

## Global hotspots of plant phylogenetic diversity

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## 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; 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, yet unrecognised 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.

**Key words:** seed plants, phylogenetic diversity, complementarity, hotspot, phylogenetic endemism, conservation, macroecology

## Introduction

Compared to 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 in a biota, PD (Faith, 1992) broadly captures diversity in form and function (Srivastava *et al.*, 2012; Tucker *et al.*, 2017; 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 has been established explicitly as a guiding measure for conservation efforts, i.e. to identify sets of areas that jointly carry the most

PD and hence should be priorities for conservation (Faith, 1992; Winter *et al.*, 2013; 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, i.e. 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 1,500 endemic plant species each (as well as high levels of anthropogenic threat). A similar train of thought can be applied to PD, using metrics such as PD endemism (Faith, 1994) 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). Such analyses can show in which parts of the world extinction would cause the largest total loss of phylogenetic (or evolutionary) history.

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 facilitated thorough 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 datasets (Qian *et al.*, 2023). For example, (Daru *et al.*, 2019) mapped PD and other diversity metrics for 6,483 (*ca.* 50%) currently accepted angiosperm genera, revealing a highly uneven distribution of angiosperm PD with hotspots in parts of South and Central America, Madagascar, Southeast Asia and Australasia. Whether species-level analyses with a more comprehensive taxon sampling will challenge or confirm these highly valuable first insights remains to be seen. Although genus- and species-level PD patterns are similar in vertebrates (Daru *et al.*, 2019) and North American angiosperm trees (Qian & Jin, 2021), this might not be the case in all plants, as also zoology and botany diverge considerably in their use of higher taxonomic ranks, with plant genera often being larger and more variable in size (Frodin, 2004; Sigwart *et al.*, 2017). 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, and thus do not effectively guide conservation attention (H2). Because of the spatial autocorrelation of diversification, areas of highest PD are often geographically adjacent and redundant in their

composition of species and lineages. We expect that hotspots based on complementarity, i.e. explicitly maximising the cumulative PD they represent, will be substantially different from the areas that individually have the highest PD.

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, Wien & 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 a high proportion of tropical and subtropical moist broadleaf forest, as well as elements of other evolutionarily divergent biomes. Along a similar vein, we expect a wider range of biomes to be important in complementarity-based hotspots compared to 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 focused 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 a high-level evaluation of global threats (deforestation, human footprint, climate change), to facilitate comparison with 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 establish a prioritised set of regions for the conservation of global plant phylogenetic diversity.

## Materials and Methods

### *Phylogeny and distribution data*

All phylogenetic measures were derived from the phylogenetic tree of Smith & Brown (2018) to which we added missing species using TACT (Chang *et al.*, 2020). Of the different trees provided by Smith & 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 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 & Brown phylogeny follow NCBI nomenclature. These were updated to follow the WCVF nomenclature using the taxonomy matching procedure of (Sun *et al.*, 2021), which uses the WCVF taxonomy data as authority. Our data includes 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.

156 Diversity indices were calculated for each botanical country. Species richness was measured as  
157 the number of species recorded in a botanical country. We estimated phylogenetic diversity  
158 (PD) as well as three measures of endemism, including PD endemism, phylogenetic endemism  
159 and weighted endemism. PD was calculated as the sum of the lengths of all branches that span  
160 members of a region (Faith, 1992), PD endemism is calculated as total amount of branch length  
161 found only in a given region (Faith, 1994), phylogenetic endemism is similar to PD but inversely  
162 weighted by species ranges (Rosauer *et al.*, 2009), and weighted endemism is species richness  
163 inversely weighted by species ranges. Indices were estimated using the R package *phyloregion*  
164 (Daru *et al.*, 2020b) functions *PD*, *phylo\_endemism* and *weighted\_endemism*. We calculated  
165 spatial correlations of diversity indices using Lee's L, an integration of Pearson's *r* and Moran's *I*  
166 (Lee, 2001).

## 167 *Hotspots*

168 We identified PD hotspots following two different approaches. First, we identified botanical  
169 countries with the highest 2.5% estimates for species richness, PD and PD endemism.  
170 Choosing the top 2.5% as hotspots is an approach that has been implemented by previous  
171 authors (e.g (Orme *et al.*, 2005; Daru *et al.*, 2019) and focuses on the total estimates for a  
172 specific area, independent from other regions. For our 368 botanical countries, the top 2.5%  
173 corresponds to the top 9.2 botanical countries, which we round up to top ten for simplicity.  
174 Second, we identified each country's contribution (=complementarity) to global species  
175 richness, PD and PD endemism. To assess complementarity we used a greedy algorithm that  
176 starts with the botanical country that has the highest PD value (or other estimate of interest) and  
177 sequentially adds botanical countries, in each step choosing the country that adds most PD to  
178 the total PD in the set. Once a group of species has been covered by adding a country to the  
179 set, these species are exempt from calculations of PD for the remaining countries. This way the  
180 algorithm identified the minimum number of countries that together contained the maximum  
181 amount of PD, which is of particular importance for conservation as it allows the optimisation of  
182 diversity in as small an area as possible. This approach focuses on the contribution of each  
183 region to the global PD, avoiding redundancy. We selected the same number of countries (ten)  
184 as was included in the top 2.5% approach to PD hotspots to facilitate comparison.

## 186 *Hotspot characteristics*

187 For each botanical country we calculated several anthropogenic and environmental  
188 characteristics (see for sources Table S1). We estimated the percent coverage of each  
189 hotspots' area with different biomes (Olson *et al.*, 2001) and the average impact of  
190 deforestation, human footprint index and future climate change as average threat values per  
191 botanical country. We collected diversification rates (mean root distance; the average number of  
192 edges from tip to root in a phylogeny of all species occurring in a botanical country) for each  
193 botanical country from (Tietje *et al.*, 2022). Quantitative differences in threats and diversification  
194 rates between hotspot and non-hotspot botanical countries were tested using Kruskal-Wallis  
195 rank sum tests.

196  
197 Analyses were done in R version 4.2.1 (R Core Team, 2022). R packages used include  
198 *data.table* (Dowle & Srinivasan, 2021), *sf* (Pebesma, 2018), *phyloregion* (Daru *et al.*, 2020b),  
199 *terra* (Hijmans, 2022a), *ggplot2* (Wickham, 2016), *cowplot* (Wilke, 2020), *raster* (Hijmans,  
200 2022b), *exactextractr* (Daniel Baston, 2022), *castor* (Louca & Doebeli, 2018), *stringr* (Wickham,  
201 2022), *spdep* (Bivand & Wong, 2018).

## 203 Results

204 Phylogenetic diversity (PD) was strongly correlated with species richness when accounting for  
205 spatial autocorrelation (Fig. 1a,b, Lee's  $L = 0.86$ ;  $P = 0.001$ ). However, the top 2.5% countries  
206 differed clearly between species richness and PD (Fig. 2a,b). While the majority of highest  
207 species richness values were concentrated in the Neotropics, the top 2.5% PD values were  
208 more evenly distributed between South America and parts of southern Asia. The highest PD  
209 values were found in Colombia followed by China South-Central and Peru, whereas Antarctica  
210 and small islands had the lowest PD values. These low PD regions were also characterised by  
211 low species richness (Fig. 1a,b).

212  
213 The ten botanical countries that were selected based on complementarity ("complementarity  
214 hotspots") were clearly different from the ten botanical countries that had the highest individual  
215 diversities, both for species richness (Fig. 2a,c) and PD (Fig. 2b,d). Importantly, the former  
216 harboured a higher total diversity than the latter (40% vs. 33.5% for species richness and 23%  
217 vs. 19% for PD). It is noteworthy that ten botanical countries can cover 40% of global species  
218 richness, but only 23% of global PD. This difference became even more apparent when  
219 comparing numbers of countries required to contain fixed proportions of global diversity. For  
220 example, while 50% of global species richness could be included in 15 botanical countries (Fig.  
221 3a), a minimum number of 33 countries was required to cover 50% of PD (Fig. 3b). This pattern  
222 was consistent across diversity thresholds between 10 and 90 percent (Fig. 4), showing that  
223 species richness could be captured in comparatively few areas, whereas PD was more evenly  
224 distributed.

225  
226 The complementarity hotspots of PD (Fig. 2d, Table 2) were almost identical to the  
227 complementarity hotspots of species richness (Fig. 2c), only differing in the inclusion of Western  
228 Australia (species richness) and Zaïre (PD). Complementarity hotspots of PD were widespread  
229 across Central- and South America, Africa, China, Madagascar, Borneo and New Guinea. They  
230 showed a significantly higher biome diversity than non-hotspot countries (Kruskal-Wallis rank  
231 sum test,  $P < 0.001$ ). These hotspots also showed higher biome coverage proportions with  
232 (sub)tropical moist and dry broadleaf forest as well as montane grasslands and shrublands than  
233 their non-hotspot counterparts (Kruskal-Wallis rank sum test,  $P < 0.005$ , Fig. S2a). Both  
234 patterns were similar for countries selected for highest 2.5% PD values (Fig. S2b). These  
235 results were consistent with the positive correlation of biome types and total PD observed  
236 (Spearman's rank correlation  $\rho = 0.57$ ,  $P < 0.001$ , Fig. S3). Diversification rates did not differ  
237 significantly between PD complementarity hotspots and other countries, but were lower in top  
238 2.5% PD countries than in other countries (Fig. S4).

239  
240 Anthropogenic and environmental characteristics varied substantially between PD  
241 complementarity hotspots (Fig. 5). Complementarity hotspots of PD had a significantly larger  
242 area affected by deforestation compared to non-hotspots (Fig. S5, Kruskal-Wallis rank sum test,  
243  $P = 0.016$ ). Borneo was particularly strongly affected by deforestation. In general, the relative  
244 area affected by deforestation within the last 20 years varied greatly from 47% on Borneo to 2%  
245 in the Cape Provinces and Australia. We found no significant difference between hotspots and  
246 non-hotspots for other threats (Fig. S5).

247  
248 Global patterns of PD endemism were correlated with species richness (Lee's  $L = 0.42$ ;  
249  $p = 0.003$ ; Fig. 1a,c), and closely matched patterns of phylogenetic endemism and weighted  
250 endemism (Fig. S1). Among the botanical countries harbouring most PD endemism were the  
251 Cape Provinces, followed by Western Australia, Madagascar and Borneo (Fig. 1c). Relatively  
252 few countries were required to cover a given proportion of global PD endemism compared to  
253 PD and species richness (Fig. 4); e.g., only twelve botanical countries were required to cover  
254 50% of global PD endemism.

## Discussion

Using a recently completed, comprehensive, open access dataset of the taxonomy and geographic distributions of all vascular plant species (Govaerts *et al.*, 2021), we dissected the distribution of global seed plant phylogenetic diversity (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 (Connor & McCoy, 1979; Rosenzweig, 1995; 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 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 focusing 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 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 recognized as hotspots, which makes prioritisation more difficult. Focusing 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.

### *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 (Table 1, Fig. S3). 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. 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). Hence, we define hotspots solely based on their contribution to global PD, using threats as an additional layer of information to inform conservation prioritisation.

### *Conservation prioritisation*

We believe that safeguarding phylogenetic diversity in the Anthropocene is a global responsibility. Attention is often focused 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; Tietje *et al.*, 2022; Guo *et al.*, 2022) which is, however, 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 (Table S2, Fig. S7–9). 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 dataset, 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 datasets 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 dataset 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), capturing both the evolutionary past and possible future evolutionary potential in a region. However, it is no panacea for conservation prioritisation, which requires a full grasp of trade-offs between different diversity measures such as basic species count, 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. We do not intend to judge the relative importance of these factors or suggest that PD is the most relevant. Instead, integrating multiple viewpoints, as suggested by (Pavoine & 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.

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## 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.

## Data availability

Code and data to repeat the analysis of this study are available in Zenodo at [[link to zenodo repository](https://github.com/Eryops1/phylogenetic_hotspots) upon publication. Currently a git repo: [https://github.com/Eryops1/phylogenetic\\_hotspots](https://github.com/Eryops1/phylogenetic_hotspots)]. All data sources are referenced in Table S1.

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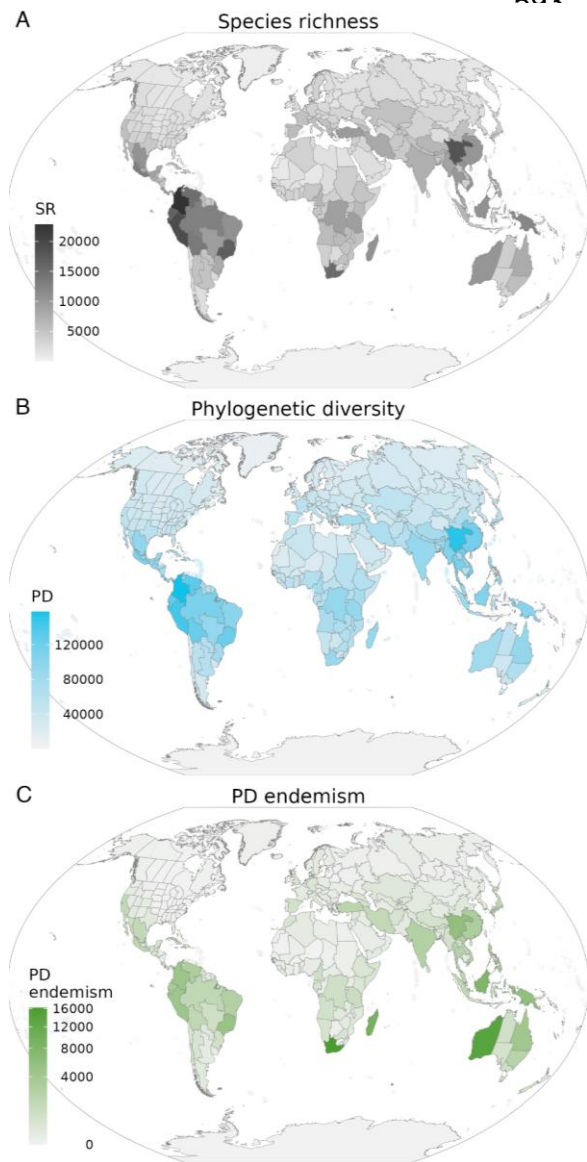
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624 Fig. 1. Three aspects of diversity: A) Species richness (SR); B) Phylogenetic diversity (PD) as per (Faith, 1992); C)  
 625 Phylogenetic diversity endemism (PD endemism). Maps in Winkel tripel projection.  
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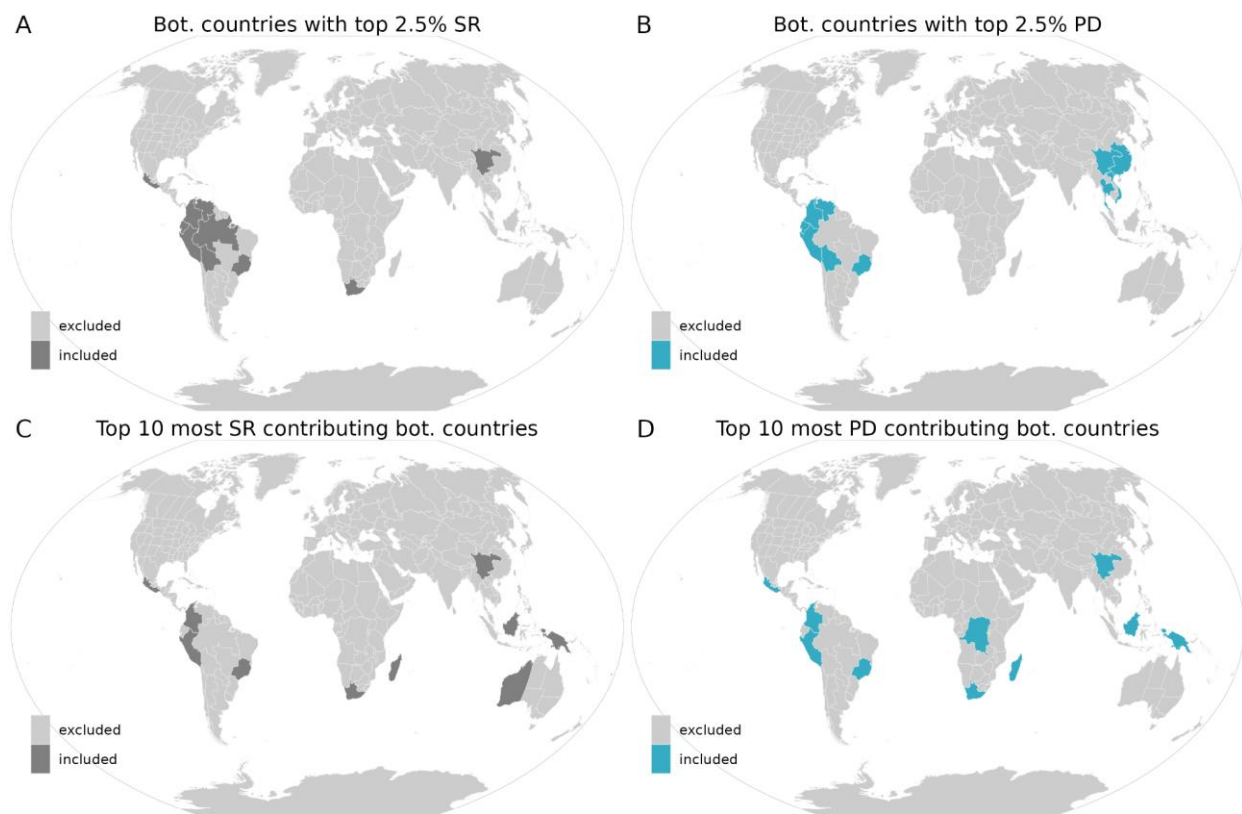


Fig. 2. Absolute values and complementarity for species richness (SR) and phylogenetic diversity (PD). Botanical countries with the top 2.5% total species richness (A) or phylogenetic diversity (B), and the top ten botanical countries with the highest contribution (complementarity) to global species richness (C) or phylogenetic diversity (D). 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.

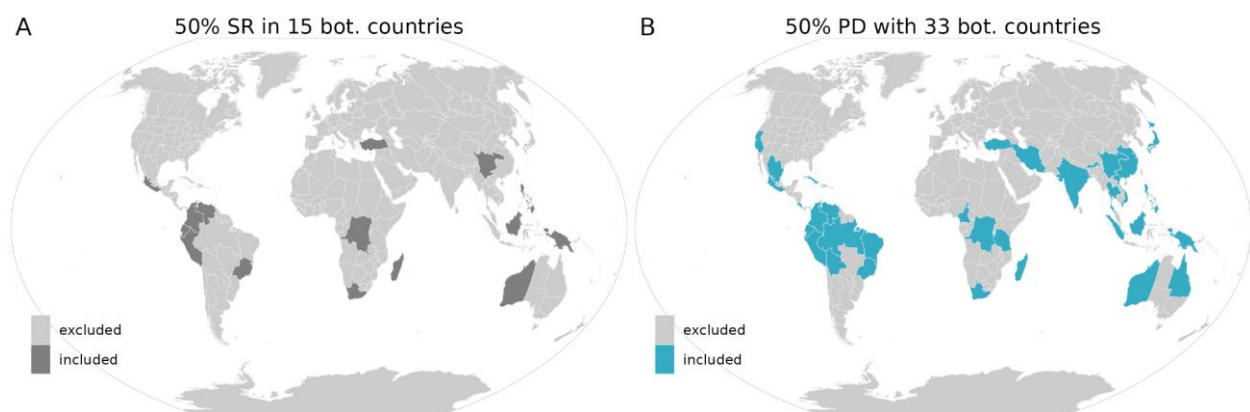


Fig. 3. The minimum number of botanical countries needed to capture 50% of global species richness (SR, A, 15 botanical countries) and phylogenetic diversity (PD, B, 33 botanical countries). Botanical countries were identified using a greedy algorithm that starts with the highest SR and PD values and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

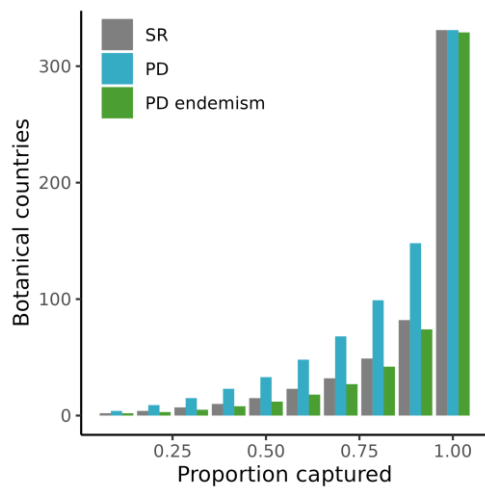


Fig 4. The number of botanical countries required to capture different percentages of species richness, phylogenetic diversity and endemic phylogenetic diversity. Half (50%) of plant species richness, phylogenetic diversity or PD endemism can be captured in either 15, 33 or 12 botanical countries, respectively.

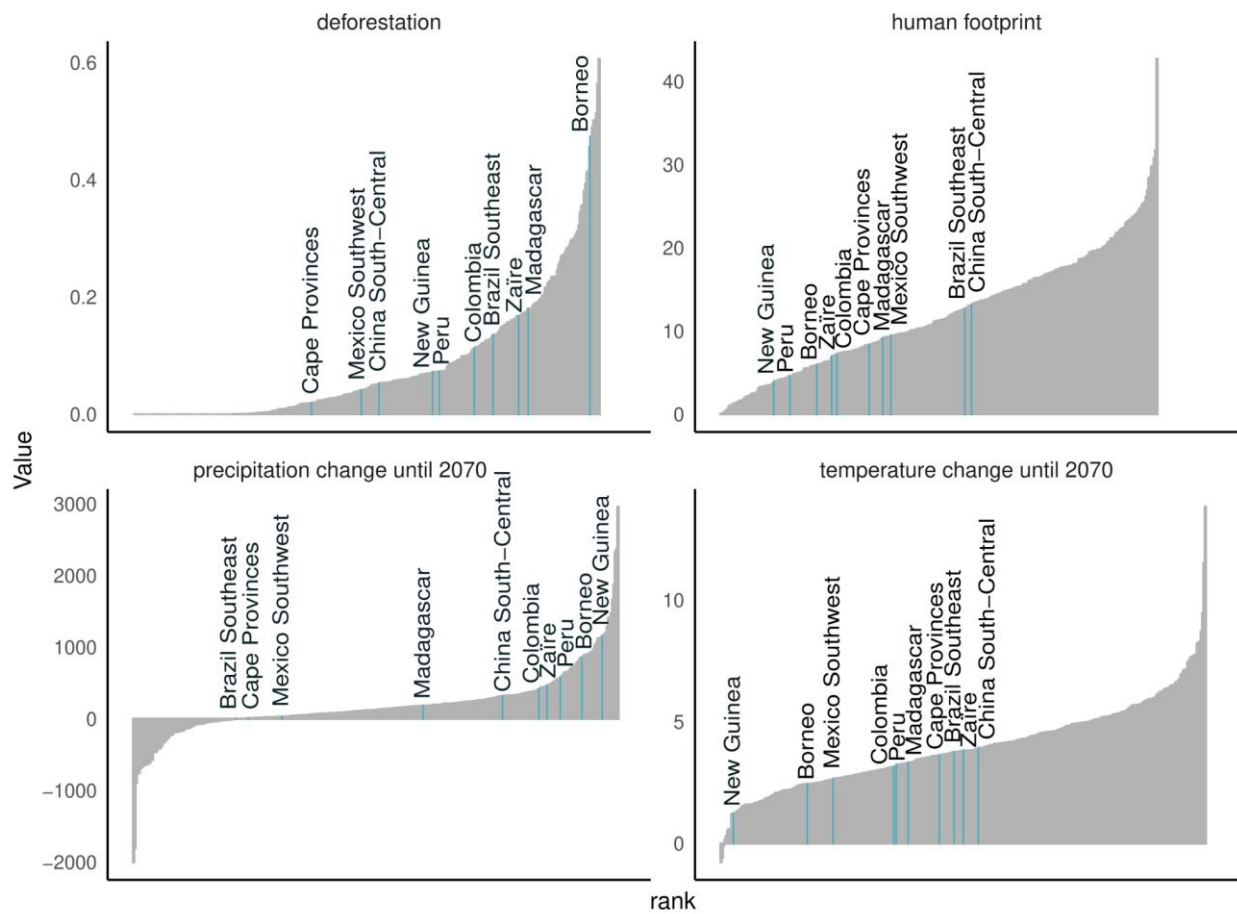


Fig. 5. Four types of threat for complementary PD hotspots. Rank of each hotspot (x-axis) with the corresponding threat value for deforestation, human footprint, predicted future change in precipitation and temperature, ordered by increasing threat values.



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Table 1. Phylogenetic diversity complementarity hotspot characteristics. 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 species richness (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.

Level name	Top 2.5% PD	Top 2.5% SR	SR complementarity top 10	PD complementarity top 10	Species richness	PD	PD endemism	Biome composition
Borneo	0	0	1	1	10782	106890	8161	
Brazil Southeast	1	1	1	1	16960	121481	4913	
Cape Provinces	0	1	1	1	15362	88425	16197	
China South-Central	1	1	1	1	18238	153301	5772	
Colombia	1	1	1	1	22833	157886	4591	
Madagascar	0	0	1	1	10720	89042	9482	
Mexico Southwest	0	1	1	1	13133	111444	1754	
New Guinea	0	0	1	1	12042	103369	5874	
Peru	1	1	1	1	19235	143769	4414	
Zaire	0	0	0	1	9094	90968	763	
Bolivia	1	1	0	0	13568	123978	1642	
China Southeast	1	0	0	0	10214	117100	3061	
Ecuador	1	1	0	0	16599	128453	3295	
Thailand	1	0	0	0	10048	113039	2262	
Venezuela	1	1	0	0	14957	130885	3012	
Vietnam	1	0	0	0	10539	118236	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