Cambridge Prisms: Extinction

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Phylogenetic diversity in conservation: A brief history, critical overview, and challenges to progress – Authors response to reviewers

Marcel Cardillo

Research School of Biology, Australian National University, Canberra, ACT, Australia

Comment

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Corresponding author:
Marcel Cardillo;
Email: marcel.cardillo@anu.edu.au

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Author's response letters to reviewers.

1. Author's response to first round of reviews

I thank the handling editor and both reviewers for their time and efforts to read and help improve my paper. Both reviews have been helpful with many constructive comments and suggestions. In reviewing the PD literature it was clear to me that a very small proportion of it has focused on critically analysing and making clear the limitations of PD. At a time when PD is beginning to become more visible to policymakers, it seemed important for a review to be published that surveys and highlights these limitations, and this is why my review is a critical one, not just a matter-of-fact summary of the literature to date. However, both reviewers and the editor felt that the wording of my manuscript was often too critical in tone, leading to the impression that the review lacked balance and was more like an opinion article. I take this point, and have now revised the ms to minimize the wording that could be interpreted in this way. In particular, I have rewritten and expanded the conclusions section so that it presents the prospects for adoption of PD into conservation practice more positively, albeit framed as a series of challenges.

It seems clear that reviewer 1 is a strong advocate for PD. Their review is quite defensive in tone and focuses largely on attempting to refute any limitations of PD that are discussed in the manuscript. It seems to me that much of the difference of opinion between myself and this reviewer stems from (1) disagreement over what constitutes evidence that PD has been adopted into conservation practice, and (2) disagreement over the equivalency of PD and EDGE or evolutionary distinctness. On the first point, most of the examples the reviewer offers for practical application of PD are not what I would regard as demonstrable evidence for the implementation of PD in conservation practice. Some refer to EDGE/evolutionarily distinct species but not phylogenetic diversity; some are academic papers, which is not evidence for policy or management adoption. On the other hand the reviewer also highlights the listing of PD as a biodiversity indicator on the IPBES and GBF reports, suggesting that PD is becoming more visible at the level of international agreements, although this still isn't evidence for the use of PD in the conservation planning, management or legislation systems of any particular countries. On the second point, EDGE and PD, while obviously related, are not equivalent and in fact differ in a way that is fundamentally important, because EDGE focuses on single species, and perhaps for this reason has been more successful at capturing public interest in evolutionary distinctness. I now discuss this difference in greater depth in the conclusions section on page 12. In short, I think my original conclusion that PD has so far had very limited impact on conservation practice still stands.

Below I have provided a specific response to each of the two reviewers points.
Many thanks,
Marcel Cardillo

Cambridge Prisms: Extinction – Decision on EXT-22-0004

Handling Editor's Comments to Author:

Handling Editor: Benson, Roger
Comments to the Author:
Thanks for submitting your review of phylogenetic diversity. I found it interesting to read, and I've sought the opinions of two referees. Both referees note some aspects of communication that could be tempered, albeit that they differ in their recommendations and the length of their reviews. And one is very positive.

I did another editorial read to evaluate the comments you have here in the longer review. In particular, I was interested whether the manuscript, in its current form, is written in a suitably objective tone. Having done that, I do have some sympathy for the comments in the longer review, and I think this is something you could address in a revised version of the manuscript.

To illustrate my impressions, I've given a few quick examples below. I only give a few examples, but I'd like you to pay attention to phrasing and accuracy throughout the ms. The paper will have a bigger influence on the field if the phrasing is fair and objective, and does not alienate people who have a different view to the one presented here. I'd also like you to address the points of scholarship and accuracy from the longer review, and to respond to each of the referees' comments in a response letter, explaining what you did to the ms (also, doing your changes using coloured text).

– "…accepted, almost uncritically" [we don't know whether people think critically or not, just by reading the text they wrote, strictly-speaking]
– "…adds nothing to…" ['adds nothing' is a strong statement from a statistical perspective. Of example, it could 'add something' even if it added a small amount of additional information]
– "…suffers from the same vulnerability to phylogenetic branch-length uncertainty" [this is a quantitative issue that is tackled only qualitatively. There is a question of effect size. For example, many of the samples given concern unequivocally very long brand distinct lineages (e.g. coelacanths). For these, the effect size of the uncertainties will be small].

Author: point taken, I have revised each of these examples, and throughout the ms I've tried to revise the tone and to remove any loose or ambiguous wording.

In summary, I'm happy to consider a raised submission of the manuscript that addresses the referees' comments. Please do use the information they have given in a constructive way.

When you do resubmit, please provide me with a list of suggested referees in your cover letter. I would like to broaden the range of invited referees here, to ensure the best quality of outcome.

Reviewer(s)' Comments to Author:

Reviewer: 1

Comments to the Author
In principle, a review of the role of PD in conservation is a welcome piece, however this paper is in practice simply an opinion piece critiquing PD, it cannot be considered a review as it omits multiple important advances and applications that have happened in recent years. As well as general misunderstandings throughout, it also misrepresents the author's previous work to fit the narrative agenda of framing PD in a negative light. The abstract and conclusion both use highly loaded, inflammatory language, unsupported by the limited evidence presented in the paper. This paper should, at the very least, be significantly revised to include the omitted aspects, as well as in presenting a more balanced view of progress. However, as it stands, the paper also does not seem to be in keeping with the stated aims and scope of the journal, and should also be reframed as such to proceed.

I present the key concerns as follows:

1. The paper claims that PD is not used or of any particular use for conservation, ignoring multiple applications, with a non-exhaustive list of applications as follows:

a) explicit recognition by IUCN of its importance with the establishment of the IUCN SSC Phylogenetic Diversity Task Force www.pdtf.org in 2019, as a consortium of experts aiming to do exactly what the author says is a challenge: "bridging the divide between academic conservation science and the scientific requirements of conservation policymakers and planners" (L381–383).

Author: the PDTF group was formed only 3 years ago and at this stage appears to be still primarily a website with a set of goals and ambitions to "promote the importance of conserving phylogenetic diversity, and so the tree of life and our evolutionary heritage, enhancing the understanding and wider adoption of phylogenetic diversity in conservation among conservation practitioners, decision-makers, business, the academic community and the public." There is currently nothing on this website, or the document outlining their principles and aims, that offers any evidence that the PDTF has yet brought about any demonstrable adoption of PD into policy or management. Indeed, they confirm what I said that "The EDGE approach represents the current primary practical methodology to apply PD to conservation." However, I do accept that the formation of this group does represent explicit recognition of the importance of PD and is a first step towards bringing about the adoption of PD into conservation policy.

b) building on the 2012 IUCN Resolution on halting the loss of evolutionarily distinct lineages https://portals.iucn.org/library/sites/library/files/resrecfiles/WCC_2012_RES_19_EN.pdf.

Author: this document is not a demonstration of the adoption of PD into conservation policy or management, it is a resolution calling for the protection of evolutionarily important and distinct lineages. Phylogenetic diversity is not explicitly mentioned anywhere in this document.

and recent call by Diaz et al. 2019 to prioritise the conservation of evolutionarily distinct lineages across the tree of life in the Convention for Biological Diversity's Global Biodiversity Framework https://www.science.org/doi/abs/10.1126/science.abe1530.

Author: this is not an example of the use of PD in conservation policy or management. It is an academic paper published in *Science* that urges the Convention on Biological Diversity to adopt targets that consider multiple levels of biodiversity, including evolutionary history.

c) PD's increasing influence on conservation activities of the IUCN SSC, recognised as important in prioritising conservation activities in multiple Specialist Groups e.g. in the goals of the Small Mammal Specialist Group, the Amphibian Specialist Group;

Author: The website of the SSC Small Mammal Specialist Group presents a list of "key species" chosen as such for their high EDGE scores. This indicates that this group values evolutionary distinctness of individual species as a conservation priority. As far as I could see, nowhere do they mention phylogenetic diversity or offer any evidence that PD guides or influences their conservation activities. The difference between EDGE and PD is an important one, and is discussed on page 12 of the ms. In the website of the SSC Amphibian Group, their emphasis is very much on prioritizing threatened species. Nowhere could I find

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any reference to or mention of phylogenetic diversity, or even evolutionary distinctness.

and the activities of many others funded through the SSC EDGE Grants https://www.iucn.org/our-union/commissions/species-survival-commission/partners-and-donors/ssc-edge-internal-grant.

Author: this is a good example of real policy impact (a grant scheme explicitly for projects to conserve EDGE species), which I now mention on page 12. But it is still not about the application of PD, but about projects for particular species that are evolutionarily distinct.

d) Dedicated and increasing donor and practitioner support globally for conserving species important to maintaining PD, specifically EDGE species and Zones, by multiple organisations, e.g. ZSL, On the Edge, re:wild, Rainforest Trust among others.

Author: once again, none of these charities appear to mention phylogenetic diversity. On the Edge emphasizes evolutionarily distinct (EDGE) species, re:wild seems to focus on Biodiversity Hotspots, Key Biodiversity Areas, and High Biodiversity Wilderness Areas, none of which are designated on the basis of phylogenetic diversity. The Rainforest Trust, as far as I can tell, emphasizes protection of threatened species by focusing on conservation of rainforests. Nowhere in their documentation could I see any mention of phylogenetic diversity.

e) the adoption of Phylogenetic Diversity by IPBES as an indicator for multiple aspects of Nature's Contributions to People in their Global and Regional assessments https://ipbes.net/global-assessment.

Author: PD is mentioned as an indicator for three of the NCP categories, which is indeed evidence for policy influence at international level (now mentioned on page 12), although this doesn't necessarily indicate that any governments have explicitly adopted PD into their conservation policy, planning or management systems.

f) The inclusion of Phylogenetic Diversity in the draft Global Biodiversity Framework as a Complementary indicator for Goal B, and the paired EDGE Index as a Component Indicator for Goal A, see here for technical submissions https://www.pdtf.org/publications leading to the most recent CBD COP15 draft document listing the indicators: https://www.cbd.int/doc/c/0524/cc9d/99da38b8be1522bd3fd97e43/cop-15-02-en.pdf, full details of the indicators as described in the pre-print https://www.biorxiv.org/content/10.1101/2021.03.03.433783v1.full.

Author: PD is mentioned as one of 57 Complementary Indicators of progress towards the achieving Draft Goal A, and one of 24 Complementary Indicators for Goal B. I accept that this is evidence for the adoption of PD into broad aspirational targets under this international agreement, although again, it still doesn't indicate adoption into actual policy or management decisions at the country level (where conservation practice generally takes place).

These two indicators were even proposed by some Parties to be considered as Alternative Headline Indicators during the CBD technical meetings in Geneva, March 2022 https://www.cbd.int/doc/c/f191/8db7/17c0a45b42a5a4fcd0bbbb8c/sbstta-24-l-10-en.pdf.

Author: this proposal wasn't adopted in the final report, and PD was not included as a Headline Indicator.

g) The inclusion of Phylogenetic Diversity in the Multi-Dimensional Biodiversity Index developed by UNEP-WCMC and already incorporated by pilot countries, Soto-Navarro et al. 2021 https://www.nature.com/articles/s41893-021-00753-z .

Author: this is an academic paper that proposes a new policy-focused biodiversity index. It is not itself evidence of policy or management uptake of PD.

h) Reporting on EDGE species by WDPA's Protected Planet e.g. https://livereport.protectedplanet.net/pdf/Protected_Planet_Report_2018.pdf.

Author: this report mentions EDGE species once, on page 12. Nowhere in the report is the word "phylogenetic" used.

i) Systematic conservation planning in Australia using PD and associated metrics, e.g., Rosauer et al. 2018 https://conbio.onlinelibrary.wiley.com/doi/10.1111/conl.12438; Laity et al. 2015 https://geobon.org/downloads/scientific-publications/2015/1-s2.0-S0048969715300498-main.pdf.

Author: these are academic papers, not evidence of policy or management impact.

Unfortunately, the author does not seem to understand the principles of ZSL's EDGE of Existence programme as the most widely cited application of PD in conservation, claiming that it is "quite far removed from PD…[shifting] focus back to the old idea of valuing individual species for their uniqueness" (L369–371). The EDGE programme, and the multiple papers presenting EDGE assessments across multiple taxonomic groups, clearly recognise PD as foundational to this work, and it is highlighted by the IUCN SSC PDTF as being a practical application of PD in conservation. It is quite a disjointed and somewhat contradictory narrative for the author to present the conservation of evolutionary history in species as then leading to the quantification of PD but then to distance the consequently developed EDGE metric from PD.

Author: As I explain in the introduction (and now expand on in the conclusions), the qualitative idea of valuing particular, single species for their distinctness is a very old one, but what PD attempted to do was turn this into something quantitative for assemblages of species using a numerical value derived from branch lengths. EDGE later presented a measure that was once again focused on single species, not assemblages (although it retains the quantitative aspect), and this is most likely why EDGE has been much more successful at finding its way into conservation policy than PD. Of course the two concepts are related, they are both based on branch lengths, but the single/multiple species difference is crucial.

I would also suggest the author may like to undertake a more rigorous review of the applications of PD in conservation than post a request on twitter https://twitter.com/MarcelCardillo/status/1549624820316286981?t=qsro5ScTF9w_Ko64gc3Kug&s=31.

Author: Actually I have often found it helpful to canvas the thoughts and suggestions of the international ecology & conservation community through Twitter. If I'd been at a conference

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I'd have done the same by talking to people. But I never use either of these media as a substitute for thorough academic scholarship.

2. The paper neglects or downplays evidence in support of the application of PD in conservation, to support a negative and unbalanced narrative, in general there is a misunderstanding of the debate, evidence and findings to date, in a variety of ways.

PD is described by the author as "a continuous-scale index of conservation value for a set of species, calculated by summing the phylogenetic branch lengths that connect them." L5 & 54. But PD is not an index of conservation value – it is a measure of biodiversity, that informs conservation. Conservation does not necessarily seek to maximise PD, but to conserve PD, an important distinction highlighted in Owen et al. 2019 https://pubmed.ncbi.nlm.nih.gov/30787282/.

Author: PD is an index of conservation value in the same way that species richness or any other measure of diversity are indices of conservation value – higher values are considered more valuable for conservation than lower values. Maximizing the PD represented in a conservation network, while minimizing associated costs, is precisely what most conservation planning algorithms that have used PD have aimed to do. A few examples:

Rodrigues & Gaston 2002: "This can be achieved if, instead of species richness, a currency of biological diversity which takes the phylogenetic relationship between species (hence evolutionary history) into account is maximised in the selection ofnetworks of reserves."

Forest et al 2007: "We argue that maximizing PD is the best bet-hedging strategy."

McCarthy & Pollock 2016: "Spatial priorities for conservation within Victoria were then analysed with Zonation, which aimed to maximise reservation of phylogenetic diversity within Victoria, subject to constraints such as total land area and suitability of cells for reservation."

Mazel et al 2018: "The phylogenetic gambit implies that maximizing phylogenetic diversity (PD), i.e., the breadth of evolutionary history, will ensure that a wide variety of forms and functions are present within a species set."

No academics, practitioners or expert groups such as the IUCN SSC PDTF lay claim to PD's "primacy as the currency of conservation" (L57) as the author asserts. This is especially important as conservation does not work this way in practice, with any single prioritisation scheme - in reality, the intention of PD-informed conservation such as the EDGE of Existence programme and other PD-initiatives (as outlined above) is to complement current conservation efforts and prioritisations, and seek to highlight where valuable species and areas may otherwise be overlooked.

Author: The superiority of PD over species richness or other biodiversity measures is precisely the claim that has been promoted by many authors for many years. All of the quotes cited above reflect this claim, but here are some more examples:

Lean & McLaurin 2016: "We conclude that the best justified general measure of biodiversity will be some form of phylogenetic diversity."

Forest et al 2007: "In an uncertain future, where we are not yet sure of the sort of plant features we will need, we argue that incorporating gains in PD into conservation planning is the best strategy."

Huang et al 2012: "PD reflects both the number and the evolutionary distinctiveness of species in an assemblage, and thus can potentially act as a 'silver bullet' ensconcing several dimensions of biodiversity."

The author does not seem to understand conservation practice, claiming "simple species richness as the primary, basic currency of conservation" (L378). For some time now, the literature has recognised that conservation efforts should not be based on species richness alone but on additional metrics, such as species composition, endemism, functional significance, and the severity of threats (and, increasingly, evolutionary distinctiveness). For example biodiversity hotspots are based on endemism, Key Biodiversity Areas on the presence of trigger (threatened) species, the IUCN Red List on extinction risk, and indeed efforts are typically made to control for species richness in spatial or species-based prioritisation analysis.

Author: To be clear, what I meant with that statement was the prevention of species extinctions, and thus maintaining species richness at a global (or national, or regional) scale. This is the ultimate aim of all of the schemes and metrics cited above, and indeed, all conservation activities. Why do we seek to protect endemic or IUCN threatened species? Because they are considered the most likely to go extinct. Why do we wish to conserve threatened habitats, Biodiversity Hotspots, Endemic Bird Areas, or KBAs? To protect the unique species they harbour. As the reviewer says, this doesn't mean species richness is always the single metric used to prioritize areas for conservation, but the point here is that for data-poor taxa, species richness will very likely be used ahead of PD. Line 413–416: "for poorly-known taxa unrealistic data requirements may make it difficult for PD to compete with simple species richness as the primary, basic currency of conservation."

The author decides throughout that feature diversity equates to all work on PD / functional relationships, despite feature diversity having a specific definition and this being cautioned against repeatedly, e.g. in Owen et al. 2019.

The inference that feature diversity and option value (and hence PD) is solely a utilitarian value of biodiversity (L122 + L222) is not supported in practice, as it is contrary to the use of PD as an indicator for multiple NCPs by IPBES and in consideration throughout the CBD (see links above), both of which's descriptions highlight its importance as a mechanism for ensuring intergenerational equity. Future benefits from biodiversity are of course not restricted to only utilitarian use and include benefits derived from non-utilitarian extrinsic values such as cultural, aesthetic, etc. as well as intrinsic values.

Author: these are still utilitarian values as defined by philosophers of biology (Maclaurin, J., and K. Sterelny. 2008. What is biodiversity?; Lean, C., and J. Maclaurin. 2016. The Value of Phylogenetic Diversity. Pages 19–37 in R. Pellens and P. Grandcolas, editors. Biodiversity Conservation and Phylogenetic Systematics: Preserving our evolutionary heritage in an extinction crisis.). I follow these authors in making the distinction between utilitarian and intrinsic value.

The author critiques data limitations around PD analyses (L379), but has omitted efforts to overcome these, such as that presented in Gumbs et al. 2018 https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0194680; note that this area is also advanced

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extensively in the pre-print https://www.biorxiv.org/content/10.1101/2022.05.17.492313v1.abstract.

Author: this paper focuses on the EDGE metric, rather than PD, and does not deal with the problems of inferring branch lengths that I discuss, but examines the very specific issue of imputing EDGE scores for species missing from existing phylogenies. I now cite this paper where I discuss incomplete data in the conclusions.

There is some mis-representation of previous findings, most notably being the author's co-authored Ritchie et al. 2021 paper, but also Kelly et al. 2014 and Mazel et al. 2018 which actually do show strong support for the PD and feature / PD and function relationship in tree space and geographic space respectively. The author dismisses Molina-Venegas's work and ignores the positive overall findings of Mazel et al. 2018; Tucker 2018,2019, and fails to cite Owen et al. 2019's response to Mazel et al. 2018.

For Ritchie et al. 2021, specific examples are as follows:

The author claims: "Again, it was found that PD values calculated from inferred phylogenies were prone to error (23–38% difference from true, simulated phylogenies)…" L339–340.

But in Ritchie et al. 2021 the average % error is 6–14% (i.e. an average of 86–94% accuracy), which in fact is very positive, particularly for true PD estimation from reconstructed trees. The values quoted here are actually the max error, and this should be represented correctly.

Author: yes that is correct, the figure quoted was the maximum rate of error across the different simulation scenarios in that study, it should have read "up to 23–38%," and I have corrected this and also quoted the mean values. But what the reviewer neglects to mention is that Ritchie et al. go on to discuss the importance of considering worst-case scenarios when it comes to conservation:

"Accounting for this risk requires accounting not only for expected average level of error, but also for the worst-case scenarios (Daniel P. Faith, 2008; Daniel P Faith, 2015)."

"An average rate of error that is considered acceptable for some uses, such as phylogeny estimation or molecular dating, might be considered unacceptably high for practical applications, such as conservation prioritization."

The key point here is that an average error rate of 6–14%, which the reviewer considers very positive, might have important implications for conservation. Of course, we don't know if this is the case, because the necessary analyses have not yet been done.

The following phrase is also incorrect "…and that the ranked positions of 100 communities differed between true and inferred community PD by an average of 10–11 places" (L341–342).

In fact, these figures are about species ED rankings (not community PD rankings), and the Ritchie et al. 2021 paper says, quite positively by comparison:

"Looking at how the position of each taxon changed when we used reconstructed ED, we found that taxa were mis-ranked by 10–11 positions on average and 20–40 positions at the 95th percentile compared to their rankings based on true ED values (BEAST, Figure 6; NPRS, Figure S4 available as Supplementary Information). Taxa that were top-ranked in the true tree were substantially more likely to be correctly ranked than those that had ED values in the middle of the ranking. An alternative way to interpret this data is to compare the proportion of the top 10, 50 (and so on) ranked species that are correctly identified under estimation. The above results are then equivalent to saying that 83–87% of the top 10 or top 50 species are correctly identified by estimation, whereas about 90% of the top 80 are correctly identified."

Author: again, whether this is a positive or gloomy result for PD is a matter of perspective, but I now quote the results for PD rankings, not ED.

3. Inflammatory language

The abstract is highly editorialised and does not match the content. This is also the case in the conclusion, claiming that PD currently has no impact on conservation decision making after omitting the multiple (and non-exhaustive) list of advances outlined above.

Author: I have responded to the list given above, and my conclusion that the conservation impact of PD is still very limited remains intact. However, I do now discuss the inroads that PD is beginning to make on international biodiversity agreements, and the potential for the wider adoption of PD into practical conservation activities.

In particular, extremely loaded language unreflective of the advances that have already been made appears in the following sentences, which should be entirely revised on the basis of the evidence above:

L8 "has had virtually no impact on conservation practice or policy."

L19–20 "it will be difficult to envisage a major role for PD in conservation policy and real-world decision making."

L385–386 "…if that is ever to happen."

L386–389 "The second will serve as a reality check on the value of PD for conservation…and help to identify the conditions under which PD might be considered to represent whatever it is that we value about biodiversity."

Author: all of the above examples, and the ms in general, have been modified to present a more neutral tone throughout.

Finally, the dramatically increasing interest in PD-informed conservation over recent years, spearheaded by concerted, cohesive and truly collaborative efforts from scientists, practitioners, donors and policy-makers highlighting the need to incorporate PD in conservation (but not as an exclusive goal), would seem to undermine the author's claim that "PD is certainly not a prominent part of the prevailing conservation paradigm." (L373).

Author: I disagree with this statement, for all of the reasons I've already outlined. In the light of the evidence available, I am still led to the conclusion that phylogenetic diversity is not yet a prominent part of the prevailing conservation paradigm. I appreciate that not everyone will share my interpretation of the evidence, but hopefully a constructive and well-informed debate will be a good thing for this area to progress. Particularly for conservation, where the consequences of poor decision-making are potentially severe, it seems important not to accept any of the science that underpins decisions uncritically.

Reviewer: 2

Comments to the Author

This opinion piece presents an overview of some of the debates and potential problems with approaches based on the concept of

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phylogenetic diversity. It is an interesting read, while I don't necessarily agree with all the points that are made here.

The section exploring why PD is popular in academic studies argue that it is caused by two factors, the ease of compiling PD and the fortuitous rise of molecular systematics in the 1990s coinciding with the introduction of PD in 1992. While that may be somewhat the case, the way it's presented makes is a bit disingenuous. Putting the conservation aspects aside, PD and associated metric have proven to be useful tools in deciphering biodiversity patterns and exploring the potential processes behind these patterns.

Author: I agree with the last sentence above, but don't see why this is necessarily in conflict with my suggestions for why PD increased in popularity during the 90's. In any case, this seems pretty close to the first reason I give in this section, that the rationale for PD is compelling.

The ability of PD to predict feature diversity is certainly a topic that has been widely debated in recent years. It would be important to mention that some of the publication cited here use a narrow view of feature diversity, as pointed out for example by Owen et al. 2019 (not cited here; https://www.nature.com/articles/s41467-019-08600-8) in the case of Mazel et al. 2018a. In some of these papers, functional diversity is equal to feature diversity, which are in fact, as pointed out by the author, two different concepts. The examples reported in lines 275 to 283 are more in line with the concept of feature diversity (i.e. usefulness of plants), which is broader than functional diversity.

Author: With limited space I did not want to explore in detail the various definitions of feature diversity, as I explain in the first paragraph of the section "How well does phylogenetic diversity predict feature diversity and ecosystem function?" As I mention in this section (page 8) I follow Tucker et al 2019 in considering feature diversity to encompass the range of conceptions of phenotypic diversity represented in the literature.

The last section of the manuscript focuses on the uncertainty in the phylogenetic inference itself, which is certainly not an issue for PD alone. Most of the points raised here are valid and I agree that additional research in this field would be necessary, especially studies using rarefication approach of real, near-complete data, rather than simulated data (such as Ritxchie et al., 2021), which have value, but might not be capturing all the complexities of phylogenetic inference. The data needed for rarefication analyses are not readily available, but hopefully these will become more common in the future.

While I would not necessarily advocate that PD is the silver bullet that can provide all the answers we need in conservation science, it is certainly important to capture the evolutionary dimension of biodiversity, an important contributor to the diversity of life on Earth, when planning conservation actions. PD should be seen as representing one of the many components of biodiversity and should be considered in conservation planning where possible. I feel that this review/opinion piece is rather dismissive in that regard, but maybe it's the way I interpreted it. In any case, it is, of course, an opinion that the author is entitled to have and several interesting points are made here.

Author: this issue should now be addressed by the expanded conclusions section.

Minor points:
L36: Family and order don't need to be capitalised

Author: corrected.

L124: I don't think that option values generally refer to financial value, so this example (i.e. pharmacologically-useful compound) might not be entirely representative of the general concept of option values.

Author: this is in fact probably the most widely-given example of the option value of biodiversity (e.g. Crozier 1997, Mclaurin & Sterelny 2008).

L143: I don't think the R package ape has functions to compile PD.

Author: no, ape has functions to handle and analyse phylogenetic data, but the other package cited (picante) can calculate PD.

Figure 2: Faith's definition of PD includes the root. The PD calculation using the tree on the right excludes the root, so this is not strictly Faith's PD and more what some have called "local PD." It doesn't affect the point that the author is attempting to make here, however.

Author: no it doesn't (its relative values that matter). This figure is the illustration of PD used by Rodrigues & Gaston 2002.

2. Author's response to second round of reviews

Dear Roger,

Thanks again for another detailed set of comments and suggestions. Again, there is much in here that helps improve the scientific quality of the manuscript. In response to this set of comments I have made further additions and alterations to improve clarity and reduce ambiguity, especially on the issue of the distinction between feature diversity and FD, if not the issue of EDGE vs. PD. I've also made a modification to the title to better reflect the current content and focus.

It does seem clear to me that this reviewer has a stake in promoting the success and uptake of PD and downplaying its limitations, and I think we may just have to disagree on some points. I don't think the subject (or conservation) will be well served by a review that is only superficially critical of PD and glosses over its limitations. Indeed, what I hope is that this review will be regarded as thought-provoking and will stimulate further research and productive discussion about the best way forward for the conservation of evolutionary history. I'm not sure if Extinction intends to publish reply articles, but that would seem to be a good avenue for ongoing debate if this paper is accepted for publication.

Many thanks,
Marcel Cardillo

Handling Editor's Comments to Author:

Handling Editor: Benson, Roger
Comments to the Author:
Thanks for resubmitting your manuscript. You will see that one referee has some further comments for you to consider, but that those comments are now more constrained in scope than before. I would welcome a resubmission of the manuscript that considers these points.

Reviewer(s)' Comments to Author:

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Reviewer: 1

Comments to the Author
I have no further comments. Thank you.

Reviewer: 2

Comments to the Author
I continue to welcome the principle of an objective review of the role of PD in conservation. However, despite some acknowledgements of the issues raised being made in the response to reviewers, this hasn't been sufficiently brought through to the manuscript revisions. This version is written more neutrally, and there are sections which present good insights and value, particularly the phylogenetic inference section. However, the overall paper is still somewhat jumbled, and lacks internal consistency. There are two major areas of concern, plus a few other elements that could be better addressed.

1. Firstly, in general the paper's approach falls into the trap of conflating research into a biodiversity metric (PD) with conservation that utilises PD along with measures of vulnerability, as is the main approach for conservation e.g. Brooks et al. 2006, and it is not appropriate to solely use the former to question the latter.

L63 "I ask if 1) PD serves as a reliable indicator of conservation-relevant phenotypic diversity." This is certainly an ambitious question, but the author does not define 'conservation-relevant phenotypic diversity' satisfactorily, and I'm uncertain if this is even possible, thus raising the question of how the author can come to a judgement. The review does not seem to adequately answer this question.

Author: Yes, this may be an ambitious question, but I don't think we can avoid it and promote the use of PD for conservation decision-making without taking steps towards testing its assumptions. I agree that I haven't defined "conservation-relevant" here, and that this adds to the uncertainty, so I've removed that phrase. That said, my view is that if we've decided that phenotypic diversity (in the form of feature diversity, FD, or whatever) is something we value and wish to conserve, then it should be absolutely critical that we know whether or not it is conservation-relevant. But this isn't the paper in which to do that.

L223–226 "Most authors of papers on PD seem to regard feature diversity implicitly as the variety or richness of phenotypic traits of any measurable kind, including physiological, phenological, morphological, and behavioural traits (Tucker et al. 2019), without explicit consideration of whether the traits are of relevance to the goals of PD."

It is unclear what is meant here: what exactly are "the goals of PD"? The goal of maximising PD (vs. conserving PD, which is different and should be clearly differentiated in this review).

Author: Again, I've removed the part of this sentence that is more ambiguous and poorly defined.

is to retain the broad suite of features precisely because we don't know what will be useful in the future, so how can it be stated (and by whom?) that any one trait is or is not of conservation relevance? However, in terms of conservation strategies, conserving PD, or maximising threatened PD, becomes the objective, and this needs to be clear if assessing the role of PD in conservation.

As part of this concern, although feature diversity is a central concept, within the manuscript feature diversity is repeatedly used interchangeably with functional diversity, which is a fundamental inaccuracy in this paper and has been cautioned against in the literature – functional diversity is only a subset of feature diversity, and this needs to be made clearer throughout. Since most of the review hinges on this point, they should both be separately defined, especially in relation to their differential use in the various studies cited. Otherwise, the review continues to misrepresent PD as a proxy for a selection of functional traits, rather than representing overall feature diversity. Specific examples as follows:

L109–111 "…PD was presented as a proxy for the diversity of unknown characters. In the age of genomic phylogenetics and open data, this is still the primary rationale for PD."

The rationale is that it is impossible to know and measure all features of all species, and PD indicates that overall diversity of features. This is not the same thing as the diversity of unknown characters that were withheld from the public domain by scientists, or that can shift in meaning as more data become available.

Author: I agree that this sentence does narrow and somewhat obscure the rationale for PD, which wasn't the intention, so I've now removed this.

L229 – "I will not dwell on the issue of definitions, but will use the term feature diversity to represent all conceptions of functional, trait, or phenotypic richness or diversity that appear in the PD literature."

Please do dwell on the issue of definitions, because this seems critical to the entire point of the review. For example, feature diversity when the target of PD conservation is often defined as the variety of different features, measured and unmeasured, represented among species or other taxa, and it is widely acknowledged that studying the link between PD and a narrow selection of traits (i.e. functional diversity) does not represent a test of the PD-feature relationship (e.g."It is important to recognise that PD-based prioritisation aims to capture the diversity of evolutionary features of species, both measurable and unmeasurable…FD is just one part of this diversity." - Griffith et al. 2023; and see Owen et al. 2019 and related articles).

By conflating studies focusing on functional trait diversity (a la Mazel et al. 2018) with tests of PD-FD relationship (a la Kelly et al. 2014), the author fails to accurately reflect the literature. This could easily be remedied by spending the necessary effort to clearly define the terms used by the author and in the papers referenced, e.g.:

L257–258 "Furthermore, because a subset of species that maximizes PD is usually distributed non randomly on the phylogeny, it can be possible for the maximum-PD set to be a worse predictor of feature diversity than a random set of species (Mazel et al. 2017)."

Mazel et al. 2017 was referring to functional diversity, not feature diversity. The two are not interchangeable.

L263–265 "This was demonstrated explicitly in a study of the spatial distribution of PD, functional diversity and species richness of plant assemblages in the Pyrenees (Pardo et al. 2017)."

The author is now talking about functional diversity, but it is not clear whether he considers this to be a component of feature diversity, or is using the terms interchangeably.

Author: I have now added some paragraphs to this section (lines 226–251) to present Owen et al.'s arguments about the difference between feature diversity and functional diversity, and provide a

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bit more clarity about the way phenotypic diversity is typically defined in the literature. This does, however, make it necessary to mention a new issue that I hadn't mentioned before – the problem of feature diversity being unquantifiable and thus untestable. I also now refer to "functional diversity" rather than "feature diversity" when describing some of the literature in the rest of this section. Hopefully this clarifies things a little bit.

2. Secondly, the author continues to provide a contradictory perception of EDGE and the link to PD. They say that "the EDGE approach represents the current primary practical method to apply PD to conservation" in the response to reviewers,

Author: This is a quote from the PDTF website, it is not my own statement. I quoted this because it confirms my observation that EDGE is the primary application of evolutionary history in conservation.

and in the paper outline how PD emerged from work on evolutionary distinctiveness, but then still distance EDGE (Evolutionary distinctiveness weighted by extinction risk) from PD when discussing PD's uptake in conservation. This arbitrary distancing is the opinion of the author, and is in opposition to the original stated aim of EDGE (from Isaac et al. 2007):

Author: Firstly, PD is a measure of diversity that can only be applied to a set of species, while EDGE is a property of a single species. Secondly, unlike PD, the EDGE score is not just a measure of evolutionary history, it is a combination of evolutionary distinctness and extinction risk, each of which contributes equally to the EDGE score. These two differences seem clear cut to me and I'm not sure how they could be regarded as either arbitrary or opinion. I've already explained why I believe the differences are important and the two metrics are not interchangeable, and why this may underlie the success of EDGE compared to PD. I think this will just have to remain a point of disagreement.

"Here, we define a simple index that measures the contribution made by different species to phylogenetic diversity and show how the index might contribute towards species-based conservation priorities."

"This paper describes a new method for measuring species' relative contributions to phylogenetic diversity."

"The EDGE approach identifies the species representing most evolutionary history from among those in imminent danger of extinction. Our methods extend the application of PD-based conservation to a wider range of taxa and situations than previous approaches."

And also contradictory to empirical data (e.g. see Redding and Mooers 2015, PLOS ONE). If the author's point is that EDGE is a species-focused approach and their personal concern is only with assemblage-based measures, this is not clearly stated in the review and needs to be brought to the fore.

Author: The purpose and scope of the review is made clear from the outset: the title is "The role of phylogenetic diversity in conservation," and the first two sentences of the abstract describe the shift from the age-old qualitative value of evolutionary distinctness of single species, to the quantitative, assemblage based diversity metric of PD. Nonetheless, I've now also added some extra sentences in the last paragraph of the Introduction (line 55–59) to better signal and justify the focus of the review on phylogenetic diversity rather than single species.

Whilst being unclear when critiquing assemblage PD and species-based measures, the author thus chooses to exclude elements such as the paired EDGE indicator, a component indicator in the CBD's GBF (explicitly linked to – and derived from – the PD indicator), from being classed as advances in PD-informed conservation, which is misleading.

3. Other points

The correction of the misrepresentations of other research is improved, though still ambiguously worded in a way that could be misconstrued, or selectively presenting certain results, e.g. L334–337. Ritchie et al. 2021 provides stimulating and insightful findings, yet only a narrow set of these findings are highlighted in this review. e.g. choosing to highlight areas of relatively weaker performance of PD while ignoring areas of strong performance, with the previously erroneously cited (and positive, from my perspective) ED results now removed entirely from the review.

Author: The sentence at lines 334–337 is a simple factual report of both the mean and maximum levels of error found by Ritchie et al, so I'm not quite sure how this can be regarded as misleading. The maximum error levels are pointed out because (as already explained), when it comes to conservation decisions it is the potential for large errors in selecting areas or species sets for their contribution to conservation targets that may be of greatest consequence.

More generally, I think the reviewer mischaracterizes the tone of my article as entirely negative, ignoring the substantial sections in which I describe studies that find PD does a good job of representing phenotypic diversity or ecosystem function (e.g. lines 295–318). Throughout the article, including the abstract, I refer to the results of studies of the PD-FD relationship as "mixed," not simply negative. In the section on phylogenetic uncertainty in which I report the Ritchie & Park results, I offer a caveat on these results: "However, it is still difficult to know how general these results are, and whether there are particular, easily-identified conditions under which the uncertainty and variability in PD values can be limited to acceptable levels."

I haven't set out to cherry-pick or selectively present results that demonstrate weaknesses and limitations of PD. However, I do think it is timely for a review to be published that casts light on these limitations, given the limited attention this has received so far in the literature. This is especially important if PD and evolutionary history are beginning to become more visible to policymakers.

Regarding the author's arguments that the researchers in the field are not concerned with the importance of uncertainty and phylogenetic inference and its implications for measuring PD and its link to feature diversity (e.g. L396–399), while the author highlights some areas that are indeed in need of greater interest, there are multiple examples to the contrary for various aspects of phylogenetic uncertainty/error – this is a very active area that is well-recognised in the literature and was even discussed in early literature around the EDGE metric (e.g. Isaac et al. 2007).

Author: I have already acknowledged (line 333–335) that from the very beginning (Faith 1992, Crozier 1997) it was recognized that PD could be sensitive to phylogenetic uncertainty. In this section I have focused on the sensitivity of branch lengths (and

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hence potential sensitivity of PD) to methods and assumptions of phylogeny inference and divergence time estimation, because this is not only a major source of uncertainty, but also the area of PD research about which the least is known – there really are very few studies that have systematically examined these effects on PD or ED in the way done by Park et al, Ritchie et and Elliott et al.

L354 – the author fails to note here the increased exploration of the impact of different phylogenetic hypotheses in phylogenetic-based work and how to incorporate or address uncertainty where possible (e.g. Jetz et al. 2014 Current Biology, Pollock et al. 2017 Nature, Stein et al. 2018 Nature Ecol Evo, Rabosky et al. 2015 Evolution, Weedop et al. 2019 Animal Conservation).

Author: I agree, there is a widespread awareness among users of phylogenies in conservation research about the effects of phylogenetic uncertainty on downstream analyses, and increasingly researchers are exploring these effects by generating alternative phylogenies under different sets of assumptions (e.g. Stein et al cited above). But there have been few systematic analyses of error or sensitivity in PD/ED along the lines of Park, Ritchie & Elliott, that try to really pin down the different forms of uncertainty and the size of their effects on PD/ED. This is still an understudied problem that needs further research.

Most of the papers cited above address the problem of missing data and imputation of ED/EDGE scores. This is also an important issue which I touch on in the penultimate paragraph, but I give less space to than the branch length issue, which I regard as the potentially biggest problem that we know the least about.

L357 – this sentence is good and should be a call to arms to phylogeneticists to tackle these issues to provide more robust PD calculations.
L42 – now classified as two species, *P. gangetica* and *P. minor*.

Author: Corrected.

Positively, I do agree with several of the author's points: around phylogenetic inference and how increased research into the conditions under which PD works best are exciting avenues, and that PD performs variably at capturing sets of functional traits, and including clarity on both points (for the former: people do care and are working on some aspects of it; for the latter: greater clarity on function vs. feature diversity as mentioned above) would go a long way to helping this transition from an opinion piece to a review. These positive elements are being overshadowed by the lack of clarity and conflation, and addressing these aspects will solve the issues outlined above.

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