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Dissimilarity of vertebrate trophic interactions reveals spatial uniqueness but functional redundancy across Europe

Highlights

- The interaction dissimilarity between networks can measure their spatial uniqueness
- Networks in southern Europe are unique and vulnerable to human footprint
- Networks in the Arctic are unique and vulnerable to future climate change
- Considering trophic groups instead of interactions, networks are rather redundant

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In brief

Gaüzère et al. estimate the spatial uniqueness of vertebrates' trophic networks in Europe based on interaction dissimilarities. Unique networks situated in southern Europe are exposed to human footprint, while Arctic ones are at risk from future climate change. In terms of functional groups, trophic networks are redundant across Europe.



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Report

Dissimilarity of vertebrate trophic interactions reveals spatial uniqueness but functional redundancy across Europe

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SUMMARY

Identifying areas that contain species assemblages not found elsewhere in a region is central to conservation planning.^{1,2} Species assemblages contain networks of species interactions that underpin species dynamics,^{3,4} ecosystem processes, and contributions to people.^{5–7} Yet the uniqueness of interaction networks in a regional context has rarely been assessed. Here, we estimated the spatial uniqueness of 10,000 terrestrial vertebrate trophic networks across Europe (1,164 species, 50,408 potential interactions⁸) based on the amount of similarity between all local networks mapped at a 10 km resolution. Our results revealed more unique networks in the Arctic bioregion, but also in southern Europe and isolated islands. We then contrasted the uniqueness of trophic networks with their vulnerability to human footprint and future climate change and measured their coverage within protected areas. This analysis revealed that unique networks in the Arctic might be at risk from future climate change. However, considering interaction networks at the level of trophic groups, rather than species, revealed that the general structure of trophic networks was redundant across the continent, in contrast to species' interactions. We argue that proactive European conservation strategies might gain relevance by turning their eyes toward interaction networks that are both unique and vulnerable.

RESULTS AND DISCUSSION

Biological conservation aims at developing conservation strategies that are both effective and ecologically relevant.⁹ For this purpose, it is important to identify areas that contain biodiversity features not found elsewhere in the region of interest.^{1,2} Such unique areas are often assumed to be worth protecting because the biodiversity features they encapsulate may entirely disappear upon a severe disturbance. In this context, it is also crucial to consider their vulnerability, i.e., the exposure of these sites to threats (sensu Margules and Pressey¹⁰). Following this rationale, most conservation strategies focus on areas that are both vulnerable and unique, i.e., following a reactive conservation approach.^{1,11} There are different ways of quantifying uniqueness.¹²⁻¹⁴ Among others, it can be defined as the lack of redundancy or similarity of a site compared with other sites in a reserve network or a region of interest.^{15–17} Similarity measures reflect the number of features (e.g., species, functions, etc.) that are shared between pairs of sites. They can thus be used to identify either a minimum set of complementary sites that maximizes overall diversity within a region, or unique sites that have characteristics not found elsewhere (or only to a limited extent) in the region of interest.^{15,18} Yet defining a region of interest when working at continental scale is challenging, and it is noteworthy that the output will be intrinsically contingent to the chosen area. For example, sites very far apart will more likely be dissimilar in respect of each other. To address this issue, one can quantify the decrease in similarity between pairs of sites with increasing spatial distance.^{2,16,19,20} A site will be considered more unique when its composition is specific to the local area and not found in other sites as the distance between sites increases (Figure 1). This decay of site similarity with distance is thought to emerge from species dispersal limitations due to physical barriers²¹ and individual species responses to spatially structured environmental variation.²² This concept of distance decay applied to species similarity has been largely described and studied across biomes and taxa through empirical studies,²³⁻²⁵ theoretical work,²⁶ and metaanalyses.²⁷ It was later extended to other dimensions, such as functional and phylogenetic diversity, to measure the degree of functional or phylogenetic redundancy between sites or communities.28-30



Figure 1. Network uniqueness measured by distance decay of interaction similarity across Europe

Two illustrative examples of the distance decay of interaction similarity (A and B) and its geographic projection (C and D) for two contrasted species assemblages. In all panels, point colors show pairwise similarity from 0 (dark blue) to 1 (light yellow), as shown in the y axis in (A) and (B). On the left (A and C), an example of species assemblage (the black dot in C) located in central Europe showing relatively low interaction uniqueness (0.59) within the region of interest because its composition (in terms of trophic interactions) is similar to many other networks in Europe. As a result, the spatial distance decay shows a large area under the curve (AUC) (A, shaded area), also shown by the large halving distance (i.e., the distance at which similarity reaches 0.5, dotted line in A and dotted circle in C). On the right (B and C), an example of a network (black dot in D) located in northern Europe showing high uniqueness (0.83), as shown by the low AUC and short halving distances are normalized to the 0–1 range (real distance is 0–3,500) to ease computations. See also Figures S1–S3.

Yet distance decay in terms of species interactions has never been investigated. Such an application will identify unique sites not only in terms of species composition but also in terms of the interactions involved. Species' trophic interactions and their wiring inside networks represent a crucial and under-considered item for conservation biogeography. They underpin species distributions and community dynamics^{3,4} but also ecosystem functioning and contributions to people.^{5–7} Hence, identifying trophic networks that are unique and vulnerable to human threats within a region of interest might inform conservation priorities that would benefit not only species but also ecosystem functioning and nature's contributions to people.⁵ Another asset of interaction networks is the notion of trophic redundancy.³¹ Indeed, just like two sites can be dissimilar in terms of species composition but similar in terms of functional traits,³² two trophic networks can be dissimilar in terms of species and interactions but similar in terms of trophic roles.³³ Depending on the redundancy of trophic roles across species, trophic groups and species interactions might show different levels of uniqueness across Europe. This has important implications for conservation,

as the loss of a functionally unique species, in terms of its trophic role, may have a higher impact on interaction networks than the loss of a trophically redundant species.³⁴

We believe that the paucity of empirical assessments of distance decay in interaction network similarity results from the triple challenge associated with (1) measuring local interaction networks across large areas and diverse environmental conditions,³⁵ i.e., the "Eltonian shortfall" of biodiversity^{36,37}; (2) using appropriate measures adapted to species interactions and networks^{38,39}; and (3) synthesizing distance decays of similarity for a given local network, i.e., "putting beta diversity on the map."16 In this study, we overcome these challenges by leveraging information on the trophic interactions of most European terrestrial vertebrates.⁸ By coupling this metaweb with spatial distributions of species across Europe,⁴⁰ we mapped potential vertebrate trophic networks at a 10-km resolution and estimated the trophic groups represented in each network using a stochastic block model.^{33,41,42} For each site, we computed a metric of uniqueness based on the distance decay of its similarity with other sites in Europe (Figure 1). Finally, we confronted the uniqueness of local trophic networks with their vulnerability to human footprint or future climate change velocity, and to their protection level, as measured by the protected area cover. Using this workflow, we identify areas of potential relevance for conservation planning that have both high uniqueness of trophic networks and are vulnerable to direct and indirect human-induced changes.

We found that unique trophic networks (uniqueness > 0.9; Figures 2A and 2B) within Europe were mostly found in the Arctic, the Macaronesian islands, Anatolia, the Mediterranean, and the Black Sea biogeographic region. Within the study area, geographic isolation seemed to play an important role in determining the uniqueness of trophic networks, in particular for the networks found in the Arctic and Macaronesian islands. Yet it is important to consider that the limitation of our analyses to the European sub-continent (i.e., not considering Asia or Africa) due to the data cover creates an artificial, non-ecological, border effect that might influence these patterns. In the eastern border of the study area, uniqueness estimates are likely overestimated, as those networks should share similarities with networks in the Middle East or Central Asia, which are not considered in our analysis. It is noteworthy that such a border effect was not pervasive, as the northwestern part of Europe showed low uniqueness, even if it was situated at the border of the study area (Figure 2A). Like any measure dependent on a given set of species or sites, uniqueness measures have to be taken with caution when the characteristics of the whole ecoregion or bioregion are not fully covered.

As expected, the spatial uniqueness of trophic interactions was related to the species composition of these networks (Figure S1). This pattern is in line with theoretical expectations³⁹ and previous empirical studies.⁴³ Trophic networks systematically showed higher uniqueness than species assemblages (\sim 10%–20% higher). The magnitude of these positive deviations varied in space, with highest values for Arctic and Mediterranean networks. The uniqueness of trophic interactions corrected by species composition was related to the intrinsic properties of the trophic networks. In particular, trophic networks with high connectance (the number of observed interactions out of the



maximum number of possible interactions) and high generality (the average number of prey per species) were also the networks with lower corrected uniqueness. Network theory hypothesizes that more connected food webs are expected to be more robust to species loss,⁴⁴ and species that are trophic generalists are more likely to have redundant interactions within their local food web.⁴⁵ Although network robustness is generally assessed from its own structural properties, we here documented an interesting transferability of the intrinsic network robustness to its uniqueness with regard to surrounding networks. In other words, trophic networks that are least unique across Europe appear to have network properties that are typically associated with higher network robustness. This observation might point to a tradeoff between the conservation of more robust networks or more unique ones. $^{5,35}\ \mathrm{To}$ our knowledge, the relationship between network properties and spatial uniqueness has not been previously described and deserves more attention. There is a need for more studies that analyze the relationships between network robustness and interaction uniqueness, with strong implications for guiding conservation at biogeographic scales. In particular, it has been shown that the bioclimatic determinants of biotic interaction variability might differ from the ones driving species distributions.^{4,46,47} Understanding the relative effects of abiotic and biotic determinants represents a promising avenue to understand why unique networks differ geographically from areas currently prioritized for biodiversity conservation. Ignoring the biogeographic and climatic context, and notably the structure and similarity of species interactions in the surrounding communities, might give a misleading picture of the robustness of a network within a spatial context.^{32,48}

Beyond their composition in interactions, most trophic networks appeared largely replaceable when looking at trophic groups (Figure S2). Only Arctic and Macaronesian networks showed low to (relatively) moderate uniqueness (>0.3). However, this low-to-moderate uniqueness was mainly due to the small number of trophic groups present in this network and found in other parts of Europe. All networks were thus redundant in terms of functional trophic group composition; hence, the "functions" they encapsulate are not unique on a European scale. As such, they do not represent unique ecosystem functions. Although it remains important to conserve these trophic groups to ensure the persistence of functions at local scale, it appears that they were not threatened regionally because of their redundancy at regional scale, ^{48–50} as long as dispersal of species between sites is preserved.

Following the irreplaceability vs. vulnerability framework of conservation planning,¹⁰ we confronted our estimates of network uniqueness with their vulnerability to human footprint^{51–53} and climate change velocity.⁵⁴ Uniqueness of trophic network was not related to human footprint of climatic velocity across Europe, although a few cells showed both very high uniqueness (i.e., >0.9) combined with very high human footprint (>75) or climatic (>10) vulnerability (Figures 3A and 3C, large red point in the top right corner). Trophic networks situated south of the continental bioregion (Mediterranean, Anatolian, and Macaronesian bioregion) and in Ireland exhibited high uniqueness and human footprint vulnerability (i.e., >50th percentile). Most islands in the study area also showed unique trophic networks linked to high human footprint vulnerability. Conversely, unique



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Figure 2. Interaction and trophic group uniqueness

(A) Spatial pattern of species uniqueness in Europe (black lines show bioregion boundaries).

(B) Density distribution of species uniqueness within each European bioregion.

(C) Spatial pattern of trophic functional groups' uniqueness in Europe (black shows bioregion boundaries).

(D) Distribution of trophic functional groups' uniqueness within each European bioregion. Darker shades indicate more vulnerable assemblages.

Note that color scales are different between (A) and (B) (ranging from 0.6 to 1) and (C) and (D) (ranging from 0 to 0.4).

trophic networks situated to the north of the continental bioregion underwent low vulnerability, as human footprint was low in these areas (Figure 3B, small blue dots in northern Europe). Interestingly, areas under high human footprint vulnerability situated in southern Europe showed low climatic vulnerability, and vice versa for areas under low human footprint vulnerability in northern Europe. Indeed, trophic networks exhibiting high uniqueness and climatic vulnerability were mostly situated in Arctic and Steppic bioregions and, to a lesser extent, in the western Mediterranean (Spain). This spatial dichotomy observed between current vulnerability driven by direct human impact and future vulnerability driven by climatic change is interesting from the irreplaceability versus vulnerability framework point of view. Indeed, unique networks under current human footprint vulnerability should be the focus of reactive conservation action directed to mitigate current adverse effects of human activities on trophic networks.¹ Conversely, unique networks not under human footprint vulnerability but facing future climate vulnerability require proactive action that would allow climate adaptation to future changes. This is particularly important concerning trophic networks, as cascading effects in response to future changes might lead to stronger than expected consequences on biodiversity.⁵⁵

By comparing the uniqueness of trophic networks with the cover of protected areas within the cell, we showed that most











(legend on next page)



unique trophic networks in the Mediterranean, Alpine, and Macaronesian bioregions are well covered in protected areas (large green dots in Figures 3E and 3F). However, unique networks found in the Anatolias and the Black Sea and Steppic bioregions did not benefit from any protected area coverage (small blue dots in Figure 3F). Importantly, those areas situated in southeastern Europe were also identified as vulnerable to human threats (Figure 3B).

The conservation planning principles of irreplaceability and vulnerability represent the basis of several biodiversity conservation prioritization frameworks.¹ For example, both the Mediterranean and Anatolia have been identified as biodiversity hotspots in Europe, based on the large number of occurring and endemic species vulnerable to habitat destruction.^{11,56} Our results show that these biodiversity hotspots also host trophically unique vertebrate assemblages at the European scale. Moreover, their network uniqueness based on trophic interactions was higher than expected based on their species composition (see supplemental information: corrected network uniqueness). This overvulnerability of trophic interactions with regard to species composition might have key implications for the conservation of the broader ecosystems that largely depend upon these networks and their particularities.^{57,58}

Describing and understanding patterns of turnover in community composition, i.e., beta diversity, is central to the long-standing fundamental question of what drives the distribution of biodiversity on Earth⁵⁹ and is directly linked to complementarity in conservation planning.⁶⁰ We here argue that dissimilarity measures and their spatial structure (spatial decay) can also represent a valuable and simple tool to identify areas or sites that have high conservation value within a region and ultimately to guide conservation strategies.^{15,18} Although we focused on spatial distance decay to estimate the uniqueness of sites regarding the study area, the same approach can be used with the consideration of environmental differences between sites instead of geographical distance. Such environmental decays that explicitly incorporate environmental drivers of dissimilarity have been previously shown to be valuable tools for biodiversity assessment.^{61,62} Using similarity measures to compare empirical interaction networks between sites could help us to understand why they differ in functioning and identify areas with unique interactions networks bearing particular ecosystem processes.

Measuring interaction uniqueness is particularly valuable because species interactions may be more sensitive to environmental change than species richness or composition,^{46,63} and their large-scale diversity patterns provide unique ecological information⁴ that appears to be particularly sensitive to human pressures on ecosystems.⁴⁷ Moreover, numerous authors⁶⁴

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have argued for a conservation of interactions as they might be keystone elements of ecosystem integrity facing global change and bear an important role in ecosystem processes.^{57,58} When planning conservation interventions at the European scale, biological interaction networks that are both unique and vulnerable to human pressure should be considered a priority. In the context of biotic homogenization representing an important and pervasive aspect of the ongoing biodiversity crisis,^{9,65,66} protecting unique sites would prevent the loss of regionally distinct interaction networks, which are more important than species composition from an ecosystemic view. In our case, using information on all terrestrial vertebrate trophic interactions allows a rich consideration of ecosystem functions and services (such as pest control, carrion elimination, seed dispersal, and wildlife watching). However, it should be pointed out that it overlooks basal ecosystem components that underpin many critical ecosystem functions, such as primary producers and invertebrates, and we furthermore do not incorporate non-trophic interactions such as mutualism or competition. It is possible that patterns of interaction uniqueness might differ if different sets of taxa, trophic levels, and interactions were considered.⁴⁶ Interaction uniqueness only measures a facet of biodiversity and should be used in combination with other indicators describing aspects of the ecosystems bearing different conservation values.⁶⁷ It is also important to note that these patterns result from locally reconstructed, probabilistic networks based on a regional metanetwork, which is locally filtered based on species distribution knowledge. Our approach differs from in situ network sampling where trophic interactions are directly observed, as it provides a comprehensive representation of the interactions that are likely to occur within a landscape or ecosystem over an extended period.^{68,69} It is, however, essential to acknowledge that these potential trophic interactions may not always be realized at a given time and location. Just as a local species pool informs about the species that should be found in a given area,⁷⁰ the local interaction network reconstructed from a regional metanetwork informs about the potential interactions that should occur in a given area.

When planning conservation interventions at the European scale, biological interaction networks that are both unique and vulnerable to human pressure should be considered a priority. We identified such unique and vulnerable networks in southern Europe, mainly in the Anatolian and Mediterranean bioregions. We further showed that Anatolian networks were also poorly covered by protected areas, which might indicate that such trophic networks are particularly endangered. These food webs are worth particular consideration because they play an important role in the regional diversity of trophic interactions⁴ and because

Figure 3. European trophic network uniqueness, vulnerability, and protection

(A) Scatterplot of trophic interaction spatial uniqueness based on Sorensen dissimilarity (y axis) against human footprint vulnerability (x axis). Each point is a trophic network colored by the combination of interaction uniqueness based on Sorensen dissimilarity (yellow to blue) and vulnerability to human activities (yellow to red). Point size corresponds to the product of standardized x and y values. Dotted black lines show the 50th percentile of values.

(B) Geographical projection of the uniqueness/human footprint vulnerability values across Europe.

(C) Scatterplot of trophic interaction spatial uniqueness based on Sorensen dissimilarity (y axis) climatic vulnerability (measured as the climatic velocity). Each point is a trophic network colored by the combination of interaction uniqueness (yellow to blue) and vulnerability to climate change (yellow to red).

(D) Geographical projection of the uniqueness/climatic vulnerability values across Europe.

(E) Scatterplot of trophic interaction spatial uniqueness (y axis) against protection (measured as the % cell covered by a protected area) (x axis). Each point is a trophic network colored by the combination of interaction uniqueness (yellow to blue) and protection (yellow to green). (F) Geographical projection of the uniqueness/protection values across Europe.

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they represent unique features within European trophic metacommunities.⁷¹ Given the existing gap between conservation and network ecology, we argue that considering uniqueness of biotic interactions can improve conservation planning by identifying unique and vulnerable communities—both in terms of species and their interactions.

STAR***METHODS**

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

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j. cub.2023.10.069.

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AUTHOR CONTRIBUTIONS

P.G. conceived the study, with early advice from W.T. C.D. computed the climate velocities. J.R. performed the extraction and estimates of protected areas within each cell. P.G. performed all other analyses and wrote the first version of the manuscript. All authors contributed substantially to the interpretation of the results and to the writing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., and Rodrigues, A.S.L. (2006). Global biodiversity conservation priorities. Science 313, 58–61. https://doi.org/10.1126/science.1127609.
- Lawler, J.J., White, D., and Master, L.L. (2003). Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. Ecol. Appl. 13, 1762–1772. https://doi.org/10.1890/02-5337.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., et al. (2013). The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. Camb. Philos. Soc. 88, 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x.
- Gaüzère, P., O'Connor, L., Botella, C., Poggiato, G., Münkemüller, T., Pollock, L.J., Brose, U., Maiorano, L., Harfoot, M., and Thuiller, W. (2022). The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity. Curr. Biol. *32*, 2093–2100.e3. https:// doi.org/10.1016/j.cub.2022.03.009.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., and Bascompte, J. (2010). Conservation of species interaction networks. Biol. Conserv. 143, 2270– 2279. https://doi.org/10.1016/j.biocon.2009.12.004.
- Windsor, F.M., van den Hoogen, J., Crowther, T.W., and Evans, D.M. (2023). Using ecological networks to answer questions in global biogeography and ecology. J. Biogeogr. 50, 57–69. https://doi.org/10.1111/jbi. 14447.
- Keyes, A.A., McLaughlin, J.P., Barner, A.K., and Dee, L.E. (2021). An ecological network approach to predict ecosystem service vulnerability to species losses. Nat. Commun. *12*, 1586. https://doi.org/10.1038/ s41467-021-21824-x.
- 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. https://doi.org/10. 1111/geb.13138.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E., and Edwards, D.P. (2016). How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31, 67–80. https://doi.org/10.1016/j.tree.2015.11.005.
- Margules, C.R., and Pressey, R.L. (2000). Systematic conservation planning. Nature 405, 243–253. https://doi.org/10.1038/35012251.
- 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. https://doi.org/10.1038/35002501.
- Carwardine, J., Rochester, W.A., Richardson, K.S., Williams, K.J., Pressey, R.L., and Possingham, H.P. (2007). Conservation planning with irreplaceability: does the method matter? Biodivers. Conserv. 16, 245–258. https://doi.org/10.1007/s10531-006-9055-4.
- Hoffmann, S., Beierkuhnlein, C., Field, R., Provenzale, A., and Chiarucci, A. (2018). Uniqueness of protected areas for conservation strategies in the European Union. Sci. Rep. 8, 6445. https://doi.org/10.1038/s41598-018-24390-3.
- Capmourteres, V., and Anand, M. (2016). "Conservation value": a review of the concept and its quantification. Ecosphere 7, e01476. https://doi. org/10.1002/ecs2.1476.
- Reyers, B., van Jaarsveld, A.S., and Krüger, M. (2000). Complementarity as a biodiversity indicator strategy. Proc. Biol. Sci. 267, 505–513. https://doi.org/10.1098/rspb.2000.1029.
- McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S., and Stuart, S.N. (2007). Putting beta-diversity on the



map: broad-scale congruence and coincidence in the extremes. PLoS Biol. 5, e272. https://doi.org/10.1371/journal.pbio.0050272.

- Ferrier, S. (2002). Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Syst. Biol. *51*, 331–363. https:// doi.org/10.1080/10635150252899806.
- Pereira Gomes, J., Bet Stedille, L.I., de Freitas Milani, J.E., Montibeller-Silva, K., Mantovani, A., and Lopes da Costa Bortoluzzi, R. (2020). Beta diversity as an indicator of priority areas for Myrtaceae assemblage conservation in subtropical Araucaria Forest. Biodivers. Conserv. 29, 1361–1379. https://doi.org/10.1007/s10531-020-01940-8.
- Nekola, J.C., and White, P.S. (1999). The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26, 867–878. https://doi.org/10. 1046/j.1365-2699.1999.00305.x.
- Nekola, J.C., and White, P.S. (2002). Conservation, the two pillars of ecological explanation, and the paradigm of distance. Nat. Areas J. 22, 305–310.
- Hubbell, S.P. (2011). The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32) (Princeton University Press). https://doi.org/10. 1515/9781400837526.
- Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. 8, 1175–1182. https://doi. org/10.1111/j.1461-0248.2005.00820.x.
- Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., and Muotka, T. (2012). Distance decay of similarity in freshwater communities: do macroand microorganisms follow the same rules? Glob. Ecol. Biogeogr. 21, 365–375. https://doi.org/10.1111/j.1466-8238.2011.00681.x.
- 24. Mammola, S., Cardoso, P., Angyal, D., Balázs, G., Blick, T., Brustel, H., Carter, J., Ćurčić, S., Danflous, S., Dányi, L., et al. (2019). Local- versus broad-scale environmental drivers of continental β-diversity patterns in subterranean spider communities across Europe. Proc. Biol. Sci. 286, 20191579. https://doi.org/10.1098/rspb.2019.1579.
- Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A.T.R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Baastrup-Spohr, L., et al. (2022). Distance decay 2.0 - a global synthesis of taxonomic and functional turnover in ecological communities. Glob. Ecol. Biogeogr. *31*, 1399–1421. https://doi.org/10.1111/geb.13513.
- Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R., and Green, J.L. (2008). A general framework for the distancedecay of similarity in ecological communities. Ecol. Lett. *11*, 904–917. https://doi.org/10.1111/j.1461-0248.2008.01202.x.
- Soininen, J., McDonald, R., and Hillebrand, H. (2007). The distance decay of similarity in ecological communities. Ecography 30, 3–12. https://doi. org/10.1111/j.0906-7590.2007.04817.x.
- Villéger, S., Ramos Miranda, J., Flores Hernandez, D., and Mouillot, D. (2012). Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. PLoS One 7, e40679. https://doi.org/10.1371/journal.pone.0040679.
- Mazel, F., Renaud, J., Guilhaumon, F., Mouillot, D., Gravel, D., and Thuiller, W. (2015). Mammalian phylogenetic diversity-area relationships at a continental scale. Ecology 96, 2814–2822. https://doi.org/10.1890/14-1858.1.
- Mazel, F., Wüest, R.O., Gueguen, M., Renaud, J., Ficetola, G.F., Lavergne, S., and Thuiller, W. (2017). The geography of ecological niche evolution in mammals. Curr. Biol. 27, 1369–1374. https://doi.org/10.1016/j.cub.2017. 03.046.
- Sanders, D., Thébault, E., Kehoe, R., and Frank van Veen, F.J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. Proc. Natl. Acad. Sci. USA *115*, 2419–2424. https://doi.org/10.1073/pnas. 1716825115.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., et al. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. USA *111*, 13757–13762. https://doi.org/10.1073/pnas.1317625111.

- 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. https://doi.org/10. 1111/jbi.13773.
- 34. Ehrlich, P., and Walker, B. (1998). Rivets and redundancy. BioScience 48, 387.
- Cumming, G.S., Bodin, Ö., Ernstson, H., and Elmqvist, T. (2010). Network analysis in conservation biogeography: challenges and opportunities. Divers. Distrib. *16*, 414–425. https://doi.org/10.1111/j.1472-4642.2010. 00651.x.
- 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. https://doi.org/ 10.1146/annurev-ecolsys-112414-054400.
- Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., and Vissault, S. (2021). Global knowledge gaps in species interaction networks data. J. Biogeogr. 48, 1552–1563. https://doi.org/10.1111/jbi.14127.
- 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. https://doi.org/ 10.1111/ele.13221.
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N., and Gravel, D. (2012). The dissimilarity of species interaction networks. Ecol. Lett. 15, 1353–1361. https://doi.org/10.1111/ele.12002.
- 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. https://doi.org/10.1371/journal.pone.0074989.
- Allesina, S., and Pascual, M. (2009). Food web models: a plea for groups. Ecol. Lett. 12, 652–662. https://doi.org/10.1111/j.1461-0248.2009.01321.x.
- Karrer, B., and Newman, M.E.J. (2011). Stochastic blockmodels and community structure in networks. Phys. Rev. E Stat. Nonlin. Soft Matter Phys. 83, 16107. https://doi.org/10.1103/PhysRevE.83.016107.
- Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A.V., and Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. Ecography 42, 295–308. https:// doi.org/10.1111/ecog.03443.
- Gilbert, A.J. (2009). Connectance indicates the robustness of food webs when subjected to species loss. Ecol. Indic. 9, 72–80. https://doi.org/10. 1016/j.ecolind.2008.01.010.
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., and Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc. Biol. Sci. 282, 20151546. https://doi.org/10.1098/rspb.2015.1546.
- Poisot, T., Guéveneux-Julien, C., Fortin, M.-J., Gravel, D., and Legendre, P. (2017). Hosts, parasites and their interactions respond to different climatic variables. Glob. Ecol. Biogeogr. 26, 942–951. https://doi.org/10. 1111/geb.12602.
- 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. https://doi.org/10.1111/ geb.12981.
- Wang, S., and Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. Ecol. Lett. 19, 510–518. https://doi. org/10.1111/ele.12582.
- Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. Proc. Natl. Acad. Sci. USA 100, 12765–12770. https://doi.org/10.1073/pnas.2235465100.
- Naeem, S., Bunker, D.E., Hector, A., Loreau, M., and Perrings, C. (2009). Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective (Oxford University Press).

Current Biology

Report

- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woolmer, G. (2002). The human footprint and the last of the wild. BioScience 52, 891. https://doi.org/10.1641/0006-3568(2002)052 [0891:THFATL]2.0.CO;2.
- Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558. https://doi.org/10.1038/ncomms12558.
- Mu, H., Li, X., Wen, Y., Huang, J., Du, P., Su, W., Miao, S., and Geng, M. (2022). A global record of annual terrestrial human footprint dataset from 2000 to 2018. Sci. Data 9, 176. https://doi.org/10.1038/s41597-022-01284-8.
- Dragonetti, C., Daskalova, G., and Marco, M.D. (2023). The exposure of the world's mountains to global change drivers. Preprint at Research Square. https://doi.org/10.21203/rs.3.rs-3008744/v1.
- Brook, B.W., Sodhi, N.S., and Bradshaw, C.J. (2008). Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460. https://doi.org/10.1016/j.tree.2008.03.011.
- 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. https://doi. org/10.1007/978-3-642-20992-5_1.
- Thébault, E., and Loreau, M. (2003). Food-web constraints on biodiversityecosystem functioning relationships. Proc. Natl. Acad. Sci. USA 100, 14949–14954.
- Thébault, E., Huber, V., and Loreau, M. (2007). Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. Oikos *116*, 163–173. https://doi.org/10.1111/j.2006.0030-1299.15007.x.
- 59. Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., et al. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. *14*, 19–28. https://doi.org/10. 1111/j.1461-0248.2010.01552.x.
- Sarkar, S. (2006). Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta discussion 141–146. Acta Biotheor. 54, 133–140. https://doi.org/10.1007/s10441-006-8259-z.
- Di Marco, M., Harwood, T.D., Hoskins, A.J., Ware, C., Hill, S.L.L., and Ferrier, S. (2019). Projecting impacts of global climate and land-use scenarios on plant biodiversity using compositional-turnover modelling. Glob. Chang. Biol. 25, 2763–2778. https://doi.org/10.1111/gcb.14663.
- Ferrier, S., Manion, G., Elith, J., and Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Divers. Distrib. *13*, 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x.
- Tylianakis, J.M., Tscharntke, T., and Lewis, O.T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445, 202–205. https://doi.org/10.1038/nature05429.
- Harvey, E., Gounand, I., Ward, C.L., and Altermatt, F. (2017). Bridging ecology and conservation: from ecological networks to ecosystem function. J. Appl. Ecol. 54, 371–379. https://doi.org/10.1111/1365-2664. 12769.

- Clavel, J., Julliard, R., and Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228. https://doi.org/10.1890/080216.
- Magurran, A.E., Dornelas, M., Moyes, F., Gotelli, N.J., and McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. Nat. Commun. 6, 8405. https://doi.org/10.1038/ncomms9405.
- O'Connor, L.M.J., Pollock, L.J., Renaud, J., Verhagen, W., Verburg, P.H., Lavorel, S., Maiorano, L., and Thuiller, W. (2021). Balancing conservation priorities for nature and for people in Europe. Science 372, 856–860. https://doi.org/10.1126/science.abc4896.
- Thuiller, W., Calderón-Sanou, I., Chalmandrier, L., Gaüzère, P., O'Connor, L.M.J., Ohlmann, M., Poggiato, G., and Münkemüller, T. (2023). Navigating the integration of biotic interactions in biogeography. Published online October 3, 2023. J. Biogeogr. https://doi.org/10.1111/jbi.14734.
- Dansereau, G., Barros, C., and Poisot, T. (2023). Spatially explicit predictions of food web structure from regional level data. Preprint at EcoEvoRxiv. https://doi.org/10.32942/X2TW2S.
- Pärtel, M., Szava-Kovats, R., and Zobel, M. (2013). Community completeness: linking local and dark diversity within the species pool concept. Folia Geobot. 48, 307–317. https://doi.org/10.1007/s12224-013-9169-x.
- Santos, M., Cagnolo, L., Roslin, T., Ruperto, E.F., Bernaschini, M.L., and Vázquez, D.P. (2021). Robustness of a meta-network to alternative habitat loss scenarios. Oikos 130, 133–142. https://doi.org/10.1111/oik.07835.
- 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. https://doi. org/10.1098/rstb.2014.0005.
- Gauzens, B., Thébault, E., Lacroix, G., and Legendre, S. (2015). Trophic groups and modules: two levels of group detection in food webs. J. R. Soc. Interface 12, 20141176. https://doi.org/10.1098/rsif.2014.1176.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10. 1111/j.1466-8238.2009.00490.x.
- Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Global terrestrial human footprint maps for 1993 and 2009. Sci. Data 3, 160067. https://doi.org/10.1038/sdata.2016.67.
- Brito-Morales, I., García Molinos, J., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., et al. (2018). Climate velocity can inform conservation in a warming world. Trends Ecol. Evol. *33*, 441–457. https://doi.org/ 10.1016/j.tree.2018.03.009.
- 77. Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., and Ackerly, D.D. (2009). The velocity of climate change. Nature 462, 1052– 1055. https://doi.org/10.1038/nature08649.
- Karger, D.N., Schmatz, D.R., Dettling, G., and Zimmermann, N.E. (2020). High-resolution monthly precipitation and temperature time series from 2006 to 2100. Sci. Data 7, 248. https://doi.org/10.1038/s41597-020-00587-y.
- Planet, P. (2021). Calculating protected and OECM area coverage. https:// www.protectedplanet.net/en/resources/calculating-protected-area-coverage.







STAR***METHODS**

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Tetrapods European distributions	Maiorano et al. ⁴⁰	https://doi.org/10.1371/journal.pone.0074989
Tetrapods Trophic interaction network	Maiorano et al. ⁸	https://doi.org/10.5061/dryad.jm63xsj7b
Biogeographical regions	https://www.eea.europa.eu/en/datahub/ datahubitem-view/11db8d14-f167-4cd5- 9205-95638dfd9618	eea_v_3035_1_mio_biogeo-regions_p_2015_ v02_r00
Trophic Functional Groups	O'Connor et al. ³³	https://doi.org/10.5061/dryad.bcc2fqz79
All formated data and code to replicate analyses and results of this study	Zenodo repository	https://doi.org/10.5281/zenodo.10036360
Software and algorithms		
R Statistical Computing language version 4.1.2	https://www.r-project.org/	https://cran.r-project.org/src/base/R-4/R-4. 1.2.tar.gz
Code to replicate analyses of this study	Zenodo repository	https://doi.org/10.5281/zenodo.10036360

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

- The raw data used in this study are from published or downloadable online sources. All references, DOI and links toward the raw data are listed in the key resources table.
- All original code along with formatted and prepared data have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request. The code shared contains analyses not with results not presented in this paper. Please contact the lead contact before reusing this code.

METHOD DETAILS

Species distributions data

We extracted the distributions for all terrestrial vertebrates naturally occurring within the study area from Maiorano et al.⁴⁰ Species distributions for 509 bird, 288 mammal, 250 reptile and 104 amphibian species for which trophic interaction data are available (see below) 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 when all three following criteria were met: the grid cell i) is within the species extent of occurrence, ii) contains at least one 300x300m patch of primary habitat for the species, and iii) meets species requirements in terms of elevation and distance from water. More details can be found in O'Connor et al.³³ and Thuiller et al.,⁷² and see Maiorano et al.⁴⁰ for a full description of species distribution data and definition of primary habitat.

Trophic interaction data and functional trophic groups

We used data on species trophic interactions for all European terrestrial vertebrates (Tetra-EU 1.0,⁸ Tetra-EU 1.0 is based on published information on known interactions, expert knowledge, and field guides published and/or collected during the last 50 years. The data provides species-level trophic interactions for all terrestrial vertebrate species occurring in the entire European sub-continent, from Macaronesia (consisting of the Azores, Madeira, and Canary islands) to the Ural Mountains, and from Fennoscandia and UK



islands to the Mediterranean. The dataset includes Turkey in order to cover the whole north-eastern Mediterranean coast. Only species introduced in historical times and currently naturalized were included (i.e recent introductions were excluded). In total the data include 288 mammals, 509 regularly breeding birds, 250 reptiles, and 104 amphibians. 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 interactions of the predator's sister species. Tetra-EU 1.0 contained 1,164 species and a total of 50,408 potential trophic interactions composing the metaweb of European terrestrial vertebrates. The full dataset and methods description can be found in Maiorano et al.⁸

We defined functional trophic groups using a stochastic block model (SBM) on the metaweb. The SBM is a random graph model defining groups of similar species in terms of the trophic interactions they have with each other.⁷³ We used the mixer R package to group species along a range of 10–50 trophic groups. We retained 28 trophic groups, as it was the number of groups that maximized the integrated classification likelihood (ICL) information criterion here used as the goodness of fit of the model.

QUANTIFICATION AND STATISTICAL ANALYSIS

Compute taxonomic and interaction pairwise dissimilarity

We used species occurrences within each 10×10 km cell to build a "site x species matrix". We used the metaweb of European terrestrial vertebrates to infer local trophic interaction networks based on the species occurring within each cell. Because pairwise dissimilarity and distances computation scale with the square of the number of sites, the computation of the full pairwise matrices would become too computationally challenging (more than 20⁹ values). We therefore limited our analyses to a random sample of 10000 cells among the 117000 cells of the dataset. We used these local interaction networks to build a "site x interaction matrix", and a "site x trophic group matrix". We then computed the Sorensen pairwise similarity between each pair of cells using the beta_diss() function from R package phyloregion (for computational efficiency) to the site x species and the site x interaction matrix separately. Note that because the local network is inferred from occurrence data, we do not account for interaction plasticity and the turnover of interactions between sites is solely due to the turnover of species. This measure is equivalent to the (dis)similarity of links from Poisot et al.³⁹ (β_{WN}, Sorensen index on links) and from Ohlmann et al.³⁸ (δ⁰_L using Hills numbers). We decomposed pairwise similarities into true turnover and nestedness-resultant components,⁷⁴ and focused on the turnover component (β_{Sim} , pairwise Simpson dissimilarity). While the Sorensen similarity index (i.e. the number of shared species (or interactions) in each site divided by the total number of species (or interactions) in both sites has the advantage of measuring the overall similarity with other sites, it is tightly linked with the richness of the site (nestedness). On the other hand, focusing on the turnover component (Simpson), namely the minimum number of unique species (or interactions) in each site divided by the richness in the same site, allows us to measure dissimilarity that is not directly linked to the richness of the site.

Model spatial distance decays

We modeled the relationship between pairwise similarity and spatial distance by fitting a power law relationship as $y \sim a^* x^b$ where y is the (species or interaction) pairwise similarity (Sorensen or turnover component) between the focal cell and all other cells (ranging from 0 to 1) and x is the geographical (euclidean) distance between the focal cell and all other cells (scaled between 0 and 1). For each cell, we calculated the maximum distance between the focal cell and all other sites in Europe. In order to make distance decay comparable between all cells, we then selected the lowest value across cells (3705km) as a threshold above which dissimilarity was not calculated between cells that were further apart than this value. Parameters a and b were fitted using non linear least square (NLS) regression using the nlsLM function from minpack.Im R package. We removed all cells for which the r² of the modeled relationship pairwise species of interaction dissimilarity and spatial distance was lower than 0.2 (4.7% of the cells), as these modeled parameters would be poor descriptors of the relationship.

Here, we selected a maximum distance of 3,507 km as it corresponds to the minimum distance of the most distant pairs across sites. Moreover, this large distance still allows most of Europe to be considered in the distance decay computation of every site.

Measure network spatial uniqueness via distance decay

We calculated the spatial uniqueness of a given trophic network based on (1 minus) the normalized Area Under the Curve (i.e. 1-AUC, Figure 1) of its distance-decay of similarity with other networks across space. We computed the area under the curve (AUC) of each spatial distance decay. AUC indicates the quantity of similarity of the site with other sites within 3,507 km. Each metric was computed for pairwise dissimilarities based on trophic interactions and trophic functional groups. The spatial uniqueness was computed as 1 - AUC. Note that we retained the AUC to measure uniqueness because it was the most integrative metric among five other metrics quantifying different aspects of distance decays. Using AUC based measures offers a natural and comparable quantification of uniqueness. It is directly interpretable with uniqueness ranging from 0 -all interactions or trophic groups of the site are shared with other sites within the region of interest-, to 1 - interactions or trophic groups are found only within (or nearby) the site of interest.

Comparing uniqueness with vulnerability and protection

Vulnerability to human activities was assessed using the Human Footprint (HFP), a multi-dimensional index estimating the direct human footprint on ecosystems as a proxy of recent human pressure on biodiversity.^{51,75} It incorporates eight variables that characterize human pressures: built environments, population density, nighttime light, croplands, pasture lands, roadways, railways, and





navigable waterways. We extracted the last version of HFP values at 1 km resolution (available from 2000-2018) and focused on the median year 2010,⁵³ and computed the average value within each 10×10 km cell.

Vulnerability to climate change was assessed using climate change velocity^{76,77} extracted from Dragonett et al.⁵⁴ The climate change velocity is calculated as the sum of the absolute values of temperature velocity of change and precipitation velocity of change. Temperature (C°) and precipitation (g/m3) data from 2020 to 2050 was extracted from Chelsa database⁷⁸ under SSP-RCP 2-4.5 scenario, and each velocity of change was estimated as the ratio between a temporal trend (the rate of change of each variable through time, estimated as a regression slope) and the corresponding spatial gradient of that variable (i.e. vector sum of longitudinal and latitudinal pairwise differences at each focal cell using a 3 x 3-cell neighborhood).

Protection was assessed as the percentage of terrestrial cell area that was covered by terrestrial protected areas. We used data from the World Database on Protected Areas (WDPA) hosted on the Protected planet website (https://www.protectedplanet.net). After cleaning the protected area data following best practices,⁷⁹ we calculated the surface of protected areas associated with any IUCN management category within each cell.