycocosm (<https://mycocosm.jgi.doe.gov/mycocosm/home>; accessed on October 22, 2024) and NCBI (<https://www.ncbi.nlm.nih.gov/datasets/genome/>; accessed on October 22, 2024) databases (Table S1). From these whole genomes, single-copy orthologous genes were searched using OrthoFinder v.2.5.4,^{36–37} and the resulting orthologous gene sequences were aligned using MAFFT v.7.110.³⁸ The best-fit substitution model of this alignment was evaluated using ModelTest-NG v.0.2.0 with default settings.³⁹ Accordingly, the phylogenomic tree was constructed using RAXML v.8.2.12.⁴⁰ Bootstrap support values were calculated based on 1000 bootstrap replicates to assess the reliability of tree topology.

Three nuclear regions (nSSU, ITS and nLSU), one mitochondrial region (mtSSU) and three ribosomal regions (*tef1a*, *rpb1* and *rpb2*) were used to construct the multilocus phylogeny of *Hymenochaetales*. All available sequences of these DNA regions were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; accessed on November 12, 2024; Table S2). These sequences were simultaneously used to represent one species only when they were generated from a single individual. Besides taxa belonging to *Hymenochaetales*, the representative taxa from other orders within *Basidiomycota* were also selected as additional ingroup taxa, while *Neurospora crassa* and *Sordaria humana* from *Ascomycota* were selected as outgroup taxa following Wang et al.^{9,14} Each of the seven regions was separately aligned using MAFFT v.7.110 under the “G-INS-i” option.^{38,41} Then, trimAl v.1.5.rev0 was used to trim the uneven 5' and 3' terminal ends of each alignment under the default parameters.⁴² SequenceMatrix v.1.8 was used to concatenate all separate alignments in the order of nSSU, ITS, nLSU, mtSSU, *tef1a*, *rpb1* and *rpb2*.⁴³ The best-fit evolutionary model of the concatenated alignment for maximum likelihood (ML) phylogenetic analysis was estimated using jModelTest v.2.1.10 under the Akaike information criterion. Following the corresponding model,^{44,45} the ML phylogenetic analysis was performed using raxmlGUI v.2.0 (Edler et al. 2020) with the phylogenomic tree generated above as a backbone. The bootstrap replicate was set to 1000 and the tree with the best score was searched.⁴⁶

Divergence time estimation

To date divergence times of Chinese taxa in *Hymenochaetales*, the penalized likelihood method implemented in treePL v.1.0 was employed,⁴⁷ based on the optimal ML phylogram obtained using raxmlGUI v.8.2.12.⁴⁰ The “prime” option was applied to identify the best optimization parameters, and then, the “thorough” analysis was accordingly carried out with the optimal parameters (opt = 5, optad = 1 and optcvad = 3). To identify the best smoothing parameter that affects the penalty for rate variation over the phylogram, the “random subsample and replicate cross-validation” was conducted using treePL. Four calibrations were chosen for dating analyses, viz. 90 million years ago (Mya) for *Agaricales*, indicated by the minimum age of *Archaeomarasmius leggetti*, a fossil agaricoid species preserved in Dominican amber,^{48,49} 125 Mya for *Hymenochaetales*, indicated by the minimum age of *Quatsinoporites cran-*

hamii, a fossil poroid species collected from Apple Bay on Vancouver Island;^{50,51} 290 Mya for *Agaricomycetes*, indicated by the mean age of *Agaricomycetes* from previous phylogenomic analyses;⁵² and 400 Mya for *Basidiomycota*, indicated by the divergence time between *Ascomycota* and *Basidiomycota* from *Paleopyrenomycites devonicus*, a fossil fungus found in Great Britain.^{53,54}

To avoid the possible inaccurate evolutionary reconstruction from an incompletely sampled phylogeny, a stochastic polytomy resolution method Taxonomic Addition for Complete Trees (TACT) was used to generate the fully sampled phylogeny.⁵⁵ TACT employs birth-death-sampling estimators across an ultrametric phylogeny to estimate branching times for unsequenced taxa with reference to their taxonomic positions, and then compatibly inserts the unsequenced taxa into the above-generated ultrametric tree. In theory, after the insertion, the divergence times at the genus level would be still same, while the divergence times of species in certain grid cells may be a little bit changed. However, in the case that the inserted unsequenced species accounts for less than 10% of all known species of *Hymenochaetales* in China, the impact on the overall divergence times at the species level will be subtle. Therefore, it is reasonable to trade off the tiny inaccuracy for a more comprehensive dataset. That may be one reason why the TACT method has been utilized in exploring evolutionary history and diversifications of various animal and plant groups.^{56–59}

Index of species and phylogenetic diversity

On the basis of a species-level phylogenetic tree and distribution data with ‘county’ as the basic unit, we selected four indices to estimate the diversity of *Hymenochaetales* in China. Species richness is a fundamental measure of biodiversity, and refers to the total number of all taxa located in a grid cell. Weighted species endemism is a biodiversity metric that quantifies the degree to which taxa in a grid cell are spatially restricted.⁶⁰ Unlike simple species endemism that counts the number of taxa unique to a grid cell, weighted species endemism assigns higher weight to taxa distributed in less grid cells.⁶¹ This approach emphasizes the conservation priority of narrowly distributed species, since these species face greater extinction risks due to the limited habitat availability. Phylogenetic diversity quantifies the evolutionary distinctiveness of taxa within a grid cell by analyzing their relationships on a phylogenetic tree, which considers both the number of taxa and their evolutionary divergence represented by phylogenetic branch lengths.^{62–65} Phylogenetic endemism quantifies the evolutionary distinctiveness and geographical restriction of lineages within a grid cell, which integrates evolutionary history represented by phylogenetic branch lengths with the spatial rarity of taxa.⁶⁶ High phylogenetic endemism indicates that grid cells possess taxa with both ancient evolutionary lineages and highly restricted distributions, and thus are critical for conserving unique evolutionary heritage.^{67,68} The above four indices of Chinese species in *Hymenochaetales* were calculated using the R package “phyloregion” based on the time-calibrated phylogeny. All of the index values in grid cells are classified into ten levels using the Jenks’ natural breaks method.

Current potential distribution prediction

According to the existing geographical distribution data, the ensemble model was used to predict the current potential distribution of species in *Hymenochaetales* in China. The specific process is as follows:

(1) To avoid data redundancy of spatial autocorrelation, we used ArcGIS v.10.8 to remove the duplication from the existing geographical distribution of fungal species in *Hymenochaetales*.⁶⁹ If the sampling locations of occurrence records were distributed within 10 km, these records were treated as replications and only one will be saved for subsequent analyses.

(2) A total of 19 climatic indicators and corresponding altitude data at a spatial resolution of 30'' (approximately 1 km²) were downloaded from the WorldClim version 2.1 database (<https://www.worldclim.org/data/worldclim21.html>; accessed on December 15, 2024). The latest version of these environmental variables (during 1970–2000) was selected for distribution prediction. In addition, host plants being considered to have a close relationship with fungi in *Hymenochaetales* were also retrieved from the Global Biodiversity Information Facility (<https://www.gbif.org/occurrence/download/>; accessed on December 15, 2024) as a biotic variable for distribution

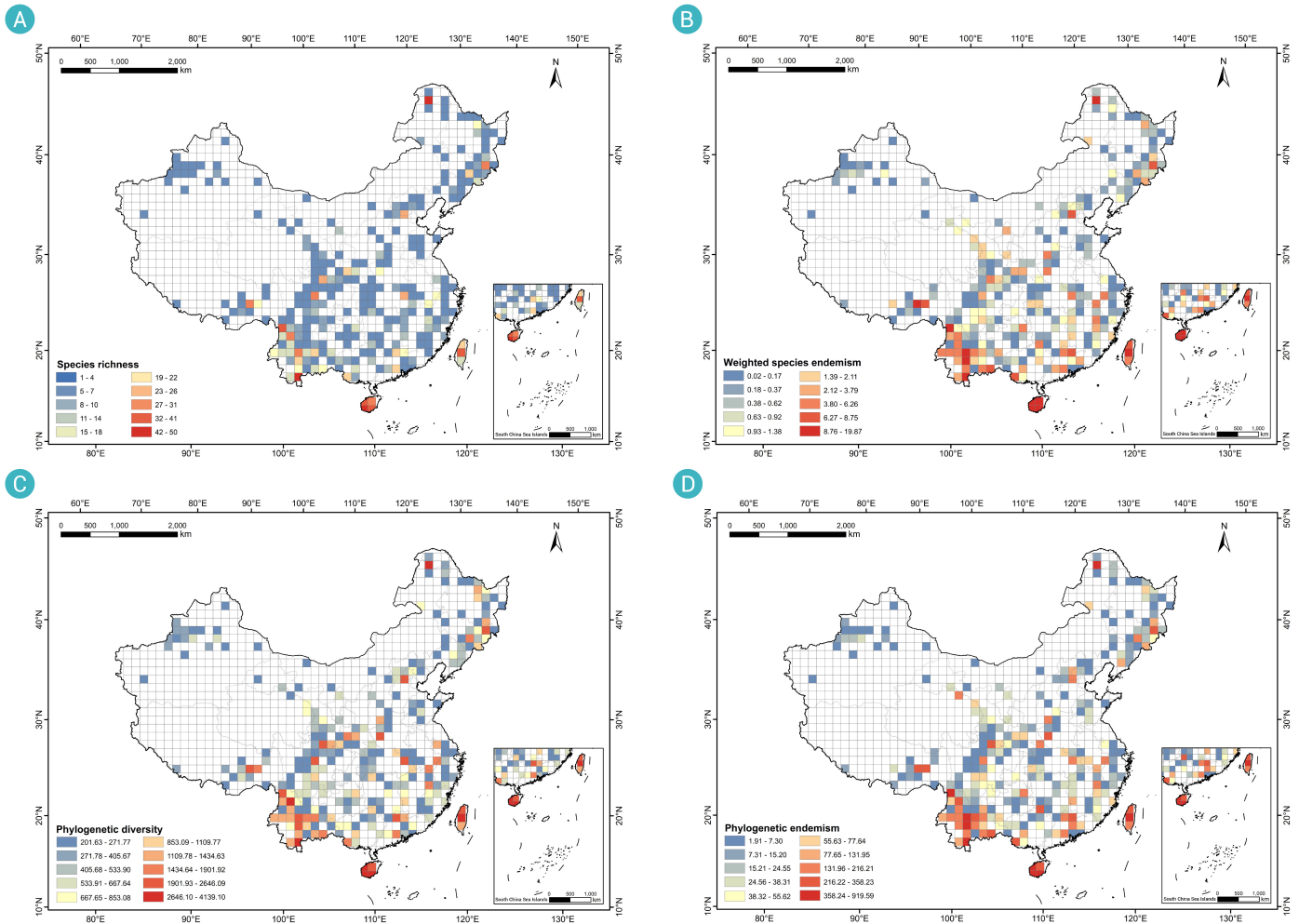


Figure 1. Patterns of species richness (A), weighted species endemism (B), phylogenetic diversity (C) and phylogenetic endemism (D) for *Hymenochaetales* in China The colors ranging from blue to red represents the values of these four diversity indices from low to high. Maps were adapted from the standard map released by the National Administration of Surveying, Mapping and Geoinformation of China (<http://bzdt.ch.mnr.gov.cn/>; review drawing number: GS(2019)1822).

prediction. The number of host plants on each coordinate was converted to raster data by ArcGIS v.10.8 at a spatial resolution of 30'' (approximately 1 km²).⁶⁹ Three categories of host plants, viz. woody angiosperms, gymnosperms, and both of them were delimited.

(3) Previous studies indicated that various bioclimatic variables may be multicollinearity.^{70,71} Therefore, to avoid over-fitting induced by the multicollinearity of variables, Pearson's correlation coefficient (r) analysis was performed to determine the correlation between primary variables using ENMTools v.5.26.⁷² When $|r| > 0.8$, two variables were considered to be auto-correlated, and then only one variable was randomly retained for further analyses (Figure S1).

(4) Ensemble model was selected to conduct the distribution prediction with four different algorithms,^{73,74} viz. Generalized additive model,⁷⁵ Generalized boosted model,⁷⁶ Generalized linear model and Random forests.^{77,78} All model-building processes were conducted by the R package biomod2 v.4.2.5. We first used random sampling methods to generate 3000 pseudo-absence data points for the entire research area. This process was repeated three times to reduce the uncertainty caused by random sampling. Secondly, each of the four algorithms was tuned by the function "bm_ModelingOptions". Thirdly, the four algorithms were evaluated and built separately by the function "BIOMOD_Modeling". A total of 75% of the filtered occurrence records were randomly selected for model calibration, while the remaining 25% for model testing with ten replications to reduce the uncertainty. A total of 120 models generated from the four algorithms, three-time replications of pseudo-absence data points and ten cross-validation runs were built. Moreover, the

accuracy of each model was evaluated separately using the values of the Area Under the receiver operator characteristic Curve (AUC) and the True Skill Statistic (TSS).^{73,79} The model will be considered to perform well, when the AUC value is higher than 0.8 and the TSS value is not lower than 0.7. Fourthly, to mix all 120 models, the ensemble model was performed by the function "BIOMOD_EnsembleModeling" using Committee Averaging (CA) and Weighted Mean (WM) methods, and each method was evaluated by both AUC and TSS values. Finally, the ensemble model was projected by the function "BIOMOD_EnsembleForecasting", which produced the raster map of distribution probability. Jenks' natural breaks method was used to divide the potential habitat into four levels following Zhao et al.⁸⁰

Spatial distribution of divergence times

To explore the spatiotemporal pattern of *Hymenochaetales* in China, the weighted mean divergence times (MDTs) of all genera and all species in each grid cell were separately calculated by integrating spatial distribution data with the dated phylogenetic tree. To verify the results from MDTs, the spatial distribution data of *Hymenochaetales* in China was also integrated with the median divergence times (MedianDTs). In addition, to identify ancient and recent divergence hotspots for *Hymenochaetales* in China, a null model test was also implemented. R program and ArcGIS v.10.8 were used to perform the above analyses following the methods of Lu et al.³ All of the divergence times in grid cells were classified into ten levels by the Jenks' natural breaks method.

To compare the MDTs of *Hymenochaetales* among various parts of China, we divided grid cells into four groups separately using two different strategies.

Table 1. Variables used for predicting the current potential distribution of *Hymenochaetales* in China and their importance scores to the ensemble model.

Variable	Description	Unit	Score
Bio1	Annual mean temperature	°C	–
Bio2	Mean diurnal temperature range	°C	0.094
Bio3	Isothermality (Bio2/Bio7) (×100)	%	–
Bio4	Temperature seasonality (standard deviation ×100)	°C	0.504
Bio5	Max temperature of the warmest month	°C	–
Bio6	Min temperature of the coldest month	°C	0.172
Bio7	Annual temperature range (Bio5–Bio6)	°C	–
Bio8	Mean temperature of the wettest quarter	°C	–
Bio9	Mean temperature of the driest quarter	°C	–
Bio10	Mean temperature of the warmest quarter	°C	–
Bio11	Mean temperature of the coldest quarter	°C	–
Bio12	Annual precipitation	mm	–
Bio13	Precipitation of the wettest month	mm	–
Bio14	Precipitation of the driest month	mm	–
Bio15	Precipitation seasonality (coefficient of variation)	%	–
Bio16	Precipitation of the wettest quarter	mm	–
Bio17	Precipitation of the driest quarter	mm	–
Bio18	Precipitation of the warmest quarter	mm	0.396
Bio19	Precipitation of the coldest quarter	mm	0.618
Altitude	Altitude	m	–
Host plant	Host plant	tree/km ²	–

The dash (–) means that the environmental variable is not included for modeling the geographic distribution due to auto correlation.

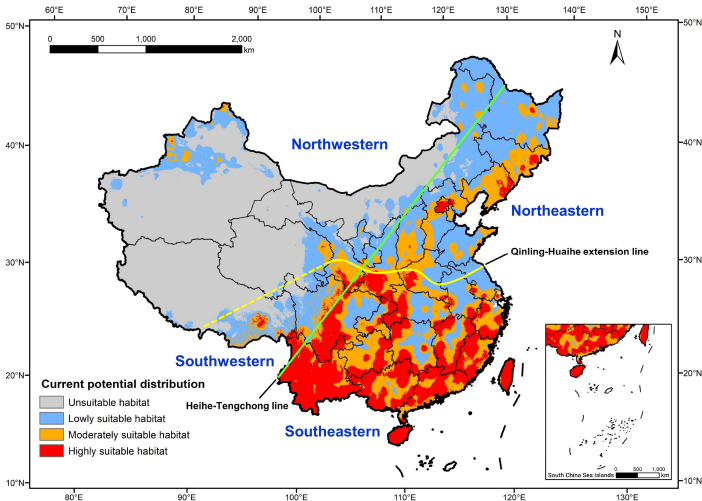


Figure 2. The current potential distribution of *Hymenochaetales* in China predicted by the ensemble model The map of China is separately divided into four groups by two strategies. The first strategy includes northeastern, southeastern, southwestern and northwestern groups according to Heihe–Tengchong line (green in color) and Qinling–Huaihe extension line (yellow in color), while the second strategy follows the four different suitable habitats (filled with four different colors). The map was adapted from the standard map released by the National Administration of Surveying, Mapping and Geoinformation of China (<http://bzdt.ch.mnr.gov.cn/>; review drawing number: GS(2019)1822).

The first strategy divided grid cells according to two geographical demarcation lines, viz. Heihe–Tengchong line dividing China into eastern and western parts, and Qinling–Huaihe extension line dividing China into southern and

northern parts. Taken together, northeastern, southeastern, southwestern and northwestern parts were delimited. The other strategy followed four different potential habitats, viz. unsuitable habitat, lowly suitable habitat, moderately suitable habitat, and highly suitable habitat. The significance of differences in the MDTs between groups were compared using Kruskal–Wallis non-parametric statistical test.⁸¹

Correlation between MDTs and bioclimatic variables

To explore the underlying mechanisms of the spatiotemporal pattern of *Hymenochaetales* in China, the MDTs of all genera and all species in each grid cell were separately regressed against abiotic and biotic variables using the Pearson's linear regression model in R program. The abiotic variables include 19 climatic one altitude variables. The climatic data were downloaded from the WorldClim Version 2.1 database (<https://www.worldclim.org/data/worldclim21.html>; accessed on December 15, 2024) with a spatial resolution of 30''. The biotic variable is represented by the host plant density in each grid cell, which was divided into three groups, viz. woody angiosperms, gymnosperms, and both of them. The distribution of each host plant family was retrieved from Global Biodiversity Information Facility (<https://www.gbif.org/occurrence/download/>; accessed on December 15, 2024) and the duplication was trimmed using the R package ENMtools v.1.1.2.⁷² The adjusted *R*² value was used to indicate the explanatory power of each bioclimatic variable.

RESULTS

Species data compilation

A total of 490 species belonging to 59 genera, 14 families in *Hymenochaetales* are known in China (as of June 13, 2024). For these species, 3950 occurrence data are recorded in China (Figure S2 & Table S3). After filtering out spatial autocorrelation of occurrence data, 607 records were

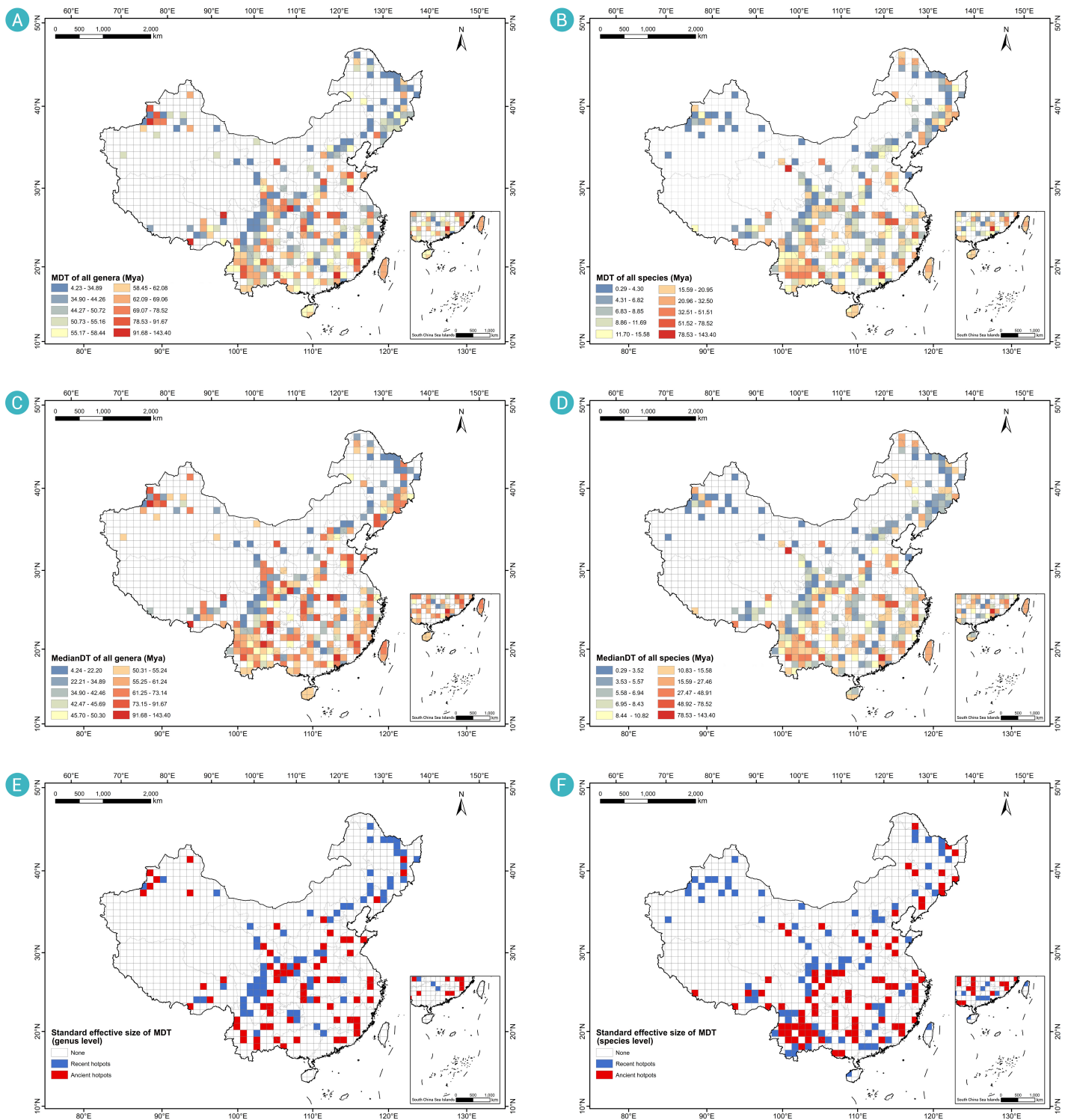


Figure 3. Geographical patterns of the mean divergence times (MDTs; A, B), median divergence times (MedianDTs; C, D), and the null-model test to identify recent (blue in color) and ancient (red in color) divergence hotspots (E, F) The colors ranging from blue to red represents the values of MDTs and MedianDTs from low to high. Maps were adapted from the standard map released by the National Administration of Surveying, Mapping and Geoinformation of China (<http://bzdt.ch.mnr.gov.cn/>; review drawing number: GS(2019)1822).

kept for distribution prediction of species in *Hymenochaetales*.

Phylogenetic relationship and divergence times of *Hymenochaetales*

A total of 292 single-copy orthologous genes were identified from 33 species for phylogenomic analysis. The best-fit substitution model of the alignment resulted from these genes was estimated as "PROTGAMMALGX". The generated phylogenomic topology received full bootstrap supports at all nodes (Figure S3).

The seven-locus dataset included 458 collections and resulted in a concatenated alignment of 9675 characters. Its best-fit evolutionary model for ML algorithm was estimated as "GTRGAMMAI". After 1000 bootstrap replicates, the best-score tree with optimal phylogeny was presented with bootstrap values labeled at the nodes (Figure S4). This phylogeny fully supported the independency of *Hymenochaetales* (BS = 100%), and each accepted family and genus was well resolved also (Figure S4).⁹

Inferred from the optimal ML phylogram, the Chinese ancestor of

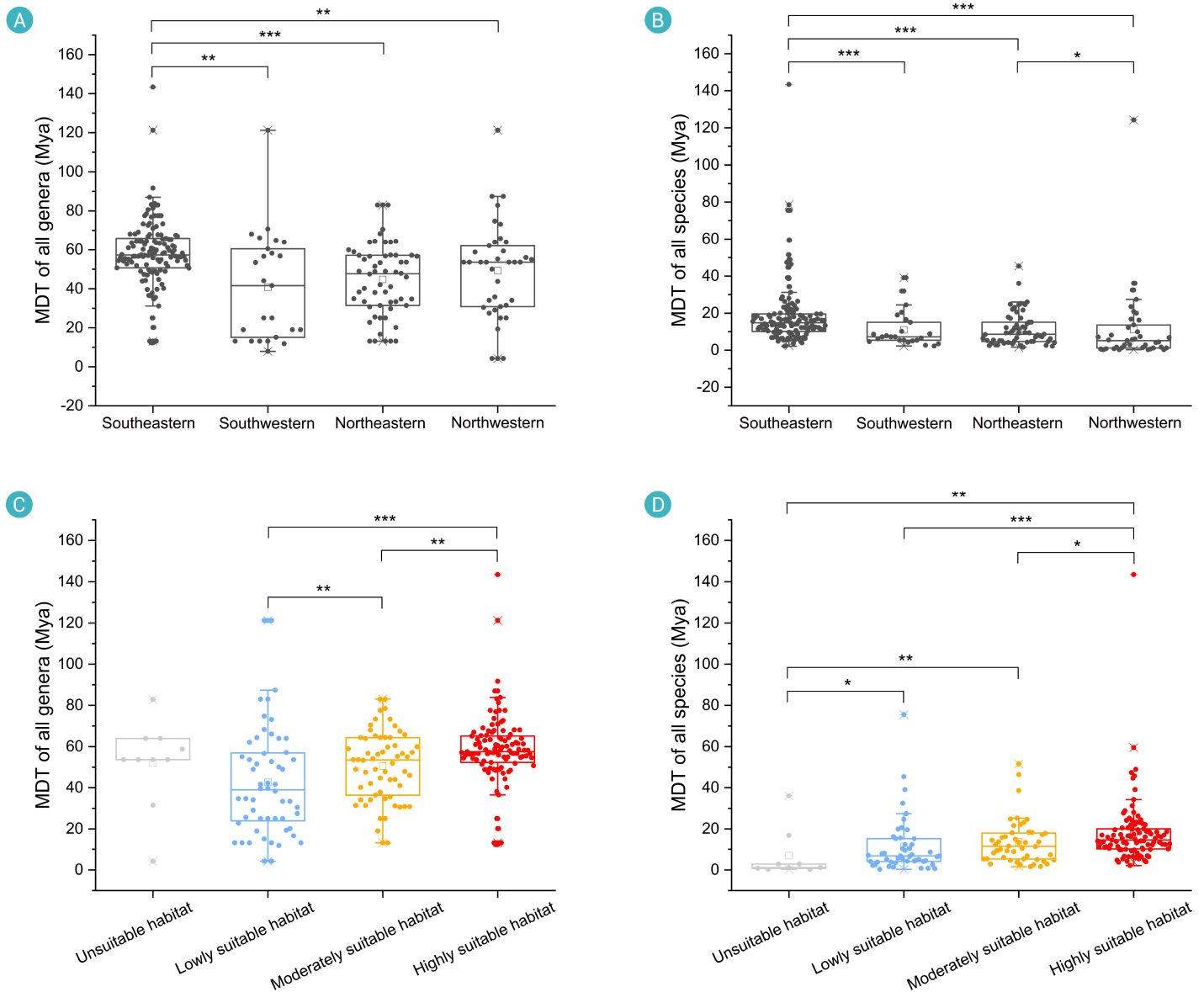


Figure 4. The Kruskal–Wallis non-parametric statistical tests of mean divergence times (MDTs) for four groups separately divided by geographical demarcation lines (A, B) and suitable habitats (C, D). *, ** and *** indicate significant difference at the level of p -value < 0.05, < 0.01 and < 0.001, respectively.

Hymenochaetales was evaluated to originate 201.63 Mya (crown age) with a 95% highest posterior density (HPD) of 183.06–231.14 Mya (Figure S5). Moreover, the divergence times of all Chinese taxa in *Hymenochaetales* were estimated and presented (Figure S5). Furthermore, additional 48 unsequenced Chinese species in *Hymenochaetales* were incorporated into the time-calibrate tree. Eventually, a fully sampled tree with the divergence times of all genera and all species in *Hymenochaetales* distributed in China was generated (Figure S6).

Overview of *Hymenochaetales* diversity

To comprehensively estimate the distribution of *Hymenochaetales* in China, four index values, viz. species richness, weighted species endemism, phylogenetic diversity and phylogenetic endemism were employed. The species richness of *Hymenochaetales* was generally higher in southern China with lower latitudes, where Hainan, Taiwan and Yunnan provinces are distributed (Figure 1A). Similarly, the index values of weighted species endemism, phylogenetic diversity and phylogenetic endemism were also higher in southern China (Figures 1B–D). Therefore, the lower latitude regions in China had the higher overall diversity of *Hymenochaetales*.

Current potential distribution of *Hymenochaetales*

Bio2 (mean diurnal temperature range), Bio4 (temperature seasonality), Bio6 (min temperature of the coldest month), altitude and host plant were estimated to be the crucial bioclimatic variables for the current potential distribution of *Hymenochaetales* in China. Among these variables, host plant, Bio4 and altitude had the highest importance scores of 0.618, 0.504 and 0.396, respectively (Table 1).

In the ensemble model, the average AUC and TSS values of the CA method were 0.943 ± 0.007 and 0.736 ± 0.036 , respectively, while the average AUC and TSS values of the WM method were 0.934 ± 0.010 and 0.712 ± 0.030 , respectively (Figure S7). Therefore, both methods supported the accuracy of the distribution modeling, and the result generated by CA method with higher statistical values is shown (Figure 2). The unsuitable habitat (0–0.18) occupied $384.937 \times 10^4 \text{ km}^2$ (40.02%), while the lowly (0.19–0.38), moderately (0.39–0.60) and highly (0.61–1) suitable habitats occupied $283.564 \times 10^4 \text{ km}^2$ (29.48%), $166.788 \times 10^4 \text{ km}^2$ (17.34%) and $126.593 \times 10^4 \text{ km}^2$ (13.16%), respectively. The highly suitable habitat mainly concentrated in the central to southern China, including Hainan, Taiwan, Guangdong, Guangxi, Fujian, Jiangxi, Zhejiang, Yunnan, Guizhou, Sichuan, Hunan, Hubei, Henan, Gansu and Shaanxi, and was also scattered in Anhui, Jiangsu, Hebei, Liaoning, Jilin,

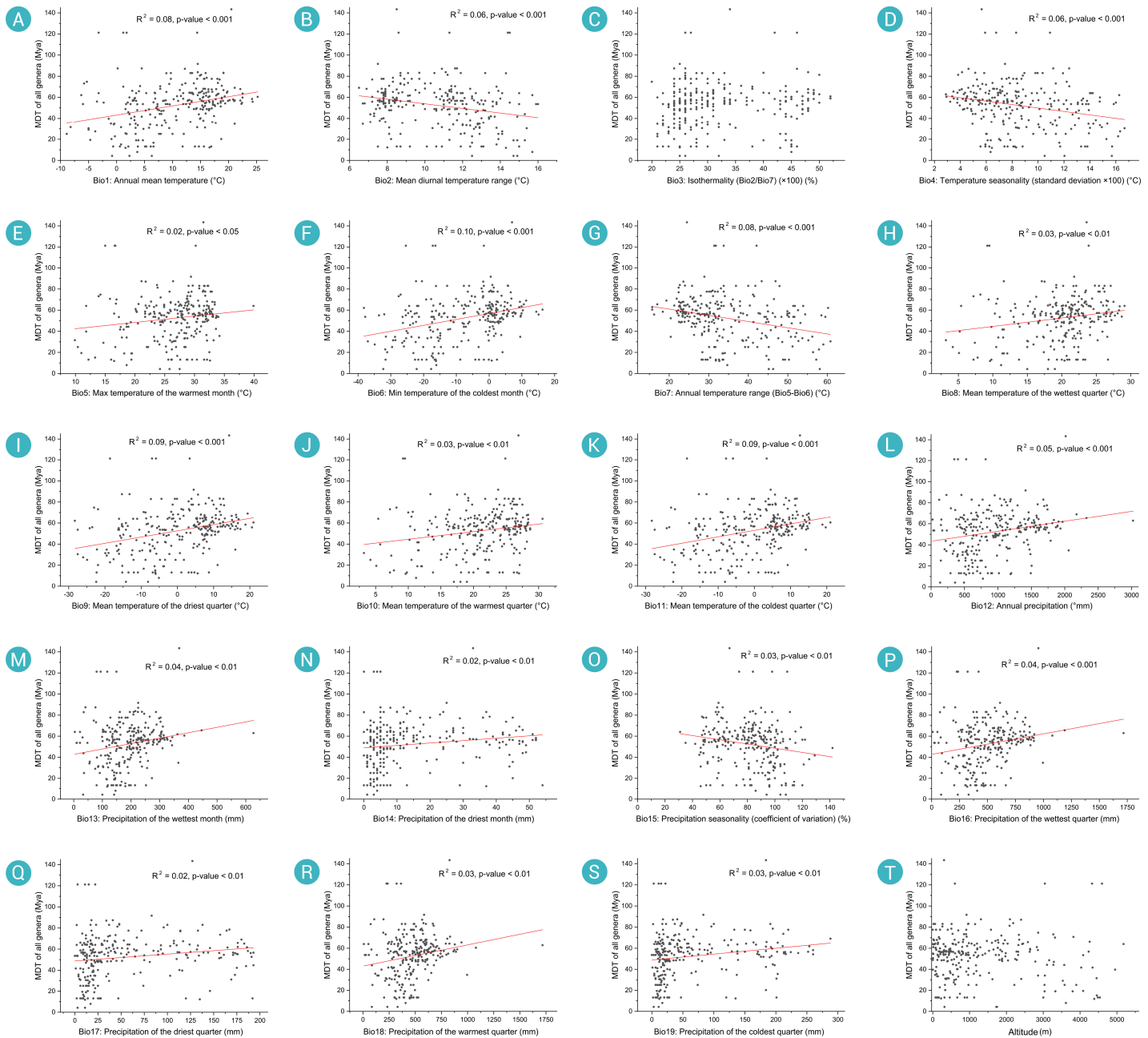


Figure 5. Correlation between 20 abiotic variables and mean divergence times (MDTs) at the genus level.

and a small part of Heilongjiang and Xizang (Figure 2).

Spatiotemporal pattern of *Hymenochaetales*

Via mapping the MDTs of all genera and all species separately to each grid cell of Chinese map, it can be observed that most taxa of *Hymenochaetales* in central to southern China had higher MDTs and MedianDTs (Figures 3A–D). In addition, most taxa at the genus level in northwestern China, that is Xinjiang, also had higher MDTs and MedianDTs, but this pattern cannot be found at the species level (Figures 3A–D). The null-model analysis at the genus level shows that most ancient lineages were distributed in central to southeastern China, while a few ancient lineages had a distribution in northwestern China (red grid cells, Figure 3E). Meanwhile, the null-model analysis at the species level shows that most ancient lineages were distributed in central to southern and also in northeastern China (red grid cells, Figure 3F), while the lineages in northwestern China diverged more recently (blue grid cells, Figure 3F).

Among the four parts divided by two geographical demarcation lines, the Kruskal–Wallis non-parametric statistical test indicates that at the genus

level the taxa of *Hymenochaetales* with the highest MDTs were distributed in southeastern China (p -value < 0.01 compared with southwestern and northwestern China, p -value < 0.001 compared with northeastern China; Figure 4A). Similarly, this pattern was also could be observed at the species level (p -value < 0.001), and moreover, the taxa of *Hymenochaetales* from northeastern China had higher MDTs than those from northwestern China (p -value < 0.05; Figure 4B).

From the suitability perspective, we found that at the genus level the taxa of *Hymenochaetales* in the highly suitable habitat had significantly higher MDTs than those in the lowly suitable (p -value < 0.001) and moderately suitable habitats (p -value < 0.01, Figure 4C), and the taxa in the moderately suitable habitat had significantly higher MDTs than those in the lowly suitable habitat (p -value < 0.01, Figure 4C). Meanwhile, at the species level the taxa in the highly suitable habitat had significantly higher MDTs than those in the unsuitable (p -value < 0.01), lowly suitable (p -value < 0.001) and moderately suitable habitats (p -value < 0.05, Figure 4D); the taxa in the unsuitable habitat had significantly lower MDTs than those in the moderately suitable (p -value < 0.01) and lowly suitable (p -value < 0.05) habitats (Figure 4D).

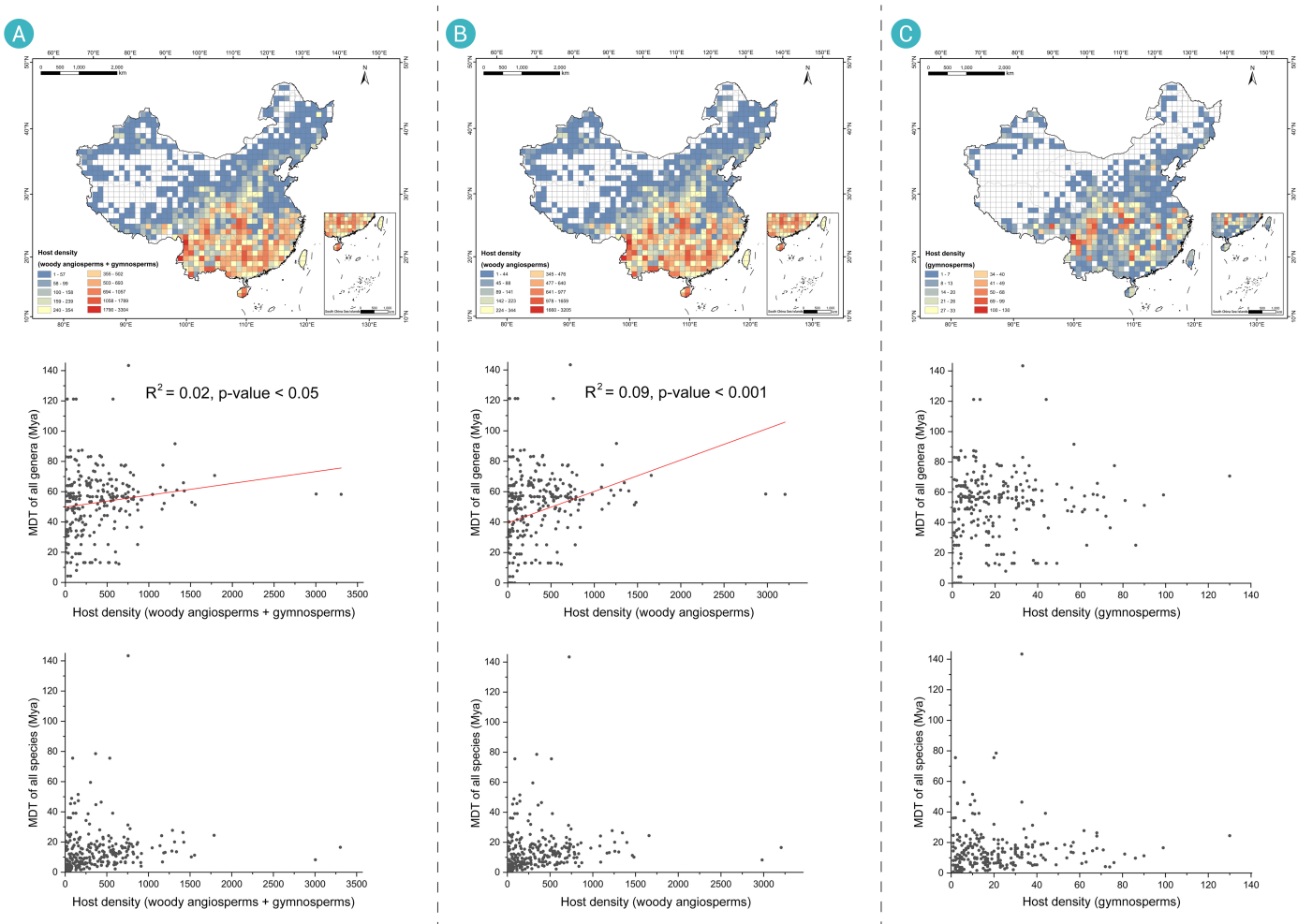


Figure 6. Patterns of host plant density (upper) in China and correlation between host plant density and mean divergence times (MDTs) of all genera (middle) and all species (bottom) (A). woody angiosperm and gymnosperm in together; (B). woody angiosperm; (C). gymnosperm.

Correlation between bioclimatic variables and MDTs

At the genus level, a total of 18 from 20 abiotic variables were significantly correlated with MDTs (Figure 5). The explanatory powers of temperature-related variables were slightly higher than those of precipitation-related variables, although both of them were not high (Figure 5). Comparably, at the species level the explanatory powers of these variables were even lower (Figure S8). In addition, altitude was not correlated with MDTs at both genus and species levels (Figures 5 & S8).

For biotic variable, that is the host plant density, the woody angiosperm and gymnosperm in together (p -value < 0.05), and woody angiosperm solely (p -value < 0.001) had significantly positive correlations with MDTs, while woody gymnosperm solely had no significantly correlation with MDTs at the genus level (Figure 6). Nevertheless, at the species level the host plant density was not significantly correlated with MDTs (Figure 6).

DISCUSSION

The first comprehensive analysis of macrofungal spatiotemporal pattern

Fungi are a group of eukaryotic life forms and have an extremely high expected species diversity (2.2–3.8 million species) with more than 90% unknown.⁸² Of them, those bearing visible fruiting bodies to the naked eyes are macrofungi, or called mushroom-forming fungi.⁸³ Macrofungi have important economic values from the edible, medicinal and biodegradation perspectives.^{84,85} On the other hand, some macrofungi are notorious pathogens of plants and animals, including human beings.⁸⁶ In the case that the recognition of macrofungal diversity is quite insufficient, to pursue advantages and avoid disadvantages, most studies in this field have been focusing on describing new species and accordingly constructing taxonomic framework.^{9,12,24,87–92} Comparably, only a few papers tried to clarify the evolutionary

history of macrofungi on either time scale or geographical distribution,^{93–95} although such works indeed provided helpful information on the conservation and utilization of macrofungal resources. Regarding macrofungal spatiotemporal pattern, to the best of our knowledge, only one preliminary paper, focusing on a small genus within *Hymenochaetales* in China, was previously published by our team.⁸ Here, we perform, for the first time, an analysis of macrofungal spatiotemporal patterns at the order level, using *Hymenochaetales* as our exemplar, and reveal the diversification scenario of this macrofungal order in China.

Diversity and distribution

In general, the four diversity indices, viz. species richness, weighted species endemism, phylogenetic diversity and phylogenetic endemism all indicate that southeastern China has the highest diversity and the most unique species of *Hymenochaetales* in China (Figure 1). This phenomenon confirms previous empirical observations in field trips for hunting macrofungi,^{96–97} and also indicates that warmer and more humid climates in southeastern China are essential to the growth of *Hymenochaetales*.^{98,99} This distribution pattern has also been found for the flowering plants and insects in China.^{5,100,101} In addition, previous research indicated that richness, diversity and endemism on islands greatly exceed those on mainland areas,¹⁰² which may explain why the diversity indices of Hainan and Taiwan islands in southeastern China are higher than those of other regions.

The ensemble model, incorporating data from several independent models to avoid the bias of selecting a single best model,^{73,74,103} predicted that most of the highly suitable habitat for *Hymenochaetales* concentrated in southeastern China (Figure 2). Taken the four diversity indices into consideration together, southeastern China can be considered to be the prior region for conservation and utilization of the high economic bioresource in

Hymenochaetales. Noteworthy, the southeastern China defined in the current study follows Heihe-Tengchong line and Qinling-Huaihe extension line, which delimit China according mainly to climate, geography and demography. Under this definition, the region of southeastern China used in the current study is not consistent with the conventional administrative divisions of China, and instead corresponds mainly to the administrative divisions of Southwest China, South China, East China and Central China.

Spatiotemporal pattern and diversification scenario

When mapping the divergence times of all Chinese genera within *Hymenochaetales* to the map of China, two ancient divergence hotspots emerged from southeastern China and the northwest of northwestern China, viz. Tianshan Mountains (Figures 3A & C–D). However, if we treated each of the four geographical parts as a whole, southeastern China had the oldest genus lineages (Figure 4A). Similarly, the highly suitable habitat concentrated mainly in southeastern China also had older genus lineages than the moderately and lowly suitable habitats (Figure 4C). At the species level, the northwest of northwestern China had no ancient hotspot (Figures 3B & D–E), but similar to the genus level southeastern China and the highly suitable habitat had the oldest lineages (Figures 4B & D). Moreover, the moderately and lowly suitable habitats both had older species than the unsuitable habitat (Figure 4D). It is reasonable to conclude that of the two ancient divergence hotspots of *Hymenochaetales* in China, the one in the northwest of northwestern China underwent less diversification since the origination, while that in southeastern China evolved highly diversity of *Hymenochaetales* during the process of evolution.

To explore why the two ancient divergence hotspots had huge difference in subsequent diversification intensity, we analyzed the correlation between bioclimatic variables and MDTs. The ancient data of these variables million years ago are not available, so we have to use the recent data instead. From such bioclimatic data, the predicted current suitability levels for *Hymenochaetales* in China corresponded well to the divergence times of taxa in this fungal order (Figures 4C–D). This indicates that even if the bioclimates changed from ancient to recent time, the changing trend all over China may be similar. So, it is practicable to use the current bioclimatic data for the correlation analyses, as if omitting the specific values of variables. Temperature, host plant and altitude were crucial variables for the potential distribution of *Hymenochaetales* (Table 1); of them, however, altitude had no significant correlation with MDTs at both genus and species levels (Figures 5 & S8). At the genus level, temperature, precipitation and woody angiosperm density were correlated with MDTs but the correlations were not high, while at the species level, the correlations between either temperature or precipitation and MDTs were weaker, and host density had no correlation with MDTs (Figures 5–6 & S8). Thus, the factors shaping the diversification intensity of *Hymenochaetales* may be beyond the current analyzed bioclimatic variables. More other kinds of variables, like the niche competition with other macrofungal groups, need to be considered when available in the future. Comparing with the ancient divergence hotspot in southeastern China, Tianshan Mountains in the northwest of northwestern China has sufficient precipitation, but lower temperature and less host plants, especially younger woody angiosperm lineages.^{3,104–107} It is well known that the diversification of macrofungi is closely related to dynamic changes of climate and their host plants.^{24,93–94, 108} Therefore, even if *Hymenochaetales* emerged quite early in Tianshan Mountains, since the origination the unsuitable niche for *Hymenochaetales* restricted its diversification intensity. On the contrary, the highly suitable niche in southeastern China facilitated the diversification rates. This phenomenon may represent a typical case of macrofungal spatiotemporal differentiation.

CONCLUSIONS

In summary, we for the first time comprehensively analyze macrofungal spatiotemporal pattern at the order level, which reveals the diversification scenario of *Hymenochaetales* in China. It is concluded that *Hymenochaetales* had two ancient divergence hotspots: one was in southeastern China where the ancient *Hymenochaetales* intensively diversified, while the other one near Tianshan Mountains in the northwest of northwestern China underwent much less diversification. The difference in evolutionary process between

these two ancient divergence hotspots may be caused by the differentiated temperature and host plant density.

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AUTHOR CONTRIBUTIONS

L.W.Z. conceived the work. X.W.W. performed analyses. L.W.Z. supervised the work. X.W.W. and L.W.Z. wrote the manuscript. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

Data are available from the corresponding author upon reasonable request.