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

Florent Mazel[1,2,3,*], Matthew W. Pennell[3,4], Marc Cadotte[5,6.$], Sandra Diaz[7,$], Giulio Valentino Dalla Riva[8,$], Richard Grenyer[9,$], Fabien Leprieur[10], Arne O. Mooers[1,$], David Mouillot[10,11,$], Caroline M. Tucker[12,$], and William D. Pearse[13]

[1] Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada
[2] Department of Botany, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;
[3] Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;
[4] Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;
[5] Biological Sciences, University of Toronto-Scarborough, Scarborough M1C 1A4, Canada
[6] Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
[7] Instituto Multidisciplinario de Biología Vegetal. FECFyN - Universidad Nacional de Córdoba. Casilla de Correo 495, 5000 Córdoba. Argentina
[8] Department of Statistics, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;
[9] School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, U.K.
[10] Marine Biodiversity, Exploitation, and Conservation (MARBEC), UMR 9190, Université Montpellier, Montpellier, France
[11] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia
[12] Department of Biology, University of North Carolina-Chapel Hill
[13] Ecology Center and Department of Biology, Utah State University, Logan, Utah
* Corresponding Author; flo.mazel@gmail.com
$ Authors listed alphabetically

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Abstract

In the face of limited funding and widespread threats to biodiversity, conserving the widest possible variety of biological traits (functional diversity, FD) is a reasonable prioritization objective. Because species traits are often similar among closely related species (phylogenetic signal), many researchers have advocated for a "phylogenetic gambit": maximizing phylogenetic diversity (PD) should indirectly capture FD. To our knowledge, this gambit has not been subject to a focused empirical test. Here we use data from >15,000 vertebrate species to empirically test it. We delineate >10,000 species pools and test whether prioritizing the most phylogenetically diverse set of species results in more or less FD relative to a random choice. We find that, across species pools, maximizing PD results in an average gain of 18% of FD relative to a random choice, suggesting that PD is a sound conservation prioritization strategy. However, this averaged gain hides important variability: for 10% of the species pools, maximizing PD can capture less FD than an averaged random scheme because of recent trait divergence and/or very strong trait conservatism. In addition, within a species pool, many random sets of species actually yield more FD than the PD-maximized selection – on average 36% of the time per pool. If the traits we used are representative of traits we wish to conserve, our results suggest that conservation initiatives focusing on PD will, on average, capture more FD than a random strategy, but this gain will not systematically yield more FD than random and thus can be considered risky.

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 a huge moral challenge [4–8]. And, to 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 forms and functions [6–12] . The biological diversity of forms and functions 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, PD 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]. While it may seem obvious that sampling species across the tree of life will capture high amounts of FD, a recent theoretical study demonstrated that PD could be a poor surrogate for FD and, in some scenarios, prioritizing species on the basis of PD could actually lead to capture *less* FD than if species were simply selected at random [16].

We clarify what our goals are in testing the utility of PD to capture FD. First, we take as given that maximizing PD is not the overarching goal *per se* of PD-maximization schemes, but rather that a PD maximization strategy is valued for its ability to capture more FD compared to a strategy that ignores phylogeny. Second, asking whether PD maximization captures more FD than a random choice is fundamentally distinct (and a lower bar) from asking whether maximizing PD also *maximizes* FD [e.g. 15,19–21,23,24]. Finally, it is important to note that we are selecting *species* sets to maximize PD or FD within a region. While this is a simplification, as conservation actions often aim to select sets of *areas* (e.g. in reserve design), the only global phylogenetically-informed conservation initiative is species-centered (EDGE; Isaac et al. 2007). More fundamentally, the framework we use here allows us to directly test the fundamental phylogenetic gambit at the heart of all PD-based conservation [16]. Critically, the question we raise has been shown to be distinct from asking whether traits have phylogenetic signal (whether closely related species tend to share similar sets of traits), since PD can be a poor surrogate for FD *even if* traits exhibit phylogenetic signal [16].

This points to the need for empirical tests of whether —within a given species pool— sets of species selected to maximize PD actually contain more FD than sets of species selected without regard to evolutionary relatedness. We evaluate the PD~FD relationship for different species pools (taxonomic families and geographical assemblages, *i.e.*, sets of species co-occurring at a given scale) using a large global dataset including trait, phylogenetic, and geographic range data for 4,616 species of mammals, 9,993 species of birds, and 1,5036 species of tropical fish. Specifically, we measure FD as functional richness (see methods) and compute, for any given species pool, an estimate of surrogacy (S_{PD_FD}, [26,27], Figure 1). S_{PD_FD} represents the amount of FD sampled by the set of species chosen to maximize PD, relative to the FD sampled by optimal set of species selected to maximize FD directly, with both components controlled for the expected FD from a random species set of the same size. S_{PD_FD} will be positive if the averaged PD-maximized set contains more FD than the averaged random set, and negative if not. S_{PD_FD} will equal 100% if the PD-maximization strategy is optimal (*i.e.* to maximize FD). We integrate S_{PD_FD} for each species pool across all deciles of species richness (Eqn. 1) but because they are many sets of species that can maximize PD or than can be chosen at random, we computed S_{PD_FD} based on the averaged FD over 1000 PD-maximized sets and 1000 random sets [16].

We find that selecting the most phylogenetically diverse sets of species within a given taxonomic family or within a given geographical location (large grid-cells across the globe) captures, on average, 18% more FD than that of randomly chosen species (i.e. S_{PD_FD} = 18%, SD +/- 6.5% across pools, see Figure 1). Although the surrogacy is generally positive, there was 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).

We next explored the drivers of surrogacies values across species pools. Surrogacy of PD appears to weaken as the species pool richness increases (on average, Spearman Rho between absolute surrogacies and species richness = -.15), most clearly seen in the tropics and in species-rich families such as the Muridae (rats mice and allies) and Columbidae (pigeons and allies) (Fig. 2-3). This is likely because our measure of FD (see Methods) rapidly saturates as the number of selected species increases and species from these large pools harbor high functional redundancy, such that a random prioritization scheme performs relatively well, or at least no worse than other strategies (Fig. S4). In contrast, FD can be greatly increased by prioritization of species using PD from species poor assemblages or clades [see also 28]. This is particularly the case in spatial assemblages containing multiple taxonomic orders, which are both phylogenetically and ecologically divergent from one another. Interestingly, the PD-FD relationship was not consistent across *taxonomic* scale: we found that, in contrast to patterns at the family level, for certain mammalian and avian orders (which are older than the families described above), using PD to select species is much worse for capturing FD than choosing species at random (see, for example, the Afrosoricidae, Chiroptera, and Charadriiformes in Fig. S5).

We explored whether it is possible to explain this variability within- and between-datasets, and in particular, why for some assemblages/clades, a PD-prioritization strategy fails to capture more FD than random choice. It is often implicitly assumed that phylogenetic signal (i.e. the degree to which closely related species tend to harbor similar sets of traits) can be used to evaluate the effectiveness of PD as a surrogate for FD [5,15–17]. Surprisingly perhaps, the 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.

For example, if the motivation for protecting FD is to maintain community-driven ecosystem functions and services [5,6,30], the value of a regional or global scale focus may be questionable [31]. This worry has motivated studies that focus on local scales [6]. This is an important area for further research; the patterns linking PD and FD in the regional pool may still be important, since this is the species pool from which local sites are assembled and maintained.

The motivator of our test of the surrogacy value of PD for FD is the fact that ecologically-relevant trait data is in short supply, especially for rare and data-deficient species. Indeed, if it were not for this relative paucity of data, we could simply prioritize species based on their unique contribution to FD directly [e.g. 36]. Although there have been massive and well-funded efforts to collect and curate trait data from across the Tree of Life [33–35], we are still far from having comprehensive coverage. Furthermore, despite recent progress [e.g. 34,35], it is still not fully understood which traits are most relevant for responses to environmental change, or that contribute most to certain ecosystem functions and services, and how these vary among systems. Our analysis suffers from a similar data limitation. We chose these traits because they are frequently collected in ecological studies, not because we know they are ecologically important. Our assumption is that their phylogenetic distribution is typical of those traits that are most desirable for the purpose of conservation and that our primary results are therefore widely applicable. We urge others to expand our simple test to other clades and traits in order to test the generality of our findings.

Conclusion

Prioritizing the most phylogenetically diverse set of taxa in a region or clade will result in an average gain of 18% functional diversity relative to applying the same conservation effort without considering phylogeny, but this gain will decrease as species richness increases. This suggests that PD is a reasonable conservation prioritization strategy, especially in species-poor clades or regions, or in the absence of meaningful data on functional traits. However, we note two important drawbacks of this strategy. First, in cases of either recent trait divergence or, alternatively, very strong trait conservatism, a PD prioritization scheme can capture less FD than a random scheme. Second, we found that while this strategy, on average, captures FD well, it is also somewhat unreliable, and 36% of the time will not capture more FD than random choice. Critically, and in opposition to what has previously been implicitly assumed [15,16], we find weak empirical evidence that the presence of phylogenetic signal in traits predicts whether PD-based conservation will prioritize FD. Assuming that the traits we have used are representative of a broader array of ecologically relevant traits, our results provide a baseline for how well we should expect PD-based prioritization to perform when ecologically important traits are unknown, unmeasured, or unmeasurable. By clearly outlining the cases and parts of the world in which phylogenetically-based conservation prioritization can (and cannot) effectively act as a surrogate for functional diversity, we hope to inform and improve conservation interventions globally.

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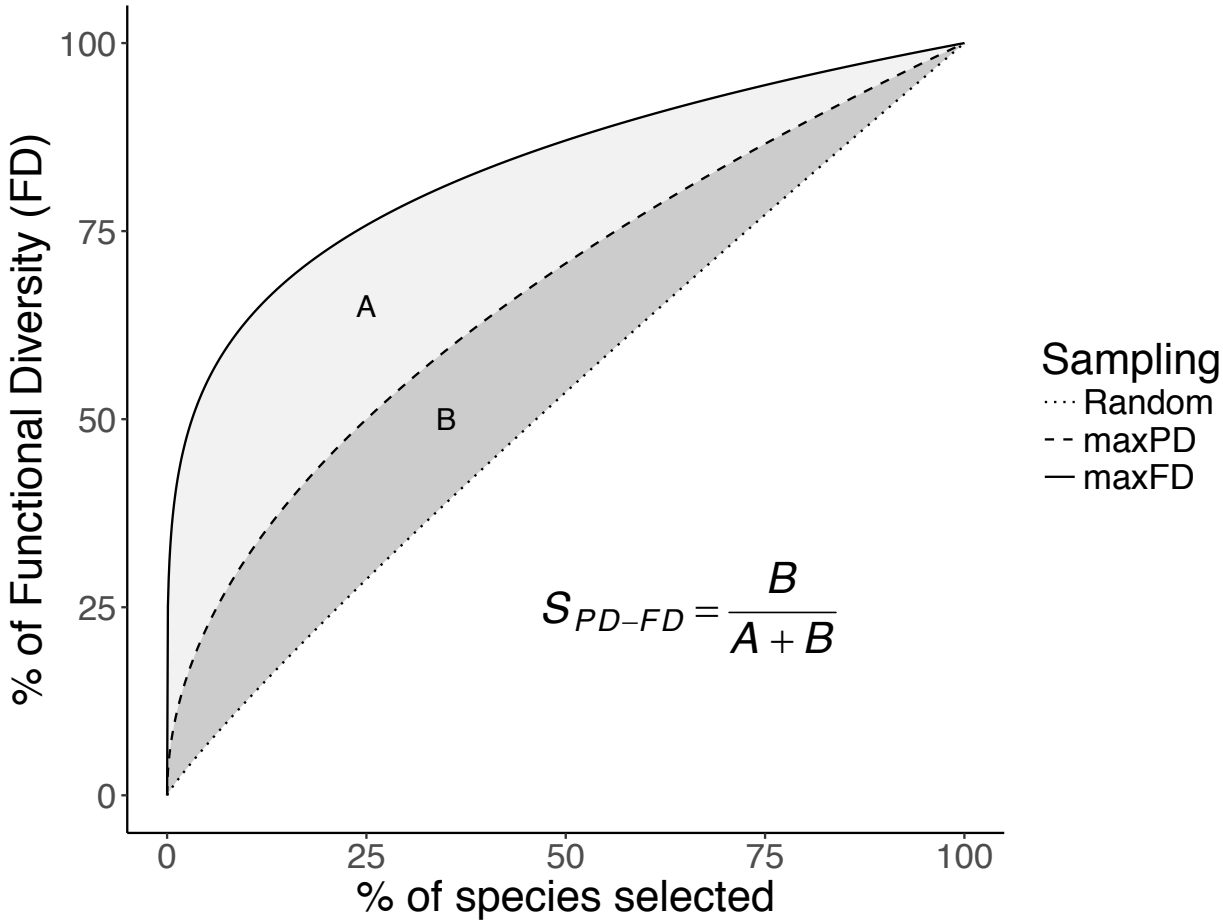

Figure 1 – A conceptual approach for evaluating if PD a good surrogate for FD. To evaluate if PD is a good surrogate of FD, we measure to what extent a species prioritization strategy that maximize PD captures FD relative to an optimal and a random strategy. To do so, we compare FD accumulation curves (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 ($SD_{PD\text{-}FD}$) 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 $SD_{PD\text{-}FD}$ is positive, PD is a good surrogate for FD (the maximum value being 1 where PD is an optimal surrogate) while when $SD_{PD\text{-}FD}$ is negative preserving species based on PD is worse than preserving them at random.

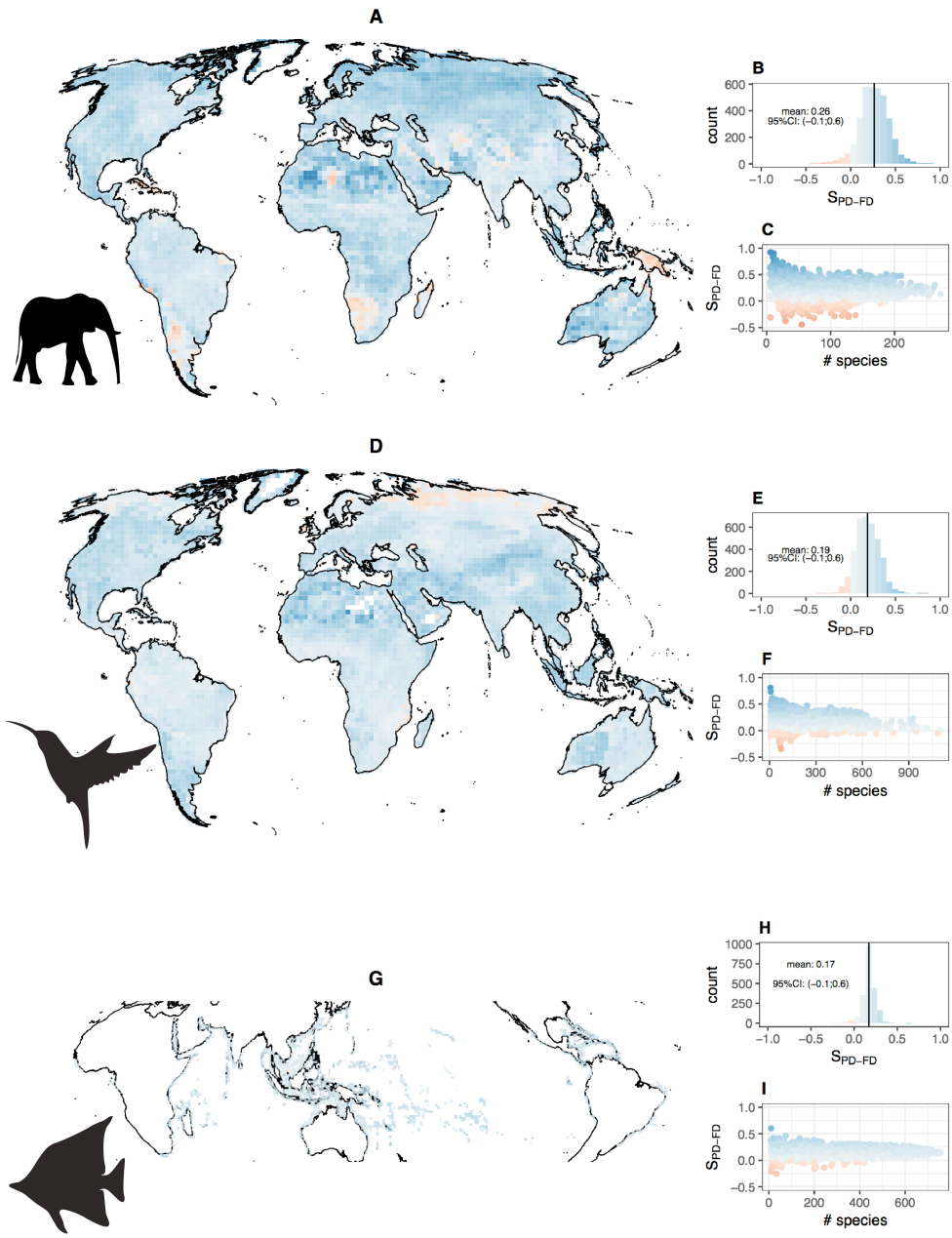

Figure 2 – PD is a good surrogate of FD across space. The figure presents the distribution and correlates of S_{PD-FD} for mammals (panels A-C), birds (panels D-F) and tropical fishes (G-I) separately across space. For each of the three groups, the SD_{PD-FD} frequency distribution is presented in top 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).

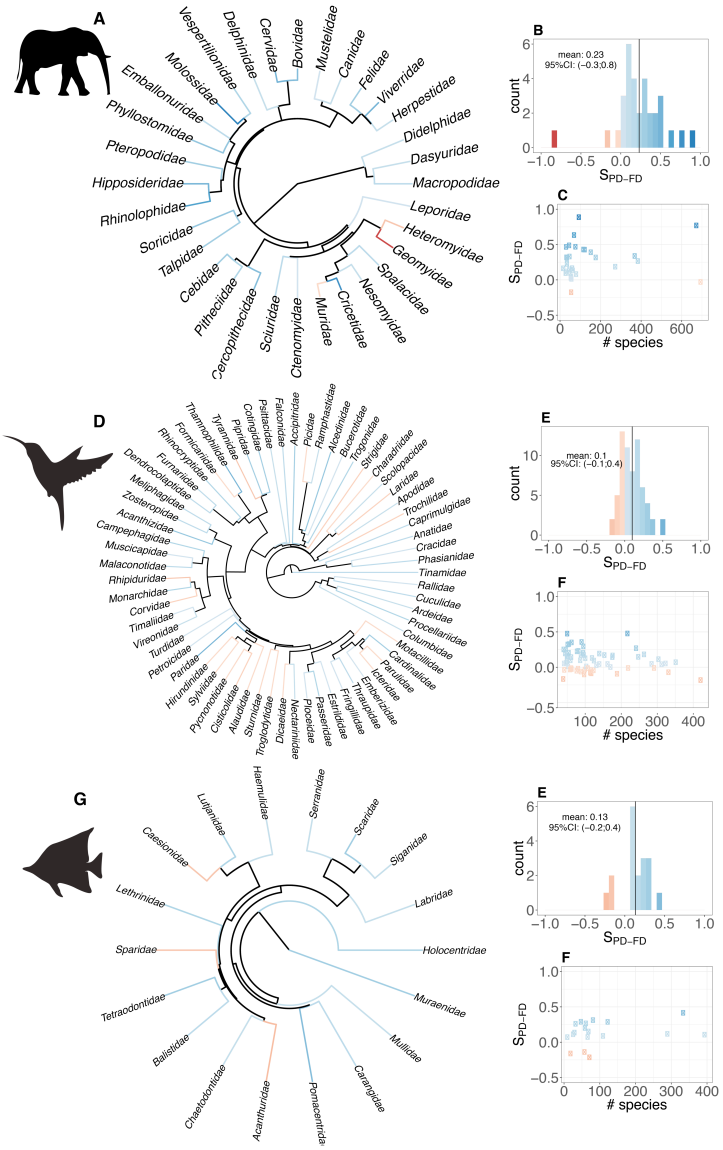

Figure 3 – PD is a good surrogate of FD across clades. The figure presents the distribution and correlates of SD_{PD-FD} for mammals (panels A-C) and birds (panels D-F) across families. For each of the two groups, the SD_{PD-FD} frequency distribution is presented (B and E) along with its mean (vertical 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).

282 **Methods**

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

290 **1. Data**

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

293 **Distribution data –** For mammals, we used the distribution maps provided by the Mammal
294 Red List Assessment (http://www.iucnredlist.org/) for 4,616 species. For birds, full (breeding
295 and wintering) and breeding ranges distribution maps were extracted from BirdLife
296 (http://www.birdlife.org/) for 9,993 species. The best resolution at which these maps should
297 be used is still under discussion in the literature, so we decided to use the 40 000km^2
298 resolution (200x200km gird cell at the equator) that is commonly used at global scale
299 [38,39]. The total number of grid cells was 3,646. Domestic and aquatic mammals were
300 excluded from the analysis. In order to make sure our results were not driven by the
301 important trait difference between volant and non volant mammals, we repeated our results
302 excluding bats. For birds we repeated our analysis using the full ranges (*i.e.*, summer and
303 winter ranges). Finally, we evaluated the robustness of our result to the spatial resolution
304 considered by repeating our analysis at a resolution of 100x100km (number of grid cells was
305 13,330) for birds and mammals; we present these results in the supplementary materials, as
306 they are qualitatively identical to those conducted at 200x200km (fig. S1). For fishes, we
307 used a database of 1536 species, for which we had distribution data, phylogenetic and
308 functional data. Distribution data were extracted from a global-scale distribution database

309 [40]. Species composition was then extracted from grid cells of 5°x5°, corresponding to
310 approximately 555x555 km at the equator [41]. This grain size of the grid was chosen
311 because it represents a good compromise between the desired resolution and the
312 geographical density of information.
313
314 **Phylogenies –** In order to prioritize species to maximize PD, phylogenies of each species pool
315 are needed. We used the first 100 published calibrated ultrametric trees of Jetz et al.[42] for
316 birds and Faurby and Svenning [43] for mammals. By repeating our analyses across a posterior
317 distribution of phylogenetic hypotheses, we control and account for phylogenetic uncertainty.
318 For tropical reef fishes, we built a phylogeny for 18 families (i.e. Labridae, Scaridae,
319 Pomacentridae, Chaetodontidae, Acanthuridae, Haemulidae, Balistidae, Carangidae,
320 Serranidae, Lutjanidae, Sparidae, Caesionidae, Holocentridae, Mullidae, Muraenidae,
321 Tetraodontidae, Lethrinidae and Siganidae) by pruning a dated molecular phylogenetic tree for
322 7,822 extant fish species [44]. These families were selected as the most representative tropical
323 reef fish families, that is, they are abundant and speciose on tropical reefs. We grafted missing
324 species on the pruned phylogenetic tree (circa 50% among the 1536 studied species) based on
325 published phylogenies for these families, supplemented by taxonomic information from fish
326 identification guides and FishBase (www.fishbase.org) [44,45]. We recorded, for each of these
327 trees, a measure of imbalance (as measured by β [46]) and 'tipiness' (as measured by Gamma
328 [47]). For both mammals and birds, we chose to group species in families and orders. We used
329 these groupings when calculating the purely phylogenetic, clade-based analyses (to address
330 question 1), but not within the spatial, assemblage-based analyses (question 2). For the
331 taxonomic analysis of mammal families we removed two families (Dipodidae and Echimyidae)
332 because of their very poor phylogenetic resolution (i.e. polytomies for an important number of
333 species).
334
335 **Traits –** For birds and mammals, four traits (diet, (log transformed) body mass, activity cycle,
336 and foraging height) were extracted from Elton Traits1.0 [35]. These traits are generally
337 assumed to appropriately represent Eltonian niche dimensions within an assemblage or clade

338 of mammals or birds [35,48,49]. For fishes, we used a previously published database [12]. We
339 used 6 categorical traits: size, mobility, period of activity, schooling, vertical position in the
340 water column, and diet (for a full description of the dataset, see Mouillot et al. [12]). These
341 traits have already been used to investigate community assembly rules [50] and to seek
342 vulnerable fish functions [11]. For each clade and assemblage, we used the raw trait (only body
343 mass was log-transformed and rescaled by the clade/assemblage range of body masses) values
344 to compute distance between species using Gower distance [19] and use PCoA to summarize
345 the trait space in few dimensions. We retained the numbers of PCoA axes necessary to
346 represent 70% of the total initial variability (using a 80% threshold did not quantitatively change
347 our conclusions, see Fig. S9). We also recorded phylogenetic signal for each PCoA axis using
348 Blomberg's K [51].
349

350 **2. Approach**

351 Our aim was to evaluate, across a wide range of clades and regions, the ability of PD-informed
352 prioritization scheme to capture FD in comparison with two other prioritization schemes:
353 selecting species to directly maximize FD ('maxFD' hereafter) and selecting species randomly
354 (Figure 1). Our premise was that we often do not know or have not measured the traits that are
355 most relevant for ecosystem function and services such that maximizing FD is not generally
356 feasible. By focusing on a subset of traits and assuming that they are representative of
357 ecologically relevant traits, we were able to get an estimate of how well PD does compared to
358 the best we could possibly do. We used performance relative to choosing on the basis of FD as
359 an upper-limit to the performance of PD as a surrogate for FD, and used random species
360 selection as a lower benchmark.

361 **Random prioritization scheme –** For each pool (i.e. each clade and each geographical
362 assemblage) and each number of selected species (10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%
363 of the total pool), 1000 random sets of species were produced, from which the average FD was
364 recorded.

Prioritization scheme maximizing PD (maxPD) – While there are many, overlapping metrics for measuring the evolutionary history encompassed by a set of species [52,53], the most common is the sum of all branch lengths (often in units of time) connecting a set of species to a common root[14], called Phylogenetic Diversity (PD). This is the metric whose maximization has most commonly been proposed as a conservation prioritization metric [14,54,55], and as a measure of phylogenetic 'richness' it most naturally maps onto our chosen FD metric [52]. We used the greedy algorithm proposed by Bordewich et al. [56] to find our maxPD set of species *S*. For a given tree there are likely multiple, and possibly very many, sets of species with the same PD as *S*. As a consequence, we produced, for each pool, each number of selected species, and each alternative phylogenetic trees, 10 maxPD sets of species. We then averaged the FD of these sets across our 100 phylogenetic tree, so that each value is an average of 1000 sets (10 sets for each of the 100 trees).

Prioritization scheme maximizing FD (maxFD) – Functional diversity was estimated using a functional richness index (FRic; [57–59]). The FRic index relies on a multidimensional Euclidean space, where the axes are traits (or factorial axes from a principal coordinates analysis (PCoA) computed using these traits) along which species are placed according to their trait values. This index measures the volume of trait space occupied by a given species assemblage by calculating the convex hull volume [59], defined by the species at the vertices of the functional space, that encompasses the entire trait space filled by all species in this assemblage. In a single dimension, this simply equals the range of values [59]. This broadly used metric in ecology is set monotonic with species richness, a property generally assumed desirable in conservation whereby the addition of a new species can never decrease the metric's value [60]. FD measures the total amount of variation in trait values, making it conceptually comparable to PD [52]. We used the FRic index instead of the FD index based on a functional dendrogram (Petchey & Gaston, 2006) since recent studies showed that the FD index may lead to biased assessments of functional diversity and inaccurate ecological conclusions [61]. The most straightforward way to obtain the maximal FD for *n* species is to compute FD for all possible combinations of *n* species and simply record the greatest value (the brute force approach). However, this is not feasible in

practice as the numbers of combinations of selected species was too high (e.g., 10^{71} possible sets for all mammal assemblages). To rapidly and efficiently find the set of species that aim to maximize FD, we developed a novel (at least in ecology) greedy algorithm. In brief, our approach iteratively (starting with two species) select the species that is the furthest from the centroid of the already selected set. To avoid selecting two species that are far from the centroid but close to each other, we penalized the distance to the centroid by the distance to the closest neighbour in the already selected set. Here we present in details the greedy algorithm we used to find the set of species that maximize FD:

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

Step 2. Compute the centroid of these two selected species

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

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

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

with K and L being penalizing factors and minD the distance between a given candidate species and the nearest species already in the selected set.

Step 5. Select the species that maximized the penalized distance

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

To avoid arbitrarily setting the penalizing parameters, we tested 1000 pairs of parameters drawn from a truncated normal distribution (mean=1, sd=.5) and retained the parameter pairs that yielded the maximal FD.

In tests of subsets of the data for which finding the true maxFD was feasible, we found our approach to adequately approximate the true maxFD and to produce a very good approximation of the true degree of PD's surrogacy for FD (fig. S10).

423 **Measuring performance and surrogacy of prioritization schemes.**
424 We use a common approach [26,27] to quantify the extent to which a given surrogate (here,
425 the maxPD choice) reaches a certain objective (here, maximize FD). Species from a given pool
426 (i.e., for each dataset (clade and assemblages) independently,) were prioritized and selected
427 according to (1) the objective, i.e. maximize FD, producing the 'optimal curve' (maxFD curve in
428 Figure 1), (2) the surrogate i.e. maximize PD, producing the 'surrogate curve' (maxPD curve in
429 Figure 1) and (3) at random (random curve in Figure 1), i.e. producing the 'random curve'
430 (Figure 1). To compute a 'surrogacy' estimate of PD ($S_{PD\text{-}FD}$), we compare the position of the
431 surrogate curve (1) to the random curve (2) relative to the optimal curve (2) (Figure 1 and Eq. 1)
432 across the deciles of species richness of the pool (given as an interval 0-1):

433 $$S_{PD\text{-}FD} = \int_0^1 \frac{FD_{maxPD}\text{-}FD_{random}}{FD_{maxPF}\text{-}FD_{random}} \qquad \text{(Equation 1)}$$

434

435 This surrogacy metric is at 100% when the surrogate perfectly meets the objective (i.e., the
436 maxFD and maxPD curves are identical and the max PD set is the maxFD set), 0% when the
437 surrogate is not better than randomly chosen sets of species (i.e., the random and maxPD
438 curves are identical) and is negative if the surrogate choice is worse than random (i.e., the
439 maxPD curve is below the random curve). Correlates of $S_{PD\text{-}FD}$ were evaluated using Spearman
440 correlations.
441 Apart from focusing on average tendencies, we quantified the variability of the FD yielded by
442 the PD—maximized selection strategy and the random selection strategy within each species
443 pools. To do so, we compute, for each species pool and for each % of selected species
444 independently, the number of cases where $FD_{random}>FD_{maxPD}$ across the 1000 random *1000
445 maxPD sets combinations (i.e. 10^6 comparisons). We then averaged theses number across % of
446 selected species and report statistics across datasets (Supp. Table 1).

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