Land-use impacts on plant functional diversity throughout Europe

Running head: Land-use impact on plant diversity in Europe

Authors: Francesca Rosa[1]*, Peter 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], Francesco Maria Sabatini[14], Franziska Schrodt[15], Domas Uogintas[16], Chaeho Byun[17], Jiri Dolezal[18], Tetiana Dziuba[19], Bruno Hérault[20, 21], Irene Martín-Forés[22], Ülo Niinemets[23], Gwendolyn Peyre[24], 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]Department of Biological, Geological, and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy

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

[16]Nature Research Centre, Vilnius, Lithuania

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

[18]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

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

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

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

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

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

[23]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

The global biodiversity loss resulting from anthropogenic land-use activities is a pressing concern, requiring precise assessments of impacts at large spatial extents. Existing models primarily focus on quantifying impacts on species richness and abundance, often overlooking the ecological relevance of species traits and their contributions to ecosystem functioning. To address this gap, we conducted a comprehensive analysis throughout Europe, investigating the effect of human land use on plant functional diversity across different land-use classes and bioregions.

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. Employing species occurrences and traits from the same databases, we computed three functional diversity metrics (functional richness, evenness, and divergence) per each plot. We assessed the impact of land use by comparing the functional diversity values in the paired.

Our findings revealed that land used and modified by humans generally exhibits lower functional richness and divergence, but higher functional evenness compared to natural habitats, across most land-use classes and bioregions. Particularly noteworthy was the impact on functional richness in croplands and urban areas, identified as having the lowest functional richness values in multiple bioregions. Furthermore, the impact of human land use on plant communities displayed less variation among land-use classes than among bioregions.

Our study emphasizes how land use impacts the functionality of species at a large scale, disclosing regional and land-use class differentiations. The results underscore the crucial need for informed conservation strategies and sustainable land management across various scales to address the escalating challenges posed by human activities to biodiversity and its associated functions.

Keywords

Anthropocene, biodiversity loss, bioregions, functional divergence, functional evenness, functional richness, vegetation.

1. Introduction

Biodiversity contributes substantially to the resilience and resistance of ecosystem functions, to the maintenance of ecosystem services, and to the mitigation of global changes (Isbell et al. 2011; Harrison et al. 2014; Tilman, Isbell, and Cowles 2014; Felipe-Lucia et al. 2018; Reader et al. 2023; Le Provost et al. 2023). At the same time, biodiversity is highly affected by habitat loss and degradation: anthropogenic land-use activities are among the major drivers of biodiversity loss (IPBES 2019). As a result of human pressures, more than 80% of the global land has now been transformed, leaving only 20% to wildland (Ellis et al. 2021). Anthropogenic transformation of natural habitats notably impacts ecosystems and their functions, which are essential for the survival and well-being of all organisms (Valladares, Magro, and Martín-Forés 2019), including humans.

Halting biodiversity loss is a major challenge that requires a multi-faceted approach, which builds on the continuous improvement of biodiversity impact assessments (Leclère et al. 2020), as well as on better quantification of the linkage between drivers and effects at different spatial scales (Chaplin-Kramer et al. 2022). However, there is currently a lack of well-established connections between individual local biodiversity assessments and global patterns (Jandt et al. 2022). This gap hampers a comprehensive analysis and suggests the demand for replicated local assessments. These assessments are particularly crucial in understanding the effect of human use of land (which encompasses activities like agriculture and urbanization and hereafter simply referred as “land use”) compared to natural habitats (Zebisch, Wechsung, and Kenneweg 2004; Dornelas et al. 2014; Jandt et al. 2022). Furthermore, biodiversity is very complex and multidimensional, while most biodiversity models focus on quantifying the number of species lost or the loss in species abundance (O’Connor et al. 2017; Bannar-Martin et al. 2018; Jandt et al. 2022). However, species counts and abundance do not inform about the ecological importance of species in a community, thus pointing to the need of considering also other biodiversity dimensions, such as functional diversity, which provide additional and complementary information (Cadotte, Carscadden, and Mirotchnick 2011; Hu et al. 2014; Rosenfield and Müller 2020; Scherer et al. 2023).

Functional diversity of plants has shown to offer better insights into ecosystem performance than taxonomic diversity (Bruelheide et al. 2018; Zambrano et al. 2019; van der Plas 2019; Jens Kattge et al. 2020; Hagan, Henn, and Osterman 2023), especially in areas affected by human activities (Bonilla-Valencia et al. 2022). To calculate functional diversity, three independent and complementary functional diversity indices can be used: functional richness, evenness, and divergence (Mason et al. 2005). These indices are derived from plant traits, i.e., plants' anatomical, physiological, biochemical, regenerative, reproductive and phenological characteristics. Functional richness measures how much trait variation in different species add up within a community. It affects aspects such as resource use, productivity, reproduction and resistance to invasions. Functional evenness looks at how evenly species abundances are distributed across the range of trait variation inside the community. It indicates if resources are being overused or underused and the level of trait redundancy. Functional divergence measures how far different species are from each other in terms of functional traits occurring in the community, and 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; Mouchet et al. 2010; Scherer, van Baren, and van Bodegom 2020).

The effect of land use on functional diversity at a large spatial extent (i.e., continental or global) has been investigated in previous studies (Flynn et al. 2009; De Souza et al. 2013; Newbold et al. 2020). However, these studies relied on relatively coarse-grained data and lack the necessary information to assess impacts at the community level where species co-occur and interact. In such studies, species occurrence data are originating from many different sources and rarely from harmonized databases. Moreover, in most cases, the results primarily aimed at obtaining global or continental aggregated values (Wolf et al. 2022; Dechant et al. 2023), without distinguishing impacts in different regions and without considering plot-level differences between areas under anthropogenic land use and their natural habitat counterparts.

The recent release of global vegetation and trait databases discloses new opportunities for exploring the effect of land use on different dimensions of functional diversity (Chytrý et al. 2016; Bruelheide et al. 2019; J. Kattge et al. 2011), especially in areas with a good coverage and representativity of data, such as Europe. The European Vegetation Archive (EVA) (Chytrý et al. 2016) is a European vegetation plot databases containing information on species co-occurrences and abundances within plant communities. Coupled with the TRY database, which provides species-level plant trait data (Jens Kattge et al. 2020), it allows for the calculation of functional diversity for millions of vegetation plots across all of Europe (Bruelheide et al. 2018). The further matching of vegetation plots and trait data with land use and land cover allows investigating the change in functional diversity in areas used and modified by humans compared to natural and close-to-natural habitats.

Given this context, our goal is to answer the following research question: how does plant functional diversity change in land actively used by humans compared to natural habitats sharing otherwise similar environmental conditions? Do biogeographical patterns emerge across different regions in Europe?

2. Materials and methods

Functional diversity indices were calculated by combining vegetation plots and trait information. To allow for a consistent comparison between anthropogenic land-use classes and natural habitats, we used the land-use and land-cover data to pair each vegetation plot sampled in land actively and predominantly used by human with a vegetation plot sampled in the natural habitat that would potentially occur there under low human pressure on the environment.

The approach we applied consisted of seven steps (see Fig. 1 and, for more details, Fig. S1.1 in the supplementary materials). 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 EVA plots and has curated a taxonomic standardization procedure to link to each species name a set of 30 gap-filled traits from the TRY database (Schrodt et al. 2015; Jens Kattge et al. 2020) (see section 2.1). Second, we assigned each of the vegetation plots to biogeographic regions (hereafter “bioregions”) 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 to be suitable for the analysis (see section 2.3). Fourth, we assigned each vegetation plot to either one of the five identified land-use classes (*Urban areas*, *Cropland*, *Pasture and rangeland*, *Mosaic*, *Planted forest*) or to one of the five identified potential natural vegetation class (*Natural forest*, *Natural grassland*, *Natural shrubland*, *Natural herbaceous wetland*, *Natural bare and sparse vegetation*) (see section 2.4). Fifth, we selected the relevant environmental covariates (i.e., bioclimatic variables and soil properties) and then performed a Principal Component Analysis (PCA) across European to obtain the scores of each vegetation plot along the PCA axes (see section 2.5). Sixth, within each bioregion, we used the distance between the PCA scores in the PCA space to pair plots sampled in a land-use class and plots representing potential natural vegetation sampled in otherwise similar environmental conditions (see section 2.6). Finally, we calculated the ratios between the values of functional richness, evenness, and divergence of each pair of plots (see section 2.7).

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

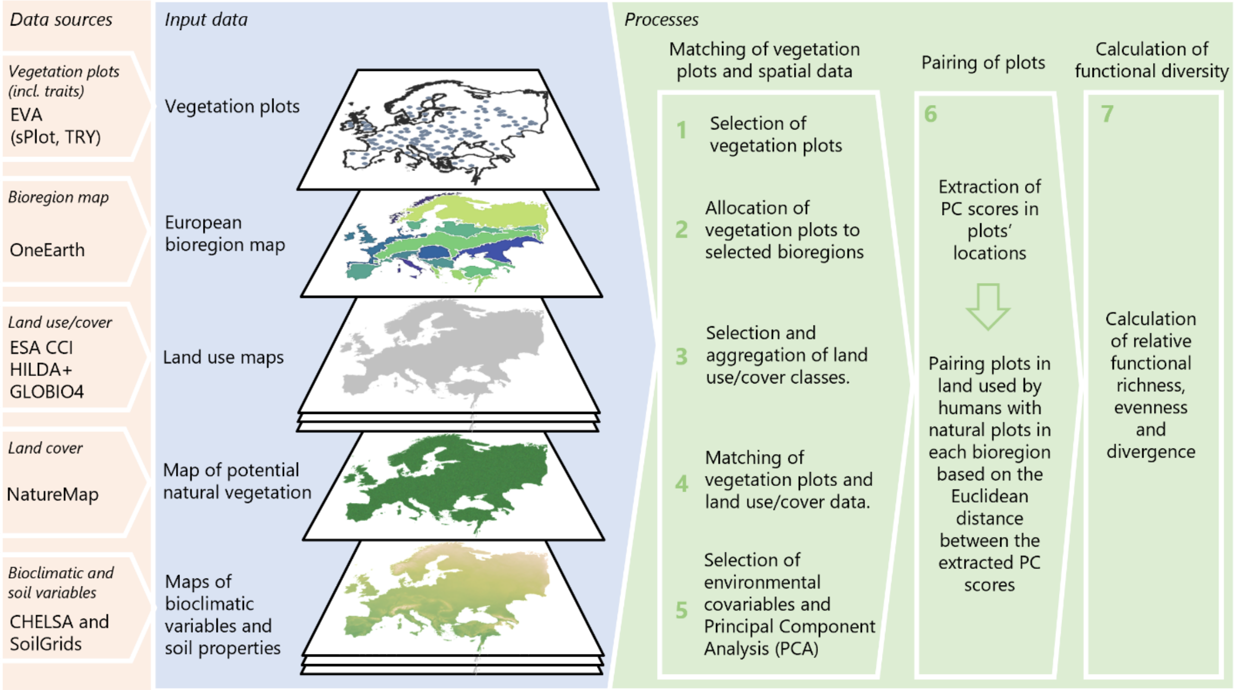

Figure 1 Overview of the methodological conceptual framework applied to this study.

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 derived data on 30 gap-filled traits from TRY (Schrodt et al. 2015; Jens Kattge et al. 2020) and an additional plot attribute (plot naturalness, used in section 2.4) from sPlot's (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 (in the supplementary materials, the full list of criteria is available in section S2 and the list of EVA datasets used for the analysis is available in section S18).

We considered only the 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 of species occurring in the plot (< 0.5), 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., 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. We retained only plots where at least 80% of the land use within the uncertainty radius was the same to 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).

2.2 Allocation to bioregions

To evaluate the spatial differences in the impacts on functional diversity, the vegetation plots were assigned to bioregions (One Earth, n.d.) (list of bioregions name available in Table S3.1 and map in Fig. 2 and S3.1 in the supplementary materials). We chose bioregions instead of the more commonly used ecoregions (Olson et al. 2001), for being geographical units internally coherent in terms of dominant biome and evolutionary history, but larger in size than ecoregions, which allows for a higher sampling size in our analysis.

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

Each vegetation plot was matched to either a land-use class or to a class of potential natural vegetation (described in more detail in sec. 2.5).

As a base layer for land-use classes, we adopted the land-cover maps 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 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 had to be excluded); and importantly (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 (PBL Netherlands Environmental Assessment Agency 2023; Schipper et al. 2019), which was built using the ESA CCI as a basis and distinguishes planted forests from the other land uses and 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 for not containing any vegetation plot in anthropogenic land uses.

Concerning the map of potential natural vegetation, the NatureMap was selected (Hengl, Jung, and Visconti 2020) as its resolution (250 m) is similar to the one on the ESA CCI map, and it allows for a distinction between multiple classes 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 in the supplementary materials for the detailed matching between the aggregated classes and, respectively, the ESA CCI classes and the NatureMap classes).

2.4 Assigning land-use and cover classes to vegetation plots

Using the geographical coordinates of the center of each vegetation plot, we extracted the corresponding land-use/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 final use classification (Table 1) is available in Table S6.1 in the supplementary materials. Two additional attributes were used to refine the matching between plots and land-use/cover classes: the type of vegetation (from the EVA database) and the level of naturalness (from the sPlot database). In the final classification, each plot was assigned to either a 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.

Land use/cover assigned to the plots		Definition
Natural and close-to-natural habitats	Natural forest	Areas where natural vegetation belongs to the same formation and vegetation 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	
Land-use classes	Planted forests	Planted forests intensively managed. It excludes forest planted for protection, ecosystem restoration, or established through planting or seeding, mimicking natural regeneration 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).
	Cropland	Agricultural land where annual or permanent crops (trees, shrubs and herbaceous) are grown with different intensities and practices.
	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 covariates

We retrieved 19 bioclimatic variables – temperature- and precipitation-related – at 1-km resolution from the CHELSA V2.1 database (Karger et al. 2017; 2018), and a selection of soil properties at 250-m resolution and less influenced by land management from the SoilGrids database (clay mass fraction, silt mass fraction, sand mass fraction, and pH) (ISRIC, n.d.; Hengl et al. 2017) (see the full list in Table S7.1 in the supplementary materials). The soil variables were 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 1km resolution and on the whole area under assessment (similarly to what was done by (F.M. Sabatini et al. 2021)) and then we extracted the scores along all the PCA axes for each vegetation plot's location. This approach was chosen as it allowed us to pair vegetation plots and remove part of the variation in functional diversity values between different plots that is likely caused by different environmental conditions as described in the next section (Wallis et al. 2021; Joswig et al. 2022).

The PCA was performed using the function rasterPCA from the package RStoolbox (which also allows for a standardization of the input data by setting spca = TRUE as argument). Figure S7.1 in the supplementary materials shows the results for the first four PCA axes.

2.6 Pairing of plots in land-use classes and plots in 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, thus minimizing the Euclidean distance between the vegetation plots' PC scores within a given pair (see Fig. S8.1 in the supplementary materials) (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).

Alternatively, the opposite situation also occurred: the same vegetation plot from a land-use class was paired to 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 having the lowest location uncertainty ranking was considered. If multiple natural plots remained paired to the same plot even after filtering out those with lower location uncertainty ranking, they were kept, and the average of their functional 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).

The final selection consisted of 72247 vegetation plots and 7185 vascular plant species (see Fig. S8.2 and Fig. S9.1 in the supplementary materials, respectively, for the spatial and density distribution of the plots after the pairing and for the ridge plot of the PC distance).

2.7 Calculation of functional richness, evenness, and divergence

We calculated the functional richness, evenness and divergence for each vegetation plot using the dbFD function from the FD package in R (Villéger, Mason, and Mouillot 2008; Laliberté et al. 2010; Ahmed, van Bodegom, and Tukker 2019). All plant traits were standardized to zero mean and unit variance. We considered all 30 traits available in sPlot (please find the full list in Table S10 in the supplementary materials), which offer a nuanced understanding of the ecological strategies and adaptations of plant species within the studied ecosystems. The traits range 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, and various genotype-related features. Since the function we used (dbFD) already performs a PCA on the traits, a selection of the traits was not necessary.

Finally, the ratio between the values of functional diversity in each plot assigned to a land-use class and its corresponding plot assigned to a natural habitat (hereafter called ‘relative functional richness’, ‘relative functional evenness’ or ‘relative functional divergence’) was calculated as follows:

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

Where $f_{i,\text{ land-use class}}$ is the functional metric (richness, evenness, or divergence) in plot *i* among those plots assigned to a land-use class and $f_{j,\text{ natural habitat}}$ is the functional metric (richness, evenness, or divergence) in the natural plot *j* paired to plot *i.* When the relative values are below (or above) 1, it means that the functional richness, evenness or divergence is lower (or higher) in the land-use class than in the natural habitat. To obtain aggregated values per bioregion, a median of all the relative functional diversity values for each metric, land-use class and bioregion was calculated. The values per land-use class across bioregions were calculated as weighted mean of the medians using the areas of bioregions as weights.

The Wilcoxon signed-rank test for paired data corrected with the Benjamini & Hochberg (hereafter "BH") correction for multiple comparisons was used to determine the significance of the shift between the absolute values of functional diversity metrics in the paired plots.

3. Results

In most bioregions, we found lower relative functional richness and divergence ($r_{fi} < 1$) but higher relative functional evenness ($r_{fi} > 1$) within habitats modified by human activities than within paired natural habitats sharing otherwise similar environmental condition (see Fig. 2, and for more details Fig. S11.1, section S12, Table S15-S17 in the supplementary materials).

The difference in functional diversity between the anthropogenic land-use classes and their paired natural counterparts was much more evident for functional richness than for functional evenness and divergence (Fig. S11.1 in the supplementary materials). 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 with similar environmental conditions. Additionally, functional evenness was 6% higher in anthropogenic areas than in natural ones.

Overall, *Cropland* and *Urban areas* appeared to be the land-use classes with the lowest relative functional richness compared to their paired potential natural vegetation (Fig. 2): the four lowest values were found for *Cropland* in PA8 *Ural Mountains & West Eurasian Taiga Forests* (0.08), for *Cropland* and *Urban areas* in PA9*Great Britain, Ireland & Faroe Islands* (both 0.1) and for Urban areas in PA18 *Aegean Sea & East Mediterranean Mixed Forests* (0.1). In four cases, the relative functional richness was above 1: for *Pasture and rangeland* in PA18 *Aegean Sea & East Mediterranean Mixed Forests* (1.5), for *Urban areas* in PA20 *Balearic Sea & West Mediterranean Mixed Forests* (1.4), and for *Planted forests* and *Pasture and rangeland* in PA16 *Pontic Steppe Grasslands* (1.2 and 1.12).

Variation among land-use classes

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 heterogeneous distribution of values of relative functional richness across bioregions.

Table 2 Mean, minimum, maximum and standard deviation of relative functional diversity values across bioregions. The alphanumeric codes in brackets correspond to the bioregion where the minimum/maximum was found.

Land-use class	Metric	Weighted mean	Minimum	Maximum	Standard deviation
Urban areas	Relative functional richness	0.38	0.10 (PA9)	1.44 (PA20)	0.43
	Relative functional evenness	1.12	0.98 (PA14)	1.36 (PA18)	0.12
	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)	0.25
	Relative functional evenness	1.02	0.95 (PA8)	1.10 (PA10)	0.04
	Relative functional divergence	0.95	0.84 (PA18)	1.21 (PA9)	0.10
Pasture and Rangeland	Relative functional richness	0.46	0.11 (PA9)	1.52 (PA18)	0.45
	Relative functional evenness	1.03	0.85 (PA16)	1.25 (PA18)	0.10
	Relative functional divergence	0.97	0.82 (PA18)	1.21 (PA9)	0.11
Mosaic	Relative functional richness	0.39	0.13 (PA9)	0.80 (PA18)	0.24
	Relative functional evenness	1.08	0.95 (PA13)	1.11 (PA9)	0.05
	Relative functional divergence	1.02	0.83 (PA15)	1.34 (PA16)	0.17
Planted forest	Relative functional richness	0.37	0.12 (PA9)	1.25 (PA16)	0.35
	Relative functional evenness	1.05	0.76 (PA16)	1.38 (PA20)	0.16
	Relative functional divergence	0.96	0.88 (PA8)	1.26 (PA20)	0.10

Cropland had the lowest weighted mean also for relative functional divergence and relative functional evenness. Relative functional divergence and relative functional divergence 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, Fig. 2). We found the opposite for *Mosaic,* negative and with similar value of functional evenness in all bioregions, except PA13 *Alps & Po Basin Mixed Forests*.

Variation among bioregions

Among bioregions (Fig. 3), PA9, being *Great Britain, Ireland & Faroe Islands* showed the most homogeneous data and the lowest values of relative functional richness for all land-use classes, except *Cropland*, which was minimum in *PA8 Ural Mountains & West Eurasian Taiga Forests*. At the same time, PA9 and PA8 depicted the highest values of relative functional divergence in various land-use classes: *PA9* in *Mosaic*, *Pasture and Rangeland*, and *Urban Areas* and *PA8* in *Cropland* and *Planted forests*.

In general, PA16, being *Pontic Steppe Grasslands* and PA20 *Balearic Sea & West Mediterranean Mixed* Forests showed the highest values of relative functional richness.

Contrary to most bioregions and for a given land-use category, PA16 being *Pontic Steppe Grasslands*, showed high relative functional richness/divergence and low relative functional evenness compared to other bioregions for the same land use. It is important to mention that this bioregion had p-values higher than 0.05 at the Wilcoxon test for most land uses (Fig. 3 and Fig. S12.1-S12.2 in the supplementary materials), which is not the case with the other bioregions.

The data for PA8 *Ural Mountains & West Eurasian Taiga Forests* were much more spread than in other bioregions for relative functional richness, but not for relative functional evenness and divergence (Fig. 3, S12.1, S12.2).

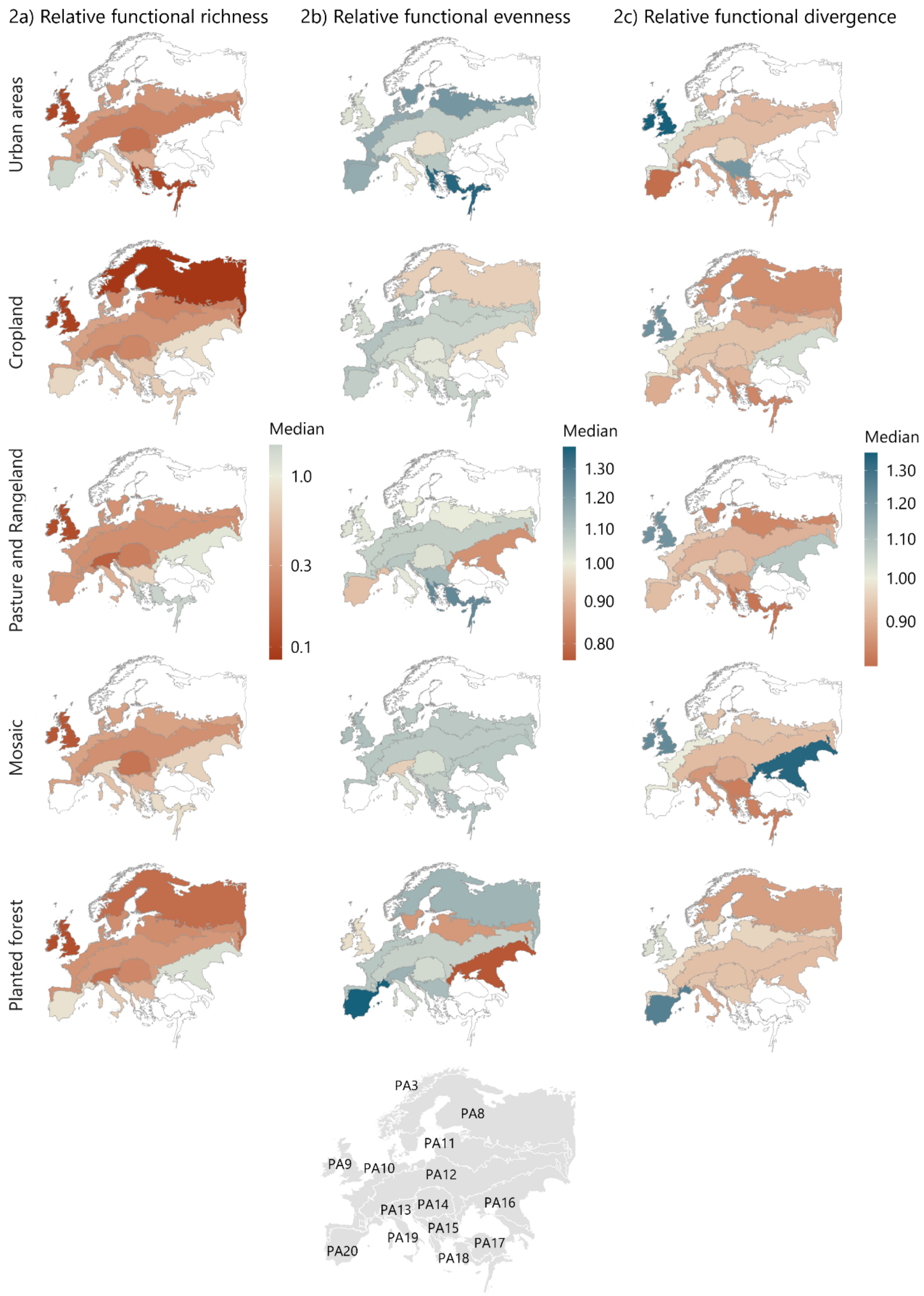

Figure 2. Median values of relative functional richness (a), evenness (b) and divergence (c) per bioregion and land-use class. Warmer colors and colder colors indicate, respectively, decreased and increased functional diversity values in relation to the potential natural vegetation. White bioregions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

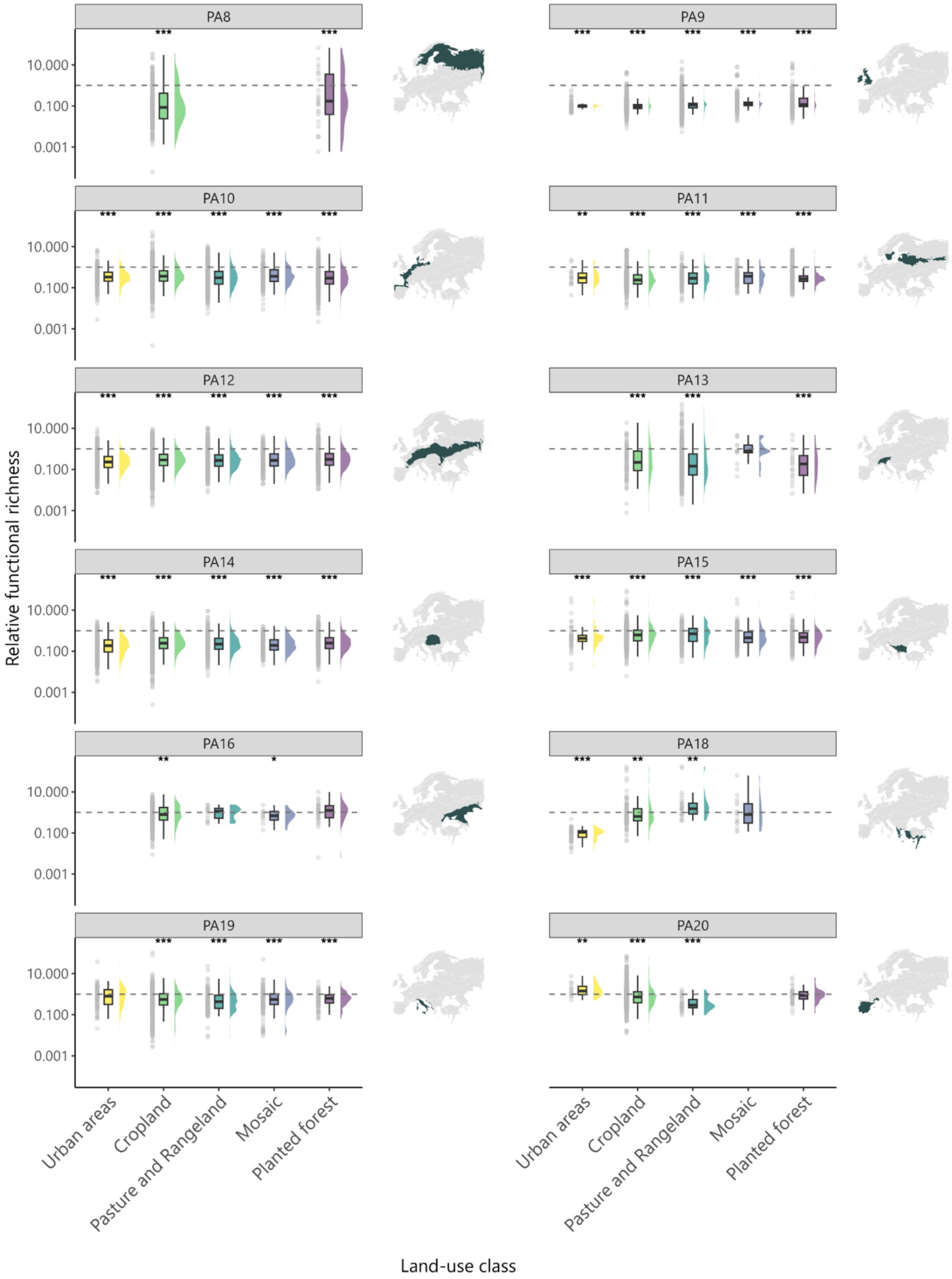

Figure 3 Relative functional richness per bioregion and per land-use class. The dotted line corresponds to 1. Results of Wilcoxon test: ***: p-value < 0.001, **: 0.001 < p-value < 0.05, *: 0.05 < p-value < 0.1, no *: p-value > 0.1.

4. Discussion

We found strong evidence that anthropogenic land use leads to a reduction in functional richness and divergence, while simultaneously promoting a slight increase in functional evenness. This was true across most of the bioregions we considered, and especially pronounced for functional richness. Notably, our study makes a significant step forward as, for the first time, vegetation plots from anthropogenic land were paired with vegetation plots from natural habitats sharing otherwise similar environmental conditions, ensuring a standardized evaluation of the effects of land use on different aspects of the functional diversity of plant communities across the entire extent of Europe. Our examination of the regionalized effects of land-use impacts on plant diversity focused specifically on functional richness, evenness, and divergence.

Our results confirm the results of (Scherer, van Baren, and van Bodegom 2020), who applied a similar approach across Germany as a whole and also found a decrease in functional richness but an increase in functional evenness in response to human land uses. Specifically, habitat filtering and disturbance – such as those caused by human land use have been identified as potential determinants reducing functional richness (Pakeman 2011; Janeček et al. 2013): functional richness is related to taxonomic richness and does not considers abundance (Villéger, Mason, and Mouillot 2008; Laliberté et al. 2010), as a result, the less natural and species-rich a habitat, the lower the functional richness. In parallel, habitat filtering and disturbance have been found to promote functional evenness. In plant communities subject to high levels of disturbance, species exhibit a broader distribution along functional trait gradients with similar abundances, reducing functional space available for redundancy and competition (Mouchet et al. 2010; Pakeman 2011). Regarding plant functional divergence, the response to human pressure is not clear yet (Pakeman 2011).

Our findings also suggest that the variation of the impact of human land uses on plant functional diversity, relative to natural habitats, is smaller among land-use classes than among bioregions. This biogeographical pattern may arise from spatial variation in environmental conditions and management practices. Environmental conditions also act as habitat filters on trait composition within the community of co-occurring plants (Diaz, Cabido, and Casanoves 1998; Cheng et al. 2022; Wallis et al. 2021; Joswig et al. 2022) and for this reason a Principal Component Analysis (PCA) was performed in order to minimize the influence of different climatic and soil conditions when pairing the plots. However, this influence cannot be entirely removed when pairing vegetation plots with natural habitats used as a baseline or reference here. Therefore, the natural vegetation of different bioregions can exhibit dissimilarities in terms of functional diversity, and this is reflected in the relative values of functional diversity. Additionally, management practices and intensity within the land use classes we considered can vary across bioregions and can be responsible for modulating the impacts on functional diversity (Laliberté et al. 2010; Janeček et al. 2013; Van Meerbeek, Helsen, and Hermy 2014). We could not consider management intensity in this study, mainly because most of the available land-use and land-cover maps are based on remote sensing products, which still lack this level of detail at the continental extent of our analysis and for sufficiently long time series. It would be valuable to include this aspect in upcoming studies to provide a more comprehensive assessment (Dullinger et al. 2021).

Our findings regarding the impacts of human land uses on plant functional diversity bear notable implications under future global change. Species community composition is expected to change in response to factors such as climate change, eutrophication, and habitat fragmentation; predictive models have found that alterations in the relative abundance of species within their natural habitat and the evolution of traits function as mechanisms for resilience (Guerin et al. 2014). Moreover, the threat of invasive alien species amplified by global trade and their impacts on ecosystem functioning depends on the functional diversity and abundance of native species (Kaushik et al. 2022; Tordoni et al. 2020). For instance, a decrease in functional richness and divergence accompanied by an increase in functional evenness following human pressures on the environment, as we report in our study, may change the tolerance or resistance of the native community to invasion risks by alien species. Shifts in functional diversity caused by anthropogenic land use may also exacerbate the response of plant community to nitrogen deposition, especially important in Europe and currently promoting broadly distributed, nitrogen-demanding plants (Staude et al. 2020). Given the observed patterns in response to human pressures on the ecosystems, we anticipate that under ongoing global changes, such as land use change, climate change and biological invasions, there will be continued alterations in plant functional diversity dynamics.

To evaluate the effects of human land use on vascular plant diversity comprehensively, we had to face a few shortcomings. Firstly, data coverage was heterogeneous across bioregions and land-use classes. Particularly in southern Europe and the Mediterranean region, limited data availability for certain land covers, like natural Grassland and natural Shrubland reduced the number of vegetation plots we could pair between natural habitats and land-use classes. The extensive history of land management in Europe, especially in Mediterranean regions, further constrained the availability of natural habitats for pairing plots (Irene Martín-Forés 2017; Francesco Maria 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. Identifying a reliable source distinguishing between natural and managed forests at a meaningful spatiotemporal resolution was the main challenge. Despite advancements in remote sensing, distinguishing unmanaged from managed forests remains difficult (Hirschmugl et al. 2017). A third source of uncertainty derived from the imprecise spatial location of the vegetation plots and their uneven level of completeness and descends from three factors: (i) the mismatch between the resolution of the land-use map and the size of the vegetation plots (53 m2 on average but with much higher or not available values for part of the plots, see Fig. S14.1), which could lead to incorrect land-use assignments; (ii) the intrinsic uncertainty of the land-use/-cover maps; and (iii) the location uncertainty of the vegetation plots (attribute available in EVA, Fig S14.2 in the supplementary materials), with which we dealt by excluding plots with high location uncertainty and ranking the others based on the homogeneity of the land use/cover within the uncertainty radius (see sec. 2.1).

In our analysis, we considered numerous traits thanks to the TRY gap-filling procedure using imputed data has proved efficient compared to a reduced species set (Scherer et al. 2023). Yet, achieving an even representativeness of the functions expressed through the traits presents some difficulty. To address this, enhancing belowground trait coverage is advisable (Carmona et al. 2021). Exploring solutions for trait distribution gaps or scaling up with methods like model predictions or remote sensing is worth investigating (Boonman et al. 2022; Schneider et al. 2017).

As an outlook, 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, Dakos, and Devictor 2023; Windsor et al. 2023).

In conclusion, our work makes a noteworthy contribution to advancing the understanding of the complex relationship between human land use and functional diversity. This study sheds more light on the nuanced impact of human land modification on functional richness, evenness, and divergence, through a regionalized approach. The methodology employed in this study not only enhances our understanding of this intricate relationship but also introduces a fresh perspective on connecting localized studies with broader regional implications.

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Code and data availability

The R code for data manipulation, analyses and data visualization will be available upon publication in a peer reviewed journal at https://github.com/francesca-git/plant-functional-diversity-Europe.git

Author contributions

F.R and L.S.: conceptualization. F.R.: project administration; methodology development under the supervision of L.S., S.H., S.P. and P.v.B.; data search, management, and analysis under the supervision of L.S.; code writing; computation; visualization; writing – original draft, review, and editing. L.S., S.H., S.P., P.v.B.: supervision; discussion on methodology and results; review and editing. I.B., S.B., M.C., R.C., M.D.F, G.D., E.G., J.L., W.A.O., J.P., F.M.S, F.S., D.U., P.v.B.: data contribution. I.B., S.B., C.B., M.C., R.C., M.D.F, G.D., J.D., T.D., E.G., B.H., J.L., I.M-F., U.N., W.A.O., J.P., G.P, F.M.S, F.S., D.U: review and editing.

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