1 **Title.** Testing the phylogenetic gambit: how much functional diversity can we reliably conserve
2 if we prioritize phylogenetic diversity?
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5 **Author list**

6 Florent Mazel[1,2,3], Matthew W. Pennell[3,4], Marc Cadotte[5,6,$], Sandra Diaz[7,$], Giulio Valentino

7 Dalla Riva[8,$], Richard Grenyer[9,$], Fabien Leprieur[10,$], Arne O. Mooers[1,$], David Mouillot[10,11,$],

8 Caroline M. Tucker[12,$], and William D. Pearse[13]

9

10 **Author affiliations**

11 [1] Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

12 [2] Department of Botany, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;

13 [3] Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;

14 [4] Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;

15 [5] Biological Sciences, University of Toronto-Scarborough, Scarborough M1C 1A4, Canada

16 [6] Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

17 [7] Instituto Multidisciplinario de Biología Vegetal. FECFyN - Universidad Nacional de Córdoba.

18 Casilla de Correo 495, 5000 Córdoba. Argentina

19 [8] Department of Statistics, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;

20 [9] School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, U.K.

21 [10] Marine Biodiversity, Exploitation, and Conservation (MARBEC), UMR 9190, Université

22 Montpellier, Montpellier, France

23 [11] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook

24 University, Townsville, QLD, Australia

25 [12] Department of Biology, University of North Carolina-Chapel Hill

26 [13] Ecology Center and Department of Biology, Utah State University, Logan, Utah

27 $ Authors listed alphabetically

28

29   **E-mail addresses of the authors**: flo.mazel@gmail.com, mwpennell@gmail.com,

30   mcadotte@utsc.utoronto.ca, sandra.diaz@unc.edu.ar, giulio.dallariva@googlemail.com,

31   grenyer@gmail.com, fabien.leprieur@umontpellier.fr, amooers@sfu.ca,

32   david.mouillot@umontpellier.fr, carolinemtucker@gmail.com, will.pearse@usu.edu

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40   and wrote the first draft of the manuscript. All authors edited the final version.

41

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43   is available upon request.

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45   **Code accessibility statement:** R functions developed in this paper are available at

46   https://github.com/FloMazel/FD_PD_Max

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49   **Corresponding Author**. Florent Mazel. Department of Botany and Biodiversity Research Centre.

50   The University of British Columbia | Vancouver Campus. 2212 Main Mall | Vancouver BC | V6T

51   1Z1 Canada. flo.mazel@gmail.com. +17783024816

52   **Abstract**

53   In the face of the biodiversity crisis, it is argued that we should prioritize species in order to

54   capture high functional diversity (FD). Because species traits often reflect shared evolutionary

55   history, many researchers have advocated for a "phylogenetic gambit": maximizing

56   phylogenetic diversity (PD) should indirectly capture FD. For the first time, we empirically test

57   this gambit using data from >15,000 vertebrate species and ecologically-relevant traits.

58   Maximizing PD results in an average gain of 18% of FD relative to random choice. However, this

59   average gain hides the fact that in over 1/3 of the comparisons, maximum PD sets contain less

60   FD than randomly chosen sets of species. These results suggest that, while maximizing PD

61   protection can help to protect FD, it represents a risky strategy.

Introduction

We are in the midst of a period of heightened biological extinction, with rates several orders of magnitude higher than background rates estimated from the fossil record[1–3]. In addition to having potentially widespread consequences for the functioning of ecosystems and the provisioning of valuable ecosystem services, this situation poses an immense moral challenge[4–8]. Since the extent that resources for conservation actions remain limited, agonizing choices as to which species most warrant attention become necessary[9,10]. To keep humanity's options open, and our common legacy as rich as possible, it is widely argued that we should seek to maximize the biological diversity of form and function in conservation strategies[6–12]. The biological diversity of form and function can be measured as functional diversity [FD] (see methods). However, in practice, it is challenging to prioritize species on the basis of FD: we have imperfect knowledge about which, and how many traits and functions are important in a given context, how these traits and functions vary among species and across space, and how the importance of traits may change in the future[13]. Many researchers have therefore advocated for a "phylogenetic gambit"; that is, if species traits reflect their shared evolutionary history, then the pattern of that evolutionary history –their phylogeny– should serve as a useful stand-in for unmeasured and unmeasurable traits[9,14,15]. 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[14–17].

Following this logic, phylogenetic diversity has formed the basis of global conservation schemes, notably the EDGE program[18] has been used by restoration biologists[19] and has been widely embraced by researchers across the biodiversity sciences[20–23]. Despite this enthusiasm, the critical question of whether maximizing PD will actually capture more FD than prioritization schemes that ignore phylogeny has, to our knowledge, never been empirically tested[16]. Some studies have discussed[24,25] and documented the relationship between FD and PD, both at regional[26] and global scales[20,22], and many of these studies have shown that maximizing PD does not *maximize* FD. However, such studies do not test the fundamental phylogenetic gambit at the heart of all PD-based conservation strategies: maximizing PD captures *more FD than*

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91 *randomly choosing species*. No one would dispute that the best way to maximize FD is to

92 prioritize FD, but phylogenetic diversity has emerged as prioritization tool because we rarely

93 have sufficient trait data to calculate FD. Here we test whether PD-based conservation passes a

94 much less stringent, but ultimately more fundamental, test: is conserving on the basis of PD

95 better than conserving at random? Worryingly, a recent theoretical study has indeed

96 demonstrated that PD could be a poor surrogate for FD and, in some scenarios, prioritizing

97 species on the basis of PD could actually lead to capture *less* FD than if species were simply

98 selected at random[16].

99 This points to the need for empirical tests of whether —within a given species pool— sets of

100 species selected to maximize PD actually contain more FD than sets of species selected without

101 regard to evolutionary relatedness. We clarify what our goals are in testing the utility of PD to

102 capture FD. First, we take as given that maximizing PD is not the overarching goal *per se* of PD-

103 maximization schemes, but rather that a PD maximization strategy is valued for its ability to

104 capture more FD compared to a strategy that ignores phylogeny. Second, it is important to note

105 that we are selecting *species* sets to maximize PD or FD within a region. While this is a

106 simplification, as conservation actions often aim to select sets of *areas* (e.g. in reserve design),

107 the only global phylogenetically-informed conservation initiative is species-centered[18] (EDGE).

108 Critically, the question we raise has been shown to be distinct from asking whether traits have

109 phylogenetic signal (whether closely related species tend to share similar sets of traits), since

110 PD can be a poor surrogate for FD *even if* traits exhibit phylogenetic signal[16].

111 We evaluate the PD~FD relationship for different species pools (taxonomic families and

112 geographical assemblages, *i.e.*, sets of species co-occurring at a given scale) using a large global

113 dataset including trait, phylogenetic, and geographic range data for 4,616 species of mammals,

114 9,993 species of birds, and 1,536 species of tropical fish. Specifically, we measure FD as

115 functional richness (see methods) and compute, for any given species pool, an estimate of

116 surrogacy[27,28] (S_{PD_FD}, Figure 1). S_{PD_FD} represents the amount of FD sampled by the set of

117 species chosen to maximize PD, relative to the FD sampled by optimal set of species selected to

118 maximize FD directly, with both components controlled for the expected FD from a random

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119   species set of the same size. S_{PD_FD} will be positive if the averaged PD-maximized set contains

120   more FD than the averaged random set, and negative if not. S_{PD_FD} will equal 100% if the PD-

121   maximization strategy is optimal (*i.e.* to maximize FD). We integrate S_{PD_FD} for each species pool

122   across all deciles of species richness but because they are many sets of species that can

123   maximize PD or than can be chosen at random, we computed S_{PD_FD} based on the averaged FD

124   over 1000 PD-maximized sets and 1000 random sets [16].


$$S_{PD-FD} = \frac{B}{A+B}$$

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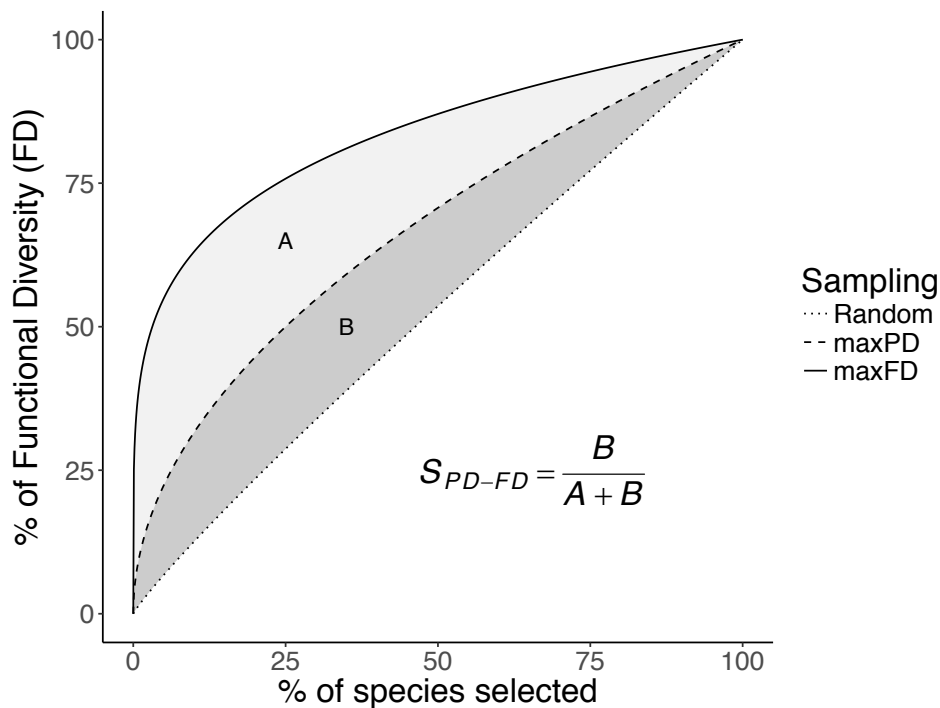
126   **Figure 1 – A conceptual approach for evaluating whether PD is a good surrogate for FD.** To

127   evaluate if PD is a good surrogate of FD, we measure to what extent a species prioritization

128   strategy that maximize PD captures FD relative to an optimal and a random strategy. To do so,

129   we compare FD accumulation curves (i.e. FD computed for increasing proportion of the species

130   pool considered) across these three different sampling strategies: the random sampling (i.e.

131   rarefaction curve, averaged over 1000 sets), the maxPD (surrogacy, averaged over 1000 sets)

132   sampling (i.e. the sets that maximize PD) and the maxFD (optimal) sampling (i.e. sets that

133   maximize FD, see legends). Then, we measure the surrogacy of PD for FD (SD_{PD-FD}) as the area

134   between the random and the maxPD curve ('A', see legend) divided by the area between the

135   random and the maxFD curve ('A+B', see legend). If SD_{PD-FD} is positive, PD is a good surrogate

136   for FD (the maximum value being 1 where PD is an optimal surrogate) while when SD_{PD-FD} is

137   negative preserving species based on PD is worse than preserving them at random.

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Results

140   We find that selecting the most phylogenetically diverse sets of species within a given

141   taxonomic family or within a given geographical location (large grid-cells across the globe)

142   captures, on average, 18% more FD than sets of randomly chosen species (i.e. S_{PD_FD} = 18%, SD

143   +/- 6.5% across pools, see Figure 1 and S1-2). Although the surrogacy is generally positive, there

144   was substantial variation across species pools. For example, the surrogacy of PD varies widely

145   from a minimum of -85% to a maximum of 92%, meaning that selecting the most

146   phylogenetically diverse sets of taxa can capture either 85% less (or 92% more) FD than sets of

147   randomly chosen taxa (Fig. 2-3 and Fig. S3-4). However, in 88% of the species pools, choosing

148   sets of species according to PD captured more FD than would be expected at random (*i.e.*,

149   surrogacy values > 0 in 88% of the cases, see Fig. 2-3). This suggests that, on average,

150   maximizing PD is a sound strategy to capture FD.

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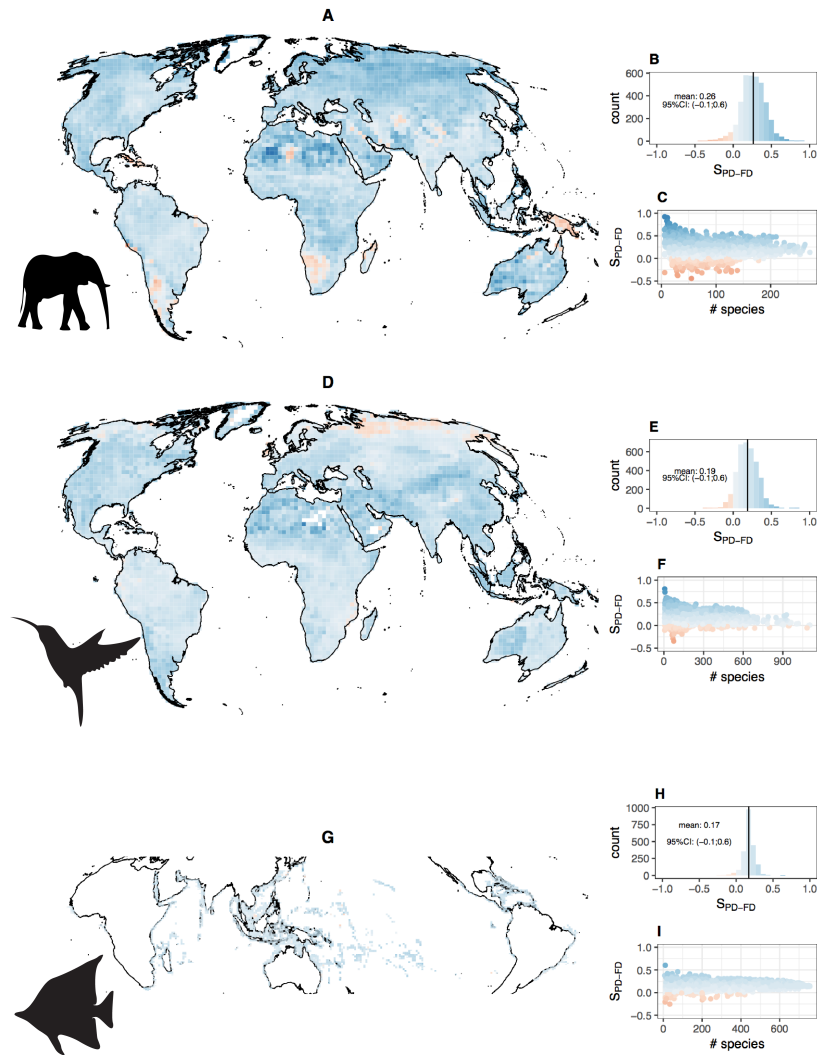
Figure 2 – PD is a good surrogate for FD across space. The figure presents the distribution and correlates of S_{PD-FD} for mammals (panels A-C), birds (panels D-F) and tropical fishes (G-I) separately across space. For each of the three groups, the SD_{PD-FD} frequency distribution is presented in top panels (B, E and H) along with its mean (vertical line) and the color code that is common to all panels, with blue indicating positive S_{PD-FD} (maximizing PD captures more FD than random). SD_{PD-FD} geographical distribution is presented in middle panels (A, D, G). Relationships between SD_{PD-FD} and species pool richness are presented in panels C, F and I. In each grid cell, SD_{PD-FD} values are based on the mean over 1000 repetitions of random and PDmax set draw (there is only one maxFD set).

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Figure 3 – PD is a good surrogate for FD across clades. The figure presents the distribution and correlates of SD_{PD-FD} for mammals (panels A-C) and birds (panels D-F) across families. For each of the two groups, the SD_{PD-FD} frequency distribution is presented (B and E) along with its mean (vertical line). The colour code that is common to all panels. SD_{PD-FD} phylogenetic distribution is presented in panels A and D. Relationships between SD_{PD-FD} and species pool richness are presented in panels C, F and I. For each taxonomic family, SD_{PD-FD} values are based on the mean over 1000 repetitions of random and maxPD set draw (there is only one maxFD set).

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171   However, even if in the majority cases maximizing PD does, on average, better than an

172   averaged random selection, this does not capture the *reliability* of its performance. The PD-

173   maximization and the random selection strategies exhibit variation: simply by chance, random

174   selection of species can capture very high (or, conversely, very low) FD, and the same may be

175   true (to a previously unstudied degree) for PD. The extent of this variation is important: if it is

176   less than the average difference, PD-maximization is a reliable strategy as it will always yield

177   more FD, but if it does not, then PD-maximization could be unreliable for individual

178   conservation interventions. To contrast these two situations, we measured the fraction of times

179   that, within each species pool, the PD-maximization strategy yielded more FD than random

180   selection (see methods). PD-based selection was the best choice in 64% of cases (SD across

181   species pool=9%, see Supplementary Table 1 and Fig. S5), making it the better strategy but not

182   a perfectly reliable one. Thus, while the PD-maximization strategy has a consistent positive

183   effect (i.e. the average PD-maximization strategy yields more FD than the average random

184   strategy), its effect is weak (i.e. the PD-maximization strategy still yields less FD than the

185   random strategy in 36% of the trials within a species pool).

186   We next explored the drivers of surrogacies values across species pools. Surrogacy of PD

187   appears to weaken as the species pool richness increases (on average, Spearman Rho between

188   absolute surrogacies and species richness = -.15), most clearly seen in the tropics and in

189   species-rich families such as the Muridae (rats, mice and allies) and Columbidae (pigeons and

190   allies) (Fig. 2-3). This is likely because our measure of FD (see Methods) rapidly saturates as the

191   number of selected species increases and species from these large pools harbor high functional

192   redundancy, such that a random prioritization scheme performs relatively well, or at least no

193   worse than other strategies (Fig. S6). In contrast, FD can be greatly increased by prioritization of

194   species using PD from species poor assemblages or clades. This is particularly the case in spatial

195   assemblages containing multiple taxonomic orders, which are both phylogenetically and

196   ecologically divergent from one another. Interestingly, the PD-FD relationship was not

197   consistent across *taxonomic* scale: we found that, in contrast to patterns at the family level, for

198   certain mammalian and avian orders (which are older than the families described above), using

199   PD to select species is much worse for capturing FD than choosing species at random (see, for

200   example, the Afrosoricidae, Chiroptera, and Charadriiformes in Fig. S7).

201   We then explored whether we can explain this variability within- and between-datasets,

202   and in particular, why for some assemblages/clades, a PD-prioritization strategy fails to capture

203   more FD than random choice. It is often implicitly assumed that phylogenetic signal (i.e. the

204   degree to which closely related species tend to harbor similar sets of traits) can be used to

205   evaluate the effectiveness of PD as a surrogate for FD [5,15–17]. Surprisingly perhaps, the value of

206   PD as a surrogate for FD was only weakly correlated with the phylogenetic signal of the

207   underlying traits (Fig. S8-9, on average Spearman Rho = 0.17). Similarly, tree imbalance, which

208   is known to affect surrogacy in simulations [16], did not explain surrogacy in these empirical data

209   (Fig. S8-9).

210   For mammals, regions where PD did worse than random were located in the Sahara,

211   south western Patagonia, southern Africa including parts of Madagascar, and New Guinea

212   (Figure 2). These latter two in particular are of concern since they are global conservation

213   priorities on the basis of species endemism and habitat loss. We suggest two historical reasons

214   for such idiosyncratic poor performance of PD. First, there is a tendency for a large carnivore

215   species, either a top predator (*e.g.*, cheetahs in the Sahara or foxes in Patagonia) or a large

216   scavenger (*e.g.*, the hyena in South Africa) to co-occur with a close relative with distinct traits in

217   these areas (*e.g.*, a desert cat with the cheetah or the aardwolf with the hyena, see Fig. S10).

218   Only one of these closely-related species will tend to be selected under prioritization schemes

219   that maximize PD, thus reducing the volume of the convex hull on average when the

220   functionally distinct one is not selected (the large predator or scavenger). This seems also to

221   drive the low surrogacy of PD in Charadriiformes (especially *Larus* and *Sterna*; see Figure S10).

222   Second, lineages in which traits evolve very slowly will contribute little to FD, even over long

223   periods of time (branch lengths) that contribute greatly to PD. For example, in New Guinea

224   many co-occurring bats with similar traits diverged long ago, such that they are always selected

225   in the PD maximizing set, but do not add much to the convex hull, resulting in a poor surrogacy

226   of PD for FD. Such strong ecological niche conservatism is common in mammals [29], e.g. in the

227 Geomyidae: two basal branches of the Geomyidae tree harbor very similar traits (species

228 descending from these branches are actually grouped in the same genus *Thomomys)* while

229 being distantly related in the phylogenies we used (Fig. S10). As such, they will be selected in

230 all PD maximizing sets, but will not contribute greatly to FD.

Discussion

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232   Maximizing PD in conservation decisions is now commonplace in the academic world[20–

233 22,30–33] and is also starting to be used in real-world conservation prioritizations, for example with

234 the EDGE program[18]. To the best of our knowledge, there are no clear direct ecosystem

235 function or health benefits that phylogenetic branch lengths provide. Rather, high PD is

236 perceived as valuable because it is assumed to be a good proxy for high diversity of traits or

237 "features"[14] (referred as to high functional diversity in this paper, FD), a hypothesis that we

238 name the "phylogenetic gambit". High FD might be valuable for a number of reasons, for

239 example ecosystem functioning, ecosystem services, future "options values"[14,15] or

240 "evolutionary potential"[15,34]. The utility of PD for conservation stems from the fact that

241 calculating PD is relatively fast and cheap, often making it an easier way to prioritize species or

242 areas than FD. Indeed, we have imperfect knowledge about which, and how many, traits and

243 functions are important in a given context, how these traits and functions vary among species

244 and across space, and how the importance of traits may change in the future[13]. Yet, even if

245 convenient, maximizing PD can only be an effective and realistic conservation strategy to

246 conserve FD if the phylogenetic gambit holds and maximizing PD yields more FD than a strategy

247 that ignores phylogeny. If maximizing PD yields *less* FD than a random strategy (i.e., the gambit

248 fails), then researchers and conservationists should reconsider whether maximizing PD as a

249 useful conservation strategy. A large body of literature has shown that maximizing PD does not

250 maximize FD empirically[20–22,30] or even in simple theoretical cases[16], but such work does not

251 test the phylogenetic gambit of whether PD prioritization captures more FD than *random*

252 selection (which has not, to our knowledge, been tested)[16]. Here we have shown that the

253 phylogenetic gambit holds: that PD *is* an effective conservation metric to capture FD. Yet we

254   also show that it remains something of a gambit: PD is good 'on average', but there is still some

255   risk associated with taking it.

256   We found that prioritizing the most phylogenetically diverse set of taxa in a region or

257   clade will result in an average gain of 18% functional diversity relative to applying the same

258   conservation effort without considering phylogeny, but this gain will decrease as species

259   richness increases. In opposition to what has previously been implicitly assumed[15,16], we find

260   weak empirical evidence that the presence of phylogenetic signal in traits predicts whether PD-

261   based conservation will prioritize FD. Our result suggests that PD is a reasonable conservation

262   prioritization strategy, especially in species-poor clades or regions, or in the absence of

263   meaningful data on functional traits. However, we note three important caveats to the use of

264   this strategy. First, 18% extra FD may not always be a useful conservation target. It is currently

265   unknown whether this added 18% of FD can actually be of enough conservation value. Second,

266   in cases of either recent trait divergence or, alternatively, very strong trait conservatism, a PD

267   prioritization scheme can capture less FD than a random scheme. Evolutionary biologists

268   commonly focus on 'unusual' clades with rapid divergences (e.g., cichlids); we show here that

269   divergence does not have to be that spectacular (e.g., African carnivores) to alter the PD-FD

270   relationship. Third, we found that while this strategy, on average, captures FD well, it is also

271   somewhat unreliable, and 36% of the time will not capture more FD than random choice. This

272   means that while the PD gambit can be a bet worth taking, it is still a bet with associated risk,

273   not a sure thing.

274   Our objective in this paper is to test the phylogenetic gambit using empirical datasets.

275   This means that we do not aim to provide a coherent prioritization strategy[35], or ready-to use

276   conservation guidelines. Indeed, we simplistically and implicitly assume that chosen species will

277   either be saved or go extinct, and we have not linked our various scenarios to any particular

278   policy position or conservation objective other than maximizing FD within a phylogenetic clade

279   or region[28,31]. In reality, conservation decisions reflect the interplay of social, economic,

280   political, and scientific priorities, and do not necessarily result in the saving of target species

281   (and therefore of their associated FD or PD). While our study is thus not directly applicable, the

282   test we are conducting is actually critical to validate (or invalidate) the use of PD in conservation

283   as a whole. While it is not clear whether our results would generalize to other taxa (although

284   we hope that others will extend our work and test the phylogenetic gambit in other systems),

285   we do feel it is important to consider the uncertainty that has been introduced into our analysis

286   as a result of uncertainty associated with the spatial scale of our analysis, our phylogenetic

287   data, and our choice of trait and measurement of FD.

288   The scale of conservation activities can vary, from the global scale of the hotspots

289   approach to local protected areas within a single country, but, unfortunately, the connection

290   between these scales remains unclear. For example, if the motivation for protecting FD is to

291   maintain community-driven ecosystem functions and services [6,36,37], the value of a regional or

292   global focus may be questionable[38], and studies are increasingly focusing on local scales[6].

293   Ecologists are refining and improving our understanding of how local assemblages assemble

294   within a regional context[39], and while the concept of the 'regional pool' of species is

295   increasingly being viewed as a simplification, it is unlikely that regional- and local-scale patterns

296   are totally disconnected. We emphasize that our results are relatively robust to variation in

297   spatial scale (see Fig. S3), but we acknowledge that future studies should test the phylogenetic

298   gambit at more local scale as well.

299   The set of species that maximize PD obviously rely on the phylogenetic hypothesis used.

300   No hypothesis is perfect or without uncertainty, and these phylogenetic uncertainties could in

301   turn impact the composition of the set of species that maximize PD and hence the surrogacy

302   values we compute. In this study, we explicitly took into account these uncertainties by using

303   100 different trees[40,41]. The explicit propagation of this phylogenetic uncertainty through into

304   our results may underlie some of the uncertainty ('risk') of our result, and we suggest it is

305   important that future studies explicitly take into account phylogenetic uncertainty when testing

306   the phylogenetic gambit.

307   The motivator of our test of the surrogacy value of PD for FD is the fact that ecologically-

308   relevant trait data is in short supply, especially for rare and data-deficient species. Indeed, if it

309   were not for this relative paucity of data, we could simply prioritize species based on their

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310 unique contribution to FD directly. Although there have been massive and well-funded efforts

311 to collect and curate trait data from across the Tree of Life[42–44], we are still far from having

312 comprehensive coverage. Furthermore, despite recent progress[45], it is still not fully understood

313 which traits are most relevant for responses to environmental change, or that contribute most

314 to certain ecosystem functions and services, and how these vary among systems. Our analysis

315 suffers from a similar data limitation. We chose these traits because they are frequently

316 collected in ecological studies, not because we know they are ecologically important. Our

317 assumption is that their phylogenetic distribution is typical of those traits that are most

318 desirable for the purpose of conservation and that our primary results are therefore widely

319 applicable. While we did test the robustness of our results to the variation of trait information

320 retained to compute FD (Figure S1), it is true that, overall, we used a rather limited set of traits.

321 We acknowledge that it is possible that many other potential valuable traits are not captured

322 by our measure of FD. One of the ideas behind the use of PD is that phylogeny might account

323 for these for unmeasured and unmeasurable traits[9,14,15], however, as this hypothesis is not

324 testable (we do not have these traits), it seems risky to assume it is true. Our objective here is

325 to test the phylogenetic gambit given the limited set of traits that we have: we consider that

326 carrying out our imperfect test is more informative than not carrying any test at all.

327 In conclusion, we found that maximizing PD results in an average gain of 18% of FD

328 relative to random choice. However, this average gain hides the fact that in over 1/3 of the

329 comparisons, maximum PD sets contain less FD than randomly chosen sets of species. These

330 results suggest that, while maximizing PD can help capture FD, it represents a risky strategy. If

331 maximizing PD is a risky strategy, then, should we abandon the use of PD in conservation? We

332 believe that before such dramatic decision, our test should be repeated across space, traits and

333 taxa, in order to narrow the uncertainties of our results. This is why we now urge others to

334 expand our simple phylogenetic gambit test to other clades and other traits in order to test the

335 generality of our findings. We hope that our study will stimulate the production of numerous

336 tests to finally rigorously assess the usefulness of PD in conservation.

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Acknowledgements

Competing interest.

No competing interest.

Material and Methods

We use two classes of data to address the question of whether choosing sets of species according to PD captures the underlying trait diversity (as measured with FD) well. First, we used taxonomic groups (clades) of species as our unit of analysis ('species pool' hereafter) and, second, we investigated broad assemblages found across the globe. The former is more explicitly evolutionary, ensuring that our results are not driven by well-established relationships across large taxonomic groups (*e.g.*, monotremes are distinct from placental mammals) and the latter is likely more relevant to actual conservation practice.

1. Data

We use distribution data to delineate geographical assemblage species pool and taxonomy to delineate clade-based species pools (namely families and orders).

Distribution data – For mammals, we used the distribution maps provided by the Mammal Red List Assessment (http://www.iucnredlist.org/) for 4,616 species. For birds, full (breeding and wintering) and breeding ranges distribution maps were extracted from BirdLife (http://www.birdlife.org/) for 9,993 species. The best resolution at which these maps should

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364 be used is still under discussion in the literature, so we decided to use the 40 000km^2

365 resolution (200x200km gird cell at the equator) that is commonly used at global scale [46,47].

366 The total number of grid cells was 3,646. Domestic and aquatic mammals were excluded

367 from the analysis. In order to make sure our results were not driven by the important trait

368 difference between volant and non volant mammals, we repeated our results excluding bats.

369 For birds, we repeated our analysis using the full ranges. Finally, we evaluated the

370 robustness of our result to the spatial resolution considered by repeating our analysis at a

371 resolution of 100x100km (number of cells was 13,330) for birds and mammals; we present

372 these results in the supplementary materials, as they are qualitatively identical to those

373 conducted at 200x200km (Fig. S1). For fishes, we used a database of 1536 species, for which

374 we had distribution data, phylogenetic and functional data. Distribution data were extracted

375 from a global-scale distribution database [48]. Species composition was then extracted from

376 grid cells of 5°x5°, corresponding to approximately 555x555 km at the equator [49]. This grain

377 size of the grid was chosen because it represents a good compromise between the desired

378 resolution and the geographical density of information.

379

380 **Phylogenies –** In order to prioritize species to maximize PD, phylogenies of each species pool

381 are needed. We used the first 100 published calibrated ultrametric trees of Jetz et al. (2012) for

382 birds and Faurby and Svenning (2015) for mammals. By repeating our analyses across a

383 posterior distribution of phylogenetic hypotheses, we control and account for phylogenetic

384 uncertainty. For tropical reef fishes, we built a phylogeny for 18 families (i.e. Labridae, Scaridae,

385 Pomacentridae, Chaetodontidae, Acanthuridae, Haemulidae, Balistidae, Carangidae,

386 Serranidae, Lutjanidae, Sparidae, Caesionidae, Holocentridae, Mullidae, Muraenidae,

387 Tetraodontidae, Lethrinidae and Siganidae) by pruning a dated molecular phylogenetic tree for

388 7,822 extant fish species [49]. These families were selected as the most representative tropical

389 reef fish families, that is, they are abundant and speciose on tropical reefs. We grafted missing

390 species on the pruned phylogenetic tree (circa 50% among the 1536 studied species) based on

391 published phylogenies for these families, supplemented by taxonomic information from fish

392 identification guides and FishBase [49,50]. We recorded, for each of these trees, a measure of

17

393   imbalance (as measured by **β** [51]) and 'tipiness' (as measured by Gamma [52]). For both mammals

394   and birds, we chose to group species in families and orders. We used these groupings when

395   calculating the purely phylogenetic, clade-based analyses (to address question 1), but not

396   within the spatial, assemblage-based analyses (question 2). For the taxonomic analysis of

397   mammal families, we removed two families (Dipodidae and Echimyidae) because of their very

398   poor phylogenetic resolution (i.e. polytomies for an important number of species).

399

400   **Traits –** For birds and mammals, four traits (diet, (log transformed) body mass, activity cycle,

401   and foraging height) were extracted from Elton Traits1.0 [44]. These traits are generally assumed

402   to appropriately represent Eltonian niche dimensions within an assemblage or clade of

403   mammals or birds [53,54]. For fishes, we used a previously published database [12]. We used 6

404   categorical traits: size, mobility, period of activity, schooling, vertical position in the water

405   column, and diet (for a full description of the dataset, see Mouill*ot et* al. 2014). These traits

406   have already been used to investigate community assembly rules [55] and to seek vulnerable fish

407   functions [11]. For each clade and assemblage, we used the raw trait (only body mass was log-

408   transformed and rescaled by the clade/assemblage range of body masses) values to compute

409   distance between species using Gower distance [19] and use PCoA to summarize the trait space

410   in few dimensions. We retained the numbers of PCoA axes necessary to represent 70% of the

411   total initial variability (using a 80% threshold did not quantitatively change our conclusions, see

412   Fig. S1). We also recorded phylogenetic signal for each PCoA axis using Blomberg's K [56].

413

414   **2. Approach**

415   Our aim was to evaluate, across a wide range of clades and regions, the ability of PD-informed

416   prioritization scheme to capture FD in comparison with two other prioritization schemes:

417   selecting species to directly maximize FD ('maxFD' hereafter) and selecting species randomly

418   (Figure 1). Our premise was that we often do not know or have not measured the traits that are

419   most relevant for ecosystem function and services such that maximizing FD is not generally

420   feasible. By focusing on a subset of traits and assuming that they are representative of

18

421 ecologically relevant traits, we were able to get an estimate of how well PD does compared to

422 the best we could possibly do. We used performance relative to choosing on the basis of FD as

423 an upper-limit to the performance of PD as a surrogate for FD, and used random species

424 selection as a lower benchmark.

425 **Random prioritization scheme –** For each pool (i.e. each clade and each geographical

426 assemblage) and each number of selected species (10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%

427 of the total pool), 1000 random sets of species were produced, from which the average FD was

428 recorded.

429 **Prioritization scheme maximizing PD (maxPD) –** While there are many, overlapping metrics for

430 measuring the evolutionary history encompassed by a set of species [15,57], the most common is

431 the sum of all branch lengths (often in units of time) connecting a set of species to a common

432 root [14], called Phylogenetic Diversity (PD). This is the metric whose maximization has most

433 commonly been proposed as a conservation prioritization metric [14,34,58], and as a measure of

434 phylogenetic 'richness' it most naturally maps onto our chosen FD metric [57]. We used the

435 greedy algorithm proposed by Bordewi*ch et* al. (2008) to find our maxPD set of species *S*. For a

436 given tree there are likely multiple, and possibly very many, sets of species with the same PD as

437 *S*. As a consequence, we produced, for each pool, each number of selected species, and each

438 alternative phylogenetic trees, 10 maxPD sets of species. We then averaged the FD of these

439 sets across our 100 phylogenetic trees, so that each value is an average of 1000 sets (10 sets for

440 each of the 100 trees).

441

442 **Prioritization scheme maximizing FD (maxFD) –** Functional diversity was estimated using a

443 functional richness index (FRic; Cornwe*ll et* al. 2006; Villég*er et* al. 2008; Pavoine & Bonsall

444 2011). The FRic index relies on a multidimensional Euclidean space, where the axes are traits

445 (or factorial axes from a principal coordinates analysis (PCoA) computed using these traits)

446 along which species are placed according to their trait values. This index measures the volume

447 of trait space occupied by a given species assemblage by calculating the convex hull volume [62],

448 defined by the species at the vertices of the functional space, that encompasses the entire trait

19

449   space filled by all species in this assemblage. In a single dimension, this simply equals the range

450   of values [62]. This broadly used metric in ecology is set monotonic with species richness, a

451   property generally assumed desirable in conservation whereby the addition of a new species

452   can never decrease the metric's value [63]. FD measures the total amount of variation in trait

453   values, making it conceptually comparable to PD [57]. We used the FRic index instead of the FD

454   index based on a functional dendrogram (Petchey & Gaston, 2006) since recent studies showed

455   that the FD index may lead to biased assessments of functional diversity and inaccurate

456   ecological conclusions [64]. The most straightforward way to obtain the maximal FD for *n* species

457   is to compute FD for all possible combinations of *n* species and simply record the greatest value

458   (the brute force approach). However, this is not feasible in practice as the numbers of

459   combinations of selected species was too high (e.g., 10^{71} possible sets for all mammal

460   assemblages). To rapidly and efficiently find the set of species that aim to maximize FD, we

461   developed a novel (at least in ecology) greedy algorithm. In brief, our approach iteratively

462   (starting with two species) select the species that is the furthest from the centroid of the

463   already selected set. To avoid selecting two species that are far from the centroid but close to

464   each other, we penalized the distance to the centroid by the distance to the closest neighbour

465   in the already selected set. Here we present in details the greedy algorithm we used to find the

466   set of species that maximize FD:

467   Step 1. Select the two species with the highest trait distance

468   Step 2. Compute the centroid of these two selected species

469   Step 3. Compute distances between species not in the set and this 'set centroid'.

470   Step 4. Penalize these distances by adding the following factor f (Eq. 1)

471                          $$f = K \times e^{L \times minD}$$ (eq. 1)

472   with K and L being penalizing factors and minD the distance between a given candidate

473   species and the nearest species already in the selected set.

474   Step 5. Select the species that maximized the penalized distance

475   Step 6. Go back to step one with this new set of species until the desired number of

476   species is reached.

477

478   To avoid arbitrarily setting the penalizing parameters, we tested 1000 pairs of parameters

479   drawn from a truncated normal distribution (mean=1, sd=.5) and retained the parameter pairs

480   that yielded the maximal FD.

481   In tests of subsets of the data for which finding the true maxFD was feasible, we found our

482   approach to adequately approximate the true maxFD and to produce a very good

483   approximation of the true degree of PD's surrogacy for FD (Fig. S2).

484

485   **Measuring performance and surrogacy of prioritization schemes.**

486   We use a common approach[27,28] to quantify the extent to which a given surrogate (here, the

487   maxPD choice) reaches a certain objective (here, maximize FD). Species from a given pool (i.e.,

488   for each dataset (clade and assemblages) independently,) were prioritized and selected

489   according to (1) the objective, i.e. maximize FD, producing the 'optimal curve' (maxFD curve in

490   Figure 1), (2) the surrogate i.e. maximize PD, producing the 'surrogate curve' (maxPD curve in

491   Figure 1) and (3) at random (random curve in Figure 1), i.e. producing the 'random curve'

492   (Figure 1). To compute a 'surrogacy' estimate of PD (S_{PD-FD}), we compare the position of the

493   surrogate curve (1) to the random curve (2) relative to the optimal curve (2) (Figure 1 and Eq. 2)

494   across the deciles of species richness of the pool (given as an interval 0-1):

495
$$S_{PD\text{-}FD} = \int_0^1 \frac{FD_{maxPD}\text{-}FD_{random}}{FD_{maxPF}\text{-}FD_{random}} \qquad \text{(Equation 2)}$$

496

497   This surrogacy metric is at 100% when the surrogate perfectly meets the objective (i.e., the

498   maxFD and maxPD curves are identical and the max PD set is the maxFD set), 0% when the

499   surrogate is not better than randomly chosen sets of species (i.e., the random and maxPD

500   curves are identical) and is negative if the surrogate choice is worse than random (i.e., the

501   maxPD curve is below the random curve). Correlates of S_{PD-FD} were evaluated using Spearman

502   correlations.

503   Apart from focusing on average tendencies, we quantified the variability of the FD yielded by

504   the PD—maximized selection strategy and the random selection strategy within each species

505   pools. To do so, we compute, for each species pool and for each % of selected species

21

506   independently, the number of cases where $FD_{random} > FD_{maxPD}$ across the 1000 random *1000

507   maxPD sets combinations (i.e. 10^6 comparisons). We then averaged theses number across % of

508   selected species and report statistics across datasets (Supp. Table 1).

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