

Spatial phylogenetics of the Chinese angiosperm flora provides insights into endemism and conservation

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Abstract

Background: The flora of China is well known for its high diversity and endemism. Identifying centers of endemism and designating conservation priorities are essential goals for biodiversity studies. We implemented a spatial phylogenetics analysis of the Chinese angiosperm flora at the generic level to identify centers of neo- and paleo-endemism. Phylogenetic endemism (PE) centers were compared with taxonomic endemism centers, and their implications for conservation were examined.

Results: (1) The majority of grid cells in China with significant PE were mixed- or paleo-endemism. The PE centers were mainly located in the mountainous regions. (2) Nine geographic centers of endemism were identified for 3,513 operational taxonomic units (OTUs). Four of these, found in northern and western China, were recognized for the first time. (3) Arid and semiarid regions were commonly linked to centers of significant PE, as has been found in other spatial phylogenetics studies worldwide. (4) Six high-priority conservation gaps were detected by overlaying the boundaries of China's nature reserves on these centers of endemism.

Conclusions: Mountainous regions are the "museums" and "cradles" for Chinese angiosperms, including both the mountains of southern and northern China. The areas we highlight as priorities are important for broad-scale conservation planning, especially in the context of evolutionary history preservation.

Background

Identifying 'centers of endemism' plays a prominent role in establishing biodiversity conservation priorities [1–5]. Centers of endemism have been widely recognized as potential refugia (i.e., paleo-endemism) or as places of more recent diversification (i.e., neo-endemism) [6, 7]. A center of paleo-endemism can be described as a location with an accumulation of many ancient lineages, which perhaps once had widespread or narrow ranges but have since contracted into their currently observed small range [3, 8, 9]. A center of neo-endemism can be considered an area that harbors many recently diverged species that have not migrated out of their area of origin [3, 8, 9]. Identifying paleo-endemism and neo-endemism centers and explaining their formation mechanism can help inform historical biogeography, evolution, and biodiversity conservation [10–13]. It should be noted that until the development of the methods applied here, centers of paleo- and neo-endemism were difficult to clearly distinguish in practice because of a lack of fossil evidence and a standard threshold for the geological time scale that can delineate temporal boundaries [14–16].

The absolute endemism concept, which is traditionally employed, identifies a center of endemism by the presence of taxa that are completely restricted to a particular area [17]. The taxonomic entity depends on the process of the taxonomic studies, which sometimes presents variable taxonomic status in different classification systems, especially at the species level. Thus, the quantitative research measures basing on the absolute endemism concept are suboptimal approaches. A more nuanced approach is to use a relative endemism concept based on range sizes of taxa [1, 18, 19], using indices of weighted endemism

(WE) and corrected weighted endemism (CWE). The relative endemism concept has been increasingly adopted in studies, because it can provide a quantitative measure to clearly and easily identify centers of endemism for a given area [1, 18, 19]. Rosauer *et al.* [20] extended the relative endemism concept to include phylogenetic trees, thereby incorporating evolutionary history into measures of endemism, and applied the concept of WE to all branches of a phylogenetic tree, which resulted in a phylogenetic endemism (PE) metric. PE methods have been developed to identify and distinguish centers of endemism using large spatial datasets [12]. Mishler *et al.* [12] proposed an integrating method called categorical analysis of neo- and paleo-endemism (CANAPE) to quantitatively distinguish between centers dominated by neo-endemism (range-restricted short branches) or paleo-endemism (range-restricted long branches). PE and CANAPE methods add an evolutionary perspective to understanding endemism and have drawn substantial attention [21–33]. Finding concentrations of endemic taxa and range-restricted OTUs provides a critical basis for conserving evolutionary history [5].

China has one of the richest floras worldwide, with more than 30,000 native vascular plant species and a high percentage of endemism (e.g., 52.1% of seed plant species are endemic) in the absolute sense [34]. China has approximately 2–8 endemic families; Ginkgoaceae and Eucommiaceae are uncontroversial paleo-endemic families, but debate remains over other several endemic families due to their variable taxonomic status [35–38]. Ying and Zhang [39] reported that China has 243 endemic genera of seed plants, and they identified three centers of endemism (Additional file 1: Figure S1a). Wang and Zhang [40] identified eight centers of endemism for 269 genera that are endemic to China (Additional file 1: Figure S1b). Using 12,980 seed plant species that are endemic to China [34], Huang *et al.* [41, 42] identified 19 centers of endemism for the Chinese flora (Additional file 1: Figure S1d). Lópes-Pujol *et al.* [3] identified 20 centers of endemism in central and southern China based on the distribution pattern of 555 Chinese endemic species (Additional file 1: Figure S1c). These studies all showed that mountainous areas harbored the largest number of endemism hotspots; in particular, the Hengduan Mountains and central China were two regions of critical conservation priority (Additional files 1 & 2). The previous studies are very helpful for understanding endemism and guiding biodiversity conservation in China, but they only focused on taxonomic endemism or used relatively coarse phylogenetic data (e.g., Huang *et al.* [41]). Therefore, a more comprehensive study from a phylogenetic perspective using more rigorous analytical measures needed to be conducted for the Chinese flora.

Mountains are frequently found to contain biodiversity hotspots and centers of endemism [3, 6, 15, 33]. Mountainous regions with high topographical diversity harbor numerous microhabitats, which can form refuges by buffering disturbances. At the same time, precipitous mountains are divided by river valleys and deep gorges shaping the highly dissected topography, which can contribute to speciation by vicariance [6, 33, 43]. Mountains are key features of China and host a substantial proportion of the plant species [44]. The mountains of southern China have been hypothesized to contain both paleo-endemics and neo-endemics [3, 6], based on the taxonomic richness of endemic seed plants. However, it has not been tested by incorporating spatial distribution and molecular phylogenetic information.

We used a spatial phylogenetics approach to study diversity and endemism in the Chinese angiosperm flora. Our goals were to: (1) explore phylogenetic diversity (PD) and PE patterns in the Chinese flora; (2) use CANAPE to identify centers of neo- and paleo-endemism; (3) examine similarities and differences between centers of endemism identified in previous studies and those found in this study; (4) evaluate the hypothesis that mountains are areas that contain a high amount of neo- and paleo-endemism; and (5) identify priority conservation gaps from a PE perspective.

Results

Observed diversity and endemism

The location of areas mentioned in this paper are illustrated in Fig. 1. Hengduan Mountains, Yunnan–Guizhou Plateau, Guangdong–Guangxi mountainous areas, Hainan Island, Taiwan Island, and east Sichuan–west Hubei had the highest generic richness (GR) and PD (Fig. 2 a, c). Southern China, especially the Yunnan–Guizhou Plateau, Guangdong–Guangxi mountainous areas, Hainan, Taiwan, Hengduan Mountains, and east Sichuan–west Hubei, had the highest WE and PE values (Fig. 2 b, d). Other areas in southern China showed moderate levels of WE and PE. A moderate level of endemism was also identified in a small number of cells in the Tianshan–Altai Mountains and Changbai Mountains. There were low levels of endemism in the hinterland of the Qinghai–Tibet Plateau (QTP), the Tarim Basin, the Inner Mongolian Plateau, North China, and Northeast China.

Spatial randomization for PD and RPD

Randomization tests of PD and RPD were conducted using both a phylogram and a chronogram. The significance test for PD using the phylogram (Fig. 3a) showed that almost all cells in western China, and scattered cells in eastern China, were significantly low in PD, while significantly high PD cells were only found on Taiwan Island (Fig. 3a). Using the chronogram, the significantly low PD areas extended to northeast China, while significantly high PD cells were identified in southern China (Fig. 3c). The significance test for RPD using the phylogram (Fig. 3b) showed widespread areas with significantly high RPD (i.e., areas that contain longer phylogenetic branches than expected) including the Daxing'anling and Changbai Mountains in Northeast China, the Tianshan–Altai Mountains and northeast Qinghai–central Gansu in Northwest China, Guangdong Province, Taiwan, and Hainan Island. Areas with significantly low RPD (i.e., areas that contain shorter branches than expected; Fig. 3b) were scattered in central China, central Tibet in the QTP, and the Kashi area in the arid regions of the Tarim Basin (Fig. 3b). Using the chronogram, grid cells with lower RPD than expected were mainly located in the northwest, while those with significantly high RPD were concentrated in southern China (Fig. 3d).

While the significant patterns between phylogram and chronogram had distinct differences, their overall trends were similar. The lower than expected PD and RPD were mainly located in western and northern regions, such as Xingjiang, Qinghai, Tibetan, Gansu, and similar arid areas (Fig. 3). Higher PD and RPD than expected were distributed in southern regions, containing Taiwan and Hainan, with a warm and humid subtropical/tropical climate.

Centers of phylogenetic endemism

A total of 113 grid cells with significantly high PE values were identified by CANAPE using the chronogram with all OTUs included (Fig. 4a). Nine geographic centers of endemism can be recognized, numbered here as labeled in Fig 4a: (1) the largest center of endemism was located south of the Tropic of Cancer in the mainland; other centers included (2) Hainan Island, (3) Taiwan Island, (4) the Lhoka Prefecture area, (5) the Shigatse area (on the periphery of Qomolangma), (6) the Ali Plateau, (7) the Kashi area, (8) the Tianshan–Altai Mountains, and (9) the Changbai Mountains. The majority of grid cells with significant PE showed mixed- or super-endemism (Fig. 4a). Of all centers of endemism, area 1 contained the most extensive amount of mixed- and super-endemism cells. Ten grid cells showed significant concentrations of neo-endemism; they were all located in the Shigatse area, the Ali Plateau and the Tianshan–Altai Mountains in western China (Fig. 4a). Fifteen grid cells dominated by paleo-endemism were scattered in the Changbai Mountains, the coastal area of Guangdong and Guangxi, Taiwan, and Hainan Island (Fig. 4a). All paleo-endemism centers were distributed in eastern China. The endemism center of Kashi area was located in the Tarim Basin, and the others were located in the mountainous regions.

To reduce border effects, we also conducted a CANAPE analysis using the chronogram for the 154 Chinese endemic genera only. Nine centers of endemism were obtained containing 61 grid cells (Fig. 4b). Of those 61 grid cells, 41 cells overlapped with significant cells found using all OTUs, which were located in four endemism centers of the mountainous areas of southern China, Hainan, Taiwan and Lhoka prefecture area–Hengduan Mountains (Fig. 4b, locations 1–4). Additionally, five small centers of endemism were identified in central and northern China (Fig. 4b, locations 5–9).

Conservation gaps

Of the total of 133 significant grid cells discovered in both of the above CANAPE analyses, 27 cells across six regions had no overlap with current nature reserves in China (Fig. 5a). Most of the conservation gaps were located in the Tianshan–Altai Mountains (Fig. 5a F), along the southwest edge of Junggar Basin in Northwest China. The other four regions were scattered in the Ali Plateau (Fig. 5a D), the Shigatse area (Fig. 5a C) and Lhoka Prefecture area (Fig. 5a B) in the QTP, the Kashi area (Fig. 5a E) in Northwest China, and the Ailao–Jinzhong–Shibalian Mountains (Fig. 5a A) in Southwest China.

Discussion

Patterns of phylodiversity

The PD patterns are commonly different between measurements using a phylogram or a chronogram, thus the interpretation for distinct PD hotspots should be carefully distinguished [21, 45]. Significantly low PD, called "phylogenetic clustering", is likely indicative of habitat filtering [46]. Closely related organisms often share an evolutionarily conservative habitat preference, thus the organisms living together in a particular habitat will tend to be more closely related than expected by chance. Past studies

[21, 28, 29, 32] have shown that this was especially prevalent in dry habitats, a pattern which was confirmed here. Significantly low PD was observed in arid areas using both phylogram and chronogram, suggesting another potential explanation for the phylogenetic clustering: recent diversification *in situ*. This explanation was supported by the significantly low RPD seen in these regions, because RPD is better designed to detect radiations since it takes into account relative branch lengths.

Significantly high PD, called "phylogenetic overdispersion", may be indicative of another ecological process, competitive exclusion [46]. This was only observed here on Taiwan Island using the phylogram, which may be because our study encompassed a very broad area covering several biomes. Interestingly, significantly high PD was noticeably clustered in southern China using the chronogram. It is likely that the phylogenetic overdispersion there may be related to the extinction of related genera over time, as these floras are composed of older elements. This interpretation is supported by the observation of significantly high RPD in the southeast.

The discovery of several areas of significantly high RPD in northern, central, and southern China (blue areas in Fig. 3b, d) indicates that the flora of those areas contains unusually long branches, i.e. those with relatively few close relatives within China. This suggests that the flora is relatively old, containing many relictual lineages, especially in southern China (Fig. 3d). In some cases, especially those close to the Chinese border, it could also indicate the presence of lineages that belong to larger clades that predominantly occur outside China, e.g., the extreme southeastern tropical area of the country. The area of significantly low RPD in the middle of the QTP and northwest China indicates that the flora there contains unusually short branches, pointing to a potential evolutionary rapid diversification of a lineage into many lineages there. All these regions would be worthy of further studies into the processes responsible for the modern phylodiversity patterns.

Centers of phylogenetic endemism in northern China

The Tianshan–Altai Mountains and Changbai Mountains are boreal mountains located in northern China; these areas and the Kashi area were identified as centers of phylogenetic endemism for the first time by our study. This result adds a crucial addition to the previous non-phylogenetic studies of centers of endemism in China (Additional file 1).

The arid Northwest China biome was influenced by significant climatic oscillations and environmental changes in the Quaternary [47]. There are multiple separate glacial refugia for plants located in the Tianshan–Altai Mountains, such as those for *Hippophae* [48], *Gymnocarpus przewalskii* [49], and *Reaumuria soonarica* [50]. Our results confirmed the above conclusions. The flora of this region was derived from Tethys coastal xerophytes or immigrated from East Asia, and the flora is xeromorphic and ancient [47, 51]. This region's aridification began in the early Miocene, and drastically increased by desert expansion during the Pleistocene [52, 53]. The lower elevation valleys or mountainous edges of the Tianshan–Altai Mountains likely served as refugia in the Quaternary [47]. During the interglacial periods, refugial lineages may have been able to expand their ranges. Meanwhile, this region's aridification also stimulated plant diversification [54–57]. These interpretations are supported by our CANAPE results,

which showed that both relictual endemics (rare long branches) and young endemics (rare short branches) are concentrated in the region. In particular, mixed-endemism is concentrated in the Tianshan Mountains, which contains long-branch genera that survived extinction events. The area from Junggar Basin to the Altai Mountains has mainly mixed-endemism. These results indicate co-occurrence of some relict genera with range-restricted long-branches and young genera with range-restricted short branches in these areas. These young genera are concentrated from the Tianshan Mountains to the Altai Mountains and show significantly low PD, especially at the edge regions between mountains and desert. The aridity of this center of endemism might drive rapid diversification in its core areas of the Gurbantunggut Desert in Junggar Basin [54–57].

The center of phylogenetic endemism discovered in the Changbai Mountains is dominated by paleo-endemism. Our results indicate that these mountains have served as refugia for multiple lineages. Some genera present here, such as *Anemarrhena*, *Mukdenia*, and *Schisandra*, are long isolated branches in the phylogenetic tree, likely because of extinction of close relatives. The preservation of some Tertiary relict plants in the Changbai Mountains refugia was confirmed by previous studies on Asian butternuts (*Juglans* section *Cardiocaryon*) [58, 59]. Fossil evidence indicated that the Asian butternuts' ancestors were widespread in higher latitudes in the northern hemisphere during the early Miocene and then migrated southward because of the late Neogene cooling climates [59]. Extant Asian butternuts are distributed in two large independent refugia, and one of them is in Northeast China with several small-scale refugia scattered across the Changbai Mountains [58].

The linkage of centers of endemism with arid regions seen in this study supports similar findings in other studies. For example, the Sonoran Desert and Chihuahuan Desert were also inferred to have concentrations of paleo-, neo-, super-, and mixed-endemism based on spatial phylogenetic studies of vascular plants in California [21] and Mexico [32]. Likewise, the relatively younger biome of arid areas in northern Chile and the interior of Australia showed mixed- and neo-endemism [28, 29]. Arid and semiarid centers of endemism generally receive less attention and conservation globally because of their lower observed richness at all taxonomic levels, yet the CANAPE approach provides a new view of the unique evolutionary history contributed by xeromorphic lineages.

Centers of phylogenetic endemism in southern China

The QTP is the largest, highest, and youngest plateau in the world, and has experienced several uplift events from the early Miocene to the Quaternary [43]. In the QTP, the Himalayan and Hengduan Mountains were previously recognized as areas of high biodiversity and endemism, with many young endemic species [41, 60]. The Shigatse and Lhoka Prefecture centers in Himalaya identified in our CANAPE results are consistent with those recognized by Huang *et al.* [41] and Zhang *et al.* [60]. The neo-endemic Ali Plateau center is identified for the first time in this study. Several previous studies indicated that most endemic genera of the QTP originated *in situ* or in adjacent regions [61–64], and we also detected several cells significantly dominated by neo-endemism. The significant centers of endemism found using all OTUs did not include the middle section of the Hengduan Mountains, which has been

identified as a center of endemism by previous studies based on traditional taxon-based measures [3, 39–41], as well as the Lhoka prefecture area–Hengduan Mountains center identified using only the endemic OTUs in this study (Fig. 4b, locations 4). This difference is mainly because we used OTUs representing genera in the present study. Several lineages on the QTP have been reported to have undergone extensive radiations in the last million years at the species level [43]; for example, *Rhododendron* is a species-rich genus of Ericaceae, and many of these species (ca. 159) have restricted distributions in the QTP [65]. Molecular data indicated that the rapid radiation of the *Rhododendron* subgenus *Hymenanthes* was driven by hybridization among lineages in the Himalayan region [66–68]. As our study was limited to the genus level, it does not address evolution at the species level. Thus, unlike paleo-endemism, neo-endemism is underrepresented in this study (as discussed in a similar genus-level analysis of the Australian flora by Thornhill *et al.* [28]). In the future, as more molecular data at species level become available, patterns of neo-endemism can be better estimated.

Southern China is mountainous with a warm and humid subtropical/tropical climate. In our CANAPE analyses, the southern Chinese mountainous areas (including Taiwan and Hainan Islands) are supported as refugia; these findings were consistent with several other lines of evidence [3, 6, 41].

Conservation concerns

CANAPE can be used to identify areas with significant concentrations of range-restricted long or short branches [26], thus areas harboring relict or new lineages. In our study, nearly all centers of phylogenetic endemism corresponded to mountain ranges. The topographic heterogeneity and relatively stable microclimate of mountains are often cited as being conducive to endemism [1, 6, 7, 69]. Compared with existing nature reserves, our results showed that the majority of the conservation gaps occur in Northwest China (Fig. 6, locations E, F). These conservation gaps in the extensive arid areas include more xeromorphic plant lineages than other areas of China. Additionally, we found that gaps in the Ailao–Jinzhong–Shibalian Mountains should receive conservation attention in the near future (Fig. 6, location A). These conservation gaps are located in the junction of the three mountains and can provide migratory corridors for plants. Several conservation gaps in QTP were also identified in the Ali Plateau, Shigatse area, and Lhoka Prefecture range (Fig. 6, location B, C, D). Consequently, it is vital to provide more protection to the conservation gaps described above by reducing human disturbance in these areas. Range-restricted taxa require long-term, stable habitats to persist. Spatial phylogenetic methods allow us to develop approaches for conserving the diversity of rare lineages from an evolutionary standpoint.

Possible limitations due to border effects

Most centers of endemism detected here are near the borders between China and its neighboring countries (Fig. 4). Unlike studies done on biogeographic islands or isolated regions (e.g., Australia [28], and the New Zealand archipelago [70]), our results are more likely to be influenced by a political border, which may cut off a broader floristic region containing lineages with restricted ranges in China but are more broadly distributed across the border. On the other hand, the high-degree of overlap between the

centers of endemism detected when using only endemic OTUs and when using all OTUs indicates that most centers near the border of China are reasonable.

WE and PE are relative only to a given study region, something that is true for all biodiversity metrics. Until the data exist to complete a global scale spatial phylogenetic study, this will remain a cause of potential problems with interpretation. Nonetheless, even if some of the relative endemism seen here is only local, it is still significant for biogeographic understanding of the region. Furthermore, it is quite significant for conservation, given that organisms that are rare within the boundaries of a country or other management areas even if present elsewhere.

Conclusions

Our investigation used an evolutionary framework to discover new and different patterns compared with traditional non-phylogenetic approaches to biodiversity assessment. These findings help us better interpret endemism patterns and their causes. We identified nine significant centers of phylogenetic endemism for 3,513 OTUs in China, four of which were not previously described, that can be used for comparison with previous taxonomic centers of endemism. Furthermore, we detected six conservation gaps among these centers. Eight endemism centers are concentrated in the mountainous regions. Our results support and develop the hypothesis that mountainous regions are both plant “museums” and “cradles”, involving the mountains of both southern and northern China. The arid and semiarid regions require additional conservation attention in the future, because these regions have been largely ignored in the past. Our results provide useful information that should be used for conservation planning that is increasingly urgent in the face of rapid land-use and climate change due to human activities.

Methods

Phylogenetic reconstruction and spatial data

The phylogenetic analyses in this study were respectively conducted based on a phylogram and a chronogram of the Chinese angiosperm genera provided by Chen *et al.* [71] and Lu *et al.* [72]. The phylogenies contained 5,864 species belonging to 2,665 native genera of angiosperms in China, which represented approximately 92% (2,665/2,884) of the Chinese vascular plant genera. Among the sampled genera, non-monophyletic genera accounted for 14.3% (380/2665). Monophyletic OTUs in the phylogeny are important for analysis and understanding of evolutionary relationships and phylogenetic patterns. Therefore each monophyletic lineage within non-monophyletic genus was made a single OTU. In total, we obtained 3,513 OTUs in the phylogeny. The phylogenies are archived in the DarwinTree website (<http://www.darwintree.cn>) and Dryad (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.p89m3>). The Chinese angiosperm flora has 199 (ca. 6.9%, 199/2884) endemic genera [34]. Among the 3,513 OTUs, 154 OTUs are sampled on the phylogenies representing 145 endemic genera.

The spatial distribution dataset is the same as that used in Lu *et al.* [72], which was normalized at the county level. A total of 1,397,452 records were contained in the dataset representing 26,973 native angiosperm species and 2,591 native angiosperm genera. We followed their methods to divide the map of China into 100 × 100 km grid cells, and used the standard map of China (<http://www.sbsm.gov.cn>; review drawing number: GS (2016)1576). Before conducting spatial phylogenetic analyses, we assessed the collection density of the spatial dataset to exclude areas with low sampling rates. Following Dagallier *et al.* [33], we adopted as a threshold of at least 100 records in a grid cell. The collection density figure is shown in additional file 3. The spatial dataset is available from http://www.darwintree.cn/resource/spatial_data

Spatial phylogenetic analysis

We used Biodiverse V2.0 [73] to calculate six metrics: GR, WE, PE, RPE, PD, and RPD [12]. Then, a total of 999 iterations of a randomization test were run using the “rand_structured” model for PE, RPE, PD, and RPD. CANAPE was carried out as described in Mishler *et al.* [12] and Thornhill *et al.* [28].

Priority conservation gap identification

To identify conservation gaps for the centers identified by CANAPE, the significant CANAPE cells were overlaid with the distribution of protected areas in China (i.e., nature reserve boundaries). Within mainland China, four different levels of nature reserves are administered by different levels of government: national, provincial, municipal, and county. The national nature reserves (NNRs) and provincial nature reserves (PNRs) have tougher regulations and receive more manpower and funding than the other two levels. Here, we used the digitization of all terrestrial nature reserves in mainland China by Zhang *et al.* [74] using geographical information system techniques in ArcGIS 10.2 software. The spatial database of nature reserves contained 319 NNRs and 835 PNRs before the end of 2012. Each one of the NNRs and PNRs had a long-established time in the map list, and protective efficacy stands the test of time. The earliest and latest reserves were established in 1956 and 2006, respectively. The protected areas of Taiwan were downloaded from the Database of Protected Areas (<https://www.protectedplanet.net/>; accessed August 2017). Grid cells with no nature reserves covered were designated as “conservation gaps”.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

All data were generated and analyzed during this study are included in published articles [71–72] and the distribution data are deposited in the DarwinTree website (http://www.darwintree.cn/resource/spatial_data).

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

ZDC and JTM conceived the project. XXZ conducted the phylogenetic analyses. SWL checked the phylogenetic results. XXZ, JFY, SWL, BDM, and AHT analyzed the results. XXZ and JFY drafted the manuscript. LML, LFM, BL, YHC, and AML participated in improving and revising the manuscript. All authors wrote, edited and approved the manuscript.

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Abbreviations

CANAPE, Categorical Analysis of Neo- and Paleo-Endemism; OTU, Operational Taxonomic Unit; GR, Generic Richness; PD, Phylogenetic Diversity; PE, Phylogenetic Endemism; RPD, Relative Phylogenetic Diversity; RPE, Relative Phylogenetic Endemism; WE, Weighted Endemism; QTP, Qinghai–Tibet Plateau

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Figures

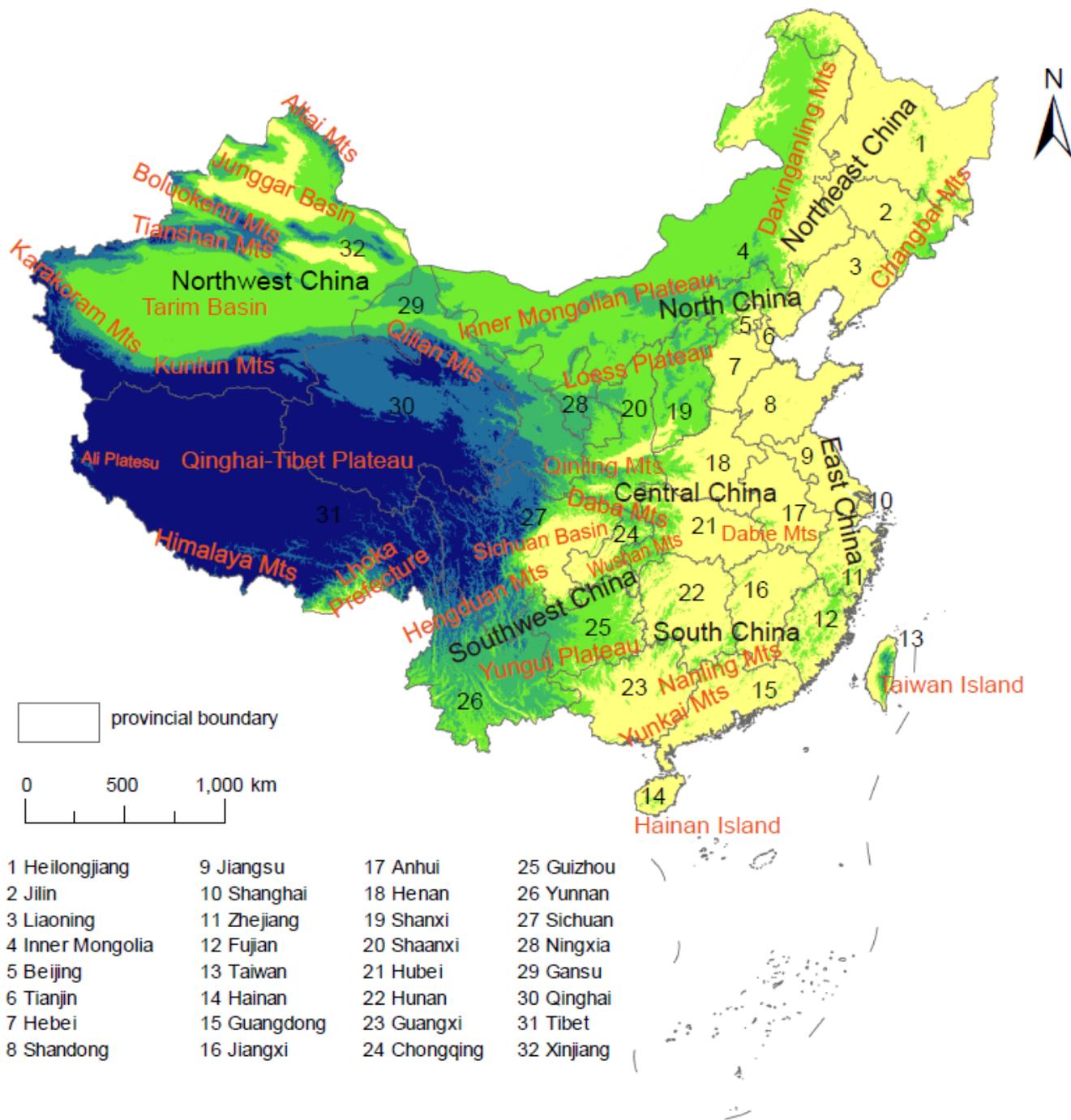
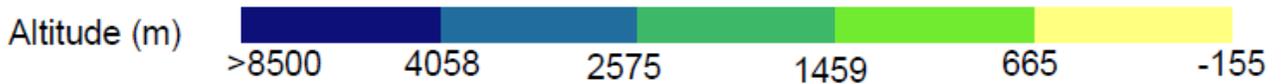


Figure 1

Topographic map of China showing locations mentioned in this study. Mts, Mountains. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

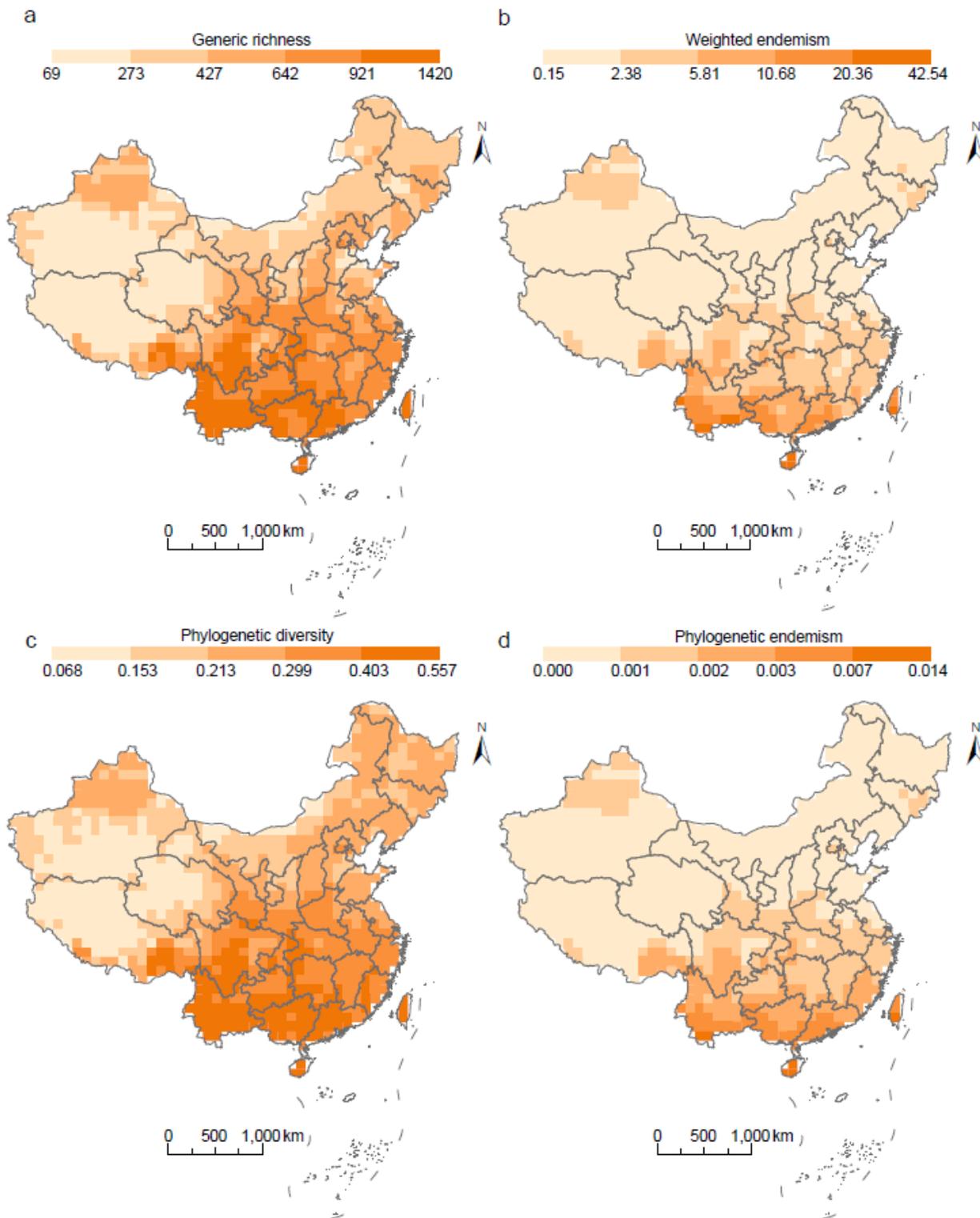


Figure 2

Observed endemism of the Chinese angiosperm genera. a Generic richness (GR), b weighted endemism (WE), c phylogenetic diversity (PD), and d phylogenetic endemism (PE). Both PD and PE are based on phylogram. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal

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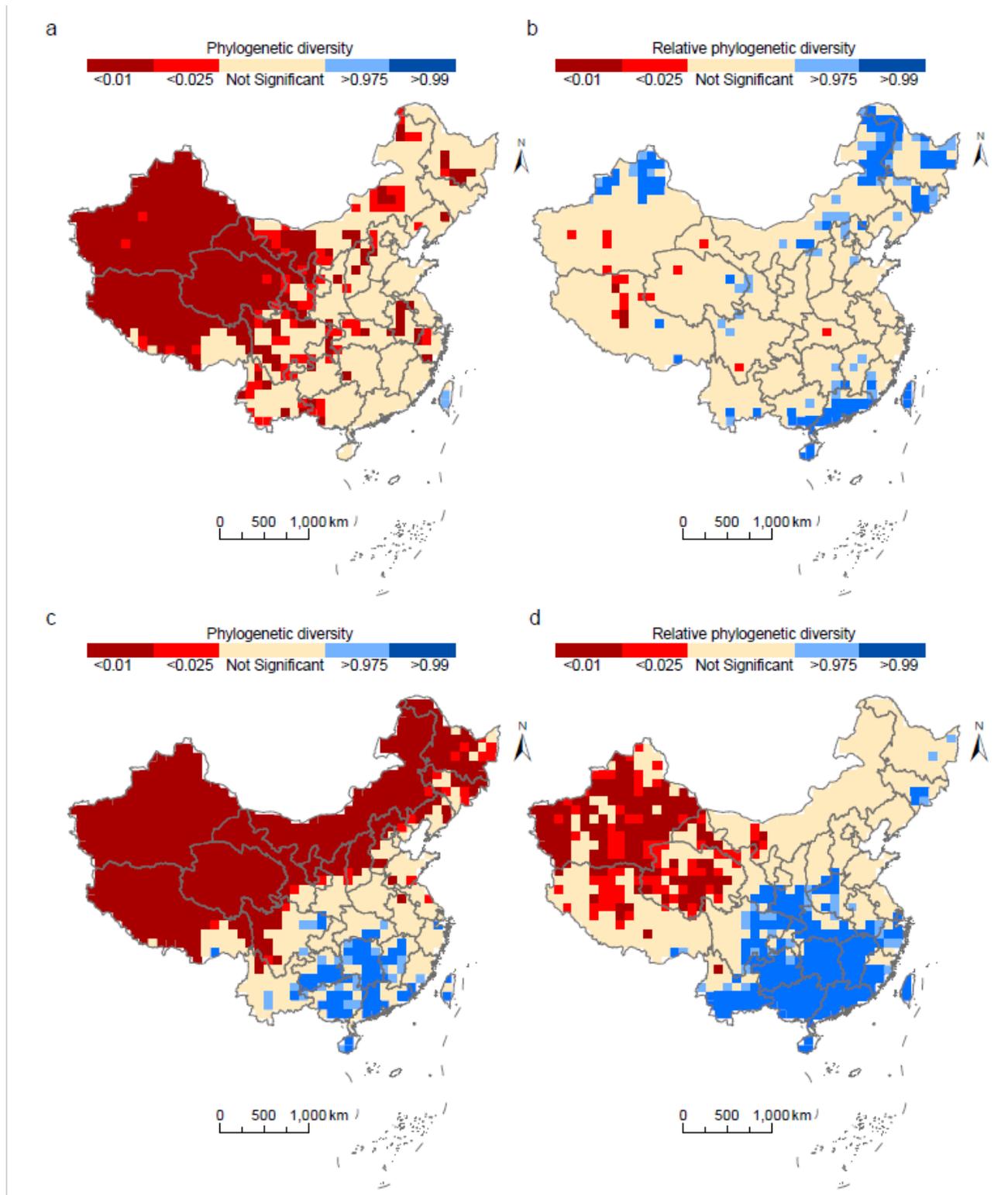


Figure 3

Significance results from randomization test. a Phylogenetic diversity using phylogram. b Relative phylogenetic diversity using phylogram. c Phylogenetic diversity using chronogram. d Relative phylogenetic diversity using chronogram. Note: The designations employed and the presentation of the

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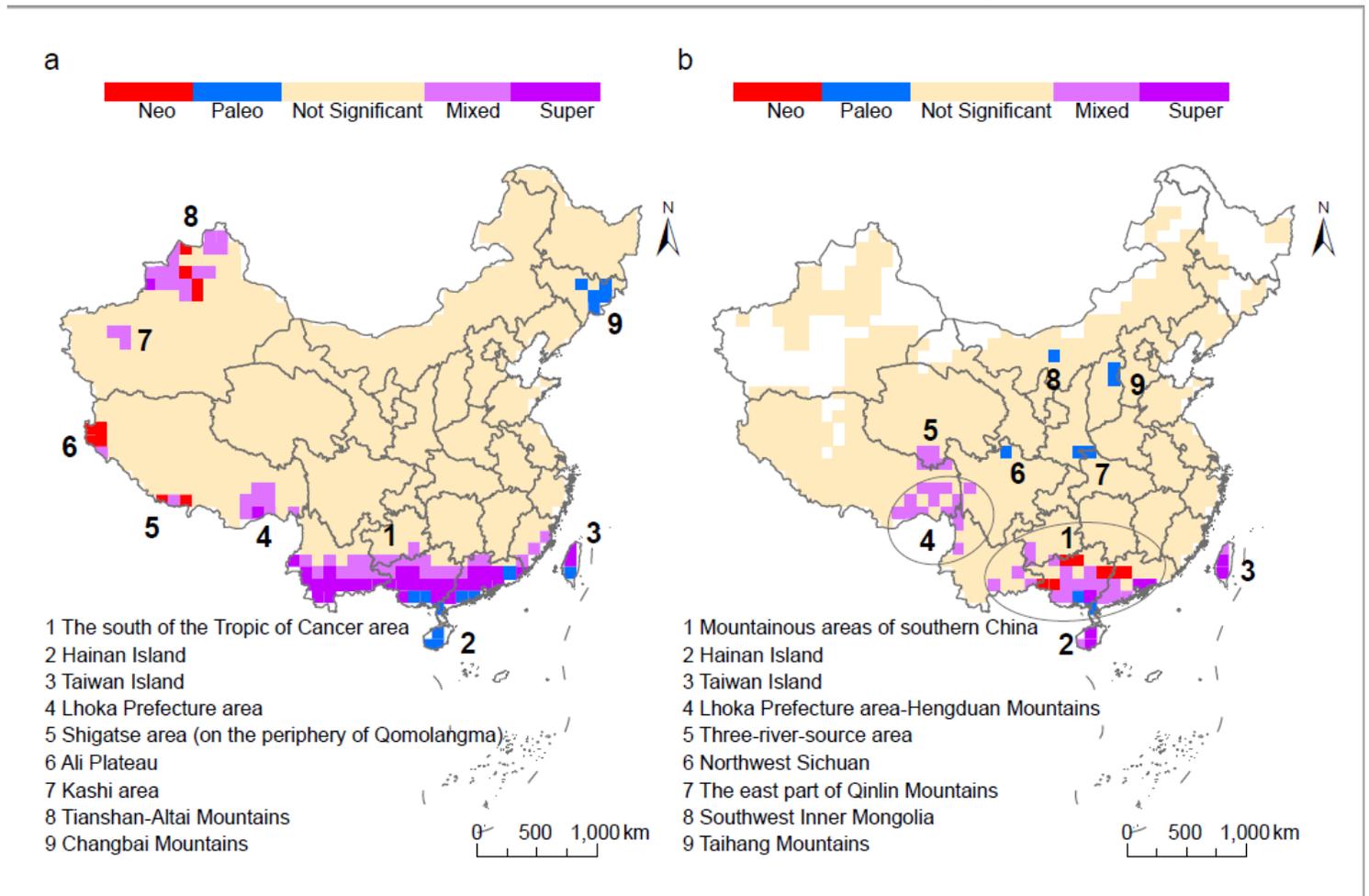


Figure 4

Centers of phylogenetic endemism discovered by CANAPE analysis using the chronogram. a Centers found using all OTUs. b Centers found using only endemic OTUs. Beige cells are not significant. Red cells indicate a concentration of neo-endemism. Blue cells indicate a concentration of paleo-endemism. Purple cells represent a mixture of neo- and paleo-endemism; darker purple cells show super-endemism (i.e., highly significant PE). The code numbers (1–9) refer to centers of endemism discussed in text. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

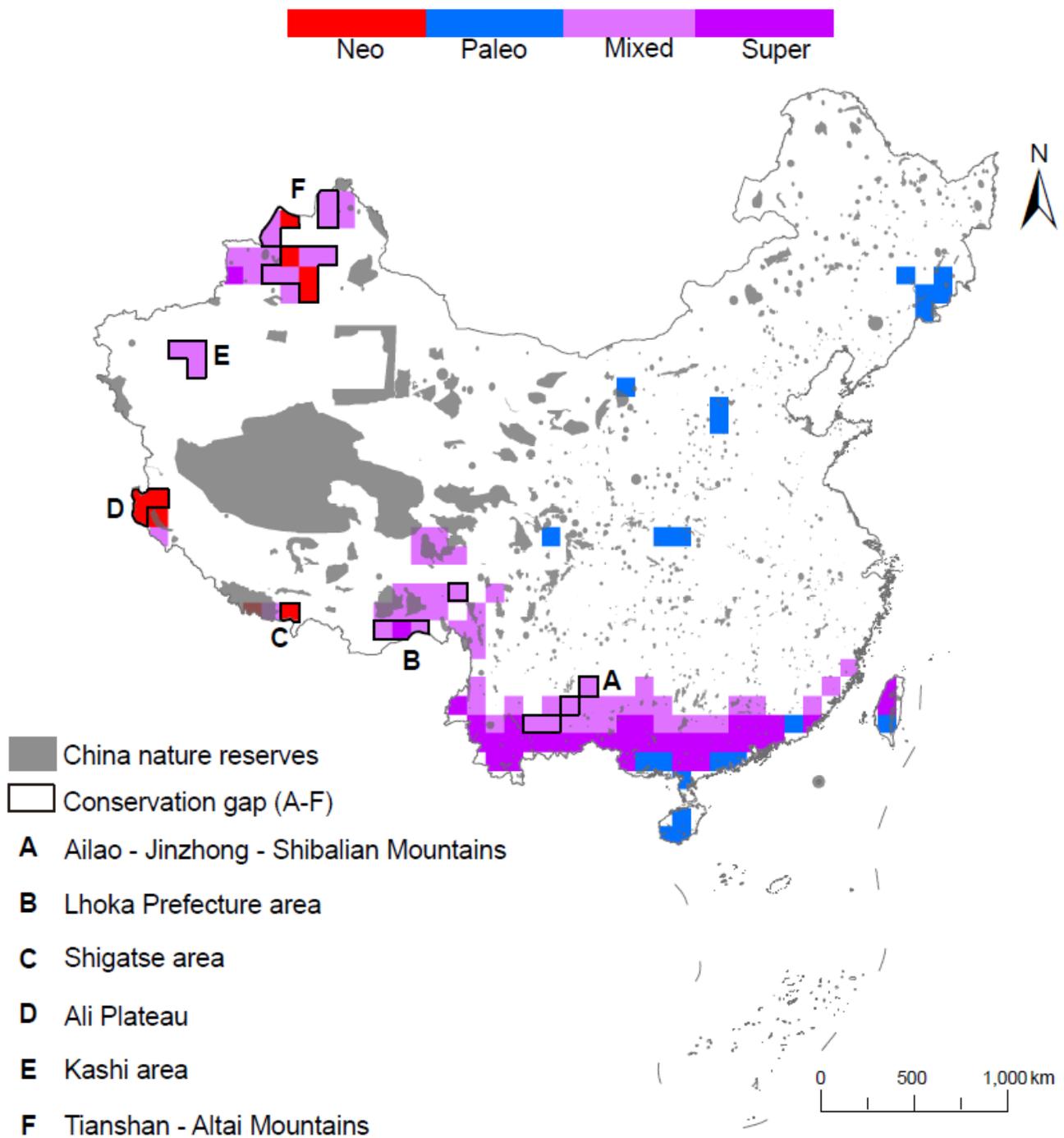


Figure 5

Overlap between grid cells with significant endemism in CANAPE and nature reserves in China. The code numbers (A–F) refer to conservation gaps discussed in the text. Grid cells with significant value were obtained from Fig. 4a and 4b. If one cell appeared both in Fig. 4a and 4b, its color was same as Fig. 4a. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any

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