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1 Manuscript

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# 3 The diversity of biotic interactions 4 complements functional and 5 phylogenetic facets of biodiversity

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## 15 Keywords

16 biodiversity, vertebrates, macroecology, biogeography, conservation

## 17 Summary

18 Taxonomic, functional and phylogenetic diversities are important facets of biodiversity. Studying them  
19 together has improved our understanding of community dynamics, ecosystem functioning and conservation  
20 values <sup>1-3</sup>. In contrast to species, traits, and phylogenies, the diversity of biotic interactions has so far been  
21 largely ignored as a biodiversity facet in large-scale studies. This neglect represents a crucial shortfall  
22 because biotic interactions shape community dynamics, drive important aspects of ecosystem functioning <sup>4-</sup>  
23 <sup>7</sup>, provide services to humans, and have intrinsic conservation value <sup>8,9</sup>. Hence the diversity of interactions  
24 can provide crucial and unique information with respect to other diversity facets. Here, we leveraged large  
25 datasets of trophic interactions, functional traits, phylogenies and spatial distributions of >1000 terrestrial  
26 vertebrate species across Europe at a 10km resolution. We computed the diversity of interactions  
27 (Interaction Diversity, ID) in addition to functional (FD) and phylogenetic diversities (PD). After controlling  
28 for species richness, surplus and deficits of ID were neither correlated with FD nor with PD, thus  
29 representing unique and complementary information to the commonly studied facets of diversity. A three-  
30 dimensional mapping allowed for simultaneously visualizing different combinations of ID-FD-PD.  
31 Interestingly, the spatial distribution of these diversity combinations closely matched the boundaries  
32 between ten European biogeographic regions, and revealed new, interaction-rich areas in the European  
33 Boreal region and interaction-poor areas in central Europe. Our study demonstrates that the diversity of  
34 interactions adds new and ecologically relevant information to multi-faceted, large-scale diversity studies  
35 with implications for understanding eco-evolutionary processes and informing conservation planning.

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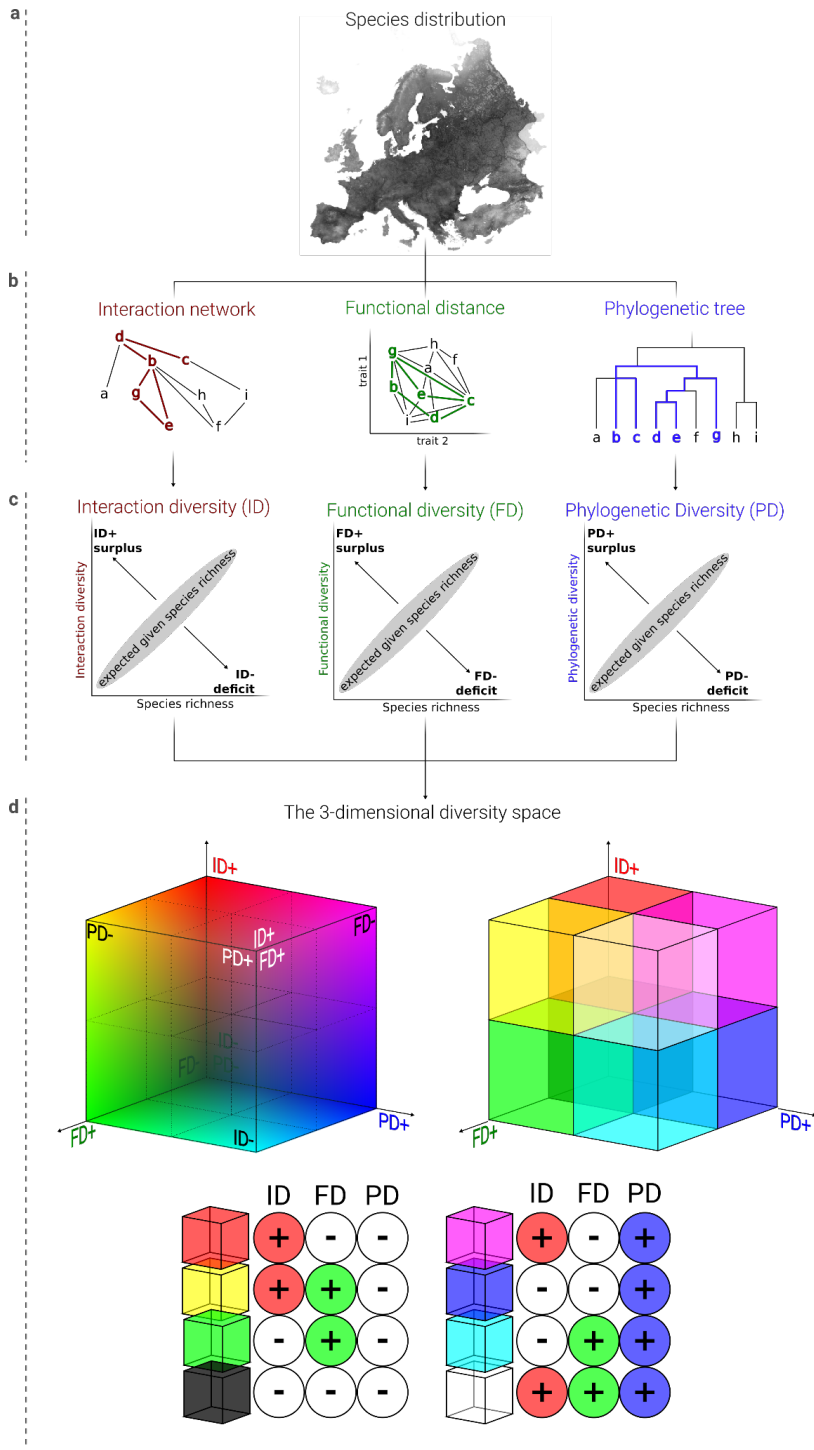
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40 Results and discussion

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43 Figure 1. Conceptual workflow for a joint analysis of phylogenetic, functional, and interaction diversity. (a) Occurrences and probability of presence for 1149 terrestrial vertebrate species on 117,000 10×10km cells across Europe are combined with (b) the phylogenetic tree, a set of functional traits, and the trophic interactions of species. (c) We combined species distribution with phylogenetic, functional and trophic species attributes to compute local terrestrial vertebrate diversities using Hills numbers ( $q = 0$ , i.e. “richness”) and statistically corrected the diversity values by the local species richness. Note that the expected relationships (gray ellipses) are not necessarily linear. (d) We projected the diversity values in a 3-dimensional space with each axis representing a diversity facet and a color in the Red-Blue-Green space ( $x = PD / blue$ ,  $y = FD / green$ ,  $z = ID / red$ ), and discretized particular types of combinations based on surplus and deficits of each diversity. Red identifies surpluses of ID and FD associated with deficits in FD and PD ( $ID > 0$ ,  $FD < 0$ ,  $PD < 0$ ); Yellow identifies surpluses of ID and FD associated with deficits in PD ( $ID > 0$ ,  $FD > 0$ ,  $PD < 0$ ); Green identifies deficits in ID and PD associated with FD surpluses ( $ID < 0$ ,  $FD > 0$ ,  $PD < 0$ ); Black identifies deficits in ID, PD and FD, Pink identifies surpluses of ID and PD associated with FD deficits; Dark blue identifies surpluses of PD associated with ID and FD deficits; Light blue identifies surpluses of PD and FD associated with ID deficits; white identifies surpluses in ID, PD and FD.

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55 Biodiversity -the diversity of life on Earth- was originally used to refer to species diversity, but it is now used  
56 to reflect a multi-faceted concept<sup>3</sup>. Given the evidence that species diversity alone cannot appropriately  
57 describe community assembly, ecosystem functioning and variation in community composition<sup>10</sup>, several  
58 complementary measures of biodiversity have emerged in the last three decades<sup>1,2</sup>. The most important  
59 are the diversity of species' evolutionary histories (i.e phylogenetic diversity, PD) and their ecological  
60 functions (i.e functional diversity, FD), but while PD and FD are becoming central to many studies<sup>11,12</sup>, the  
61 diversity of biotic interactions (i.e interaction diversity, ID) has been poorly considered as a biodiversity  
62 facet in large-scale studies (but see refs<sup>8,13</sup>). This is a major gap since biological interactions are tightly  
63 linked to species coexistence<sup>14</sup>, ecosystem productivity and functioning<sup>4-7</sup>.

64 In its simplest form, ID is the total number of interactions shared by all species of a given assemblage<sup>9</sup>.  
65 Interactions considered can be of different types and nature, e.g antagonistic (competition for resources),  
66 mutualistic (pollination<sup>15,16</sup>), or trophic (predation<sup>17</sup>). Although the concept of interaction diversity is not  
67 novel<sup>8,13</sup> and has its own methodological tools<sup>18,19</sup>, the lack of information available on biotic interactions  
68<sup>20,21</sup> has limited its study across large taxonomical and spatial scales<sup>22-26</sup>. Here, we leveraged unique and  
69 valuable data combining spatial distributions<sup>27</sup> (Figure 1.a), trophic interactions (Figure 1.b), functional  
70 traits<sup>28</sup>, and phylogenies<sup>29</sup> of most terrestrial vertebrate species in Europe<sup>30</sup> at a 10 km resolution. Within  
71 each 10km cell, we computed interaction diversity (ID, as the number of trophic interactions), functional  
72 diversity (FD, as the sum of functional pairwise Gower distances between species in the cell), and  
73 phylogenetic diversity (PD, as the sum of the branch lengths of the phylogenetic tree containing all species  
74 present in the cell<sup>1</sup>) using Hill numbers<sup>31</sup><sup>18</sup>. We statistically corrected each diversity by the local species  
75 richness<sup>32,33</sup> in order to measure and map deficits and surpluses of ID, FD, and PD (Figure 1.c). We also  
76 investigated the correlation and complementarity between the three facets, and created a 3-dimensional  
77 diversity space that reveals different local combinations of ID-FD-PD (Figure 1.d) and their distribution  
78 across biogeographical regions in Europe.

#### 79 Surpluses and deficits of diversities

80 Trophic networks of terrestrial vertebrates found within 10km cells in Europe contained up to 4834 trophic  
81 interactions with an average of 1958 interactions across cells (Figure 2a). Once corrected for species  
82 richness, ID ranged from a deficit of -942 interactions (1667 observed interactions with 202 species involved)  
83 to a surplus of +968 interactions (3730 interactions with 210 species involved, see [Supplemental  
84 information - Trophic network examples](#)). Because highly connected assemblages are often considered as  
85 the signature of functional and resilient ecosystems<sup>34,35</sup>, areas with high ID are important from a  
86 conservation point of view<sup>34,36</sup>. Further, comparing spatial distributions of surplus and deficit IDs with those  
87 of FD or PD can complement our understanding of community dynamics and underlying processes.  
88 Because phylogenetic and trait data contain information about evolutionary history and species niches, the  
89 spatial distribution of their diversity (Figure 2b-c) is thought to hold the signature of the eco-evolutionary  
90 drivers that shape biodiversity patterns<sup>37-39</sup>. For example, for a given species richness, observed surplus of  
91 FD (Figure 1d, and Figure 2b, green color) could result from competitive exclusion between species with  
92 similar traits, while a deficit of FD might result from environmental filtering constraining the range of locally  
93 viable traits or hierarchical competition where a given set of traits is the best adapted locally<sup>40</sup>. PD surplus  
94 (Figure 1d and Figure 2c, dark blue color) could result from slow extinction rates of old and distant lineages  
95 (i.e., museums of biodiversity<sup>41</sup>), and PD deficit from rapid recent speciation (i.e., cradles of biodiversity).  
96 ID surplus and deficit brings additional information, as observed ID surplus (Figure 1d and Figure 2a, red  
97 color) indicates particularly dense or long trophic networks, such as those emerging from high levels of  
98 omnivory and intraguild predation<sup>42</sup>, or from bottom-up control when large amounts of basal resources  
99 sustain longer trophic chains and the presence of top predators. ID deficits can result from weakened top-  
100 down control when top predators are absent from local assemblages, for example following human-induced  
101 removal<sup>43-45</sup>.

102 Overall, the different facets of diversity are shaped by eco-evolutionary drivers which are not mutually  
103 exclusive<sup>46</sup>. Any combination of ID-FD-PD could potentially exist locally and bring complementary  
104 information to the others, although one can expect the facets of diversity to be (partly) correlated when  
105 similar drivers influence multiple diversity facets. We showed that FD and PD were clearly and positively  
106

108 correlated (Figure 3b). This correlation is due to the fact that species tend to retain their ancestral traits  
 109 through evolution <sup>38,47-49</sup>, and suggests an important effect of evolution and phylogenetic niche conservatism  
 110 on biodiversity patterns <sup>47,50,51</sup>. While one could expect ID to be related to FD (because of the link between  
 111 trait similarity and competition for resources) or PD (because biotic interactions can drive the  
 112 (co)evolutionary history of the species <sup>46,52</sup>), this was not what we observed (Figure 3c-d). Instead, ID  
 113 represented unique and complementary information to the commonly studied facets of diversity.

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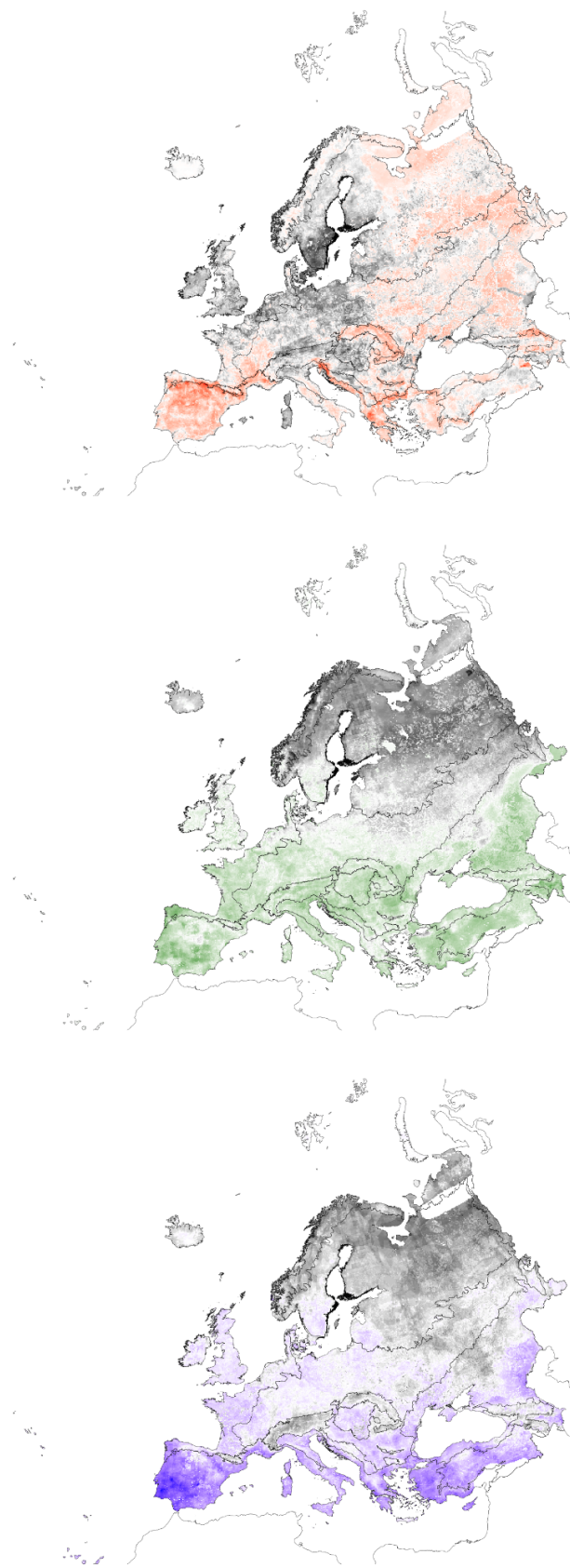
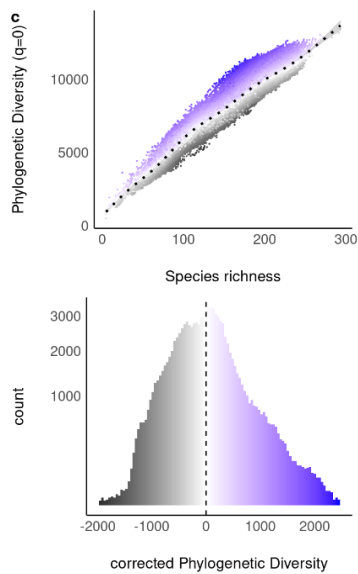
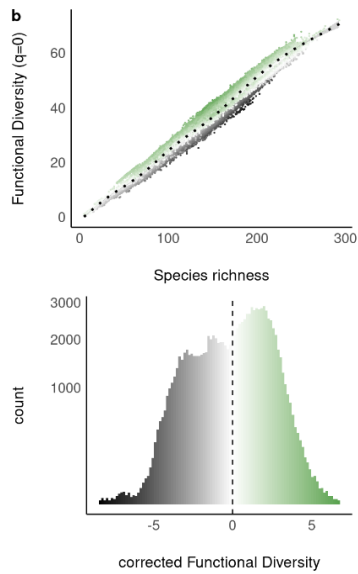
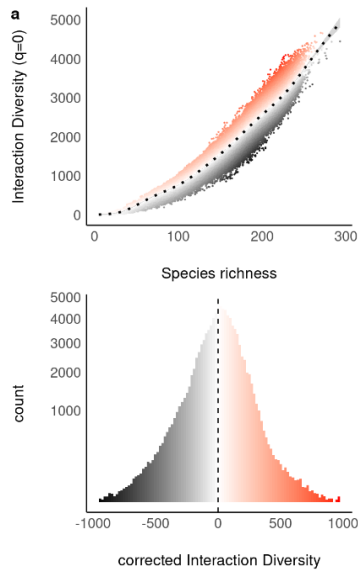
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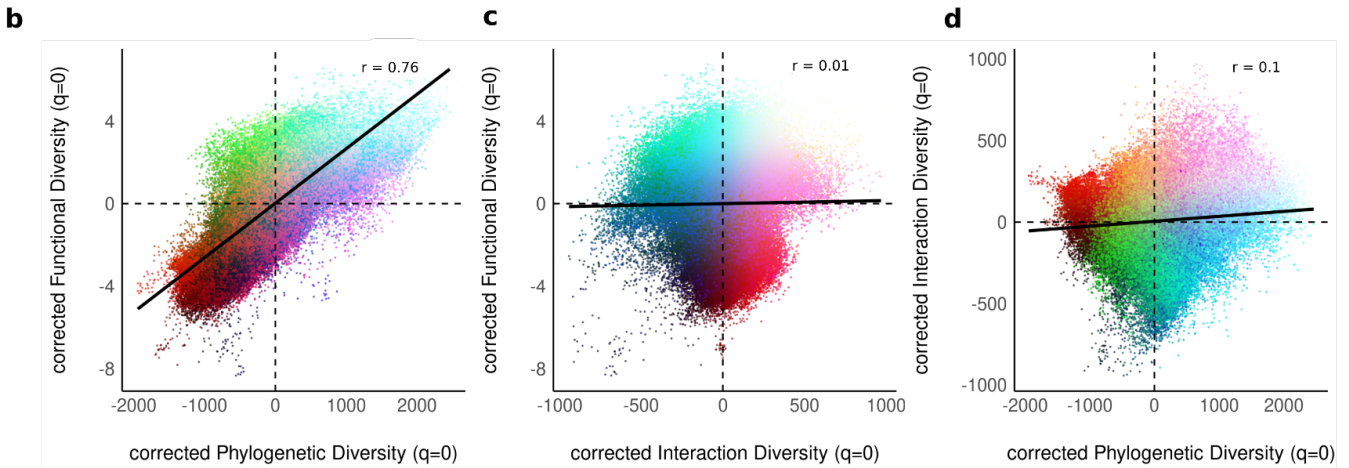
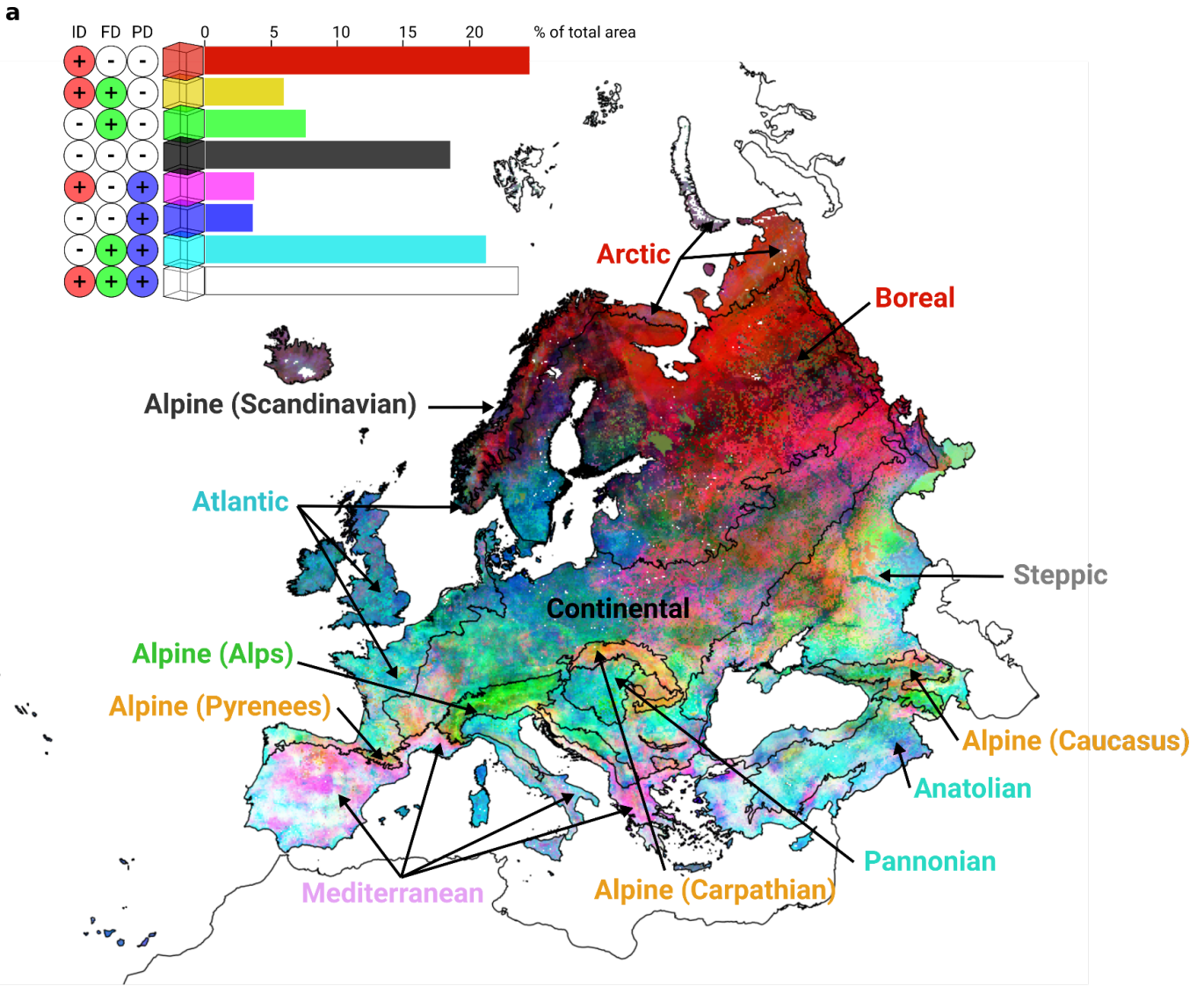
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**Figure 2.** Patterns of Interaction diversity ID (a, in red), Functional diversity FD (b, in green), and Phylogenetic diversity PD (c, in blue). Top left: Relationship between each diversity facet and the species richness. Dotted lines show relationships as fitted by Generalized Additive Models. Bottom left: Distribution of deficits and surpluses of diversities, where model residuals correspond to “corrected diversity” values with deficits (dark shades) and surpluses (red for ID, green for FD, blue for PD). Right: spatial distribution of corrected values for each biodiversity facet, color corresponds to distributions on the left.

141 To investigate the congruence between the interaction, functional and phylogenetic facets of biodiversity,  
142 we created a 3-dimensional space where each dimension represents one diversity facet. We further  
143 attributed a color channel for each diversity facet (red = ID, green = FD, blue = PD) to visualize all possible  
144 combinations of biodiversity facets (Figure 1d). Each combination of three color channels (Red, Blue,  
145 Green) resulted in a particular color in the RGB color space that corresponds to a given combination of  
146 three diversity facets, and allowed us to identify a continuum of ID-FD-PD combinations (Figure 1d). We  
147 also interpreted particular types of combinations by discretizing colors based on the combinations of  
148 surplus and deficits of each diversity facet (Figure 1d).

149 This joint analysis of diversity facets highlighted various local combinations of ID-FD-PD, with all kinds of  
150 combinations being observed in different proportions (Figure 3a). The most commonly observed  
151 combinations were ID surpluses with FD and PD deficits (covering 21.8% of the total study area); surpluses  
152 in ID, FD, and PD (white, 21.6%); surpluses of FD and PD with deficits in ID (light blue 19.6%); and deficits  
153 in ID, FD, and PD (black, 17.3%), which is consistent with the positive correlation observed between FD  
154 and PD (Figure 3b). The spatial structure of diversity combinations aligned well with many boundaries of  
155 European biogeographical regions (Figure 3a), a striking spatial congruency considering that the  
156 identification and delimitation of bioregions are based on geographic distribution of vegetation types <sup>53</sup>.  
157 Beyond species distribution, biodiversity facets such as phylogenetic diversity already have been shown to  
158 match some ecological regions across the globe <sup>54</sup>. ID strongly varies between different regions (e.g  
159 between the Mediterranean region and the Alps, or between the Continental region and the Carpathian  
160 mountains) and thus further refines boundaries between them. These results suggest that species  
161 interactions (along with species co-occurrences and phylogeny) could have a strong structuring effect on  
162 (bio)regional species pools. Such a question, however, would require a deeper analysis based on the  
163 turnover of interactions within and between regions as regional diversity is connected to local diversity by  
164 the turnover in composition between locations. Interestingly, the mapping of diversity combinations also  
165 revealed the specificity of several sub-regions within their biogeographical region, e.g the Balkan peninsula  
166 sub-region in the Mediterranean region, or the Carpathian mountains in the Alpine region. These results  
167 further highlight that biotic interaction diversity adds new and independent information and that a dense  
168 network of trophic interactions can occur in areas of poor functional and phylogenetic diversity.



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**Figure 3.** (a) Spatial projection of the 3-dimensional diversity space. In the top left barplot, we created 8 discrete categories based on the combinations of deficits (-) and surpluses (+) of each diversity and reported the number of cells falling in each category. In the map, points are colored by their location in the Red-Green-Blue 3-dimensional color space, with each diversity facet corresponding to a distinct channel: Red channel = Interaction Diversity, Green Channel = Functional Diversity, Blue channel = Phylogenetic Diversity. black shows lowest ID-FD-PD values, white shows highest ID-FD-PD, and so on for each combination. Black lines show the boundaries of the European biogeographical regions. (b) Pair plot of corrected FD (y-axis) VS corrected PD (x-axis), (c) corrected FD (y-axis) VS corrected ID (x-axis), (d) corrected ID (y-axis) VS corrected PD (x-axis). In top right,  $r$  is the value of Pearson's product-moment correlation between  $y$  and  $x$ . Points colors correspond to colors in the map.

Southern Europe showed strong diversity surpluses in all diversity facets (white / light color shades in Figure 3a), which confirms the Mediterranean bioregion as a multifaceted biodiversity hotspot<sup>55,56</sup>. This result shows that, for a given number of species, local assemblages of Mediterranean terrestrial vertebrate species were particularly rich in terms of ecological strategies, contained long evolutionary history, and had

183 particularly dense trophic networks. In the Mediterranean basin, the warm climate and the geographical  
184 proximity with Africa and Asia explains the high diversity of amphibians and reptiles, as well as the  
185 presence of unique evolutionary lineages, leading to high functional and phylogenetic diversities compared  
186 to the rest of Europe ([Supplemental information - Groups and species distributions across Europe](#)). In  
187 addition to these high levels of functional and phylogenetic diversities, the Mediterranean region showed  
188 surpluses in interaction diversity, in particular in the subregion of the Balkan peninsula. The densely  
189 connected trophic networks observed in the Mediterranean region resulted from (i) numerous top predators  
190 in this region ([Supplemental information - Maps of relevant network properties](#)) previously identified as  
191 birds, felids, and snakes preying upon small reptiles and rodents <sup>22</sup>; and (ii) to a lesser extent from a high  
192 degree of omnivory in the Iberian peninsula <sup>23</sup>.

193  
194 Conversely, the northernmost areas tended to show low levels of diversities (black areas in North of  
195 Scandinavia and Iceland, Figure 3a). The Boreal and Arctic bioregions showed deficits in functional and  
196 phylogenetic diversities, but tended to sustain surpluses in interaction diversity (red areas, Figure 3a). In  
197 these regions, FD deficits were likely to be driven by the cold climate constraining the range of functional  
198 traits that can be found in these regions, and similarly for PD via trait conservatism. In particular, the fact  
199 that cold temperature limits the presence of ectotherms (amphibians and reptiles) in high latitudes reduces  
200 functional and phylogenetic diversities, in line with the expected effect of environmental filtering on these  
201 diversity facets <sup>37,38</sup>. The consideration of ID brings additional and complementary information since FD-PD  
202 deficits are associated with ID surpluses in Northern Europe. The presence of ID surpluses in the Boreal  
203 and Arctic bioregions likely resulted from a high degree of omnivory ([Supplemental information - Maps of  
204 relevant network properties](#)), which is known to increase trophic network connectance <sup>26,57</sup>. Species that live  
205 under high latitudes tend to be trophic generalists <sup>23</sup> because the higher seasonality in high latitudes  
206 promotes the evolution of larger niche breadth, in accordance with the latitude–niche breadth hypothesis  
207 <sup>57,58</sup>.

208  
209 Within the Alpine bioregion, different mountain ranges displayed contrasting diversity combinations. The  
210 marked differentiation between the Alps and the Carpathian mountains subregions is a striking example  
211 supporting the consideration of interaction diversity in biodiversity studies and conservation biogeography.  
212 These two mountain ranges located in Central Europe are part of the same Alpine bioregion, which partly  
213 explains their similarity in terms of functional surpluses and phylogenetic deficits (Figure 2b-c). Based on  
214 functional and phylogenetic diversities alone, these two mountain ranges would be considered as similarly  
215 diverse - but they are markedly different in terms of interaction diversity. The Carpathians displayed a clear  
216 ID surplus in (Figure 3, yellow), while the Alps were deficitary (Figure 3, green). The proximate cause of  
217 such difference was the rarity of top predators in the Alps compared to the Carpathians (see [Supplemental  
218 information - Maps of relevant network properties](#)). Human influence likely explains this discrepancy  
219 because many apex-predators (bears, wolves, lynx) that are often trophic generalists are still present in the  
220 Carpathians, while they were exterminated in the Alps <sup>59</sup>.

221  
222  
223 Potential drivers of diversity facets

224 While environmental filtering is likely to drive the decrease of FD and PD observed in high latitudes, ID  
225 might be more influenced by human activities than climate. As such, local deficits of trophic interactions  
226 appeared as a marker of high human impact across Europe. This is in line with the negative correlation  
227 between connectance and human influence previously reported for the same study system <sup>23</sup>, and suggests  
228 that the diversity of interactions is influenced by different drivers than functional and phylogenetic diversity.  
229 It is, however, noteworthy that other studies reported higher connectance in more human impacted systems  
230 <sup>9,46</sup>. Indeed, the human-induced relative increase of generalist intermediate predators could counterbalance  
231 the decrease in ID due to the loss of a few top predators. The human influence on large-scale diversity has  
232 been considered and studied in terms of phylogeny and traits <sup>60</sup>. However, its consequences on large-scale  
233 patterns of interaction diversity have been largely overlooked, although they are probably stronger. Indeed,  
234 human activities have been (and still are) particularly detrimental to large-bodied species <sup>60–63</sup>. While this



235 observation is generally viewed as a trait-induced consequence (humans are more detrimental to larger  
236 animals), it might also be a trophic-induced consequence (humans are more detrimental to apex and  
237 generalist predators) <sup>45,64</sup>.

238  
239 The importance of interaction diversity

240 A clear understanding of the impact of human activities on ID has yet to emerge. More generally, ID is likely  
241 to be highly context and taxa dependent, and the understanding of its multi-scale drivers represents a  
242 research agenda for the years to come. Among others, the Eltonian shortfall is one big challenge that  
243 currently limits the description of ID in many parts of the world where information on biotic interactions is  
244 lacking <sup>21</sup>. Here, we overcame this challenge for trophic interactions by inferring local interactions from  
245 species distributions and their known potential trophic interactions from the literature and expert knowledge  
246 (as commonly done, see for example refs <sup>19,25</sup>). While this approach overestimates interactions at a given  
247 time, “realized” and “potential” number of interactions are very likely to converge in the long term. On the  
248 contrary, a field sampling approach would underestimate the realized ID. This underestimation can be quite  
249 severe and a massive sampling effort is required to detect most interactions <sup>65</sup>. Combining both approaches  
250 (inferring interactions from a metanetwork and species distribution, vs. observing interactions), and  
251 comparing their accuracy across a range of temporal and spatial scales will provide valuable insights in  
252 community ecology and biogeography <sup>66</sup>.

253  
254 Although ID patterns appear robust to data depletion and spatial contexts (see [Supplemental information -  
255 Robustness of diversity patterns](#)), whether the patterns described in this study can be extrapolated to other  
256 biomes remains an open question. For example, our conclusions from European terrestrial vertebrates  
257 might not hold true for tropical rainforests which shelter many trophic specialist species with narrow  
258 ecological niches (but comprehensive data on traits and interactions are lacking). Nonetheless, we argue  
259 that interaction diversity is a particularly valuable facet for biogeography and conservation planning.  
260 Although this view has been empirically challenged <sup>36</sup>, more densely connected trophic networks are  
261 generally considered as desirable from a conservation point of view <sup>9</sup>. Areas with surpluses of interactions  
262 represent interaction networks that are expected to be more robust to cascading species extinctions <sup>34</sup>, and  
263 consequently more resilient to perturbations. Coupled with its apparent sensitivity to human activities <sup>23</sup>,  
264 interaction diversity might be viewed as a marker of both ecosystem degradation and resistance to future  
265 degradation. We argue that a general consideration of interaction diversity as an important and meaningful  
266 diversity facet alongside the functional and phylogenetic diversities should be a priority for macroecology  
267 and conservation biogeography.

## STAR Methods

### Study area and data

Study area. The study area, hereafter referred to as “Europe”, included the entire European subcontinent (with Macaronesia and Iceland) plus Anatolia to include a complete picture of the North Mediterranean coast (Figure 1a). The study area was divided into 117,000 cells on a 10×10 km equal-size area grid (ETRS89). Within the study area, we considered ten biogeographical regions defined by the European Environment Agency<sup>67</sup>: Alpine, Anatolian, Arctic, Atlantic, Boreal, Black Sea, Continental, Macaronesia, Mediterranean, and Steppic. These bioregions are large scale ecological units based on an interpretation of geobotanical data<sup>68</sup>, and represent areas with homogeneous ecological context.

Species distributions. We extracted the distributions for all terrestrial vertebrates naturally occurring within the study area from Maiorano et al. (2013). Species distributions for 509 bird, 288 mammal, 250 reptile and 104 amphibian species were mapped by combining the IUCN extent of occurrence for each species with their habitat requirements. A species was considered potentially present in a 10×10 km cell if the grid cell met the three following criteria: i) is within the species extent of occurrence, ii) contains at least one 300x300m area of primary habitat for the species, i.e. habitat where the species can persist (defined by experts and published literature) and iii) meets species requirements in terms of elevation and distance from water. A full description of species distribution data and definition of primary habitat can be found in Maiorano et al. 2013<sup>27</sup>. In addition, we used the percentage of primary habitat of the species in each cell as a proxy for the probability to find the species in a random locality within this cell. For example, we considered that if the primary habitat of a species covered 80% of the cell, the probability to find the species in a random locality of the cell was 0.8. As such, it represents a proxy for the probability of presence of the species within the cell and was used as a weight in the entropy-based diversity measures (i.e when q=1) provided as supplementary analyses.

Functional traits. We gathered biological trait data from Thuiller et al. 2015<sup>28</sup>, excluding traits describing diet (and thus trophic interactions) and traits for larvae and juveniles. Our analysis was based on four life-history and ecological traits common to mammals, amphibians, birds and reptiles. The only quantitative trait was body mass [grams, log-transformed]. The three other traits were multichoice nominal variables coded by binary values. Feeding behavior was coded by four binary columns: opportunistic feeder, active hunter, browser, grazer. Nesting location was coded by eleven binary columns: tree/hole/fissure in bark, ground, rocks, building/artificial, underground water, cave/fissures/burrows, lodge, temporary water, brooks/springs/small rivers, puddles/ponds/pools/small lakes, brackish waters. Activity time was coded by four binary columns: nocturnal, crepuscular, diurnal, arrhythmic. These traits were selected because they represent informative niche dimensions linked to the use and acquisition of resources in space and time, and are related to ecosystem functioning<sup>69,70</sup>. A thorough description of traits and the list of publications where the data were gathered is available in supplementary material from<sup>28</sup> available at <https://royalsocietypublishing.org/doi/suppl/10.1098/rstb.2014.0005>.

We computed the pairwise dissimilarities (distances) of this trait matrix using a mixed variable coefficient of distance (using function `dist.ktab` in `ade4`) that generalizes Gower's general coefficient of distance to allow the treatment of various statistical types of variables when calculating distances<sup>71</sup>. Euclidean distance was used for body mass, and Jaccard index was used for the four other multichoice nominal variables (S3 coefficient of in Gower and Legendre 1986<sup>72</sup>).

Phylogenetic tree. We used the 100 phylogenetic trees for European terrestrial vertebrates assembled and published by Roquet et al. 2014<sup>29</sup>. We chose these phylogenetic trees as they are the only species-level phylogenies encompassing all European vertebrates, and have already been valuably used to depict phylogenetic diversity in this context vertebrates in the past<sup>28,32,73,74</sup>.

319 Trophic networks. We used data on species trophic interactions from the metaweb of European terrestrial  
320 vertebrates, (Tetra-EU 1.0, <sup>30</sup>). This metaweb is based on expert knowledge, published information and field  
321 guides. Potential trophic links between a predator and a prey were identified from published accounts of  
322 their observation, morphological similarities between potential prey and literature-referenced prey or -in the  
323 absence of this information- the diet of the predator's sister species. The metaweb of European terrestrial  
324 vertebrates contained 1,164 species and a total of 50,408 potential trophic interactions. The full dataset and  
325 methods description can be found in ref <sup>30</sup>.

326  
327 In order to maximize the species coverage for each diversity, we allowed for different sets of species to be  
328 used to compute ID, FD and PD. For ID we retained 1149 species for which we had information on their  
329 European distribution range and trophic interactions; for FD we retained 1009 species for which we had  
330 information on their European distribution range and functional traits; for PD we retained 993 species for  
331 which we had information on their European distribution range and phylogeny. This varying set of species  
332 should have low impact on the assessment of diversities as ID, FD and PD were corrected by their  
333 corresponding taxonomic richness to compute surpluses and deficits. In order to investigate the potential  
334 bias resulting from the variation of species coverage across space and diversities, we computed diversities  
335 based on the same set of 884 species for which we had all shared information. The resulting diversity  
336 patterns were similar when considering the 884 species or varying set of species (see [Supplemental  
337 information - Diversities based on the same set of 884 species](#)).

338  
339 Diversity measures and the 3-dimensional diversity space

340 Within each 10x10km cell, we used Hill numbers <sup>31</sup> to compute FD, PD, and ID. In this framework, diversity  
341 values are converted into effective numbers of species, the Hill numbers. When considering taxonomic  
342 diversity, the effective number of species is the number of equally abundant species necessary to produce  
343 the observed value of diversity (an analogue to the concept of effective population size in genetics). This  
344 approach has then been generalized to incorporate species phylogenetic relatedness and species  
345 functional distances. We used the framework from Chao et al. 2014 <sup>31</sup> implemented in the R package hillR  
346 for phylogenetic and functional diversity and in the package econetwork <sup>18</sup> for interaction diversity. We  
347 computed each diversity as a Hill number analogous to a measure of richness by setting  $q=0$  (ignoring  
348 abundance). The ID richness was the sum of trophic links formed by the species present in the cell, the FD  
349 richness was the sum of functional pairwise gower distances between species in the cell, and the PD  
350 richness was the mean sum of the branch lengths of the phylogenetic tree connecting all species present in  
351 the cell <sup>1</sup> across the 100 trees.

352 We focused our study on richness-based results ( $q=0$ ) as they are the easiest to interpret, but we also  
353 analyzed and showed results based on Shannon entropy in the [Supplemental information - Results based  
354 on Shannon entropy](#). To compute the results as a Shannon entropy, we set  $q=1$  and used the % of species'  
355 primary habitat within the cell as the probability to find the species in the cell. More precisely, when  $q=1$  the  
356 ID entropy is the Shannon entropy over the interaction weights (product of the two species abundances),  
357 the FD is the Shannon entropy of effective number of species-pairs with unit-distance between species,  
358 and the PD is the mean Shannon entropy of the effective total branch length across the 100 trees. More  
359 details on the calculations of FD and PD can be found in Chao et al. 2014 <sup>31</sup>, and in Ohlmann et al. 2019 <sup>18</sup>  
360 for ID.

361  
362 We corrected FD, PD, ID richness and Shannon entropy for the number of species in the cell (i.e taxonomic  
363 richness) based on the set of species used to compute each diversity. We fitted a thin plate spline  
364 regression, a particular Generalized Additive Model (GAM), to predict each diversity measure from species  
365 richness. The residuals of each model (one for each diversity facet and order  $q$ ) were retained as the  
366 species richness corrected value of the diversity, with positive residuals considered as surplus and negative  
367 residuals considered as deficits given the species richness <sup>32,33</sup>. In other words, a deficit (or surplus)  
368 indicates a lower (or higher, respectively) diversity value than expected given the local species richness  
369 (Figure 1) .

371 To investigate the congruence between the interaction, functional and phylogenetic facets of biodiversity,  
372 we created a 3-dimensional space where each dimension represents one diversity facet. In order to  
373 visualize all possible combinations of biodiversity facets, we attributed a color channel for each diversity  
374 facet (red = ID, green = FD, blue = PD) where the residual values for each diversity were rescaled to 0-255  
375 value in the corresponding color channel (Figure 1). Hence, each combination of three color channels (Red,  
376 Blue, Green) results in a particular color in the RGB color space that corresponds to a given combination of  
377 three diversity facets, and allows us to identify a continuum of ID-FD-PD combinations depicted in figure  
378 1.d. We can also interpret particular types of combinations by discretizing colors based on the combinations  
379 of surplus and deficits of each diversity. As shown in Figure 1d and Figure 3a, Red identifies surpluses of  
380 ID and FD associated with deficits in FD and PD ( $ID > 0$ ,  $FD < 0$ ,  $PD < 0$ ); Yellow identifies surpluses of ID and  
381 FD associated with deficits in PD ( $ID > 0$ ,  $FD > 0$ ,  $PD < 0$ ); Green identifies deficits in ID and PD associated  
382 with FD surpluses ( $ID < 0$ ,  $FD > 0$ ,  $PD < 0$ ); Black identifies deficits in ID, PD and FD, Pink identifies surpluses  
383 of ID and PD associated with FD deficits; Dark blue identifies surpluses of PD associated with ID and FD  
384 deficits; Light blue identifies surpluses of PD and FD associated with ID deficits; white identifies surpluses  
385 in ID, PD and FD.

## 386 SUPPLEMENTAL INFORMATION

387 Supplemental Information includes six appendix and can be found at:

## 388 AUTHOR CONTRIBUTIONS

389 P.G and W.T. conceived the study, with early advice from L.O.C, C.B, G.P. and T.M. P.G. performed all  
390 analyses and wrote the first version of the manuscript with inputs from W.T, L.O.C, C.B, G.P. and T.M. All  
391 authors contributed substantially to the interpretation of the results and to the writing of the manuscripts and  
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400

401

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## References

- 403 1. Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* *61*, 1–10.
- 404 2. Tilman, D. (2001). Functional diversity. *Encyclopedia of biodiversity* *3*, 109–120.
- 405 3. Pollock, L.J., O'Connor, L.M.J., Mokany, K., Rosauer, D.F., Talluto, M.V., and Thuiller, W. (2020).  
406 Protecting Biodiversity (in All Its Complexity): New Models and Methods. *Trends Ecol. Evol.* *35*, 1119–  
407 1128.
- 408 4. Grime, J.P. (1997). Biodiversity and Ecosystem Function: The Debate Deepens. *Science* *277*, 1260–  
409 1261.
- 410 5. Tilman, D., Isbell, F., and Cowles, J.M. (2014). Biodiversity and Ecosystem Functioning. *Annu. Rev.*  
411 *Ecol. Evol. Syst.* *45*, 471–493.
- 412 6. Brose, U., Blanchard, J.L., Eklöf, A., Galiana, N., Hartvig, M., R. Hirt, M., Kalinkat, G., Nordström,  
413 M.C., O'Gorman, E.J., Rall, B.C., et al. (2017). Predicting the consequences of species loss using size-  
414 structured biodiversity approaches. *Biol. Rev. Camb. Philos. Soc.* *92*, 684–697.
- 415 7. Schneider, F.D., Brose, U., Rall, B.C., and Guill, C. (2016). Animal diversity and ecosystem functioning  
416 in dynamic food webs. *Nat. Commun.* *7*, 12718.
- 417 8. Thompson, J.N. (1997). Conserving Interaction Biodiversity. In *The Ecological Basis of Conservation:*  
418 *Heterogeneity, Ecosystems, and Biodiversity*, S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E.  
419 Likens, eds. (Springer US), pp. 285–293.
- 420 9. Tylianakis, J.M., Laliberté, E., Nielsen, A., and Bascompte, J. (2010). Conservation of species  
421 interaction networks. *Biol. Conserv.* *143*, 2270–2279.
- 422 10. Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchmann, N., Degrange, V., Grime,  
423 P., Hulot, F., Mermillod-Blondin, F., et al. (2002). Species diversity, functional diversity and ecosystem  
424 functioning. *Biodiversity and ecosystem functioning: synthesis and perspectives*, 195–208.
- 425 11. De Palma, A., Kuhlmann, M., Bugter, R., Ferrier, S., Hoskins, A.J., Potts, S.G., Roberts, S.P.M.,  
426 Schweiger, O., and Purvis, A. (2017). Dimensions of biodiversity loss: Spatial mismatch in land-use  
427 impacts on species, functional and phylogenetic diversity of European bees. *Divers. Distrib.* *23*, 1435–  
428 1446.
- 429 12. Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R.,  
430 Tilman, D., and Gamon, J.A. (2018). Plant spectral diversity integrates functional and phylogenetic  
431 components of biodiversity and predicts ecosystem function. *Nat Ecol Evol* *2*, 976–982.
- 432 13. Dyer, L.A., Walla, T.R., Greeney, H.F., Stireman, J.O., III, and Hazen, R.F. (2010). Diversity of  
433 Interactions: A Metric for Studies of Biodiversity: Interaction Diversity. *Biotropica* *42*, 281–289.
- 434 14. Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., and Gravel, D.  
435 (2016). No complexity–stability relationship in empirical ecosystems. *Nat. Commun.* *7*, 1–8.
- 436 15. Burkle, L.A., and Alarcón, R. (2011). The future of plant-pollinator diversity: understanding interaction  
437 networks across time, space, and global change. *Am. J. Bot.* *98*, 528–538.
- 438 16. Burkle, L.A., Myers, J.A., and Belote, R.T. (2016). The beta-diversity of species interactions:  
439 Untangling the drivers of geographic variation in plant-pollinator diversity and function across scales.  
440 *Am. J. Bot.* *103*, 118–128.
- 441 17. Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W.D., Lenoir, J., Sandel, B., Trøjelsgaard, K., Ejrnaes,  
442 R., and Svenning, J.-C. (2013). Mammal predator and prey species richness are strongly linked at  
443 macroscales. *Ecology* *94*, 1112–1122.
- 444

- 445 18. Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L., and Thuiller, W. (2019). Diversity  
446 indices for ecological networks: a unifying framework using Hill numbers. *Ecol. Lett.* 22.
- 447 19. Poisot, T., Canard, E., Mouillot, D., Mouquet, N., and Gravel, D. (2012). The dissimilarity of species  
448 interaction networks. *Ecol. Lett.* 15, 1353–1361.
- 449 20. Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., and Ladle, R.J. (2015). Seven  
450 Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 46, 523–549.
- 451 21. Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C.,  
452 Vissault, S., and Chapman, D. (2021). Global knowledge gaps in species interaction networks data. *J.*  
453 *Biogeogr.* 48, 1552–1563.
- 454 22. O'Connor, L.M.J., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez-Almoyna, C.,  
455 Montemaggiore, A., Ohlmann, M., and Thuiller, W. (2020). Unveiling the food webs of tetrapods across  
456 Europe through the prism of the Eltonian niche. *J. Biogeogr.* 47, 181–192.
- 457 23. Braga, J., Pollock, L.J., Barros, C., Galiana, N., Montoya, J.M., Gravel, D., Maiorano, L.,  
458 Montemaggiore, A., Ficetola, G.F., Dray, S., et al. (2019). Spatial analyses of multi-trophic terrestrial  
459 vertebrate assemblages in Europe. *Glob. Ecol. Biogeogr.* 28, 1636–1648.
- 460 24. Cumming, G.S., Bodin, Ö., Ernstson, H., and Elmqvist, T. (2010). Network analysis in conservation  
461 biogeography: Challenges and opportunities. *Diversity and Distributions* 16, 414–425.
- 462 25. Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.P., Martinez, N.D., Nyman, T., Poisot, T., Stouffer, D.B.,  
463 Tylianakis, J.M., Wood, S.A., et al. (2019). Bringing Elton and Grinnell together: a quantitative  
464 framework to represent the biogeography of ecological interaction networks. *Ecography* 42, 401–415.
- 465 26. Baiser, B., Gravel, D., Cirtwill, A.R., Dunne, J.A., Fahimipour, A.K., Gilarranz, L.J., Grochow, J.A., Li,  
466 D., Martinez, N.D., McGrew, A., et al. (2019). Ecogeographical rules and the macroecology of food  
467 webs. *Glob. Ecol. Biogeogr.* 28, 1204–1218.
- 468 27. Maiorano, L., Amori, G., Capula, M., Falcucci, A., Masi, M., Montemaggiore, A., Pottier, J., Psomas, A.,  
469 Rondinini, C., Russo, D., et al. (2013). Threats from climate change to terrestrial vertebrate hotspots in  
470 Europe. *PLoS One* 8, e74989.
- 471 28. Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G.F., Lavergne, S., Renaud, J., Roquet,  
472 C., and Mouillot, D. (2015). Conserving the functional and phylogenetic trees of life of European  
473 tetrapods. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 370, 20140005.
- 474 29. Roquet, C., Lavergne, S., and Thuiller, W. (2014). One tree to link them all: a phylogenetic dataset for  
475 the European tetrapoda. *PLoS Curr.* 6.
- 476 30. Maiorano, L., Montemaggiore, A., Ficetola, G.F., O'Connor, L., and Thuiller, W. (2020). TETRA-EU 1.0:  
477 A species-level trophic metaweb of European tetrapods. *Glob. Ecol. Biogeogr.* 29, 1452–1457.
- 478 31. Chao, A., Chiu, C.-H., and Jost, L. (2014). Unifying Species Diversity, Phylogenetic Diversity,  
479 Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. *Annu.*  
480 *Rev. Ecol. Evol. Syst.* 45, 297–324.
- 481 32. Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N.,  
482 Renaud, J., and Thuiller, W. (2014). Spatial mismatch of phylogenetic diversity across three vertebrate  
483 groups and protected areas in Europe. *Diversity and Distributions* 20, 674–685.
- 484 33. Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K., and Diniz-Filho, J.A.F. (2011).  
485 Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R.*  
486 *Soc. Lond. B Biol. Sci.* 366, 2536–2544.
- 487 34. Gilbert, A.J. (2009). Connectance indicates the robustness of food webs when subjected to species  
488 loss. *Ecol. Indic.* 9, 72–80.
- 489 35. Thébault, E., and Fontaine, C. (2010). Stability of ecological communities and the architecture of  
13

- 490 mutualistic and trophic networks. *Science* 329, 853–856.
- 491 36. Heleno, R., Devoto, M., and Pocock, M. (2012). Connectance of species interaction networks and  
492 conservation value: Is it any good to be well connected? *Ecol. Indic.* 14, 7–10.
- 493 37. McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from  
494 functional traits. *Trends Ecol. Evol.* 21, 178–185.
- 495 38. Webb, C.O., Ackerly, D.D., McPeck, M.A., and Donoghue, M.J. (2002). Phylogenies and Community  
496 Ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505.
- 497 39. Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F.,  
498 Mokany, K., Roquet, C., Smyčka, J., et al. (2020). Dos and don'ts when inferring assembly rules from  
499 diversity patterns. *Glob. Ecol. Biogeogr.* 164, S165.
- 500 40. Mayfield, M.M., and Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic  
501 structure of communities. *Ecol. Lett.* 13, 1085–1093.
- 502 41. Stebbins, G.L. (1974). *Flowering Plants: Evolution Above the Species Level* (Belknap Press of Harvard  
503 University Press).
- 504 42. Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E., and Loreau, M. (2007). The  
505 functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol. Lett.* 10, 522–538.
- 506 43. Estes, J. a., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R.,  
507 Essington, T.E., Holt, R.D., Jackson, J.B.C., et al. (2011). Trophic downgrading of planet Earth.  
508 *Science* 333, 301–306.
- 509 44. de Visser, S.N., Freymann, B.P., and Olf, H. (2011). The Serengeti food web: empirical quantification  
510 and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* 80, 484–494.
- 511 45. Pauly, D., Christensen, V., V., Dalsgaard, J., Froese, R., and Torres, F., Jr (1998). Fishing down  
512 marine food webs. *Science* 279, 860–863.
- 513 46. Tylianakis, J.M., and Morris, R.J. (2017). Ecological Networks Across Environmental Gradients. *Annu.*  
514 *Rev. Ecol. Evol. Syst.* 48, 25–48.
- 515 47. Wiens, J.J., and Graham, C.H. (2005). Niche Conservatism: Integrating Evolution, Ecology, and  
516 Conservation Biology. *Annu. Rev. Ecol. Evol. Syst.* 36, 519–539.
- 517 48. Peterson, A.T., Soberon, J., and Sanchez-Cordero, V., V. (1999). Conservatism of ecological niches in  
518 evolutionary time. *Science* 285, 1265–1267.
- 519 49. Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. (2010). Biodiversity and Climate Change:  
520 Integrating Evolutionary and Ecological Responses of Species and Communities. *Annu. Rev. Ecol.*  
521 *Evol. Syst.* 41, 321–350.
- 522 50. Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I.,  
523 Jonathan Davies, T., Grytnes, J.-A., Harrison, S.P., et al. (2010). Niche conservatism as an emerging  
524 principle in ecology and conservation biology. *Ecol. Lett.* 13, 1310–1324.
- 525 51. Münkemüller, T., Boucher, F., Thuiller, W., and Lavergne, S. (2015). Common conceptual and  
526 methodological pitfalls in the analysis of phylogenetic niche conservatism. *Funct. Ecol.* 29, 627–639.
- 527 52. Williams, R.J., and Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature* 404, 180–  
528 183.
- 529 53. Noirfalise, A. (1987). *Map of the Natural Vegetation: Of the Member Countries of the European*  
530 *Economic Community and the Council of Europe.*
- 531 54. Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H.,  
532 Graham, C.H., Graves, G.R., Jønsson, K.A., et al. (2013). An update of Wallace's zoogeographic

- 533 regions of the world. *Science* 339, 74–78.
- 534 55. Myers, N., Fonseca, G. a. B., Mittermeier, R. a., Fonseca, G. a. B., and Kent, J. (2000). Biodiversity  
535 hotspots for conservation priorities. *Nature* 403, 853–858.
- 536 56. Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., and Gascon, C. (2011). Global  
537 Biodiversity Conservation: The Critical Role of Hotspots. In *Biodiversity Hotspots: Distribution and*  
538 *Protection of Conservation Priority Areas*, F. E. Zachos and J. C. Habel, eds. (Springer Berlin  
539 Heidelberg), pp. 3–22.
- 540 57. Cirtwill, A.R., Stouffer, D.B., and Romanuk, T.N. (2015). Latitudinal gradients in biotic niche breadth  
541 vary across ecosystem types. *Proc. Biol. Sci.* 282.
- 542 58. Vázquez, D.P., and Stevens, R.D. (2004). The latitudinal gradient in niche breadth: concepts and  
543 evidence. *Am. Nat.* 164, E1–19.
- 544 59. Kaczensky, P., Chapron, G., Von Arx, M., Huber, D., Andrén, H., and Linnell, J. (2013). Status,  
545 Management and Distribution of Large Carnivores - Bear, Lynx, Wolf & Wolverine - in Europe (Verlag  
546 nicht ermittelbar).
- 547 60. Fritz, S.A., Bininda-Emonds, O.R.P., and Purvis, A. (2009). Geographical variation in predictors of  
548 mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* 12, 538–549.
- 549 61. Gaston, K.J., and Blackburn, T.M. (1995). Birds, body size and the threat of extinction. *Philos. Trans.*  
550 *R. Soc. Lond. B Biol. Sci.* 347, 205–212.
- 551 62. Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L.,  
552 and Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science* 309,  
553 1239–1241.
- 554 63. Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M.,  
555 Bielby, J., and Collen, B. (2016). Correlates of extinction risk in squamate reptiles: the relative  
556 importance of biology, geography, threat and range size. *Glob. Ecol. Biogeogr.* 25, 391–405.
- 557 64. Brose, U. (2010). Improving nature conservancy strategies by ecological network theory. *Basic Appl.*  
558 *Ecol.* 11, 1–5.
- 559 65. Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., and Padrón, B. (2012).  
560 Evaluating sampling completeness in a desert plant-pollinator network. *J. Anim. Ecol.* 81, 190–200.
- 561 66. Fortuna, M.A., Nagavci, A., Barbour, M.A., and Bascompte, J. (2020). Partner Fidelity and Asymmetric  
562 Specialization in Ecological Networks. *Am. Nat.* 196, 382–389.
- 563 67. European Environmental Agency, EEA (2016). Biogeographical regions.  
564 <https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3>.
- 565 68. Roekaerts, M. (2002). The Biogeographical Regions Map of Europe. Basic principles of its creation  
566 and overview of its development (European Environmental Agency, EEA).
- 567 69. Luck, G.W., Lavorel, S., McIntyre, S., and Lumb, K. (2012). Improving the application of vertebrate  
568 trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology* 81, 1065–1076.
- 569 70. Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. *Trends Ecol. Evol.* 21,  
570 464–471.
- 571 71. Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., and Daniel, H. (2009). On the challenge of treating  
572 various types of variables: application for improving the measurement of functional diversity. *Oikos*  
573 118, 391–402.
- 574 72. Gower, J.C., and Legendre, P. (1986). Metric and Euclidean properties of dissimilarity coefficients. *J.*  
575 *Classification* 3, 5–48.



- 576 73. Pearman, P.B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N.E., and Thuiller, W. (2014).  
577 Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. *Glob.*  
578 *Ecol. Biogeogr.* *23*, 414–424.
- 579 74. Saladin, B., Thuiller, W., Graham, C.H., Lavergne, S., Maiorano, L., Salamin, N., and Zimmermann,  
580 N.E. (2019). Environment and evolutionary history shape phylogenetic turnover in European tetrapods.  
581 *Nat. Commun.* *10*, 249.
- 582 75. Cadotte, M.W., Cardinale, B.J., and Oakley, T.H. (2008). Evolutionary history and the effect of  
583 biodiversity on plant productivity. *Proc. Natl. Acad. Sci. U. S. A.* *105*, 17012–17017.
- 584 76. Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E., and Oakley, T.H. (2010).  
585 Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance  
586 and evolutionary history. *Ecol. Lett.* *13*, 96–105.
- 587 77. Davies, T.J., and Buckley, L.B. (2011). Phylogenetic diversity as a window into the evolutionary and  
588 biogeographic histories of present-day richness gradients for mammals. *Philos. Trans. R. Soc. Lond. B*  
589 *Biol. Sci.* *366*, 2414–2425.
- 590 78. Pollock, L.J., Thuiller, W., and Jetz, W. (2017). Large conservation gains possible for global  
591 biodiversity facets. *Nature* *546*, 141–144.
- 592 79. Cadotte, M.W., Carscadden, K., and Mirotnick, N. (2011). Beyond species: functional diversity and  
593 the maintenance of ecological processes and services. *J. Appl. Ecol.* *48*, 1079–1087.
- 594 80. Díaz, S., and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem  
595 processes. *Trends Ecol. Evol.* *16*, 646–655.
- 596 81. Cadotte, M.W., Dinnage, R., and Tilman, D. (2012). Phylogenetic diversity promotes ecosystem  
597 stability. *Ecology* *93*, S223–S233.
- 598 82. Brun, P., Zimmermann, N.E., Graham, C.H., Lavergne, S., Pellissier, L., Münkemüller, T., and Thuiller,  
599 W. (2019). The productivity-biodiversity relationship varies across diversity dimensions. *Nat. Commun.*  
600 *10*, 5691.
- 601 83. de Bello, F., Lavorel, S., Hallett, L.M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland, T.,  
602 Goberna, M., Májeková, M., et al. (2021). Functional trait effects on ecosystem stability: assembling  
603 the jigsaw puzzle. *Trends Ecol. Evol.* *36*, 822–836.
- 604 84. Loreau, M. (2014). Reconciling utilitarian and non-utilitarian approaches to biodiversity conservation.  
605 *Ethics Sci. Environ. Polit.* *14*, 27–32.
- 606 85. Mazel, F., Wüest, R.O., Gueguen, M., Renaud, J., Ficetola, G.F., Lavergne, S., and Thuiller, W.  
607 (2017). The Geography of Ecological Niche Evolution in Mammals. *Curr. Biol.* *27*, 1369–1374.
- 608 86. Chesson, P., and Kuang, J.J. (2008). The interaction between predation and competition. *Nature* *456*,  
609 235–238.
- 610 87. Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet,  
611 R.M., and Case, T.J. (2002). The interaction between predation and competition: a review and  
612 synthesis. *Ecol. Lett.* *5*, 302–315.
- 613 88. Stouffer, D.B., Sales-Pardo, M., Siner, M.I., and Bascompte, J. (2012). Evolutionary conservation of  
614 species' roles in food webs. *Science* *335*, 1489–1492.
- 615 89. Poisot, T., Mouquet, N., and Gravel, D. (2013). Trophic complementarity drives the biodiversity-  
616 ecosystem functioning relationship in food webs. *Ecol. Lett.* *16*, 853–861.
- 617 90. Vane-Wright, R.I., Humphries, C.J., and Williams, P.H. (1991). What to protect?—Systematics and the  
618 agony of choice. *Biol. Conserv.* *55*, 235–254.
- 619 91. Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., and Baillie, J.E.M. (2007). Mammals on the  
16

- 620 EDGE: conservation priorities based on threat and phylogeny. PLoS One 2, e296.
- 621 92. Rodrigues, A.S.L., and Gaston, K.J. (2002). Maximising phylogenetic diversity in the selection of  
622 networks of conservation areas. *Biol. Conserv.* 105, 103–111.
- 623 93. Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., and Mouquet, N. (2010). Spatial  
624 mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for  
625 integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040.
- 626 94. Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., and  
627 Bastos Araujo, M. (2011). *Ecological niches and geographic distributions* (Princeton University Press).
- 628 95. Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman,  
629 K., Butchart, S., et al. (2020). Summary for policymakers of the global assessment report on  
630 biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity  
631 and Ecosystem Services (IPBES).

632