Title. Testing the phylogenetic gambit: how much functional diversity can we reliably conserve if we prioritize phylogenetic diversity?

Author list

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Code accessibility statement: R functions developed in this paper are available at https://github.com/FloMazel/FD_PD_Max

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Abstract

In the face of the biodiversity crisis, it is argued that we should prioritize species in order to capture high functional diversity (FD). Because species traits often reflect shared evolutionary history, many researchers have advocated for a “phylogenetic gambit”: maximizing phylogenetic diversity (PD) should indirectly capture FD. For the first time, we empirically test this gambit using data from >15,000 vertebrate species and ecologically-relevant traits. Maximizing PD results in an average gain of 18% of FD relative to random choice. However, this average gain hides the fact that in over 1/3 of the comparisons, maximum PD sets contain less FD than randomly chosen sets of species. These results suggest that, while maximizing PD 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*

randomly choosing species. No one would dispute that the best way to maximize FD is to prioritize FD, but phylogenetic diversity has emerged as prioritization tool because we rarely have sufficient trait data to calculate FD. Here we test whether PD-based conservation passes a much less stringent, but ultimately more fundamental, test: is conserving on the basis of PD better than conserving at random? Worryingly, a recent theoretical study has indeed 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].

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 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, 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[18] (EDGE). 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].

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 1,536 species of tropical fish. Specifically, we measure FD as functional richness (see methods) and compute, for any given species pool, an estimate of surrogacy[27,28] (S_{PD_FD}, 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 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].

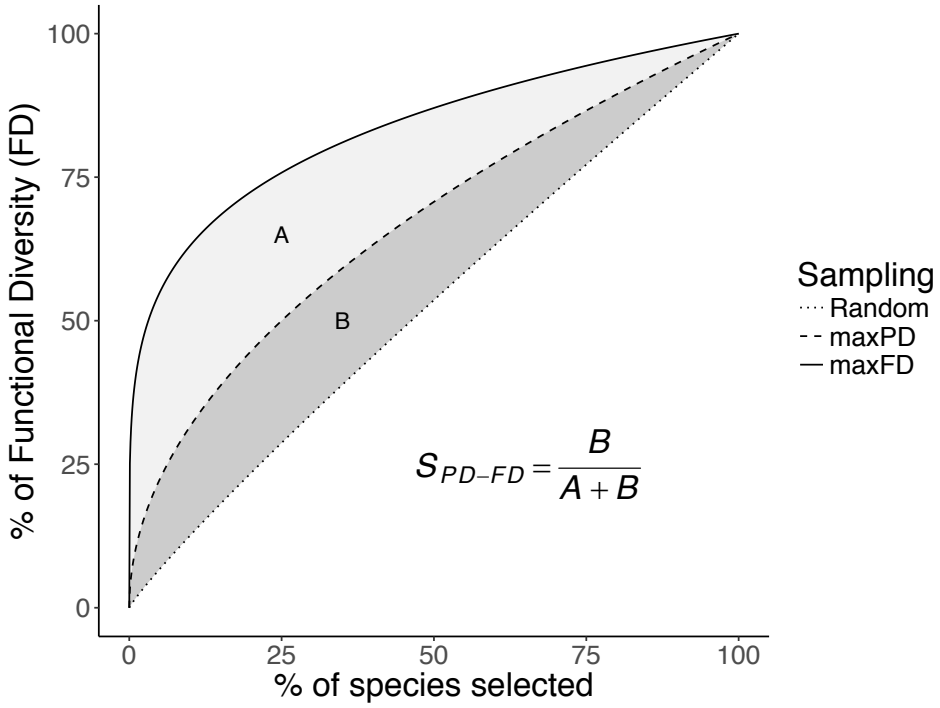

Figure 1 – A conceptual approach for evaluating whether PD is a good surrogate for FD. To evaluate if PD is a good surrogate of FD, we measure to what extent a species prioritization strategy that maximize PD captures FD relative to an optimal and a random strategy. To do so, we compare FD accumulation 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.

138

139 **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.

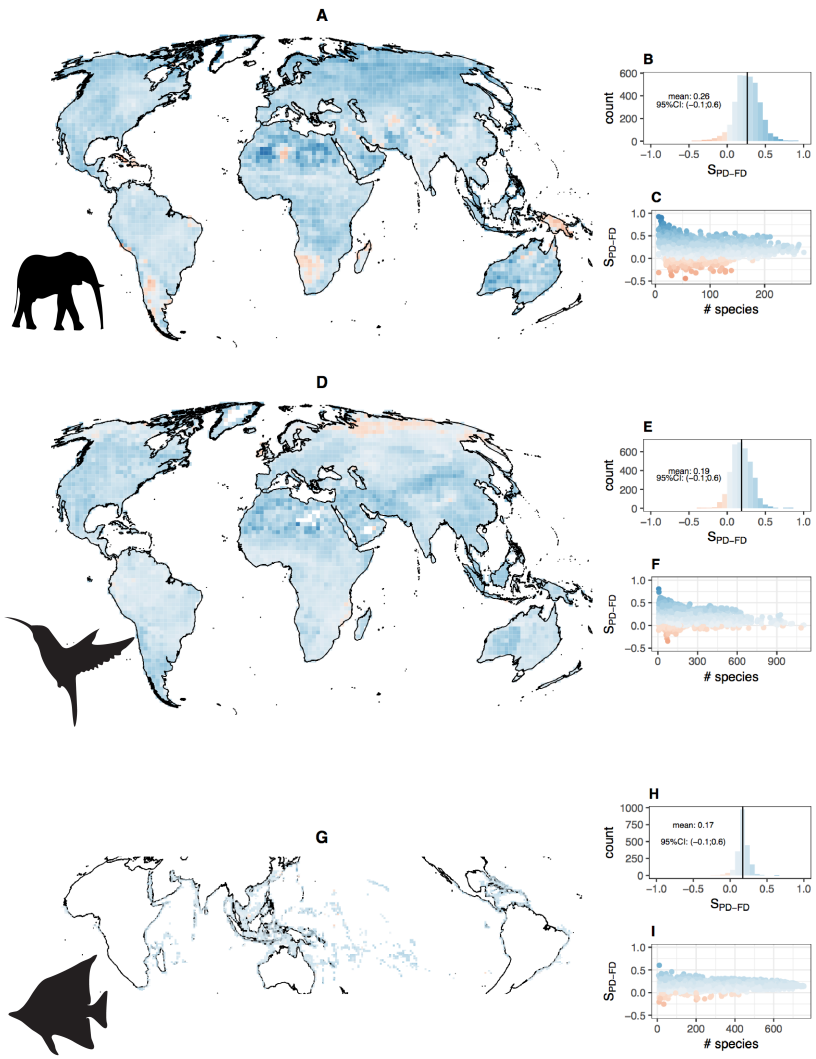

Figure 2 – PD is a good surrogate for FD across space. The figure presents the distribution and correlates of S_{PD-FD} for mammals (panels A-C), birds (panels D-F) and tropical fishes (G-I) separately across space. For each of the three groups, the SD_{PD-FD} frequency distribution is presented in top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

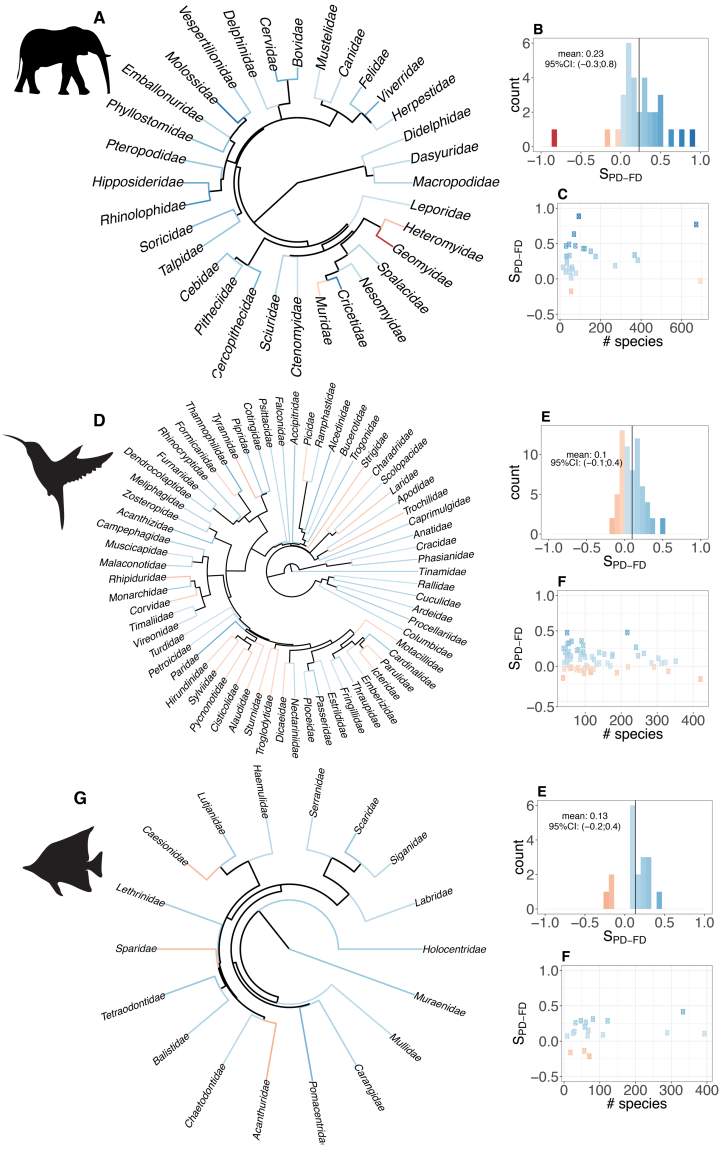

Figure 3 – PD is a good surrogate for FD across clades. The figure presents the distribution and correlates of SD_{PD-FD} for mammals (panels A-C) and birds (panels D-F) across families. For each of the two groups, the SD_{PD-FD} frequency distribution is presented (B and E) along with its mean (vertical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

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.

231 **Discussion**

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

also show that it remains something of a gambit: PD is good 'on average', but there is still some risk associated with taking it.

We found that 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. 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. Our result 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 three important caveats to the use of this strategy. First, 18% extra FD may not always be a useful conservation target. It is currently unknown whether this added 18% of FD can actually be of enough conservation value. Second, 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. Evolutionary biologists commonly focus on 'unusual' clades with rapid divergences (e.g., cichlids); we show here that divergence does not have to be that spectacular (e.g., African carnivores) to alter the PD-FD relationship. Third, 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. This means that while the PD gambit can be a bet worth taking, it is still a bet with associated risk, not a sure thing.

Our objective in this paper is to test the phylogenetic gambit using empirical datasets. This means that we do not aim to provide a coherent prioritization strategy[35], or ready-to use conservation guidelines. Indeed, we simplistically and implicitly assume that chosen species will either be saved or go extinct, and we have not linked our various scenarios to any particular policy position or conservation objective other than maximizing FD within a phylogenetic clade or region[28,31]. In reality, conservation decisions reflect the interplay of social, economic, political, and scientific priorities, and do not necessarily result in the saving of target species (and therefore of their associated FD or PD). While our study is thus not directly applicable, the

test we are conducting is actually critical to validate (or invalidate) the use of PD in conservation as a whole. While it is not clear whether our results would generalize to other taxa (although we hope that others will extend our work and test the phylogenetic gambit in other systems), we do feel it is important to consider the uncertainty that has been introduced into our analysis as a result of uncertainty associated with the spatial scale of our analysis, our phylogenetic data, and our choice of trait and measurement of FD.

The scale of conservation activities can vary, from the global scale of the hotspots approach to local protected areas within a single country, but, 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 [6,36,37], the value of a regional or global focus may be questionable[38], and studies are increasingly focusing on local scales[6]. Ecologists are refining and improving our understanding of how local assemblages assemble within a regional context[39], and while the concept of the 'regional pool' of species is increasingly being viewed as a simplification, it is unlikely that regional- and local-scale patterns are totally disconnected. We emphasize that our results are relatively robust to variation in spatial scale (see Fig. S3), but we acknowledge that future studies should test the phylogenetic gambit at more local scale as well.

The set of species that maximize PD obviously rely on the phylogenetic hypothesis used. No hypothesis is perfect or without uncertainty, and these phylogenetic uncertainties could in turn impact the composition of the set of species that maximize PD and hence the surrogacy values we compute. In this study, we explicitly took into account these uncertainties by using 100 different trees[40,41]. The explicit propagation of this phylogenetic uncertainty through into our results may underlie some of the uncertainty ('risk') of our result, and we suggest it is important that future studies explicitly take into account phylogenetic uncertainty when testing the phylogenetic gambit.

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

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.
337
338

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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

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

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

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; Villé*ger 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

space filled by all species in this assemblage. In a single dimension, this simply equals the range of values [62]. 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 [63]. FD measures the total amount of variation in trait values, making it conceptually comparable to PD [57]. 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 [64]. 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 distances by adding the following factor f (Eq. 1)

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

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. S2).

Measuring performance and surrogacy of prioritization schemes.

We use a common approach[27,28] to quantify the extent to which a given surrogate (here, the maxPD choice) reaches a certain objective (here, maximize FD). Species from a given pool (i.e., for each dataset (clade and assemblages) independently,) were prioritized and selected according to (1) the objective, i.e. maximize FD, producing the 'optimal curve' (maxFD curve in Figure 1), (2) the surrogate i.e. maximize PD, producing the 'surrogate curve' (maxPD curve in Figure 1) and (3) at random (random curve in Figure 1), i.e. producing the 'random curve' (Figure 1). To compute a 'surrogacy' estimate of PD ($S_{PD\text{-}FD}$), we compare the position of the surrogate curve (1) to the random curve (2) relative to the optimal curve (2) (Figure 1 and Eq. 2) across the deciles of species richness of the pool (given as an interval 0-1):

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

This surrogacy metric is at 100% when the surrogate perfectly meets the objective (i.e., the maxFD and maxPD curves are identical and the max PD set is the maxFD set), 0% when the surrogate is not better than randomly chosen sets of species (i.e., the random and maxPD curves are identical) and is negative if the surrogate choice is worse than random (i.e., the maxPD curve is below the random curve). Correlates of $S_{PD\text{-}FD}$ were evaluated using Spearman correlations.

Apart from focusing on average tendencies, we quantified the variability of the FD yielded by the PD—maximized selection strategy and the random selection strategy within each species pools. To do so, we compute, for each species pool and for each % of selected species

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).

509 **References**

510 1. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution,
511 and protection. *Science (80-.).* **344,** (2014).
512 2. Hull, P. M., Darroch, S. A. F. & Erwin, D. H. Rarity in mass extinctions and the future of
513 ecosystems. *Nature* **528,** 345–51 (2015).
514 3. Ceballos, G., Ehrlich, P. R. & Dirzo, R. Biological annihilation via the ongoing sixth mass
515 extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.*
516 *S. A.* **114,** E6089–E6096 (2017).
517 4. Tilman, D., Wedin, D. & Knops, J. Productivity and Sustainability Influenced by
518 Biodiversity in Grassland Ecosystems. *Nature* **379,** 718–720 (1996).
519 5. Srivastava, D. S. D., Cadotte, M. M. W., MacDonald, A. A. M., Marushia, R. G. &
520 Mirotchnick, N. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15,**
521 637–48 (2012).
522 6. Cadotte, M. W., Carscadden, K. & Mirotchnick, N. Beyond species: functional diversity
523 and the maintenance of ecological processes and services. *J. Appl. Ecol.* **48,** 1079–1087
524 (2011).
525 7. Isbell, F. *et al.* Linking the influence and dependence of people on biodiversity across
526 scales. *Nature* **546,** 65–72 (2017).
527 8. Pascual, U. *et al.* Valuing nature's contributions to people: the IPBES approach. *Curr.*
528 *Opin. Environ. Sustain.* **26–27,** 7–16 (2017).
529 9. Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. What to protect?—Systematics and
530 the agony of choice. *Biol. Conserv.* **55,** 235–254 (1991).
531 10. Bottrill, M. C. *et al.* Is conservation triage just smart decision making? *Trends in Ecology &*
532 *Evolution* **23,** 649–654 (2008).
533 11. Mouillot, D. *et al.* Rare species support vulnerable functions in high-diversity ecosystems.
534 *PLOS Biol.* **11,** (2013).
535 12. Mouillot, D. *et al.* Functional over-redundancy and high functional vulnerability in global
536 fish faunas on tropical reefs. *Proc. Natl. Acad. Sci.* **111,** 13757–13762 (2014).
537 13. Cadotte, M. W., Davies, J. T. & Peres-Neto, P. R. Why phylogenies do not always predict

538 ecological differences. *Ecol. Monogr.* (2017). doi:10.1002/ecm.1267
539 14. Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61,** 1–10
540 (1992).
541 15. Winter, M., Devictor, V. & Schweiger, O. Phylogenetic diversity and nature conservation:
542 where are we? *Trends Ecol. Evol.* (2013).
543 16. Mazel, F., Mooers, A. O. A. O., Riva, G. V. D. G. V. D. & Pennell, M. W. M. W. Conserving
544 Phylogenetic Diversity Can Be a Poor Strategy for Conserving Functional Diversity. *Syst.*
545 *Biol.* (2017). doi:10.1093/sysbio/syx054
546 17. Kelly, S., Grenyer, R. & Scotland, R. W. Phylogenetic trees do not reliably predict feature
547 diversity. *Divers. Distrib.* **20,** 600–612 (2014).
548 18. Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the
549 EDGE: conservation priorities based on threat and phylogeny. *PLoS One* **2,** e296 (2007).
550 19. Barak, R. S. *et al.* Taking the Long View: Integrating Recorded, Archeological,
551 Paleoecological, and Evolutionary Data into Ecological Restoration. *Int. J. Plant Sci.* **177,**
552 90–102 (2016).
553 20. Pollock, L. J., Thuiller, W. & Jetz, W. Large conservation gains possible for global
554 biodiversity facets. *Nature* **546,** 141–144 (2017).
555 21. Brum, F. T. *et al.* Global priorities for conservation across multiple dimensions of
556 mammalian diversity. *Proc. Natl. Acad. Sci. U. S. A.* 201706461 (2017).
557 doi:10.1073/pnas.1706461114
558 22. Mazel *et al.* Multifaceted diversity–area relationships reveal global hotspots of
559 mammalian species, trait and lineage diversity. *Glob. Ecol. Biogeogr.* **23,** 836–847 (2014).
560 23. Thuiller, W. *et al.* Conserving the functional and phylogenetic trees of life of European
561 tetrapods. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **370,** 20140005 (2015).
562 24. Mason, N. W. H. & Pavoine, S. Does trait conservatism guarantee that indicators of
563 phylogenetic community structure will reveal niche-based assembly processes along
564 stress gradients? *J. Veg. Sci.* **24,** 820–833 (2013).
565 25. Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V. & Prinzing, A. Phylogenetic patterns are
566 not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.* **29,**

567 600–614 (2015).
568 26. Devictor, V. *et al.* Spatial mismatch and congruence between taxonomic, phylogenetic
569 and functional diversity: the need for integrative conservation strategies in a changing
570 world. *Ecol. Lett.* **13,** 1030–1040 (2010).
571 27. Ferrier, S. & Watson, G. An evaluation of the effectiveness of environmental surrogates
572 and modelling techniques in predicting the distribution of biological diversity. *Armidale*
573 *NSW Environ. Aust.* (1997).
574 28. Rodrigues, A. S. L. & Brooks, T. M. Shortcuts for Biodiversity Conservation Planning: The
575 Effectiveness of Surrogates. *Annu. Rev. Ecol. Evol. Syst.* **38,** 713–737 (2007).
576 29. Mazel, F. *et al.* The Geography of Ecological Niche Evolution in Mammals. *Curr. Biol.* **27,**
577 1369–1374 (2017).
578 30. Thuiller, W. *et al.* Conserving the functional and phylogenetic trees of life of European
579 tetrapods. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **370,** 20140005 (2015).
580 31. Carvalho, S. B. *et al.* Spatial conservation prioritization of biodiversity spanning the
581 evolutionary continuum. *Nat. Ecol. Evol.* **1,** 151 (2017).
582 32. Jetz, W. *et al.* Global distribution and conservation of evolutionary distinctness in birds.
583 *Curr. Biol.* **24,** 919–30 (2014).
584 33. Thévenin, C., Mouchet, M., Robert, A., Kerbiriou, C. & Sarrazin, F. Reintroductions of
585 birds and mammals involve evolutionarily distinct species at the regional scale. *Proc.*
586 *Natl. Acad. Sci. U. S. A.* **115,** 3404–3409 (2018).
587 34. Forest, F. *et al.* Preserving the evolutionary potential of floras in biodiversity hotspots.
588 *Nature* **445,** 757–760 (2007).
589 35. Brooks, T. M. *et al.* Global biodiversity conservation priorities. *Science* **313,** 58–61 (2006).
590 36. Srivastava, D. D. S., Cadotte, M. M. W., MacDonald, A. A. M., Marushia, R. G. &
591 Mirotchnick, N. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15,**
592 637–48 (2012).
593 37. Díaz, S. *et al.* Incorporating plant functional diversity effects in ecosystem service
594 assessments. *Proc. Natl. Acad. Sci. U. S. A.* **104,** 20684–9 (2007).
595 38. Srivastava, D. S. & Vellend, M. Biodiversity-Ecosytem Function Research: Is It Relevant to

596 Conservation? *Annu. Rev. Ecol. Evol. Syst.* **36,** 267–294 (2005).
597 39. HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M. & Mayfield, M. M. Rethinking
598 Community Assembly through the Lens of Coexistence Theory. *Annu. Rev. Ecol. Evol.*
599 *Syst.* **43,** 227–248 (2012).
600 40. Faurby, S. & Svenning, J.-C. A species-level phylogeny of all extant and late Quaternary
601 extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Mol.*
602 *Phylogenet. Evol.* **84,** 14–26 (2015).
603 41. Jetz, W., Thomas, G., Joy, J. & Mooers, A. Ø. The global diversity of birds in space and
604 time. *Nature* **491,** 444–448 (2012).
605 42. Kattge, J. *et al.* TRY--a global database of plant traits. *Glob. Chang. Biol.* **17,** 2905–2935
606 (2011).
607 43. Kate E. Jones, J. B. *et al.* PanTHERIA: a species-level database of life history, ecology, and
608 geography of extant and recently extinct mammals. *Ecology* **90,** 2648–2648 (2009).
609 44. Wilman, H. *et al.* EltonTraits 1.0: Species-level foraging attributes of the world's birds and
610 mammals. *Ecology* **95,** 2027–2027 (2014).
611 45. Lavorel, S. & Garnier, E. Predicting changes in community composition and ecosystem
612 functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* **16,** 545–556 (2002).
613 46. Hurlbert, A. H. & Jetz, W. Species richness, hotspots, and the scale dependence of range
614 maps in ecology and conservation. *Proc. Natl. Acad. Sci. U. S. A.* **104,** 13384–9 (2007).
615 47. Holt, B. G. *et al.* An Update of Wallace's Zoogeographic Regions of the World. *Science*
616 *(80-.).* **339,** 74–78 (2013).
617 48. Parravicini, V. *et al.* Global patterns and predictors of tropical reef fish species richness.
618 *Ecography (Cop.).* **36,** 1254–1262 (2013).
619 49. Leprieur, F. *et al.* Plate tectonics drive tropical reef biodiversity dynamics. *Nat. Commun.*
620 **7,** 11461 (2016).
621 50. Ottimofiore, E. *et al.* Responses of coral reef fishes to past climate changes are related to
622 life-history traits. *Ecol. Evol.* **7,** 1996–2005 (2017).
623 51. Blum, M., François, O. & Steel, M. Which Random Processes Describe the Tree of Life? A
624 Large-Scale Study of Phylogenetic Tree Imbalance. *Syst. Biol.* **55,** 685–691 (2006).

625 52. Pybus, O. & Harvey, P. Testing macro–evolutionary models using incomplete molecular
626 phylogenies. *Proc. R. Soc. London, Ser. B* **267,** 2267–2272 (2000).
627 53. Safi, K. *et al.* Understanding global patterns of mammalian functional and phylogenetic
628 diversity. *Philos. Trans. R. Soc. London, Ser. B* **366,** 2536–2544 (2011).
629 54. Belmaker, J. & Jetz, W. Relative roles of ecological and energetic constraints,
630 diversification rates and region history on global species richness gradients. *Ecol. Lett.* **18,**
631 563–571 (2015).
632 55. Guillemot, N. *et al.* Functional Redundancy Patterns Reveal Non-Random Assembly Rules
633 in a Species-Rich Marine Assemblage. *PLoS One* **6,** e26735 (2011).
634 56. Blomberg, S. P., Garland, T. J. R. & Ives, A. Testing for phylogenetic signal in compartive
635 data : behavioral traits are more labile. *Evolution (N. Y).* **57,** 717–745 (2003).
636 57. Tucker, C. M. C. M. *et al.* A guide to phylogenetic metrics for conservation, community
637 ecology and macroecology. *Biol. Rev. Camb. Philos. Soc.* (2017). doi:10.1111/brv.12252
638 58. Rodrigues, A. S. L. & Gaston, K. J. Maximising phylogenetic diversity in the selection of
639 networks of conservation areas. *Biol. Conserv.* **105,** 103–111 (2002).
640 59. Bordewich, M., Rodrigo, A., Semple, C. & Collins, T. Selecting Taxa to Save or Sequence:
641 Desirable Criteria and a Greedy Solution. *Syst. Biol.* **57,** 825–834 (2008).
642 60. Villéger, S., Mason, N. & Mouillot, D. New multidimensional functional diversity indices
643 for a multifaceted framwork in functional ecology. *Ecology* **89,** 2290–2301 (2008).
644 61. Pavoine, S. & Bonsall, M. B. Measuring biodiversity to explain community assembly: a
645 unified approach. *Biol. Rev.* **86,** 792–812 (2011).
646 62. Cornwell, W. K. W. K., Schwilk, D. W. W., Ackerly, D. D. D. D. & Schwilk, L. D. W. A trait-
647 based test for habitat filtering: convex hull volume. *Ecology* **87,** 1465–1471 (2006).
648 63. Ricotta, C. A note on functional diversity measures. *Basic Appl. Ecol.* **6,** 479–486 (2005).
649 64. Villéger, S., Maire, E. & Leprieur, F. On the risks of using dendrograms to measure
650 functional diversity and multidimensional spaces to measure phylogenetic diversity: a
651 comment on Sobral *et al* . (2016). *Ecol. Lett.* **20,** 554–557 (2017).
652
653