Land-use impacts on plant functional diversity throughout Europe

Authors: Francesca Rosa[1]*, Peter M. van Bodegom[2], Stefanie Hellweg[1], Stephan Pfister[1], Idoia Biurrun[3], Steffen Boch[4], Milan Chytrý[5], Renata Ćušterevska[6], Michele Dalle Fratte[7], Gabriella Damasceno[8, 9], Emmanuel Garbolino[10], Jonathan Lenoir[11], Wim A Ozinga[12], Josep Penuelas[13, 14], Francesco Maria Sabatini[15, 16], Franziska Schrodt[17], Domas Uogintas[18], Chaeho Byun[19], Jiri Dolezal[20], Tetiana Dziuba[21], Bruno Hérault[22, 23], Irene Martín-Forés[24] Ülo Niinemets[25], Gwendolyn Peyre[26], Laura Scherer[2]

[1]Institute of Environmental Engineering, ETH Zürich, 8093 Zürich, Switzerland

[2]Institute of Environmental Sciences (CML), Leiden University, Leiden, The Netherlands

[3]Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country UPV/EHU, Bilbao, Spain

[4]WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[5]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

[6]Faculty of Natural Sciences and Mathematics, Ss. Cyril and Methodius University, Skopje, North Macedonia

[7]Department of Biotechnology and Life Science, University of Insubria, 21100, Varese, Italy

[8]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany

[9]Martin-Luther University, Institute of Biology and Geobotany and Botanical Garden, Halle-Wittenberg, Halle, Germany

[10]ISIGE, MINES Paris PSL, 77300 Fontainebleau, France

[11]UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, Amiens, France

[12]Wageningen Environmental Research, Wageningen University & Research, P.O. Box 430, 6700 AK Wageningen, the Netherlands

[13]CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, 08193 Barcelona, Catalonia, Spain

[14]CREAF, 08193 Cerdanyola del Vallès, Barcelona, Catalonia, Spain

[15]BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum University of Bologna, Bologna, Italy

[16]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, 165 00, Prague, Czech Republic

[17]School of Geography, University of Nottingham, University Park, Nottingham, NG7 2RD, UK

[18]Nature Research Centre, Vilnius, Lithuania

[19]Department of Biological Sciences, Andong National University, Andong, 36729, Republic of Korea

[20]Institute of Botany, The Czech Academy of Sciences, Dukelská 135, 37901, Třeboň, Czech Republic, and Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 1760, 37005, České Budějovice, Czech Republic

[21]Department of Geobotany and Ecology, M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

[22] UPR Forêts et Sociétés, F-34398 Montpellier, France

[23]Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

[24]Department of Ecology & Evolutionary Biology, School of Biological Sciences, The University of Adelaide 5005, Adelaide, South Australia, Australia

[25]Estonian University of Life Sciences, Kreutzwaldi 1, 51006 Tartu, Estonia

[26]Department of Civil and Environmental Engineering, University of the Andes, Bogotá, Colombia

***Correspondence to**

Francesca Rosa, ETH Zürich

Institute of Environmental Engineering, chair of Ecological Systems Design

HIF D 11, Laura-Hezner-Weg 7, 8093 Zürich, Switzerland

+41 44 633 99 49

rosa@ifu.baug.ethz.ch

Abstract

Aim: Global biodiversity loss resulting from anthropogenic land-use activities is a pressing concern, requiring precise assessments of impacts at large spatial extents. Existing models mainly focus on species richness and abundance, lacking insights into ecological mechanisms and species' roles in ecosystem functioning. To bridge this gap, we conducted an extensive analysis of the impact of human land use on vascular plant functional diversity, across diverse land-use classes and bioregions in Europe, comparing it to traditional metrics.

Location: Europe **Time period**: 1992-2019 **Major taxa studied**: Vascular plants

Methods: Integrating extensive databases of vegetation plots with spatial data on land use and land cover, we paired plots from areas actively used and modified by humans with plots from natural habitats under similar environmental conditions. Using species occurrences and traits, in each plot we computed three complementary functional diversity metrics (functional richness, evenness, and divergence), species richness and abundance. We assessed the impact of land use by comparing the metrics in the paired plots.

Results: Our findings revealed that, compared to natural habitats, anthropogenic land use exhibits lower functional richness and divergence but higher functional evenness across most land-use classes and bioregions. The response of functional richness was more marked than the other two metrics and especially pronounced in croplands and urban areas and in northern bioregions. Functional richness exhibited a pattern that did not fully overlap with the trend in species richness, providing useful complementary information.

Main conclusions: We provide a large-scale precise assessment of anthropogenic land-use impacts on functional diversity across Europe. Our findings indicate that: (i) human disturbance significantly alters plant functional diversity compared to natural habitats; (ii) this alteration goes in the direction of functional homogenization; (i) functional diversity metrics complement traditional metrics by offering deeper insights into the ecological mechanisms in response to anthropogenic land use.

Keywords

Land use, Biodiversity loss, Functional diversity, Functional divergence, Functional evenness, Functional richness, Vascular plants, Species richness, Bioregions, Species abundance.

1. Introduction

Biodiversity plays a crucial role in bolstering ecosystem functions, maintaining services vital for all organisms, including humans, and mitigating some global changes (Isbell et al. 2011; Harrison et al. 2014; Tilman et al. 2014; Felipe-Lucia et al. 2018; Valladares et al. 2019; Le Provost et al. 2023; Reader et al. 2023). Anthropogenic activities, particularly habitat loss and degradation, pose significant threats to biodiversity (IPBES 2019; Pereira et al. 2024). With over 80% of global land transformed due to human actions (Ellis et al. 2021)e, ecosystems and their functions face severe impacts, underlining the urgent need for comprehensive strategies to halt biodiversity loss (Leclère et al. 2020; Carmona et al. 2021) and for a better understanding of the linkage between drivers and effects at different spatial scales (Chaplin-Kramer et al. 2022).

To effectively tackle this challenge, it is essential to expand our comprehension of biodiversity beyond conventional metrics like species richness or abundance, which are frequently employed in current biodiversity models given their availability (O'Connor et al. 2017; Bannar-Martin et al. 2018; Jandt et al. 2022). However, these metrics often fail to capture the ecological significance of species within a community or their role in ecosystem functioning (Suárez-Castro et al. 2022) and exhibit considerable variability in trends (Dornelas et al. 2023; Valdez et al. 2023). Therefore, it is imperative to explore additional dimensions of biodiversity, such as functional diversity, here defined as the variation and distribution of species' functional traits within communities. Functional diversity enhances and complements traditional metrics by providing deeper knowledge into ecological mechanisms through the integration of functional information (Cadotte et al. 2011; Hu et al. 2014; Rosenfield and Müller 2020; Scherer et al. 2023). Particularly, the functional diversity of plants has been shown to offer further insights into ecosystem performance than taxonomic diversity (Bruelheide et al. 2018; van der Plas 2019; Zambrano et al. 2019; Kattge et al. 2020; Hagan et al. 2023), especially in areas affected by human activities (Bonilla-Valencia et al. 2022).

To calculate functional diversity, three independent and complementary indices are commonly used: functional richness, evenness, and divergence (Mason et al. 2005). These indices, derived from traits encompassing anatomical, physiological, biochemical, regenerative, reproductive, and phenological characteristics, provide valuable insights into ecosystem dynamics (Villéger et al. 2008). Functional richness represents the amount of functional niche space filled by a species assemblage. Functional evenness describes how regularly species abundances are distributed in the functional niche space. Functional divergence measures to which degree species abundances are distributed from the centre of the functional space to its extremes; it is sensitive to the presence and abundance of species with extreme trait values, e.g., highly specialized or functionally rare species (Mason et al. 2005; Villéger et al. 2008; Mouchet et al. 2010; Scherer et al. 2020).

Along with the need of complementary biodiversity metrics, currently there is a lack of well-established connections between individual local biodiversity assessments and global patterns (Jandt et al. 2022), hindering a comprehensive analysis and suggesting the need for replicated local assessments (Knollová et al. 2024). These assessments are particularly crucial in understanding the effect of human use of land, which encompasses activities like agriculture and urbanization (hereafter simply referred to as “land use”), compared to natural habitats (Zebisch et al. 2004; Dornelas et al. 2014; Jandt et al. 2022).

Previous studies have explored the effect of land use on plant functional diversity at a large spatial extent, from national to global (Flynn et al. 2009; De Souza et al. 2013; Carmona et al. 2020; Newbold et al. 2020; Scherer et al. 2020). However, these studies often used different and less comprehensive indices, failed to distinguish impacts across regions, only focused on a specific land-use class or did not compare functional diversity with more common metrics.

In this research work, we leverage the recent release of global vegetation and trait databases to explore the effect of land use on different dimensions of functional diversity, especially in regions with good data coverage and representativeness, such as Europe (Chytrý et al. 2016; Bruelheide et al. 2019; Kattge et al. 2020). We utilized data from the European Vegetation Archive (EVA) (Chytrý et al. 2016), a vegetation

plot database containing information on species co-occurrences and abundances within plant communities. Coupled with the TRY database, which provides species-level plant trait data (Kattge et al. 2020), it allows for the calculation of functional diversity for approximately two millions of vegetation plots across all of Europe (Bruelheide et al. 2018). By matching vegetation plots and trait data with land use and land cover, we investigated the change in functional diversity in anthropogenic land compared to natural and close-to-natural habitats across Europe.

Given this context, our goal was to answer the following research questions: How does plant functional diversity change in land actively used by humans compared to natural habitats? Which additional information does functional diversity provide compared to other metrics? Are the biogeographic conditions affecting the response?

2. Materials and methods

We compared the functional diversity in vegetation plots located in anthropogenic and natural land by combining species and trait information with land-use and land-cover maps.

We applied seven steps (see Fig. 1 and, for more details, Fig. S1.1). First, we retrieved and filtered the suitable vegetation plots from the European Vegetation Archive (EVA) (Chytrý et al. 2016), while matching them to the sPlot database (Bruelheide et al. 2019), which contains all of the EVA plots and has curated a taxonomic standardization procedure to link each species name to a set of 30 gap-filled traits from the TRY database (Schrodt et al. 2015; Kattge et al. 2020) (see section 2.1). Second, we assigned each vegetation plot to a biogeographic region (hereafter "bioregion") to enable a spatially explicit analysis while including a sufficient sample size per spatial unit (see section 2.2). Third, based on land-use and potential natural vegetation maps, we aggregated land-use classes into broader ones suitable for the analysis (see section 2.3). Fourth, we assigned each vegetation plot to one of the five identified anthropogenic land-use classes (*Urban areas*, *Cropland*, *Pasture and rangeland*, *Mosaic*, *Planted forest*) or to one of the five identified potential natural vegetation classes (*Natural forest*, *Natural grassland*, *Natural shrubland*, *Natural*

herbaceous wetland, *Natural bare and sparse vegetation*) (see section 2.4). Fifth, we selected the relevant environmental variables (i.e., bioclimatic variables and soil properties) and then performed a Principal Component Analysis (PCA) of these variables across Europe to obtain the scores of each vegetation plot along the PCA axes (see section 2.5). Sixth, to allow for a consistent comparison between anthropogenic land-use classes and natural habitats, we paired each vegetation plot sampled in anthropogenic land with a vegetation plot sampled in the natural habitat that would potentially occur there under low human pressure. To do that, we selected the pairs from the same bioregion with minimal distance of PC scores in the PCA space (see section 2.6). Finally, we computed functional richness, functional evenness, functional divergence, species richness, and total abundance in each plot; we then calculated the relative values of these metrics in each vegetation plot sampled in anthropogenic land compared to the paired vegetation plot in natural habitat (see section 2.7).

All analyses were performed in R version 4.0.5 (2021-03-31) (R Core Team 2021).

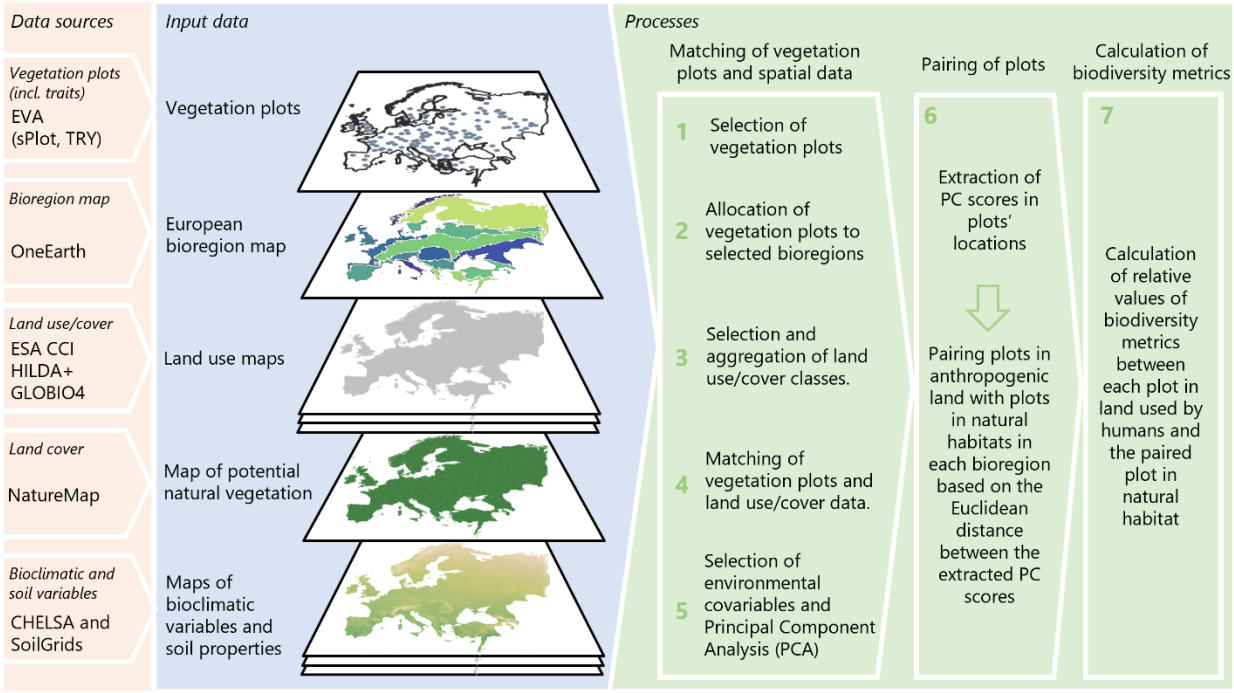

Figure 1 Overview of the methodological conceptual framework applied to this study.

2.1 Selection and processing of vegetation plots

We extracted vegetation plot data from EVA (Chytrý et al. 2016). It currently contains more than 2 million vegetation plots and has a representative geographical coverage for Europe, especially for West, South and Central Europe. We used data on 30 gap-filled plant traits from TRY (Schrodt et al. 2015; Kattge et al. 2020) and an additional plot attribute (plot naturalness, used in section 2.4) from sPlot (Bruelheide et al. 2019). Not all the vegetation plots were suitable for the analysis, as some do not report, for example, geographical coordinates and/or the year of the survey. Therefore, we applied various filtering criteria (see section S2 for the full list) and selected a subset of datasets from EVA (see Table S16 for the list).

We considered only those vegetation plots for which species abundance data were available, as this information was needed to calculate functional evenness and divergence. Furthermore, we retained only vascular plant species with available traits. Additional vegetation plots were excluded from the analysis for various reasons: e.g., when trait information was known for a small proportion (< 0.5) of species occurring in the plot, or the location uncertainty was too high (Engel et al. 2023).

We set a threshold for location uncertainty of 10 km, because a stricter threshold would exclude almost all plots from some regions (e.g., the Iberian Peninsula). Since this threshold is considerably higher than the resolution of the land-use maps (300 m, see section 2.3), for plots with location uncertainty higher than 150 m, we applied an additional filter based on the homogeneity of the land use of the area falling within the uncertainty radius of the plot. After matching land-use and land-cover classes to the vegetation plots (as explained in section 2.4), we retained only plots where at least 80% of the land use or land cover within the uncertainty radius was the same as that occurring at the location of the plot coordinates. A ranking was made to keep track of this procedure (ranking 1: location uncertainty < 150 m; ranking 2: location uncertainty > 150 m and land use 100% homogeneous within the uncertainty radius; ranking 3: location uncertainty > 150 m and land use being 80 to < 100% homogeneous within the uncertainty radius). The ranking was later used to refine the pairing between vegetation plots in anthropogenic land and vegetation plots in natural habitats (as explained in section 2.6).

2.2 Allocation to bioregions

To assess spatial variations in the effects on functional diversity, we assigned vegetation plots to bioregions (One Earth). This approach enabled regionalization, while facilitating an appropriate sampling size, as higher resolution of other more commonly used regionalizations (e.g., (Olson et al. 2001), would have drastically reduced the sample size (list of bioregions' names available in Table S3.1 and map in Fig. 2 and S3.1).

2.3 Selection and processing of land use, land cover and potential natural vegetation maps

Each vegetation plot was matched to either an anthropogenic land-use class or to a class of natural vegetation (described in more detail in section 2.4).

As a base layer for land-use classes, we adopted the land-use and land-cover map from the European Space Agency for the Climate Change Initiative (ESA CCI) (ESA Land Cover CCI project team and Defourny 2019). The ESA CCI map had several advantages: (1) it has a 300 m spatial resolution, which we deemed adequate for our goals; (2) it includes most of the land uses and land covers we are addressing in this study (urban areas, cropland, natural vegetation), although not all (e.g., it does not distinguish between natural and managed grassland or forest); (3) it has a yearly resolution, although it goes back only to 1992 (so plots sampled before that year had to be excluded); and (4) it is open access. To fill the gaps concerning some land-use classes, we integrated the ESA CCI data with: (i) the HILDA+ map (Winkler et al. 2021), which covers the period 1960-2019 on a yearly basis and distinguishes between natural grass/shrubland and human-modified pasture/rangeland) and (ii) the GLOBIO4 map (Schipper et al. 2019; PBL Netherlands Environmental Assessment Agency 2023), which was built using the ESA CCI as a basis and distinguishes planted forests from the other land uses and land covers. GLOBIO4 provides data for 1992, 1995, 2000, 2005, 2010, 2015. The land use of the intermediate years was assumed to be the same as the closest year for which the map was available (e.g., for 1993, 1992's data were used). Bioregions PA1 (Russian Arctic Desert Islands) and PA2 (Iceland) were excluded, as they did not contain any vegetation plot in anthropogenic land uses.

Concerning the map of potential natural vegetation, the NatureMap was selected (Hengl et al. 2020), as its resolution (250 m) is similar to the one of the ESA CCI map, and it allows for a distinction between multiple types of natural vegetation (e.g., forest, grassland, shrubland, etc.).

ESA CCI contains 38 land-use/cover classes and the NatureMap 17 land-cover classes. An aggregation was performed to reduce the number of classes and align the classification with the scope of the study (see Table S4.1 and Table S5.1 for the detailed matching between the aggregated classes and, respectively, the ESA CCI classes and the NatureMap classes).

2.4 Assigning vegetation plots to anthropogenic land-use classes or classes of natural habitat, and to the potential natural vegetation

Using the geographical coordinates of the center of each vegetation plot and its sampling date, we extracted the corresponding land-use and land-cover classes. The list of land-use and land-cover classes retrieved from the spatial sources described in the previous section and how they were combined to define the finally used classification (Table 1) is available in Table S6.1. Two additional attributes were used to refine the matching between plots and land-use/cover classes: (i) the type of vegetation from the EVA database (forest, shrubland, grassland, sparse vegetation or wetland); (ii) and the level of naturalness from the sPlot database (1: natural, 2: semi-natural, 3: anthropogenic) (sPlot 2024). In the final classification, each plot was assigned to either a anthropogenic land-use class or a natural habitat (Table 1).

Table 1 List and definition of the land-use/cover classes considered in this study, retrieved from the combination of spatial data, and assigned to the vegetation plots. The list of original land-use and land-cover classes and how they were combined is shown in Table S6.1.

Land use/cover assigned to the plots		Definition
Natural and close-to-natural habitats	Natural forest	Areas where vegetation belongs to the same formation and type that would occupy the site without human interference. This includes forests with sporadic wood extraction or natural grasslands that are grazed at such low intensity that the natural vegetation type is not replaced.
	Natural grassland	
	Natural shrubland	

	Natural herbaceous wetland	
	Natural bare and sparse vegetation	
Anthropogenic land-use classes	Planted forests	Planted, intensively managed forests. It excludes forest planted for protection, ecosystem restoration, or established through planting or natural regeneration, mimicking natural forest stands at maturity.
	Pasture and rangeland	Herbaceous land or shrubland used for livestock and grazing with different intensities and practices. It excludes areas grazed at very low intensity (see two rows above). Vegetation plots assigned to *Pasture and rangeland* do not necessarily have *Natural grassland* as potential natural vegetation, because in most of Europe potential natural vegetation is *Natural forest*, even where now there are pastures and rangelands.
	Cropland	Agricultural land where annual or permanent crops (trees, shrubs and herbaceous) are grown.
	Urban areas	Human settlements, including artificial surfaces, built-up areas, industrial areas, and urban green spaces.
	Mosaic	Areas characterized by a combination of natural vegetation and cropland to varying degrees.

2.5 PCA on the environmental variables

We retrieved 19 bioclimatic variables – temperature- and precipitation-related – at 1-km resolution from the CHELSA V2.1 database (Karger et al. 2017; Karger et al. 2018), and a selection of soil properties that are less influenced by land management (clay mass fraction, silt mass fraction, sand mass fraction, and pH) at 250-m resolution from the SoilGrids database (ISRIC; Hengl et al. 2017) (see the full list in Table S7.1). The soil variables were spatially aggregated to match the resolution of the bioclimatic variables by calculating their mean in each 1-km square. The PCA was performed for these variables at 1-km resolution and on the whole area under assessment, similarly to what was done by (Sabatini et al. 2021). Then we extracted the scores along all the PCA axes for each vegetation plot's location. This approach enabled us to assign each vegetation plot to a position in the PCA space defined by the environmental conditions (Wallis et al. 2021; Joswig et al. 2022), which was later used to pair the plots (see section 2.6).

The PCA was performed using the function rasterPCA from the package RStoolbox, which also allows for a standardization of the input data (see Fig. S7.1 for the results of the first four PCA axes).

2.6 Pairing of vegetation plots in anthropogenic land use and natural habitats

After extracting the PC scores, we paired each vegetation plot sampled in an area assigned to a land-use class with a vegetation plot sampled in the corresponding potential natural land and sharing similar environmental conditions. This approach paired vegetation plots that are close to each other in the environmental space of the PCA as well as belonging to the same bioregion, minimizing the Euclidean distance between the vegetation plots' PC scores within a given pair (see Fig. S8.1) (Elmore and Richman 2001). To calculate the Euclidean distance, each PC score was weighted according to the explained variance of the corresponding PCA axis. Multiple pairings were possible for the same vegetation plot in a natural habitat if the plot had a minimum distance with multiple vegetation plots in human-used land (Fig. S8.1).

The opposite situation also occurred: the same vegetation plot from an anthropogenic land-use class was paired with multiple vegetation plots belonging to natural habitats if the environmental distance within the PCA space was the same. When this occurred, only the vegetation plot from natural habitats with the lowest location uncertainty ranking was considered. If multiple natural plots remained paired to the same plot even after filtering out those with higher location uncertainty ranking, they were kept, and the average of their biodiversity metrics (see next section) was calculated.

Any combinations of bioregion and land-use class with fewer than 10 pairings were removed from the subsequent analyses for statistical reasons, and this caused the exclusion of two additional bioregions not fulfilling this requirement: PA3 (Scandinavian Birch & Coastal Conifer Forests) and PA17 (Black Sea, Caucasus-Anatolian Mixed Forests & Steppe).

2.7 Calculation of relative functional and species diversity

We calculated functional richness, evenness and divergence for each vegetation plot using the dbFD function from the FD package in R (Villéger et al. 2008; Laliberté et al. 2010; Ahmed et al. 2019). All plant traits were standardized to zero mean and unit variance. As our aim was to assess the response of the overall ecosystem functioning and not of specific ecosystem functions, we considered all 30 traits available in sPlot (full list in Table S10.1) from the gap-filled TRY database, as using imputed data was shown to be robust compared to a reduced species set (Scherer et al. 2023).The traits ranged from morphological and nutritional to reproductive characteristics, including stem-specific density, rooting depth, specific leaf area, leaf carbon and nitrogen content, plant height, seed characteristics, leaf dimensions. The function used to calculate functional diversity (dbFD) performs a Principal Coordinate Analysis on the traits and removes information redundancy. We also calculated species richness and total abundance (sum of the number of individuals per species).

Finally, we calculated the ratio between the values of each biodiversity metric in each plot assigned to an anthropogenic land use and its paired plot assigned to a natural habitat (hereafter called "relative functional richness", "relative functional evenness", "relative functional divergence", "relative species richness" and "relative total abundance") as follows:

$$r_{fi} = \frac{bd_{i,\, land-use\ class}}{bd_{j,\, natural\ habitat}}$$

Where $bd_{i,\ \text{anthropogenic land-use class}}$ is the biodiversity metric in anthropogenic vegetation plot *i* and $bd_{j,\ \text{natural habitat}}$ is the biodiversity metric in the natural vegetation plot *j* paired to plot *i*. We also calculated the relative number of species shared between each plot *i* in anthropogenic land and the paired plot in natural habitats *j* compared to the total number of species in the plot in anthropogenic land (hereafter "relative natural species richness"). This metric is a relative value by definition and has the purpose of quantifying how much of the original composition contributes to the new species pool.

Relative values below one indicate that the absolute value is smaller in anthropogenic land use than in the natural habitat. Relative values above one indicate the opposite trend. To obtain aggregated values per bioregion, a median of all the relative values for each metric, land-use class and bioregion was calculated. The values per land-use class across bioregions were calculated as the weighted mean of the medians using the areas of bioregions as weights.

Given the assumptions made, we tested the sensitivity of the results by removing vegetation plots ranked 3 in terms of location uncertainty, imposing an upper threshold on the distance between PC scores of 0.01 (this threshold was selected, as it would remove most of data dispersion, Fig. S9.1), and excluding vegetation plots in anthropogenic land with a naturalness level of 2. The Wilcoxon signed-rank test for paired data with the Benjamini & Hochberg (hereafter "BH") correction for multiple comparisons was used to determine the significance of the shift between the absolute values of biodiversity metrics in the paired plots.

3. Results

The final selection consisted of 73,074 vegetation plots (Fig. S11.1) and 7,185 vascular plant species, out of an estimated 20,000–25,000 European species (Bilz et al. 2011; POWO 2021) (see Fig. S8.2 and Fig. S9.1 for the spatial and density distribution of the plots after the pairing and for the ridge plot of the PC distance, respectively).

In most bioregions, we found lower relative functional richness and divergence ($r_{fi} < 1$) but higher relative functional evenness ($r_{fi} > 1$) in anthropogenic land than in the corresponding paired natural habitats (see Fig. 2, Tables S17-S19).

The difference in functional diversity between anthropogenic land-use classes and their paired natural counterparts was much more evident for functional richness than for functional evenness and divergence. On average, across all bioregions and land-use classes, functional richness and divergence were,

respectively, 66% and 4% lower in anthropogenic areas compared to natural habitats. Functional evenness was 6% higher in anthropogenic areas than in natural ones.

The results of the sensitivity analysis did not significantly differ from the default settings (Figs. S12.1-S12.3).

3.1 Variation among land-use classes

Overall, *Cropland* and *Urban areas* were the land-use classes with the lowest relative functional richness compared to their paired natural vegetation (Fig. 2 and Fig. 3), especially in PA8 *Ural Mountains & West Eurasian Taiga Forests* and PA9 *Great Britain, Ireland & Faroe Islands*, where their values ranged between 0.08 and 0.1 (Table S18).

Averaging the relative functional richness values per land-use class across bioregions (Table 2), we found the lowest weighted mean for *Cropland* and the highest one for *Pasture and rangeland*. *Cropland* and *Pasture and rangeland* were also the categories with the lowest minimum value and the highest maximum value, respectively. *Mosaic* showed the most homogeneous distribution of values of relative functional richness across bioregions (see Fig. 2 and relative weighted standard deviation in Table 2).

Table 2 Mean, minimum, maximum, and standard deviation of relative functional diversity values averaged per land-use class. The alphanumeric codes in brackets correspond to the bioregion where the minimum/maximum was found.

Land-use class	Metric	Weighted mean	Minimum	Maximum	Relative weighted standard deviation
Urban areas	Relative functional richness	0.38	0.10 (PA9)	1.44 (PA20)	1.02
	Relative functional evenness	1.12	0.98 (PA14)	1.36 (PA18)	0.09
	Relative functional divergence	1.01	0.81 (PA20)	1.36 (PA9)	0.18
Cropland	Relative functional richness	0.32	0.08 (PA8)	0.79 (PA16)	0.75
	Relative functional evenness	1.02	0.95 (PA8)	1.10 (PA10)	0.05
	Relative functional divergence	0.95	0.84 (PA18)	1.21 (PA9)	0.12
Pasture and Rangeland	Relative functional richness	0.46	0.11 (PA9)	1.52 (PA18)	0.93
	Relative functional evenness	1.03	0.85 (PA16)	1.25 (PA18)	0.09
	Relative functional divergence	0.97	0.82 (PA18)	1.21 (PA9)	0.13
Mosaic	Relative functional richness	0.39	0.13 (PA9)	0.80 (PA18)	0.55
	Relative functional evenness	1.08	0.95 (PA13)	1.11 (PA9)	0.03

	Relative functional divergence	1.02	0.83 (PA15)	1.34 (PA16)	0.17
Planted forest	Relative functional richness	0.37	0.12 (PA9)	1.26 (PA16)	0.87
	Relative functional evenness	1.05	0.75 (PA16)	1.38 (PA20)	0.14
	Relative functional divergence	0.95	0.88 (PA8)	1.26 (PA20)	0.10

Cropland had the lowest weighted mean also for relative functional divergence (together with *Planted forest*) and relative functional evenness. Relative functional divergence and relative functional evenness showed the highest weighted mean, respectively, in *Mosaic* and in *Urban areas.* The highest variation in terms of impact on functional evenness was found for *Planted forest* (the values are the most heterogeneous across bioregions, see Fig. 2 and weighted relative standard deviation in Table 2). We found the opposite for *Mosaic:* similar values of functional evenness in all bioregions and almost all above one, except PA13 *Alps & Po Basin Mixed Forests*.

3.2 Variation among bioregions

The variation of the response appeared to be more pronounced among bioregions than among land-use classes. PA9 *Great Britain, Ireland & Faroe Islands* showed the most homogeneous values of functional diversity and the lowest values of median relative functional richness for all land-use classes except *Cropland*, which had its minimum in *PA8 Ural Mountains & West Eurasian Taiga Forests* (Fig. 3). At the same time, PA9 depicted the highest values of relative functional divergence in *Urban areas*, *Cropland* and *Pasture and rangeland*. PA16 *Pontic Steppe Grasslands* had the largest number of land-use classes with relative functional richness above one (*Pasture and rangelands* and *Planted forest*) and did not show significant difference from natural habitat according to the Wilcoxon test. PA18 *Aegean Sea & East Mediterranean Mixed Forests*, PA19 *Adriatic Sea & Central Mediterranean Mixed Forests* and PA20 *Balearic Sea & West Mediterranean Mixed Forests*, all in southern Europe, had higher values of relative functional richness compared to the more northern bioregions (Fig. 2), even above one in two cases, resulting from a lower absolute value of functional richness for the two natural vegetation classes occurring there, *Natural forest* and *Natural shrubland* (Fig. S13.1).

3.3 Comparison with other biodiversity metrics

The impact of anthropogenic land use on relative species richness did not yield the same results as those of relative functional richness (Fig. 3), and their relationship followed a logarithmic pattern (see Figs. S14.1 and S14.2). In 25 combinations of land-use classes and bioregions, the medians of both relative species richness and relative functional richness were below one, and, in most cases, the decrease in functional richness appeared more pronounced. In 23 other combinations, especially for the land-use class *Pasture and rangelands*, the median relative species richness was around one or slightly above one, whereas the median relative functional richness was below one. Conversely, in three combinations distributed in PA16 *Pontic Steppe Grasslands* and in PA20 *Balearic Sea & West Mediterranean Mixed Forests*, the opposite occurred. *Pasture and rangeland* in PA18 *Aegean Sea & East Mediterranean Mixed Forests* was the only case where both metrics were above one.

The relative natural species richness (Fig. 3) was very close to zero for all combinations of anthropogenic land-use classes and bioregions and the relative total abundance had a median value smaller than one in most combinations of land-use classes and bioregions (Fig. 3), with a few exceptions in southern Europe.

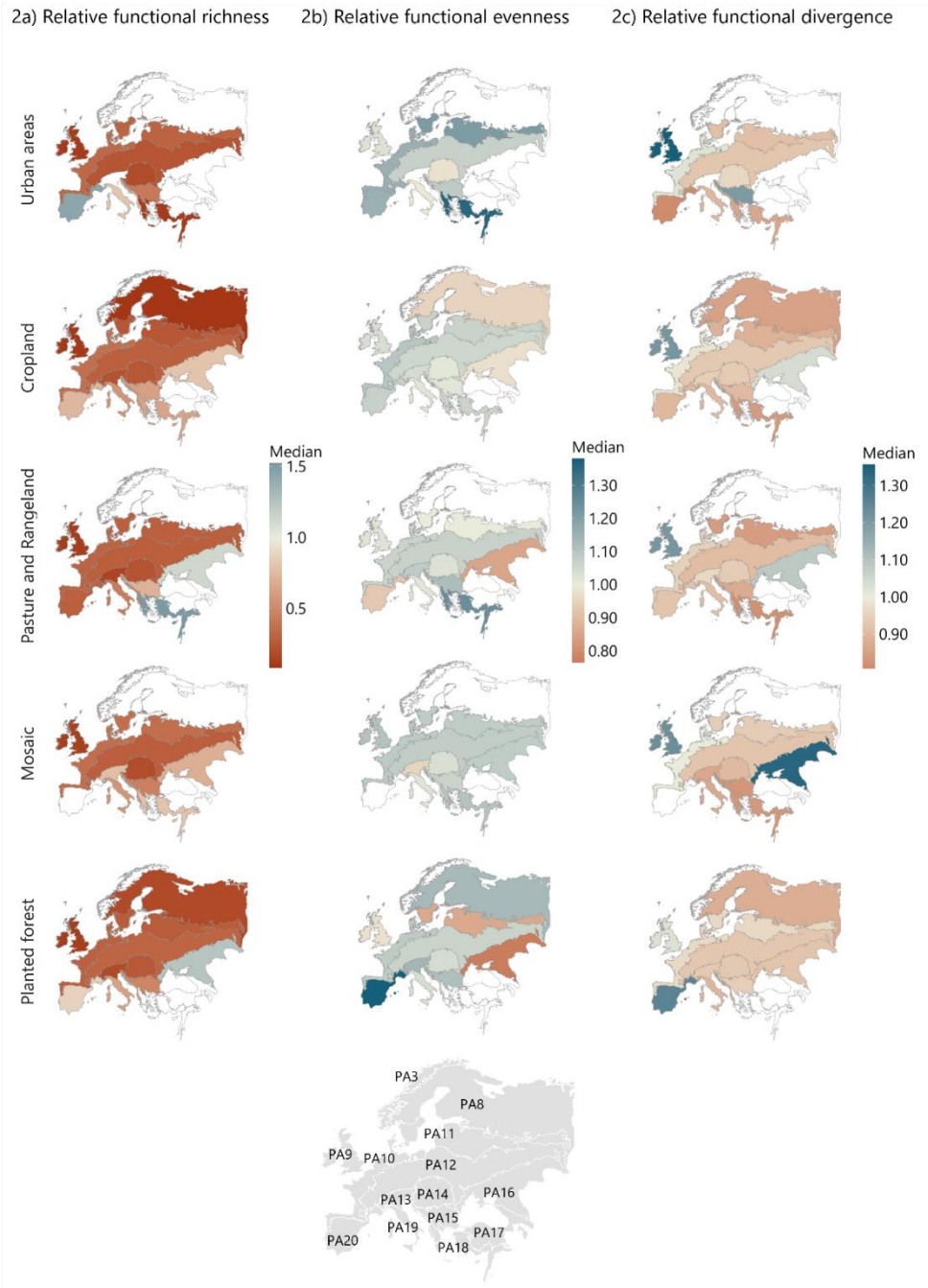

Figure 2. Median values of relative functional richness (a), evenness (b) and divergence (c) per bioregion and land-use class. Warmer colors and colder colors indicate decreased and increased functional diversity values, respectively, in relation to the potential natural vegetation. White bioregions are those for which not enough pairings were available.

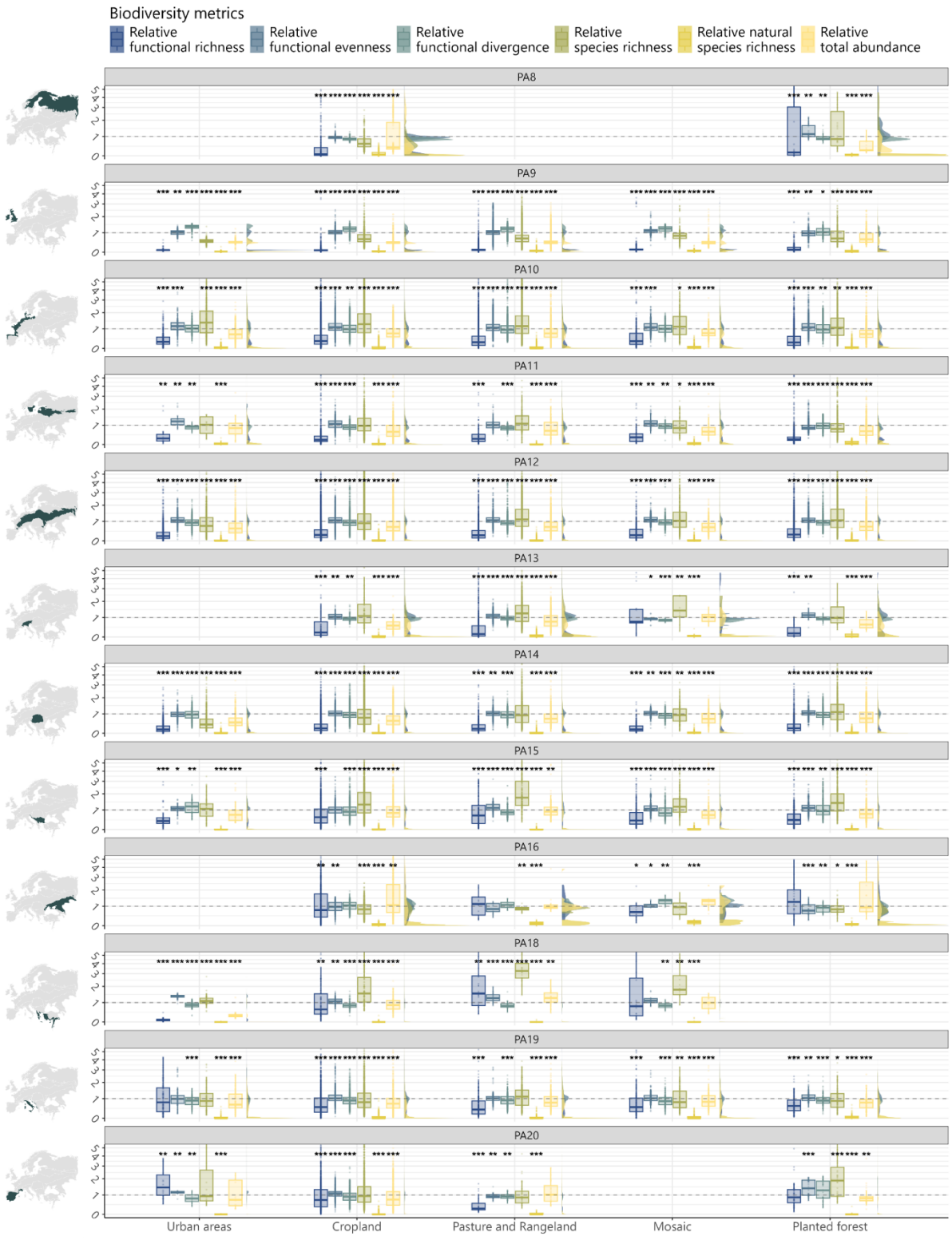

Figure 3 Relative functional and species diversity per bioregion and per land-use class, zoomed between 0 and 5 to improve readability. The dotted lines correspond to 1. Results of Wilcoxon test: ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.05, *: 0.05 < p-value ≤ 0.1, no *: p-value > 0.1.

4. Discussion

We found evidence that anthropogenic land use leads to a reduction in functional richness and divergence while simultaneously promoting an increase in functional evenness. This trend was consistent across most of the bioregions we examined, with a particularly pronounced effect observed for functional richness. Our results confirm those of Scherer *et al.* (2020) at a smaller spatial extent in Europe but diverge from the findings of Flynn *et al.* (2008), who reported no clear pattern of diversity change due to anthropogenic land use for plants in the Americas. The disparity in results may be attributed to differences in the metric used for assessing functional diversity. Flynn *et al.* (2008), along with De Souza *et al.* (2014), which is mostly based on data from Flynn *et al.* (2008), calculated a single functional diversity metric, which was quantified based on a dendrogram and relied on only eight functional traits, including four categorical traits, found to decrease the quality of the measure (Maire et al. 2015).

Regarding the response of each functional diversity metric, the observed decrease in functional richness aligns with previous studies (Pakeman 2011; Janeček et al. 2013; Carmona et al. 2020): human disturbance occurring with anthropogenization of land tends to diminish functional richness. Concerning functional divergence, previous studies have reported mixed responses to land use (Bonilla-Valencia et al. 2022). The decrease recorded in our study suggests that anthropogenic land use reduces the degree of niche differentiation among species within communities and increases the trait similarity of dominant species (Mason et al. 2005; Mouchet et al. 2010). Conversely, human disturbance appeared to promote functional evenness. Functional evenness is higher when species and their abundance are more regularly distributed along functional trait gradients (Mouchet et al. 2010; Pakeman 2011). When coupled with a reduction of traits' multidimensional space (reduced functional richness) and with a lower degree of niche differentiation (reduced functional divergence), the response of functional evenness suggests that the dominant species exhibit a higher level of similarity in anthropogenic land than in natural habitats (Mouchet et al. 2010; Pakeman 2011). These findings may indicate that species populating anthropogenic areas are more functionally homogeneous than those in natural habitats. Previous studies have reported disruption of

interactions among specialized partners following the removal of natural and semi-natural habitats, resulting in extensive community restructuring towards a less diverse community dominated by generalist and widespread species (Newbold 2018; Le Provost et al. 2021). These effects are likely linked to the extensive change in species composition observed when comparing anthropogenic land use with natural habitats (Fig. 3). For example, plots in anthropogenic land in PA16 *Pontic Steppe Grasslands* had higher relative natural species richness and functional richness than other bioregions, suggesting that species turnover plays a big role in determining functional richness under disturbance.

The logarithmic relationship between species richness and functional richness has been observed in prior studies (Villéger et al. 2008; Biswas and Mallik 2011; Aros-Mualin et al. 2021; Boonman et al. 2021), likely accounting for the occasionally divergent behavior observed in these metrics. Notably, natural habitats tended to exhibit higher functional richness than anthropogenic land use at equivalent levels of species richness (Fig. S14.1). Moreover, as species richness increased, the corresponding rise in functional richness did not occur at the same rate. Conversely, lower species richness was associated with more pronounced variations in functional richness. This underscores the distinct information conveyed by these indices and emphasizes how functional diversity can detect adverse changes even when species richness remains unchanged or seemingly improves.

Regarding species richness alone, we acknowledge that, in contrast with our findings, many studies with site-specific comparisons focusing on populations have found evidence of decline in all land-use classes (Newbold et al. 2015). In addition, there are inherent uncertainties in our study due to the quality of the datasets, which suggests pairing refinement should be prioritized once additional data becomes available (see Limitations section). Compared to previous studies, we implemented a different and more systematic approach, not based on meta-analyses but on harmonized datasets and coupling anthropogenic land with the potential natural vegetation occurring there and not the natural vegetation nearby, which might differ from the original natural vegetation. The differences may emerge from these elements. Furthermore, a global review of land-use effects on plant species richness found a positive trend in managed grasslands

compared to natural habitats (Gerstner et al. 2014). Additionally, recent research indicates that global median species richness may either increase or remain stable when comparing different types of natural forests (namely, natural deciduous broadleaf forest, evergreen needleleaf forests, and mixed forests, which are the same natural forests considered in our study) to minor or major human modification (Deng et al. 2024). Furthermore, Flynn *et al.* (2009) did not find a significant difference between plant species richness in anthropogenic and natural land.

Variability in response among bioregions, compared to land-use classes, may stem from differences in environmental conditions and management practices. Environmental factors can act as filters on trait composition within plant communities, influencing their functional diversity (Bruelheide et al. 2018; Wallis et al. 2021; Cheng et al. 2022; Joswig et al. 2022). While PCA was utilized to minimize this influence when pairing vegetation plots, distinct levels of functional variation may still be exhibited across bioregions due to their specific natural vegetation and environment. For instance, Mediterranean bioregions (PA18, PA19, PA20) exhibited lower absolute functional richness compared to northerly ones (Fig. S13.1). Certain forest types, such as mixed forests (mostly spread in central Europe) and coniferous forests (occurring at high latitudes or high elevations, e.g. in PA8 or PA13, which we recorded having the highest absolute values of functional richness, Fig. 13.1), can exhibit larger trait hypervolumes than Mediterranean woodlands or temperate grasslands (Echeverría-Londoño et al. 2018), corroborating our findings. Furthermore, the relationship between trait hypervolume and latitude has been recorded to differ from that of species richness, indicating distinct ecological dynamics (Lamanna et al. 2014).

Additionally, management practices and intensity within land-use classes vary across bioregions and likely modulate their impacts on functional diversity (Laliberté et al. 2010; Janeček et al. 2013; Van Meerbeek et al. 2014). While our study could not incorporate management intensity due to data limitations, future research should consider this aspect for a more comprehensive assessment (Dullinger et al. 2021).

Our study's findings on how human land use affects plant functional diversity have significant implications for future global change. Predictive models suggest that trait evolution aids resilience (Guerin et al. 2014),

while the threat of invasive alien species, amplified by global trade, is influenced by the functional diversity and abundance of native species (Tordoni et al. 2020; Kaushik et al. 2022; Díaz et al. 2023). For instance, the changes we observed, like decreased functional richness and divergence alongside increased functional evenness due to human pressures, may alter the native communities' ability to resist invasive species. Shifts in functional diversity may also heighten plant communities' response to nitrogen deposition, particularly relevant in Europe, where it fosters nitrogen-demanding plants (Staude et al. 2020). Considering these observed patterns, we anticipate ongoing alterations in plant functional diversity dynamics under global changes such as land use change.

Limitations

To evaluate the effects of human land use on vascular plant diversity comprehensively, we had to face a few challenges. Firstly, data coverage varied across bioregions and land-use classes, particularly in southern Europe and the Mediterranean region, where the number of natural vegetation plots available for analysis was limited by data availability and by the long history of land management (Martín-Forés 2017; Sabatini et al. 2018; Ellis et al. 2021). Secondly, the absence of a consistent spatial data source for land-use classification led us to combine multiple maps, introducing uncertainty. The main challenge lays in identifying a reliable source capable of distinguishing between natural and managed forests at a meaningful spatiotemporal resolution, which remains difficult despite advancements in remote sensing (Hirschmugl et al. 2017). Thirdly, the matching between the vegetation plots and the land-use and land-cover classes introduced uncertainty, mainly because of three factors: (i) the location uncertainty of the vegetation plots (see Fig. S15.2), which we addressed by excluding plots with high location uncertainty and ranking the others based on the homogeneity of land use/cover within the uncertainty radius (see sec. 2.1); (ii) the intrinsic uncertainty of the land-use and land-cover maps; and (iii) the mismatch between the resolution of the land-use map and the size of the vegetation plots (53 m^2 on average but with much higher or not available values for part of the plots (see Fig. S15.1), which could lead to incorrect land-use assignments.

Outlook

Our analysis stands out for its comprehensive consideration of a high number of traits, surpassing previous studies. To increase even more the trait representativeness, enhancing belowground trait coverage is advisable (Carmona, Bueno, et al. 2021). Exploring solutions for trait distribution gaps or scaling up with methods like model predictions or remote sensing is worth investigating (Schneider et al. 2017; Boonman et al. 2020; Hauser, Timmermans, et al. 2021; Hauser, Féret, et al. 2021).

An improvement in the ecological relevance of the assessment and an in-depth comprehension of the effect of land-use change from natural to human-modified could be achieved by considering not only plants' traits but also traits of other taxonomic groups. This advancement would make it possible to trace the effect along the trophic chain and on species interactions, given the essential interplay between them (Haddad et al. 2009; Rigal et al. 2023; Windsor et al. 2023).

Conclusion

Our study offers valuable insights into the multifaceted relationship between anthropogenic land modification and biodiversity and highlights the significance of incorporating diverse metrics, notably functional diversity, which yields unique and complementary insights beyond traditional measures. We integrate information across different databases, enabling data interoperability and merging various sources of information at a continental scale. Through our regionalized approach and novel methodology, we enhanced our understanding of this intricate relationship and introduced a fresh perspective on connecting localized studies with broader regional implications. Such efforts are crucial in addressing the urgent challenge of halting biodiversity loss.

Code and data availability

The code and the data on which the analysis is based are available for the review process on Dryad at: https://datadryad.org/stash/share/50nM9Rbd-qMSoiREeLir9CekoiFLG39bt3V5PiUdj4s

References

Ahmed DA, van Bodegom PM, Tukker A. 2019. Evaluation and selection of functional diversity metrics with recommendations for their use in life cycle assessments. Int J Life Cycle Assess. 24(3):485–500. doi:10.1007/s11367-018-1470-8.

Aros-Mualin D, Noben S, Karger DN, Carvajal-Hernández CI, Salazar L, Hernández-Rojas A, Kluge J, Sundue MA, Lehnert M, Quandt D, et al. 2021. Functional Diversity in Ferns Is Driven by Species Richness Rather Than by Environmental Constraints. Front Plant Sci. 11(January). doi:10.3389/fpls.2020.615723.

Bannar-Martin KH, Kremer CT, Ernest SKM, Leibold MA, Auge H, Chase J, Declerck SAJ, Eisenhauer N, Harpole S, Hillebrand H, et al. 2018. Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (CAFE) approach. Ecol Lett. 21(2):167–180. doi:10.1111/ele.12895.

Bilz M, Kell SP, Maxted N, Lansdown R V. 2011. European Red List of Vascular Plants. Publicatio. http://data.iucn.org/dbtw-wpd/edocs/RL-4-016.pdf.

Biswas SR, Mallik AU. 2011. Species diversity and functional diversity relationship varies with disturbance intensity. Ecosphere. 2(4):1–10. doi:10.1890/ES10-00206.1.

Bonilla-Valencia L, Castillo-Aguero S, Zavala-Hurtado JA, García FJE, Lindig-Cisneros R, Martínez-Orea Y. 2022. Linking functional diversity to ecological indicators: a tool to predict anthropogenic effects on ecosystem functioning. Environ Rev. 30(2):175–183. doi:10.1139/er-2021-0093.

Boonman CCF, Benítez-López A, Schipper AM, Thuiller W, Anand M, Cerabolini BEL, Cornelissen JHC, Gonzalez-Melo A, Hattingh WN, Higuchi P, et al. 2020. Assessing the reliability of predicted plant trait distributions at the global scale. Glob Ecol Biogeogr. 29(6):1034–1051. doi:10.1111/geb.13086.

Boonman CCF, Huijbregts MAJ, Benítez-López A, Schipper AM, Thuiller W, Santini L. 2022. Trait-

based projections of climate change effects on global biome distributions. Divers Distrib. 28(1):25–37. doi:10.1111/ddi.13431.

Boonman CCF, Santini L, Robroek BJM, Hoeks S, Kelderman S, Dengler J, Bergamini A, Biurrun I, Carranza ML, Cerabolini BEL, et al. 2021. Plant functional and taxonomic diversity in european grasslands along climatic gradients. J Veg Sci. 32(3):1–12. doi:10.1111/jvs.13027.

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-alfaro B, Hennekens SM, Botta-dukát Z, Chytrý M, Field R, Jansen F, et al. 2018. Global trait–environment relationships of plant communities. Nat Ecol Evol. 2(December):1906–1917. doi:10.1038/s41559-018-0699-8. http://dx.doi.org/10.1038/s41559-018-0699-8.

Bruelheide H, Purschke O, Pillar D, Jansen F, Kattge J, Haider S, Jandt U, Arnst E, Attorre F, Berg C, et al. 2019. sPlot – A new tool for global vegetation analyses. J Veg Sci. 30(2):161–186. doi:10.1111/jvs.12710.

Cadotte MW, Carscadden K, Mirotchnick N. 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. J Appl Ecol. 48(5):1079–1087. doi:10.1111/j.1365-2664.2011.02048.x.

Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R. 2021. Fine-root traits in the global spectrum of plant form and function. Nature. 597(7878):683–687. doi:10.1038/s41586-021-03871-y. http://dx.doi.org/10.1038/s41586-021-03871-y.

Carmona CP, Guerrero I, Peco B, Morales MB, Oñate JJ, Pärt T, Tscharntke T, Liira J, Aavik T, Emmerson M, et al. 2020. Agriculture intensification reduces plant taxonomic and functional diversity across European arable systems. Funct Ecol. 34(7):1448–1460. doi:10.1111/1365-2435.13608.

Carmona CP, Tamme R, Pärtel M, De Bello F, Brosse S, Capdevila P, González RM, González-Suárez M, Salguero-Gómez R, Vásquez-Valderrama M, et al. 2021. Erosion of global functional diversity across

the tree of life. Sci Adv. 7(13):1–12. doi:10.1126/sciadv.abf2675.

Chaplin-Kramer R, Brauman KA, Cavender-Bares J, Díaz S, Duarte GT, Enquist BJ, Garibaldi LA, Geldmann J, Halpern BS, Hertel TW, et al. 2022. Conservation needs to integrate knowledge across scales. Nat Ecol Evol. 6(2):118–119. doi:10.1038/s41559-021-01605-x.

Cheng X, Ping T, Li Z, Wang T, Han H, Epstein HE. 2022. Effects of environmental factors on plant functional traits across different plant life forms in a temperate forest ecosystem. New For. 53(1):125–142. doi:10.1007/s11056-021-09847-0.

Chytrý M, Knollov I, Hennekens SM, Jim B, Jansen F, Landucci F, Schamin JHJ, Agrillo E, Ambarlı D, Angelini P, et al. 2016. European Vegetation Archive (EVA): an integrated database of European vegetation plots r. Appl Veg Sci. 19:173–180. doi:10.1111/avsc.12191.

Deng S, Beale CM, Platts PJ, Thomas CD. 2024. Human modification of land cover alters net primary productivity, species richness and their relationship. Glob Ecol Biogeogr. 33(3):385–399. doi:10.1111/geb.13795.

Díaz JG, de la Riva EG, Martín-Forés I, Vilà M. 2023. Which features at home make a plant prone to become invasive? NeoBiota. 86:1–20. doi:10.3897/NEOBIOTA.86.104039.

Dornelas M, Chase JM, Gotelli NJ, Magurran AE, McGill BJ, Antão LH, Blowes SA, Daskalova GN, Leung B, Martins IS, et al. 2023. Looking back on biodiversity change: Lessons for the road ahead. Philos Trans R Soc B Biol Sci. 378(1881):1–15. doi:10.1098/rstb.2022.0199.

Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE. 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science (80-). 344(6181):296–299. doi:10.1126/science.1248484.

Dullinger I, Essl F, Moser D, Erb K, Haberl H, Dullinger S. 2021. Biodiversity models need to represent land-use intensity more comprehensively. Glob Ecol Biogeogr.(February):924–932.

doi:10.1111/geb.13289.

Echeverría-Londoño S, Enquist BJ, Neves DM, Violle C, Boyle B, Kraft NJB, Maitner BS, McGill B, Peet RK, Sandel B, et al. 2018. Plant functional diversity and the biogeography of biomes in North and South America. Front Ecol Evol. 6(DEC):1–12. doi:10.3389/fevo.2018.00219.

Ellis EC, Gauthier N, Goldewijk KK, Bird RB, Boivin N, Díaz S, Fuller DQ, Gill JL, Kaplan JO, Kingston N, et al. 2021. People have shaped most of terrestrial nature for at least 12,000 years. Proc Natl Acad Sci U S A. 118(17):1–8. doi:10.1073/pnas.2023483118.

Elmore KL, Richman MB. 2001. Euclidean Distance as a Similarity Metric for Principal Component Analysis. Mon Weather Rev. 129:540–549. doi:10.1175/1520-0493(2001)129<0540:EDAASM>2.0.CO;2.

Engel T, Bruelheide H, Hoss D, Sabatini FM, Altman J, Arfin-Khan MAS, Bergmeier E, Černý T, Chytrý M, Dainese M, et al. 2023. Traits of dominant plant species drive normalized difference vegetation index in grasslands globally. Glob Ecol Biogeogr. 32(5):695–706. doi:10.1111/geb.13644.

ESA Land Cover CCI project team, Defourny P. 2019. ESA Land Cover Climate Change Initiative (Land_Cover_cci): Global Land Cover Maps, Version 2.0.7. :Centre for Environmental Data Analysis. https://catalogue.ceda.ac.uk/uuid/b382ebe6679d44b8b0e68ea4ef4b701c.

Felipe-Lucia MR, Soliveres S, Penone C, Manning P, van der Plas F, Boch S, Prati D, Ammer C, Schall P, Gossner MM, et al. 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. Nat Commun. 9(1). doi:10.1038/s41467-018-07082-4.

Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett. 12(1):22–33. doi:10.1111/j.1461-0248.2008.01255.x.

Gerstner K, Dormann CF, Stein A, Manceur AM, Seppelt R. 2014. Effects of land use on plant diversity -

A global meta-analysis. J Appl Ecol. 51(6):1690–1700. doi:10.1111/1365-2664.12329.

Guerin GR, Martín-Forés I, Biffin E, Baruch Z, Breed MF, Christmas MJ, Cross HB, Lowe AJ. 2014. Global change community ecology beyond species-sorting: A quantitative framework based on mediterranean-biome examples. Glob Ecol Biogeogr. 23(10):1062–1072. doi:10.1111/geb.12184.

Haddad NM, Crutsinger GM, Gross K, Haarstad J, Knops JMH, Tilman D. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecol Lett. 12(10):1029–1039. doi:10.1111/j.1461-0248.2009.01356.x.

Hagan JG, Henn JJ, Osterman WHA. 2023. Plant traits alone are good predictors of ecosystem properties when used carefully. Nat Ecol Evol. 7(3):332–334. doi:10.1038/s41559-022-01920-x.

Harrison PA, Berry PM, Simpson G, Haslett JR, Blicharska M, Bucur M, Lommelen E, Meiresonne L, Turkelboom F. 2014. Linkages between biodiversity attributes and ecosystem services : A systematic review. Ecosyst Serv. 9:191–203. doi:10.1016/j.ecoser.2014.05.006.

Hauser LT, Féret JB, An Binh N, van der Windt N, Sil ÂF, Timmermans J, Soudzilovskaia NA, van Bodegom PM. 2021. Towards scalable estimation of plant functional diversity from Sentinel-2: In-situ validation in a heterogeneous (semi-)natural landscape. Remote Sens Environ. 262(December 2020). doi:10.1016/j.rse.2021.112505.

Hauser LT, Timmermans J, van der Windt N, Sil ÂF, César de Sá N, Soudzilovskaia NA, van Bodegom PM. 2021. Explaining discrepancies between spectral and in-situ plant diversity in multispectral satellite earth observation. Remote Sens Environ. 265(September). doi:10.1016/j.rse.2021.112684.

Hengl T, Jung M, Visconti P. 2020. Potential distribution of land cover classes (Potential Natural Vegetation) at 250 m spatial resolution (v0.1). https://doi.org/10.5281/zenodo.3631254.

Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, Blagotić A, Shangguan W, Wright MN, Geng X, Bauer- Marschallinger B, et al. 2017. SoilGrids250m: Global

gridded soil information based on machine learning. PLoS One. 12(e0169748). doi:doi.org/10.1371/journal.pone.0169748.

Hirschmugl M, Gallaun H, Dees M, Datta P, Deutscher J, Koutsias N, Schardt M. 2017. Methods for Mapping Forest Disturbance and Degradation from Optical Earth Observation Data: a Review. Curr For Reports. 3(1):32–45. doi:10.1007/s40725-017-0047-2.

Hu G, Jin Y, Liu J, Yu M. 2014. Functional diversity versus species diversity: relationships with habitat heterogeneity at multiple scales in a subtropical evergreen broad-leaved forest. Ecol Res. 29(5):897–903. doi:10.1007/s11284-014-1178-6.

IPBES. 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Brondízio ES, Settele J, Diaz S, Ngo HT, editors. IPBES secretariat.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-lorenzen M, Schmid B, Tilman D, Ruijven J Van, et al. 2011. High plant diversity is needed to maintain ecosystem services. Nature. 477:5–9. doi:10.1038/nature10282.

ISRIC. Webdav - Index of soilgrids latest data. https://files.isric.org/soilgrids/latest/data/.

Jandt U, Bruelheide H, Jansen F, Bonn A, Grescho V, Klenke RA, Sabatini FM, Bernhardt-Römermann M, Blüml V, Dengler J, et al. 2022. More losses than gains during one century of plant biodiversity change in Germany. Nature. 611(7936):512–518. doi:10.1038/s41586-022-05320-w.

Janeček Š, de Bello F, Horník J, Bartoš M, Černý T, Doležal J, Dvorský M, Fajmon K, Janečková P, Jiráská Š, et al. 2013. Effects of land-use changes on plant functional and taxonomic diversity along a productivity gradient in wet meadows. J Veg Sci. 24(5):898–909. doi:10.1111/jvs.12012.

Joswig JS, Wirth C, Schuman MC, Kattge J, Reu B, Wright IJ, Sippel SD, Rüger N, Richter R, Schaepman ME, et al. 2022. Climatic and soil factors explain the two-dimensional spectrum of global

plant trait variation. Nat Ecol Evol. 6(1):36–50. doi:10.1038/s41559-021-01616-8.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann N., Linder HP, Kessler M. 2018. Data from: Climatologies at high resolution for the earth's land surface areas. EnviDat. https://doi.org/10.16904/envidat.228.v2.1.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M. 2017. Climatologies at high resolution for the earth's land surface areas. Sci Data. 4:1–20. doi:10.1038/sdata.2017.122.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, et al. 2020. TRY plant trait database – enhanced coverage and open access. Glob Chang Biol. 26(1):119–188. doi:10.1111/gcb.14904.

Kaushik P, Pati PK, Khan ML, Khare PK. 2022. Plant functional traits best explain invasive species' performance within a dynamic ecosystem - A review. Trees, For People. 8(April):100260. doi:10.1016/j.tfp.2022.100260. https://doi.org/10.1016/j.tfp.2022.100260.

Knollová I, Chytrý M, Bruelheide H, Dullinger S, Jandt U, Bernhardt-Römermann M, Biurrun I, de Bello F, Glaser M, Hennekens S, et al. 2024. ReSurveyEurope: A database of resurveyed vegetation plots in Europe. J Veg Sci. 35(2). doi:10.1111/jvs.13235.

Laliberté E, Wells JA, Declerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, et al. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol Lett. 13(1):76–86. doi:10.1111/j.1461-0248.2009.01403.x.

Lamanna C, Blonder B, Violle C, Kraft NJB, Sandel B, Šímová I, Donoghue JC, Svenning JC, McGill BJ, Boyle B, et al. 2014. Functional trait space and the latitudinal diversity gradient. Proc Natl Acad Sci U S A. 111(38):13745–13750. doi:10.1073/pnas.1317722111.

Leclère D, Obersteiner M, Alkemade R, Almond R, Barrett M, Bunting G, Burgess ND, Butchart SHM,

Chaudhary A, Cornell S, et al. 2020. Towards pathways bending the curve of terrestrial biodiversity trends within the 21st century. Nature. 585:551–556. doi:10.1038/s41586-020-2705-y. http://pure.iiasa.ac.at/id/eprint/15241/1/https://doi.org/10.1038/s41586-020-2705-y.pdf.

Maire E, Grenouillet G, Brosse S, Villéger S. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Glob Ecol Biogeogr. 24(6):728–740. doi:10.1111/geb.12299.

Martín-Forés I. 2017. Exotic Plant Species in the Mediterranean Biome: A Reflection of Cultural and Historical Relationships. In: Borna Fuerst-Bjelis, editor. Mediterranean Identities - Environment, Society, Culture. Croatia: InTech Open. p. 414.

Mason Norman W H, Mouillot D, Lee WG, Wilson JB. 2005. Functional richness , functional evenness and functional divergence: The primary components of functional diversity. (October). doi:10.1111/j.0030-1299.2005.13886.x.

Mason N.W.H., Mouillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. Oikos. 111(1):112–118. doi:10.1111/j.0030-1299.2005.13886.x.

Van Meerbeek K, Helsen K, Hermy M. 2014. Impact of land-use intensity on the conservation of functional and phylogenetic diversity in temperate semi-natural plant communities. Biodivers Conserv. 23(9):2259–2272. doi:10.1007/s10531-014-0720-8.

Mouchet MA, Villéger S, Mason NWH, Mouillot D. 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol. 24(4):867–876. doi:10.1111/j.1365-2435.2010.01695.x.

Newbold T. 2018. Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. PLoS Biol.:1–24. doi:10.5519/0066354.

Newbold T, Bentley LF, Hill SLL, Edgar MJ, Horton M, Su G, Şekercioğlu ÇH, Collen B, Purvis A. 2020. Global effects of land use on biodiversity differ among functional groups. Funct Ecol. 34(3):684–693. doi:10.1111/1365-2435.13500.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature. 520(7545):45–50. doi:10.1038/nature14324. https://www.nature.com/articles/nature14324#Tab2.

O'Connor MI, Gonzalez A, Byrnes JEK, Cardinale BJ, Duffy JE, Gamfeldt L, Griffin JN, Hooper D, Hungate BA, Paquette A, et al. 2017. A general biodiversity–function relationship is mediated by trophic level. Oikos. 126(1):18–31. doi:10.1111/oik.03652.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA, Itoua I, Strand HE, Morrison JC, et al. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. Bioscience. 51(11):933. doi:10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2.

One Earth. Bioregions. https://www.oneearth.org/bioregions/.

Pakeman RJ. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. J Ecol. 99(5):1143–1151. doi:10.1111/j.1365-2745.2011.01853.x.

PBL Netherlands Environmental Assessment Agency. 2023. Globioweb. Providing biodiversity information to the broad audience. Technical documentation of the Globioweb datasets. https://www.globio.info/wp-content/uploads/2023/03/GlobioWeb_technical_documentation_20230219.pdf.

Pereira HM, Martins IS, Rosa IMD, Kim H, Leadley P, Popp A, Vuuren DP van, Hurtt G, Anthoni P, Arneth A, et al. 2024. Global trends in biodiversity and ecosystem services from 1900 to 2050. Science (80-). 465(384):458–465. doi:10.1126/science.adn3441. https://www.biorxiv.org/content/10.1101/2020.04.14.031716v2%0Ahttps://www.biorxiv.org/content/10.1

101/2020.04.14.031716v2.abstract.

van der Plas F. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biol Rev. 94(4):1220–1245. doi:10.1111/brv.12499.

POWO. 2021. Plants of the world online. Facilitated by the royal botanic gardens, Kew. http://www.plantsoftheworldonline.org.

Le Provost G, Schenk N V., Penone C, Thiele J, Westphal C, Allan E, Ayasse M, Blüthgen N, Boeddinghaus RS, Boesing AL, et al. 2023. The supply of multiple ecosystem services requires biodiversity across spatial scales. Nat Ecol Evol. 7(2):236–249. doi:10.1038/s41559-022-01918-5.

Le Provost G, Thiele J, Westphal C, Penone C, Allan E, Neyret M, van der Plas F, Ayasse M, Bardgett RD, Birkhofer K, et al. 2021. Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nat Commun. 12(1). doi:10.1038/s41467-021-23931-1.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing,. https://www.r-project.org/.

Reader MO, Eppinga MB, de Boer HJ, Damm A, Petchey OL, Santos MJ. 2023. Biodiversity mediates relationships between anthropogenic drivers and ecosystem services across global mountain, island and delta systems. Glob Environ Chang. 78(October 2022):102612. doi:10.1016/j.gloenvcha.2022.102612. https://doi.org/10.1016/j.gloenvcha.2022.102612.

Rigal S, Dakos V, Devictor V. 2023. Farmland practices are driving bird population decline across Europe. Proc Natl Acad Sci. 120(21). doi:10.1073/pnas. http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2216830120/-/DCSupplemental.https://doi.org/10.1073/pnas.2216830120.

Rosenfield MF, Müller SC. 2020. Plant Traits Rather than Species Richness Explain Ecological Processes in Subtropical Forests. Ecosystems. 23(1):52–66. doi:10.1007/s10021-019-00386-6.

Sabatini FM, Burrascano S, Keeton WS, Levers C, Lindner M, Pötzschner F, Verkerk PJ, Bauhus J, Buchwald E, Chaskovsky O, et al. 2018. Where are Europe's last primary forests? Divers Distrib. 24(10):1426–1439. doi:10.1111/ddi.12778.

Sabatini FM, Lenoir J, Hattab T, Arnst EA, Chytrý M, Dengler J, De Ruffray P, Hennekens SM, Jandt U, Jansen F, et al. 2021. sPlotOpen – An environmentally balanced, open-access, global dataset of vegetation plots. Glob Ecol Biogeogr.(December 2020):geb.13346. doi:10.1111/geb.13346. https://onlinelibrary.wiley.com/doi/10.1111/geb.13346.

Scherer L, van Baren SA, van Bodegom PM. 2020. Characterizing land use impacts on functional plant diversity for life cycle assessments. Environ Sci Technol.(April). doi:10.1021/acs.est.9b07228. https://pubs.acs.org/doi/10.1021/acs.est.9b07228.

Scherer L, Boom HA, Barbarossa V, van Bodegom PM. 2023. Climate change threats to the global functional diversity of freshwater fish. Glob Chang Biol. 29(13):3781–3793. doi:10.1111/gcb.16723.

Schipper AM, Hilbers JP, Meijer JR, Antão LH, Benítez-López A, de Jonge MMJ, Leemans LH, Scheper E, Alkemade R, Doelman JC, et al. 2019. Projecting terrestrial biodiversity intactness with GLOBIO 4. Glob Chang Biol. doi:10.1111/gcb.14848.

Schneider FD, Morsdorf F, Schmid B, Petchey OL, Hueni A, Schimel DS, Schaepman ME. 2017. Mapping functional diversity from remotely sensed morphological and physiological forest traits. Nat Commun. 8(1). doi:10.1038/s41467-017-01530-3. http://dx.doi.org/10.1038/s41467-017-01530-3.

Schrodt F, Kattge J, Shan H, Fazayeli F, Joswig J, Banerjee A, Reichstein M, Bönisch G, Díaz S, Dickie J, et al. 2015. BHPMF - a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. Glob Ecol Biogeogr. 24(12):1510–1521. doi:10.1111/geb.12335.

De Souza DM, Flynn DFB, Declerck F, Rosenbaum RK, De Melo Lisboa H, Koellner T. 2013. Land use

impacts on biodiversity in LCA: Proposal of characterization factors based on functional diversity. Int J Life Cycle Assess. 18(6):1231–1242. doi:10.1007/s11367-013-0578-0.

sPlot. 2024. Contributing vegetation-plot databases to sPlot. Documentation. https://www.idiv.de/fileadmin/content/Files_sPlot/Documents/Contributing_data_sPlot_Draft_01.pdf.

Staude IR, Waller DM, Bernhardt-Römermann M, Bjorkman AD, Brunet J, De Frenne P, Hédl R, Jandt U, Lenoir J, Máliš F, et al. 2020. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. Nat Ecol Evol. 4(6):802–808. doi:10.1038/s41559-020-1176-8. http://dx.doi.org/10.1038/s41559-020-1176-8.

Suárez-Castro AF, Raymundo M, Bimler M, Mayfield MM. 2022. Using multi-scale spatially explicit frameworks to understand the relationship between functional diversity and species richness. Ecography (Cop). 2022(6):1–18. doi:10.1111/ecog.05844.

Tilman D, Isbell F, Cowles JM. 2014. Biodiversity and Ecosystem Functioning. Annu Rev Ecol Evol Syst. 45:471–493. doi:10.1146/annurev-ecolsys-120213-091917.

Tordoni E, Petruzzellis F, Nardini A, Bacaro G. 2020. Functional divergence drives invasibility of plant communities at the edges of a resource availability gradient. Diversity. 12(4). doi:10.3390/D12040148.

Valdez JW, Callaghan CT, Junker J, Purvis A, Hill SLL, Pereira HM. 2023. The undetectability of global biodiversity trends using local species richness. Ecography (Cop). 2023(3):1–14. doi:10.1111/ecog.06604.

Valladares F, Magro S, Martín-Forés I. 2019. Anthropocene, the challenge for Homo sapiens to set its own limits. Geogr Res Lett. 45(1):33–59. doi:10.18172/cig.3681.

Villéger S, Mason NWH, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology. 89(8):2290–2301. doi:10.1890/07-1206.1.

Wallis CIB, Tiede YC, Beck E, Böhning-Gaese K, Brandl R, Donoso DA, Espinosa CI, Fries A, Homeier

J, Inclan D, et al. 2021. Biodiversity and ecosystem functions depend on environmental conditions and resources rather than the geodiversity of a tropical biodiversity hotspot. Sci Rep. 11(1):1–14. doi:10.1038/s41598-021-03488-1. https://doi.org/10.1038/s41598-021-03488-1.

Windsor FM, van den Hoogen J, Crowther TW, Evans DM. 2023. Using ecological networks to answer questions in global biogeography and ecology. J Biogeogr. 50(1):57–69. doi:10.1111/jbi.14447.

Winkler K, Fuchs R, Rounsevell M, Herold M. 2021. Global land use changes are four times greater than previously estimated. Nat Commun. 12(1):1–10. doi:10.1038/s41467-021-22702-2. http://dx.doi.org/10.1038/s41467-021-22702-2.

Zambrano J, Garzon-Lopez CX, Yeager L, Fortunel C, Cordeiro NJ, Beckman NG. 2019. The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? Oecologia. 191(3):505–518. doi:10.1007/s00442-019-04505-x. https://doi.org/10.1007/s00442-019-04505-x.

Zebisch M, Wechsung F, Kenneweg H. 2004. Landscape response functions for biodiversity - Assessing the impact of land-use changes at the county level. Landsc Urban Plan. 67(1–4):157–172. doi:10.1016/S0169-2046(03)00036-7.