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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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14

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 ¹⁻³. 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 ⁴⁻
23 ⁷, provide services to humans, and have intrinsic conservation value ^{8,9}. 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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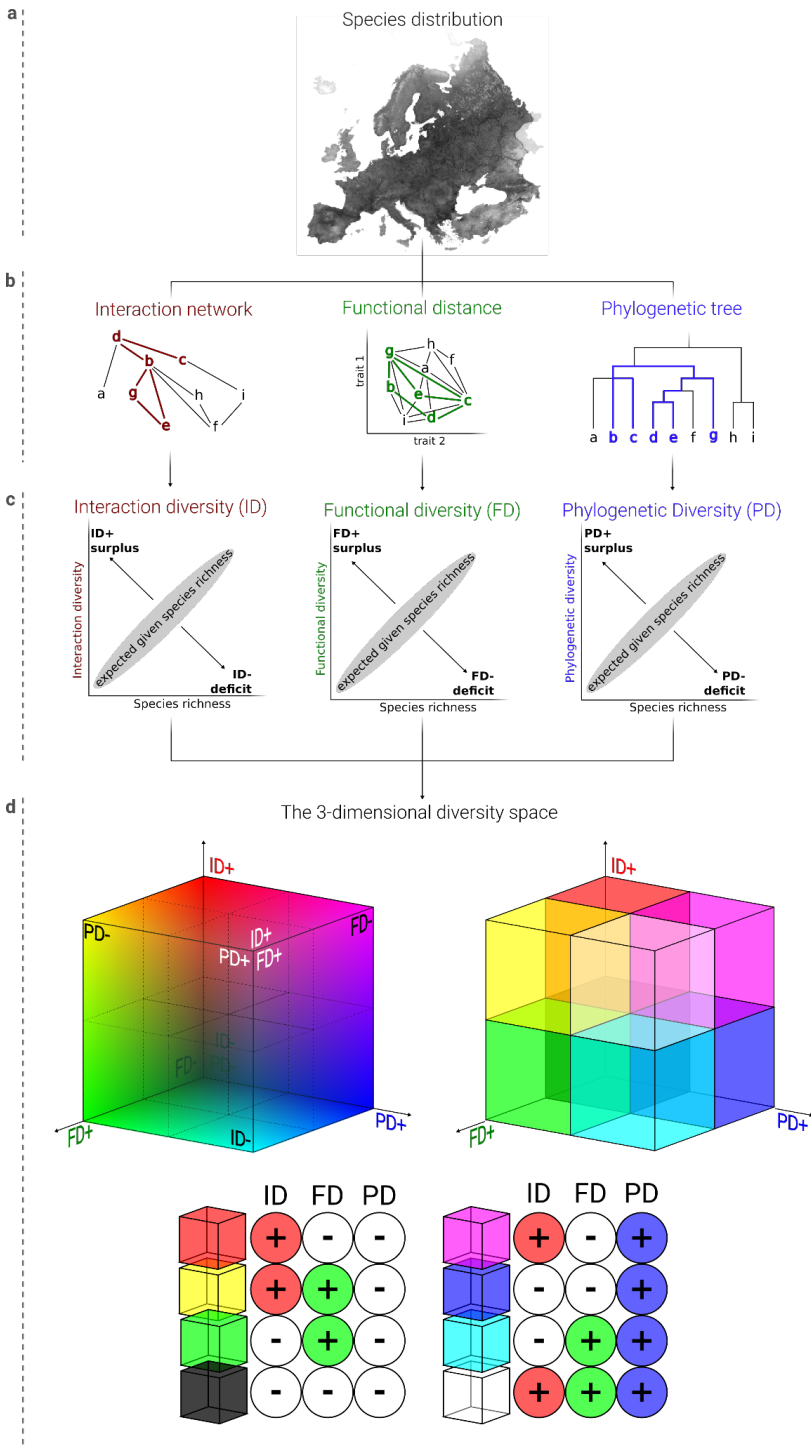
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40 Results and discussion

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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*
 44 *traits, and the trophic interactions of species. (c) We combined species distribution with phylogenetic, functional and trophic species attributes to*
 45 *compute local terrestrial vertebrate diversities using Hills numbers ($q = 0$, i.e. “richness”) and statistically corrected the diversity values by the local*
 46 *species richness. Note that the expected relationships (gray ellipses) are not necessarily linear. (d) We projected the diversity values in a 3-*
 47 *dimensional space with each axis representing a diversity facet and a color in the Red-Blue-Green space ($x = PD / blue$, $y = FD / green$, $z = ID / red$),*
 48 *and discretized particular types of combinations based on surplus and deficits of each diversity. Red identifies surpluses of ID and FD*
 49 *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 ($ID > 0$, $FD > 0$,*
 50 *$PD < 0$); 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*
 51 *identifies surpluses of ID and PD associated with FD deficits; Dark blue identifies surpluses of PD associated with ID and FD deficits; Light blue*
 52 *identifies surpluses of PD and FD associated with ID deficits; white identifies surpluses in ID, PD and FD.*
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54

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 ³. Given the evidence that species diversity alone cannot appropriately
57 describe community assembly, ecosystem functioning and variation in community composition ¹⁰, several
58 complementary measures of biodiversity have emerged in the last three decades ^{1,2}. 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 ^{11,12}, 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 ^{8,13}). This is a major gap since biological interactions are tightly
63 linked to species coexistence ¹⁴, ecosystem productivity and functioning ⁴⁻⁷.

64 In its simplest form, ID is the total number of interactions shared by all species of a given assemblage⁹.
65 Interactions considered can be of different types and nature, e.g antagonistic (competition for resources),
66 mutualistic (pollination ^{15,16}), or trophic (predation ¹⁷). Although the concept of interaction diversity is not
67 novel ^{8,13} and has its own methodological tools ^{18,19}, the lack of information available on biotic interactions
68 ^{20,21} has limited its study across large taxonomical and spatial scales ²²⁻²⁶. Here, we leveraged unique and
69 valuable data combining spatial distributions²⁷ (Figure 1.a), trophic interactions (Figure 1.b), functional
70 traits²⁸, and phylogenies²⁹ of most terrestrial vertebrate species in Europe ³⁰ 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 ¹) using Hill numbers ^{31 18}. We statistically corrected each diversity by the local species
75 richness ^{32,33} 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 ^{34,35}, areas with high ID are important from a
86 conservation point of view ^{34,36}. 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 ³⁷⁻³⁹. 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 ⁴⁰. 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 ⁴¹), 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 ⁴², 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 ⁴³⁻⁴⁵.

102 Overall, the different facets of diversity are shaped by eco-evolutionary drivers which are not mutually
103 exclusive ⁴⁶. 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 ^{38,47-49}, and suggests an important effect of evolution and phylogenetic niche conservatism
 110 on biodiversity patterns ^{47,50,51}. 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 ^{46,52}), 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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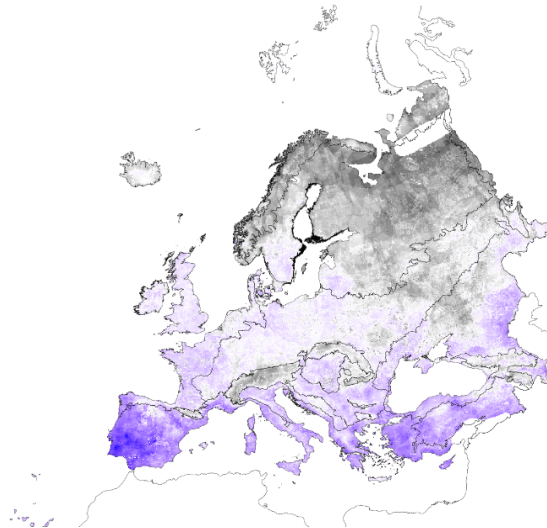
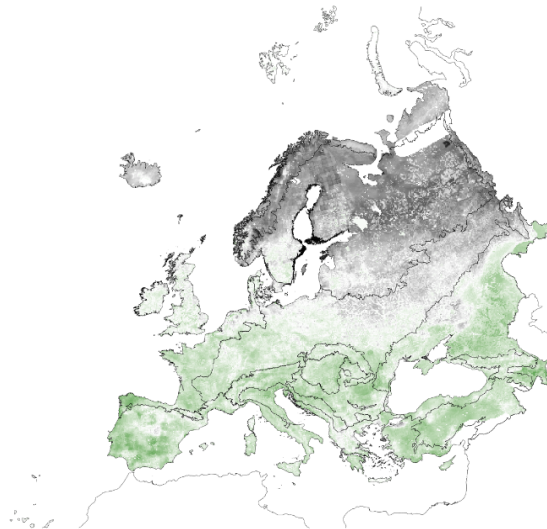
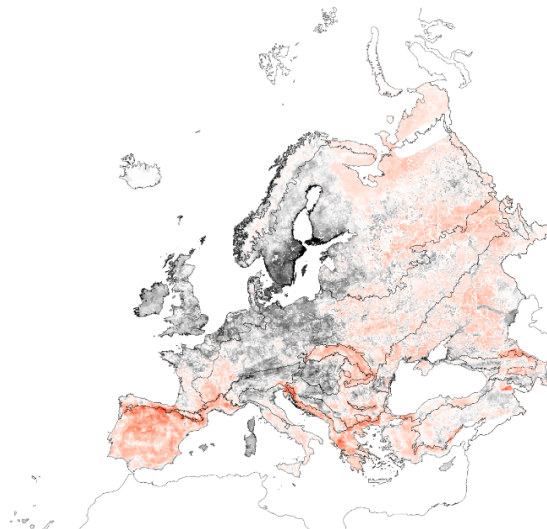
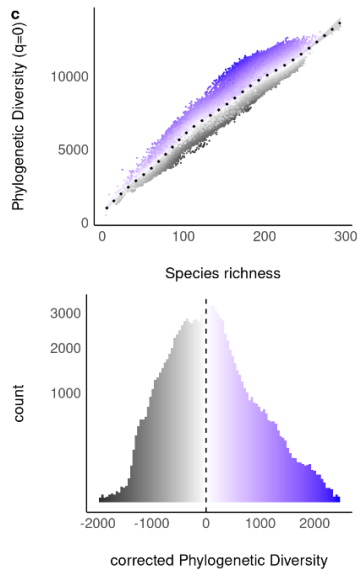
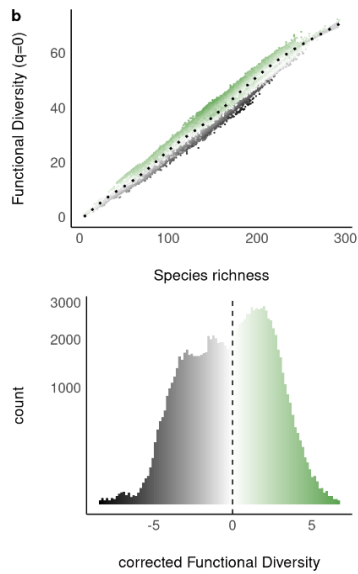
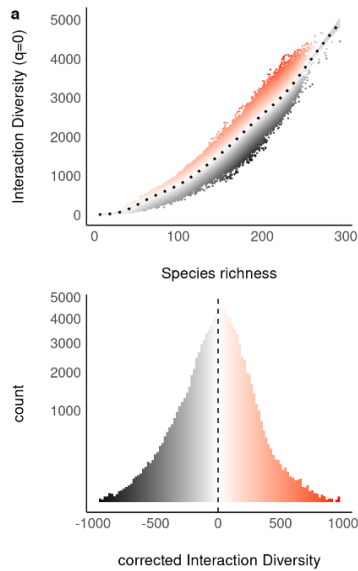
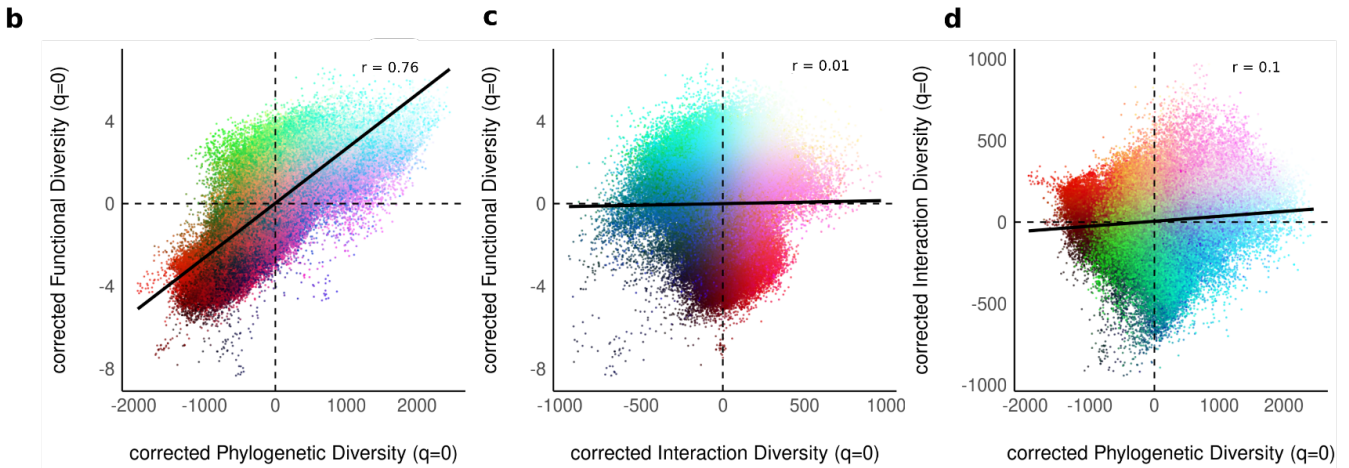
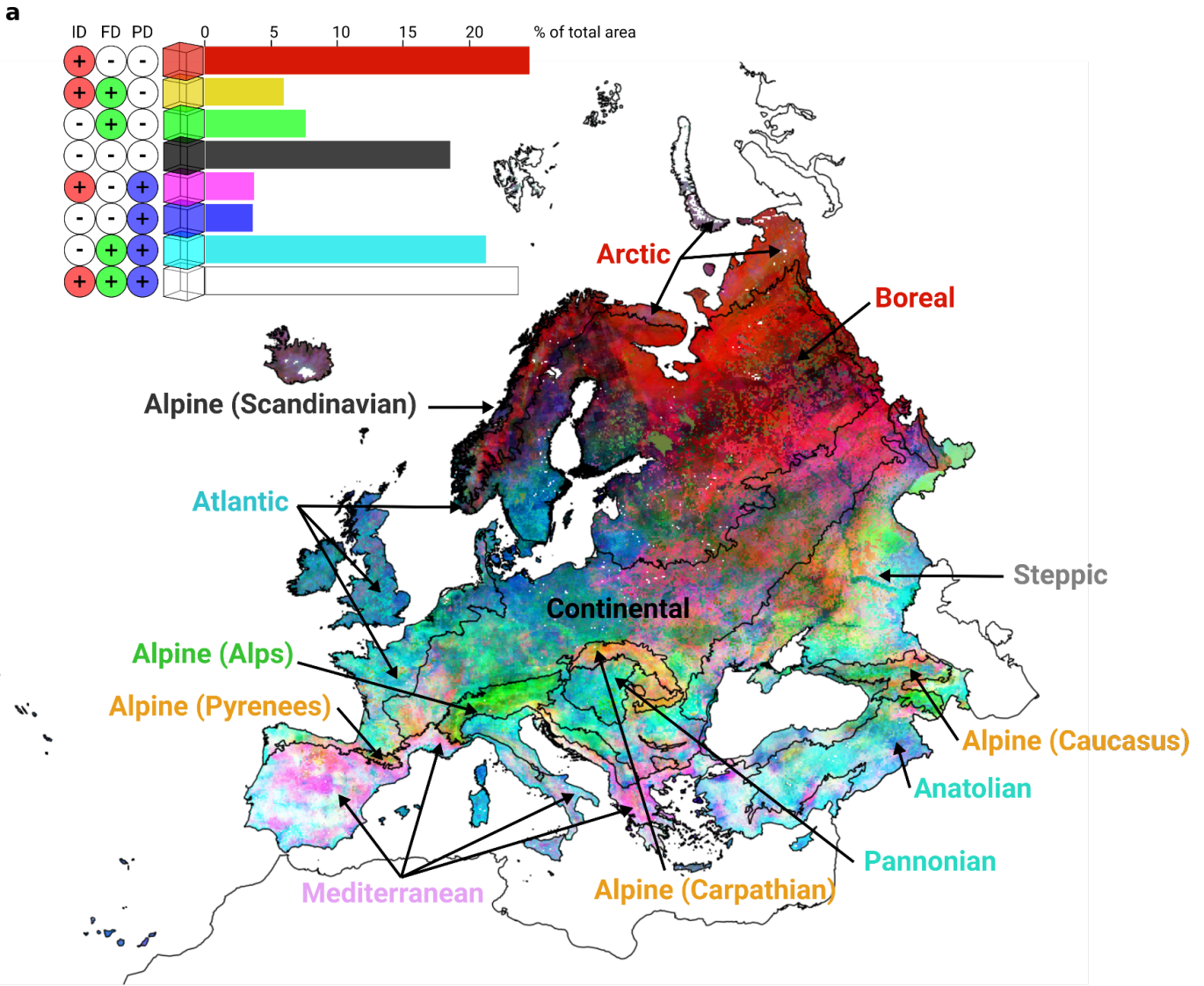


Figure 2. Patterns of Interaction diversity ID (a, in red), Functional diversity FD (b, in green), and Phylogenetic diversity PD (c, in blue). Top left: Relationship between each diversity facet and the species richness. Dotted lines show relationships as fitted by Generalized Additive Models. Bottom 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 ⁵³.
157 Beyond species distribution, biodiversity facets such as phylogenetic diversity already have been shown to
158 match some ecological regions across the globe ⁵⁴. 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.



169 **Figure 3.** (a) Spatial projection of the 3-dimensional diversity space. In the top left barplot, we created 8 discrete categories based on the
 170 combinations of deficits (-) and surpluses (+) of each diversity and reported the number of cells falling in each category. In the map, points are
 171 colored by their location in the Red-Green-Blue 3-dimensional color space, with each diversity facet corresponding to a distinct channel: Red
 172 channel = Interaction Diversity, Green Channel = Functional Diversity, Blue channel = Phylogenetic Diversity. black shows lowest ID-FD-PD values,
 173 white shows highest ID-FD-PD, and so on for each combination. Black lines show the boundaries of the European biogeographical regions. (b) Pair
 174 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
 175 (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.
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 179 Southern Europe showed strong diversity surpluses in all diversity facets (white / light color shades in
 180 Figure 3a), which confirms the Mediterranean bioregion as a multifaceted biodiversity hotspot^{55,56}. This
 181 result shows that, for a given number of species, local assemblages of Mediterranean terrestrial vertebrate
 182 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 ²²; and (ii) to a lesser extent from a high
192 degree of omnivory in the Iberian peninsula ²³.

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 ^{37,38}. 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 ^{26,57}. Species that live
205 under high latitudes tend to be trophic generalists ²³ because the higher seasonality in high latitudes
206 promotes the evolution of larger niche breadth, in accordance with the latitude–niche breadth hypothesis
207 ^{57,58}.

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 ⁵⁹.

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 ²³, 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 ^{9,46}. 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 ⁶⁰. 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 ^{60–63}. 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) ^{45,64}.

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 ²¹. 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 ^{19,25}). 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 ⁶⁵. 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 ⁶⁶.

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 ³⁶, more densely connected trophic networks are
261 generally considered as desirable from a conservation point of view ⁹. Areas with surpluses of interactions
262 represent interaction networks that are expected to be more robust to cascading species extinctions ³⁴, and
263 consequently more resilient to perturbations. Coupled with its apparent sensitivity to human activities ²³,
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

269 Study area and data

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

277
278
279 Species distributions. We extracted the distributions for all terrestrial vertebrates naturally occurring within
280 the study area from Maiorano et al. (2013). Species distributions for 509 bird, 288 mammal, 250 reptile and
281 104 amphibian species were mapped by combining the IUCN extent of occurrence for each species with
282 their habitat requirements. A species was considered potentially present in a 10×10 km cell if the grid cell
283 met the three following criteria: i) is within the species extent of occurrence, ii) contains at least one
284 300x300m area of primary habitat for the species, i.e. habitat where the species can persist (defined by
285 experts and published literature) and iii) meets species requirements in terms of elevation and distance
286 from water. A full description of species distribution data and definition of primary habitat can be found in
287 Maiorano et al. 2013 ²⁷. In addition, we used the percentage of primary habitat of the species in each cell as
288 a proxy for the probability to find the species in a random locality within this cell. For example, we
289 considered that if the primary habitat of a species covered 80% of the cell, the probability to find the
290 species in a random locality of the cell was 0.8. As such, it represents a proxy for the probability of
291 presence of the species within the cell and was used as a weight in the entropy-based diversity measures
292 (i.e when q=1) provided as supplementary analyses.

293
294 Functional traits. We gathered biological trait data from Thuiller et al. 2015 ²⁸, excluding traits describing
295 diet (and thus trophic interactions) and traits for larvae and juveniles. Our analysis was based on four life-
296 history and ecological traits common to mammals, amphibians, birds and reptiles. The only quantitative trait
297 was body mass [grams, log-transformed]. The three other traits were multichoice nominal variables coded
298 by binary values. Feeding behavior was coded by four binary columns: opportunistic feeder, active hunter,
299 browser, grazer. Nesting location was coded by eleven binary columns: tree/hole/fissure in bark, ground,
300 rocks, building/artificial, underground water, cave/fissures/burrows, lodge, temporary water,
301 brooks/springs/small rivers, puddles/ponds/pools/small lakes, brackish waters. Activity time was coded by
302 four binary columns: nocturnal, crepuscular, diurnal, arrhythmic. These traits were selected because they
303 represent informative niche dimensions linked to the use and acquisition of resources in space and time,
304 and are related to ecosystem functioning ^{69,70}. A thorough description of traits and the list of publications
305 where the data were gathered is available in supplementary material from ²⁸ available at
306 <https://royalsocietypublishing.org/doi/suppl/10.1098/rstb.2014.0005>.

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

312
313 Phylogenetic tree. We used the 100 phylogenetic trees for European terrestrial vertebrates assembled and
314 published by Roquet et al. 2014 ²⁹. We chose these phylogenetic trees as they are the only species-level
315 phylogenies encompassing all european vertebrates, and have already been valuably used to depict
316 phylogenetic diversity in this context vertebrates in the past ^{28,32,73,74}.

319 Trophic networks. We used data on species trophic interactions from the metaweb of European terrestrial
320 vertebrates, (Tetra-EU 1.0, ³⁰). 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 ³⁰.

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 ³¹ 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 ³¹ implemented in the R package hillR
346 for phylogenetic and functional diversity and in the package econetwork ¹⁸ 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 ¹ 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 ³¹, and in Ohlmann et al. 2019 ¹⁸
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 ^{32,33}. 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

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