

Global hotspots of plant phylogenetic diversity

Responses to general comments

For this resubmission we made vast adjustments to our manuscript, hence we provide here first of all the responses to the most pressing issues found with the previous version of our paper as identified by the editor, which concerns novelty, integration with state-of-the-art literature, and our diversity metrics. For the remaining reviewer suggestions, we added our responses to their comments below in italics with references to the changed parts of the manuscript.

Novelty

We have adjusted our manuscript as suggested by reviewer 1 by changing the angle of our study which also allowed us to address significant increments from previous work.

ACTION:

1. We dedicated the third paragraph in our introduction to existing literature, describing limitations of these studies and still missing research aspects; this includes particularly Daru 2019 (as suggested by reviewer 1) and also the newer Qian 2023 paper.
2. We changed the focus of our analysis: we have implemented the main criticism of reviewer 2 by including PD complementarity values for each botanical country and comparing those to absolute PD values, which also differentiates our study further from Daru et al. 2019 and put a spotlight on complementarity. Adding the complementary analysis also helped us to better integrate our point about spatial scaling differences between species richness and PD.

Connection with state of the art literature

We are grateful for literature suggestions made by the reviewers. Due to the vast changes in the manuscript, some suggestions did not fit any longer in our manuscript, but we added literature e.g. on methods and challenges in conservation ([Sarkar et al. 2006](#); [Kukkala and Moilanen 2013](#)).

Diversity metrics

As mentioned in the novelty statement, we acknowledge the critique on the used phylogenetic diversity metrics, especially on the PD standardisation, and agree that this standardisation might be of more theoretical value than applicable for conservation questions. The comments by reviewer 2 have prompted us to remove the standardisation of our diversity metrics. Instead, we discuss the non-equal area resolution of our data and the meaningfulness of botanical countries as spatial unit for global scale conservation questions.

Responses to specific comments by referees:

Referee: 1

Comments to the Author

In this manuscript, Tietje et al. explore global phylodiversity patterns (Phylogenetic Diversity PD sensu Faith 1992 and Phylogenetic Endemism PE) using level-3 TDWG regions as sampling units to identify what they called phylodiversity hotspots, that is, level-3 TDWG regions with high PD and SR (species richness) or PE and WE (weighted endemism), and they further characterized them in

terms of biome representativeness, diversification rates, and biodiversity threats. The statistical analyses are rather simple (for a specialized reader) and, overall, they clearly described (but see below). The authors present the research as hypothesis-driven, yet I think they are not particularly sharp but rather kind of obvious, at least for a specialized reader (see comments). Concerning the English, I must say that I am not a native English speaker, yet I have the feeling that language needs improvement. As an illustrative example, the second paragraph of the abstract includes four sentences, all of them starting with “we”. I think there is room for polishing the English style throughout the text.

[We have paid particular attention to improving language in our revisions.](#)

The topic addressed in the manuscript is interesting, and I concur with the authors that exploring phylodiversity patterns can be highly informative, yet there is an issue that, to my judgement, raises the need for a change in the perspective; this analysis has been already done in the recent past (as the authors recognize in the text). It is true that the research by Daru et al. (2018) was conducted at the genus-level using an incompletely resolved phylogeny, but it is essentially the same type of analysis. Moreover, Daru et al. (2018) reported strong correlations between phylodiversity hotspots defined at the genus- and species-level, which cast doubt on the author’s arguments for revisiting the topic. Of course, revisiting research questions is highly valuable and necessary for pushing the frontiers of knowledge forward, but I think the circumstances of this research requires a change of perspective; what have we learnt here? What is the incremental novelty relative of the findings by Daru et al. (2018)? I do not think this ‘epistemological’ obstacle is insurmountable, yet it requires reformulating the manuscript in accordance.

[We agree that our study needs to put a heavier spotlight on novelty and hence have made substantial changes. Please see above the statement on novelty where the new line of argument in our paper is outlined.](#)

That said, I now provide some comments and suggestions that may hopefully help to improve the research.

I concur that “optimising PD has the potential to stabilise the resilience of key ecosystem functions” (line 48), yet I think the authors may further provide extant empirical evidence on this matter. For example, Forest et al. (2007) found that maximum PD levels capture more plant-related benefits than random sampling in the Cape (the analysis is somewhat ‘hidden’ in the Supplementary of the cited article, but it is there), and Molina-Venegas (2021) found a similar outcome at the global scale. Both papers are indeed cited in the text, but I think moving these citations earlier will much increases the strength of the introductory idea of the manuscript. I would edit the sentence like: “optimising PD has the potential to stabilise the resilience of key ecosystem functions (Mazzochini et al., 2019) and services (Forest et al. 2007; Molina-Venegas et al. 2021)”.

[Thank you for the suggestion! Keeping in mind reviewer 2 comments on how PD optimisation could even include targeted extinctions, we included the Molina-Venegas study but avoided “optimising”. The sentence now reads “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)” (lines 45 - 49).

Later in the same paragraph, the authors posit that identifying phylodiversity hotspots is essential for retaining “the evolutionary history and potential of plants”. I wonder potential for what? If the authors refer to ‘evolutionary potential’, as suggested by the title of the citation (Forest et al. 2007), I will argue that such idea is controversial, as the relationship between higher PD and greater evolutionary potential remains unclear (see Winter et al. 2013). If the authors refer to ‘beneficial potential for humans’, then I would just reword a bit for clarification and to avoid redundancy with the previous sentence.

Thank you, this sentence is now framed more generally focussing on identifying preservation goals (lines 49 - 52).

Concerning the importance of using PE to complement PD-based results (lines 55 – 63), I got the idea because I am familiar with the eco-phylogenetic literature, but I think it may be a bit cryptic for non-specialized readers. I would suggest the authors to further describe what “how important” means in the context of the paragraph.

This part became obsolete with the restructuring of the manuscript, we no longer jointly maximise these two measures of diversity aspects.

The authors cited Molina-Venegas et al. (2021) as an example of global plant phylodiversity analysis (lines 68-70), but I would also suggest citing Carta et al. (2022) as another example, this time from the bioregionalization angle.

This part has been rewritten and now focuses on studies explicitly looking at two major studies on global plant PD.

Concerning the hypothesis, I will argue that they are not particularly persuasive but rather obvious. As such, it is expected that sister species co-occur at the level-3 TDWG region level regardless of the mode of speciation (of course, there are exceptions to this generally expected pattern), which undoubtedly will lead to phylogenetic clustering relative to the global species pool that is defined by the randomization scheme used by the authors. Also, the fact that “conservation hotspots imperfectly capture plant phylodiversity hotspots” is neither surprising because the former were not delimited based on level-3 TDWG regions but manually on the basis of expert opinion.

We revised our hypotheses which are now stated right in the summary as well as more outlined in the introduction (lines 87 - 118). In short, our hypotheses are: 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.

The spatial overlap with conservation hotspots hypothesis got removed since we agree that a comparison is difficult due to different identification techniques and spatial resolution.

The authors used the method described in Chang et al. (2020) to expand the molecular phylogeny they used in the study. I have no problem at all with this, but I think they should briefly describe the procedure, especially because it seems a sort of parametric expansion based on diversification models, which has been criticized in the recent past (Rabosky 2015).

We added a more detailed description of how TACT works to the text (lines 137 - 140)

Concerning the Kruskal-Wallis rank sum and pairwise Wilcoxon rank sum tests conducted by the authors, it is not clear to me what are the two groups being compared. After going through the results, it seems the authors compared phylodiversity hotspots versus conservation hotspots, yet I would suggest clarifying this already from the methods.

Text on group comparisons using rank sum tests was reworded for clarity (lines 192f).

The authors estimated a diversification rate per sampling unit using the methods described in Tietje et al. (2022). I would suggest further describing the procedure to save the readers the visit to Tietje et al. (2022) for a better understanding of this analysis. Note that in many cases, the representative species of the lineages (let's say genera) inhabiting a given level-3 TDWG region will represent a minor fraction of the entire lineages, and this may have an impact in determining diversification rates for delimited spatial units. I am not sure if this issue was addressed in Tietje et al. (2022), yet I think it may be worth discussing here.

We followed the suggestion and added a description of the diversification rate measure (MRD) to the text (lines 191f). Since this data was based on a complete (=including all described species) phylogeny, we do not have representative sample fractions of taxonomic units that could interfere with diversification rate estimates.

The authors argued that greater PD towards the tropics may be due to slower diversification rates resulting in more evolutionarily distinct species and thus substantial increase in PD relative to SR. I wonder if higher extinction rates in certain lineages may also lead to the same pattern? The largely tropical nature of the identified phylodiversity hotspot suggest that extinction may have had a minor role in shaping high PD levels therein, yet I think it may be worth discussing a bit from this angle.

The contribution of extinction rates is something that hopefully future methods can shed more light on, high extinction rates in certain lineages could certainly lead to slow diversification rates that we (and others) observe in the tropics. However, due to our new focus on complementarity and scaling patterns in our study, we prefer to abstain from speculating in detail on this topic further (lines 311 - 314).

Finally, the authors discuss the discrepancy between conservation hotspots and phylodiversity hotspots, I would also add the classic biodiversity hotspots, while valuable, were defined in a

somewhat arbitrarily manner. As such, they were delimited based on the level of endemism, but Myers et al. (2000) did not quantify such levels of endemism using sampling units but simply using an expert criterium. I think this may worth a brief discussion, because after all, any species is endemic to the world (note that I am now criticizing Myers et al. 2000 nor the author's study)

[This is no longer part of the study.](#)

Further comments by line:

Line 19. Add "it" before "remains"

Line 45. Add "ancestor-descendant" between "the" and "relationships", otherwise reword for clarification.

Line 67. You closed and opened brackets between Zhang et al., 2015 and Vamosi & Queenborough, 2010. Typo?

Line 76. I think you missed something here, as "iffering" means nothing to me

Line 80. Please, change "diversity hotspots" into "biodiversity hotspots"

Line 100-101. Here you refer to standardized PD/PE, so please, clarify to avoid confusion.

Line 336. I guess by "limited niche evolution" you mean that species do have ecological constraints causing environmental filtering? Please, clarify.

Line 357. A "more faceted approach" is a pretty vague. I would suggest rewording into a more specific statement.

[All changed where still applicable](#)

References (others than those already cited in the text)

Carta, A., Peruzzi, L., & Ramírez-Barahona, S. (2022). A global phylogenetic regionalization of vascular plants reveals a deep split between Gondwanan and Laurasian biotas. *New Phytologist*, 233(3), 1494–1504.

Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth–death polytomy resolvers for downstream comparative analyses. *Evolution*, 69(12), 3207–3216.

Referee: 2

Comments to the Author

This study sets out to "use newly available species-level distribution data from a taxonomic and geographic checklist for all 330,527 seed plant species –the World Checklist for Vascular Plants (Govaerts et al., 2021)– to estimate the global patterns of plant phylogenetic diversity and endemism."

This is an important, timely, topic - phylogenetic diversity (PD sensu Faith 1992) is a hot topic in global biodiversity conservation. It now provides an indicator for one of the Nature's Contributions to People: maintenance of options, in multiple IPBES assessments (see

<https://danielpfaith.wordpress.com/phylogenetic-diversity/phylogenetic-diversity-and-ipbes/>).

This phylogenetic diversity indicator is also listed as an indicator for the new CBD global

biodiversity framework. PD/ phylogenetic diversity also is the basis for the important global conservation program for species called EDGE. As a form of biodiversity, the value of PD to society is now increasingly appreciated - see eg "Valuation and Appreciation of Biodiversity: The "Maintenance of Options" Provided by the Variety of Life"

<https://www.frontiersin.org/articles/10.3389/fevo.2021.635670/full> .

This global use of PD is revealing in illustrating how PD is a form of biodiversity ("feature diversity"). This biodiversity is a goal for conservation but to achieve that in practice we use calculations (e.g. of gains and losses) based on the PD framework. Indeed, the examples in Faith 1992 never calculated total PD, but instead calculations of gains and losses etc. See <https://danielpfaith.wordpress.com/phylogenetic-diversity/> . Similarly, the IPBES "phylogenetic diversity" indicator is a PD calculation of expected PD loss; EDGE is based on PD and now uses scores based on averted expected PD loss.

PD endemism (Faith 2004 etc) is a special case of the PD complementarity introduced in Faith 1992 – it is the amount of PD that is restricted to a nominated place (the PD complementarity if all other areas are taken as given). The first study on PD and global hotspots (Sechrest et al 2002) used this.

See for example

Faith et al 2004 "Integrating Phylogenetic Diversity, Complementarity, and Endemism for Conservation Assessment" http://www.amphibia.be/Courses/Faith_2004.pdf

"Phylogeny and Conservation" <https://academic.oup.com/sysbio/article/56/4/690/1685473>

"The PD Phylogenetic Diversity Framework: Linking Evolutionary History to Feature Diversity for Biodiversity Conservation" https://link.springer.com/chapter/10.1007/978-3-319-22461-9_3

"Phylogenetic Diversity (PD) and Biodiversity Conservation: Some Bioinformatics Challenges" <https://journals.sagepub.com/doi/10.1177/117693430600200007>

"Chapter 1 Phylogenetic Diversity and Conservation Evaluation: Perspectives on Multiple Values, Indices, and Scales of Application" <https://danielpfaith.files.wordpress.com/2018/12/faith-chapter-phylogenetic-diversity-and-conservation-evaluation.pdf>

And many other papers.

While ecologists tend to look at PD as one index, in reality phylogenetic diversity is a form of biodiversity with a broad "calculus". We sometimes refer to all the sorts of indices we might calculate from a phylogeny as "phylodiversity" indices (analogous to the vast number of ecological "diversity" indices based on species). But that is a vague term - not all such indices are part of the PD calculus. Further, we would not set a goal to generally preserve "phylodiversity" as this includes some measures that increase when a species goes extinct! In contrast, we do seek to conserve "phylogenetic diversity", and that is the growing strong goal in global conservation work. Unfortunately, this submission, while proposing to "estimate the global patterns of plant phylogenetic diversity and endemism." neglects all this background. The title claims to be about conserving phylodiversity, but that should be "phylogenetic diversity".

[We removed the term "phylodiversity" from our manuscript. Instead we use the names of each phylogeny-derived diversity index throughout the study to avoid confusion.](#)

The authors do say "Phylogenetic diversity (PD) can also serve as a proxy for form and function aspects of biodiversity" but perhaps should make it clearer that this feature diversity link is the basis for lots of useful calculations.

We have restructured this paragraph in the introduction and also added e.g. the review by Tucker et al. (Tucker et al. 2017) as reference for an overview on phylogenetic metrics in conservation and macroecology.

Failure to appreciate the PD calculus has unfortunate consequences. The paper as a consequence wrongly says “Phylogenetic diversity has been established explicitly as a guiding measure for conservation efforts, i.e. to identify areas that carry the most evolutionary diversity and hence are most preferable to conserve (Faith, 1992...” – but that 1992 paper prioritises areas with high PD complementarity, not total PD within the area.

Similarly the statement “the identification of regions with high PD is therefore essential (Forest et al., 2007)” is unclear – such big regions are of interest but Forest et al looked at complementarity within the region of interest.

Thank you for this clarification. To address this we have rephrased this paragraph, which states now “...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). “ (lines 49 - 52).

Additionally to the necessary adjustments in the text regarding the usage of PD and complementarity for conservation, we also made PD complementarity one of the foci in our analysis, please see our response to general comments above for this.

This reveals the core misleading aspect of the paper – the claim is “While PD measures the total amount of evolutionary history represented by an assemblage, it does not reflect how important that particular assemblage is for preserving this history (which could also be represented elsewhere, if species are widespread). This is measured with Phylogenetic endemism (PE),...” Thus, they adopt the less informative range standardised PE measure, without considering the basic simple idea of PD complementarity (the marginal gain in PD) and its extreme case, PD endemism.

We have streamlined our study to now use 3 measures of diversity: species richness, phylogenetic diversity (PD), and PD endemism.

In addition to the absolute values per botanical country, we have estimated complementarity estimates for each of these metrics using a greedy algorithm that maximises PD estimates in as few countries as possible.

We moved PE for a comparison with PD endemism and weighted endemism to the supplementary information (Fig. S1).

Most critically, the study then surely must calculate not only total PD but also basic PD endemism of areas/regions – this is the quantity that is analogous to species level endemism for the Myer 2002 type hotspots criteria etc.

Done, see above.

The study then states “We will refer to PD and PE together as phylodiversity.” – but really PE is just one of several popular aspects of the PD calculus - they all serve to help preserve phylogenetic diversity, not “phylodiversity” – a term which invites confusion.

Done as well, see above.

The study then departs even more from established global conservation of phylogenetic diversity by using standardised versions of both PD and PE: “Phylogenetic diversity was estimated as the standardised effect size of Faith’s phylogenetic diversity (Faith, 1992; Kembel, 2009) ... Phylogenetic endemism was calculated with phylo_endemism and standardised for weighted endemism in the same manner as phylogenetic diversity” . Yet conservation policy seeks to conserve the biodiversity – not a standardised effect size of biodiversity (conservation policy seeks to conserve phylogenetic diversity – not a standardised effect size of phylogenetic diversity).

We understand that standardising PD for species richness is not the most informative PD measure for conservation policy. Hence, as stated in the General comments part above (diversity metrics), we removed the standardisation from our estimates and instead focused on absolute values, and complementarity of the diversity metrics.

This confusion means also that this core important claim is false: “we use the phylogenetic equivalents of species richness and endemism”. This would be a nice claim to make – but it requires calculating PD and PD endemism for the areas, and this was not done.

We removed this claim from the manuscript as part of the revision.

The conclusion of the paper is therefore not well justified: “Phylodiversity hotspots provide upan important addition to conservation knowledge by adding another layer to the puzzle of how plant variety is distributed globally. This additional layer depicts an evolutionary perspective on diversity beyond the number of species...”

Not only is their standardised calc not particularly useful compared to established PD endemism, but also the supposed novelty is inflated, given that the other background literature of using PD in this context is neglectd (e.g. the classic Sechrest et al study on PD and globalhotspots is not even cited).

Given the vast changes we made to the manuscript, we believe that our new conclusions are better supported and in more in accordance with conservation research and policies. We would like to note though that our study does not intend to review the use of PD or other phylogeny-derived metrics in the past literature, hence we focus on citing studies that have used PD for macroecological analysis including a lot of species, ideally plants. The here mentioned classic study is unfortunately outside of the scope of our work as it focuses on primates and other carnivores.

Noting that “the journal can only publish the most innovative studies that substantially advance the field” and regarding “The significance of the findings; this can be from two perspectives (1) the

scientific importance and relevance of the research, and (2) the novelty of the work itself.”, I think the paper would benefit from a major revision. A major revision would need to provide more of this background context, including reference to the status of PD and its societal value in global conservation work; would need to calculate PD endemism of countries and existing global hotspots; would need to make the PD calculus clear (and avoiding jumping between alternative vague terminologies such as “evolutionary history”).

Daniel P Faith

daniel.faith@sydney.edu.au

- “reference to the status of PD and its societal value in global conservation work.”

We include the value and purpose of using PD in conservation in the first paragraph of our introduction. However, our study is not tailored to address the societal value of PD beyond the fact that it is an important metric for conservation policy makers, which is now part of the introduction. We hence keep our focus in this study on the global patterns of phylogenetic diversity.

- “would need to calculate PD endemism of countries and existing global hotspots”

We have now included PD endemism in our study (Figure 1). Unfortunately though, we do not see an option to calculate PD endemism (or other metrics) specifically for existing global hotspots as the spatial resolution between botanical countries and e.g. Myers 2000 conservation hotspots does not allow for it. Calculating the average or complimentary PD of all botanical countries connected to a hotspot would quickly include an area that is much larger than the hotspot, hence quite unsuitable. For the same reason we now also excluded the measure for the amount of overlap between our and other hotspots, as this has been rightfully criticised by reviewer 1 as well. We instead focus more on a qualitative comparison of our complementarity hotspots with hotspots of other studies in the discussion (lines 286 ff).

- “would need to make the PD calculus clear (and avoiding jumping between alternative vague terminologies such as “evolutionary history”).”

The revisions of our manuscript included dropping the standardised estimates in favour of adding a focus on estimates for PD complementarity. We think this reorientation has benefited the general structure and also use of terminology in our manuscript.

Referee: 3

Comments to the Author

Dear colleagues,

Your study on the “Global hotspots of plant phylodiversity” is interesting and potentially very important for identifying unique areas of evolutionary history (or phylodiversity). It compares phylodiversity with species richness, identified phylodiversity hotspots and compared them with global biodiversity hotspots. Additionally, your analyses of the current state of these regions under

anthropogenic disturbance and climate change could help to better understand the level of conservation of these regions. The paper is nicely written and you made very nice figures.

In general, I found this study interesting, but there are two major issues worries me. First, it is somehow strange that PD does not correlate with species richness, mainly because at the regional level, this usually does. Here are some examples of this:

-<https://www.sciencedirect.com/science/article/pii/S2589004221002078#fig2>

-<https://www.sciencedirect.com/science/article/abs/pii/S1055790317301379>

-<https://bsapubs.onlinelibrary.wiley.com/doi/full/10.1002/ajb2.1848>

-<https://onlinelibrary.wiley.com/doi/10.1111/jse.12590>

Even in Colombia for crop wild relatives PD and species richness also correlate -

<https://onlinelibrary.wiley.com/doi/pdfdirect/10.1111/eva.13295>

The high correlation of SR and PD is also found in our dataset, however we seem to have failed to communicate the standardisation procedure we used on PD in the old version of the manuscript. Since we removed this standardisation, Fig 1 now shows more clearly the strong connection between species richness and PD.

You acknowledge that using botanical countries as a spatial unit for the analyses can be a disadvantage because as you said, it could affect diversity measures. So why not do your analyses at grid cells of more representative spatial resolutions, which could be more close to species distribution?

We agree that using an equal-area approach would be great, however currently this data is not available for all angiosperms (yet). We therefore favour taxonomic completeness over spatial resolution. We argue this as well as the meaningfulness of botanical countries for conservation due to their close relation with political units in lines 351 - 361.

The second thing that calls my attention, is that phylogenetic endemism can be more deeply analyzed and used to prioritize evolutionary history. For example, I was expecting to see an analysis to identify places that hold old evolutionary diversity and areas of more recent radiations. The latter was addressed in the discussion, but it would be nice to have a spatial representation and develop it more.

While this specific aspect of endemism is certainly interesting, analysing the temporal aspects of endemism origins is currently outside the scope of our work, and we prefer to keep our focus here on comparing phylodiversity hotspots with complementarity hotspots for a more streamlined story.

Finally, including anthropogenic threats in this type of analysis is very important, because as I said before, it allows us to have an idea of the current state of biodiversity. However this is not addressed in the introduction and the discussion, nor you gave any detail of the source and temporal coverage of the anthropogenic threats variables. For example, do deforestation and human footprint represents the same time frame? What does it mean that some regions have high deforestation but a low human footprint? For climate change variables, which GCM, scenarios and periods were used? What was the spatial resolution of all of these variables? For the sake of

reproducibility and openness, it is necessary to have these details, and in general, I would recommend addressing them fully.

Thanks, we added the missing link to data sources listed in Table S1 in the material and methods part.

Now that I am going through my notes, it is possible that I didn't fully understand why including anthropogenic threats. It was not clear if you include this to identify the threats of phylodiversity regions or to show that it should not be included in the definition of the phylodiversity hotspots. What was it for?

We added threats as "an additional layer of information to inform conservation prioritisation" and now state this in the discussion in lines 340f.