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Land-Use Impacts on Plant Functional Diversity Throughout Europe

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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 homogenisation within sites; (iii) functional diversity metrics complement traditional metrics by offering deeper insights into the ecological mechanisms in response to anthropogenic land use.

1 | Introduction

Biodiversity plays a crucial role in bolstering ecosystem functions, maintaining services vital for all organisms, including humans, and mitigating some global changes (Tilman, Isbell, and Cowles 2014; Le Provost 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), ecosystems and their functions face severe impacts, such as alterations in ecosystem structure and disruption of ecological processes (IPBES 2019), which underlines the urgent need for comprehensive strategies to halt biodiversity loss (Leclère et al. 2020; Carmona, Tamme, et al. 2021). Equally important is the need to better understand 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 commonly used in current biodiversity models due to their widespread availability (Bannar-Martin et al. 2018; Pollock et al. 2020). 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, Carscadden, and Mirotchnick 2011; 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; Kattge

et al. 2020), 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, Mason, and Mouillot 2008). Functional richness represents the amount of functional niche space filled. Functional evenness describes how regularly species abundances are distributed in the functional niche space. Functional divergence measures how species abundances are distributed from the centre of the functional space to its extremes and is sensitive to highly specialised or functionally rare species (Mason et al. 2005; Villéger, Mason, and Mouillot 2008).

Along with the need for complementary biodiversity metrics, currently there is also 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 urbanisation (hereafter simply referred to as 'land use'), when comparing anthropogenic land to natural habitats (Zebisch, Wechsung, and Kenneweg 2004; Dornelas et al. 2014; Jandt et al. 2022).

Studies examining the impact of land use on plant functional diversity at national to global scales have yielded mixed results. Some found no significant changes in functional richness due to land use (Flynn et al. 2009; De Souza et al. 2013). Others reported significant alterations in functional richness and more subtle changes in functional evenness or divergence when comparing anthropogenic land use to natural habitats (Carmona

et al. 2020; Scherer, van Baren, and van Bodegom 2020). These inconsistencies highlight the need for further investigation into the relationship between land use and functional diversity. Furthermore, previous studies often performed analyses by using 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 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 utilised 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), the EVA dataset allows for the calculation of functional diversity for approximately two million 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 Figure 1 and, for more details, Figure 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 standardisation 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
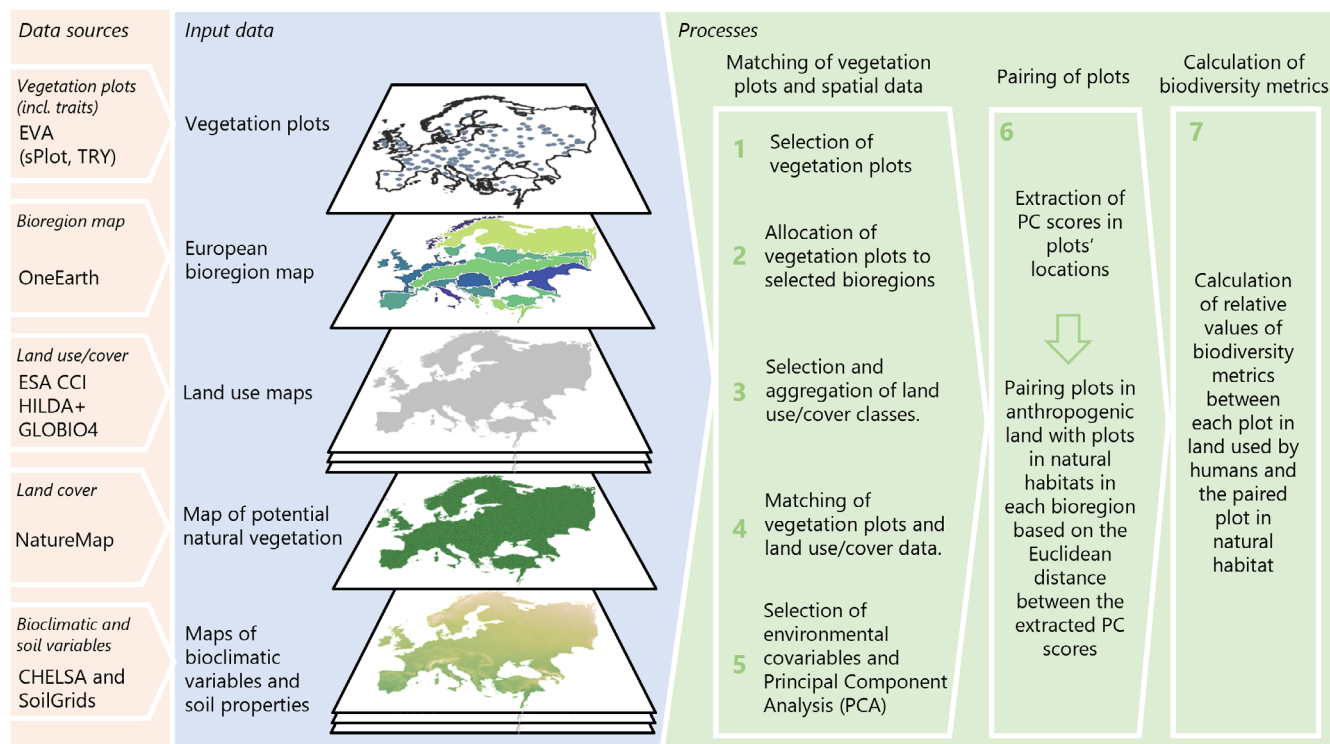
FIGURE 1 | Overview of the methodological framework applied to this study.

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).

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 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.

We considered only those vegetation plots for which species abundance data were available, as this information was needed to calculate functional evenness and divergence. Additional vegetation plots were excluded from the analysis for various reasons, for example, 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). After filtering, on average the proportion of species with traits per vegetation plot was 98%. Furthermore, we retained only vascular plant species with trait information; vascualr plants accounted for 90% of the total species pool of the selected vegetation plots.

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 response of functional diversity, we assigned vegetation plots to bioregions (One Earth 2020). This approach enabled regionalisation while facilitating an appropriate sampling size, as higher resolution of other more commonly used regionalisations (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 Figure 2 and Table 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 were 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 and 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, Jung, and Visconti 2020), as its resolution (250 m) is similar to ESA CCI map's resolution, and it allows for a distinction between multiple types of natural vegetation (e.g., forest, grassland, shrubland, etc.). This map estimates the potential natural vegetation that would occur in present time without human intervention based on biophysical conditions over land (i.e., atmospheric, climatic and lithologic variables) and was validated with occurrence records.
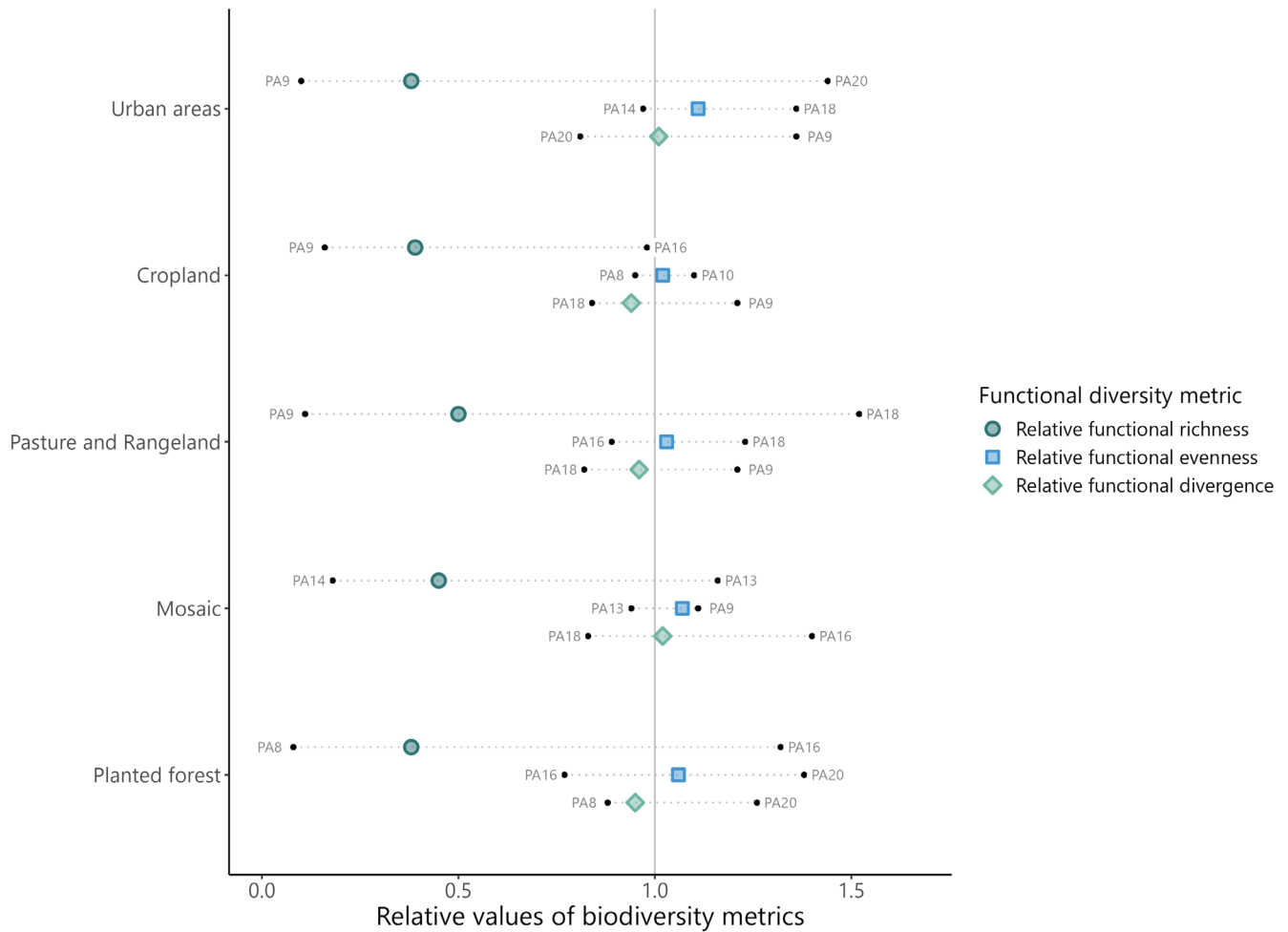
FIGURE 2 | Summary statistics of relative functional diversity values averaged per land-use class: Weighted mean across bioregions (dots in grey scale with darker border), minimum and maximum (black dots). The alphanumeric codes next to the minimum and maximum correspond to the bioregion where the minimum/maximum was found.

ESA CCI contains 38 land-use/cover classes, and the NatureMap has 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 Tables S4.1 and 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 Potential Natural Vegetation

Using the geographical coordinates of the centre 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); and (ii) 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 an anthropogenic land-use class or a natural habitat (Table 1).

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, 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 2022; 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

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 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 forests 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 is 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 characterised by a combination of natural vegetation and cropland to varying degrees.

Note: The list of original land-use and land-cover classes and how they were combined is shown in Table S6.1.

(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 standardisation of the input data (see Figure 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 from a human-modified land-use class with a plot representing the potential natural vegetation for that location, based on environmental similarity. We measured environmental similarity using the Euclidean distance between plots' PC scores, which we refer to as 'PC distance'. For example, a plot assigned to *Cropland* in an area where the potential natural vegetation is natural forest was paired with the natural forest plot having the smallest PC distance. This approach minimised environmental differences between paired plots within the same bioregion (Figure S8.1), ensuring similarity while accounting for regional context (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 (Figure S8.1). The distance between the PC scores had a mean value of 0.09 (distribution in Figure S9.1).

The opposite situation also occurred: a single vegetation plot from an anthropogenic land-use class was paired with multiple natural habitat plots due to equal environmental distances in the PCA space. This occurred for roughly 25% of the vegetation plots in anthropogenic land use. In these cases, we applied the following hierarchical criteria to select the most appropriate natural vegetation plot:

1. Similarity in plot size between the paired plots. Vegetation plots in natural habitats had, on average, larger sizes than plots in anthropogenic land use (Figure S10.1 for the distribution of plot sizes and Figure S10.2 for the comparison). To mitigate this discrepancy, we prioritised plot size as the primary selection criterion.

2. Similarity in proportion of species with trait information between paired plots. While consistently high across all vegetation plots (Figures S10.3 and S10.4), this factor is crucial for functional diversity calculations and was thus chosen as the second criterion.

3. Geographic proximity between paired plots. With a median of 180 km between paired plots (Figure S10.5), this was selected as the third criterion to account for spatial variations.

4. Lowest location uncertainty of plot in natural vegetation. Previously filtered and ranked (Section 2.1) and subject to sensitivity analysis (see end of next section), this factor was applied as the final criterion (Figure S10.6).

If multiple plots remained after applying the above criteria, 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, Mason, and Mouillot 2008; Laliberté et al. 2010; Ahmed, van Bodegom, and Tukker 2019). The function requires two inputs: a species-by-trait matrix containing trait values and the corresponding species abundance data for each community. Functional richness is calculated as the volume of the minimum convex hull defined by the values of the traits in the multi-dimensional trait space. Functional evenness is based on the minimum spanning tree (a tree that links all trait values in the trait space via Euclidean distance with a minimum sum of linking branches), weighted by the abundance of each species and ranging between 0 and 1. Functional divergence measures how abundance-weighted species deviate from the community's centre of gravity in trait space and ranges from 0 to 1. Prior to calculations, the function performs a Principal Coordinates Analysis (PCoA) on traits to obtain orthogonal axes and reduce dimensionality, addressing potential trait correlations. All plant traits were standardised to zero mean and unit variance. As our aim was to assess the response of the overall ecosystem functioning rather than specific ecosystem functions, we utilised all 30 traits available in sPlot (full list in Table S11.1). These traits were sourced from the TRY database (Kattge et al. 2011), which included gap-filled data as described in Schrodt et al. (2015). Our use of a gap-filled dataset has been supported by research showing that inputted data is 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 and leaf dimensions. We also calculated species richness and total abundance (sum of the total cover across the species in a plot).

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:

$$r_{\mathrm{fi}} = \frac{\mathrm{bd}_{\mathrm{fi,land\text{-}use\ class}}}{\mathrm{bd}_{\mathrm{fj,\ natural\ habitat}}}.$$

where r_{fi} represents the relative value of biodiversity metric f in anthropogenic vegetation plot i, $\mathrm{bd}_{\mathrm{fi,\ land\text{-}use\ class}}$ is the value of biodiversity metric f in anthropogenic vegetation plot i and $\mathrm{bd}_{\mathrm{fj,\ natural\ habitat}}$ is the value of biodiversity metric f 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.

Despite the pairing refinement based on the relative plot size (Section 2.6), the discrepancy between plot size in natural habitats and in anthropogenic land use cannot be completely removed. To prevent an underestimation of relative functional richness, species richness and total abundance, which are positively correlated with relative plot size, an adjustment was performed. The correction was defined using a log–log linear regression model relating the biodiversity metric to the relative plot size. This model was fit separately for each unique combination of human land-use class and bioregion, and a few constraints were applied to the correction approach to ensure that it did not over-adjust the data (Sections S10.2 and S10.3). The resulting regression coefficients were then used to calculate a correction factor to standardise the biodiversity metrics.

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 the data dispersion; Figure S9.1) and excluding vegetation plots in anthropogenic land with a naturalness level of 2. The Wilcoxon signed-rank test for paired data was used to determine the significance of the shift between the absolute values of functional and species diversity metrics in the paired plots (with the Benjamini & Hochberg correction for multiple comparisons—hereafter 'BH') and between the relative values of species richness and functional richness across all plots.

3 | Results

The final selection consisted of 68,368 vegetation plots from 57 datasets (Table S12) and 7,185 vascular plant species, out of

an estimated 20,000–25,000 European species (Bilz et al. 2011; POWO 2021). The spatial and density distribution of the plots after the pairing is illustrated in Figure S13.1.

In most bioregions, we found lower relative functional richness and divergence ($r_{\text{fi}} < 1$) but higher relative functional evenness ($r_{\text{fi}} > 1$) in anthropogenic land than in the corresponding paired natural habitats (see Figure 2, Tables S14–S17).

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 (Figure S18.1). On average, across all bioregions and land-use classes, functional richness and divergence were, respectively, 50% 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 (Figures S19.1–S19.3).

The correction implemented to account for the correlation between relative functional richness, relative species richness, relative total abundance and relative plot size reduced the R^2_{adjusted} to be smaller than 0.1 for most of the combinations of human land-use classes and bioregion codes (Figures S20.1–S20.3). The geographical distance between paired plots and the proportion of species with traits did not appear to affect the outcomes (see Figures S20.4 and S20.5).

3.1 | Variation Among Land-Use Classes

Overall, *Cropland, Urban areas* and *Planted forest* were the land-use classes with the lowest relative functional richness compared to their paired natural vegetation (Figures 2 and 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 S15).

Averaging the relative functional richness values per land-use class across bioregions (Figure 1 and Table S21.1), we found the lowest weighted mean for *Cropland* and the highest one for *Pasture and rangeland*. *Planted forest* and *Pasture and range-land* were the categories with the lowest minimum value and the highest maximum value, respectively. *Cropland* showed the most similar values of relative functional richness across bioregions (see Figure 3).

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 Figure 3 and weighted relative standard deviation in Table S21.1). 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. Planted forest had the lowest value of median relative functional richness in *PA8 Ural Mountains & West Eurasian Taiga Forests* and Mosaic in *PA14 Carpathian Mountain & Plains Mixed Forests*, while the other land-use classes had their minimum in *PA9 Great Britain, Ireland & Faroe Islands* (Figure 4). 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 a 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 (Figure 3), 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* (Figure S22.1).

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 (Figure 4), and their relationship followed a logarithmic pattern (see Figures S23.1 and S23.2). In 19 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 28 other combinations, especially for the land-use class *Pasture and rangelands*, the median relative species richness was equal to or larger than 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. Mosaic in P13 *Alps & Po Basin Mixed Forests*, Pasture and rangeland in P15 *Dinaric Mountains & Balkan Mixed Forests* and *Pasture and rangeland* in PA18 *Aegean Sea & East Mediterranean Mixed Forests* were the three cases where both metrics were above one. In most combinations of land-use and land-cover classes and bioregions, the difference between relative species richness and relative functional richness was significant (see Table S23.1).

The relative natural species richness (Figure 4) 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 (Figure 4), with a few exceptions in southern Europe and PA9 *Great Britain, Ireland & Faroe Islands*.

4 | Discussion

We found evidence that anthropogenic land use leads to a reduction in functional richness and divergence while simultaneously
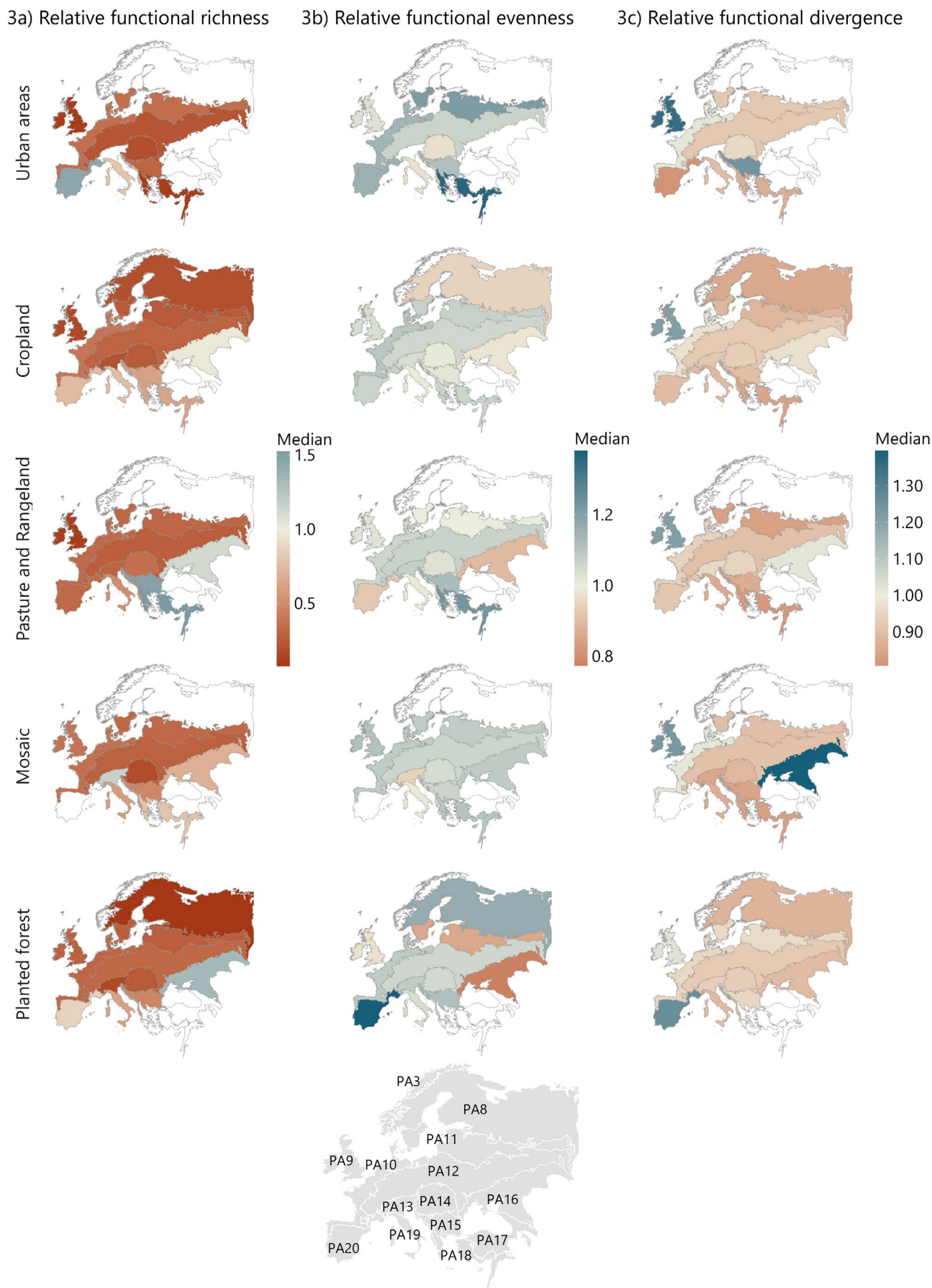
3a) Relative functional richness

3b) Relative functional evenness

3c) Relative functional divergence

FIGURE 3 | Legend on next page.

FIGURE 3 | Median values of relative functional richness (a), evenness (b) and divergence (c) per bioregion and land-use class. Warmer colours and colder colours 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.

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, van Baren, and van Bodegom (2020) at a smaller spatial extent in Europe but diverge from the findings of Flynn et al. (2009), 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. (2009), along with De Souza et al. (2013), calculated a single functional diversity index using a dendrogram-based metric, which measures the complementarity among species' trait values (Petchey and Gaston 2002). Furthermore, the index was based on eight traits, including four categorical ones, 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 the anthropogenisation of land tends to filter species based on their traits. The disturbances associated with human land use, which may include altered resource availability, changes in soil properties and increased disturbance frequency, can narrow the range of viable functional traits present in the community, for example, by favouring generalist species sharing high dispersal capacity, rapid growth, or stress tolerance (Mayfield et al. 2010). The reduction in functional richness may have direct implications for ecosystem functioning, as it limits the diversity of functional roles species can perform, which is critical for maintaining ecosystem processes and services (Cadotte, Carscadden, and Mirotchnick 2011).

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). This could be due to the simplification of habitat structure or reduced resource heterogeneity in anthropogenically modified landscapes, leading to increased competition among species with overlapping niches. As a result, species with more extreme expressions of functional traits may be outcompeted or unable to persist, driving the decline in functional divergence.

Conversely, human disturbance appeared to promote functional evenness, which suggests that species' abundances are more regularly distributed along functional trait gradients in anthropogenic landscapes (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). This response could be driven by a reduction in redundancy among species, where the competition for limited resources in anthropogenic landscapes forces species into a more regular distribution within the trait space.

These findings may indicate that species populating anthropogenic areas are more functionally homogeneous than those in natural habitats, which may reduce ecosystems' ability to respond to environmental changes, as fewer unique functional strategies are retained within the community. Previous studies have reported disruption of interactions among specialised 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 (Figure 3). For example, in PA16 *Pontic Steppe Grasslands*, functional richness was higher than in other bioregions and coupled with higher relative natural species richness, suggesting that species turnover plays a big role in determining functional richness under disturbance. The systematic decline in community abundance may also impact fundamental ecosystem processes, as community abundance, mediated by species traits, is positively associated with ecosystem function (Grime 1998; Winfree et al. 2015).

The logarithmic relationship between species richness and functional richness, observed in prior studies (Villéger, Mason, and Mouillot 2008; Biswas and Mallik 2011; Aros-Mualin et al. 2021; Boonman et al. 2021), explains the occasionally divergent behaviour of these metrics. Natural habitats often showed higher functional richness than anthropogenic land use at similar species richness levels (Figure S23.1). 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 highlights how functional diversity can detect adverse changes even when species richness appears stable or improved.

Our findings on species richness contrast with some site-specific population studies showing declines across all land-use classes (e.g., Newbold et al. 2015). On the one hand, we acknowledge that there are inherent uncertainties in our study, and pairing refinement should be prioritised once additional data becomes available (see Limitations section). On the other hand, discrepancies may stem from our novel approach: using harmonised datasets to systematically compare anthropogenic land with potential natural vegetation, rather than relying on meta-analyses or nearby natural vegetation comparisons. Furthermore, some studies align with our results, such as positive trends in managed grasslands compared to natural habitats (Gerstner et al. 2014) and stable or increased median global species richness when
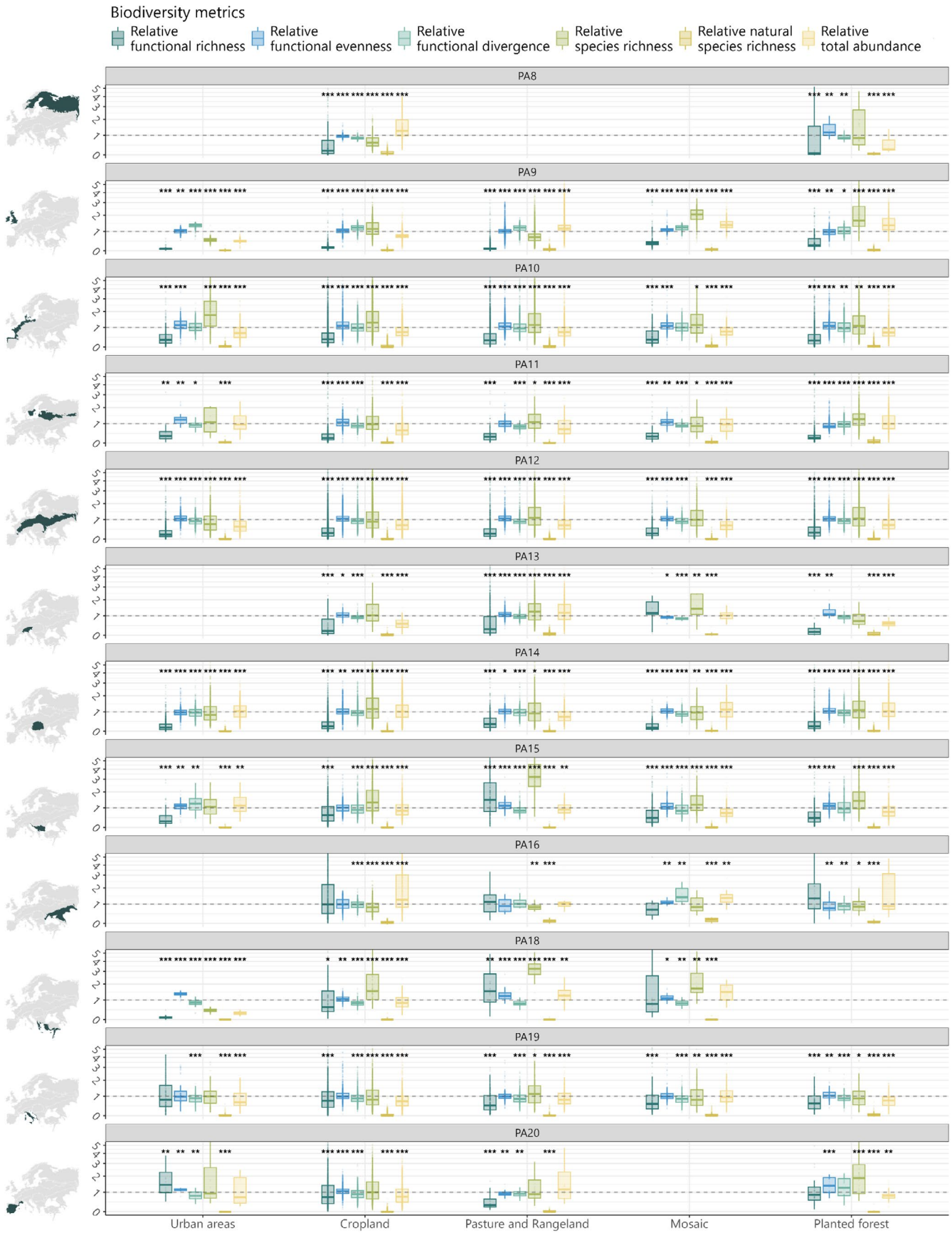
FIGURE 4 | Relative functional and species diversity per bioregion and per land-use class, zoomed between 0 and 5 to improve readability. The dotted lines correspond to 1. Results of Wilcoxon test: ***: p-value ≤ 0.001, **: $0.001 < p$-value ≤ 0.05, *: $0.05 < p$-value ≤ 0.1, no *: p-value > 0.1.

comparing the types of natural forests considered in our study to human-modified land (Deng et al. 2024). Flynn et al. (2009) also found no significant difference in plant species richness between 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 utilised to minimise 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 (Figure 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, Figure S13.1), 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, Helsen, and Hermy 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.

4.1 | Limitations

To evaluate the effects of human land use on vascular plant diversity comprehensively, we had to face a few challenges. (1) 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). (2) Our study's spatial comparative approach overlooks temporal dynamics such as land-use history or species introductions and invasions, which have substantially shaped European landscape and species composition. (3) The absence of a consistent spatial data source for land-use classification led us to combine multiple maps, introducing uncertainty. The main challenge lies 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). (4) 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 Figure 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 Section 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 Figure S15.1]), which could lead to incorrect land-use assignments. (5) Most vegetation plots in anthropogenic land were paired with vegetation plots in natural forest, according to the maps of potential natural vegetation used in the study. However, this may oversimplify the landscape structure of natural vegetation, which recent research suggests was more diverse (Pearce et al. 2023). (6) Vegetation plots in natural habitats (especially forests) typically have a larger sampling area than vegetation plots in anthropogenic land use. Despite applying statistical corrections for plot size differences, we acknowledge that sampling area differences remain a methodological challenge in our study. While our corrections help address this constraint, it should be considered when interpreting our results (Sections 2.6 and 2.7). These limitations could potentially introduce biases in our results. Specifically, our analysis may underrepresent certain regions and oversimplify temporal dynamics (limitations 1 and 2). Uncertainties in land-use and land-cover classification and in plot assignments could affect the accuracy of our comparisons (limitations 3, 4 and 5). Differences in plot sizes between paired plots may lead to a conservative assessment of biodiversity changes, particularly for some anthropogenic landscapes, potentially overestimating the impacts on functional richness (limitation 6). On the other hand, it is worth noting that our analysis revealed that geographical distance between the paired plots and the proportion of species with traits did not significantly impact our findings, lending additional robustness to our results.

4.2 | 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 below-ground 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, Féret, et al. 2021; Hauser, Timmermans, 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, Dakos, and Devictor 2023; Windsor et al. 2023).

4.3 | 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 regionalised approach and novel methodology, we enhanced our understanding of this intricate relationship and introduced a fresh perspective on connecting localised studies with broader regional implications. Such efforts are crucial in addressing the urgent challenge of halting biodiversity loss.

Author Contributions

F.R. and L.S.: conceptualization. FR: 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 LS; code writing; computation; visualisation; writing – original draft, review and editing; supervision; discussion on methodology and results; review and editing. I.B., S.B., M.C., R.Ć., M.D.F., G.D., E.G., J.L., W.A.O., J.P., F.M.S., F.S., D.U. and P.v.B.: data contribution. I.B., S.B., C.B., M.C., R.Ć., 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. and D.U.: review and editing.

Data Availability Statement

The code and the data on which the analysis is based are available on Dryad at: https://doi.org/10.5061/dryad.bg79cnpjw.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.