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Geographical patterns in phylogenetic diversity of Chinese woody plants and its application for conservation planning

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Abstract

Aim: Biodiversity hotspots are widely used as conservation priorities to preserve the tree of life. However, many conservation practices identify biodiversity hotspots without considering phylogenetic diversity (PD), which reflects total evolutionary history and feature diversity of a region. Moreover, conservation planning rarely distinguishes between neo- and palaeo-biodiversity hotspots despite their differences. Here, we (a) estimated large-scale patterns in PD of woody plants, (b) identified neo- and palaeo-biodiversity hotspots and (c) demonstrated their implication in conservation planning, with special focus on Hengduan Mountains and southern China.

Location: China.

Methods: Distributions of 11,405 woody species from the *Atlas of Woody Plants in China* were updated and were transformed into a grid of 50 × 50 km². By integrating distribution maps with a genus-level phylogeny of angiosperms, we estimated Faith's PD of each grid cell and evaluated the contribution of species relatedness to PD at given levels of species diversity (i.e. standardized PD, sPD) using regressions and three null models. Then, we identified areas with significantly lower or higher sPD than expected as neo- and palaeo-hotspots and estimated the coverage of protected areas in these regions.

Results: Species diversity and PD decreased towards the north. Southern China had high species diversity, PD and sPD, while Hengduan Mountains had high species diversity and PD but low sPD. The coverage of protected areas in southern China was less than half of that in Hengduan Mountains and entire China.

Main conclusions: Our results identified Hengduan Mountains as a neo-hotspot and southern China as a palaeo-hotspot, highlighting their importance for biodiversity conservation. Compared to Hengduan Mountains, southern China has low coverage of protected areas, which calls for more conservation attention. Our study demonstrates a way of incorporating the phylogenetic component in the identification of neo- and palaeo-hotspots, and hence of achieving a more complete perception of biodiversity patterns for conserving the tree of life.

KEYWORDS

biodiversity hotspots, biological conservation planning, Hengduan Mountains, phylogenetic diversity, species richness pattern, woody plants

1 | INTRODUCTION

The increase in human population and human activities has driven the current rate of species extinction to c. 100 to 1,000 times of the background extinction rate (Pimm et al., 2014; Steffen et al., 2015). Identifying conservation priorities is critical for the spatial planning of protected areas. Several criteria have been widely used to identify conservation priorities, including the number of total (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000), endemic (Mittermeier et al., 2003) and threatened species (Beger et al., 2015), land tenure (Olson & Dinerstein, 1998) and habitat loss (Hoekstra et al., 2005; Sanderson et al., 2002). However, most of these criteria hardly reflect phylogenetic diversity (PD; Faith, 1992), which is acknowledged as an important biodiversity dimension representing feature diversity and the option values of biodiversity (Carstensen et al., 2013; Faith, 2013). Several indices have been used to evaluate PD (Dan et al., 2009; Isaac et al., 2007; Tucker et al., 2016; Webb, 2000), among which Faith's PD, defined as the total branch lengths of the minimum tree spanning all species of an area (Faith, 1992), has been most widely used.

As illustrated by Faith (1992, 2018), feature diversity represents the amount of species features within an area or community. As species features are not all directly measurable, PD has often been used as a quantitative measure to evaluate feature diversity based on the hypothesis that shared features can be explained by shared ancestry (Faith, 1992, 1994). Using the permutation tail probability test (Faith & Cranston, 1991) and other methods, several studies have identified the positive linkage between feature diversity and PD based on empirical trait data for different groups (e.g. Mazel et al., 2018; Slowinski & Crother, 1998; Tucker, Davies, Cadotte, & Pearse, 2018; Wilkinson, Peres-Neto, Foster, & Moncrieff, 2002). These studies suggest that PD reflects the accumulation of species features (Faith, 2016) and is complementary to the measures representing other dimensions of biodiversity (Faith, 1994, 2010).

Studies have also highlighted the positive relationship between feature diversity and biodiversity option values—the potential unanticipated needs that future generations may be able to benefit from biodiversity (International Union for Conservation of Nature, &

World Wildlife Fund, 1980). Studies indicate that species with different features will have different adaptations and resilience capacity to respond to biodiversity change drivers (such as climate change, habitat fragmentation and biological invasion, Fletcher et al., 2019; Groot et al., 2007; Liao, Bearup, & Blasius, 2014; Yachi & Loreau, 1999), and therefore, communities with higher feature diversity tend to ensure a larger range of option values in the long term (Forest et al., 2007). Due to the positive linkage between feature and PD, these findings suggest that PD can also reflect biodiversity option values. Larsen et al. (2012) argued that biodiversity option values would be maximized if we maximize the conservation of PD. Incorporating both taxonomic diversity and PD in the selection of conservation priorities is increasingly recognized and is acknowledged to be helpful in conserving different dimensions of biodiversity (Devictor et al., 2010; Faith, 2013, 2016). For example, Forest et al. (2007) suggested that it is important to preserve regions with high PD for the retention of species' features and their option values. Recently, PD has been included in the assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, an independent intergovernmental body aiming to strengthen the link between science and decision making for biodiversity conservation and sustainable development (Diaz et al., 2019).

Mishler et al. (2014) proposed that conservation planning should distinguish between centres of neo- and palaeo-endemism. Neo-endemic centres are regions with a relative high proportion of recently diverged young endemic species, while palaeo-endemic centres are regions with a relative high proportion of old endemic species (Mishler et al., 2014). Studies have demonstrated that the distinction between neo- and palaeo-endemic centres could provide critical information for identifying priority areas for biodiversity conservation of both plants and vertebrate communities (González-Orozco et al., 2016; López-Pujol et al., 2011; Rosauer, Pollock, Linke, & Jetz, 2017). Similarly, biodiversity hotspots can also be divided into two types: neo- and palaeo-hotspots based on their PD at given levels of species diversity. A neo-hotspot is a biodiversity hotspot where species have more extant recently diverged relatives than expected and usually consists of more young species with short branches. The formation of a neo-hotspot is likely due to fast radiations of

different groups and/or elevated net diversification rates (Couvreur et al., 2011; Fritz & Rahbek, 2012; Moreau & Bell, 2013). Thus, a neo-hotspot tends to contain lower PD than expected at given levels of species diversity. In contrast, a palaeo-hotspot is a biodiversity hotspot where species have fewer extant recently diverged relatives than expected and usually consists of more old species with long branches. The formation of a palaeo-hotspot is likely due to long-term environmental stability and low extinction rates (López-Pujol et al., 2011; Schley et al., 2018; Tamma & Ramakrishnan, 2015). Thus a palaeo-hotspot tends to contain higher PD than expected at given levels of species diversity.

As neo- and palaeo-hotspots contain different lengths of evolutionary histories, they may also have different feature diversity and biodiversity option values (Faith, 2013). Specifically, a palaeo-hotspot tends to contain higher feature diversity and biodiversity option values than other regions with similar species diversity. Meanwhile, a neo-hotspot tends to contain species that are normally closely related to each other and may have experienced high net diversification (Cowling & Pressey, 2001; Levin, 2019; Lópezpujol, Zhang, Sun, Ying, & Ge, 2011; Soltis et al., 2016). These findings highlight the importance of both palaeo- and neo-hotspots for the retention of species' features and their potential benefits. One of the major aims in biodiversity conservation is to conserve evolutionary processes and to maintain the completeness of the tree of life (Forest et al., 2007), which could only be achieved if conservation covers regions with not only high species diversity, but also species with distinct evolutionary histories and the evolutionary front of the tree of life. Therefore, distinguishing neo- and palaeo-hotspots could provide new insight for identifying conservation priorities to better conserve the tree of life.

China has a great number of threatened plant species (>3,700 species, Qin et al., 2017) due to the rich flora therein and a long history of strong human disturbances, and hence requires wide conservation attention. Previous identification of biodiversity hotspots in China has been based on species diversity and endemics, with little consideration of PD, especially the distinction between neo- and palaeo-hotspots of PD. Moreover, researchers have paid much attention to the conservation in the Hengduan Mountains (Figure 1) in south-western China due to high diversity of species and endemics (e.g. the Yunnan Great Rivers Project, Ma, Moseley, Chen, & Zhou, 2007). Listed as one of the world's most important biodiversity hotspots by Wilson (1992) and Myers et al. (2000), the Hengduan Mountains contain about 9,000 vascular plant species in an area of about 500,000 km^2 (Wu, 1988), ranking top among the mountain ranges surrounding the Qinghai–Tibetan Plateau. Additionally, the species diversity in this region is far beyond other regions at similar latitudes in the Northern Hemisphere, such as eastern North America (Qian, Ricklefs, & White, 2005). However, compared to other regions (e.g. eastern North America) the PD in the Hengduan Mountains remains poorly explored. Similar to the Hengduan Mountains, southern China (including southern Yunnan, south-western Guangxi, south-western Guangdong, southern Taiwan and Hainan; Figure 1a) also contains high species diversity and has been identified as the hotspot of both threatened (Zhang, He, Li, & Tang, 2015) and palaeo-endemic plant species (López-Pujol et al., 2011). However, southern China attracts much less attention in conservation practices than the Hengduan Mountains and its PD of plants also remains poorly studied. Recent development in mega-phylogenies of Chinese vascular plants (Chen et al., 2016; Lu et al., 2018) makes it possible
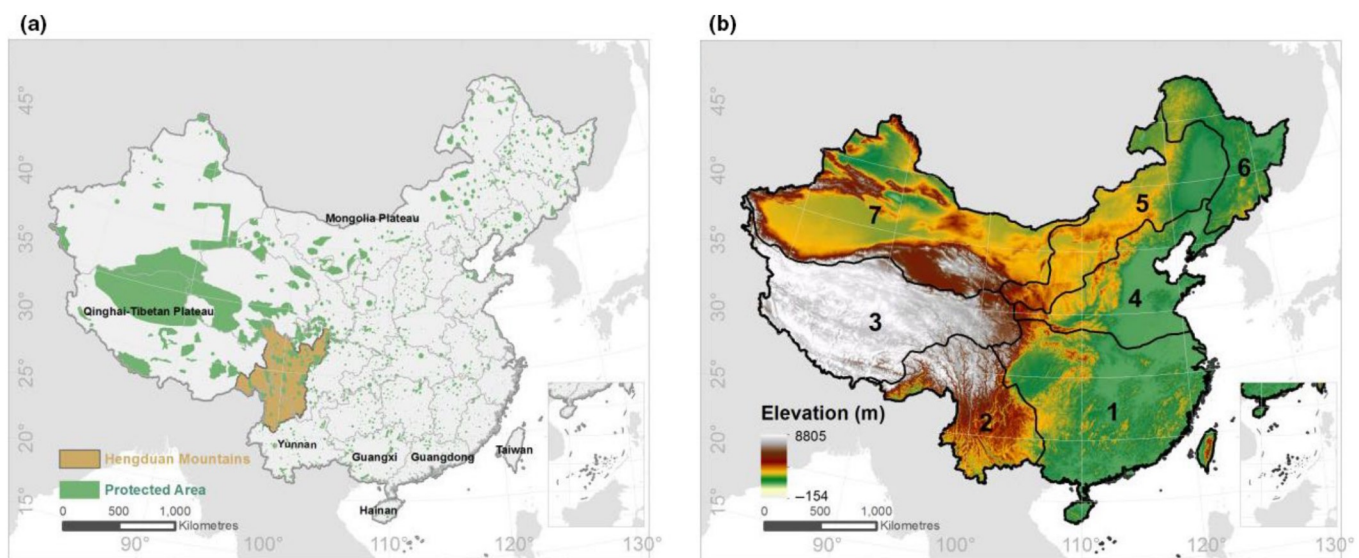

FIGURE 1 The geographical locations of Hengduan Mountains shown together with the network of nature reserves (a) and the seven biogeographical regions (b) in China. In (b), the seven biogeographical regions are as follows: (1) southeast China (including Hainan and Taiwan Island); (2) eastern Himalayas; (3) the Qinghai–Tibetan Plateau; (4) north China; (5) the Mongolian Plateau; (6) northeast China; and (7) northwest China. In our analyses, southern China was referred to the geographical area covering southern Yunnan, south-western Guangxi, south-western Guangdong, southern Taiwan and Hainan. Figure (b) was redrawn from Wang, Fang, Tang, and Lin (2012) with permission

to compare PD of plant species between southern China and the Hengduan Mountains, and to incorporate phylogenetic information in biodiversity conservation.

Here, by integrating a genus-level phylogeny with high-resolution species distributions of all woody plants in China, we tested whether the patterns in species and PD of woody plants are congruent with each other in Hengduan Mountains and southern China. We constructed null models based on three species pools with different sizes to estimate standardized PD (sPD) at given levels of species diversity. Then, we identified areas with significantly higher or lower PD than expected at given levels of species diversity, and explored the possible macroevolutionary mechanisms underlying these patterns. We especially emphasized on the comparison of sPD and proportions of protected areas between Hengduan Mountains and southern China (Figure 1). Finally, we discussed the relevance of our findings to future conservation planning in China.

2 | METHODS

2.1 | Species distribution data

Distributions of Chinese woody species were obtained from the updated *Database of China's Woody Plants*, which contains a total of 11,405 native woody species from 1,175 genera (Fang et al., 2011; Wang, Brown, Tang, & Fang, 2009). The distribution data in this database were compiled from all national and provincial floras in China, as well as regional floras and inventory reports published before 2009. The spatial resolution of the distribution data was at county level, with the median area of all counties to be 2,081 km^2 (skewness = 9.93). The taxonomy of this database followed *Flora of China* (http://www.efloras.org/). We substantially updated the distribution data using more than 40 volumes of national and regional floras published in 2009–2018, and from ca. six million specimen records in China recently published (http://www.nsii.org.cn/).

The county-level distribution maps were transformed into an equal-area grid with a spatial resolution of 50 × 50 km^2 to eliminate the effects of area on the estimation of species diversity. The grid cells along the border and coasts with more than 50% of their area in China were kept. In total, 3,794 grid cells were remained for the following analyses. Species distribution data were matched with the genus-level phylogeny of Chinese vascular plants (Chen et al., 2016), and a total of 11,050 woody species belonging to 1,077 genera had both distribution and phylogenetic information.

As spatial resolution may influence species diversity patterns and their drivers (Rahbek & Graves, 2001), we repeated all analyses using species distribution data transformed into a grid of 100 × 100 km^2. We found that all results were consistent with those based on distribution data with spatial resolution of 50 × 50 km^2. We therefore included the results based on 50 × 50 km^2 data in the main text, and those based on 100 × 100 km^2 data in Supporting Information (Appendix S1, Figures S1–S4).

2.2 | Phylogenetic trees

As species-level phylogenies based on molecular data for all woody species in China are not available yet, we used a genus-level phylogeny of Chinese vascular plants (Chen et al., 2016) and added all species to their corresponding genera as basal polytomies. As some genera in this phylogeny are not monophyletic, we used two methods to add polytomies to these genera, that is adding species to the monophyletic lineage (a) containing the largest number of descendants (method 1), or (b) with the oldest age (method 2) within each genus. Method 2 tended to result in older genus ages than method 1, and hence might lead to relatively inflated estimation of the number of palaeo-hotspots. We repeated all analyses with the phylogenies generated by these two methods, and the results were virtually identical. Therefore, the results based on method 1 were presented in the main text and those based on method 2 in Supporting Information (Appendix S1, Figures S5–S8).

To evaluate the potential influences of polytomies within these phylogenies on the calculation of PD, we randomly resolved the polytomies of genera with more than one species using a birth–death (Yule) bifurcation process (see Thuiller et al., 2011 for more details), which leads to random relationships between species within each genus. This was done for the phylogenies generated by the two methods (i.e. non-monophyletic genera being represented by either their oldest or largest clades) separately. We generated 100 random trees for each of these two genus-level phylogenies, and repeated all phylogenetic analyses with them. The results based on these random trees were then averaged. The averaged results were consistent with those based on the two trees with polytomies (Appendix S1, Figures S9–S16), suggesting that polytomies may not significantly bias our findings.

2.3 | PD estimation

For each grid cell, we calculated Faith's PD, hereafter termed PD for short (Faith, 1992). In our study, the branch length in the phylogeny represents the evolutionary time of each clade, and hence, PD here evaluates the total evolutionary history of the species in an assemblage (Kling, Mishler, Thornhill, Baldwin, & Ackerly, 2019). Specifically, the calculation of PD here did not include the root of the minimum spanning tree, that is the brunch length from the most recent common ancestor of all species in an assemblage back to the root of all woody plants. The phylogeny used is a regional one with some close relatives of the covered taxa missed from it. This may influence the estimation of taxa ages, but is unlikely to bias the estimation of PD (Lu et al., 2018).

To evaluate the net contribution of phylogenetic relationship to PD, we first used a LOESS (locally weighted scatterplot smoothing) regression of PD over species diversity and extracted the residuals (hereafter termed residual PD; Forest et al., 2007; Fritz & Rahbek, 2012). For comparison, we also extracted the residuals of a power function of PD over species diversity and found consistent results with those

based on the LOESS regression (see Appendix S1, Figure S17). Then, three null models were also used to evaluate the net contribution of phylogenetic relationship to PD (see the next section).

2.4 | Null models with different species pools

Although PD has been found to be positively correlated with species diversity (Fritz & Rahbek, 2012; Mishler et al., 2014; Rodrigues & Gaston, 2002), studies show that biodiversity loss under anthropogenic threats can be quite different when conservation priorities are selected using phylogenetic or species diversity (Forest et al., 2007; Yesson & Culham, 2006). The separation of the contributions of species diversity and species relatedness to PD may enhance the use of the biodiversity dimensionality in conservation planning. Null models have been used to divide Faith PD (Faith, 1992) of a species assemblage into two interacting components: (a) species diversity, and (b) phylogenetic relationships between these species. To separate the contributions of species diversity and species, phylogenetic relationships to PD may enhance the usage of PD in identifying conservation priorities.

Therefore, we developed a null model approach based on species pools of different sizes. In general, for each focal grid cell, we randomly drew the same number of species given by the species richness of this grid cell from a defined species pool and calculated the PD of this random species assemblage. This was repeated for 1,000 times. Then, we calculated the mean and standard deviation of the PD of these random assemblages and used the following formula to estimate the standardized PD (hereafter termed as sPD) for the focal grid cell:

$$sPD = \left(PD_{observed} - meanPD_{randomized}\right) / \left(sdPD_{randomized}\right).$$

$PD_{observed}$ represented the observed PD of the focal grid cell, and $meanPD_{randomized}$ and $sdPD_{randomized}$ represented the mean and standard deviation of 1,000 PD values based on random assemblages, respectively. The mathematical formula of sPD that we used was the same as those for the calculation of standardized effect size in previous studies (Gotelli & McCabe, 2002; Gurevitch et al., 1992; Sanders, Gotelli, Heller, & Gordon, 2003).

In this study, sPD reflects the contribution of phylogenetic relationship to PD after controlling for species diversity. sPD values lower than −1.96 (or higher than 1.96) indicate significantly lower (or higher) PD than expected at given levels of species richness (Gotelli & McCabe, 2002; Sanders et al., 2003), respectively. Values between −1.96 and 1.96 were considered as not significantly different from null expectation.

Null models require an ecologically explicit definition of species pools (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012). Studies on species assembly of ant communities in North America (Lessard, Belmaker, et al., 2012; Lessard, Borregaard, et al., 2012) and woody plant communities in the mountains of China (Wang, Tang, et al., 2012) found that species pools with different sizes (or at

different spatial scales) may be influenced by different evolutionary and ecological processes and hence may affect the outputs of null models. We used three species pools with different sizes: (a) full species pool, (b) similarity weighted dispersion-field species pool and (c) biogeographical-region species pool. For a certain grid cell, the size of its species pool decreases across these three species pools. Then, we repeated the null models using each of these species pools.

2.4.1 | Species pool 1: Full species pool

A full species pool contained all woody plant species (i.e. 11,050 species) used in our study. This definition assumed that all the grid cells share the same species pool and all species within the species pool could appear in the focal grid cell, which is less realistic given the large extent in space in our study (Lessard, Belmaker, et al., 2012).

2.4.2 | Species pool 2: Similarity weighted dispersion-field species pool

The species pool for a focal grid cell was defined as all species occurring in the dispersion field of the focal grid cell, that is, all grid cells that share at least one species with the focal one. A dispersion field of a focal grid cell could be visualized by overlaying the geographic distributions of all species occurring in the focal grid cell (Graves & Rahbek, 2005). As the distributions of some widespread species could be very large, the traditional dispersion fields of different grid cells would remain relatively similar across large space. Therefore, we used similarity weighted dispersion field to further refine the species pool of each grid cell (Lessard, Borregaard, et al., 2012). First, for a grid cell i within the dispersion field of a focal grid cell j, we estimated the number of shared species between i and j (S_{ij}), and then calculated the selection probability of i as: $P_{ij} = \frac{S_{ij}}{\sum_{i=1}^{n} S_{ij}}$, where n was the number of grid cells within the dispersion field of j. Second, a grid cell was randomly selected from j's dispersion field with the estimated selection probability and a species was randomly sampled from this cell. This process was repeated until the number of selected species reached the species richness of the focal grid cell j. The similarity weighted dispersion-field species pool gives high selection probability to grid cells with similar species composition to the focal grid cell, leading to relatively high similarity in species compositions between the random and actual communities (Carstensen et al., 2013; Lessard, Borregaard, et al., 2012).

2.4.3 | Species pool 3: Biogeographical-region species pool

Following Wang, Fang, Tang, and Lin (2012), we divided our study area into 7 biogeographical-regions (Figure 1b): (1) southeast China
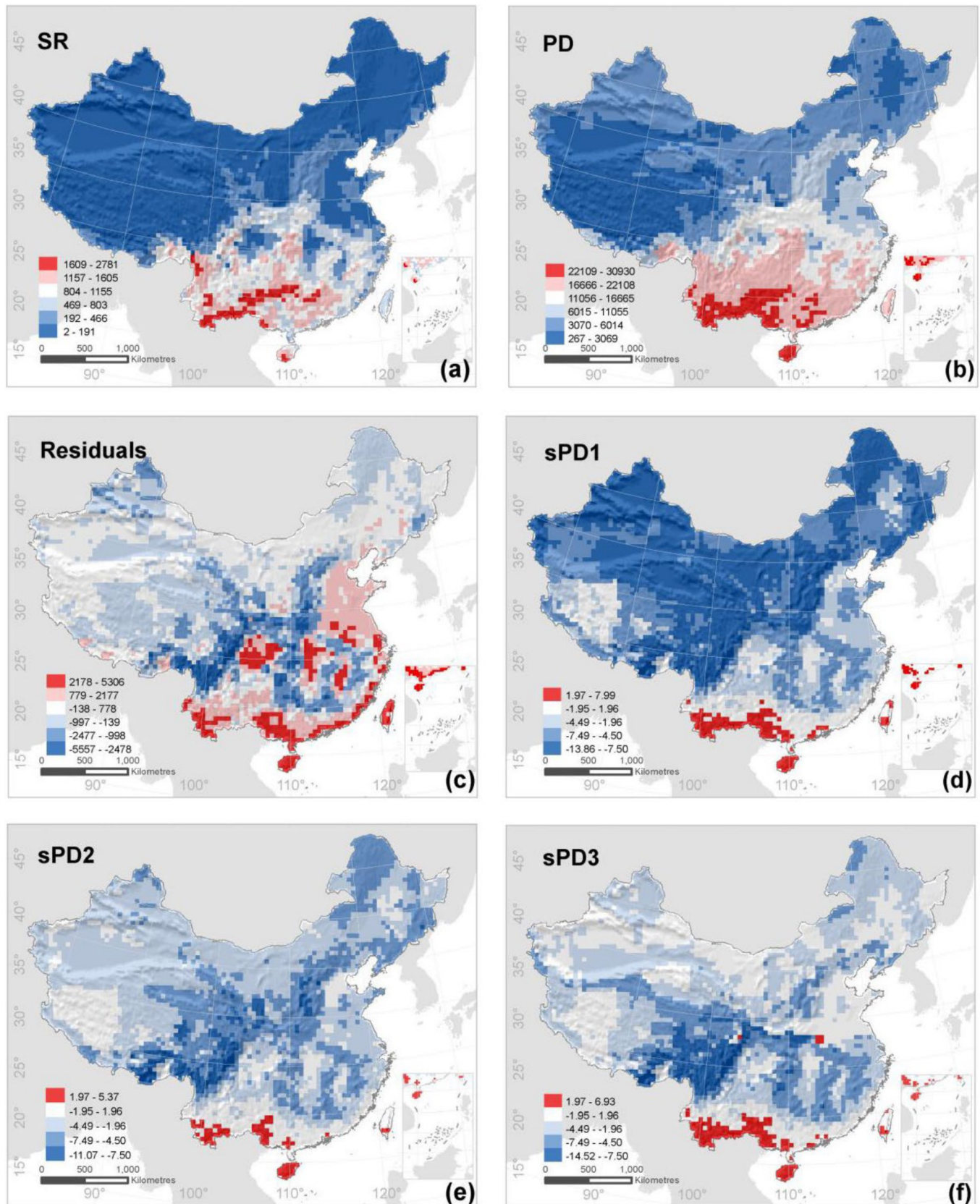
FIGURE 2 Patterns of (a) species diversity (SR), (b) Faith's phylogenetic diversity (PD), (c) residuals from a LOESS (locally weighted scatterplot smoothing) regression of PD over species diversity (residual PD), and (d–f) three standardized PD indices (sPD) of woody plants in China. The three sPDs were estimated by three null models based on species pools with different sizes, that is the full species pool (sPD1), similarity weighted dispersion-field species pool (sPD2) and biogeographical-region species pool (sPD3), respectively. In figure (d–f), regions in red and blue had significantly higher or lower PD than expected given the levels of their species diversity, while values between −1.96 and 1.96 (not significant) were shown in white. Figure (a) was redrawn from Wang et al. (2011) with permission using a substantially updated database of woody species in China
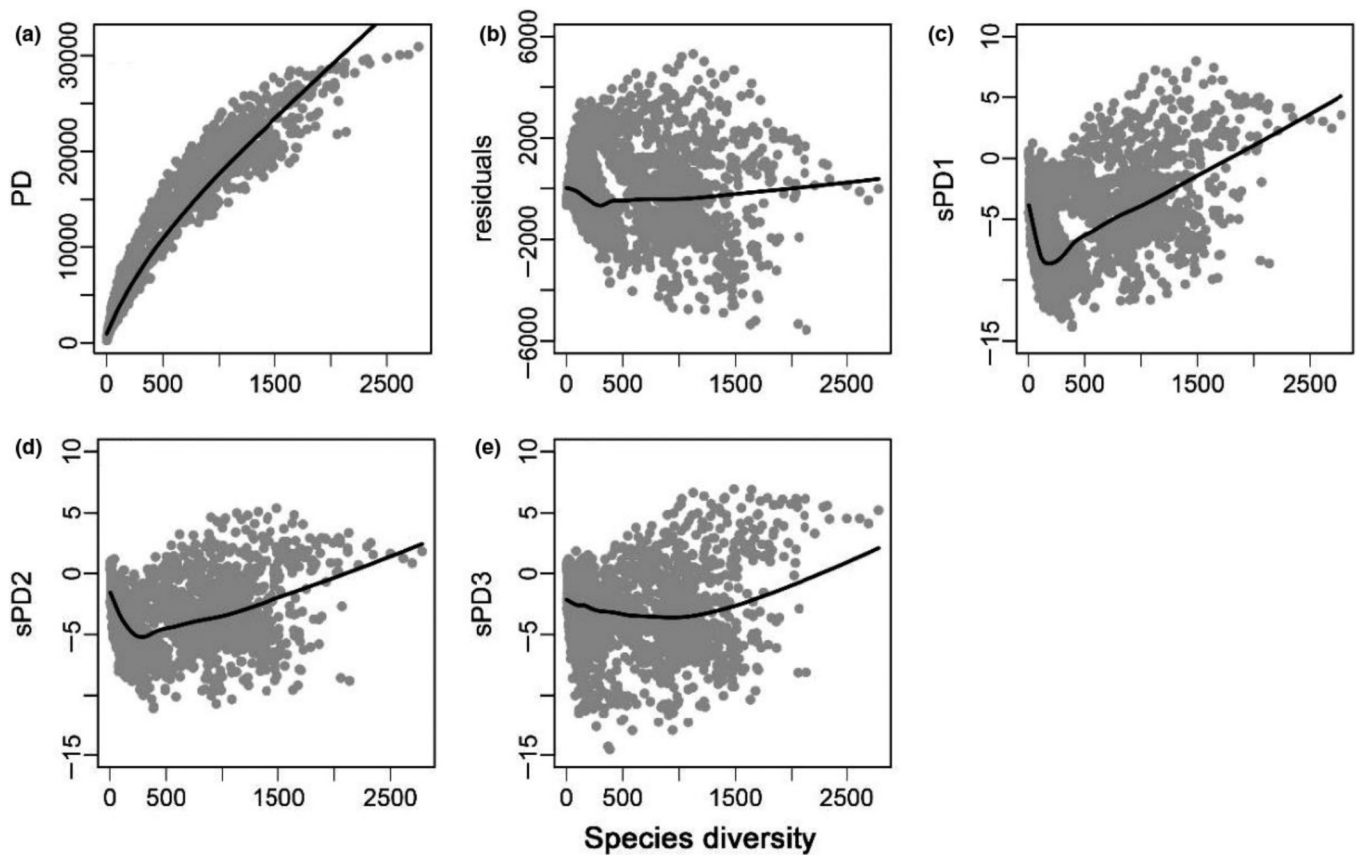
FIGURE 3 Relationships between phylogenetic diversity (PD) and species diversity. (a) Faith's PD; (b) residual PD; (c–e) standardized PD estimated by null models with the full (c), similarity weighted dispersion-field (d) and biogeographical-region (e) species pools. The relationships were evaluated using LOESS (locally weighted scatterplot smoothing) regressions

(including Hainan and Taiwan Island); (2) eastern Himalayas; (3) the Qinghai–Tibetan Plateau; (4) north China; (5) the Mongolian Plateau; (6) northeast China; and (7) northwest China. For more details of these biogeographical regions (see Wang, Fang, et al., 2012). The species pool for each grid cell consisted of all woody plants occurring in the biogeographical region where this grid cell was located.

2.5 | Hotspots of woody plant diversity based on species and PD

We identified hotspots and coldspots (areas where biodiversity is relatively low) of woody plant diversity separately using species diversity, PD, residual PD and the three indices of sPD based on different species pools. Following previous studies (Kareiva & Marvier, 2003; Orme et al., 2005; Price, 2002), hotspots and coldspots were referred to grid cells where species diversity (or PD) was within the top and bottom 2.5% quantile of species diversity (or PD) of all grid cells, respectively. However, PD was contributed by both species diversity and species relatedness, and thus, the hotspots of PD could result from both high species diversity and long branches between species. The hotspots (or coldspots) of residual PD and sPD represented regions with higher (or lower) PD than expected at given levels of species diversity. In other words, species in these hotspots (or coldspots) had fewer

or more extant recently diverged relatives than expected. Therefore, these hotspots and coldspots identified from the residual PD and sPD could be termed as palaeo- and neo-biodiversity hotspots, respectively. Then, the maps of hotspots and coldspots based on the three indices of sPDs were merged using a spatial union method to generate an integrated map of palaeo- or neo-biodiversity hotspots, which was then intersected with the map of nature reserves in China (Zhang et al., 2015). The intersected region within each grid cell was considered as protected. Finally, we calculated the proportions of protected areas within neo- and palaeo-biodiversity hotspots covered by nature reserves at different conservation levels (i.e. national, provincial, and county-level).

All statistical analyses were performed in R 3.3.1 (R Development Core Team).

3 | RESULTS

Phylogenetic diversity was strongly positively correlated with species diversity ($r = .961$), suggesting that the species diversity pattern of woody plants across China was highly similar to that of PD (Figures 2a,b and 3a; Appendix S1, Figures S1–S2, S5–S6, S9, S10, S13, S14). Specifically, species diversity and PD decreased from the tropics to high latitudes. Southern China (including southern
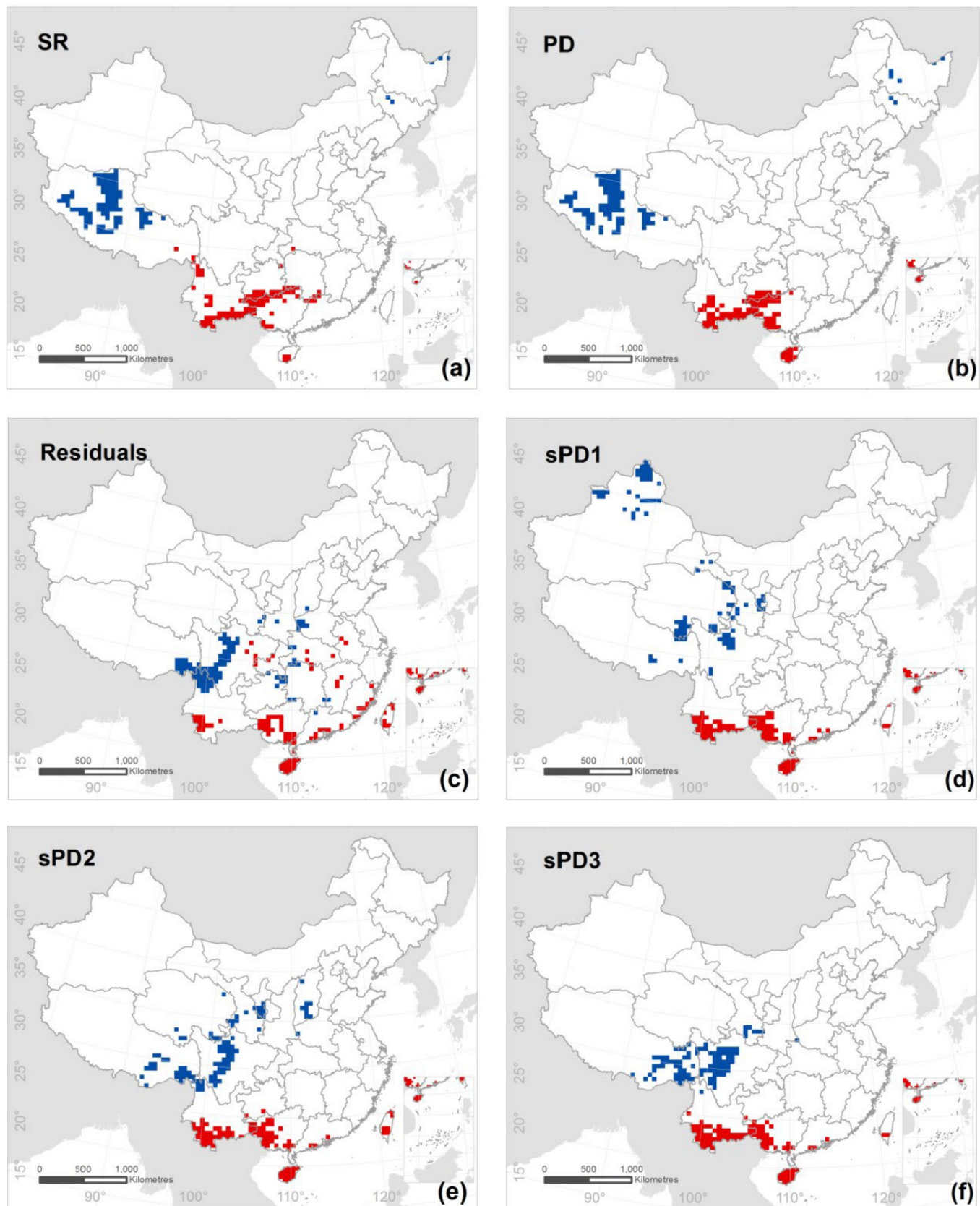
FIGURE 4 Geographical patterns in the hotspots and "coldspots" of woody plant diversity. Hotspots (red) and coldspots (blue) were identified as the top and bottom 2.5% of the grid cells after all grid cells were sorted in a decreasing order of species diversity (a), Faith's phylogenetic diversity (PD) (b), residual PD (c) and three standardized PD (sPD) estimated by null models with the full species pool (sPD1), similarity weighted dispersion-field species pool (sPD2) and biogeographical-region species pool (sPD3) (d–f). SR, species diversity

FIGURE 5 Distribution (a) and coverage (b) of nature reserves in the merged neo- (blue) and palaeo-hotspots (red) based on the three measures of standardized PD (sPD). (a) The distribution of nature reserves (green) in the merged neo-and palaeo-hotspots. (b) The bars show the area coverage of nature reserves at different levels, and the green solid line shows the total area coverage of all nature reserves in entire China (c. 15.28%)
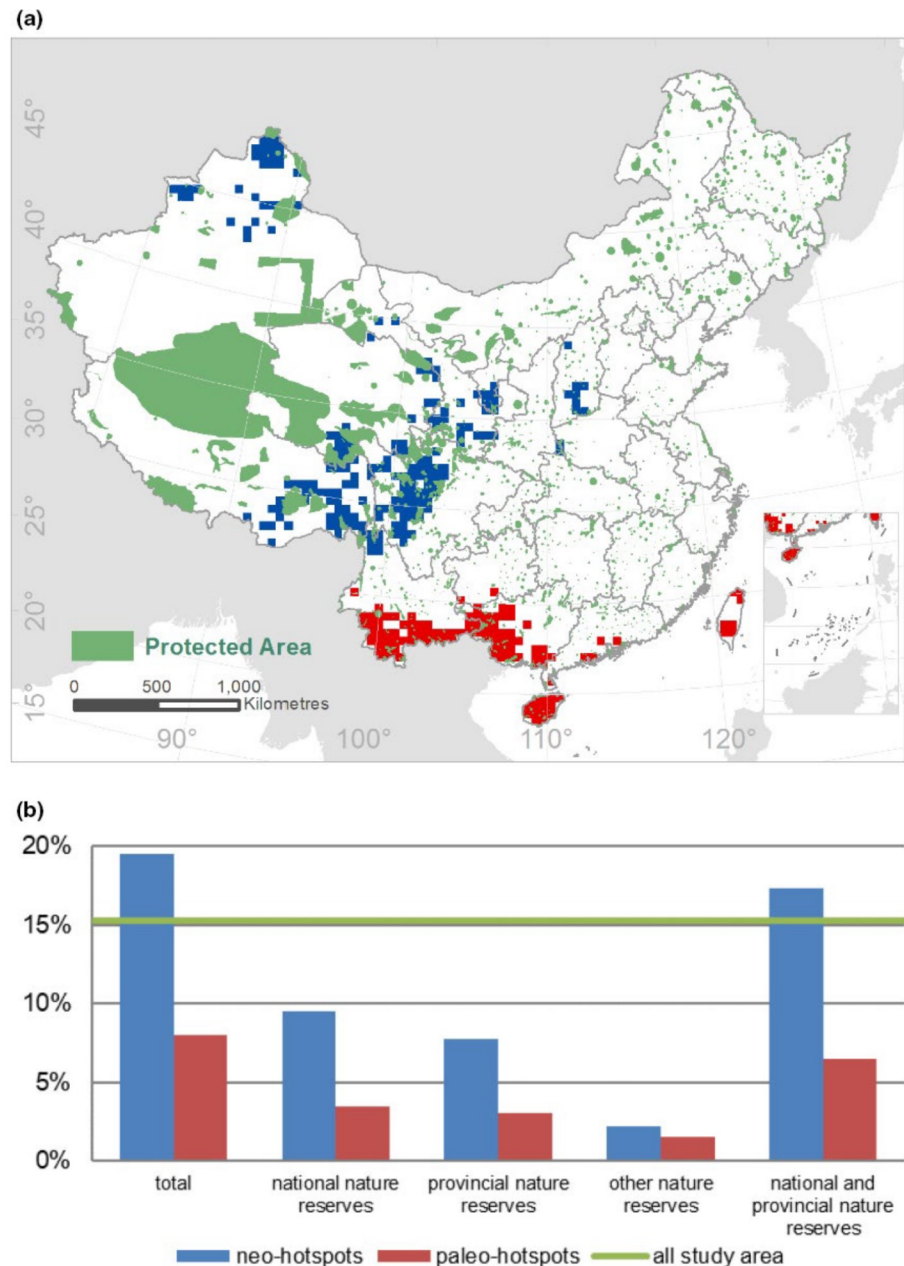
Yunnan, south-western Guangxi, south-western Guangdong, southern Taiwan and Hainan) had the highest species diversity and PD while the Qinghai–Tibetan Plateau had the lowest (Figure 2a,b; Appendix S1, Figures S1, S5, S9, S13).

The geographical patterns in the residual PD and the three sPD indices obtained from null models (i.e. sPD1, sPD2 and sPD3) were consistent with each other (Figure 2c–f; Appendix S1, Figures S1, S5, S9, S13). The patterns of different indices were strongly correlated with each other (Appendix S1, Table S1), but were not or only weakly correlated with the species diversity pattern (residual PD, $r = -.086$; sPD1, $r = .472$; sPD2, $r = .104$; sPD3, $r = .016$; Figure 3b–e; Appendix S1, Figures S2, S6, S10, S14). Among the sPD based on three null models, the patterns of sPD2 and sPD3 were more similar to each other, but were relatively more different from that of sPD1. These patterns indicated areas with significantly higher or lower PD at given levels of species diversity.

Specifically, southern China had significantly higher PD than expected given the levels of species diversity there (Figures 2c–f, 4; Appendix S1), while most other areas had lower PD than expected. The south-eastern Qinghai–Tibetan Plateau and Hengduan Mountains had extremely low PD after controlling for species diversity (Figures 2c–f, 4; Appendix S1, Figures S3, S7, S11, S15). The hotspots and coldspots of PD, that is areas with the top and bottom 2.5% quantile of residual PD or sPD, respectively, were strongly overlapped between results based on different indices (Figure 4; Appendix S1, Figures S3, S7, S11, S15, Table S2), suggesting that our results were robust to the selection of species pools.

The proportion of protected areas in Hengduan Mountains was higher than that in southern China, and this result was consistent across all levels of nature reserves (Figure 5a; Appendix S1, Figures S4, S8, S12, S16). Specifically, Hengduan Mountains had relatively large

nature reserves and the proportion of protected area in this region was higher than the average proportion of the entire country. In contrast, southern China contained small nature reserves and the proportion of protected area there was only half of the average proportion of the entire country (Figure 5a,b; Appendix S1, Figures S4, S8, S12, S16).

4 | DISCUSSION

4.1 | Patterns of species and PD of Chinese woody plants

We found strong correlations between the geographical patterns in phylogenetic and species diversity of Chinese woody plants (Figure 2a,b), which is consistent with previous studies (Forest et al., 2007; Fritz & Rahbek, 2012; Mishler et al., 2014; Morlon et al., 2011). Ecological and evolutionary processes leading to more symmetric phylogenies, relatively long tip branches and relatively coarse spatial resolution may have all contributed to the strong richness-PD correlation (Tucker & Cadotte, 2013). Additionally, our results showed that floras in many mountains (such as the Hengduan Mountains, Tianshan Mountains, Qilian Mountains, Taihang Mountains, Changbai Mountains and Qinling Mountains; Figure 2c–f) contained relatively lower PD than expected given their levels of species diversity, which may suggest that these mountains tend to be neo-hotspots. In comparison with those in lowlands, some woody plant lineages in mountains may have undergone rapid net diversification due to strong isolation and ecological opportunities created by the emergence of new habitats and low competition (Hughes & Eastwood, 2006; Parra-Olea et al., 2012; Schwery et al., 2015). Geographically isolated habitats in mountains may have acted as dispersal barriers to reduce gene flows among populations (Polato et al., 2018), leading to higher net diversification of plants and more phylogenetically closely related species in mountains than in lowlands (Schluter & Pennell, 2017). The high levels of environmental heterogeneity in mountains could also support the maintenance of these lineages (Rangel et al., 2018; Wen, Zhang, Nie, Zhong, & Sun, 2014). Fast diversification in mountains has also been found in groups other than plants, such as mammals in the eastern slopes of Andes (Rosauer & Jetz, 2015). In contrast to these mountains, southern China has significantly higher PD than expected given the levels of species diversity there (Figure 2c–f), and hence may represent a palaeo-hotspot of woody plants in China.

4.2 | Macroevolutionary mechanisms underlying neo- and palaeo-biodiversity hotspots

Our results suggest that the Hengduan Mountains are a neo-biodiversity hotspot containing relatively high species diversity but lower PD than expected given its species diversity (Figure 2a,c–f), which is consistent with the findings of previous studies (Liu et al., 2016; Lópezpujol et al., 2011). Geological evidence suggests that the Hengduan Mountains uplifted rapidly between the late Miocene and

late Pliocene and are younger than the Qinghai–Tibetan Plateau and the Himalayas (Clark et al., 2005; Kirby et al., 2002; Meng et al., 2016; Sun et al., 2011; Wang et al., 2014). The high species diversity in the Hengduan Mountains is partly due to the extremely complex and dissected topography of this region, which provides diverse climates and vegetation types for new lineages to diversify and to be preserved (Hewitt, 2000; Li & Li, 1993; Myers et al., 2000; Tzedakis, Lawson, Frogley, Hewitt, & Preece, 2003). Moreover, the low sPD in this region suggests that the Hengduan Mountains contain high proportion of species with more extant recently diverged relatives than expected, which could be due to rapid radiation and high in situ net diversification together with low Quaternary extinction in this region. The Hengduan Mountains have been shown as a centre of in situ net diversification for many alpine taxa, many of which experienced accelerated net diversification since late Miocene and are believed to be still actively giving rise to new species (Ding et al., 2020; Sun, 2002; Sun & Li, 2003; Zhang, Zhang, Boufford, & Sun, 2009). For example, a recent study shows that the rate of in situ net diversification of 19 plants clades in the Hengduan Mountains increased at c. 8 Ma, suggesting recent radiation of these groups in this region (Xing & Ree, 2017). Elevated net diversification in the Hengduan Mountains may have generated many species-rich young clades with relatively short branches. Indeed, a recent study suggests that the medium age of woody genera in the Hengduan Mountains is relatively young (Lu et al., 2018). Moreover, the Hengduan Mountains may have also acted as a refuge for plants during the Quaternary and prevented species from extinction (Rahbek et al., 2019). A recent study suggests that the extinction rate of plants during the Quaternary was lower in the Hengduan Mountains than in the Himalayas and the Qinghai–Tibet Plateau (Ding et al., 2020). All these macroevolutionary processes may have contributed to the lower PD of the Hengduan Mountains than expected given the species diversity there.

In contrast the Hengduan Mountains, our results suggest that southern China is a palaeo-hotspot containing both high species diversity and higher PD than expected given the level of species diversity, indicating that this region harbours species that have fewer extant recently diverged relatives than expected and likely consists of more old species with long branches. Southern China lies at the confluence of two different floristic regions (i.e. between Eastern Asiatic Region and Indochinese Region, Takhtajan, 1986) and between tropical and temperate regions. Despite the controversy on the boundary between tropical and temperate regions in China, it is agreed that southern China contains the northern boundary of the tropical zone (Zhu, 2013; Zhu, Ma, Yan, & Hu, 2007). Moreover, southern China has very diverse climates (Song et al., 2009)—ranging from tropical to temperate climates—and is the only place in China where savanna exists (e.g. semi-arid savanna in Yuanjiang Savanna Ecological Station; Fei et al., 2017). Different climates provide diverse habitats for different woody species to establish and persist. These biogeographic and climatic characteristics of southern China may be one of reasons for its high species diversity.

The high proportion of species with fewer extant recently diverged relatives than expected in southern China may be due to the long history of stable habitats. Previous studies identified southern China as one of the refugia for plants during climate shifts since the Cenozoic. Palaeo-ecological evidence suggests that southern China has been extensively connected with tropical regions since the Cenozoic (Hall, 1998), and lacked major geographic barriers for north–south dispersal (Zhu, Cao, & Hu, 2006). Therefore, temperate and subtropical plant species might have migrated to lower latitudes when the climate became colder, whereas tropical species might have moved poleward when the climate became warmer (López-Pujol et al., 2011; Yu et al., 2000). Previous Quaternary vegetation reconstructions also suggest that even during the Quaternary glacial–interglacial cycles southern China contained extensive subtropical forests as it does today (Harrison et al., 2001; Wang & Sun, 1994; Wang et al., 2017). These large forests acted as refugia and thus helped preserve many old lineages (such as Magnoliaceae, *Litsea*, *Liriodendron*, *Styrophyton*; Wu, Sun, Zhou, Peng, & Li, 2005; Zhu, 2011, 2017).

4.3 | Neo- and palaeo-biodiversity hotspots for biological conservation

According to the Aichi Biodiversity Target 11, at least 17% of terrestrial areas should be conserved by 2020 (https://www.cbd.int/decisions/cop/?m=cop-10). The zero draft report of the post-2020 global biodiversity framework suggests that the percentage should be increased to 30% by 2030 (Convention on Biological Diversity, 2020). To date, about 15% of terrestrial areas in China are covered by protected areas (http://www.stats.gov.cn). To meet the currently proposed post-2020 conservation target, the protected areas in China should be doubled in the following decade. Future expansion of the protected areas and improvement in protecting China's biodiversity will require a targeted effort (Pimm, Jenkins, & Li, 2018). PD, representing feature diversity and biodiversity option values, should be maintained to preserve the tree of life during the expansion of protecting areas (Mace, Gittleman, & Andy, 2003; Scholes et al., 2018). In addition, due to the limitation of resources, conservation priorities should cover as many threatened species and areas as possible with the least costs. To achieve this, the location of conservation priorities is more important than the quantities of protected areas (Pimm et al., 2018).

As an important biodiversity hotspot due to its high diversity of species and endemics, Hengduan Mountains has attracted increasing attention from conservation biologists in China (e.g., Chen et al., 2017; Ma et al., 2007; Ye, Liu, Li, Wang, & Zeng, 2015). This region has large nature reserves and high proportion of protected areas (Figure 5). However, our analysis reveals that Hengduan Mountains contain low PD relative to the number of species present. In contrast, southern China contains both high species diversity and high PD, hence has more feature diversity and biodiversity option values than other regions, which highlights its importance for biodiversity

conservation. However, the nature reserves in this region are fragmented and the coverage of protected areas is only about half of the average level in China (Figure 5; Xu et al., 2017), suggesting that southern China has attracted much less conservation efforts than Hengduan Mountains. Therefore, our findings argue for the establishment of more nature reserves or expansion of the existing ones in southern China, given the need to preserve the completeness of the tree of life (Mace et al., 2003). However, we do not attempt to deny Hengduan Mountains as a conservation priority, but would like to emphasize the importance of southern China as well in biological conservation and in the selection of conservation priorities.

In terms of feature diversity and biodiversity option values, a palaeo-hotspot contains more ancestral or phylogenetically isolated taxa that carry unique or rare gene combinations and the corresponding feature diversity and biodiversity option values (Faith, 2018; Mace et al., 2003). As ancestral or phylogenetically isolated taxa usually lack close relatives, the extinction of them may lead to loss of some unique utilitarian uses and unanticipated benefits (i.e. biodiversity option value; Faith, 1992, 2016), which should not be ignored in conservation assessments (Vane-Wright, Humphries, & Williams, 1991). In contrast, a neo-hotspot normally contains species that may reflect the evolutionary front of the tree of life (Cowling & Pressey, 2001; Crozier, 1997; Levin, 2019; Lópezpujol et al., 2011; Soltis et al., 2016). Therefore, in order to face the uncertain future of the Anthropocene, both neo- and palaeo-biodiversity hotspots should be taken into consideration in the preservation of the tree of life.

In conservation practice, species diversity has been most frequently used for the identification of conservation priorities, which normally ignores other facets of biodiversity. As maximizing the conservation of evolutionary processes and the tree of life has been increasingly suggested as an efficient strategy to face the uncertain future (Forest et al., 2007; Mace et al., 2003; Winter, Devictor, & Schweiger, 2013), PD has been increasingly used for the identification of priorities in conservation planning. Although some studies argue that certain species features may be poorly captured by PD because of the widespread homoplasy in phylogenies (e.g. Jansky et al., 2006; Kelly & Scotland, 2014; Mazel, Mooers, Riva, & Pennell, 2017; Winter et al., 2013), the rationale of using PD for biological conservation is its positive link to the diversity of a broader set of species features and option values rather than a single feature or character (Carstensen et al., 2013; Davies et al., 2016; Mazel et al., 2017; Owen, Gumbs, Gray, & Faith, 2019). Our analyses suggest that the null model approach for identifying neo- and palaeo-biodiversity hotspots based on PD provides a quantitative way to incorporate phylogenetic component into conservation assessments so as to complement traditional strategies in the planning of biodiversity conservation (i.e. those mainly focusing on species diversity and endemism). This method embraces the multifaceted nature of biodiversity and hence provides a more complete perception of biodiversity hotspots.

Although the hotspot approach has been frequently used for the selection of conservation priorities in previous studies and

conservation practices, it does have some drawbacks. For example, a previous study suggests the efficiency of the hotspot approach for biodiversity conservation may depend on the sampling design and the character of the study area (Kati et al., 2004). Moreover, biodiversity hotspots identified by different species groups often fail to overlap (Margules & Pressey, 2000; Orme et al., 2005; Shrestha & Wang, 2018). In addition to the hotspot approach, several other methods have also been developed for conservation planning, for example complementarity approach maximizing both species diversity and PD (Mazel et al., 2018; Pressey, Humphries, Margules, Vane-Wright, & Williams, 1993; Pressey, Possingham, & Margules, 1996; Rodrigues & Gaston, 2002), network approach based on graph theory (Davies et al., 2016) and assessment of evolutionary distinctiveness (e.g. Evolutionary Distinctiveness Globally Endangered, EDGE, Isaac et al., 2007). Recent studies suggest that these later approaches may provide more cost-efficient selections of conservation priorities, especially for rare species requiring more conservation attention (Shrestha, Shen, & Wang, 2019; Véron, Saito, Padilla-García, Forest, & Bertheau, 2019). Selecting priority regions for the conservation of the tree of life at large spatial scales by integrating these approaches with the multiple facets of biodiversity (e.g. species, genetic, phylogenetic and functional diversity, and option values) represents one of the central challenges in studies and practices of conservation planning.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13180.

DATA AVAILABILITY STATEMENT

The distribution data are available from *Atlas of Woody Plants in China: Distribution and Climate* (Fang et al., 2011). Phylogeny data are available at https://onlinelibrary.wiley.com/doi/full/10.1111/jse.12219#support-information-section. The maps of nature reserves in China are available at https://www.sciencedirect.com/science/article/pii/S0006320715301440. Calculation results and R scripts used for this study are in Supporting Information (see Appendices S2 and S3).

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BIOSKETCH

Hongyu Cai is a PhD candidate at Peking University and is mainly interested in macroecology and macroevolutionary. Her work focuses on investigating the patterns in phylogenetic diversity of Chinese plants and the macroevolutionary mechanisms underlying them.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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