Current Biology

The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity

Highlights

- Biotic interactions (ID) can be considered and studied as a biodiversity facet

- ID is not correlated to FD and PD

- ID patterns reveal new interaction-rich areas in the European Boreal region

- ID adds new and ecologically relevant information to FD and PD

Authors

Pierre Gaüzère, Louise O'Connor, Christophe Botella, ..., Luigi Maiorano, Michael Harfoot, Wilfried Thuiller

Correspondence

pierre.gauzere@gmail.com

In brief

Gaüzère et al. show that the diversity of biotic interactions (ID) brings unique and complementary information to the FD and PD. Once corrected by species richness, ID was not correlated with FD and PD. Mapping combinations of ID/FD/PD reveals new interaction-rich areas in European Boreal region.

CellPress

Report

The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity

Pierre Gaüzère,[1,7,8,*] Louise O'Connor,[1] Christophe Botella,[1] Giovanni Poggiato,[1] Tamara Münkemüller,[1] Laura J. Pollock,[2] Ulrich Brose,[3,4] Luigi Maiorano,[5] Michael Harfoot,[6] and Wilfried Thuiller[1]

[1]University Grenoble Alpes, University Savoie Mont Blanc, CNRS, LECA, 38000 Grenoble, France
[2]Biology Department, McGill University, Montréal, QC H3A 1B1, Canada
[3]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany
[4]German Center for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany
[5]Department of Biology and Biotechnologies "Charles Darwin," "Sapienza" University of Rome, Rome, Italy
[6]United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, UK
[7]Twitter: @pierregauz
[8]Lead contact
*Correspondence: pierre.gauzere@gmail.com
https://doi.org/10.1016/j.cub.2022.03.009

SUMMARY

Taxonomic, functional, and phylogenetic diversities are important facets of biodiversity. Studying them together has improved our understanding of community dynamics, ecosystem functioning, and conservation values.[1–3] In contrast to species, traits, and phylogenies, the diversity of biotic interactions has so far been largely ignored as a biodiversity facet in large-scale studies. This neglect represents a crucial shortfall because biotic interactions shape community dynamics, drive important aspects of ecosystem functioning,[4–7] provide services to humans, and have intrinsic conservation value.[8,9] Hence, the diversity of interactions can provide crucial and unique information with respect to other diversity facets. Here, we leveraged large datasets of trophic interactions, functional traits, phylogenies, and spatial distributions of >1,000 terrestrial vertebrate species across Europe at a 10-km resolution. We computed the diversity of interactions (interaction diversity [ID]) in addition to functional diversity (FD) and phylogenetic diversity (PD). After controlling for species richness, surplus and deficits of ID were neither correlated with FD nor with PD, thus representing unique and complementary information to the commonly studied facets of diversity. A three-dimensional mapping allowed for visualizing different combinations of ID-FD-PD simultaneously. Interestingly, the spatial distribution of these diversity combinations closely matched the boundaries between 10 European biogeographic regions and revealed new interaction-rich areas in the European Boreal region and interaction-poor areas in Central Europe. Our study demonstrates that the diversity of interactions adds new and ecologically relevant information to multifacetted, large-scale diversity studies with implications for understanding eco-evolutionary processes and informing conservation planning.

RESULTS AND DISCUSSION

Biodiversity—the diversity of life on Earth—was originally used to refer to species diversity, but it is now used to reflect a multifaceted concept.[3] Given the evidence that species diversity alone cannot appropriately describe community assembly, ecosystem functioning, and variation in community composition,[10] several complementary measures of biodiversity have emerged in the last three decades.[1,2] The most important measure is 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,[11,12] the diversity of biotic interactions (i.e., interaction diversity [ID]) has been poorly considered as a biodiversity facet in large-scale studies (but see Thompson et al.[8] and Dyer

et al.[13]). This is a major gap since biological interactions are tightly linked to species coexistence,[14] ecosystem productivity, and functioning.[4–7]

In its simplest form, ID is the total number of interactions shared by all species of a given assemblage.[9] Interactions considered can be of different types and nature, for example, antagonistic (competition for resources), mutualistic (pollination[15,16]), or trophic (predation[17]). Although the concept of ID is not novel[8,13] and has its own methodological tools,[18,19] the lack of information available on biotic interactions[20,21] has limited its study across large taxonomical and spatial scales.[22–26] Here, we leveraged unique and valuable data combining spatial distributions[27] (Figure 1A), trophic interactions (Figure 1B), functional traits,[28] and phylogenies[29] of most terrestrial vertebrate species in Europe[30] at a 10-km resolution.
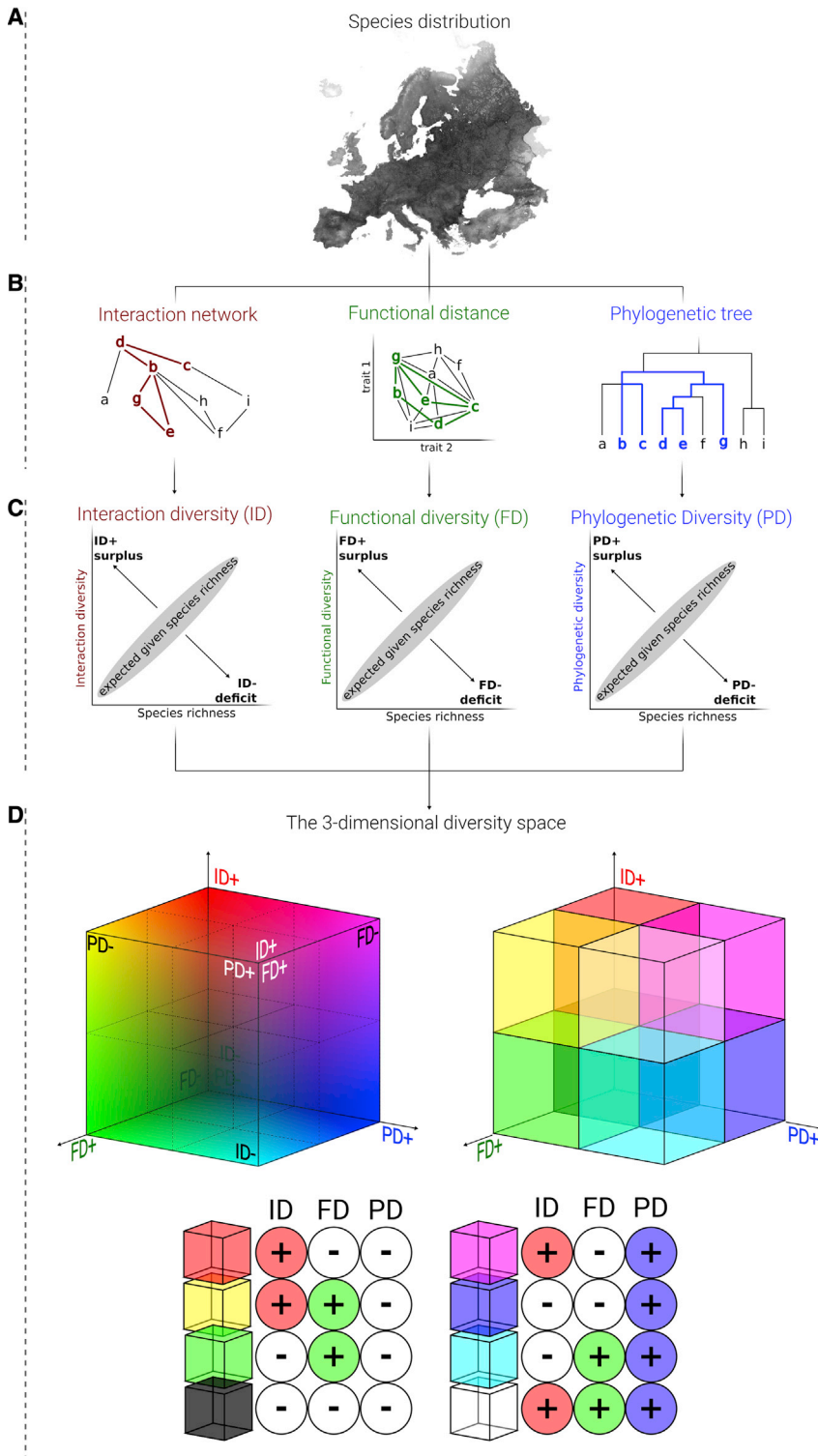
Figure 1. Conceptual workflow for a joint analysis of phylogenetic, functional, and interaction diversity (ID)

(A and B) Occurrences and probability of presence for 1,149 terrestrial vertebrate species on 117,000 10 × 10 km cells across Europe (A) are combined with the phylogenetic tree, a set of functional traits, and the trophic interactions of species (B).

(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 three-dimensional space with each axis representing a diversity facet and a color in the red-blue-green space (x = PD/blue, y = FD/green, and 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, and PD < 0); yellow identifies surpluses of ID and FD associated with deficits in PD (ID > 0, FD > 0, and PD < 0); green identifies deficits in ID and PD associated with FD surpluses (ID < 0, FD > 0, and 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.

richness[32,33] to measure and map deficits and surpluses of ID, FD, and PD (Figure 1C). We also investigated the correlation and complementarity between the three facets and created a three-dimensional diversity space that reveals different local combinations of ID-FD-PD (Figure 1D) and their distribution across biogeographical regions in Europe.

Surpluses and deficits of diversities

Trophic networks of terrestrial vertebrates found within 10-km cells in Europe contained up to 4,834 trophic interactions with an average of 1,958 interactions across cells (Figure 2A). Once corrected for species richness, ID ranged from a deficit of −942 interactions (1,667 observed interactions with 202 species involved) to a surplus of +968 interactions (3,730 interactions with 210 species involved). Because highly connected assemblages are often considered as the signature of functional and resilient ecosystems,[34,35] areas with high ID are important from a conservation point of view.[34,36] Furthermore, 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
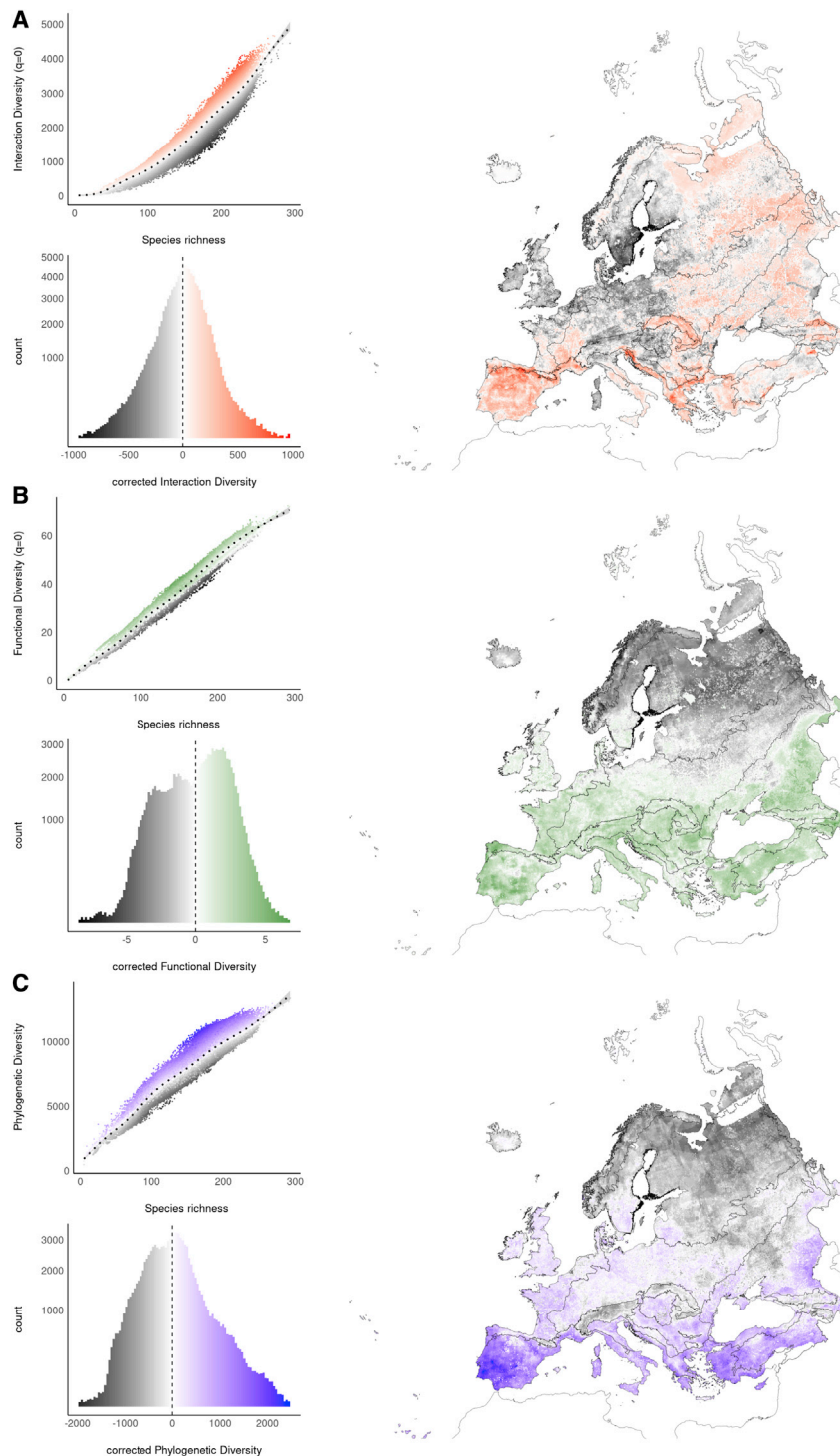
Within each 10-km cell, we computed ID (as the number of trophic interactions), FD (as the sum of functional pairwise Gower distances between species in the cell), and PD (as the sum of the branch lengths of the phylogenetic tree containing all species present in the cell[1]) using Hill numbers.[18,31] We statistically corrected each diversity by the local species

Figure 2. Patterns of diversity facets

(A) Interaction diversity (ID), in red.
(B) Functional diversity (FD), in green.
(C) Phylogenetic diversity (PD), 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, and blue for PD). Right: spatial distribution of corrected values for each biodiversity facet color corresponds to distributions on the left. See also Figures S1–S3.

and trait data contain information about evolutionary history and species niches, the spatial distribution of their diversity (Figures 2B and 2C) is thought to hold the signature of the eco-evolutionary drivers that shape biodiversity patterns.[37–39] For example, for a given species richness, an observed surplus of FD (Figures 1D and 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.[40] PD surplus (Figures 1D and 2C, dark blue color) could result from slow extinction rates of old and distant lineages (i.e., museums of biodiversity[41]) and PD deficit from rapid recent speciation (i.e., cradles of biodiversity). ID surplus and deficit bring additional information, as observed ID surplus (Figures 1D and 2A, red color) indicates particularly dense or long trophic networks, such as those emerging from high levels of omnivory and intraguild predation[42] 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.[43–45]

Overall, the different facets of diversity are shaped by eco-evolutionary drivers that are not mutually exclusive.[46] 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[38,47–49] and suggests an important effect of evolution and phylogenetic niche conservatism on biodiversity patterns.[47,50,51] 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[46,52]), this was not what we observed (Figures 3C and 3D). Instead, ID represented unique and complementary information to the commonly studied facets of diversity.
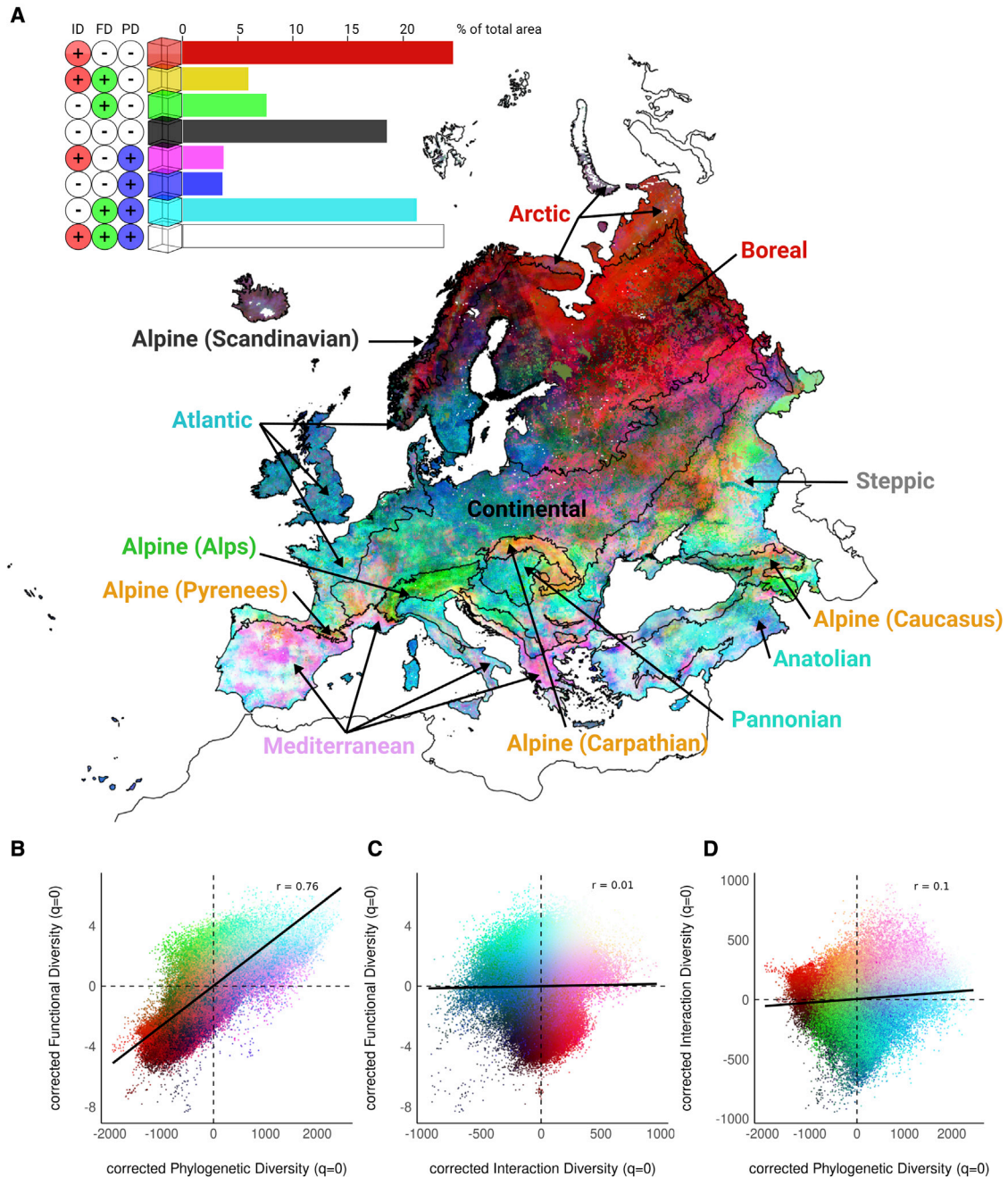
Figure 3. The combinations of diversities in the three-dimensional diversity space

(A) Geographic projection of the three-dimensional diversity space. In the top left barplot, we created eight 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 three-dimensional color space, with each diversity facet corresponding to a distinct channel: red channel, ID; green channel, FD; blue channel, PD. 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) versus corrected PD (x axis).

(C) Corrected FD (y axis) versus corrected ID (x axis).

(D) Corrected ID (y axis) versus corrected PD (x axis). In top right, r is the value of Pearson's product-moment correlation between y and x axes. Points' colors correspond to colors in the map.

Distribution of diversity combinations

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

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

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.[55,56] 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 explain the high diversity of amphibians and reptiles, as well as the presence of unique evolutionary lineages, leading to high

functional and phylogenetic diversities compared with the rest of Europe. In addition to these high levels of functional and phylogenetic diversities, the Mediterranean region showed surpluses in ID, in particular in the subregion of the Balkan peninsula. The densely connected trophic networks observed in the Mediterranean region resulted from (1) numerous top predators in this region previously identified as birds, felids, and snakes predating upon small reptiles and rodents[22] and (2) to a lesser extent from a high degree of omnivory in the Iberian peninsula.[23]

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 ID (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.[37,38] 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,[23] which is known to increase trophic network connectance.[26,57] Species that live under high latitudes tend to be trophic generalists[23] because the higher seasonality in high latitudes promotes the evolution of larger niche breadth, in accordance with the latitude-niche breadth hypothesis.[57,58]

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 ID 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 (Figures 2B and 2C). 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 ID. The Carpathians displayed a clear ID surplus (Figure 3, yellow), while the Alps displayed ID deficit (Figure 3, green). The proximate cause of such difference was the rarity of top predators in the Alps compared with the Carpathians (see maps of relevant network properties in supplemental information). Human influence likely explains this discrepancy because many apex predators (bears, wolves, and lynx) that are often trophic generalists are still present in the Carpathians, while they were exterminated in the Alps.[59]

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[23] and suggests that the diversity of interactions is influenced by different drivers than functional and PD. It is, however, noteworthy that other studies reported higher connectance in more human-impacted systems.[9,46] 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.[60] However, its consequences on large-scale patterns of ID have been largely overlooked although they are probably stronger. Indeed, human activities have been (and still are) particularly detrimental to large-bodied species.[60–63] 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).[45,64]

The importance of ID

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.[21] 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, e.g., Poisot et al.[19] and Gravel et al.[25]). 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.[65] Combining both approaches (inferring interactions from a metanetwork and species distribution versus observing interactions) and comparing their accuracy across a range of temporal and spatial scales will provide valuable insights in community ecology and biogeography.[66]

Although ID patterns appear robust to spatial contexts (Figure S1) and data depletion (Figure S2), whether the patterns described in this study can be extrapolated to other biomes remain 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 ID is a particularly valuable facet for biogeography and conservation planning. Although this view has been empirically challenged,[36] more densely connected trophic networks are generally considered as desirable from a conservation point of view.[9] Areas with surpluses of interactions represent interaction networks that are expected to be more robust to cascading species extinctions[34] and consequently more resilient to perturbations. Coupled with its apparent sensitivity to human activities,[23] ID might be viewed as a marker of both ecosystem degradation and resistance to future degradation. We argue that a general consideration of ID as an important and meaningful diversity facet alongside the functional and phylogenetic diversities should be a priority for macroecology and conservation biogeography.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- METHOD DETAILS
  - Study area and data
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Diversity measures and corrections
  - Building 3-dimensional diversity space

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 input 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.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. Biol. Conserv. *61*, 1–10.

2. Tilman, D. (2001). Functional diversity. In Encyclopedia of Biodiversity, S.A. Levin, ed. (Elsevier), pp. 109–120.

3. Pollock, L.J., O'Connor, L.M.J., Mokany, K., Rosauer, D.F., Talluto, M.V., and Thuiller, W. (2020). Protecting biodiversity (in all its complexity): new models and methods. Trends Ecol. Evol. *35*, 1119–1128.

4. Grime, J.P. (1997). Biodiversity and ecosystem function: the debate deepens. Science *277*, 1260–1261.

5. Tilman, D., Isbell, F., and Cowles, J.M. (2014). Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. *45*, 471–493.

6. Brose, U., Blanchard, J.L., Eklöf, A., Galiana, N., Hartvig, M., R Hirt, M., Kalinkat, G., Nordström, M.C., O'Gorman, E.J., Rall, B.C., et al. (2017). Predicting the consequences of species loss using size-structured biodiversity approaches. Biol. Rev. Camb. Philos. Soc. *92*, 684–697.

7. Schneider, F.D., Brose, U., Rall, B.C., and Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. Nat. Commun. *7*, 12718.

8. Thompson, J.N. (1997). Conserving interaction biodiversity. In The Ecological Basis of Conservation: Heterogeneity, Ecosystems and Biodiversity, S.T.A. Pickett, R.S. Ostfeld, M. Shachak, and G.E. Likens, eds. (Springer), pp. 285–293.

9. Tylianakis, J.M., Laliberté, E., Nielsen, A., and Bascompte, J. (2010). Conservation of species interaction networks. Biol. Conserv. *143*, 2270–2279.

10. Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchmann, N., Degrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., et al. (2002). Species diversity, functional diversity and ecosystem functioning. Biodivers. Ecosyst. Functioning Synth. Perspect. 195–208.

11. De Palma, A., Kuhlmann, M., Bugter, R., Ferrier, S., Hoskins, A.J., Potts, S.G., Roberts, S.P.M., Schweiger, O., and Purvis, A. (2017). Dimensions of biodiversity loss: spatial mismatch in land-use impacts on species, functional and phylogenetic diversity of European bees. Divers. Distrib. *23*, 1435–1446.

12. Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., Madritch, M.D., Wang, R., Tilman, D., and Gamon, J.A. (2018). Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. Nat. Ecol. Evol. *2*, 976–982.

13. Dyer, L.A., Walla, T.R., Greeney, H.F., Stireman, J.O., III, and Hazen, R.F. (2010). Diversity of interactions: a metric for studies of biodiversity: interaction diversity. Biotropica *42*, 281–289.

14. Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., and Gravel, D. (2016). No complexity–stability relationship in empirical ecosystems. Nat. Commun. *7*, 12573.

15. Burkle, L.A., and Alarcón, R. (2011). The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. Am. J. Bot. *98*, 528–538.

16. Burkle, L.A., Myers, J.A., and Belote, R.T. (2016). The beta-diversity of species interactions: untangling the drivers of geographic variation in plant-pollinator diversity and function across scales. Am. J. Bot. *103*, 118–128.

17. Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W.D., Lenoir, J., Sandel, B., Trøjelsgaard, K., Ejrnaes, R., and Svenning, J.C. (2013). Mammal predator and prey species richness are strongly linked at macroscales. Ecology *94*, 1112–1122.

18. Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L., and Thuiller, W. (2019). Diversity indices for ecological networks: a unifying framework using Hill numbers. Ecol. Lett. *22*, 737–747.

19. Poisot, T., Canard, E., Mouillot, D., Mouquet, N., and Gravel, D. (2012). The dissimilarity of species interaction networks. Ecol. Lett. *15*, 1353–1361.

20. Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., and Ladle, R.J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. Annu. Rev. Ecol. Evol. Syst. *46*, 523–549.

21. Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., Vissault, S., and Chapman, D. (2021). Global knowledge gaps in species interaction networks data. J. Biogeogr. *48*, 1552–1563.

22. O'Connor, L.M.J., Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez-Almoyna, C., Montemaggiori, A., Ohlmann, M., and Thuiller, W. (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. J. Biogeogr. *47*, 181–192.

23. Braga, J., Pollock, L.J., Barros, C., Galiana, N., Montoya, J.M., Gravel, D., Maiorano, L., Montemaggiori, A., Ficetola, G.F., Dray, S., et al. (2019). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. Glob. Ecol. Biogeogr. *28*, 1636–1648.

24. Cumming, G.S., Bodin, Ö., Ernstson, H., and Elmqvist, T. (2010). Network analysis in conservation biogeography: challenges and opportunities. Divers. Distrib. *16*, 414–425.

25. Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.P., Martinez, N.D., Nyman, T., Poisot, T., Stouffer, D.B., Tylianakis, J.M., Wood, S.A., et al. (2019). Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. Ecography *42*, 401–415.

26. Baiser, B., Gravel, D., Cirtwill, A.R., Dunne, J.A., Fahimipour, A.K., Gilarranz, L.J., Grochow, J.A., Li, D., Martinez, N.D., McGrew, A., et al. (2019). Ecogeographical rules and the macroecology of food webs. Glob. Ecol. Biogeogr. *28*, 1204–1218.

27. Maiorano, L., Amori, G., Capula, M., Falcucci, A., Masi, M., Montemaggiori, A., Pottier, J., Psomas, A., Rondinini, C., Russo, D., et al. (2013). Threats from climate change to terrestrial vertebrate hotspots in Europe. PLoS One *8*, e74989.

28. Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G.F., Lavergne, S., Renaud, J., Roquet, C., and Mouillot, D. (2015). Conserving the functional and phylogenetic trees of life of European tetrapods. Philos. Trans. R. Soc. Lond. B Biol. Sci. *370*, 20140005.

29. Roquet, C., Lavergne, S., and Thuiller, W. (2014). One tree to link them all: a phylogenetic dataset for the European Tetrapoda. PLoS Curr. *6*, ecurrent-s.tol.5102670fff8aa5c918e78f5592790e48.

30. Maiorano, L., Montemaggiori, A., Ficetola, G.F., O'Connor, L., and Thuiller, W. (2020). Tetra-EU 1.0: a species-level trophic metaweb of European tetrapods. Glob. Ecol. Biogeogr. *29*, 1452–1457.

31. Chao, A., Chiu, C.-H., and Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu. Rev. Ecol. Evol. Syst. *45*, 297–324.

32. Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N., Renaud, J., and Thuiller, W. (2014). Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. Divers. Distrib. *20*, 674–685.

33. Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K., and Diniz-Filho, J.A.F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 2536–2544.

34. Gilbert, A.J. (2009). Connectance indicates the robustness of food webs when subjected to species loss. Ecol. Indic. *9*, 72–80.

35. Thébault, E., and Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. Science *329*, 853–856.

36. Heleno, R., Devoto, M., and Pocock, M. (2012). Connectance of species interaction networks and conservation value: is it any good to be well connected? Ecol. Indic. *14*, 7–10.

37. McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends Ecol. Evol. *21*, 178–185.

38. Webb, C.O., Ackerly, D.D., McPeek, M.A., and Donoghue, M.J. (2002). Phylogenies and community ecology. Annu. Rev. Ecol. Syst. *33*, 475–505.

39. Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F., Mokany, K., Roquet, C., Smyčka, J., et al. (2020). Dos and don'ts when inferring assembly rules from diversity patterns. Glob. Ecol. Biogeogr. *164*, S165.

40. Mayfield, M.M., and Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecol. Lett. *13*, 1085–1093.

41. Stebbins, G.L. (1974). Flowering Plants: Evolution Above the Species Level (Belknap Press of Harvard University Press).

42. Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E., and Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol. Lett. *10*, 522–538.

43. Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., et al. (2011). Trophic downgrading of planet Earth. Science 333, 301–306.

44. de Visser, S.N., Freymann, B.P., and Olff, H. (2011). The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. J. Anim. Ecol. 80, 484–494.

45. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. Science 279, 860–863.

46. Tylianakis, J.M., and Morris, R.J. (2017). Ecological networks across environmental gradients. Annu. Rev. Ecol. Evol. Syst. 48, 25–48.

47. Wiens, J.J., and Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519–539.

48. Peterson, A.T., Sober n, J., and Sanchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.

49. Lavergne, S., Mouquet, N., Thuiller, W., and Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. Annu. Rev. Ecol. Evol. Syst. 41, 321–350.

50. Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.A., Harrison, S.P., et al. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13, 1310–1324.

51. Münkemüller, T., Boucher, F.C., Thuiller, W., and Lavergne, S. (2015). Common conceptual and methodological pitfalls in the analysis of phylogenetic niche conservatism. Funct. Ecol. 29, 627–639.

52. Williams, R.J., and Martinez, N.D. (2000). Simple rules yield complex food webs. Nature 404, 180–183.

53. Noirfalise, A. (1987). Map of the Natural Vegetation of the Member Countries of the European Economic Community and the Council of Europe (European Commission).

54. Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.H., Graham, C.H., Graves, G.R., Jønsson, K.A., et al. (2013). An update of Wallace's zoogeographic regions of the world. Science 339, 74–78.

55. Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

56. Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., and Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas, F.E. Zachos, and J.C. Habel, eds. (Springer), pp. 3–22.

57. Cirtwill, A.R., Stouffer, D.B., and Romanuk, T.N. (2015). Latitudinal gradients in biotic niche breadth vary across ecosystem types. Proc. Biol. Sci. 282.

58. Vázquez, D.P., and Stevens, R.D. (2004). The latitudinal gradient in niche breadth: concepts and evidence. Am. Nat. 164, E1–E19.

59. Kaczensky, P., Chapron, G., Von Arx, M., Huber, D., Andrén, H., and Linnell, J. (2013). Status, management and distribution of large carnivores - bear, lynx, wolf & wolverine – in Europe (European Commission).

60. Fritz, S.A., Bininda-Emonds, O.R.P., and Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol. Lett. 12, 538–549.

61. Gaston, K.J., and Blackburn, T.M. (1995). Birds, body size and the threat of extinction. Phil. Trans. R. Soc. Lond. B 347, 205–212.

62. Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., and Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.

63. Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., and Collen, B. (2016). Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

64. Brose, U. (2010). Improving nature conservancy strategies by ecological network theory. Basic Appl. Ecol. 11, 1–5.

65. Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., and Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. J. Anim. Ecol. 81, 190–200.

66. Fortuna, M.A., Nagavci, A., Barbour, M.A., and Bascompte, J. (2020). Partner fidelity and asymmetric specialization in ecological networks. Am. Nat. 196, 382–389.

67. European Environmental Agency (2016). Biogeographical regions. https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3.

68. Roekaerts, M. (2002). The Biogeographical Regions Map of Europe. Basic Principles of Its Creation and Overview of Its Development (European Environmental Agency).

69. Luck, G.W., Lavorel, S., McIntyre, S., and Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. J. Anim. Ecol. 81, 1065–1076.

70. Sekercioglu, C.H. (2006). Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.

71. Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., and Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118, 391–402.

72. Gower, J.C., and Legendre, P. (1986). Metric and Euclidean properties of dissimilarity coefficients. J. Classif. 3, 5–48.

73. Pearman, P.B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N.E., and Thuiller, W. (2014). Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. Glob. Ecol. Biogeogr. 23, 414–424.

74. Saladin, B., Thuiller, W., Graham, C.H., Lavergne, S., Maiorano, L., Salamin, N., and Zimmermann, N.E. (2019). Environment and evolutionary history shape phylogenetic turnover in European tetrapods. Nat. Commun. 10, 249.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Tetrapods European distributions	[27]	N/A
Tetrapods Traits	[28]	N/A
Tetrapods Phylogenetic tree	[29]	N/A
Tetrapods Trophic interaction network	[30]	N/A
Biogeographical regions	[67]	https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3
Software and algorithms		
R package hillR	[31]	https://github.com/daijiang/hillR
R package econetwork	[18]	https://plmlab.math.cnrs.fr/econetproject/econetwork
R package NetIndices	N/A	https://CRAN.R-project.org/package=NetIndices
R code used to perform analyses of this paper	N/A	https://doi.org/10.5281/zenodo.5960930

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Pierre Gaüzère (pierre.gauzere@gmail.com).

Materials availability
This study did not generate new unique reagents.

Data and code availability
All data used in this paper are from published or downloadable online sources. See key resources table for links toward the basal data. The code used to run analyses is available in the following zenodo repository: https://doi.org/10.5281/zenodo.5960930

METHOD DETAILS

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:[67] 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,[68] 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.[27] 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.[27] 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,[28] 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.[69,70] A thorough description of traits and the list of publications where the data were gathered is available in supplementary material from Thuiller et al.[28] 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.[71] 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[72]).

Phylogenetic tree

We used the 100 phylogenetic trees for European terrestrial vertebrates assembled and published by Roquet at al. 2014.[29] 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.[28,32,73,74]

Trophic networks

We used data on species trophic interactions from the metaweb of European terrestrial vertebrates, (Tetra-EU 1.0[30]). 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 Maiorano et al. 2020.[30]

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 (not shown).

QUANTIFICATION AND STATISTICAL ANALYSIS

Diversity measures and corrections

Within each 10x10km cell, we used Hill numbers[31] 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[31] implemented in the R package hillR for phylogenetic and functional diversity and in the package econetwork[18] 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[1] 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 Figure S3. 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,[31] and in Ohlmann et al. 2019[18] 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.[32,33] In other words, a deficit (or surplus) indicates a lower (or higher, respectively) diversity value than expected given the local species richness (Figure 1) .

Building 3-dimensional diversity space

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 1D. 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 Figures 1D and 3A, 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.