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RESEARCH ARTICLE

Human modification of land cover alters net primary productivity, species richness and their relationship

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Abstract

Aim: Humans have altered ecosystem productivity and biodiversity worldwide by changing land-cover types and management. High local species richness is commonly found in geographic areas and ecosystems with high net primary productivity (NPP), but the long-term effects of modification on productivity and biodiversity change, and particularly on the relationship between the two, are poorly understood. Here we evaluate whether human modification tends to increase biodiversity in low-productivity ecosystems (where human management is likely to increase productivity) and decrease biodiversity in ecosystems that were originally high-productive.

Location: Global.

Time Period: 2001–2013.

Major Taxa Studied: Plants, mammals, birds, hexapods, arachnids, other terrestrial invertebrates, amphibians, reptiles and fungi.

Methods: We assembled a large worldwide dataset of NPP and associated species richness from MODIS land cover and NPP products and the PREDICTS biodiversity database, involving 11,849 sites. This enabled comparisons of species richness and NPP differences between samples of relatively natural and human-modified vegetation within the same geographic regions, considering 102 types of land-cover transitions.

Results: (1) Modification from non-forest vegetation to forests on average increased NPP by 7.76%, and vice versa. (2) Human modification of less productive areas tended to increase NPP and vice versa, with stronger effects of major modification. (3) However, site-level species richness decreases were associated with nearly all land-cover transitions from relatively natural to modified vegetation. (4) Despite expectations, we found no significant relationship between species richness differences (between relatively natural and modified vegetation) and productivity differences, when considering conversions across land-cover types and excluding human-appropriated productivity in croplands.

Main Conclusions: Human modification tends to increase NPP in low-productivity ecosystems, but species richness declines are associated with most major human-induced land-cover changes. Therefore, increasing or decreasing NPP did not generate corresponding increases or decreases in species richness, contrary to expectations of the general species richness-productivity relationship.

KEYWORDS
biodiversity change, global change, human-associated drivers, land-cover change, MODIS, PREDICTS project

1 | INTRODUCTION

Land-cover change represents a major transformation of the Earth's surface, influencing the diversity and distributions of species (De Palma et al., 2016; Ellis & Ramankutty, 2008; Guenat et al., 2019; Newbold et al., 2015; Winkler et al., 2021) and the primary productivity of ecosystems (Running et al., 2004; Krausmann et al., 2013). Understanding these changes and how they relate to one another represents a major challenge since land-cover changes are widespread. Around 80% of the terrestrial biosphere has been transformed into a variety of land uses that vary in both purpose and intensity of management (Ellis et al., 2021). Hence, landscapes commonly contain mosaics of different human-modified land-cover types (Martins et al., 2022), which we term 'modified vegetation' (MV) types. These might include novel land covers such as urban areas and intensive farmland, as well as less heavily modified grazing land and commercially harvested forests. They also contain remnants of historic land cover, that is the land-cover type before modification and transition, which we refer to as 'relatively natural vegetation' (RNV) in recognition that all such locations are at least indirectly impacted by human activity. In a world of human-modified landscapes, land-cover changes are critical determinants of both biodiversity and ecosystem productivity (linked to CO_2 uptake), both of which are of global policy relevance. Although extensive research has documented the impact of land-cover change on both biodiversity (Jung et al., 2019; Kehoe et al., 2015; Millard et al., 2021; Newbold et al., 2020) and productivity (Hernández et al., 2016; Houghton & Nassikas, 2017; Liu et al., 2019), few have attempted to quantify these impacts together.

Impacts of land-cover change on local species richness (the measure of biodiversity considered here) have previously been studied by comparing the species richness of each human-modified land-cover type with species richness in primary vegetation – with the conclusion that local diversity has, on average, declined with human modification (Newbold et al., 2015). However, 'primary' is a coarse category. Primary vegetation (which we call 'relatively natural') and the local species diversity associated with it vary geographically, and hence the observed impacts of land transformation on local species richness will depend on the type of relatively natural vegetation that was present in a particular area historically, as well as on the vegetation type to which it is converted (Thomas, 2020). 'Historically' here represents a space-for-time deduction based on the biotic conditions observed in the least obviously modified (relatively natural) ecosystems in a region, while land-cover changes and modifications in other ecosystems have accumulated over time scales ranging from recent decades to millennia. This diversity of combinations of 'starting' and 'modified' land-cover types (adopting a space-for-time comparison approach following Newbold et al., 2015) could help explain why some studies report higher species richness in human-modified environments than in some relatively natural ecosystems (Hiley et al., 2016) and why time series analyses often find increases in species richness in some locations and declines in others (Dornelas et al., 2014; Martins et al., 2022). Therefore, it is important to test the impacts on species richness of all possible comparisons between different modified and relatively natural land-cover types to assess both the impacts of historic land-cover modifications and to evaluate the potential implications of future changes (including restoration projects).

Previous work has shown that humans have altered ecosystem productivity (Haberl et al., 2007, 2014; Krausmann et al., 2013; Kastner et al., 2022; Reiter et al., 2023), which is a key measurement of ecosystem function, CO_2 flux, and a potential determinant of species richness (Migliavacca et al., 2021). Regional and global analyses suggest that increased greening and productivity have occurred (but not everywhere) since at least 1981, with land-use changes such as afforestation, forest management, irrigation and agricultural fertilisers increasing vegetation greenness in some regions, at least in some times of the year (Haberl et al., 2007; Trant et al., 2016; Chen et al., 2019; Piao et al., 2020). However, croplands with high maximum productivity might lie fallow at other times of the year and hence might either increase or decrease overall annual productivity. In addition, much crop production is then directly or indirectly exploited for human purposes, and hence not necessarily available for biodiversity. The human appropriation of net primary productivity (NPP) has doubled from 1910 to 2005 (Krausmann et al., 2013). Humans only represent 0.5% of the heterotrophic biomass on Earth, yet we appropriate 20%–30% of the planet's annual NPP for our own use (Wright, 1990). The range of published human appropriation of NPP estimates is large, however, ranging from 10% to 55%, mainly because researchers define 'appropriation' in different ways, and hence include (or exclude) different sets of processes and their associated errors (Haberl et al., 2014; Imhoff et al., 2004; Krausmann et al., 2013; Rojstaczer et al., 2001). The appropriation of primary productivity derived from human-modified ecosystems implies lower availability for biodiversity. Understanding the relationship between biodiversity and productivity change is important and challenging in the global change context (Mori et al., 2021).

Species richness has long been hypothesised to be at least partly dependent on ecosystem productivity (Connell & Orias, 1964; Mittelbach et al., 2001), and hence it is important to consider biodiversity and primary productivity together. Theoretical and empirical results indicate that NPP is sometimes significantly correlated with species richness (Tilman et al., 2001), but the relationship is not consistent among ecosystems: species richness and productivity are more strongly correlated in relatively natural ecosystems than in modified ones (Flombaum & Sala, 2008), and richness-productivity relationships change with evenness (Hordijk et al., 2023), based on regional and experimental studies. However, the extent to which primary productivity and biodiversity co-vary in relation to relatively natural and human-modified land-cover types has not previously been examined across multiple sites at continental to global scales with empirical data. Here, we integrate databases on ecosystem productivity (MODIS) and biodiversity (PREDICTS) (Table 1) to undertake such an analysis. We investigate how global patterns of NPP and species richness vary in relation to human-associated land-cover changes, and whether species richness changes correlate with primary productivity and with changes in primary productivity. Our hypotheses are (a) NPP decreases with modification in naturally productive ecosystems, but increases in low productivity ecosystems, (b) species richness changes (increases and decreases) will also depend on the specific transition being considered, and (c) species richness will decline (i.e. be lower in modified vegetation) when modification is predicted to decrease ecosystem productivity (particularly where relatively natural vegetation has high productivity) and richness potentially increase where modification is expected to increase productivity (particularly where relatively natural vegetation has low productivity).

2 | METHODS

Our analyses are based on sample sites where biodiversity has been measured 'in the field', and where it is also possible to estimate the type of ecosystem present and the ecosystem productivity at those sites. The sites are drawn from those in the PREDICTS database (see below), which provides collated species richness data from around the world, with individual sample 'site' data nested within 'studies'. Each PREDICTS study that we considered enables comparisons of locally measured species richness of one or more taxonomic groups in relatively natural sites and human-modified sites in a given region, as a measure of differences between less and more human-modified environments, and as a space-for-time proxy for biodiversity change (Figure 1). More strictly, these comparisons represent a counterfactual examination to consider differences in diversity between the current diversity of modified vegetation and the diversity it might have been expected to contain today, had it not been modified in the past (given that diversity might have changed since the time of modification within relatively unmodified vegetation too). We refined the PREDICTS ecosystem classifications using satellite-based data from the MODIS data source (see below), so as to compare the consequence of land-cover change associated with different 'original' vegetation types. The taxonomic groups considered were plants, mammals, birds, hexapods (insects as well as Collembola, Protura and Diplura), arachnids, amphibians, reptiles, fungi, and 'other terrestrial invertebrates'.

We estimated net primary productivity (NPP) at the same locations, comparing relatively natural and modified sites within each region, as a space-for-time proxy for productivity change associated with human ecosystem modification (a counterfactual, as described for biodiversity above). NPP estimates are satellite-based annual NPP measurements, derived from MODIS (see below). This enables us to compare species richness and productivity differences associated with different 'relatively natural vegetation' (RNV) and 'modified vegetation' (MV) types around the world and to deduce the consequences of specific vegetation transitions.

2.1 | Data sources

We sourced species data from paired 'primary vegetation' versus modified land-cover types as defined by the PREDICTS database (Hudson et al., 2014, 2017). We used the PREDICTS database released in 2016, which includes sites sampled up to 2013. The PREDICTS database is a global database that reports field-based measurements of local biodiversity, which can be used to evaluate how human activities, such as land use, affect biological communities. 'Sites' are nested within 'studies', whereby a single 'study' represents multi-site data for one taxonomic group that originated from an individual source publication or equivalent data source. So defined, we considered 666 studies. Across all studies, there are 26,112 sites, of which 22,489 (588 studies) record abundance data, 3493 (70 studies) record presence-only data and 132 (eight studies) record richness-only data. We converted all of these into species richness estimates (species counts), retaining the structure of the data within all analyses such that any differences in recording methodologies between studies and taxa were taken into account. These sites were classified in the PREDICTS database into 'primary vegetation', eight secondary or modified land-cover types and a 'cannot decide' land-cover type category (Table 1). 328 out of the 666 studies (11,779 out of 26,112 sites, step one in Figure S1) have both 'primary vegetation' sites *and* modified land-cover sites (excluding 'cannot decide' sites) and were retained for analysis.

To establish land-cover types and transitions, we refined the information in the PREDICTS database using the MODIS land-cover product (MCD12Q1 v006: Friedl & Sulla-Menashe, 2019). Land cover estimates are available annually in MODIS, from 2001 to 2019, at 500 m resolution and include six classification schemes. We used Boston University's UMD classification scheme (Running & Zhao, 2019), which is a global land cover classification including 14 separate land cover classes, produced by the Department of Geography of the University of Maryland in 1998 using AVHRR satellite images between 1981 and 1994. We used this classification to

TABLE 1 Land-cover and modification class terminology.

Vegetation type in this paper	Identification	Examples
A. Vegetation types		
Relatively natural vegetation (RNV)	Sites that are classified as 'primary vegetation' in PREDICTS	Evergreen broadleaf forest with limited disturbance
Modified vegetation (MV)	Sites that are classified as any land-use types other than 'primary vegetation' in PREDICTS in the same study	Secondary evergreen broadleaf forest (e.g. following logging) or croplands
Vegetation type in this paper	**'Predominant land use' in the PREDICTS database**	**'Land-cover type' in MODIS products[a]**
B. Comparing land cover types from different sources		
Relatively natural vegetation (RNV)	Primary vegetation	Evergreen needleleaf forests Evergreen broadleaf forests Deciduous needleleaf forests Deciduous broadleaf forests Mixed forests Closed shrublands Open shrublands Woody savannas Savannas Grasslands
Modified vegetation (MV)	Young secondary vegetation Intermediate secondary vegetation Mature secondary vegetation Secondary vegetation (indeterminate age) Plantation forest Pasture Cropland Urban	Evergreen needleleaf forests Evergreen broadleaf forests Deciduous broadleaf forests Mixed forests Closed shrublands Open shrublands Woody savannas Savannas Grasslands Cropland and natural vegetation mosaics Croplands Urban and built-up lands
Unknown (Excluded from this study)	Cannot decide	Multiple types
C. Modification intensities		
	Change in MODIS land-cover types (from RNV to MV)[b]	
	No	Yes
Modification intensities for modified vegetation	Minor modification (minor MV)	Major modification (major MV)
Definition	Sites recognised as modified (from PREDICTS) but where MODIS (see above) classifies the modified site as having the same land cover as RNV sites in the same study	Modified sites where MODIS classifies the site as a different land cover to the original RNV in the same study. These land covers are mainly associated with human activity, such as farming and urbanisation
Examples	A secondary evergreen broadleaf forest which has been modified from a relatively natural evergreen broadleaf forest	Cropland sites in regions that were originally grasslands, or plantations in areas that were previously natural mixed forests

[a] Some of the MODIS land-cover types appear in both relatively natural vegetation (RNV) and modified vegetation (MV) classes because PREDICTS classifies some of these sites as 'primary vegetation' and others as modified (not primary) vegetation. Hereafter, we use the MODIS classification of vegetation types, combined with the PREDICTS assessment of whether that vegetation is RNV ('primary') or MV.

[b] We generated biodiversity differences between relatively natural vegetation and modified vegetation as a space-for-time proxy for changes from RNV to MV.

ensure consistency with the MODIS (MOD17) NPP data, which also employs this classification (Running & Zhao, 2019). We derived maps of annual NPP for the period 2001–2019 from the MOD17A3HGF v006 product (Running & Zhao, 2019). This product estimates NPP by combining the absorbed solar energy and satellite-derived spectral indices of vegetation, at 500 m resolution.

We classified all 'primary vegetation' sites in PREDICTS as relatively natural vegetation (RNV) and other sites as modified vegetation (MV), based on the PREDICTS land-cover types. However, the PREDICTS database does not provide a detailed land cover classification for the primary and secondary vegetation. In order to identify different primary vegetation types, we

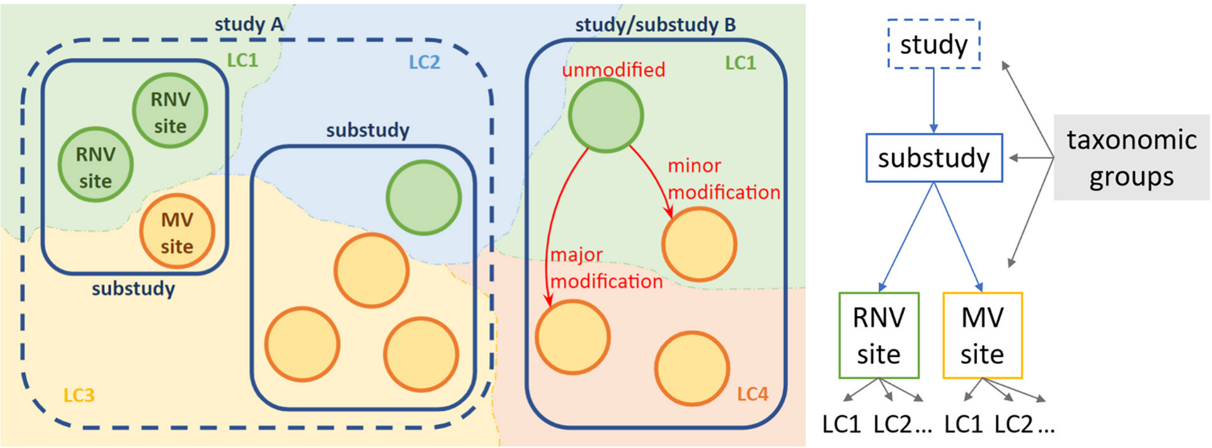

FIGURE 1 Structure of the dataset. All data used enable comparisons of species richness of a given taxonomic group in two or more land-cover types (LC1, LC2...) that are either relatively natural (green circles, RNV) or modified (orange circles, MV), within a single 'landscape' (substudy). Study A shows how we separated the geographically disjunct studies, based on geographic distances (100 km buffer) between groups of sites. Study/Substudy B shows how we define the intensity of modification: minor modification when modified sites are in the same general land-cover type as relatively natural vegetation sites (LC1; e.g. comparing 'primary' and 'secondary' forest) and major modification when MV sites are in a different land-cover type (e.g. comparing LC1 'primary' forest sites with LC4 urban sites).

extracted the MODIS land-cover type for each site in its sampling end year (last year of biodiversity sampling data in PREDICTS), uniting the 'predominant land use' in PREDICTS and 'land-cover type' in MODIS (Table 1; Figure 1; additional details are provided in Tables S1 and S2).

2.2 | Land-cover type reclassification and harmonisation

MODIS and PREDICTS land-cover classifications may differ, requiring harmonisation. Comparing MODIS and PREDICTS data identified 206 (of 5183) relatively natural sites where classifications could not be reconciled, which we removed, resulting in 4977 relatively natural sites (see Appendix S1 for Supplementary methods). We also controlled the geographical separation of sites within PREDICTS studies by grouping sites with overlapping 100 km buffers (see Supplementary methods and Sensitivity analyses, which consider different buffer sizes, in Appendix S1), resulting in splitting 4.7% of the original 363 studies into 28 substudies that contained both relatively natural and modified sites. This gave us 374 acceptable studies/substudies with 12,454 sites in total (Figures S1 and S2).

2.3 | Net primary productivity and species richness

We identified the land-cover type during the final year of PREDICTS sampling for each site (or 2001 for those sites sampled before 2001), and calculated the average NPP for the site for all preceding years where MODIS identified the same land-cover type as the final year (up to a 19-year-averaged estimation of NPP, see Appendix S1 Supplementary methods). Following some further refining of the data to remove sites where harmonised land cover did not exist within a 1 km buffer during the 19 years, we kept 11,849 sites for the analyses (step 12 in Figure S1). We also adjusted NPP values in modified sites to reflect the level of human appropriation (but not when reporting the main results for primary productivity, see Table S3).

To estimate the species richness differences caused by human modification, we compared richness between relatively natural vegetation and modified vegetation within individual substudies (sharing taxon and sampling methods). Among substudies we identified nine taxonomic groupings (Figure S3): plants, mammals, birds, hexapods, arachnids, other terrestrial invertebrates, amphibians, reptiles and fungi. We modelled *species richness differences* as the log of the proportional species richness 'change from' (difference between) the mean richness of relatively natural vegetation sites to each of the modified vegetation sites within a substudy ($\log[S_{MV}/S_{RNV}]$) (Hautier et al., 2015; Supp & Ernest, 2014; Vellend et al., 2013), with taxonomic groups separated (see Appendix S1 Supplementary methods).

2.4 | Analysis

The PREDICTS dataset is compiled as sites (PREDICTS category: SSBS, source-study-block-site) nested within the study (SS, which we further subdivided into spatially-coherent 'substudies'), with data for different *taxonomic groups*. We therefore applied mixed-effects models with the random effect *substudy* nested within *study*, to control for spatial heterogeneity, sampling effort and period (for species richness), and a partially crossed random effect, *taxonomic group*. We used a negative-binomial regression to model the species richness change as a function of land-cover types and intensity of modifications. As most (90%) of substudies (274 out of 306 studies) only covered a single taxonomic group (10% of substudies recorded two or three different taxa), we were unable to estimate site-level effects and excluded this from the hierarchical structure. To model the NPP difference as a function of land-cover types and intensity of modifications, we applied linear mixed-effects models with the nested random effect *substudy/study*. To evaluate whether NPP in relatively natural vegetation is a predictor of species richness differences (between relatively natural and modified vegetation), we applied linear mixed-effects models for different taxonomic groups with the nested random effect *substudy/study* and *land-cover type and NPP in relatively natural vegetation* as fixed effects. Model assumptions were verified by plotting residuals versus fitted values and each covariate in the model. The importance of the interaction term was inferred from Akaike information criterion (AIC) differences and a likelihood-ratio test (model details are provided in Tables S8–S10).

We checked for spatial autocorrelation by plotting semi-variograms of the model residuals between pairs of data points (Appendix S1 Supplementary methods). We also tested whether the elapsed time since conversion for an ecosystem affected the results by applying a sensitivity analysis (see Sensitivity analysis in Appendix S1).

All statistical analyses were performed in R 4.0.3 using the *lme4* package (Bates et al., 2007).

3 | RESULTS

3.1 | Effects of land-cover modification on net primary productivity

Year-averaged net primary productivity (NPP) varied among relatively natural ecosystem types, with evergreen broadleaf forests (including most tropical and subtropical moist forests) having the highest productivity of 1402.07 gC/m^2/year, while open shrublands (including shrubby deserts, semi-deserts and tundra) having the lowest of 272.83 gC/m^2/year (Figure 2a, Figure S5, Table S6). Compared to relatively natural sites, the productivity of modified land covers was, across all land-cover types, 13.4% higher in sites with minor modification (exploited/modified, but still within the same broad vegetation class) and 5.3% lower in sites with major modification (converted to a different land-cover category). However, ecosystem modification affected NPP in complex ways, depending on the 'original' relatively natural vegetation (i.e. the vegetation type that would have existed in a region prior to modification), as well as whether land-cover modification was relatively minor or major. We found a significant interaction between land-cover type and modification intensity on NPP ($\chi^2 = 1723.7$; df = 16; $p < 0.001$; $\triangle$AIC = −1691; Table S8, Figure S5) such that major modification led to higher NPP in woody savannas, grasslands and open shrublands but lower NPP in other vegetation types (e.g. in areas that naturally support evergreen forests and deciduous broadleaf forests) (Figure 2a) and major modification in evergreen broadleaf forests led to an obvious decrease in NPP compared to minor modification (Figure S6). Likewise, our models showed that minor modification has diverse effects, in some instances leading to the highest overall productivity (e.g. in deciduous broadleaf forests and mixed forest areas, where secondary growth might have higher NPP than established forest) and in some instances leading to the lowest (in woody savanna and savanna, which, showed in the next section, were more likely to be modified into high human-associated land-cover types) (Figure S5). The predicted NPP values from the mixed-effect model (Figure S5, Table S6) confirmed patterns in the raw data (Figure 2a) with small differences attributable to the models correcting for the nested structure of the data.

The models (Figures 2a, Figure S5) confirmed the empirical NPP pattern (Figure 2a) that major modification increased mean NPP in relatively natural grasslands and open shrublands, but strongly decreased NPP in most forest types. The interaction between land-cover type (land cover in relatively natural vegetation prior to transformation) and modification intensity (major, minor) significantly improved the fit, decreasing the model's AIC ($\chi^2 = 539.65$; df = 8; $p < 0.001$; $\triangle$AIC = −524; Table S8, Figure S5).

3.2 | Effects of specific ecosystem transformations on net primary productivity differences

Year-averaged NPP differences between relatively natural and modified vegetation depended on the specific land-cover transition considered, particularly where there were either increases or decreases in amounts of woody vegetation (Figures 3, Figure S6). Transitions from open shrublands, grassland and savanna to evergreen needleleaf forests, and open shrublands to croplands and woody savannas typically showed the greatest increases in NPP (blue cells in Figure 3), while transitions from broadleaf forests to open shrublands and urban or croplands showed the greatest reductions. In general, major modification of forests reduced NPP by 31.8% (Figures 2a and 3, Figure S7) while modification of other land uses to forest types normally increased NPP by 7.76% (Figure S8). NPP was reduced to the greatest extent when transformed to open shrublands with a 4.0% reduction in NPP from relatively natural shrublands to modified shrublands and a 35.8% reduction from different relatively natural vegetation to open shrublands (Figure 3b,c, Figure S8).

Because NPP changes were influenced by the 'original' vegetation (relatively natural vegetation), by the level of modification (major, minor), and by what the derived modified vegetation type is (Figure S8), the multi-way interaction among all of these variables generated the greatest AIC reduction: there was a significant effect of the interaction between land-cover type in modified vegetation and modification intensity on the NPP difference ($\chi^2 = 451.11$; df = 8; $p < 0.001$; $\triangle$AIC = −435; Table S8, Figure S8). This interaction arises, for example, because transitions from a non-forest relatively natural

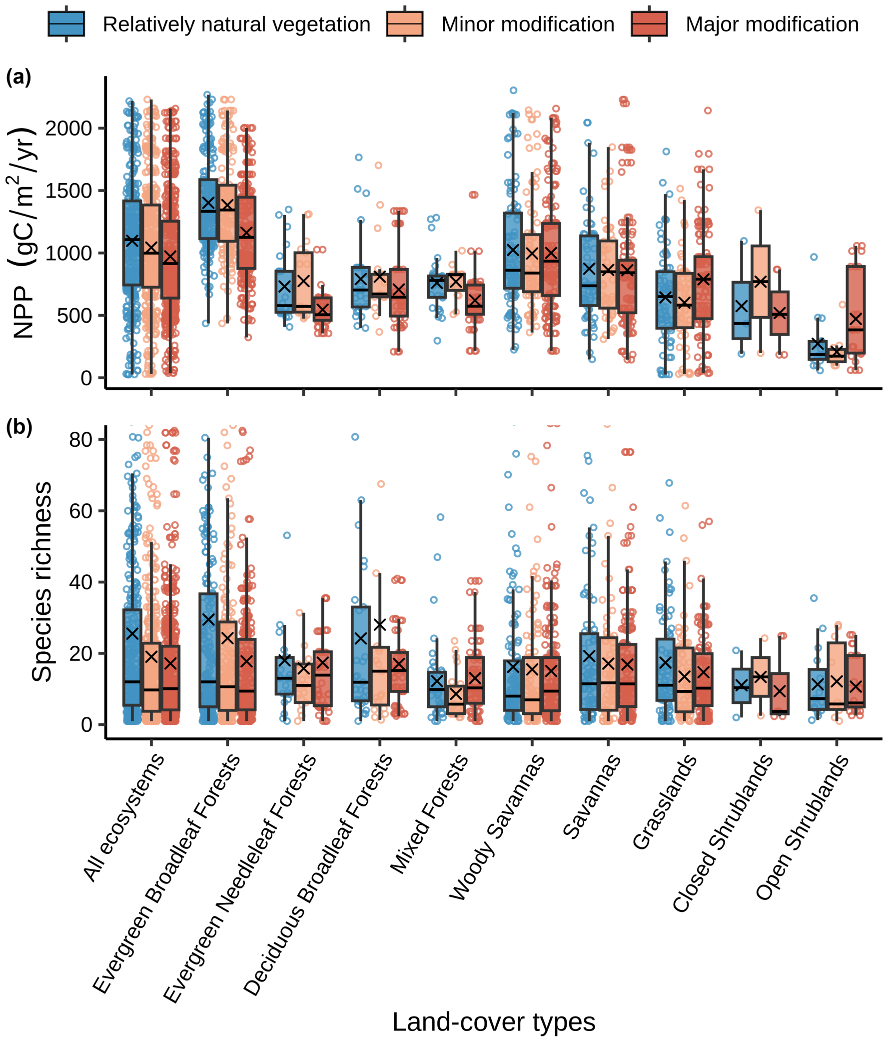

FIGURE 2 Ecosystem net primary productivity (year-averaged NPP, a) and species richness (b) in relatively natural vegetation (blue) and in modified vegetation (minor modification, fawn; major modification, rust). Land-cover types on the *x*-axis are types of relatively natural sites in a substudy (presumed 'original' vegetation). 'All ecosystems' combines the data from all land-cover types. Major modification is where the vegetation is altered sufficiently to fall into a different land-cover class. Each circle represents the substudy mean NPP and richness value, respectively, for each land-cover type and modification combination. The central line in boxes represents the median, the lower and upper box limits correspond to the 25th and 75th percentiles, the whiskers extend to ±1.5 times the interquartile range, and the cross represents the mean.

type to a modified forest usually increase NPP, but transitions of non-forest relatively natural vegetation to other modified categories usually reduce NPP.

3.3 | Relationship between original net primary productivity and productivity differences

Modification of more productive sites tended to result in decreases in NPP, while modification at less productive sites led to increases in average NPP (Figure 4). This result was stronger for major than minor modifications. There was a significant effect of NPP in relatively natural vegetation (*x*-axis in Figure 4: $\chi^2 = 2741.1$; df = 1; $p < 0.001$; $\triangle$AIC = −2739.2), the modification intensity ($\chi^2 = 25.06$; df = 1; $p < 0.001$; $\triangle$AIC = −23), and the interaction between these two variables ($\chi^2 = 100.86$; df = 1; $p < 0.001$; $\triangle$AIC = −99; Table S8) on productivity difference.

3.4 | Effects of minor and major ecosystem modification on species richness

The mean species richness in modified sites was, on average, 18.3% lower for minor modification and 23.8% lower for major modification relative to their comparator relatively natural vegetation sites. However, there was considerable overlap, variation and possible differences in responses in regions that contained different relatively natural vegetation types (Figure 2b, Table S7). In statistical models, there was a significant interaction between relatively natural vegetation type and modification intensity on species richness ($\chi^2 = 162.23$; df = 16;

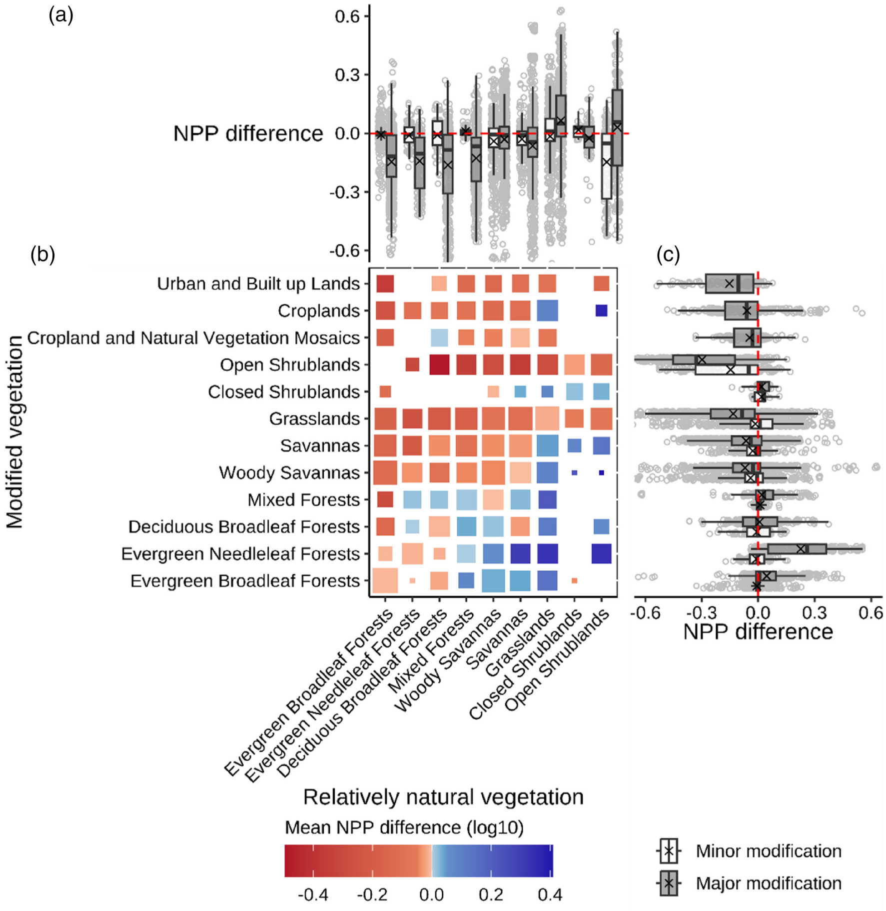

FIGURE 3 Net primary productivity differences (log10) between relatively natural and modified vegetation in different land-cover combinations. Squares in the main plot (b) are mean net primary productivity (NPP) values (values refer to Figure S5) of the land-cover type transition between relatively natural vegetation on the *X*-axis and each modified vegetation type on the *Y*-axis. The size of the points is proportional to the number of available NPP values for each land-cover type transition. The marginal boxplots show the effects of minor (open) and major (grey) levels of modification, depending on (a) the original relatively natural vegetation category and (c) the vegetation type to which sites have been transformed. The central line in boxes represents the median, the lower and upper box limits correspond to the 25th and 75th percentiles, the whiskers extend to ±1.5 times the interquartile range, and the crosses on the boxplots show the mean adjusted NPP differences, and small circles indicate individual sites.

$p<0.001$; $\triangle$AIC$=-130$; model 4.1 in Table S8), indicating that the directions and magnitudes of species richness differences (between relatively natural vegetation, minor modified vegetation, major modified vegetation) varied when considering different original relatively natural vegetation types. In general, major modification reduced richness by more than minor modification in forested landscapes (except deciduous broadleaf), while the two intensities of modification had similar impacts in savannas (decrease) and open shrublands (increase) (Figures S9, S11, S12).

Nonetheless, there was variation within and among ecosystem transition types (Figure 5, Figure S10) and across the world (Figure S13). There was a significant difference between different land-cover types in relatively natural vegetation and modification intensity ($\chi^2=31.29$; df$=8$; $p<0.001$; $\triangle$AIC$=-15.29$; Table S8, Figure S11). The 'destination' (modified vegetation) land-cover type also interacted significantly with the modification intensity ($\chi^2=73.37$; df$=8$; $p<0.001$; $\triangle$AIC$=-57.37$; Table S8, Figure S12). Globally, species richness decreased by modification in Africa, the Americas and Asia, but not significantly in Europe and Oceania (Figure S14).

3.5 | Relationships between species richness and NPP differences

Overall, we found no significant effects of landscape-scale, relatively natural vegetation productivity (Figure S15; $\chi^2=0.34$; df$=1$; $p=0.56$; $\triangle$AIC$=1.67$; adjusting cropland productivity for human appropriation) or productivity change (comparing modified with relatively natural vegetation; Figure S16; $\chi^2=2.41$; df$=1$; $p=0.12$; $\triangle$AIC$=-0.41$) on the species richness differences between relatively natural vegetation and modified vegetation, in most taxonomic groups. Overall, species richness tended to decline after modification, regardless of the original productivity of the relatively natural vegetation, or the estimated change in productivity associated

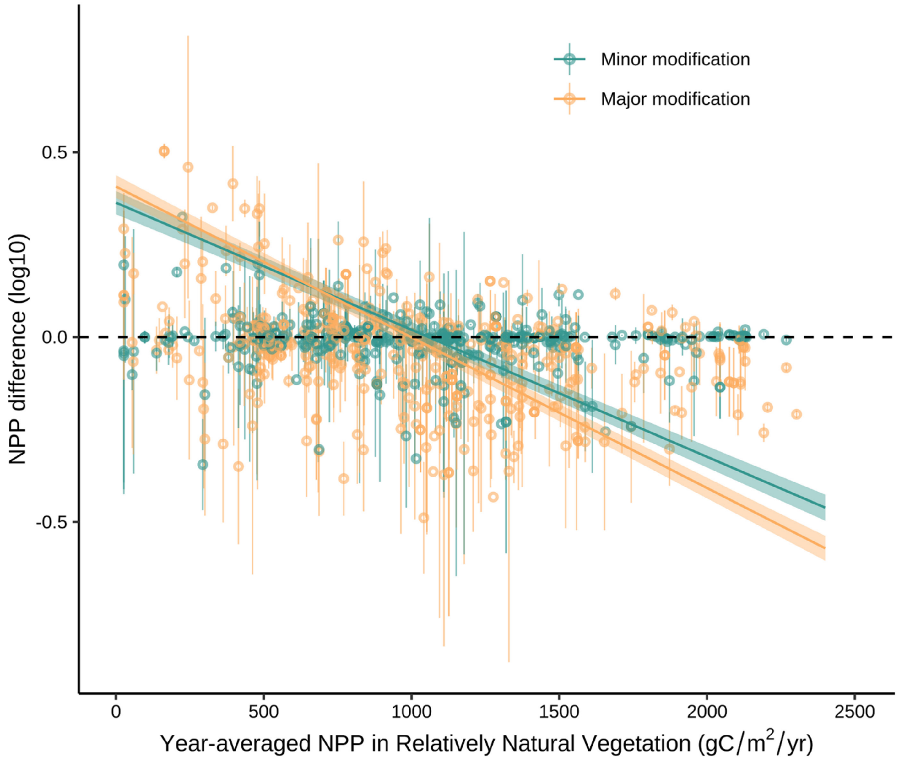

FIGURE 4 Effect of net primary productivity (NPP) in relatively natural vegetation on log 10 difference in the NPP between relatively natural and modified vegetation. Dashed line: no change in NPP. Solid lines: predicted values from the mixed-effects model, with 95% confidence interval. Single circles indicate the mean NPP values for each relatively natural vegetation land-cover type * modification combination within substudies (lines attached to circles show the standard deviation of the NPP difference). Circles without lines are substudies that only have one valid value.

with human-caused land cover changes. However, there could still be richness-productivity changes affecting the conversion of specific 'original' land-cover types (i.e. the relatively natural vegetation types present in a given substudy; Figure 6, Figure S17). The combined effect of the 'original' land-cover types and modification levels (minor or major modification) did have a significant influence on the biodiversity-difference versus productivity-difference relationship (Figure 6; $\chi^2=230.81$; df = 25; $p<0.001$; $\triangle$AIC = −180.81; adjusting cropland productivity for human appropriation), but the slope differences were mostly driven by the land-cover types that had relatively small sample sizes (e.g. evergreen needleleaf forests, Figure 6, Figure S17). These results suggest that the overall 'all ecosystems' impact of productivity changes on species richness change is not significant (Figure 6, top-left panel), but there are weak, heterogeneous trends that may vary among ecosystem types.

4 | DISCUSSION

Our results confirm that high net primary productivity (NPP) ecosystems, particularly forests, experienced reductions in productivity associated with modification by people, especially following major modification (Figure 4). In contrast, land that was converted from relatively open vegetation types to more forested ecosystem types showed 7.76% increases in NPP with modification (Figure 3). Somewhat unexpectedly, we did not find any evidence that species richness differences ('changes') were related to either the NPP of the 'original' vegetation (Figure S17) or to differences in NPP between the 'original' relatively natural vegetation and the derived modified vegetation types (Figure 6). Instead, we found a consistent decrease in species richness with vegetation modification (except for shrublands), regardless of whether human modification increased or decreased productivity, with an average decrease of 18.3% in minor-modified vegetation and 23.8% in major-modified vegetation. Therefore, we find support for the hypotheses that human modification has often led to decreased ecosystem productivity in highly productive parts of the world, and typically increased it in low-productivity regions; but human modification is associated with reductions in species richness, regardless of the original productivity (in relatively natural vegetation) or change in productivity (between relatively natural and modified vegetation) of the ecosystems considered. As a general global trend, productivity is positively correlated with species richness (Liang et al., 2016). Since we found human modification decreases the productivity of originally highly productive landscapes, the decline in species richness we found in high-productivity sites is expected and fits the global pattern. However, human modification of low-productivity areas tended to increase productivity, which we had anticipated could increase species richness, and we did not find this pattern. Testing the relationship between richness changes and productivity changes directly,

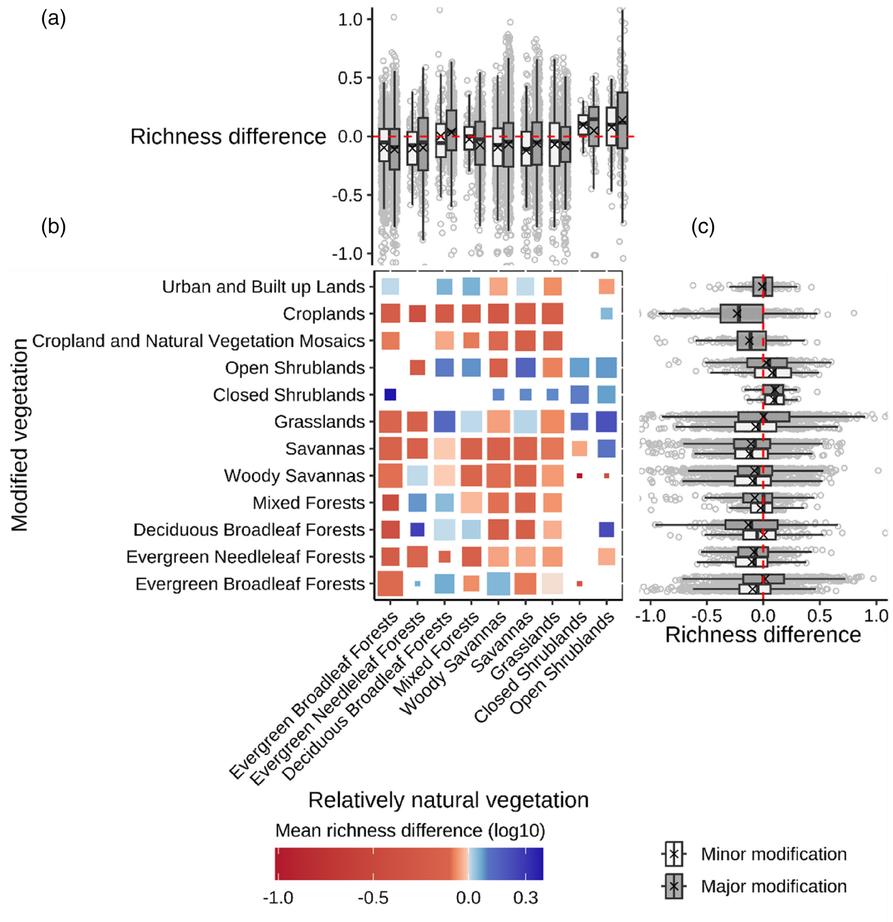

FIGURE 5 Species richness differences between relatively natural vegetation and modified vegetation in different land-cover type combinations. Squares in the main plot (b) are mean species richness differences (values refer to Figure S9) for each land-cover type transition between relatively natural vegetation on the *X*-axis and modified vegetation on the *Y*-axis. The size of the points is proportional to the Log number of available sites in each land-cover type transition. The marginal boxplots show the effects of minor (open) and major (grey) levels of modification, depending on (a) the original relatively natural vegetation category and (c) the vegetation type to which sites have been transformed. Boxplots show the distribution of Log richness change. The central line in boxes represents the median, the lower and upper box limits correspond to the 25th and 75th percentiles, the whiskers extend to ±1.5 times the interquartile range, and the crosses in the boxplot show mean species richness differences, and small dots indicate individual sites.

we found no clear evidence to support our initial hypothesis. Human modification, therefore, appears to break general relationships between ecosystem productivity and richness at least over the timescales represented in the PREDICTS datasets.

We found an overall tendency for ecosystem modification to result in a reduction of productivity within high-productivity sites but an increase in low-productivity sites, confirming the earlier regional findings that humans act to reduce spatial variation in NPP (Williams et al., 2005). Previous studies showed that areas currently under forestry are the most productive, followed by areas used today as cropland (Haberl et al., 2007). In high-productivity tropical forests, land-cover change usually decreases productivity (Krause et al., 2022), although a transition to a highly productive arable cropland can increase maximum productivity (DeFries et al., 1999; Gosling et al., 2017). However, the average annual productivity of croplands, which includes productivity across the whole cropping cycle, is reduced even though the proportion of the productivity that can be consumed by humans and livestock has increased. This was our expected result, based on the literature and because the global NPP appropriated by humans has approximately doubled since 1910 (Krausmann et al., 2013; Lepers et al., 2005; Zika & Erb, 2009).

Confirming our basic assumption and previous work (Cavanaugh et al., 2014; Lambers et al., 2004; Liang et al., 2016), we found a positive relationship between species richness and year-averaged NPP (Figure S19). The existence of this relationship underpinned our hypothesis that species richness should decrease with human modification in productive ecosystems, but increase in less productive ones. Unexpectedly, we found that species richness decreased even in areas where land-cover changes resulted in productivity increases, providing evidence that human modification on biodiversity change is relatively independent of the original status of the ecosystem, in both high productivity-biodiversity and low productivity-biodiversity ecosystems. This may imply different lag times for ecosystem

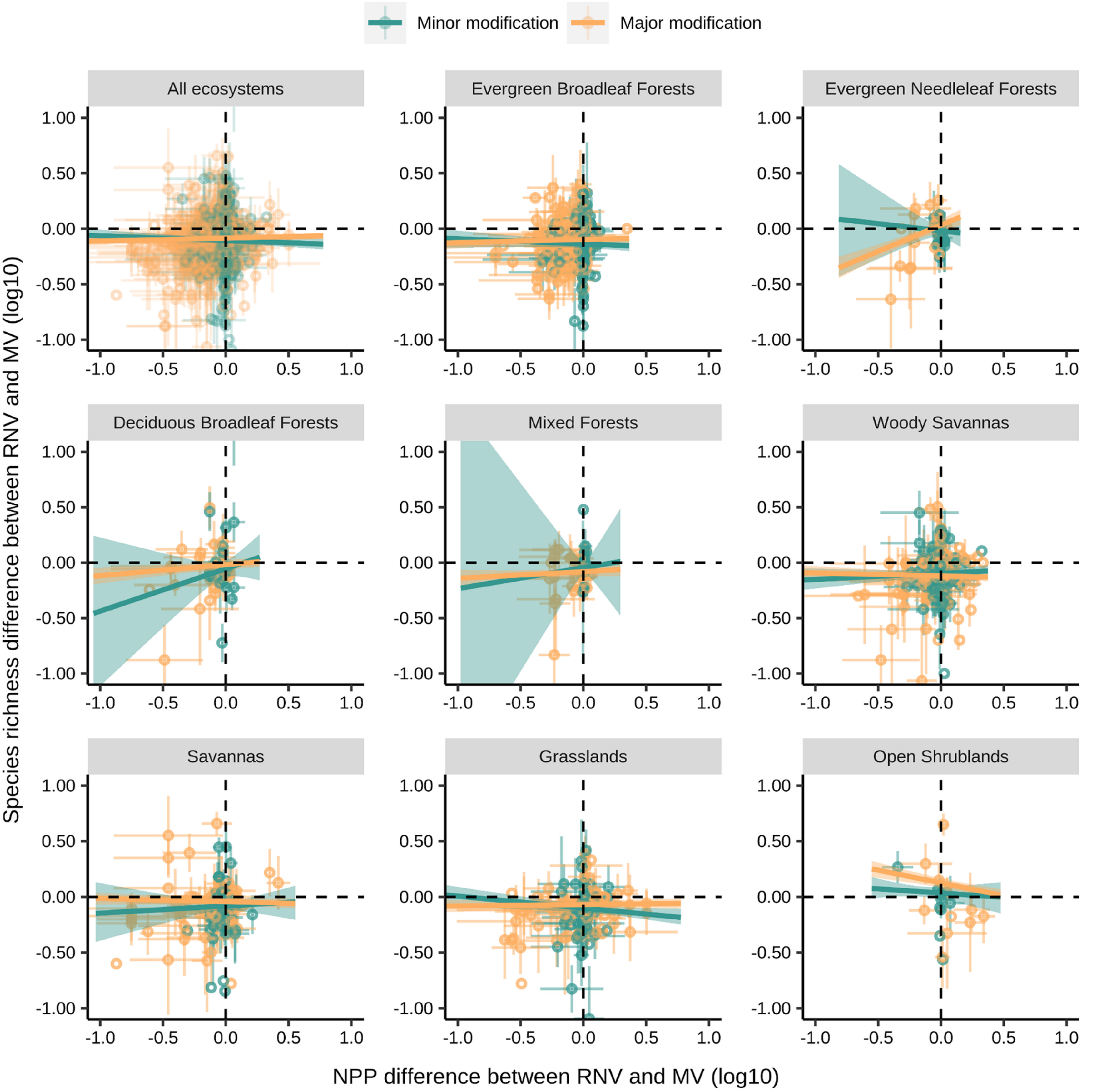

FIGURE 6 Relationship between species richness difference and net primary productivity (NPP) difference for different relatively natural land cover types. Richness differences are the log10 of the proportional species richness differences between every modified site (MV) and the mean value of relatively natural sites (RNV) for a specific land-cover type in the same substudy. Year-averaged NPP shown; adjusting cropland productivity for human appropriation. Single circles indicate the mean species richness difference values for each relatively natural land-cover type and modification combination within substudies (vertical and horizontal lines show standard deviations). Closed shrublands not shown as an individual plot because of small sample size.

productivity (and carbon pools) and biodiversity in the period after initial modification (Essl et al., 2015; Martin et al., 2013). In general, extinction and colonisation debts that lead to biodiversity lag times are worthy of future investigation (Millard et al., 2021). For example, the time lag between landscape change and extinction of half of the species that ultimately are lost from tropical forest remnants following fragmentation could take about 50 years (Brooks et al., 1999), although species additions around new forest edges could also take place. There are also potential delays in the establishment of species in novel ecosystems, with species richness recovery taking more than 10 years in some landscapes (Jung et al., 2019). The relative lags in species extirpations and colonisations are not known for most of the individual ecosystem transitions considered here. Nonetheless, we found no significant influence of time since conversion on our results in the subset of data that provided information on dates of conversion (Sensitivity analysis Table S3 in Appendix S1).

Despite these caveats (also see Appendix S1 Supplementary discussion), the clear result is nonetheless that, on average, species richness is reduced by most inferred land-cover 'transitions' (Figure 5), which is consistent with previous space-for-time analyses (Millard et al., 2021; Newbold et al., 2015, 2016). It contrasts starkly with time series analyses, which identify a great deal of variability (which is also present in the data considered here), but no overall decline in richness over time (Dornelas et al., 2014; Vellend et al., 2013), suggesting no overall trend towards reduced local biodiversity, despite ongoing land-cover and intensification changes. Gonzalez et al. (2016) have critiqued time-series analyses, but both sets of observations (space-for-time average declines, time-series lack of net decline) do appear to be well supported by empirical data. We suggest that this difference may arise for a number of potential reasons: (a) the PREDICTS database by definition focuses on often paired contrasts between 'primary' and modified vegetation types and is therefore a poor representation of modification frequency at the landscape level (and could potentially be slightly biased in site/ecosystem selection towards relatively large biodiversity differences), while time series might be slightly biased away from the largest modifications (meadow quadrats for plants are rarely repeated once they have been converted to concrete), (b) space-for-time comparisons effectively include changes over centuries while time series only observe a subset of these; only a modest proportion of the world surface is transformed to a fundamentally different land use each decade, which makes it hard to detect clear trends within short duration studies (Gonzalez et al., 2016), (c) Major transformations might lead to a rapid decline in local diversity, but then slower recovery as new species gradually colonise novel ecosystems. This could result in a preponderance of time series with flat (untransformed) or positive (recovering) trends and a few with large declines, generating no overall trend (Gonzalez et al., 2016). These transformed sites might still show reduced richness (in space-for-time analyses) compared to relatively natural sites if those positive trends have not yet returned richness to original levels.

The lack of relationship between primary productivity (in either the 'original' ecosystem or of difference in productivity between unmodified and modified vegetation) and species richness change is interesting, if slightly surprising, given the overall positive relationship at a global scale between productivity and richness (Hawkins et al., 2003; Hawkins et al., 2003a,b; Reiter et al., 2023). The absence of a positive relationship between productivity change and species richness change in our analyses could be related to lags in the system, if few species from low-productivity ecosystems are adapted to higher productivity (modified) systems, and vice versa; species of high productivity systems likely perform poorly in low production systems. Alternatively, or additionally, altered productivity associated with high levels of human intervention might, on average, be environments that include relatively high levels of chemical additions, including pesticides, and where there is direct human exploitation that removes animals and plants (including the appropriation of primary productivity for our livestock and ourselves directly). Alternatively, the overall global positive association between productivity and diversity may not be causally linked, but mere correlations in space (Colville et al., 2020; Hordijk et al., 2023). The challenge for this study is that it is not possible to directly test the overall species richness-productivity relationship before and after modification empirically because of the large variation in the sampling effort, time periods and taxonomic groups, as well as geographical area, for each study. Nonetheless, we found inconsistent relationships between richness change and productivity change within different land covers. Further research is required to identify the extent to which diversity and productivity are (or are not) causally linked at different temporal and spatial scales.

Overall, our results demonstrated the changing patterns of net primary productivity and species richness globally associated with human-induced land-cover change. We operated the analysis in two dimensions, modification level and the land-cover type, which revealed the complexity and diversity of productivity and biodiversity responses across landscapes. Although the overall pattern for the relationship between species richness difference and the initial vegetation productivity is less clear, it shows productivity increases and decreases and biodiversity gains and losses in particular human-modified ecosystems at the landscape scale. Showing results from all possible ecosystem transitions, this study helps us to enhance the knowledge of the potential effect of human modification on biodiversity and ecosystem function relationships on the Earth.

AUTHOR CONTRIBUTIONS

Chris D. Thomas conceived of the study, and all authors planned analyses. Shuyu Deng extracted and analysed the data with assistance from Colin M. Beale and drafted the manuscript. All authors contributed to the manuscript editing and revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw species data were downloaded from the PREDICTS database (2016 release). Lawrence Hudson; Tim Newbold; Sara Contu;

Samantha L L Hill et al. (2016). The 2016 release of the PREDICTS database [Data set]. Natural History Museum. https://doi.org/10.5519/0066354. Net primary productivity maps and land use maps downloaded from MODIS and processed by Google Earth Engine and R. Running, S., Zhao, M. (2019). MOD17A3HGF MODIS/Terra Net Primary Production Gap-Filled Yearly L4 Global 500 m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD17A3HGF.006. Friedl, M., Sulla-Menashe, D. (2019). MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500 m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MCD12Q1.006. The selected data used in this article and the R script used to generate the main results of the study are archived online on Zenodo: https://doi.org/10.5281/zenodo.10245343.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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