

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

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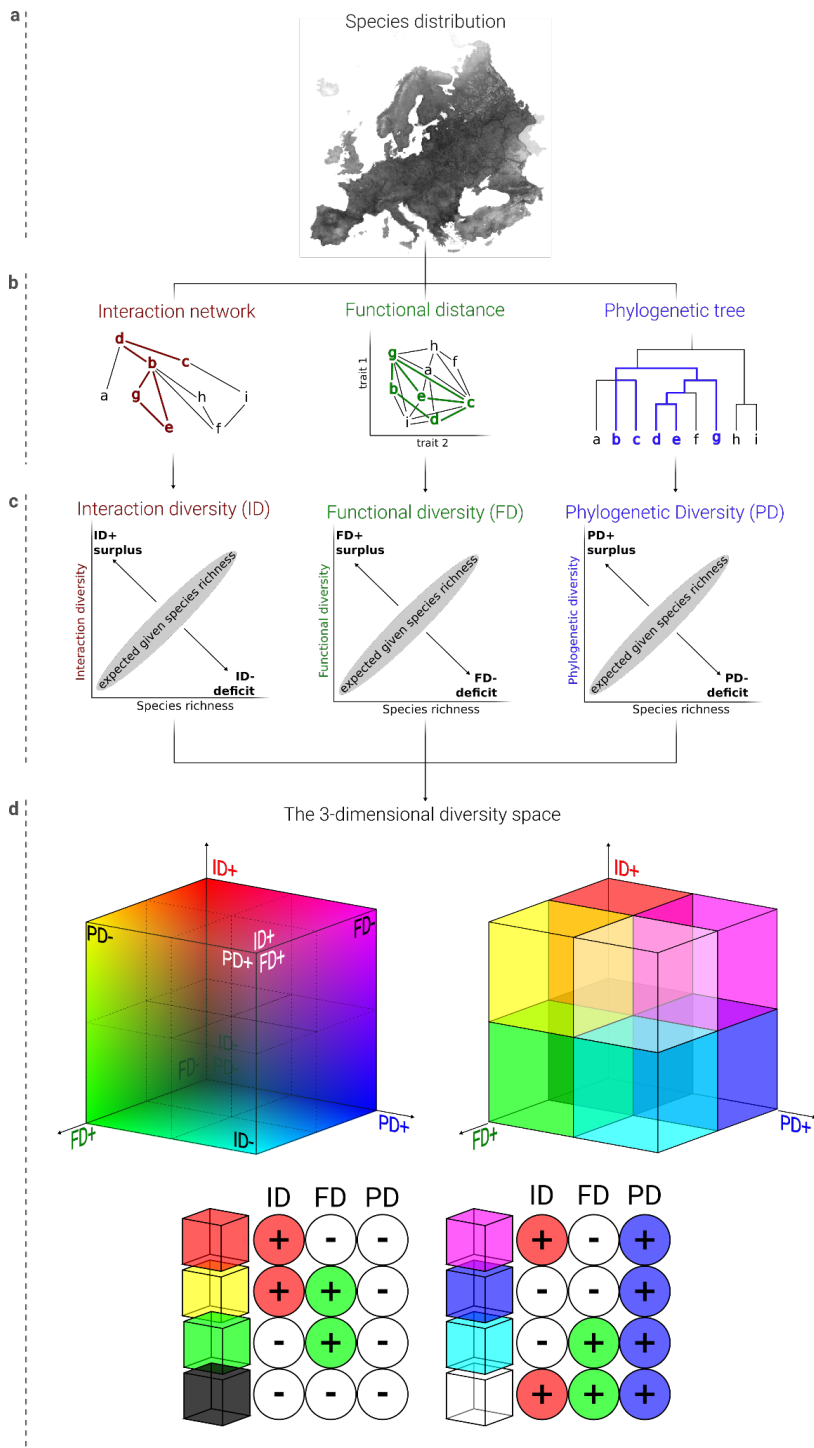
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## 15 Keywords

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.



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 10x10km 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,  $z = ID$  /  
48 red), 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 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.

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

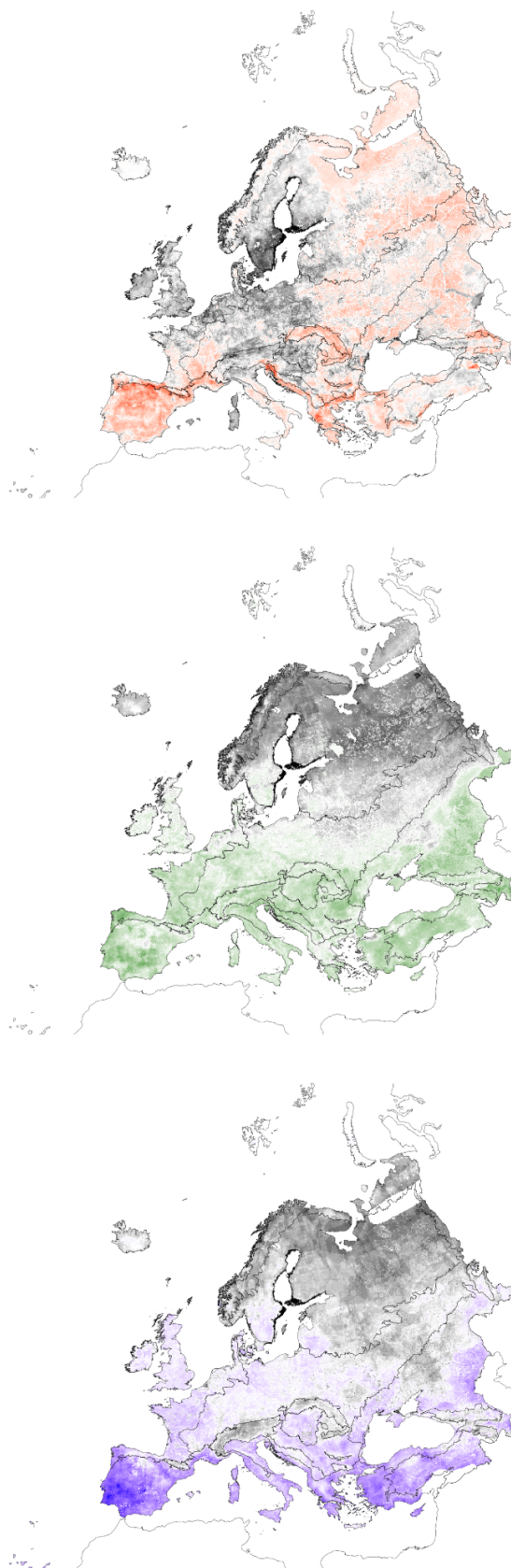
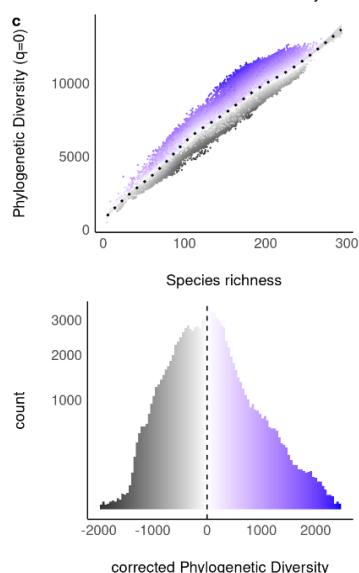
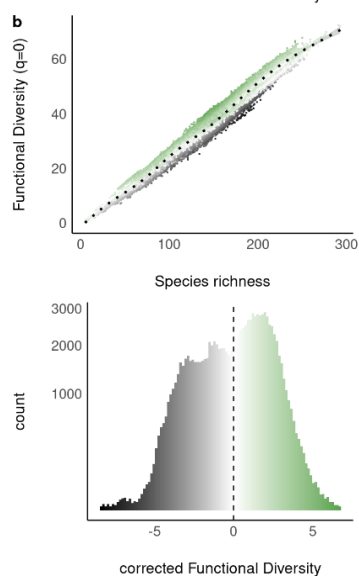
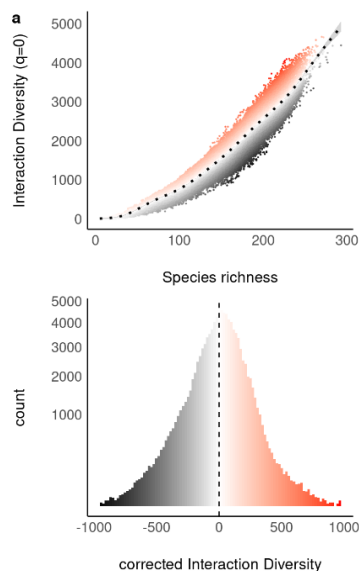
In its simplest form, ID is the total number of interactions shared by all species of a given assemblage<sup>9</sup>. Interactions considered can be of different types and nature, e.g antagonistic (competition for resources), mutualistic (pollination<sup>15,16</sup>), or trophic (predation<sup>17</sup>).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

#### Surpluses and deficits of diversities

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

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

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

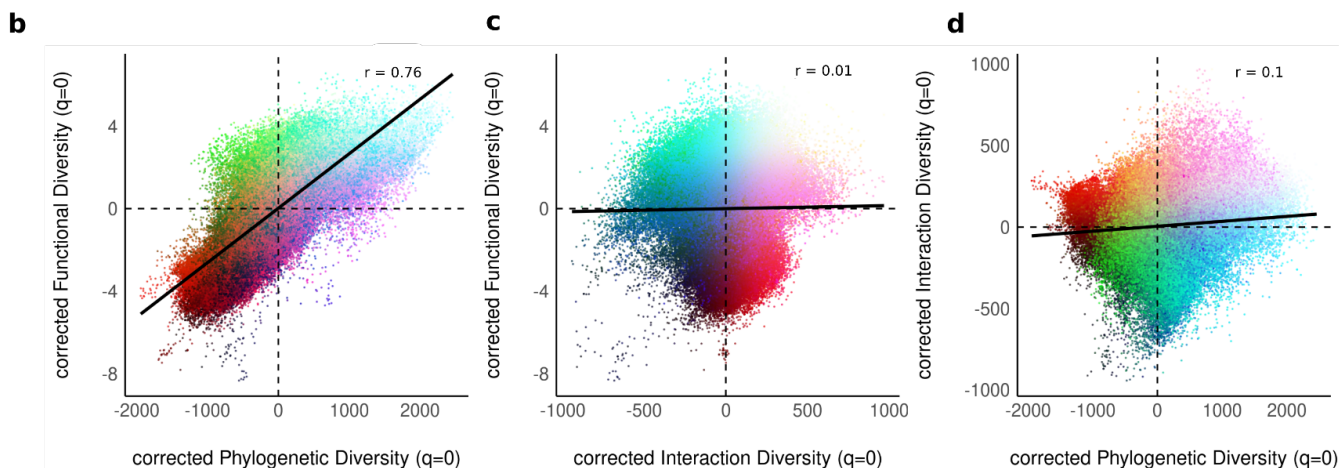
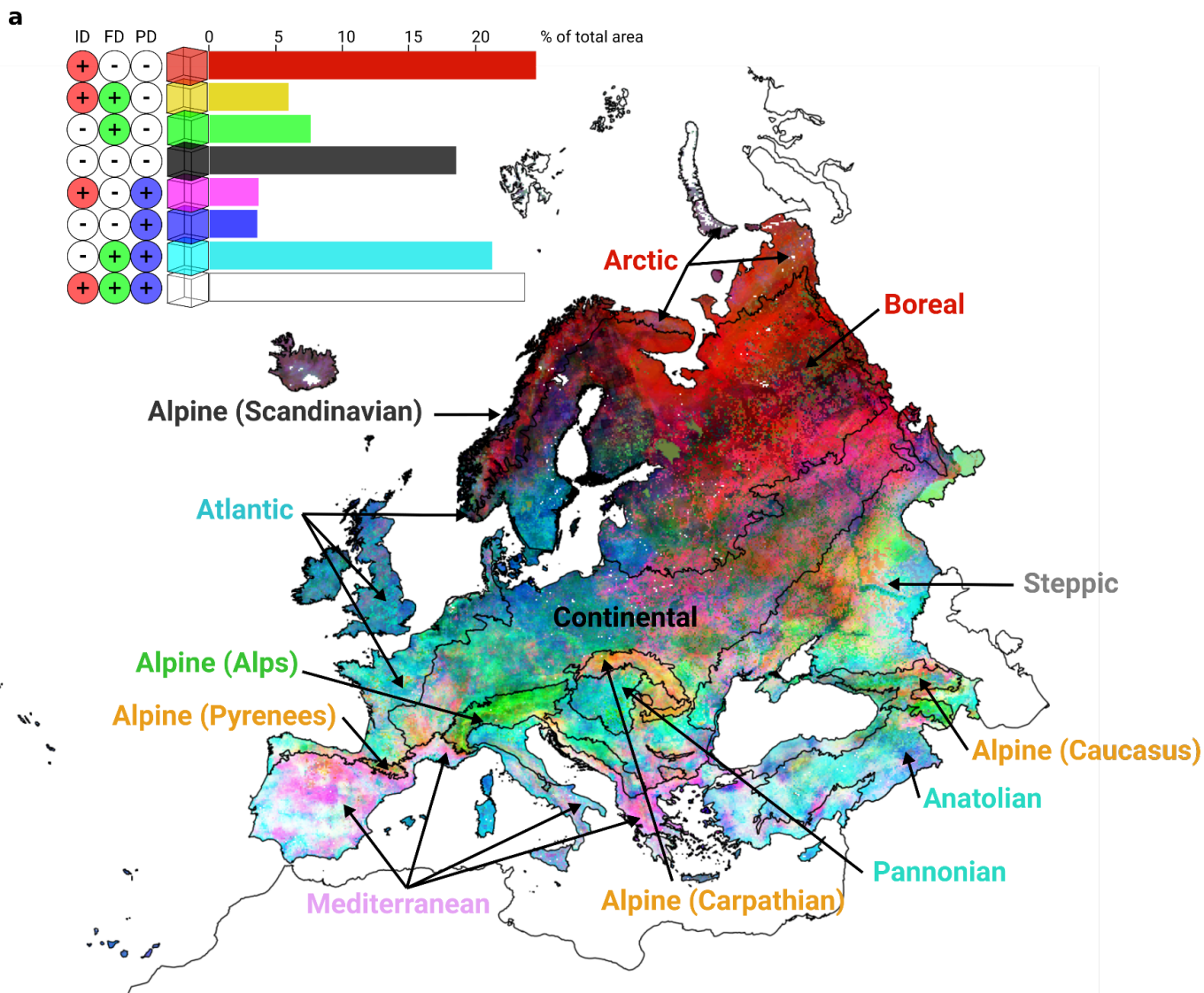


**Figure 2.** Patterns of Interaction diversity ID (a, in red), Functional diversity FD (b, in green), and Phylogenetic diversity PD (c, in blue). Top left: Relationship between each diversity facet and the species richness. Dotted lines show relationships as fitted by Generalized Additive Models. Bottom 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.





**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

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

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

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

#### Potential drivers of diversity facets

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

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

The importance of interaction diversity

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

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



## 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>.

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

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

Diversity measures and the 3-dimensional diversity space

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

We focused our study on richness-based results ( $q=0$ ) as they are the easiest to interpret, but we also analyzed and showed results based on Shannon entropy in the [Supplemental information - Results based on Shannon entropy](#). To compute the results as a Shannon entropy, we set  $q=1$  and used the % of species' primary habitat within the cell as the probability to find the species in the cell. More precisely, when  $q=1$  the ID entropy is the Shannon entropy over the interaction weights (product of the two species abundances), the FD is the Shannon entropy of effective number of species-pairs with unit-distance between species, and the PD is the mean Shannon entropy of the effective total branch length across the 100 trees. More 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> for ID.

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

To investigate the congruence between the interaction, functional and phylogenetic facets of biodiversity, we created a 3-dimensional space where each dimension represents one diversity facet. In order to visualize all possible combinations of biodiversity facets, we attributed a color channel for each diversity facet (red = ID, green = FD, blue = PD) where the residual values for each diversity were rescaled to 0-255 value in the corresponding color channel (Figure 1). Hence, each combination of three color channels (Red, Blue, Green) results in a particular color in the RGB color space that corresponds to a given combination of three diversity facets, and allows us to identify a continuum of ID-FD-PD combinations depicted in figure 1.d. We can also interpret particular types of combinations by discretizing colors based on the combinations of surplus and deficits of each diversity. As shown in Figure 1d and Figure 3a, Red identifies surpluses of ID and FD associated with deficits in 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.

## SUPPLEMENTAL INFORMATION

Supplemental Information includes six appendix and can be found at:

## AUTHOR CONTRIBUTIONS

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 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 authors contributed substantially to the interpretation of the results and to the writing of the manuscripts and its revisions.

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