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Is phylogenetic diversity a surrogate for functional diversity across clades and space?

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29 **Abstract**

30 In the face of limited funding and widespread threats to biodiversity, conserving the widest

31 possible variety of biological traits (functional diversity, FD) is a reasonable prioritization

32 objective. Because species traits are often similar among closely related species (phylogenetic

33 signal), many researchers have advocated for a "phylogenetic gambit": maximizing

34 phylogenetic diversity (PD) should indirectly capture FD. To our knowledge, this gambit has not

35 been subject to a focused empirical test. Here we use data from >15,000 vertebrate species to

36 empirically test it. We delineate >10,000 species pools and test whether prioritizing the most

37 phylogenetically diverse set of species results in more or less FD relative to a random choice.

38 We find that, across species pools, maximizing PD results in an average gain of 18% of FD

39 relative to a random choice, suggesting that PD is a sound conservation prioritization strategy.

40 However, this averaged gain hides important variability: for 10% of the species pools,

41 maximizing PD can capture less FD than an averaged random scheme because of recent trait

42 divergence and/or very strong trait conservatism. In addition, within a species pool, many

43 random sets of species actually yield more FD than the PD-maximized selection – on average

44 36% of the time per pool. If the traits we used are representative of traits we wish to conserve,

45 our results suggest that conservation initiatives focusing on PD will, on average, capture more

46 FD than a random strategy, but this gain will not systematically yield more FD than random and

47 thus can be considered risky.

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51 We are in the midst of a period of heightened biological extinction, with rates several orders of

52 magnitude higher than background rates estimated from the fossil record [1–3]. In addition to

53 having potentially widespread consequences for the functioning of ecosystems and the

54 provisioning of valuable ecosystem services, this situation poses a huge moral challenge [4–8].

55 And, to the extent that resources for conservation actions remain limited, agonizing choices as

56 to which species most warrant attention become necessary [9,10]. To keep humanity's options

57 open, and our common legacy as rich as possible, it is widely argued that we should seek to

58 maximize the biological diversity of forms and functions [6–12] . The biological diversity of

59 forms and functions can be measured as functional diversity [FD] (see methods). However, in

60 practice, it is challenging to prioritize species on the basis of FD: we have imperfect knowledge

61 about which, and how many traits and functions are important in a given context, how these

62 traits and functions vary among species and across space, and how the importance of traits may

63 change in the future [13]. Many researchers have therefore advocated for a "phylogenetic

64 gambit"; that is, if species traits reflect their shared evolutionary history, then the pattern of

65 that evolutionary history –their phylogeny– should serve as a useful stand-in for unmeasured

66 and unmeasurable traits [9,14,15]. The phylogenetic gambit implies that maximizing

67 phylogenetic diversity (PD), i.e. the breadth of evolutionary history, will ensure that a wide

68 variety of forms and functions are present within a species set [14–17].

69 Following this logic, PD has formed the basis of global conservation schemes, notably the EDGE

70 program [18], has been used by restoration biologists [19], and has been widely embraced by

71 researchers across the biodiversity sciences [20–23]. Despite this enthusiasm, the critical

72   question of whether maximizing PD will actually capture more FD than prioritization schemes

73   that ignore phylogeny has, to our knowledge, never been empirically tested [16]. While it may

74   seem obvious that sampling species across the tree of life will capture high amounts of FD, a

75   recent theoretical study demonstrated that PD could be a poor surrogate for FD and, in some

76   scenarios, prioritizing species on the basis of PD could actually lead to capture *less* FD than if

77   species were simply selected at random [16].

78   We clarify what our goals are in testing the utility of PD to capture FD. First, we take as given

79   that maximizing PD is not the overarching goal *per se* of PD-maximization schemes, but rather

80   that a PD maximization strategy is valued for its ability to capture more FD compared to a

81   strategy that ignores phylogeny. Second, asking whether PD maximization captures more FD

82   than a random choice is fundamentally distinct (and a lower bar) from asking whether

83   maximizing PD also *maximizes* FD [e.g. 15,19–21,23,24]. Finally, it is important to note that we

84   are selecting *species* sets to maximize PD or FD within a region. While this is a simplification, as

85   conservation actions often aim to select sets of *areas* (e.g. in reserve design), the only global

86   phylogenetically-informed conservation initiative is species-centered (EDGE; Isaac et al. 2007).

87   More fundamentally, the framework we use here allows us to directly test the fundamental

88   phylogenetic gambit at the heart of all PD-based conservation [16]. Critically, the question we

89   raise has been shown to be distinct from asking whether traits have phylogenetic signal

90   (whether closely related species tend to share similar sets of traits), since PD can be a poor

91   surrogate for FD *even if* traits exhibit phylogenetic signal [16].

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

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

94   regard to evolutionary relatedness. We evaluate the PD~FD relationship for different species

95   pools (taxonomic families and geographical assemblages, *i.e.*, sets of species co-occurring at a

96   given scale) using a large global dataset including trait, phylogenetic, and geographic range data

97   for 4,616 species of mammals, 9,993 species of birds, and 1,5036 species of tropical fish.

98   Specifically, we measure FD as functional richness (see methods) and compute, for any given

99   species pool, an estimate of surrogacy (S_{PD_FD}, [26,27], Figure 1). S_{PD_FD} represents the amount

100 of FD sampled by the set of species chosen to maximize PD, relative to the FD sampled by

101 optimal set of species selected to maximize FD directly, with both components controlled for

102 the expected FD from a random species set of the same size. S_{PD_FD} will be positive if the

103 averaged PD-maximized set contains more FD than the averaged random set, and negative if

104 not. S_{PD_FD} will equal 100% if the PD-maximization strategy is optimal (*i.e.* to maximize FD). We

105 integrate S_{PD_FD} for each species pool across all deciles of species richness (Eqn. 1) but because

106 they are many sets of species that can maximize PD or than can be chosen at random, we

107 computed S_{PD_FD} based on the averaged FD over 1000 PD-maximized sets and 1000 random sets

108 [16].

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

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

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

112 +/- 6.5% across pools, see Figure 1). Although the surrogacy is generally positive, there was

113 variation across species pools. For example, the surrogacy of PD varies widely from a minimum

114   of -85% to a maximum of 92%, meaning that selecting the most phylogenetically diverse sets of

115   taxa can capture either 85% less (or 92% more) FD than that of randomly chosen taxa (Fig. 2-3

116   and Fig. S1-2). However, in 88% of the species pools, choosing sets of species according to PD

117   captured more FD than would be expected at random (*i.e.*, surrogacy values > 0 in 88% of the

118   cases, see Fig. 2-3). This suggest that, on average, maximizing PD is a sound strategy to capture

119   FD.

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

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

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

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

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

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

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

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

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

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

130   species pool=9%, see Supplementary Table 1 and Fig. S3), making it the better strategy but not

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

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

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

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

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

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

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

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

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

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

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

142   worse than other strategies (Fig. S4). In contrast, FD can be greatly increased by prioritization of

143   species using PD from species poor assemblages or clades [see also 28]. This is particularly the

144   case in spatial assemblages containing multiple taxonomic orders, which are both

145   phylogenetically and ecologically divergent from one another. Interestingly, the PD-FD

146   relationship was not consistent across *taxonomic* scale: we found that, in contrast to patterns

147   at the family level, for certain mammalian and avian orders (which are older than the families

148   described above), using PD to select species is much worse for capturing FD than choosing

149   species at random (see, for example, the Afrosoricidae, Chiroptera, and Charadriiformes in Fig.

150   S5).

151   We explored whether it is possible to explain this variability within- and between-

152   datasets, and in particular, why for some assemblages/clades, a PD-prioritization strategy fails

153   to capture more FD than random choice. It is often implicitly assumed that phylogenetic signal

154   (i.e. the degree to which closely related species tend to harbor similar sets of traits) can be used

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

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

157 underlying traits (Fig. S6-7, on average Spearman Rho = 0.17). Similarly, tree imbalance, which

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

159 data (Fig. S6-7).

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

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

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

163 priorities on account of species endemism and habitat loss. We suggest two historical reasons

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

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

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

167 these areas (*e.g.*, a desert cat with the cheetah or the aardwolf with the hyena, see Fig. S8).

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

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

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

171 drive the low surrogacy of PD in Charadriiformes (especially *Larus* and *Sterna*; see Figure S8).

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

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

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

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

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

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

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

179 being distantly related in the phylogenies we used (Fig. S8). As such, they will be selected in all

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

181   In summary, while in specific cases maximizing PD actually captures less FD than a

182 random set, in the majority of cases PD performs well (at least, better than random) as a

183 surrogate (in 88% of the species pool sets the mean surrogacy value ≥0). This represents an

184 important and necessary test of the motivations of conservation planning activities that

185 incorporate PD. However, we simplistically and implicitly assume that chosen species will either

186 be saved or will go extinct and we have not linked our various scenarios to any particular policy

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

188 region [16]. In reality, conservation decisions reflect the interplay of social, economic, political,

189 and scientific priorities, and do not necessarily result in the saving of target species (and

190 therefore of their associated FD or PD). However, our approach allows us to test a long-

191 standing idea in biodiversity science, and identify two critical ways in which PD-based

192 conservation can become disconnected from FD. We have not made any assumptions regarding

193 the macroevolutionary history of these traits (for example, assuming some particular model of

194 trait evolution) or how phenotypes are distributed across geographical and ecological gradients,

195 and therefore hope that our results generalize beyond the species we study here.

196   The spatial scale of our analysis reflects the scale of available data appropriate for

197 making a general statement about the surrogacy value of PD for FD. The scale of conservation

198 activities can vary, from the global scale of the hotspots approach to local protected areas

199 within a single country. Unfortunately, the connection between these scales remains unclear.

200   For example, if the motivation for protecting FD is to maintain community-driven ecosystem

201   functions and services [5,6,30], the value of a regional or global scale focus may be

202   questionable [31]. This worry has motivated studies that focus on local scales [6]. This is an

203   important area for further research; the patterns linking PD and FD in the regional pool may still

204   be important, since this is the species pool from which local sites are assembled and

205   maintained.

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

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

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

209   unique contribution to FD directly [e.g. 36]. Although there have been massive and well-funded

210   efforts to collect and curate trait data from across the Tree of Life [33–35], we are still far from

211   having comprehensive coverage. Furthermore, despite recent progress [e.g. 34,35], it is still not

212   fully understood which traits are most relevant for responses to environmental change, or that

213   contribute most to certain ecosystem functions and services, and how these vary among

214   systems. Our analysis suffers from a similar data limitation. We chose these traits because they

215   are frequently collected in ecological studies, not because we know they are ecologically

216   important. Our assumption is that their phylogenetic distribution is typical of those traits that

217   are most desirable for the purpose of conservation and that our primary results are therefore

218   widely applicable. We urge others to expand our simple test to other clades and traits in order

219   to test the generality of our findings.

220   **Conclusion**

221   Prioritizing the most phylogenetically diverse set of taxa in a region or clade will result in an

222   average gain of 18% functional diversity relative to applying the same conservation effort

223   without considering phylogeny, but this gain will decrease as species richness increases. This

224   suggests that PD is a reasonable conservation prioritization strategy, especially in species-poor

225   clades or regions, or in the absence of meaningful data on functional traits. However, we note

226   two important drawbacks of this strategy. First, in cases of either recent trait divergence or,

227   alternatively, very strong trait conservatism, a PD prioritization scheme can capture less FD

228   than a random scheme. Second, we found that while this strategy, on average, captures FD

229   well, it is also somewhat unreliable, and 36% of the time will not capture more FD than random

230   choice. Critically, and in opposition to what has previously been implicitly assumed [15,16], we

231   find weak empirical evidence that the presence of phylogenetic signal in traits predicts whether

232   PD-based conservation will prioritize FD. Assuming that the traits we have used are

233   representative of a broader array of ecologically relevant traits, our results provide a baseline

234   for how well we should expect PD-based prioritization to perform when ecologically important

235   traits are unknown, unmeasured, or unmeasurable. By clearly outlining the cases and parts of

236   the world in which phylogenetically-based conservation prioritization can (and cannot)

237   effectively act as a surrogate for functional diversity, we hope to inform and improve

238   conservation interventions globally.

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

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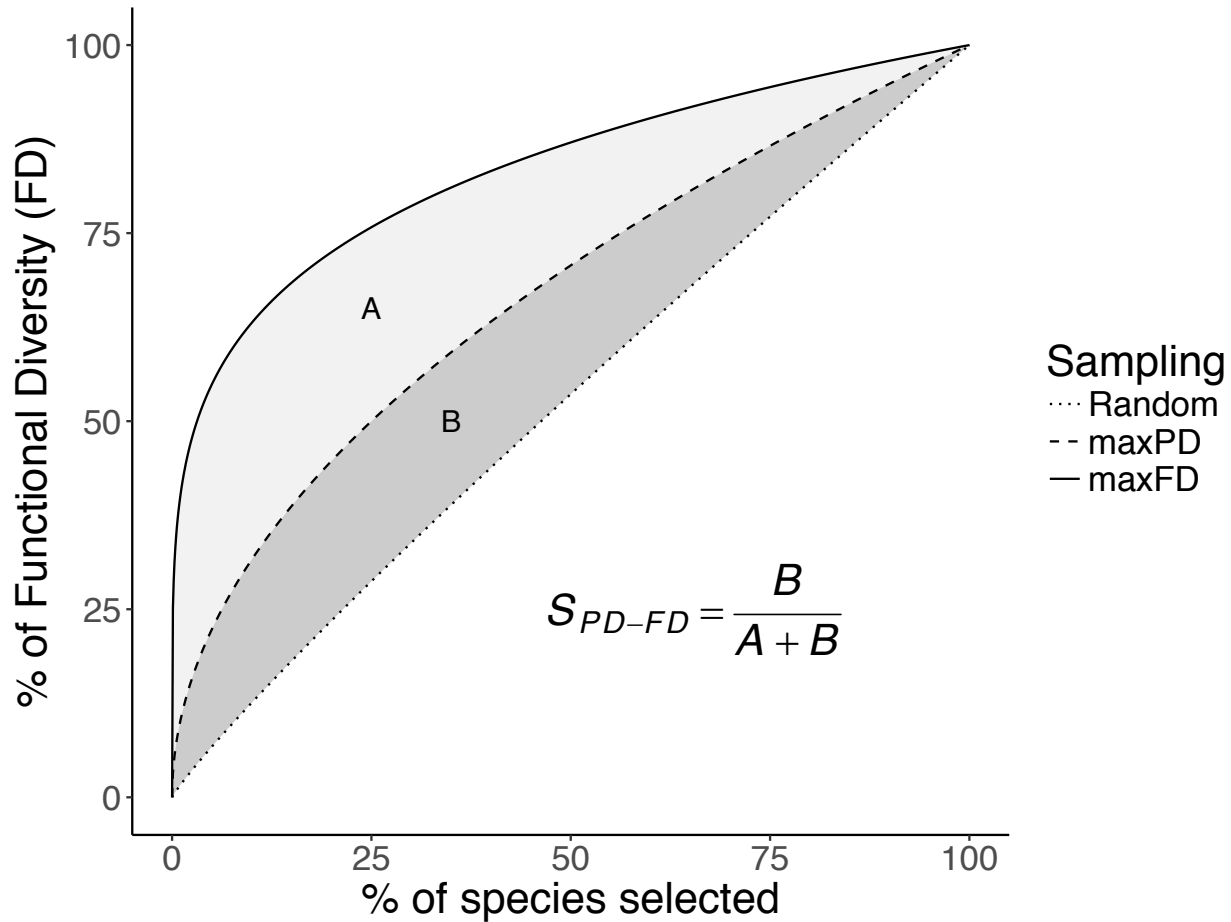
Figure 1 – A conceptual approach for evaluating if PD a good surrogate for FD. To evaluate if
PD is a good surrogate of FD, we measure to what extent a species prioritization strategy that
maximize PD captures FD relative to an optimal and a random strategy. To do so, we compare
FD accumulation curves (i.e. FD computed for increasing proportion of the species pool
considered) across these three different sampling strategies: the random sampling (i.e.
rarefaction curve, averaged over 1000 sets), the maxPD (surrogacy, averaged over 1000 sets)
sampling (i.e. the sets that maximize PD) and the maxFD (optimal) sampling (i.e. sets that
maximize FD, see legends). Then, we measure the surrogacy of PD for FD (SD_{PD-FD}) as the area
between the random and the maxPD curve ('A', see legend) divided by the area between the
random and the maxFD curve ('A+B', see legend). If SD_{PD-FD} is positive, PD is a good surrogate
for FD (the maximum value being 1 where PD is an optimal surrogate) while when SD_{PD-FD} is
negative preserving species based on PD is worse than preserving them at random.

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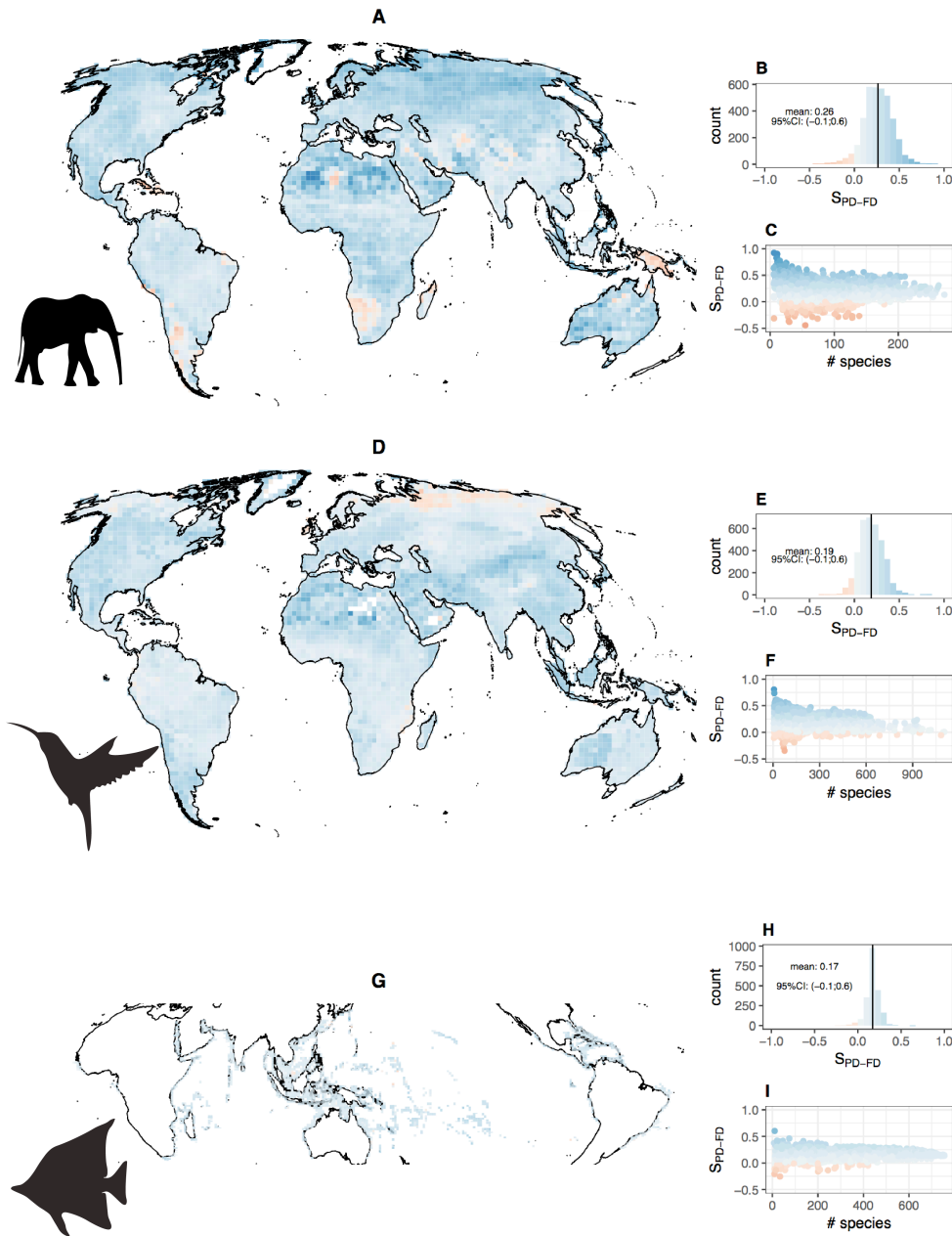
Figure 2 – PD is a good surrogate of FD across space. The figure presents the distribution and correlates of S_{PD-FD} for mammals (panels A-C), birds (panels D-F) and tropical fishes (G-I) separately across space. For each of the three groups, the SD_{PD-FD} frequency distribution is presented in top 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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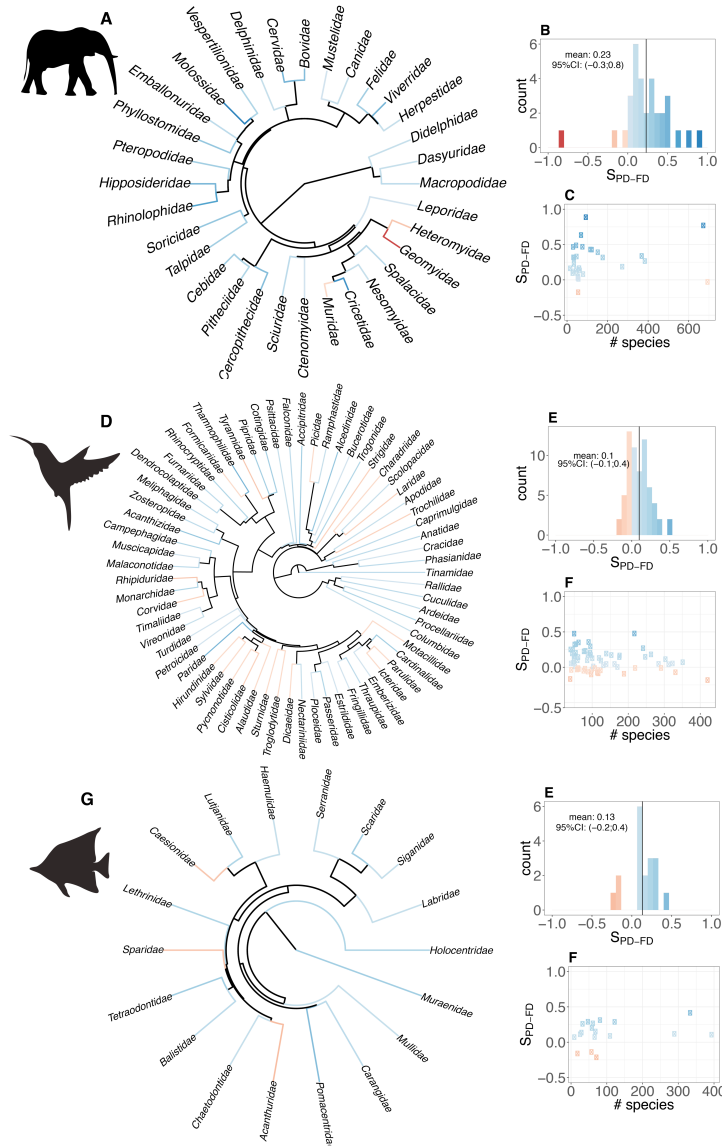
Figure 3 – PD is a good surrogate of FD across clades. The figure presents the distribution and correlates of SD$_{PD-FD}$ for mammals (panels A-C) and birds (panels D-F) across families. For each of the two groups, the SD$_{PD-FD}$ frequency distribution is presented (B and E) along with its mean (vertical 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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276   **Methods**

277   We use two classes of data to address the question of whether choosing sets of species

278   according to PD captures the underlying trait diversity (as measured with FD) well. First, we

279   used taxonomic groups (clades) of species as our unit of analysis ('species pool' hereafter) and,

280   second, we investigated broad assemblages found across the globe. The former is more

281   explicitly evolutionary, ensuring that our results are not driven by well-established relationships

282   across large taxonomic groups (*e.g.*, monotremes are distinct from placental mammals) and the

283   latter is likely more relevant to actual conservation practice.

284   **1. Data**

285   We use distribution data to delineate geographical assemblage species pool and taxonomy to

286   delineate clade-based species pools (namely families and orders).

287   **Distribution data –** For mammals, we used the distribution maps provided by the Mammal

288   Red List Assessment (http://www.iucnredlist.org/) for 4,616 species. For birds, full (breeding

289   and wintering) and breeding ranges distribution maps were extracted from BirdLife

290   (http://www.birdlife.org/) for 9,993 species. The best resolution at which these maps should

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

292   resolution (200x200km gird cell at the equator) that is commonly used at global scale

293   [38,39]. The total number of grid cells was 3,646. Domestic and aquatic mammals were

294   excluded from the analysis. In order to make sure our results were not driven by the

295   important trait difference between volant and non volant mammals, we repeated our results

296   excluding bats. For birds we repeated our analysis using the full ranges (*i.e.,* summer and

297   winter ranges). Finally, we evaluated the robustness of our result to the spatial resolution

298   considered by repeating our analysis at a resolution of 100x100km (number of grid cells was

299   13,330) for birds and mammals; we present these results in the supplementary materials, as

300   they are qualitatively identical to those conducted at 200x200km (fig. S1). For fishes, we

301   used a database of 1536 species, for which we had distribution data, phylogenetic and

302   functional data. Distribution data were extracted from a global-scale distribution database

303 [40]. Species composition was then extracted from grid cells of 5°x5°, corresponding to

304 approximately 555x555 km at the equator [41]. This grain size of the grid was chosen

305 because it represents a good compromise between the desired resolution and the

306 geographical density of information.

307

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

309 are needed. We used the first 100 published calibrated ultrametric trees of Jetz et al.[42] for

310 birds and Faurby and Svenning [43] for mammals. By repeating our analyses across a posterior

311 distribution of phylogenetic hypotheses, we control and account for phylogenetic uncertainty.

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

313 Pomacentridae, Chaetodontidae, Acanthuridae, Haemulidae, Balistidae, Carangidae,

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

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

316 7,822 extant fish species [44]. These families were selected as the most representative tropical

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

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

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

320 identification guides and FishBase (www.fishbase.org) [44,45]. We recorded, for each of these

321 trees, a measure of imbalance (as measured by β [46]) and 'tipiness' (as measured by Gamma

322 [47]). For both mammals and birds, we chose to group species in families and orders. We used

323 these groupings when calculating the purely phylogenetic, clade-based analyses (to address

324 question 1), but not within the spatial, assemblage-based analyses (question 2). For the

325 taxonomic analysis of mammal families we removed two families (Dipodidae and Echimyidae)

326 because of their very poor phylogenetic resolution (i.e. polytomies for an important number of

327 species).

328

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

330 and foraging height) were extracted from Elton Traits1.0 [35]. These traits are generally

331 assumed to appropriately represent Eltonian niche dimensions within an assemblage or clade

332   of mammals or birds [35,48,49]. For fishes, we used a previously published database [12]. We

333   used 6 categorical traits: size, mobility, period of activity, schooling, vertical position in the

334   water column, and diet (for a full description of the dataset, see Mouillot et al. [12]). These

335   traits have already been used to investigate community assembly rules [50] and to seek

336   vulnerable fish functions [11]. For each clade and assemblage, we used the raw trait (only body

337   mass was log-transformed and rescaled by the clade/assemblage range of body masses) values

338   to compute distance between species using Gower distance [19] and use PCoA to summarize

339   the trait space in few dimensions. We retained the numbers of PCoA axes necessary to

340   represent 70% of the total initial variability (using a 80% threshold did not quantitatively change

341   our conclusions, see Fig. S9). We also recorded phylogenetic signal for each PCoA axis using

342   Blomberg's K [51].

343

2. Approach

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

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

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

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

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

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

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

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

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

354   selection as a lower benchmark.

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

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

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

358   recorded.

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

360   measuring the evolutionary history encompassed by a set of species [52,53], the most common

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

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

363   commonly been proposed as a conservation prioritization metric [14,54,55], and as a measure

364   of phylogenetic 'richness' it most naturally maps onto our chosen FD metric [52]. We used the

365   greedy algorithm proposed by Bordewich et al. [56] to find our maxPD set of species *S*. For a

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

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

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

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

370   each of the 100 trees).

371

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

373   functional richness index (FRic; [57–59]). The FRic index relies on a multidimensional Euclidean

374   space, where the axes are traits (or factorial axes from a principal coordinates analysis (PCoA)

375   computed using these traits) along which species are placed according to their trait values. This

376   index measures the volume of trait space occupied by a given species assemblage by calculating

377   the convex hull volume [59], defined by the species at the vertices of the functional space, that

378   encompasses the entire trait space filled by all species in this assemblage. In a single dimension,

379   this simply equals the range of values [59]. This broadly used metric in ecology is set monotonic

380   with species richness, a property generally assumed desirable in conservation whereby the

381   addition of a new species can never decrease the metric's value [60]. FD measures the total

382   amount of variation in trait values, making it conceptually comparable to PD [52]. We used the

383   FRic index instead of the FD index based on a functional dendrogram (Petchey & Gaston, 2006)

384   since recent studies showed that the FD index may lead to biased assessments of functional

385   diversity and inaccurate ecological conclusions [61]. The most straightforward way to obtain

386   the maximal FD for *n* species is to compute FD for all possible combinations of *n* species and

387   simply record the greatest value (the brute force approach). However, this is not feasible in

388   practice as the numbers of combinations of selected species was too high (e.g., 10^{71} possible

389   sets for all mammal assemblages). To rapidly and efficiently find the set of species that aim to

390   maximize FD, we developed a novel (at least in ecology) greedy algorithm. In brief, our

391   approach iteratively (starting with two species) select the species that is the furthest from the

392   centroid of the already selected set. To avoid selecting two species that are far from the

393   centroid but close to each other, we penalized the distance to the centroid by the distance to

394   the closest neighbour in the already selected set. Here we present in details the greedy

395   algorithm we used to find the set of species that maximize FD:

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

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

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

399   Step 4. Penalize these distance by adding the following factor f (Eq. 4)

400                            $$f = K \times e^{L \times minD}$$ (eq. 4)

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

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

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

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

405   species is reached.

406

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

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

409   that yielded the maximal FD.

410

411

412

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

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

415   approximation of the true degree of PD's surrogacy for FD (fig. S10).

416

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

418 We use a common approach [26,27] to quantify the extent to which a given surrogate (here,

419 the maxPD choice) reaches a certain objective (here, maximize FD). Species from a given pool

420 (i.e., for each dataset (clade and assemblages) independently,) were prioritized and selected

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

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

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

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

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

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

427 $$S_{PD\text{-}FD} = \int_0^1 \frac{FD_{maxPD}\text{-}FD_{random}}{FD_{maxPF}\text{-}FD_{random}} \qquad \text{(Equation 1)}$$

428

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

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

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

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

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

434 correlations.

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

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

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

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

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

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

441

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