Research

New Phytologist

Global hotspots of plant phylogenetic diversity

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Received: *18 April 2023*
Accepted: *24 June 2023*

New Phytologist (2023) **240:** 1636–1646
doi: 10.1111/nph.19151

Key words: conservation, hotspot, macroecology, PD endemism, phylogenetic diversity (PD), phylogenetic endemism, seed plants.

Summary

- Regions harbouring high unique phylogenetic diversity (PD) are priority targets for conservation. Here, we analyse the global distribution of plant PD, which remains poorly understood despite plants being the foundation of most terrestrial habitats and key to human livelihoods.
- Capitalising on a recently completed, comprehensive global checklist of vascular plants, we identify hotspots of unique plant PD and test three hypotheses: (1) PD is more evenly distributed than species diversity; (2) areas of highest PD (often called 'hotspots') do not maximise cumulative PD; and (3) many biomes are needed to maximise cumulative PD.
- Our results support all three hypotheses: more than twice as many regions are required to cover 50% of global plant PD compared to 50% of species; regions that maximise cumulative PD substantially differ from the regions with outstanding individual PD; and while (sub-) tropical moist forest regions dominate across PD hotspots, other forest types and open biomes are also essential.
- Safeguarding PD in the Anthropocene (including the protection of some comparatively species-poor areas) is a global, increasingly recognised responsibility. Having highlighted countries with outstanding unique plant PD, further analyses are now required to fully understand the global distribution of plant PD and associated conservation imperatives across spatial scales.

Introduction

Compared with species diversity patterns, the global distribution of phylogenetic diversity (PD) is poorly understood. Phylogenetic diversity is a more meaningful proxy for 'feature diversity' than simple species counts (Faith, 1992). By accounting for the total amount of phylogenetic history represented by a set of taxa, PD (Faith, 1992) broadly captures diversity in form and function (Owen *et al.*, 2019), and is connected to the resilience of key ecosystem functions (Mazzochini *et al.*, 2019) and services (Forest *et al.*, 2007; Molina-Venegas *et al.*, 2021). Phylogenetic diversity is also a widely accepted indicator of the 'option value' of biodiversity for future uses and benefits to people (Faith, 2021). It has been established explicitly as a guiding measure for conservation efforts, that is to identify areas that maximise the amount of protected PD and hence feature diversity (Faith, 1992; Véron *et al.*, 2019). However, this requires a robust knowledge of the spatial distribution of PD.

Crucially, the regions that are richest in species or PD are not necessarily the regions of biggest conservation concern. Instead, conservation tends to focus on hotspots of *unique* (endemic) diversity, that is regions that harbour many species or lineages that occur nowhere else, and consequently cannot be conserved anywhere else. For example, the classic *biodiversity hotspots for conservation priorities* (Myers *et al.*, 2000) were selected to contain at least 1500 endemic plant species each (as well as high levels of anthropogenic threat). A similar train of thought has been applied to PD, using metrics such as PD endemism (Faith, 1994; Sechrest *et al.*, 2002) or phylogenetic endemism (Rosauer *et al.*, 2009). Alternatively, complementarity analyses can be used to identify the set of areas that most efficiently maximises PD (Faith *et al.*, 2003; Kukkala & Moilanen, 2013). Analyses of PD endemism and complementarity can show which parts of the world harbour particularly high amounts of unique evolutionary history, either globally or relative to other regions, thus guiding conservation attention.

Considering that plants are the trophic and structural foundation of most terrestrial habitats and hence also a cornerstone of human livelihoods, exploring and explaining the distribution of their diversity is clearly a priority. However, due to limitations in both geographic and phylogenetic data (Meyer *et al.*, 2016; Rudbeck *et al.*, 2022), global plant PD remains incompletely understood. This is in stark contrast to most vertebrates, which are well-served with geographic and phylogenetic data that have

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facilitated exploration of their global PD patterns (Davies & Buckley, 2011; Safi *et al*., 2011; Fritz & Rahbek, 2012; Voskamp *et al*., 2017; Daru *et al*., 2019; Gumbs *et al*., 2020). Previous studies on global plant PD were either limited in their taxonomic sampling and resolution (Daru *et al*., 2019), or based on incompletely documented, closed-access data sets (Qian *et al*., 2023). Additionally, it is also important to note that neither of these studies adequately addressed complementarity from a conservation perspective.

To establish the distribution of plant PD, its relationship to species richness, and its conservation requirements, we frame three hypotheses. First, we hypothesise that PD is more evenly distributed across the surface of the Earth than species diversity (H1). While the world's plant species are concentrated in relatively few 'hyperdiverse' regions (Pimm & Joppa, 2015), PD is unlikely to behave in the same way because closely related species and lineages are spatially autocorrelated (i.e. occur in close proximity at a global scale; Kissling *et al*., 2012b; Eiserhardt *et al*., 2013). Typically, 'hyperdiverse' regions are dominated by local diversification and therefore include many close relatives (e.g. Schnitzler *et al*., 2011; Hughes & Atchison, 2015). Thus, while hyperdiverse regions capture species richness and shallow phylogenetic history, many different regions are required to represent deep phylogenetic history and maximise PD. This challenges the prevailing worldview that places conservation responsibility primarily with countries that harbour 'hyperdiverse' biota.

Second, we hypothesise that the areas of highest PD, which are often designated as hotspots (e.g. Daru *et al*., 2019; Qian *et al*., 2023) do not maximise cumulative PD (Faith *et al*., 2004; Pollock *et al*., 2017), and thus do not effectively guide conservation attention (H2). Because lineages usually diversify within certain geographic boundaries, set either by dispersal constraints or limited ability to adapt to new environments or both (Eiserhardt *et al*., 2013), adjacent areas are often similar in their biotic composition. Thus, we expect that the areas of highest PD are often geographically close and redundant in their composition of species and lineages. By contrast, we expect that hotspots based on complementarity, that is explicitly maximising the cumulative PD they represent, will be substantially different from the areas that individually have the highest PD, sampling geographically distant areas that harbour phylogenetically distant floras.

Third, we hypothesise (H3) that absolute phylogenetic diversity is highest in tropical and subtropical moist broadleaf forest, where species richness is overall high and diversification rates low (Igea & Tanentzap, 2020; Sun *et al*., 2020; Tietje *et al*., 2022) and many old lineages persist (tropical conservatism hypothesis; Wiens & Donoghue, 2004). However, as different biomes represent different lineages (biome conservatism hypothesis; Crisp *et al*., 2009), we expect that the highest values of PD would be attained by regions with both a high proportion of tropical and subtropical moist broadleaf forest and elements from other evolutionarily divergent biomes. Along a similar vein, we expect a wider range of biomes to be important in complementarity-based hotspots compared with high-PD regions, in line with the idea that diversification is not only spatially, but also environmentally autocorrelated (Wiens & Donoghue, 2004; Crisp *et al*., 2009; Eiserhardt *et al*., 2013).

Here, we test these hypotheses in a global analysis of phylogenetic diversity focussed on seed plants (Spermatophyta). With > 330 000 accepted species, seed plants constitute > 90% of extant land plant diversity and dominate almost all terrestrial vegetation. Our analyses capitalise on the recently completed World Checklist of Vascular Plants (Govaerts *et al*., 2021), a publicly accessible, comprehensive taxonomic checklist of vascular plants and their geographic distributions, in conjunction with a complete phylogeny of seed plants (Smith & Brown, 2018). We extend our test of these hypotheses with an evaluation of global threats (deforestation, human footprint and climate change), to facilitate comparison with the existing literature on conservation hotspots, which have traditionally accounted for degree of threat (Myers *et al*., 2000). By integrating these resources within a complementarity framework for the first time, we highlight a set of regions within which a large proportion of global plant phylogenetic diversity could be conserved.

Materials and Methods

Phylogeny and distribution data

All phylogenetic measures were derived from the phylogenetic tree of Smith and Brown (2018) to which we added missing species using TACT (Chang *et al*., 2020). Of the different trees provided by Smith and Brown (2018), we used the one that contained only species with molecular data and a backbone from Magallón *et al*. (2015; GBMB). TACT adds missing species to a time-calibrated phylogeny using a taxonomic guide tree and birth–death models to estimate branching times. Since TACT has a stochastic component, we used averages across 100 replicate phylogenetic trees produced by TACT in all our analyses.

The geographic distribution of each species was derived from the World Checklist of Vascular Plants (Govaerts *et al*., 2021), which provides the presence and absence data for each World Geographical Scheme for Recording Plant Distributions (WGSRPD) level 3 unit (hereafter 'botanical country'; Brummitt *et al*., 2001). These botanical country names follow in some cases alternative spellings (e.g. Sumatera for Sumatra), we follow here the names as provided in Brummitt *et al*. (2001).

Species names in the Smith and Brown phylogeny follow NCBI nomenclature. These were updated to follow the WCVP nomenclature using the taxonomy matching procedure as previously described (Sun *et al*., 2021), which uses the WCVP taxonomy data as authority. Our data include 330 527 described species of seed plants. Bryophytes, clubmosses and ferns are not included in our analysis as geographic and/or phylogenetic data were unavailable.

Diversity indices

Diversity indices were calculated for each botanical country. Species richness was measured as the number of species recorded in a botanical country and species endemism as the number of endemic species. We calculated PD as the sum of the lengths of all branches that span members of a region (Faith, 1992), and PD endemism as the total amount of branch length found only in a given region (Faith, 1994). Because species richness, and by extension, PD are known to correlate with area, we additionally standardised all indices by area. Indices were estimated using the R package PHYLOREGION (Daru *et al.*, 2020b) functions *PD*, *phylo_endemism* and *weighted_endemism*. We calculated spatial correlations of diversity indices using Lee's L, an integration of Pearson's r, and Moran's I (Lee, 2001).

Hotspots

We identified PD hotspots following two different approaches. First, we identified botanical countries with the highest 2.5% estimates for species richness, PD and PD endemism, following previous authors (e.g. Orme *et al.*, 2005; Daru *et al.*, 2019). For our 368 botanical countries, the top 2.5% corresponds to the top 9.2 botanical countries, which we round up to top 10 for simplicity. Second, we identified each country's contribution (= complementarity) to global species richness, PD, species endemism and PD endemism. To assess complementarity, we used a greedy algorithm that starts with the botanical country that has the highest PD value (or other estimate of interest) and sequentially adds botanical countries, in each step choosing the country that adds most PD to the total PD in the set. Once a group of species has been covered by adding a country to the set, these species are exempt from calculations of PD for the remaining countries. This way the algorithm identified the minimum number of countries that together contained the maximum amount of PD in as small an area as possible. We selected the set of 10 countries that jointly maximised PD to facilitate comparison with top 2.5% countries.

Hotspot characteristics

For each botanical country, we calculated several anthropogenic and environmental characteristics (see for sources Supporting Information Table S1). We estimated the percent coverage of each hotspots' area with different biomes (Olson *et al.*, 2001) and the impact of deforestation, human footprint index and future climate change (annual precipitation and mean annual temperature) as average threat values per botanical country. All values were calculated as averages for each botanical country (Table S1). Quantitative differences in threats between hotspot and nonhotspot botanical countries were tested using Kruskal–Wallis rank sum tests.

Analyses were made in R v.4.2.1 (R Core Team, 2022). R packages used include DATA.TABLE (Dowle & Srinivasan, 2021), SF (Pebesma, 2018), PHYLOREGION (Daru *et al.*, 2020b), TERRA (Hijmans, 2022a), GGPLOT2 (Wickham, 2016), COWPLOT (Wilke, 2020), RASTER (Hijmans, 2022b), EXACTEXTRACTR (Baston, 2022), CASTOR (Louca & Doebeli, 2018), STRINGR (Wickham, 2022), SPDEP (Bivand & Wong, 2018).

Results

Phylogenetic diversity was strongly correlated with species richness (Fig. 1a,b; Lee's $L = 0.86$; $P = 0.001$). However, the top 2.5% countries differed clearly between species richness and PD (Fig. 2a,b). While the majority of highest species richness values were concentrated in the Neotropics, the top 2.5% PD values were more evenly distributed between South America and parts of southern Asia. The highest PD values were found in Colombia followed by China South-Central and Peru, whereas Antarctica and small islands had the lowest PD values. These low PD regions were also characterised by low species richness (Fig. 1a,b). Area-standardised PD was consistently highest on small islands, but it did not reveal any meaningful patterns for continental floras (Fig. S1).

The 10 botanical countries that were selected based on complementarity ('complementarity hotspots') were clearly different from the 10 botanical countries that had the highest individual diversities, both for species richness (Fig. 2a,c) and PD (Fig. 2b,d). Importantly, the former harboured a higher total diversity than the latter (40% vs 33.5% for species richness and 23% vs 19% for PD). It is noteworthy that 10 botanical countries can cover 40% of global species richness, but only 23% of global PD. This difference became even more apparent when comparing numbers of countries required to contain fixed proportions of global diversity. For example, while 50% of global species richness could be included in 15 botanical countries (Fig. 3a), a minimum number of 33 countries was required to cover 50% of PD (Fig. 3b). This pattern was consistent across diversity thresholds between 10% and 90% (Fig. 4), showing that species richness could be captured in comparatively few areas, whereas PD was more evenly distributed.

The complementarity hotspots of PD (Fig. 2d; Table 1) were almost identical to the complementarity hotspots of species richness (Fig. 2c), only differing in the inclusion of Western Australia (species richness) and Zaïre (PD). Complementarity hotspots of PD were widespread across Central- and South America, Africa, China, Madagascar, Borneo and New Guinea. They showed a significantly higher number of biomes than nonhotspot countries (Kruskal–Wallis rank sum test; $P < 0.001$). These hotspots also showed higher biome coverage proportions with (sub)tropical moist and dry broadleaf forest as well as montane grasslands and shrublands than their nonhotspot counterparts (Kruskal–Wallis rank sum test; $P < 0.005$; Fig. S2a). Both patterns were similar for countries selected for highest 2.5% PD values (Fig. S2b). These results were consistent with the positive correlation of biome types and total PD observed (Fig. S3; Spearman's rank correlation $\rho = 0.57$; $P < 0.001$).

The complementarity hotspots of species richness were, with one exception (Mexico Southwest), also the countries with the highest species endemism (Fig. 2c,e). There was also a large overlap between the PD complementarity hotspots and the countries with the highest PD endemism (Fig. 2d,f). Notably, two Australian states (Queensland and Western Australia) were among the top 10 countries with highest PD endemism but were not

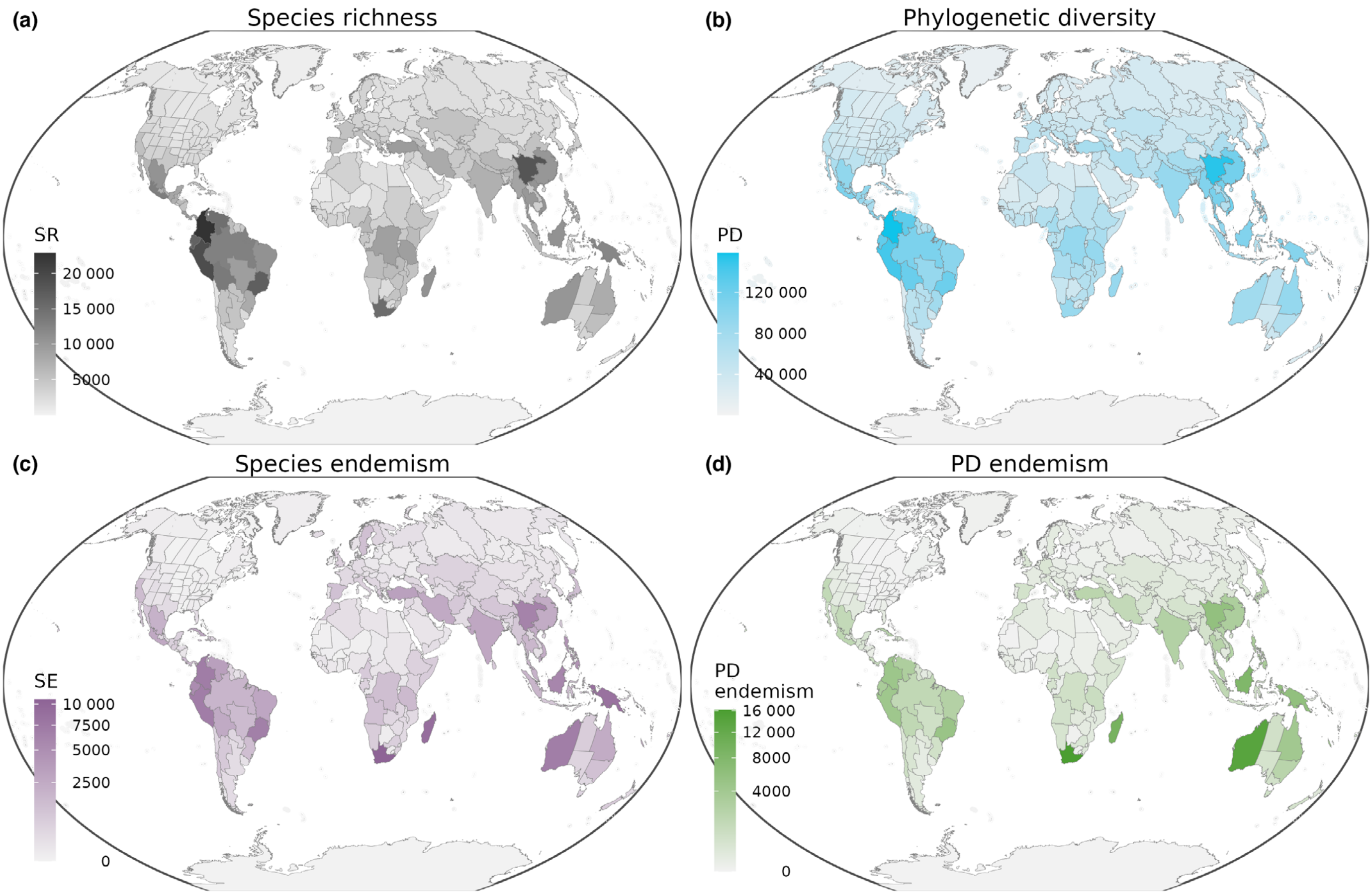

Fig. 1 Four aspects of diversity: (a) species richness (SR), (b) phylogenetic diversity (PD) as per (Faith, 1992), (c) species endemism, and (d) PD endemism. Colour saturation shows respective diversity values. Maps in Winkel tripel projection.

selected as PD complementarity hotspots. Conversely, Mexico Southwest and Zaïre had lower PD endemism, but did qualify as PD complementarity hotspots. Relatively few countries were required to cover a given proportion of global PD endemism compared with PD and species richness (Fig. 4); for example, only 12 botanical countries were required to cover 50% of global PD endemism.

Anthropogenic and environmental characteristics varied substantially between PD complementarity hotspots (Fig. 5). Complementarity hotspots of PD had a significantly larger area affected by deforestation compared with nonhotspots (Fig. S4; Kruskal–Wallis rank sum test; $P = 0.016$). Borneo was particularly strongly affected by deforestation. In general, the relative area affected by deforestation within the last 20 yr varied greatly from 47% on Borneo to 2% in the Cape Provinces and Australia. We found no significant difference between hotspots and nonhotspots for other threats (Fig. S4).

Discussion

Using a recently completed, comprehensive, open access data set of the taxonomy and geographic distributions of all vascular plant species (Govaerts *et al.*, 2021), we dissected the distribution of global seed plant PD using a complementarity-based approach. We found that (1) PD is more evenly distributed across the globe than species richness; (2) absolute PD (Daru *et al.*, 2019; Qian *et al.*, 2023) is no substitute for cumulative PD derived from complementarity-based analyses; and (3) tropical rain forests are important for sustaining high levels of PD, but a variety of biomes are implicated in the conservation of global seed plant PD.

Phylogenetic diversity is more evenly distributed across the globe than species richness

Our results support hypothesis H1, demonstrating that, for seed plants, PD is more evenly distributed across the globe than species richness. Because PD increases more slowly with area than species richness (Morlon *et al.*, 2011; Helmus & Ives, 2012), more than twice as many botanical countries are needed to represent 50% of global PD than to achieve the same for species richness (Fig. 3). This discrepancy is due to the spatial autocorrelation of diversification. If the area of a given sampling unit is increased, new species are added, but those species are likely close relatives to the ones that are already in the set. Biologically, this pattern results from the limited niche evolution and dispersal of

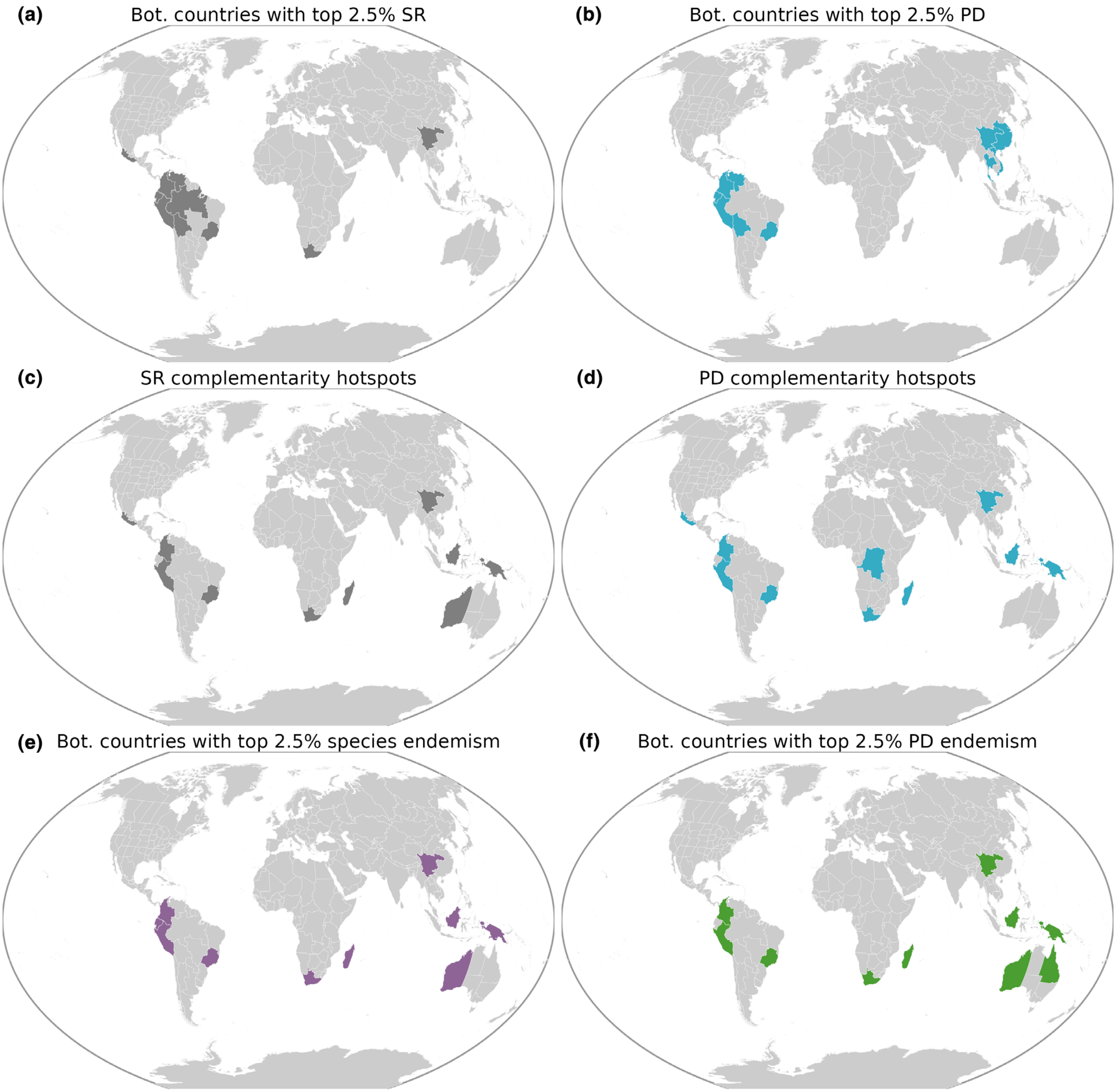

Fig. 2 Absolute values and complementarity for species richness (SR) and phylogenetic diversity (PD). Botanical countries with the top 2.5% total species richness (a) or PD (b), and the top 10 botanical countries with the highest contribution (complementarity) to global species richness (c) or PD (d). (e, f) Show the top 10 botanical countries for species endemism and PD endemism. Complementarity was assessed using a greedy algorithm that identifies the minimum number of countries containing the maximum number of species richness or phylogenetic diversity. The algorithm starts with the highest SR and PD value and subsequently adds countries with the next highest remaining contribution to SR and PD to the set.

diversifying clades (Wiens *et al*., 2010; Eiserhardt *et al*., 2013). Well-known examples of this phenomenon are local radiation events such as those driven by the uplift of the Andes (Hughes & Eastwood, 2006; Pérez-Escobar *et al*., 2017), where species-rich regions contain disproportionately many closely related species. These results highlight the risks of focussing purely on species richness in area prioritisation for conservation (Rodrigues *et al*., 2005).

Absolute phylogenetic diversity is no substitute for complementarity

In line with our hypothesis H2, we found that hotspots selected for PD complementarity outperformed hotspots selected for highest total PD in representing global diversity. The two approaches selected substantially different sets of regions. Evidently, many of the regions of highest PD were not only spatially

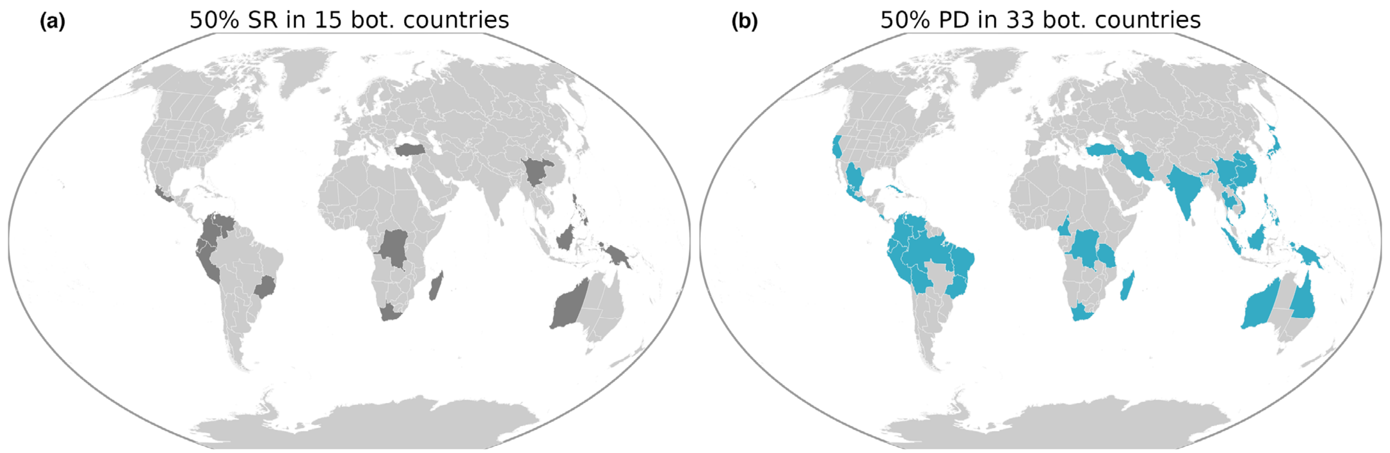

Fig. 3 Minimum number of botanical countries needed to capture 50% of global species richness (SR; (a) 15 botanical countries) and phylogenetic diversity (PD; (b) 33 botanical countries). Botanical countries were identified using a greedy algorithm that starts with the highest SR and PD values and subsequently adds countries with the next highest remaining contribution to SR and PD to the set.

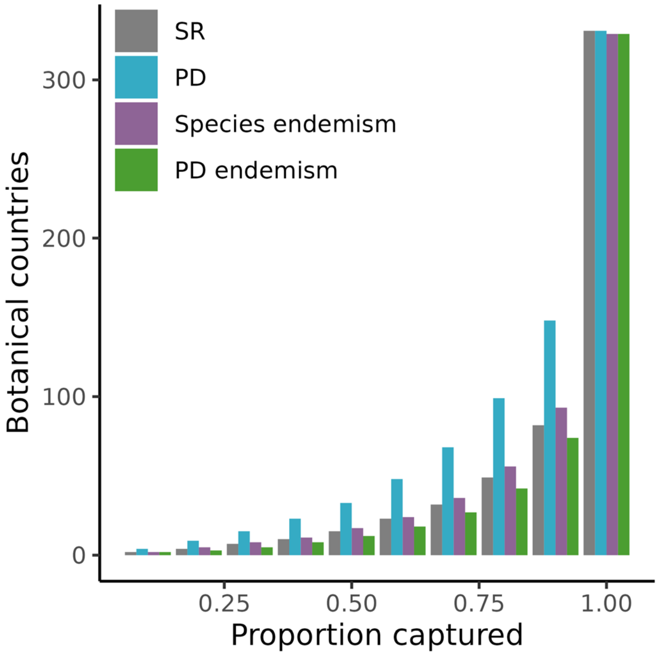

Fig. 4 Number of botanical countries required to capture different percentages of species richness (SR), phylogenetic diversity (PD) and endemic phylogenetic diversity. Half (50%) of plant SR, PD, PD endemism or species endemism can be captured in either 15, 33, 12, or 17 botanical countries, respectively.

adjacent, but also significantly redundant in their composition of species and lineages. For example, the botanical countries with the highest PD included clusters of adjacent countries in north-western South America and continental Asia (Fig. 2b). The complementarity approach showed that several of these were redundant in maximising PD in 10 botanical countries, instead highlighting the importance of Sub-Saharan Africa and Australasia for global PD. Of note, these areas were also identified by Qian *et al.* (2023) by ranking absolute PD, but using a much lower threshold (10%), leading to many more regions being recognised as hotspots, which makes prioritisation more difficult. Focussing on the areas with the highest individual PD as 'hotspots' (Daru *et al.*, 2019; Qian *et al.*, 2023) risks attention being diverted from parts of the world that are essential to safeguarding seed plant PD globally.

Ranking botanical countries by their PD endemism (Fig. 2f) identified many of the same areas as our complementarity analysis (Fig. 2d), which is expected since areas with much endemic PD can by definition always contribute many lineages that are not already represented by other areas (Faith, 1994). However, there are notable differences suggesting that the two approaches are not redundant. The Australian states that were not selected as complementarity hotspots despite high PD endemism likely overlapped too much in their phylogenetic composition with the geographically close New Guinea (Joyce *et al.*, 2021); thus, the geographically distant and hence likely phylogenetically less similar Mexico Central and Zaïre were able to contribute more to the set of hotspots. While PD endemism outperforms raw PD in selecting areas that are important for global PD, the two approaches emphasise slightly different aspects of the global distribution of PD.

Tropical rain forests are important, but a variety of biomes are required to conserve global PD

The distribution of high-PD regions and complementarity hotspots (Table 1) across biomes largely supports our hypothesis H3. As anticipated, regions of high individual PD had high coverage of (sub)tropical moist broadleaf forest (Fig. S3; Table 1). Due to biome conservatism (Crisp *et al.*, 2009), we also expected PD to be highest in regions that harbour many other biomes in addition to (sub)tropical moist broadleaf forest. This expectation was also confirmed (Fig. S3). However, the biome composition of high-PD regions (Table 1) suggests that the type of biomes included matters too. High-PD regions typically include several other forest types, specifically (sub)tropical dry forest, (sub)tropical coniferous forest, or temperate broadleaf or coniferous forest.

Table 1 Phylogenetic diversity (PD) complementarity hotspot characteristics.

	Top 2.5%		Complementarity top 10						
Level name	PD	SR	SR	PD	SR	PD	Species endemism	PD endemism	Biome composition
Borneo	0	0	1	1	10782	106890	5967	8161	
Brazil Southeast	1	1	1	1	16960	121481	6686	4913	
Cape Provinces	0	1	1	1	15362	88425	10590	16197	
China South-Central	1	1	1	1	18238	153301	6313	5772	
Colombia	1	1	1	1	22833	157886	7096	4591	
Madagascar	0	0	1	1	10720	89042	9040	9482	
Mexico Southwest	0	1	1	1	13133	111444	2681	1754	
New Guinea	0	0	1	1	12042	103369	8465	5874	
Peru	1	1	1	1	19235	143769	7008	4414	
Zaïre	0	0	0	1	9094	90968	1280	763	
Bolivia	1	1	0	0	13568	123978	2602	1642	
China Southeast	1	0	0	0	10214	117100	2443	3061	
Ecuador	1	1	0	0	16599	128453	5286	3295	
Thailand	1	0	0	0	10048	113039	1718	2262	
Venezuela	1	1	0	0	14957	130885	3369	3012	
Vietnam	1	0	0	0	10539	118236	2335	2453	

■ (Sub)Tropical moist broadleaf forests
■ (Sub)Tropical dry broadleaf forests
■ (Sub)Tropical coniferous forests
■ Temperate broadleaf and mixed forests
■ Temperate coniferous forests
■ (Sub)Tropical grasslands, savannas, shrublands
■ Montane grasslands and shrublands
■ Mediterranean forests, woodlands, scrub
■ Deserts and xeric shrublands
■ Mangroves

Hotspots were identified using a greedy algorithm that starts with the highest PD value and subsequently adds countries with the next highest remaining contribution to PD to the set. The first 10 selected countries are defined as hotspots. Top 2.5% columns indicate if the country is among the top 2.5% total PD or species richness (SR) countries (0 = no, 1 = yes). Complementarity top 10 columns indicate if the country is among the top 10 first selected countries using SR or PD. Grey rows show countries with top 2.5% PD values that have not been picked as PD complementarity hotspot. The biome column depicts the biome composition of each hotspot country.

Whether this is because forest generally harbours older and/or more divergent lineages than open vegetation, or because these forest biomes just happen to be spatially adjacent to the phylogenetically highly diverse (sub)tropical moist broadleaf forest, is unclear and worthy of further study. Our expectation that complementarity hotspots jointly cover a wider range of biomes than high-PD regions is primarily supported by the observation that complementarity hotspots encompass more open biomes than the primarily forested high-PD regions. This is particularly evident from the inclusion of the Cape Provinces of South Africa, which are exclusively covered by open biomes (at the scale of the biome maps used here). This confirms that while (sub)tropical moist broadleaf forest is, on its own, the most phylogenetically diverse biome, other ecologically and evolutionarily divergent biomes are required to appropriately represent global seed plant PD.

Threats to phylogenetic diversity

Countries identified as PD complementarity hotspots were not consistently more or less threatened by human impact than non-hotspot areas except for deforestation, which affected hotspots more strongly. The deforestation result is plausible, since hotspots also showed on average larger proportions of (sub)tropical moist broadleaf forest, with the notable exception of Cape Provinces. This biome is known to be under intense deforestation pressure (Lindquist *et al.*, 2012). Human footprint did not show clear results, possibly due to the large spatial scale our study was conducted on, which averages footprint over large areas, not differentiating between heavily affected urban areas and remote untouched landscapes. Since the majority of high diversity areas were located at low latitudes, anticipated future climate changes were naturally rather low since the absolute extent of climate change is predicted to be larger near the poles (Rantanen *et al.*, 2022). Threat status, usually represented as some form of habitat loss of a region, has been used as one of the defining criteria of conservation hotspots (Myers *et al.*, 2000). However, the example of New Guinea with its extraordinary flora, high contribution to global PD, but insufficient threat to qualify as conservation hotspot demonstrates potential challenges with the inclusion of threat in hotspot criteria (Cámara-Leret *et al.*, 2020), especially since anthropogenic habitat loss can be rapid (Gaveau *et al.*, 2014; Gamoga *et al.*, 2021). Due to the dynamic nature of threats, we defined hotspots solely based on their contribution to global PD.

Conservation prioritisation

We believe that safeguarding phylogenetic diversity in the Anthropocene is a global responsibility. Attention is often

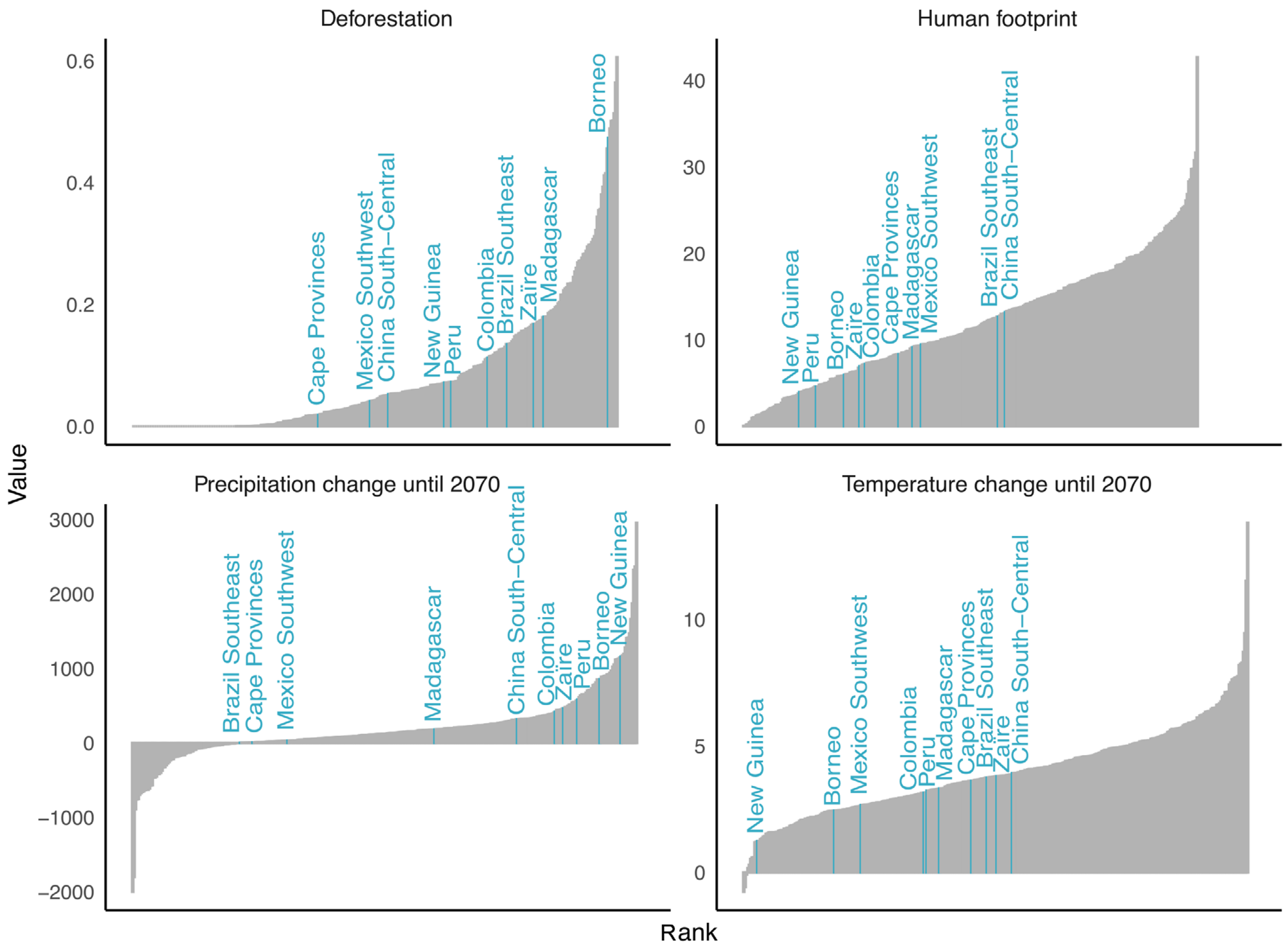

Fig. 5 Four types of threat for phylogenetic diversity (PD) complementarity hotspots. Rank of each hotspot (*x*-axis) with the corresponding threat value for deforestation, human footprint, predicted future change in precipitation and temperature, ordered by increasing threat values.

focussed on exceptionally species-rich regions, such as the Neotropics (Antonelli & Sanmartín, 2011; Cazzolla Gatti *et al.*, 2022), which also are highlighted by our analyses of absolute, country-level PD. However, complementarity-based analyses clearly show that many more biogeographic regions and biomes are needed for effective conservation of global PD, and hence global feature diversity. This includes regions of the world that are known for their comparatively low species richness, such as parts of the African continent (Couvreur, 2015). Because our analyses are conducted at the scale of botanical countries, most of which correspond to political or administrative units (Brummitt *et al.*, 2001), our findings can in principle directly inform conservation policy in those units. In our view, this advantage of botanical countries outweighs their disadvantage of being variable in size, which complicates their use in ecological and evolutionary research (but see e.g. Kissling *et al.*, 2012a; Guo *et al.*, 2022; Tietje *et al.*, 2022) but is less problematic in a conservation context. While larger (botanical) countries are more likely to be identified as priority regions for conservation, these do also in fact hold larger proportions of global PD. Of note, the countries that were most implicated in the conservation of global PD were largely unaffected by the somewhat arbitrary division of the largest countries into lower-level administrative units (Figs S5–S8; Table S2). Importantly, we stress that countries that are not selected in our complementarity analysis can still play a major role in the conservation of global plant PD, as their PD may largely overlap with adjacent, selected countries. Not being flagged as a priority country for global PD complementarity thus does not imply that a country has no role to play in conservation.

Prospects

Our findings are a first pass at revealing not only where centres of plant PD are located, but also how broadly plant PD is distributed across the planet. By taking complementarity into account and using a taxonomically comprehensive, open access data set, our analysis goes substantially beyond previous studies (Daru *et al.*, 2019; Qian *et al.*, 2023). However, due to data availability, our analysis is limited to a relatively large spatial scale, and further studies are warranted to fully explore how the distribution and complementarity of plant PD is affected by spatial scaling (Morlon *et al.*, 2011; Helmus & Ives, 2012; Daru *et al.*, 2020a). While analyses at finer spatial resolution are needed to more accurately pinpoint the locations of PD hotspots, these may not necessarily improve insights from PD complementarity for conservation prioritisation (Daru *et al.*, 2019). Analyses at intermediate spatial resolution using units that do not vary in area could provide invaluable insights. However, the point occurrence data sets needed for such analyses are notoriously incomplete and biased (Meyer *et al.*, 2016), making such an analysis impractical for the time being and underlining the value of the taxonomically and geographically complete data set used here. Further investment in the assembly of global distribution datasets is clearly needed.

Phylogenetic diversity provides substantially deeper insights into total 'feature diversity' than simple species counts (Faith, 1994). It captures both the evolutionary past and possible future evolutionary potential in a region, as well as the 'option value' of biodiversity for future human uses. However, it is no panacea for conservation prioritisation, which requires a full grasp of trade-offs between different diversity measures such as basic species counts, phylogenetic diversity metrics, functional and trait diversity and anthropogenic factors, including rapid changes in land use and the ubiquitous effects of climate change and plant distribution and diversity (Pollock *et al.*, 2017; Faith, 2021). We do not intend to judge the relative importance of these factors or suggest that PD is the most relevant. Instead, integrating phylogenetic measures (including PD) with other diversity metrics, as suggested by Pavoine and Bonsall (2011) might be the most appropriate way to explore and understand the current biodiversity crisis and its potential future implications. We also acknowledge that complementarity analysis in conservation practice requires multivariate optimisation processes guided by spatial, political, financial and social aspects and limitations (Sarkar *et al.*, 2006; Kukkala & Moilanen, 2013). Thus, while our results provide important insights into the global distribution of plant PD, future studies need to integrate these findings with other aspects of plant diversity as well as the political and socioeconomic context of real-world conservation.

Acknowledgements

We thank Dan Faith and three anonymous reviewers for insightful comments on previous drafts that materially improved the manuscript. MT's postdoc was funded by Villum Fonden (grant 00025354 to WLE) and an Aarhus University Research Foundation research grant (to WLE). AA acknowledges financial support from the Swedish Research Council (2019-05191) and the Royal Botanic Gardens, Kew. SAS was supported by the National Science Foundation under grant agreement DBI 1930030. Some of the computing for this project was performed on the GenomeDK cluster.

Competing interests

The authors declare no competing interests.

Author contributions

MT, WJB and WLE conceived the research ideas and designed the project. RG collected the data. MT analysed the data. MT, AA, FF, WJB, SAS and WLE interpreted the results. MT, WJB and WLE wrote the manuscript with contributions by AA, SAS, FF and in consultation with RG and MS. WJB and WLE contributed equally to this work.

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Data availability

Code and data to repeat the analysis of this study are available in Zenodo at 10.5281/zenodo.8084423. All data sources are referenced in Table S1. Machine-readable estimates for each botanical country are provided as Dataset S1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Data summary including each botanical countries metrics.

Fig. S1 Four aspects of diversity, divided by area of the botanical country.

Fig. S2 Proportional coverage of top 2.5% phylogenetic diversity (PD) and PD complementarity hotspots with biome types compared to remaining botanical countries.

Fig. S3 Number of biomes and phylogenetic diversity per botanical country.

Fig. S4 Threat estimates for top 10 phylogenetic diversity complementarity hotspots and remaining botanical countries.

Fig. S5 Area of the phylogenetic diversity (PD) complementarity hotspots and 50% PD botanical countries compared to remaining botanical countries.

Fig. S6 Political countries with the top 2.5% and highest complementarity for species richness and phylogenetic diversity.

Fig. S7 Political countries needed to capture 50% of global species richness or phylogenetic diversity.

Fig. S8 Number of political countries required to capture increasing percentages of species richness, phylogenetic diversity (PD) and endemic PD.

Table S1 Data sources.

Table S2 Botanical countries merged into political units.