Ecological Indicators 147 (2023) 110001

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Transitional areas of vegetation as biodiversity hotspots evidenced by multifaceted biodiversity analysis of a dominant group in Chinese evergreen broad-leaved forests

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ARTICLE INFO

Keywords:
Spatial pattern
Multifaceted diversity
Transitional areas
Evergreen broad-leaved forests
Hotspots
Conservation

ABSTRACT

Species in transitional areas often display adaptive responses to climate change and such areas may be crucial for long-term biodiversity conservation. Evaluation of spatial multidimensional biodiversity patterns and the identification of biodiversity hotspots and priority conservation areas may help mitigate the effects of climate change. Here, we examine the spatial distribution patterns, evolutionary and functional levels of Lauraceae from Chinese evergreen broad-leaved forests. The results show species richness (SR), corrected weighted endemism (CWE), phylogenetic diversity (PD), and phylogenetic endemism (PE) for Chinese Lauraceae are congruent, whereas evolutionarily distinct and globally endangered (EDGE) and function diversity (FD) are incongruent. Areas of paleo-endemism are present in the border region of Yunnan and Guangxi, whereas neo-endemic regions are distributed mainly along the Yarlung Zangbo River and the Himalayas in southern Tibet. Priority conservation areas are located in southern Tibet, the northern Hengduan Mountains, the north–south boundary of Qinling and Huaihe River, southern and south-eastern Yunnan, and south China. Biodiversity hotspots for Chinese Lauraceae overlap with transitional zones for several other vegetation types in adjacent areas. Climate factors are estimated to account for 82.72% of the SR and 86.86% of the PD for Lauraceae spatial distribution patterns, reflecting higher diversity under warmer and wetter conditions. This study confirms the conservation value of transitional areas and the significance of using multiple diversity facets as part of integrative approaches to maximize biodiversity protection in Chinese broad-leaved forests, especially under climate change.

1. Introduction

Climate change and biodiversity loss are important and interconnected environmental challenges facing the world at present. Evidence suggests that conservation actions can simultaneously and significantly mitigate anthropogenic climate change (Smith et al., 2021). Conservation strategies should focus on biodiversity hotspots (Myers et al., 2000), with such areas identified using multiple biodiversity metrics, including the number of species and their abundance (species richness, SR), evolutionary history (phylogenetic diversity, PD), and diversity of form and function (functional diversity, FD). As measures for assessing protection, these biodiversity components each

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https://doi.org/10.1016/j.ecolind.2023.110001
Received 7 November 2022; Received in revised form 3 February 2023; Accepted 7 February 2023
Available online 11 February 2023
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provide different information for assessing protection (Vane-Wright et al., 1991; Faith, 1992; Swenson, 2011; Cianciaruso, 2012), but may not respond uniformly under climate change (Myers et al., 2000;Flynn et al., 2009; Monnet et al., 2014).

Species in transitional areas often display adaptive responses to climate change and such areas may be crucial for long-term biodiversity conservation (Smith et al., 2001). There is also evidence that transitional areas are sensitive to climate change and human activities (Smith et al., 1997) and have high diversity (Smith et al., 2001), but this is not always the case (Morandi et al., 2020). Accordingly, it is essential to determine whether transitional regions are biodiversity hotspots and deserve special conservation attention and whether biodiversity hotspots overlap with transitional areas when examined using multifaceted diversity measures.

China's highly diverse evergreen broad-leaved forests (EBLF) cover > 26 % of the land area (Zhou et al., 2013) and play an important role in the maintenance of ecosystem services (Song, 2013; Zhou et al., 2013). The EBLF is surrounded by deciduous broadleaf forests to the north, Qinghai–Tibet Plateau alpine floras to the west and by tropical forests to the south-west (Ashton & Zhu, 2020), with two different vegetation types forming a transitional area between them in East Asia. Within EBLF and adjacent forests, Lauraceae grows mainly as trees and shrubs in the middle and lower canopy layers and is major floristic component, together with Magnoliaceae, Theaceae, and Fagaceae. The Lauraceae family shows high species richness (Gentry, 1988), ancient origins (Chanderbali et al., 2001), and rapid diversification rates (Xiao et al., 2022) and should be considered a high priority for protection because it is prone to higher extinction risk (Fu et al., 2022). In addition, Lauraceae displays the highest endemism (71 %) amongst the Chinese plant lineages (Huang, 2011; Yang & Liu, 2015; Zhou et al., 2017; Zheng et al., 2018), as well as important economic, industrial, medicinal uses, and ecological value (Li et al., 1984; Li & Li, 2004). Considering the diversity and importance of Lauraceae within the EBLF, this family is therefore ideal for studying the relationships between high concentrations of diversity and transitional areas to identify priority-based multifaceted regions for protection. Similarly, understanding the importance of environmental heterogeneity, evolutionary history and species-level ecological variation within a family is essential for providing basic data for protecting these forests.

Nature reserves are often identified as the most effective way to protect biodiversity, especially considering funding constraints. However, it is challenging to determine how to generate the best biodiversity metrics for conservation priorities and protected area selection (Rodrigues & Gaston, 2002; Wilson et al., 2006; Forest et al., 2007). There is also evidence that the spatial distribution patterns of multifaceted diversity may lack congruence owing to evolutionary and ecological constraints. For example, if there are more ecological niches and less competition in an area, the number of functional traits and species is expected to increase rapidly when a new taxon enters the area, resulting in high functional diversity and low phylogenetic diversity. Alternatively, when ecological niches are scarce, the diversity of functional traits is limited, and functional diversity is expected to be lower than phylogenetic or species diversity (Wiens et al., 2013).

The evolutionary history of species can also affect the relationship between species diversity and phylogenetic diversity (Rodrigues & Gaston, 2002). For example, areas undergoing rapid speciation or limited species migration tend to have lower phylogenetic diversity, whereas areas with slower speciation and more frequent long-distance dispersal tend to display higher phylogenetic diversity (Davies & Buckley, 2012). Species evolutionary distinctiveness (ED) is the sum of the terminal branch lengths of a species on a clade and the weighted value of its common ancestor. Therefore, this measure reflects the contribution of each species to the total evolutionary history of the clade, as well as giving greater conservation value to species with lower shared evolutionary history (Redding & Mooers, 2006; Isaac et al., 2007).

Phylogenetic diversity (PD) is the sum of the branch lengths of a group of species on the phylogenetic tree (Faith, 1992) and can identify areas with the largest evolutionary history, which is key to promoting future evolutionary selection diversity (Moritz, 2002; Rodrigues et al., 2005; Forest et al., 2007), although it generally tends to resemble the patterns observed for species richness (Thornhill et al., 2016). Phylogenetic endemism (PE) range-weights phylogenetic information using the spatial distribution of taxa to indicate the extent to which phylogenetic diversity is restricted to a specific area (Rosauer et al., 2009; Huang et al., 2013). In contrast, functional diversity (FD) reflects the diversity of morphological, physiological and ecological traits within biological communities and explains ecosystem function better than other diversity measures (Hooper & Chapin, 2005; Petchey & Gaston, 2006).

These evolution- and function-linked diversity metrics have been increasingly used in conjunction with traditional species-level diversity measures to prioritize protected areas (Forest et al., 2007; Devictor et al., 2010; Barratt et al., 2017; Millar et al., 2017; Funk & Burns, 2018; Spalink et al., 2018). Relative phylogenetic diversity (RPD), relative phylogenetic endemism (RPE) and categorical analysis of neo- and paleo-endemism (CANAPE) based on the concepts of PD or PE have been developed to identify areas of endemism with significant concentrations of rare long branches (i.e., paleo-endemism), rare short branches (i.e., neo-endemism), or mixtures of the two (Mishler et al., 2014; Kling et al., 2018). These evolutionary metrics enable the definition and quantitative mapping of 'museum' and 'cradle' areas for better conservation management (Mishler et al., 2014; Spalink et al., 2018).

Although 474 national or other nature reserves (e.g., provincial nature reserves) have been established in China up to 2019, covering 15 % of the land area (MEE of China, 2019), a nationwide assessment of the effectiveness of China's nature reserves suggests that they are insufficient to safeguard either biodiversity or key ecosystem services (Xu et al., 2017). Specifically, these reserves currently only utilize species-level biodiversity metrics, such as species richness, Shannon–Wiener, and Simpson diversity indices (Simpson, 1949; Ma & Liu, 1994; Rodrigues et al., 2005), rather than the evolutionary or genetic conservation value of the taxa present. Therefore, to identify high diversity areas better, the present study examines: (a) whether multiple aspects of biodiversity are spatially congruent or conflicted; (b) the extent to which Lauraceae biodiversity hotspots overlap with transitional areas of various vegetation types; and (c) the extent to which current nature reserves protect Lauraceae diversity when considering multiple biodiversity measures.

To achieve these goals, we integrated geographical distribution and phylogenetic information, as well as functional diversity data to create a systematic overview of Chinese Lauraceae. The study focused on using multifaceted diversity approaches: (1) mapping and identify spatial patterns of SR, PD, and FD; (2) defining areas of neo- and paleo-endemism for Chinese Lauraceae; (3) identifying priority areas for conservation; (4) determining whether transitional areas serve as convergent centers of biodiversity hotspots; and (5) evaluating the effectiveness of multifaceted biodiversity for assessing Lauraceae conservation within existing nature reserves.

2. Material and methods

Our study area comprises the geographical regions of the People's Republic of China (PRC). We arranged a grid of 50 × 50 km cells over the shapefile of the Chinese vector map available from the National Geomatics Center of China (NGCC, www.ngcc.cn/ngcc/). The position of each grid cell is arbitrary and not predefined by any political or natural borders, resulting in a total of 1483 grids for the analyses.

2.1. Species distribution data and species distribution models

Occurrence data for all native Lauraceae species were obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn), and National Specimen Information Infrastructure (NSII, https://www.nsii.org.cn), as well as herbarium specimens at the Kunming Institute of Botany (KUN) and Xishuangbanna Tropical Botanical Garden of Chinese Academy of Sciences (HITBC). Erroneous or questionable GBIF records were excluded, following the *Flora of China* (Li et al., 2008) and The Plant List (https://www.plantlist.org). For herbarium records that only had a location name with no coordinates, we used Google Earth (https://www.google.cn/maps/) to determine the approximate latitude and longitude.

Current climatic variables were represented by 19 bioclimatic variables (bio1–bio19) at a spatial resolution of 1 × 1 km obtained from the WorldClim 2.1 database (https://www.worldclim.org) (Fick & Hijmans, 2017). To reduce collinearity between bioclimatic variables, we conducted correlation analyses of the 19 bioclimatic variables and selected only those with correlation coefficients of$<$0.7. In addition, digital elevation models (DEM), the normalized difference vegetation index (NDVI), and soil of China data (including soil pH (T_PH_H2O), organic carbon content (T_OC), exchangeable base salts (T_TEB), exchangeable sodium salts (T_ESP), soil available water content (AWC_CLASS), etc.) with a 30-arcsecond spatial resolution were retrieved from the Resource and Environment Science and Data Center (https://www.resdc.cn/). Slope of China data were also derived from the DEM using the slope tool in ArcGIS 10.2, resulting in a final set of 17 environmental variables (Table S1) that were then aligned to fit the same dimensions as the Chinese map and converted to ASCII files.

Some Lauraceae species in border areas (e.g., Guangxi, Yunnan and Xizang provinces) have few records, making it difficult to determine accurate distribution ranges (Yang & Liu, 2015). To compensate for collection bias, we used a species distribution model (SDM) to model the predicted distributions. Species distribution data were also trimmed to a maximum of one occurrence per species in a raster cell of 10 km to reduce autocorrelation between the environmental variables. In order to reduce the risk of overfitting in the models, we removed erroneous records, duplicate records and pseudoreplication. In total, we retained 25 genera, 440 species, and 18,837 records of Lauraceae, ranging from 18.22° N to 41.99° N and 85.29° E to 125.96° E, and converted these to CSV files. We used the maximum entropy (MaxEnt) distribution model and downloadable version 3.4.1, as this performed best among many other species distribution models (Elith et al., 2006; Merow et al., 2013). The available Lauraceae coordinates ranged from 6 to 676, which all conform to MaxEnt's criteria for acceptable data (Pearson et al., 2007) and for each of the 440 species SDM was developed based on its unique presence records and the 17 environmental predictors. For species with$>$25 spatial records, 75 % were used for the model training and 25 % were used as test data. The jackknife method was used for simulation of species with$<$25 coordinate points (Pearson et al., 2007). The areas under curves (AUC) of the receiver operator characteristic (ROC) were used to evaluate the reliability of the simulation results. The range of the AUC value is [0, 1], and the closer the value is to 1, the higher the reliability of the simulation (Raes & Steege, 2007). When the AUC value is [0.9, 1], the simulation result is very accurate; the AUC value is [0.8, 0.9] the results are deemed accurate; when [0.7, 0.8), the results are average; and when$<$0.7, the simulation results are not considered to be credible (Elith et al., 2006). In addition, a 10 % training presence value was selected as the application threshold rule for each scale model (Raes et al, 2009). Cross-validation was maintained in the replicate run, and iterations were fixed at 20, with default values used for the other parameters. The final outputs of the model predictions were exported to ArcGIS 10.2 for further analysis. Altogether, the results were obtained for 440 Lauraceae species and 64,604 potential distribution sites.

2.2. Phylogenetic data

Although our recent studies have demonstrated that chloroplast genomes can resolve phylogenetic relationships effectively (Liu et al., 2021; Liu et al., 2022), there are only about 130 chloroplast genome records available for Chinese Lauraceae species. Furthermore, cytonuclear discordance between the plastid and nuclear DNA has been identified in Lauraceae and certain taxa exhibit conflicting nuclear and plastome phylogenomic analyses, creating a challenge for phylogenetic construction based on the combined plastid and nuclear DNA sequences. In addition, based on the previous studies using four plant DNA barcoding loci (*rbc*L, *mat*K, *trn*H–*psb*A and ITS) to reconstruct the species level relationships of the Chinese Lauraceae, ITS was more informative than the other three fragments and provided better phylogenetic resolution (Liu et al., 2017), as well as ITS being the most widely available species-level sequences for the Chinese Lauraceae. Therefore, we used ITS sequence data to construct phylogenetic relationships in the family, obtaining ITS sequences for 286 species of Lauraceae, with 209 species from our previous studies, 42 species downloaded from the National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov) and 35 new species records from this study (Table S2). Three species of Monimiaceae were selected as outgroups, following Chanderbali et al. (2001). All sequences were aligned with MAFFT and analysed under the Maximum Likelihood (ML) criterion using the RAxML-HPC Blackbox program (Stamatakis, 2006) with the GTR + I + G model in the CIPRES Portal (https://www.phylo.org).

2.3. Functional traits and functional diversity

To quantify the functional diversity of Lauraceae in China, we scored three continuous and five categorical traits for each species: stem length, diameter at breast height (DBH), leaf area, growth form (tree, shrub, and herb), life form (evergreen and deciduous), leaf quality (membranous, papery and leathery), venation pattern (pinninerved, trinerved and triplinerved) and buds (scaly or naked), using descriptions from *Flora of Reipublicae Popularis Sinicae* (Li et al., 1984) and *Flora of China* (Li et al., 2008). These characteristics were selected to represent species niche dimensions, and resource requirements and assess the relationships between biodiversity and ecosystem function (Flynn et al., 2009; Safi et al., 2011). This index is also appropriate for mixed data, including quantitative (e.g., body mass) and nominal (e.g., habitat mode and feeding niche) data. The functional dispersion metric, which is the average Gower distance in the ordinated trait space between individual species in a cell and the ordination centroid was used to measure functional diversity, as it is unaffected by species richness (Laliberte & Legendre, 2010). Functional dispersion was calculated using the FD package in R (https://cran.r-project.org/web/packages/FD/FD.pdf), with all continuous traits scaled.

2.4. Diversity and endemism analyses

The distribution patterns of SR, CWE, PD, and PE were calculated for equal-area square grid cells of 50 × 50 km using the Biodiverse software, version 3.1 (Laffan et al., 2010), based on the SDM results and phylogenetic trees. Evolutionary distinctiveness and threat were combined in the EDGE (evolutionary distinctiveness and global endangerment) metric to evaluate the conservation value of each Lauraceae species, using the following formula:

$$\mathrm{EDGE} = \ln(1 + \mathrm{ED}) + \mathrm{GE} \times \ln \tag{2}$$

as EDGE can identify species with few extant relatives and/or those that face higher risk of extinction (Isaac et al., 2007).

The values of Evolutionary Distinctiveness (ED) and Global Endangerment (GE) were measured separately for each species. The ED was calculated using the PICANTE package of R (Redding & Mooers, 2006). GE corresponds to the conservation status of each species on the *Red List of Biodiversity in China – Volume of Higher Plants* (https://www.mee.gov.cn/gkml/hbb/bgg/201309/W020130917614244055331.pdf) and Qin et al. (2017) (LC, NT, VU, EN, and CR); see Isaac et al. (2007) for more information on the category weight of each conservation status. Because EDGE represents the amount of unique evolutionary history and threat status for a species and does not fitted naturally to complementarity approaches for areas, we generated per-cell scores from mean species values (Daru et al., 2015).

2.5. Significance of diversity and CANAPE

Significant grid cell values of PD, RPD, PE, and RPE were assessed by running 999 randomizations with the “rand_structured” option in Biodiverse 3.1. Randomization was performed by redistributing the occurrence of taxa found in each grid cell, maintaining the total taxa per cell and the total number of cells unchanged (Mishler et al., 2014). Based on the randomization test for PE and RPE, the categorical analysis of neo- and paleo-endemism (CANAPE) can identify further four grid cell types based on the range-restricted branches’ lengths: paleo-endemic, neo-endemic, mixed- and super-endemic (Mishler et al., 2014). A cell with an overrepresentation of rare short branches is considered neo-endemic (two-tailed test, $\alpha < 0.05$), a feature commonly considered to indicate centers of speciation (Mishler et al., 2014) and “cradle of evolution” (Dagallier et al., 2020). Cells with an over-representation of rare long-branches are considered paleo-endemic (two-tailed test, $\alpha > 0.95$), indicating refugial areas and “museums of evolution” (Dagallier et al., 2020) and where clades may have historically suffered high extinction and/or range contractions (Mishler et al., 2014). Areas with a mixture of both rare long and short branches are considered to have mixed endemism or super-endemism (areas of mixed endemism that were highly significant, i.e., $p < 0.01$), suggesting that the cells act as both “museums” and “cradles”. Super-endemic areas are further subdivisions of mixed endemism at the $\alpha > 0.01$ level (Mishler et al., 2014). Accordingly, the output files from the PE and RPE randomizations were reclassified further in SDMtoolbox 2.3 (Brown et al., 2017) to conduct CANAPE.

2.6. Identification of Chinese Lauraceae diversity hotspots and analysis of conservation gaps

We used the top 10 % and 20 % of the SR, CWE, PD, PE, FD, and EDGE, as well as paleo-endemic and neo-endemic scores, to identify priority conservation areas. Superimposing the map of China’s nature reserves (Zhang et al., 2015) with priority conservation areas enables the evaluation of the protection value of nature reserves. It also helps to identify unprotected areas with high conservation value, enabling the development of practical suggestions for constructing and managing of nature reserves (Fig. 1).

3. Results

3.1. Spatial patterns of Chinese Lauraceae diversity

We assembled a phylogeny of native Chinese Lauraceae, comprising 286 species (64 %) in 23 genera (92 %), using the combined datasets from NCBI, as well as previous and novel sequences by our team (Fig. 2). We obtained a well-resolved and supported ML tree, where the bootstrap value for the basal group (e.g., *Cryptocarya* R.Br.) within Lauraceae was 80.96 %, and the bootstrap values of each monophyletic branch were>50 %. *Cryptocarya*, *Cinnamomum* Schaeff., *Machilus* Nees and *Neolitsea* (Benth. & Hook.f.) Merr. were each monophyletic, whereas *Beilschmiedia* Nees, *Litsea* Lam. and *Lindera* Thunb. were paraphyletic, consistent with previous studies (Li et al., 2007; Huang et al., 2016a; Liu et al., 2017, 2021).

The overall distribution range of Lauraceae in China consists of 1483 50×50 km grid cells, covering an area of 3,707,500 km^2. The mapped values for SR, CWE, PD, PE, and EDGE are shown in Fig. 3. The relationship between species and phylogenetic diversity was a significantly positive ($r = 0.957$, $p < 0.01$; Table 1). The spatial distribution patterns of Lauraceae showed that the SR increased from north to south in China (Fig. 3A) which is a similar pattern to that of PD (Fig. 3B). CWE was correlated significantly and positively with PE ($r = 0.847$, $p < 0.01$; Table 1), and the spatial distribution patterns of the two indices were similar, increasing from north to south (Fig. 3C, D). Although SR, PD, CWE, and PE showed similar spatial distribution patterns, the spatial pattern of EDGE was different from the others and increased from the northeast to the southwest (Fig. 3E). However, the spatial distribution of FD showed an opposite trend of increasing from south to north, forming a regional belt of high FD along the north–south junction of the Hengduan Mountains and the Qinling-Huai River, decreasing sharply to the north (Fig. 3F). FD was not correlated with any of the other diversity indicators ($r = 0.096$–0.346, $p < 0.01$; Table 1).

3.2. Significant diversity and CANAPE

The randomization-based significance tests of PD, RPD, PE, and RPE showed that regions with significantly high PD scores were distributed in southern and south-eastern Yunnan and central Hainan, whereas low PD values were distributed broadly north of 24° N (Fig. 4A). Southern and south-eastern Yunnan and central Hainan had more species from the range of the phylogeny than would be expected by chance, suggesting phylogenetic dispersal, whereas northern China had fewer species, indicating phylogenetic clustering. RPD showed a similar pattern to PD, with significantly high RPD scores in southern and south-eastern Yunnan and Hainan (Fig. 4B), indicating the phylogenetic over-representation of long branches. However, unlike PD, significantly low RPD values were limited to eastern Sichuan, central Guizhou and northern Hunan (Fig. 4B), suggesting a phylogenetic overrepresentation of short branches within these areas and the randomization test results for PE were very similar to those observed for PD (Fig. 4C, D).

Areas of concentrated paleo-endemism were small and occurred in the border region of eastern Yunnan and western Guangxi (Fig. 5). A greater number of neo-endemic cells were distributed mainly along the Yarlung Zangbo River and the Himalayas in southern Tibet, although central Sichuan and southern Guangxi also had neo-endemic cells (Fig. 5). Areas of mixed endemism occurred in Yunnan, Hainan, Taiwan and Tibet (Fig. 5), indicating that over-representation of both relatively long and short branches was rare in these areas. Super-endemics were distributed in southern Yunnan, Hainan and southern Taiwan (Fig. 5).

3.3. Hotspots and priority areas for Lauraceae in China

Regardless of whether the top 10 % or 20 % were used as hotspot areas, the proportion of overlapping hotspot areas of nature reserves and diversity indicators of Lauraceae (SR, PD, CWE, PE, EDGE, and FD) in China was very low (Fig. 6). Only 4.6–20.8 % of the hotspot areas were distributed in nature reserves, with large conservation gaps (Table 2; Fig. 7). The distribution patterns of hotspot areas for SR, PD, CWE, and PE were consistently similar and were mainly distributed in southern and south-eastern Yunnan, Guangxi and Guangdong and other areas of southern China areas (Fig. 7A, B, C, D).

EDGE cells were mainly distributed in southern Yunnan, with a few in south-eastern Tibet (Fig. 6E). The hotspot areas for FD were scattered, but mainly distributed in the northern section of the Hengduan Mountains and at the north–south junction of the Qinling Mountains and Huaihe Rivers, while other cells were distributed in the Tianmu Mountains (Fig. 6F).

The paleo-endemic center of Lauraceae is located at the junction of Yunnan and Guangxi; the neo-endemic center is in south-eastern Tibet, while mixed and super-endemism occurred in Yunnan, Hainan, Taiwan, and Tibet (Fig. 5). Therefore, the priority areas of conservation for Lauraceae are southeast Tibet, the northern section of the Hengduan Mountains, the north–south junction of the Qinling Mountains and Huaihe River, Tianmu Mountains, southern and south-eastern Yunnan, Guangxi, Guangdong, Hainan and Taiwan (Fig. 7A, C). Overall, these

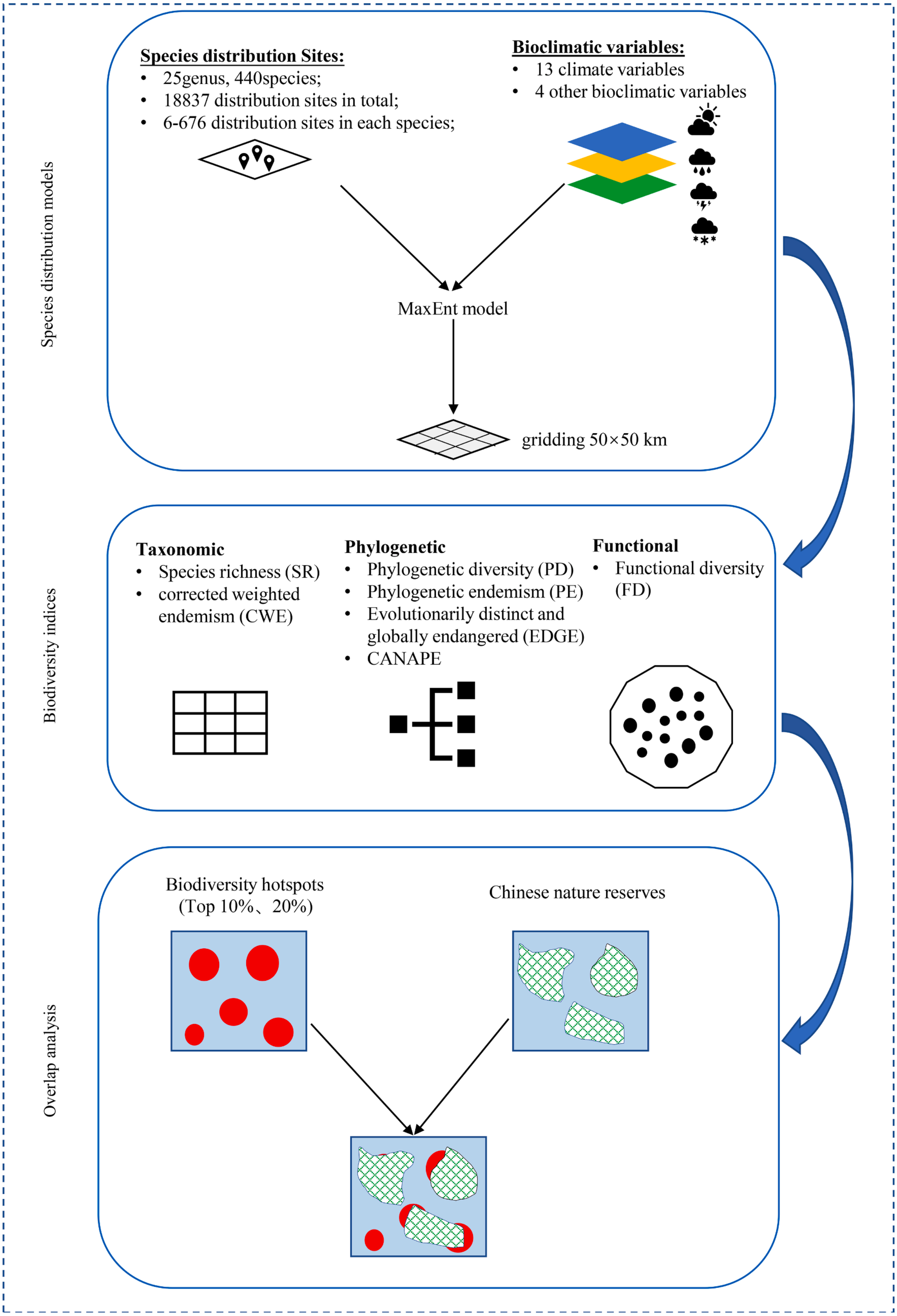

Fig. 1. Workflow diagram depicting.

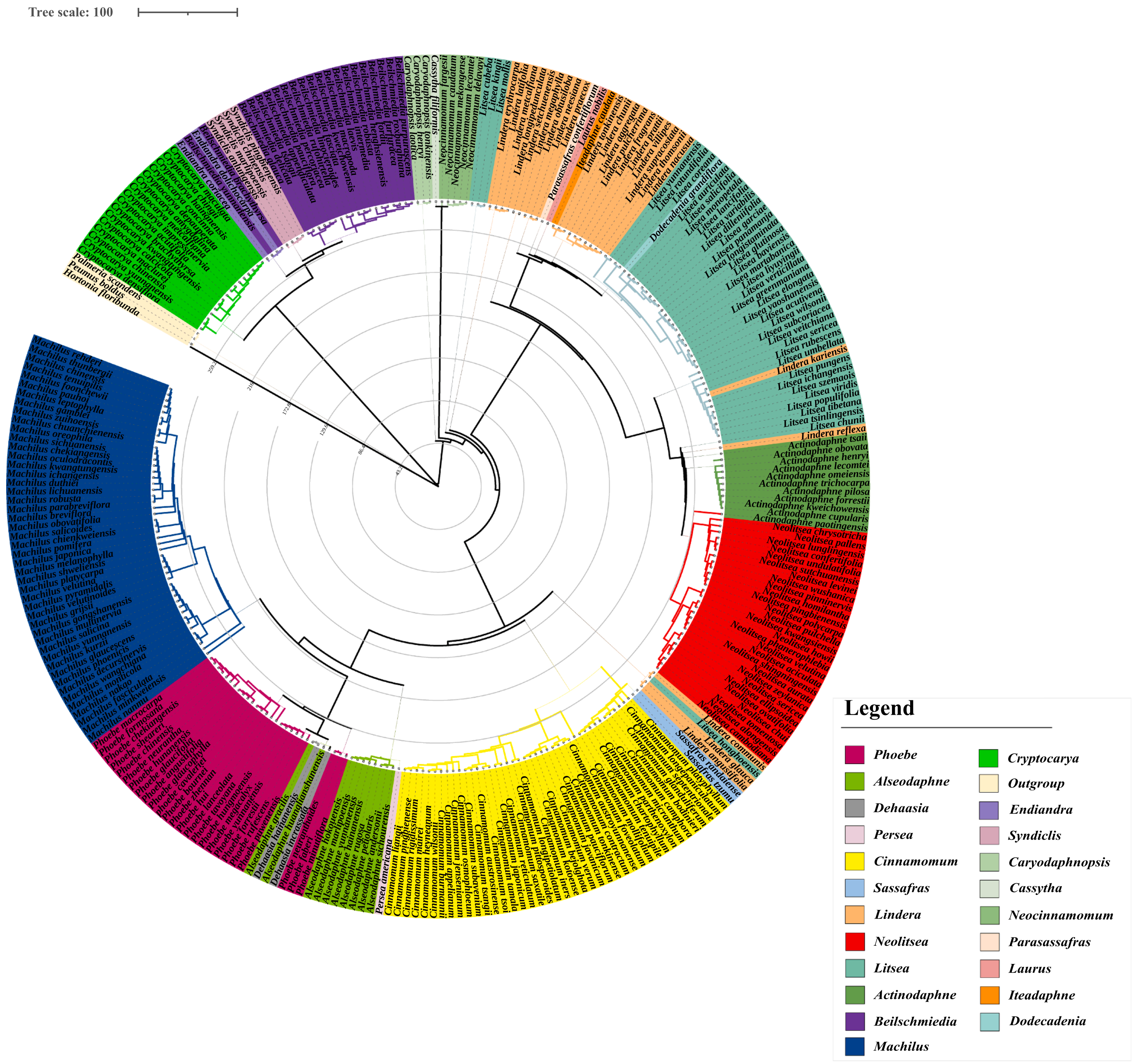

Fig. 2. Maximum Likelihood tree for 286 Chinese Lauraceae species constructed using ITS sequences in RAxML.

biodiversity hotspots were mainly located in transitional zones between the EBLF and other vegetation types (Fig. 7A).

3.4. *Environmental drivers of diversity indexes*

The regression analyses between the six diversity indicators and the 13 climatic factors are shown in Table 3. The overall regression for all diversity indicators was significant ($p = <0.01$) and the adjusted R^2 values for SR, PD, CWE, PE, EDGE, and FD were 0.8272, 0.8686, 0.4768, 0.6227, 0.4627, and 0.3798 respectively (Table 3), indicating that climatic factors could explain the spatial diversity patterns of SR and PD better than those of CWE, PE, EDGE, and FD. Pearson correlation analysis also showed that climatic factors were significantly correlated with SR and PD. The lowest temperature in the coldest month (r = 0.823–0.835) showed the strongest correlation, followed by precipitation in the wettest season (r = 0.788–0.793) and annual mean precipitation (r = 0.792) (Table 4). However, the correlations between these climate factors and CWE, PE, EDGE, and FD were all low (r = -0.06–0.6) (Table 4).

4. Discussion

Lauraceae is one of the four dominant components of the Chinese EBLF, and is a viable model for describing regional patterns of plant diversity. Multi-dimensional diversity patterns for Chinese Lauraceae show that spatial patterns of species, evolutionary and functional levels vary considerably among assemblages. Furthermore, diversity hotspots overlap with EBLF transition zones, emphasizing the importance of transition zones for protection in areas with diverse vegetation types. Thus, in order to increase conservation effectiveness under a changing climate, multi-dimensional assessments of diversity are desirable to enhance the resolution of species patterns and provide better insights into both diversity and phylogenetically based conservation efforts.

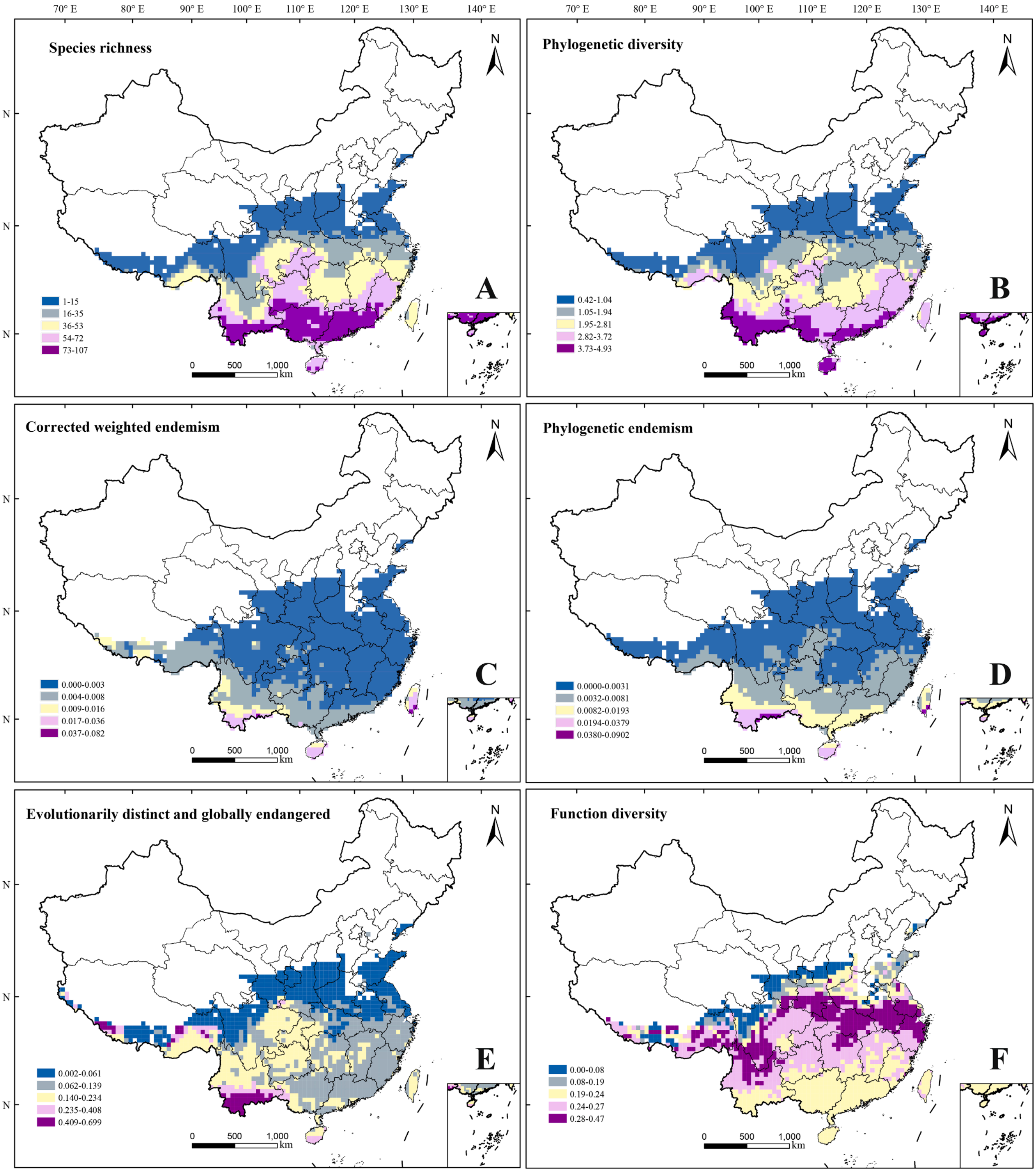

Fig. 3. Map showing spatial patterns of six diversity indices offor Chinese Lauraceae speciesin China, from purple to bule, show the highest value to the lowest value. A, Species richness (SR). B, Phylogenetic diversity (PD). C, Corrected weighted endemism (CWE). D, Phylogenetic endemism (PE). E, Evolutionarily distinct and grobally endangered (EDGE). F, Function diversity (FD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Spatial patterns of multifaceted diversity in Chinese Lauraceae

Although using ITS for DNA barcoding provides the best ability to solve the phylogenetic relationship of Lauraceae (Liu et al., 2017; Liu et al., 2021), uncertain branches still exist in the ITS trees. However, some studies have concluded that tree uncertainty has virtually no effect of on spatial phylogenetics results (Thornhill et al., 2017), and different input trees and uncertainty have modest or little influence on phylogenetic diversity, especially on landscape scales (Allen et al., 2019). Therefore, using imperfect phylogenetic data to study spatial patterns of diversity is tolerable within the context of rapid biodiversity loss due to climate change (Thornhill et al., 2017; Allen et al., 2019).

Table 1
Pearson correlation coefficient values (*r*) between diversity indicators for Lauraceae in China.

	Species richness	Phylogenetic diversity	Phylogenetic endemism	Function diversity	Corrected weighted endemism
Phylogenetic diversity	0.957**				
Phylogenetic endemism	0.650**	0.721**			
Function diversity	0.331**	0.332**	0.12**		
Corrected weighted endemism	0.387**	0.469**	0.847**	0.096**	
Evolutionarily Distinct and Globally Endangered	0.509**	0.560**	0.637**	0.346**	0.57**

Note ** indicates a significant correlation at the 0.01 level (two tailed).

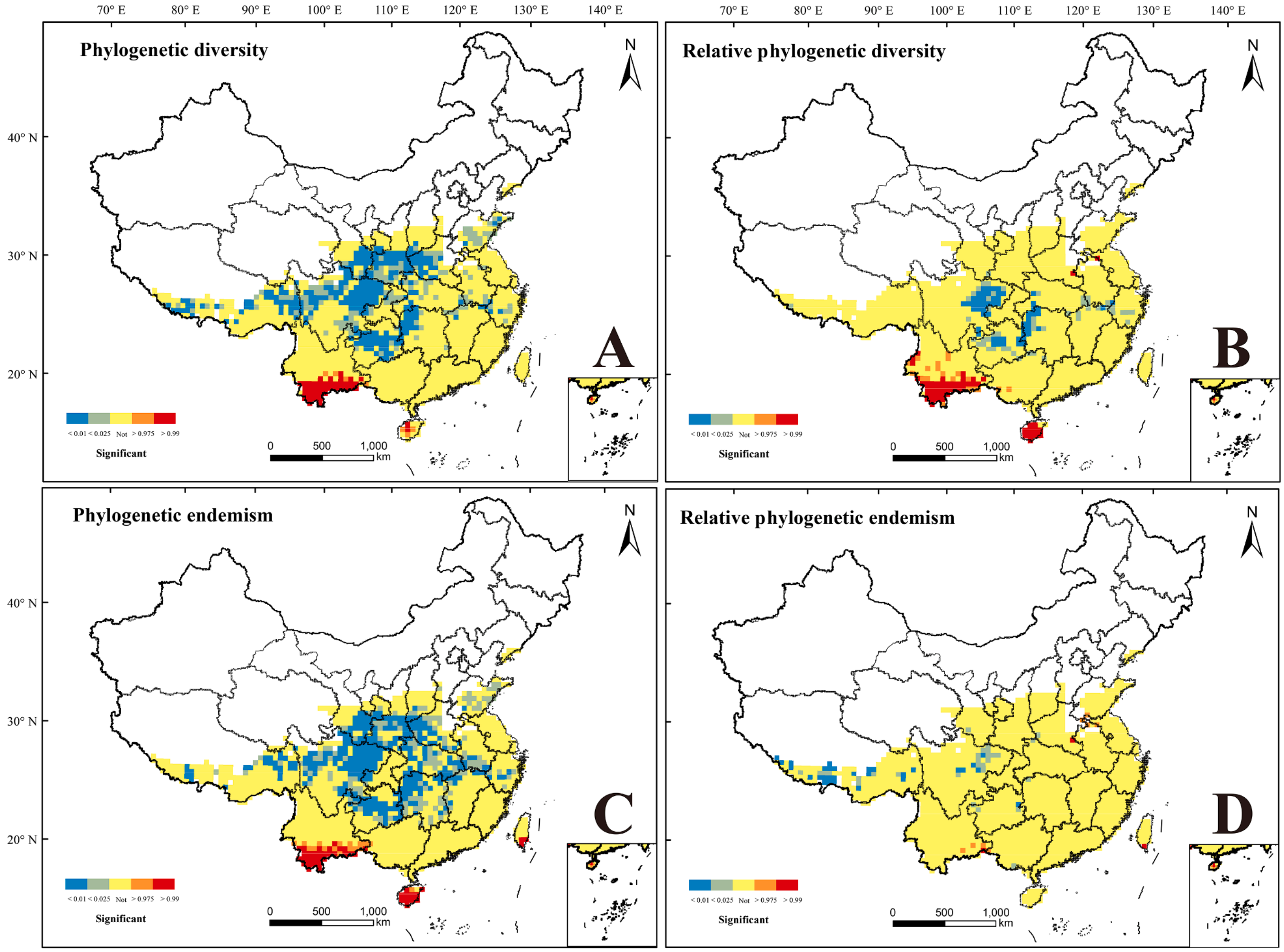

Fig. 4. Map showing significant results from two-tailed randomization tests of Chinese Lauraceae in China. White cells contain no records, yellow cells are no significant, red cells conatin significantly more than expected; blue cells contain signicantly less than expected. A, Phylogenetic diversity (PD), B, Relative phylogenetic diversity (RPD), C, Phylogenetic endemism (PE) and D, Relative phylogenetic endemism (RPE). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Spatial congruence and mismatch between diversity metrics can provide insights into the processes structuring diversity, helping to explain diversity gradient patterns of the Chinese Lauraceae. The SR showed a latitudinal gradient that increased from north to south, with Guangdong, Guangxi and southern Yunnan having the highest numbers of species. These results were strongly congruent with PD, indicating that species-rich areas tend to harbor multiple distinct lineages of Lauraceae, which is consistent with previous studies on other plant taxa (e.g., Forest et al., 2007; Mishler et al., 2014; Thornhill et al., 2016; Cai et al., 2021; Zhang et al., 2022). The spatial patterns for CWE and PE also increased from north to south, with hotspots concentrated in southern-southeastern Yunnan, Hainan, and Taiwan, consistent with previously recognized patterns for seed plants in China (López-Pujol et al., 2011a; Huang et al., 2016b). In constrast, the EDGE mismatches with other diversity indices possibly reflect the fact that they are more relevant to the endangerment levels of the taxa (Isaac et al., 2007); FD mismatches with other diversity indices may reflect historical, environmental, and ecological processes of the study areas (Gómez-Ortiz et al., 2017). Any estimated measure of FD (or even the true FD that would capture all functional traits) can also be decoupled from PD if some functional traits are subjected to strong stabilizing selection and/or competitive interactions within lineages (Prinzing et al., 2008). Parallel evolution of morphological characters is not uncommon in Lauraceae (Li, 1995; Yang et al., 2022), which may also have contributed to the mismatch between FD and other indices seen here. The decoupling patterns of these two diversity indices highlight the complementarity of

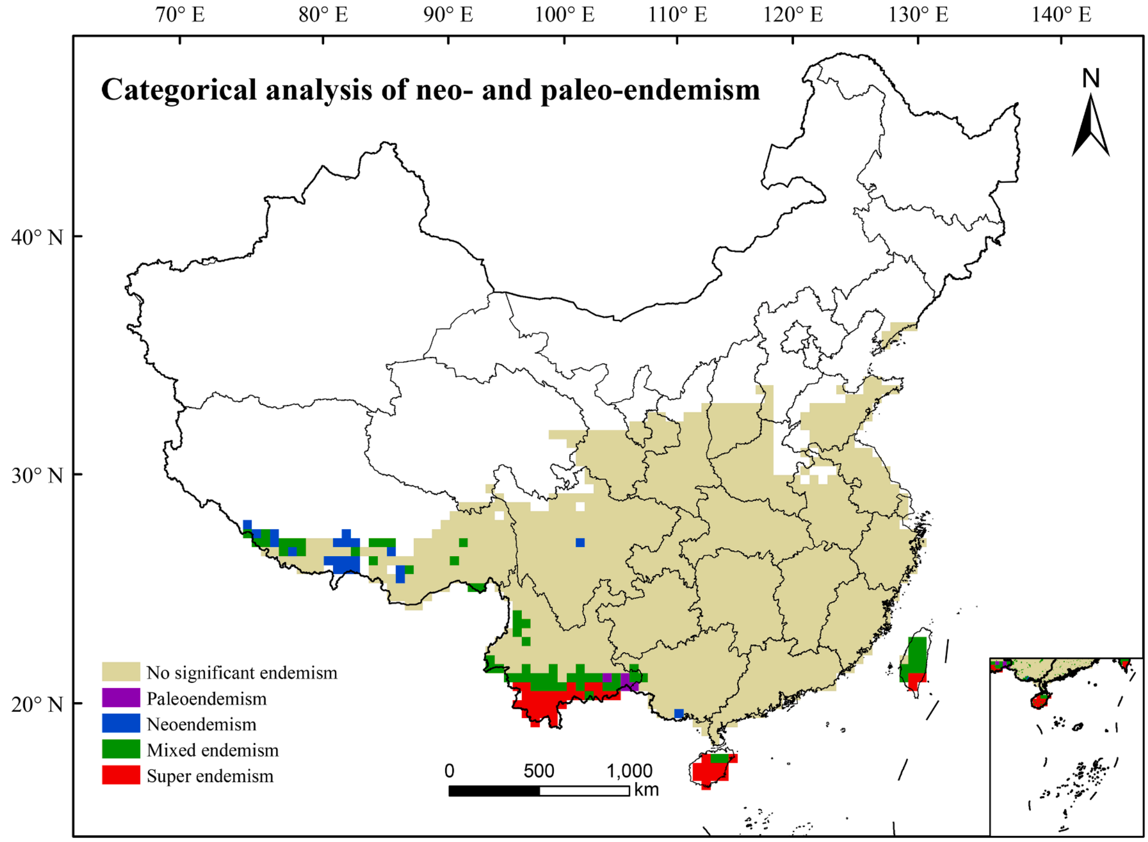

Fig. 5. Centers of phylogenetic endemism of Chinese Lauraceae in China inferred by analysis distribution patterns of neo- and palaeo-endemism (CANAPE). Red cells indicate cneters of Super endemism, green cells indicate cneters of Mixed endemism, blue cells indicate cneters of Neo-endemism, purple cells indicate cneters of Paleo-endemism. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the different biodiversity indices and their respective utility for assessing conservation value.

There are 66, 29, and 28 species of Lauraceae restricted to southern-south-eastern Yunnan, Hainan, and Taiwan respectively (Li et al., 2008); however, this is not unexpected, as endemic tropical plants constitute an important component of the Chinese flora. For example, the China-wide floristic endemism study by Zhang et al. (2022) concluded that the mountains of southern and northern China contained areas of both paleo- and neo-endemics. López-Pujol et al. (2011a) identified 20 centers of plant endemism in China, with south-eastern Yunnan, Hainan and Taiwan all recognized as priority hotspots for endemism. Zhu et al. (2021) delineated three major vegetational zones in Hainan and Huang et al. (2016b) identified 19 hotspots of Chinese endemic seed plants using species - and phylogeny-based metrics, with southern Yunnan, the mountainous areas of eastern Yunnan and western Guangxi and Hainan, roughly overlapping with the Lauraceae hotspots identified in this study.

Generally, SR and PD are products of evolutionary and ecological processes. Throughout the Cenozoic, paleoecological evidence suggests that southern-southeast Yunnan and southern China had extensive contact with other tropical regions (Jacques et al., 2014; Spicer et al., 2016; Ding et al., 2020). Simultaneously, floristic and phylogenetic studies have revealed that southern-southeast Yunnan and southern China are key evolutionary hotspots in Southeast Asia (Bruyn et al., 2014). Lauraceae are assumed to have originated in the tropics and later radiated into the subtropics (Li, 1995; Huang et al., 2016a; Xiao et al., 2022). As southern Yunnan, Hainan and southern Taiwan are the only remaining extant tropical regions in China, these regions may have served as refugia for Lauraceae during Cenozoic climatic fluctuations.

EDGE values increased from northeast to southwest China, with hotspots primarily located in southern Yunnan and southeastern Tibet (Fig. 2.2E, 2.5E), where species are phylogenetically isolated and some are threatened with extinction (Isaac et al., 2007; Cadotte & Davies, 2010). EDGE combines ED and extinction risk to identify species that are evolutionarily distinct and globally endangered (Isaac et al., 2007); however, because our measure of ED only considered relationships among native Chinese Lauraceae, possibly our results depended more on extinction risk and that these high-scoring EDGE regions, including southern Yunnan and south-eastern Tibet, may include more endangered Lauraceae than have been identified in this study.

In contrast to SR, FD, CWE, PE, and EDGE, the spatial distribution pattern of FD increased and then decreased going from south to north across China and the hotspots were concentrated mainly in the northern section of the Hengduan Mountains and Dujiangyan area and the north–south boundary between the Qinling Mountains and Huaihe River. As an evolutionary convergence zone, the northern section of the Hengduan-Dujiangyan region has recently been recognized as a biodiversity hotspot (López-Pujol et al., 2011b; Liu et al., 2016). The region also was a refuge for plants during the Fourth Glacial Period (Feng et al., 2016), with lower plant extinction rates leading to a complex regional floristic composition (Rahbek et al., 2019; Ding et al., 2020), including Lauraceae taxa that are considered to represent both ancestral and more derived lineages (Li, 1992). This area also acts as a large-scale ecological transition zone between the Hengduan Mountains and Central China floras and includes numerous Lauraceae with different functional traits, including species of *Phoebe*, *Machilus*, *Lindera*, *Litsea* and *Nothaphoebe*. Therefore, the complex provenance of the Dujiangyan flora at the northern end of the Hengduan Mountains, as well as the region's possible roles as both a refuge and cradle of evolution, may help to drive the formation of diverse functional characteristics of Lauraceae, resulting in the exceedingly high FD scores observed in the region.

The north–south boundary of the Qinling Mountains and Huaihe River straddles a transition zone between the warm temperate and

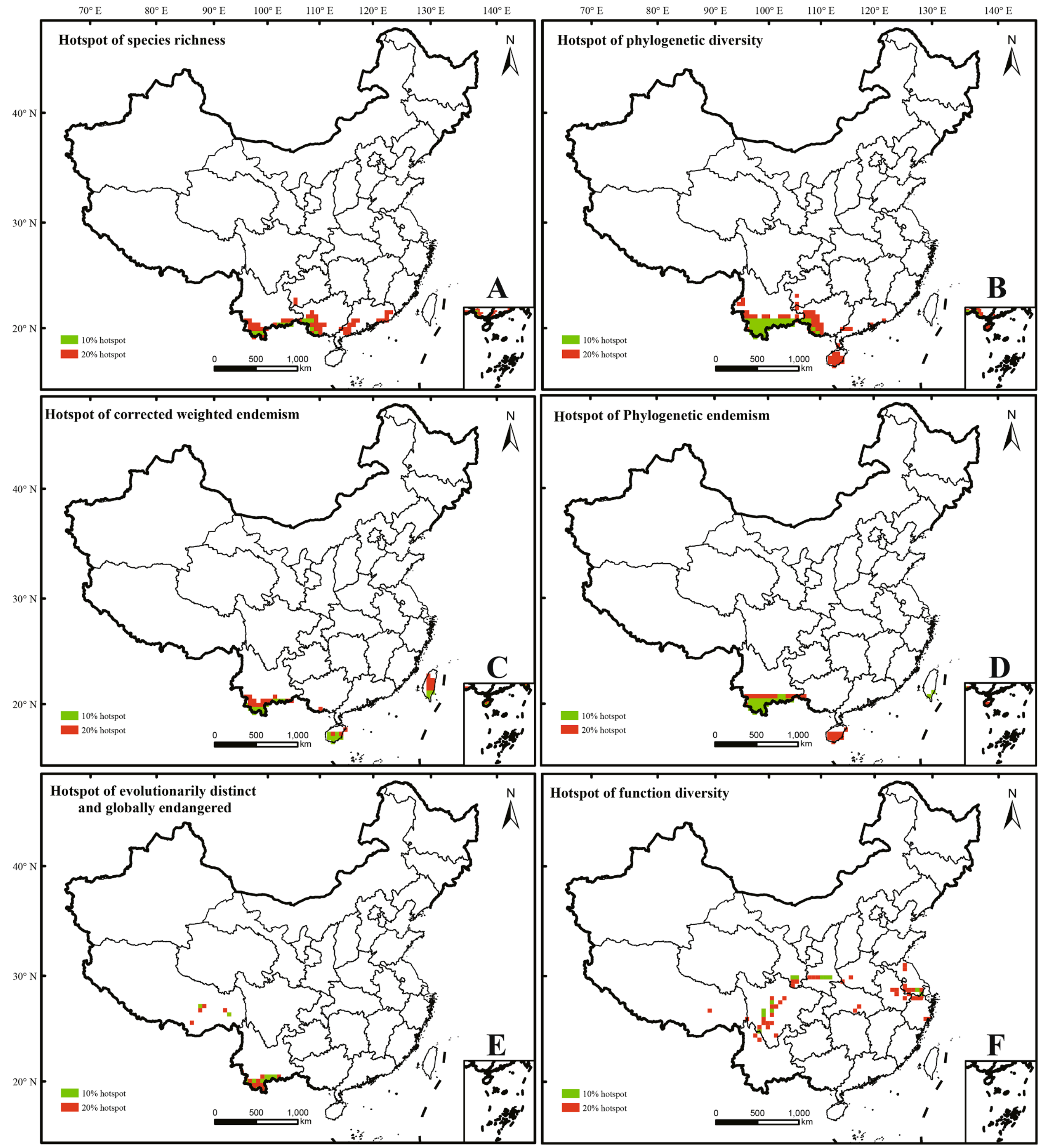

Fig. 6. Hotspot maps for six diversity indices of Chinese Lauraceae. Red cells show top 20% hospots, green cells show top 10% hospots. A, Species richness (SR). B, Phylogenetic diversity (PD). C, Corrected weighted endemism (CWE). D, Phylogenetic endemism (PE). E, Evolutionarily distinct and grobally endangered (EDGE). F, Function diversity (FD). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subtropical zones and is a major climatic convergence zone in China. Furthermore, the Qinling Mountains are located at the intersection of the vegetation of North China, Central China, and the Hengduan Mountains, whereas the Huaihe River is often seen as the boundary between the central Chinese deciduous broad-leaf and northern evergreen broad-leaf forests. As a result, intersecting and complex local patterns of ecological niches indicate that a mixture of cold-tolerant, dry-tolerant, moisture-tolerant and heat-tolerant Lauraceae all occur in this region (Li, 1979; Li, 1992; Li, 1995; Huang et al., 2016a), possibly explaining the higher observed FD values.

Although extant Chinese Lauraceae are now restricted mainly to tropical and subtropical regions, with only a few temperate species, fossil evidence shows that the family was once widely distributed across the higher latitudes of Europe, Asia and North America (Friis et al.,

Table 2
The proportion of Lauraceae found in protected plant diversity hotspots in China.

	Species richness	Phylogenetic diversity	Corrected weighted endemism	Phylogenetic endemism	Functional diversity	Evolutionarily Distinct and Globally Endangered
Top 10 % hotspot	12 %	7.9 %	9.1 %	8.95 %	4.6 %	20.75 %
Top 20 % hotspot	7.1 %	7.4 %	8.99 %	8 %	13.33 %	18.54 %

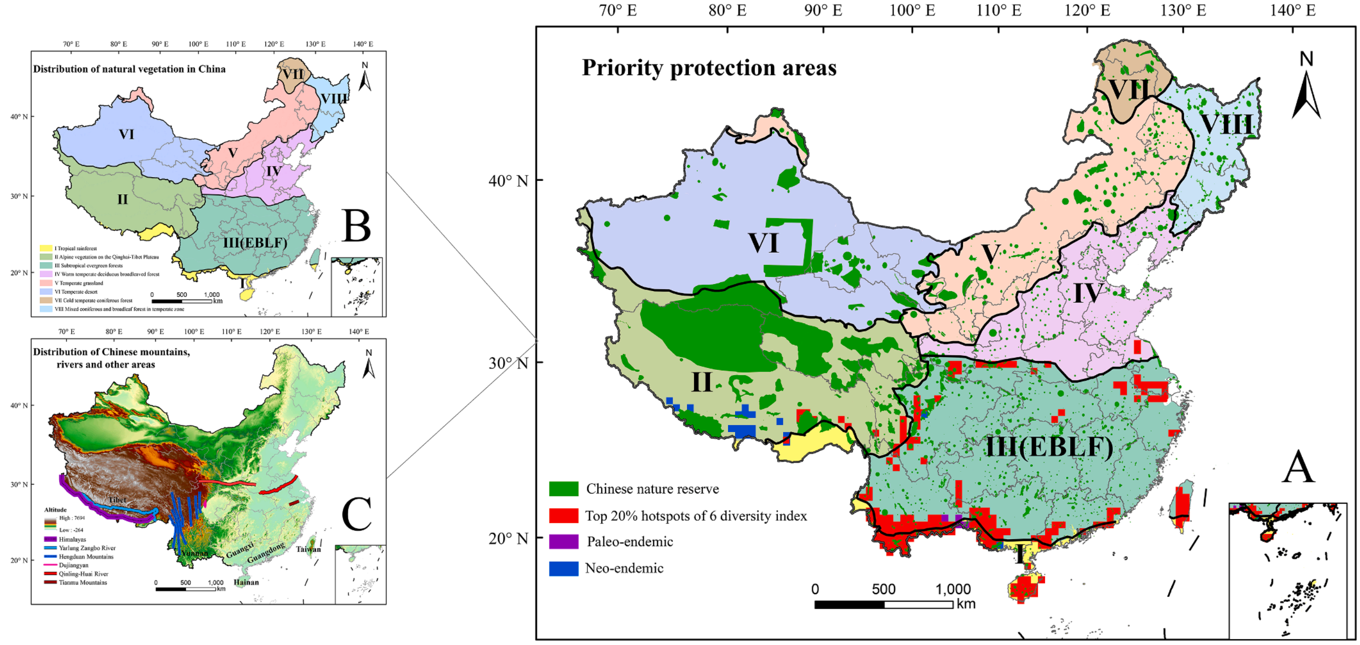

Fig. 7. A, Priority protection areas (overlap of nature reserves and top 20% hotspots for Chinese Lauraceae diversity indices); B, Distribution of natural vegetation in China (the bold black lines indicate the boundary between vegetation types (I, Tropical Forest; II, Qinghai–Tibet Plateau alpine vegetation; III, EBLF; IV, Deciduous Broadleaf Forest; V, Temperate grassland; VI, Temperate desert; VII, Cold temperate coniferous forest; VIII, Mixed coniferous and broadleaf forest in temperate zone); C, Distribution of Chinese mountains, rivers and other areas.

2011; Huang & Li, 2018), as well as the Southern Hemisphere (Cantrill et al., 2011; Bannister et al., 2012; Carpenter et al., 2012), implying higher past temperatures in these present-day temperate regions. This suggests it is necessary to exercise caution when inferring the possible causes or the refugial status of modern patterns for ancient lineages with previously wider distributions.

4.2. Neo- and paleo-endemism

Centers of endemism may arise either from newly differentiated species that have not expanded their distribution or from remnants of formerly widespread ancient species that are now confined to smaller areas. The CANAPE analysis identified that Lauraceae paleo-endemism occurs mainly at the border of Yunnan and Guangxi in South China in regions that also display high SR, PD, and PE. These metrics suggest that the region has fewer recently differentiated, closely related species than expected and conversely contains more ancient species with long branches. Southern China is recognized as one of the most important refugia for lineages that evolved prior to the late Neogene and Quaternary glaciations owing to the absence of severe continental glaciations during the Plio-Pleistocene (Myers et al., 2000; Gong et al., 2016). This region is also located at the intersection of East Asian and Indochinese flora, and climatic heterogeneity at local scales appears to have provided multiple, potentially long-term stable habitats for relict taxa to persist, including Lauraceae.

Neo-endemic centers of Lauraceae diversity mainly occur near the Yarlung Zangbo River and the middle section of the Himalayas in southern Tibet, where numerous heterogeneously complex habitats exist. The southern part of this area is adjacent to the northern edge of tropical Southeast Asia, and the northern and northwestern parts transition to the alpine zone of the Qinghai–Tibet Plateau. During the early Cenozoic, Lauraceae was the dominant group in the eastern Himalayas (Sun 2002). However, the uplift of the Qinghai–Tibet Plateau and subsequent development of the monsoons resulted in habitat heterogeneity and potential barriers for species dispersal, helping to drive rapid radiation events and leading to localized endemics that gradually became common components of the evergreen broad-leaved forests (Liu et al., 2017). Our study also found numerous mixed and super-endemic centers in southern Yunnan, Hainan and Taiwan, consistent with previous findings that southwest and South China represent a mixture of ancient and modern lineages, making them simultaneously “museums” and “cradles” of plant diversity (López - Pujol et al., 2011b; Lu et al., 2018; Zhu et al., 2021; Zhang et al., 2022).

4.3. Transitional areas as hotspots and priority areas for Lauraceae in China

If spatial biodiversity patterns are strongly congruent between SR, PD, and FD, conserve biodiversity by protecting a single indicator such as SR is possible (Rodrigues et al., 2005; Brooks et al., 2006; Spalink et al., 2018). In previous studies, a high degree of consistency between different components of biodiversity has been found (Barker, 2002; Tucker & Cadotte, 2013; Spalink et al., 2018); thus, it is easy to identify hotspots based on SR. However, hotspots based on SR do not adequately

Table 3

Stepwise regression equations and adjusted R^2 values of six Lauraceae diversity indices and environmental factors.

Biodiversity index	Intercept	Adjusted R^2	F value	Residual standard deviation	Significance
Species richness	36.6772	0.8278	793.3	11.61	2.2×10^{-16}***
Regression equation	SR = 36.6772 + 31.47bio2-27.38bio3-37.72bio5 + 66.44bio6 + 7.27bio12-4.45bio14 + 9.42bio16-9.24bio18-7.2bio19				
Corrected weighted endemism	3.927×10^{-3}	0.4768	226.3	0.003216	2.2×10^{-16}***
Regression equation	CWE = 3.9×10^{-3}-7.992×10^{-3}bio2 + 8.725×10^{-3}bio3 + 5.003×10^{-3}bio5-7.672×10^{-3}bio6 + 2.531×10^{-4}bio15 + 1.233×10^{-3}bio16				
Phylogenetic diversity	1.98221	0.8686	1634	0.4554	2.2×10^{-16}***
Regression equation	PD = 1.98221 + 0.12bio3-0.45bio4 + 0.69bio6 + bio14 + 0.47bio16-0.28bio18				
Phylogenetic endemism	0.0043	0.6227	350.4	0.003989	2.2×10^{-16}***
Regression equation	PE = 0.0044–0.011bio2 + 0.012bio3-0.002bio4 + 0.013bio5-0.015bio6 + 0.002bio16-0.0006bio19				
Function diversity	0.227	0.3798	125	0.05894	2.2×10^{-16}***
Regression equation	FD = 0.23 + 0.034bio3 + 0.1bio4-0.12bio5 + 0.17bio6-0.039bio14-0.039bio15 + 0.046bio17-0.028bio19				
Evolutionarily Distinct and Globally Endangered	0.122	0.4627	141.8	0.08144	2.2×10^{-16}***
Regression equation	EDGE = 0.12–0.24bio2 + 0.2bio3-0.122bio4-0.361bio6-0.088bio12-0.02bio15 + 0.066bio16 + 0.029bio19				

Note *** indicates a significant correlation at the < 0.001 level (two tailed).

capture PD and FD for some taxa (Tucker et al., 2012; D'agata et al., 2014) and in our study, there was a mismatch of spatial patterns among multifaceted biodiversity indices for Chinese Lauraceae. Therefore, more multifaceted biodiversity approaches are needed to explore priority areas for biodiversity conservation, as in other studies (Strecker et al., 2011; Pool et al., 2014; Xu et al., 2019; Zhu et al., 2021; Zhang et al., 2022). The hotspots of Chinese Lauraceae diversityare distributed mainly in transitional areas of the EBLF and other adjacent vegetation, similar to some of those reported for Chinese endemic plants (Huang et al., 2012) and evolutionary hotspots of seed plants in subtropical China (Fan et al., 2018).

Transitional zones between ecological communities are critical for conserving biodiversity (Allen & Starr, 1982; Smith et al., 2001) and although such zones are often underappreciated compared to hotspots, their significance for biodiversity conservation should not be ignored, especially in the context of climate change. SR and PD tend to peak in transitional zones (Kark & van Rensburgb, 2006; Gómez-Ortiz et al., 2017; Silva-Pereira et al., 2020) and these areas often contain many rare species (Kark et al., 2007), due to high local-scape spatial heterogeneity (Kark 2012). Transition zones also often correspond with sharp environmental gradients, contain more adaptive variation for species, communities, or ecosystems and have been considered areas of evolutionary novelty and centers for important ecological and evolutionary processes such as speciation in previous studies (Smith et al., 1997, 2001; Schilthuizen, 2000; Kark et al., 2007), where they are more adaptable to future climate and environmental changes. For example, some Chinese Lauraceae hotspots not included in transitional zones are distributed in the mountains with heterogeneous physiognomy, climates and environments, such as the Tianmu Mountains (Huang et al., 2012).

The biodiversity hotspots of southwest China and South China have attracted increasing attention because they serve as "museums" and "cradles" of plant diversity (Lopez-Pujol et al., 2011b; Lu et al., 2018; Zhu et al., 2021; Zhang et al., 2022); In addition, Hainan and Taiwan islands have dispersal barriers as they are isolated from the continental part of China, resulting in accelerated speciation, differentiation and endemism (Lomolino et al., 2006). Therefore, these areas should be considered priority targets for biodiversity conservation. However, for Lauraceae, our results showed that only 7.1–12 % of SR-, CWE-, PD-, and PE-defined diversity hotspots in southwest China and South China are currently protected. In addition, the coverage of protected areas in southwest China and South China is only approximately half of the average level in China (Cai et al., 2021) and the nature reserves in these areas are often fragmented and discontinuous. Accordingly, nature reserves located in these areas with high biodiversity should be optimized by improving connectivity for gene flow between adjacent nature reserves, establishing more nature reserves and/or expanding existing reserves to help protect regional biodiversity (Cai et al., 2021; Xu et al., 2019). Based on the spatial patterns of transitional zones and priority areas for Lauraceae, it is suggested that new conservation areas for Lauraceae and similar groups should be built or expanded to include transitional zones.

4.4. Climate factors drive the diversity pattern of Lauraceae

The effects of climate on plant diversity patterns are generally explained by a combination of the environmental energy hypothesis (Wright, 1983), water-energy dynamic hypothesis (O'Brien, 1998, 2006; O'Brien et al., 2000) and the cold tolerance hypothesis (Currie & Francis, 2004). However, there is no consensus on interpreting the climate and diversity patterns across different scales and taxonomic groups. For example, in the extremely arid regions of northwest China, water is considered to be the main limiting factor for explaining plant diversity; thus, the hydrothermal dynamic hypothesis is strongly supported (Li et al., 2011; Li et al., 2013; Wang et al., 2016); In contrast, in the forests of eastern China, the environmental energy hypothesis is used to explain tree diversity patterns (Wang et al., 2009).

In the present study, stepped regression and Pearson correlation analyses showed that the coldest month and lowest temperature had the highest explanatory rate and were significantly correlated with SR and PD, consistent with the cold tolerance hypothesis proposed in previous studies (Sakai & Weiser, 1973; Sakai & Malla, 1981; Currie & Francis, 2004; Nagalingum et al., 2015). This suggests that many species cannot survive in some areas because of their intolerance to low temperatures (Hawkins, 2001; Hawkins et al., 2003). Some Lauraceae species, such as *Lindera obtusiloba* Blume, *L. communis* Hemsl., *Cinnamomum septentrionale* Hand.-Mazz. and *C. camphora* (L.) J.Presl, have managed to spread to more northern subtropical and temperate regions by evolving functional characteristics to adapt to low temperatures (Li et al., 2008). Nevertheless, many members of the family, such as *Syndiclis* J.D.Hook., *Actinodaphne* Nees and *Cryptocarya* R.Br., are still confined mainly to the warmer region of South China (Li et al., 2008) and appear to have no mechanisms to resist cold.

In addition to temperature, water may also affect Lauraceae diversity, as SR and PD were significantly correlated with both average annual rainfall and average rainfall in the wettest season. Water allows plants to absorb and transport nutrients and plays an important role in biochemical reactions (Gurevitch et al., 2002; Clarke & Gaston, 2006; O 'Brien, 2006), seed maturation (Roberts, 1973), dormancy and phenology (Xu et al., 2014). Many Lauraceae are affected by water availability, including *Phoebe chekiangensis* C.B.Shang (Wu et al., 2016) and *Sassafras tzumu* (Hemsl.) Hemsl. (Liu et al., 2018). Thus, energy and water may jointly help determine the physiological and ecological mechanisms that affect the spatial distribution patterns observed in Lauraceae for SR and PD.

Although climate factors had a high explanatory rate for the SR and PD patterns observed in Chinese Lauraceae, they did not explain the observed patterns for CWE, PE, EDGE, and FD ($R^2 = 0.3798$–0.6227), suggesting that other factors contributed to the distribution patterns of these diversity indicators. For example, soil, altitude, habitat

Table 4
Standardized coefficient of regression equations and Pearson correlation coefficient.

Biodiversity index	Bioclimatic variables	Standardized coefficient	*t*-test	Significance	Pearson's *r*
Species richness	Bio2	31.47	11.808	$< 2 \times 10^{-16***}$	-0.621^{**}
	Bio3	-27.38	-11.2	$< 2 \times 10^{-16***}$	-0.08
	Bio5	-37.72	-16.825	$< 2 \times 10^{-16***}$	0.475^{**}
	Bio6	66.44	19.872	$< 2 \times 10^{-16***}$	0.835^{**}
	Bio12	7.27	3.682	$2.39 \times 10^{-4***}$	0.792^{**}
	Bio14	4.45	3.081	$2.1 \times 10^{-3**}$	0.564^{**}
	Bio16	9.42	5.1	$3.84 \times 10^{-7***}$	0.788^{**}
	Bio18	-9.24	-6.492	$1.15 \times 10^{-10***}$	0.740^{**}
	Bio19	-7.20	-4.725	$2.52 \times 10^{-6***}$	0.542^{**}
Corrected weighted endemism	Bio2	-7.992×10^{-3}	-11.377	$< 2 \times 10^{-16***}$	-0.06*
	Bio3	8.725×10^{-3}	13.563	$< 2 \times 10^{-16***}$	0.439^{**}
	Bio5	5.003×10^{-3}	8.414	$< 2 \times 10^{-16***}$	-0.06*
	Bio6	-7.672×10^{-3}	-8.633	$< 2 \times 10^{-16***}$	0.314^{**}
	Bio15	2.531×10^{-4}	2.353	$1.87 \times 10^{-2*}$	0.089^{**}
	Bio16	1.233×10^{-3}	8.252	$3.4 \times 10^{-16***}$	0.414^{**}
Phylogenetic diversity	Bio3	0.13	3.921	$9.21 \times 10^{-5***}$	0.144^{**}
	Bio4	-0.45	-14.995	$< 2 \times 10^{-16***}$	-0.646^{**}
	Bio6	0.69	28.991	$< 2 \times 10^{-16***}$	0.823^{**}
	Bio14	0.10	4.351	$1.45 \times 10^{-5***}$	0.521^{**}
	Bio16	0.47	8.423	$< 2 \times 10^{-16***}$	0.793^{**}
	Bio18	-0.28	-5.893	$4.69 \times 10^{-9***}$	0.751^{**}
Phylogenetic endemism	Bio2	-0.011	-10.774	$< 2 \times 10^{-16***}$	-0.219*
	Bio3	0.012	14.846	$< 2 \times 10^{-16***}$	0.35^{**}
	Bio4	-0.002	-2.888	$3.93 \times 10^{-3**}$	-0.6^{**}
	Bio5	0.013	7.54	$8.2 \times 10^{-14***}$	0.182^{**}
	Bio6	-0.015	-6.816	$1.36 \times 10^{-11***}$	0.54^{**}
	Bio16	0.002	11.704	$< 2 \times 10^{-16***}$	0.588^{**}
	Bio19	-0.0006	-3.972	$7.46 \times 10^{-5***}$	0.165^{**}
Function diversity	Bio3	0.034	6.056	$1.74 \times 10^{-9***}$	-0.103^{**}
	Bio4	0.1	8.763	$< 2 \times 10^{-16***}$	-0.203^{**}
	Bio5	-0.12	-11.134	$< 2 \times 10^{-16***}$	0.269^{**}
	Bio6	0.17	12.285	$< 2 \times 10^{-16***}$	0.434^{**}
	Bio14	-0.039	-3.559	$3.83 \times 10^{-4***}$	0.291^{**}
	Bio15	-0.039	-16.705	$< 2 \times 10^{-16***}$	-0.449^{**}
	Bio17	0.046	3.53	$4.28 \times 10^{-4***}$	0.305^{**}
	Bio19	-0.028	-4.283	$1.95 \times 10^{-5***}$	0.285^{**}
Evolutionarily Distinct and Globally Endangered	Bio2	-0.24	-11.238	$< 2 \times 10^{-16***}$	-0.104^{**}
	Bio3	0.20	12.659	$< 2 \times 10^{-16***}$	0.414^{**}
	Bio4	-0.122	-5.662	$2.22 \times 10^{-8***}$	-0.589^{**}
	Bio6	-0.361	-7.904	$4.95 \times 10^{-15***}$	0.359^{**}
	Bio12	-0.088	-5.206	$2.18 \times 10^{-7***}$	0.293^{**}
	Bio15	-0.02	-6.255	$5.09 \times 10^{-10***}$	-0.083^{**}
	Bio16	0.066	4.715	$2.62 \times 10^{-6***}$	0.349^{**}
	Bio19	0.029	3.718	$2.08 \times 10^{-4***}$	0.089^{**}

Note *, **, *** indicates a significant correlation at the 0.01, 0.001, 0.00 level respectively (two-tailed).

heterogeneity, and human activities may also play a role, as complex habitats can result in isolation, promotion of speciation, and impeding dispersal (Cun & Wang, 2010; Xing & Ree, 2017), resulting in higher CWE and PE values. Similarly, land clearing and other human-induced impacts can also lead to population fragmentation, isolation, and an increased risk of plant extinction, resulting in higher EDGE scores.

4.5. *Conservation implications*

Our findings showed that functional diversity and other diversity measures for Chinese Lauraceae are not spatially congruent, emphasizing the significance of incorporating various aspects of biodiversity as complementary surrogates of biodiversity into planning processes (Devictor et al., 2010; Safi et al., 2011; Xue et al., 2022) to meet the biodiversity goals of the United Nations 2030 Agenda for Sustainable Development (Hoban et al., 2020). The study also suggests that very few hotspots for priority conservation are currently located in nature reserves, with existing reserves are only partially protecting the variety of the Lauraceae. However, creating extensive nature reserves is challenging because the areas where Lauraceae are the most diversified are also eastern China's economic development hubs and densely populated. Therefore, it is advised that hotspots within these areas are protected by implementing the protection model of plant micro-reserves using a policy framework designed for Plant Species with Extremely Small Populations (PSESP) (Ma et al., 2013). In addition, our findings show that the biodiversity hotspots of Lauraceae in China overlap with transition areas for different vegetation types, indicating the significant conservation relevance of these sites for related taxa. Thus, in order to optimize protected areas in these regions, it may be necessary to recognize and preserve transitional zones between the EBLF and other vegetation type.

To improve the efficacy of conservation efforts for various taxa, we must particularly focus on the characteristic groups with have high species richness, ancient origins, and/or rapid rates of diversification. To achieve this, we must evaluate the spatial patterns of diversity using multifaceted approaches. Identifying biodiversity hotspots and undertaking gap analyses are both essential for bridging the evolutionary history, ecological traits, and practical conservation planning. Methodologies for the integration of diversity indices to identify hotspots still need to be improved in the future so that biodiversity assessment can lead to more successful conservation results.

In addition, the main drawbacks of the spatial pattern research caused by incomplete species distribution data, the limitations of the model simulation itself, and insufficient phylogenetic trees can hopefully be mitigated by future expansion of field surveys and collections, improving models, and better-resolved phylogenetic trees using NGS data.

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

Data will be made available on request.

Acknowledgements

We thank Dr. ZY Tang from Peking University for sharing the map of China's nature reserves. This study was supported by Yunnan Fundamental Research Projects (No. 202201AS070055), the National Natural Science Foundation of China (No. 31770569, No. 31500454), the Science and Technology Basic Resources Investigation Program of China (No. 2017FY100100, No. 2017FY100102), and Biodiversity Conservation Program of the Chinese Academy of Sciences (No. ZSSD-013).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110001.

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