

Availability and proximity of natural habitat influence cropland biodiversity in forest biomes globally

Charlotte L. Outhwaite¹  | A. Monica D. Ortiz² | Fiona E. B. Spooner^{1,3,4} | Carole Dalin² | Tim Newbold¹

¹Centre for Biodiversity and Environment Research, University College London, London, UK

²Institute for Sustainable Resources, Bartlett School of Environment, Energy and Resources, University College London, London, UK

³European Centre for Environment and Health, University of Exeter Medical School, Truro, UK

⁴Institute of Data Science and Artificial Intelligence, University of Exeter, Exeter, UK

Correspondence

Charlotte L. Outhwaite, Centre for Biodiversity and Environment Research, University College London, Gower Street, London, WC1E 6BT, UK.

Email: charlotte.outhwaite.14@ucl.ac.uk

Funding information

Natural Environment Research Council, Grant/Award Number: NE/N01524X/1 and NE/R010811/1

Handling Editor: Petr Keil

Abstract

Aim: Agriculture is one of the greatest pressures on biodiversity. Regional studies have shown that the presence of natural habitat and landscape heterogeneity are beneficial for biodiversity in agriculture, but it remains unclear whether their importance varies geographically. Here, we use local biodiversity data to determine which local and landscape variables are most associated with biodiversity patterns and whether their association varies between tropical and non-tropical regions.

Location: Global terrestrial area in forest biomes.

Major taxa studied: More than 21,000 species of vertebrates, invertebrates, plants and other taxa.

Methods: We used generalized linear mixed-effects models to analyse the relationships between either community total abundance or species richness (derived from the PREDICTS database) and a number of site-level (predominant land use and land-use intensity) and landscape-level variables (distance to forest, the percentage of natural habitat in the surrounding landscape, landscape homogeneity, the number of land-cover types in the landscape, and total fertilizer application). We compared the associations of these variables with biodiversity in tropical and non-tropical regions.

Results: In most cases, changes in biodiversity associated with landscape-level variables were greater than those associated with local land use and land-use intensity. Increased natural habitat availability was associated with the most consistent increases in biodiversity. Landscape homogeneity was also important but showed different directions of biodiversity change between regions. Associations with fertilizer application or the number of land-cover types were generally weaker, although still of greater magnitude than for the local land-use measures.

Main conclusions: Our results highlight similarities and differences in the association of local- and landscape-scale variables with local biodiversity in tropical and non-tropical regions. Landscape natural habitat availability had a consistent positive association with biodiversity, highlighting the key role of landscape management in the maintenance of biodiversity in croplands. Landscape-scale variables were almost always associated with greater changes in biodiversity than the local-scale measures.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

KEYWORDS

biodiversity, cropland, forest, land use, landscape complexity, landscape composition, natural habitat, PREDICTS database, sustainability, tropical

1 | INTRODUCTION

With the global human population continuing to rise, there is a need to determine how to produce sufficient food while also conserving biodiversity. To meet the increasing demand for food, it is likely that further expansion and intensification of agricultural systems will be necessary, with resulting negative impacts on biodiversity (Kehoe et al., 2017). Agriculture is a major driver of biodiversity change; therefore, considering how to address the problem of feeding the global population while limiting the negative impacts of food production is key (Mehrabi et al., 2018). Indeed, land-use change, particularly conversion of land for agriculture, is already a major threat to biodiversity (Maxwell et al., 2016). The richness and abundance of species are significantly reduced and the composition of communities is altered in croplands relative to areas of primary vegetation (Newbold et al., 2015, 2016). Maintaining biodiversity within agricultural systems is not only desirable for conservation, but also necessary for the functioning and resilience of agro-ecosystems, because it underpins the provision of many essential ecosystem services (Millennium Ecosystem Assessment, 2005), including pollination, pest control and nutrient cycling.

The establishment of the factors that influence biodiversity within croplands has enabled some farming systems to be developed with conservation and sustainability in mind (Garibaldi et al., 2017). Characteristics of the landscape, such as composition and configuration, have an important role in shaping biodiversity patterns at both local and landscape scales (Tscharntke et al., 2012). Characteristics identified as important for cropland biodiversity include the availability and proximity of natural or semi-natural habitat (Carvalho et al., 2010; Dainese et al., 2015; Garibaldi et al., 2011; Kohler et al., 2007; Öckinger & Smith, 2007; Plath et al., 2021; Ricketts et al., 2008). Nearby natural habitats can provide additional or alternative resources to local biodiversity or act as a source of biodiversity itself (Tscharntke et al., 2005). Likewise, the biophysical characteristics of agricultural systems themselves have important effects on biodiversity. In addition to biodiversity declines with the conversion of natural habitats to croplands, inputs such as fertilizer (Kleijn et al., 2009) and pesticides (Geiger et al., 2010) can also result in negative impacts on biodiversity, as can increasing field size (Ricciardi et al., 2021).

Although the effects of certain landscape characteristics (such as landscape composition) on biodiversity have been assessed at local and regional scales, and on specific taxa (e.g., (Garibaldi et al., 2011; Martin et al., 2019; Redlich, Martin, & Steffan-Dewenter, 2018), to our knowledge there has been no global assessment of the relative importance of both local and landscape variables on biodiversity (although for an assessment of habitat amount, patch size and isolation effects specifically, see Watling et al., 2020). It is also unlikely

that biodiversity responses will be the same in both tropical and non-tropical regions, given their very different contexts in terms of land-use history, wider habitat availability and the composition of ecological communities. In non-tropical regions, particularly in the Northern Hemisphere, there has been a long history of anthropogenic land use (Ellis et al., 2021), which has substantially altered species composition, filtering out sensitive species from communities (Balmford, 1996). Indeed, species at low latitudes have shown greater sensitivity to disturbance compared with those at higher latitudes (Betts et al., 2019). Understanding variation across global regions in how landscape composition and complexity affect local biodiversity will ensure that the most appropriate conservation management responses can be implemented.

Here, we investigate globally the effects of agricultural land-use intensity and of landscape composition and complexity on local biodiversity. We assess the relative importance of these variables for biodiversity and establish whether patterns differ between tropical and non-tropical regions. To do this, we use biodiversity data from the PREDICTS database (Hudson et al., 2014, 2016, 2017). This work builds on previous studies using this database, which have shown the effects of local land use and land-use intensity on biodiversity (Newbold et al., 2015), and the differences in these responses across biomes (Newbold et al., 2020), by assessing an additional set of landscape-scale variables. We fit sampled species richness and total sampled abundance to site-level land-use variables (predominant land use and land-use intensity) and five landscape-scale variables (distance to forest, the percentage of natural habitat in the surrounding landscape, landscape homogeneity, the number of land cover types in the landscape, and total fertilizer application). We predict that species richness and abundance will be: (1) negatively associated with landscape-scale variables reflecting reduced availability of natural resources, such as long distance to forest and low percentage of surrounding natural habitat; (2) negatively associated with higher application of fertilizers within the landscape; (3) negatively associated with increasing landscape homogeneity, owing to simplification of the landscape; and (4) positively associated with the number of land-cover types, owing to the presence of additional habitat types that could support greater biodiversity. We expect that local-scale variables, although coarse in their classification, will be most important to local biodiversity, because they will best reflect the environmental conditions experienced by species. Of the landscape-scale variables, we expect those associated with natural habitat availability to be most important, because nearby natural habitat can provide alternative resources for biodiversity. We also predict that differences in the tropics will be greater than those in the non-tropics, because there is a greater proportion of rare and/or specialist species relative to the non-tropics.

2 | MATERIALS AND METHODS

2.1 | Biodiversity data: The PREDICTS database

The PREDICTS database (Hudson et al., 2014, 2016, 2017) contains data from 666 published studies, describing measures of individual species abundance (83% of records) or presence/absence (17% of records) or, alternatively, overall species richness (<1% of records) for assemblages sampled at specific sites, across gradients of land use or land-use intensity. The database has a hierarchical structure, whereby studies contain data sampled using the same methods, from one or more spatial blocks that form distinct spatial clusters, each of which contains data from one or more specific sites with geographical coordinates (Hudson et al., 2014). Finally, for each site there is a list of abundance, presence/absence or richness records for individual taxa (Hudson et al., 2014). One of the landscape variables we were interested in was the effect of nearby natural habitat on biodiversity. Given that the only natural habitat to have been mapped globally at a resolution fine enough to answer this question adequately is forest, we focused here on data from naturally forested biomes. We used an updated version of the WWF Terrestrial Ecoregions of the World map (Olson et al., 2001) to select sites found within biomes where the potential natural vegetation is expected to be forest. Of the 14 biomes listed, seven constitute forests.

We calculated within-sample species richness as the total count of species sampled at each site, and total abundance as the sum of recorded abundance measurements (for those records that captured some measure of abundance). Some measures required correction for sampling effort where effort varied within a study. To do so, sampling effort was rescaled within each study such that the most-sampled site had an effort value of one, and then raw abundance measurements were divided by this relative sampling effort. This correction assumes that recorded abundance scales linearly with sampling effort (Newbold et al., 2015). It is not possible to include sampling effort directly in the models, to account for variation in sampling effort among studies, because each study measured sampling effort in a different way. Such variation in sampling effort should be accounted for, at least in part, by including study identity as a random effect. We tested the robustness of our species richness results using estimates of species richness that accounted for incomplete sampling, using the Chao estimator (Chao et al., 2005). Given that we did not always have an integer measure of abundance, we could determine Chao-estimated richness for only 2143 sites in the tropics (out of 3719 in the main analysis) and 3706 sites in the non-tropics (out of 6674 in the main analysis). Although the number of sites was reduced considerably, results were generally similar to those from the models based on uncorrected species richness (Supporting Information Appendix S1). In a few cases, significant terms became non-significant, which might be attributable, in part, to the reduction in the number of sites available.

To compare the influence of landscape characteristics in cropland compared with sites of natural vegetation, we selected only sites from land uses specified as primary vegetation, secondary vegetation and cropland that were present within naturally forested

biomes, and for which data on all landscape characteristics were available (see next section). The remaining sites were then split into tropical and non-tropical sites by latitude: sites between -23.44 and 23.44° of latitude (the Tropics of Capricorn and Cancer) were classified as tropical sites and those outside of this region as non-tropical. This resulted in two data subsets: the tropical subset, which contained species richness estimates from 3719 sites across 224 studies and abundance estimates from 3314 sites across 202 studies; and the non-tropical subset, which contained species richness estimates from 6674 sites across 257 studies and abundance estimates from 5740 sites across 228 studies. These sites were distributed in a relatively even manner across forest biomes, although fewer sites were available from tropical coniferous, tropical dry broadleaf and temperate conifer forest systems (Figure 1; Supporting Information Table S6.1). The datasets include biodiversity estimates for >21,000 species of vertebrates, invertebrates, plants and other taxa (for a breakdown, see Supporting Information Table S6.1).

2.2 | Site-level data

Site-level information on land use and a coarse classification of land-use intensity are available within the PREDICTS database. Selected land uses were “cropland” (areas used for growing herbaceous crops), “primary vegetation” (natural habitat with no record of past vegetation destruction) and “secondary vegetation” (areas where the natural habitat is known to have been destroyed by human actions or extreme natural events but is now recovering). Land-use intensity within the database is specified as one of three classes: “minimal use”, “light use” or “intense use”. Sites where there was insufficient information to classify land-use intensity ($n = 1403$) were removed from our analysis. The criteria used to classify intensity varied among land-use types and was based on information given within the source papers. For primary and secondary vegetation, this is classified by the level and spatial extent of human impact (for example, hunting or selective logging), and for cropland it is based on cropping approach (mixed or monoculture), tillage, mechanization, irrigation and the application of chemical inputs (Hudson et al., 2014).

2.3 | Landscape-level data: Agricultural land-use intensity

Landscape-scale data on agricultural land-use intensity were extracted from datasets available from EarthStat (www.earthstat.org). These datasets represent global, gridded maps at a 5 arcmin \times 5 arcmin resolution (c. 10 km \times 10 km at the Equator) describing total production, yield, fertilizer application (total and per hectare) and area harvested (fractional area and hectares) averaged over the period 1997–2003 (Monfreda et al., 2008; Mueller et al., 2012; West et al., 2014). The area harvested and production data cover 175 crop types (Monfreda et al., 2008), and the fertilizer data cover 17 major crops (Mueller et al., 2012; West et al., 2014). Values were summed

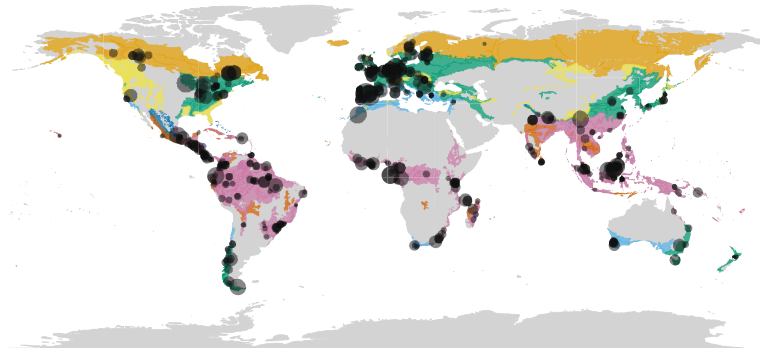


FIGURE 1 Global spread of the PREDICTS studies from naturally forested areas used in this analysis. The size of points represents the number of sites per study. Coloured regions correspond to the forest biomes, from the WWF terrestrial ecoregions of the world map (Olson et al., 2001). Dashed lines show -23.44 and 23.44° latitude; sites within this region are classified as tropical sites and those outside of this region as non-tropical sites.

across all crops within a grid cell (either 175 or 17) to obtain a total value across all crop types for each variable. Estimates of production and fertilizer application were divided by the area harvested to determine per-hectare estimates. For each of the variables, we overlaid the PREDICTS sites onto each aggregated map and extracted values using the *extract* function from the *raster* R package v.2.8-4 (Hijmans, 2018).

Although the EarthStat data might be inaccurate at the grid-cell level (Mueller et al., 2012), they offer the best available quantitative estimates of global agricultural intensity. Given that we are interested in spatial differences in use intensity, and not in absolute values, these data should be a suitable proxy for relative agricultural use intensity in terms of crop production and fertilizer application across the globe. More information on the EarthStat datasets can be found in the Supporting Information (Appendix S2).

2.4 | Landscape-level data: Landscape composition and complexity

Data on landscape composition and complexity included information on the distance of each site to forest, the percentage of natural habitat in the surrounding landscape, a measure of the homogeneity of the surrounding landscape, and the number of land-cover types in the surrounding landscape.

To estimate distance to forest, we used data from Global Forest Watch (<https://www.globalforestwatch.org/>) on tree cover density (Hansen et al., 2013) and calculated the distance of each site from any $30\text{m} \times 30\text{m}$ cell with forest of $\geq 80\%$ density, assuming that such dense forest represents mature natural forest that might harbour source populations of species or offer resources to biodiversity in nearby areas. In contrast to the biomes map, which was used to filter

sites found with areas where the natural vegetation is expected to be forest, the Global Forest Watch map represents contemporary actual forest distribution. We first processed the Global Forest Watch dataset such that cells were either one (forest of $\geq 80\%$ density) or zero (forest of $< 80\%$ density or not forest). We then determined the distance (in kilometres) from each site to the nearest cell containing $\geq 80\%$ dense forest using the *pointDistance* function from the *raster* R package (Hijmans, 2018).

We estimated the percentage of natural habitat in the landscape using downscaled land-use data (Hoskins et al., 2016). This dataset consists of estimates of the proportional cover of five major land-use classes (primary habitat, secondary habitat, cropland, pasture and urban) at 30arc-s resolution (c. 1 km at the Equator) for all global terrestrial areas. This dataset was created by downscaling data detailing 61 bio-realms using the relationships between these bio-realms and fine-grained data on climate, land cover, landform and anthropogenic layers determined using statistical models (Hoskins et al., 2016). We projected the maps of primary and secondary vegetation onto a Behrmann equal-area projection at 1 km resolution and summed the values in these two maps to obtain estimates of the proportional cover of natural habitat. The data were then aggregated to $5\text{ km} \times 5\text{ km}$ blocks, calculating the average percentage cover across the block. Finally, we overlaid our sites onto this map and extracted values as above to obtain estimates of the percentage of surrounding natural habitat for each site.

The number of land-cover types surrounding each site was determined using the global land-system classification by Kehoe et al. (2017), which is a map characterizing broad land-cover categories at 30arc-s resolution (c. 1 km at the Equator). For our purposes, we ignored the classifications based on suitability for crops and/or livestock and combined land-use categories with the same broad land-cover type (e.g., *Dense_forest* and *Dense_forest_CropSuitable*);

this left 12 land-cover types. We determined the number of surrounding land covers for each site by creating a 5 km buffer, within which we summed the number of land covers. This was carried out using the *buffer* and *extract* functions, respectively, in the *raster* R package (Hijmans, 2018). Initially, a selection of buffer zones was tested across a range of distances often considered in landscape studies (radius of 100m, 500m, 1 km, 3 km and 5 km). We chose to use the 5 km buffer in the final analysis because it is an important landscape size in other studies (Crouzeilles & Curran, 2016; Potts et al., 2010) and for consistency with the other metrics used here. Smaller buffer sizes did not have a good range of values across possible numbers of land covers owing to the resolution of the land-cover dataset.

Our measure of landscape homogeneity was taken from the study by Tuanmu and Jetz (2015). We used the “homogeneity” metric which, using the MODIS enhanced vegetation index (EVI) product (a vegetation index derived from satellite images that measure the reflectance in the red, near-infrared and blue wavebands), describes vegetation similarity between adjacent pixels. This metric ranges between zero and one, with one representing homogeneous areas. We used the 2.5 arcmin resolution homogeneity map (c. 5 km at the Equator) and for each PREDICTS site extracted the homogeneity value associated with its location, as above. We would expect a negative relationship between homogeneity and the number of land-cover metrics, which was the case (Supporting Information Figure S5.1). However, we do not expect this correlation to be problematic because the correlation was relatively weak ($r = -0.35$), and each variable measures a different characteristic of the environment. We sought alternative metrics of homogeneity that account for whether the landscape is natural or modified, which this dataset does not, but did not find anything suitable. Maps of landscape-level variables can be found in the Supporting Information (Figures S5.2 and S5.3), along with dataset details (Supporting Information Table S6.2).

2.5 | Statistical analysis

All statistical analyses were conducted in R v.3.6.2 (R Core Team, 2016). To avoid overly complex models with high-order interaction terms, analyses were conducted separately on tropical and non-tropical data subsets. Initially, correlations between all landscape-scale variables were tested using the *cor* function (calculating Pearson's correlation coefficient). As expected, many of the agricultural variables from the EarthStat data were highly correlated (Supporting Information Figure S5.4). We therefore used only the “total fertiliser application” variable in our final analyses. We selected this variable because the application of chemical inputs is an important aspect of agricultural intensification. This left five landscape-scale variables for analysis: total fertilizer application, distance to forest, percentage of natural habitat, homogeneity of the surrounding landscape and the number of land covers in the surrounding landscape; the two site-specific categorical variables: predominant land use and use intensity; and the forest biome in which the site was located (Table 1; Supporting Information Figure S5.5).

Each measure of biodiversity (species richness and total abundance) was modelled separately for each realm as a function of the final set of variables using mixed-effects models. For all models, a random effect of study identity was included to account for differences in sampling methods between studies and differences in overall abundance and richness between broad taxonomic groups and geographical regions, and also a nested random effect of spatial block within study to account for the spatial arrangement of sites (Newbold et al., 2015). For the species richness model, site was also included as a random effect (nested within spatial block, nested within study) to account for overdispersion (Newbold et al., 2015; Rigby et al., 2008). To account further for differences in abundance and richness between taxonomic groups, we tested the inclusion of a random effect of study identity nested within major taxonomic group (birds, mammals, amphibians, reptiles, invertebrates, fungi and slime moulds, and plants). These models had slightly improved Akaike information criterion values compared with the main models and produced very similar results to models without this random effect. However, the modelling algorithm produced convergence warnings, hence they were not taken further.

Interactions between each of the continuous variables and both predominant land use and use intensity were included, because we expect effects of landscape-scale variables to vary across different types and intensities of land use. An interaction between predominant land use and use intensity was also included. The distance to forest and total fertilizer application estimates were skewed, and were therefore ln-transformed before analysis (adding a value of one to deal with zeroes), as were the abundance estimates. Analyses were also tested using an inverse hyperbolic sine transformation for the fertilizer and distance to forest data [this transformation allows the retention of zero-value observations (Bellemare & Wichman, 2020)]. The results were unchanged, hence they are not presented. All landscape-scale variables were rescaled to have a mean of zero and standard deviation of one. The best fixed-effects structure was determined by backward stepwise model selection, conducting likelihood-ratio tests (χ^2) to select variables (Supporting Information Tables S6.3 and S6.4). Species richness was modelled using a generalized linear mixed-effects model, assuming Poisson-distributed errors. We modelled ln-transformed total abundance (adding one to handle zero values) using a linear mixed-effects model, assuming normally distributed errors. We used this approach because the PREDICTS database contains many abundance estimates that are not true counts (e.g., relative densities, percentage cover of plants), hence assuming a Poisson or similar count distribution is suboptimal. Previous studies using the PREDICTS database have shown that alternative distributions (such as the zero-inflated negative-binomial distribution) give very similar results to the log-normal distribution used here (Millard et al., 2021). The final model structures are presented in the Supporting Information (Appendix S3). Models were run in R using the *lme4* package v.1.1-21 (Bates et al., 2015). Checks were carried out to ensure that model assumptions were met and to check for spatial autocorrelation in the residuals (Supporting

TABLE 1 Explanatory variables used to determine local- and landscape-scale characteristics that are likely to influence biodiversity

Variable	Source	Reference	Description	Unit	Range in dataset
Land use	PREDICTS database	Hudson et al. (2016)	A metric based on the authors' description of the site. Assigned to one of six categories: primary vegetation, secondary vegetation, cropland, plantation, pasture and urban	Categorical variable	Primary, secondary, cropland
Use intensity	PREDICTS database	Hudson et al. (2016)	A metric based on the authors' description of the site. Assigned to one of four categories: minimal, light or intense use or "cannot decide" during database creation	Categorical variable	Minimal, light, intense
Total fertilizer application (17 crops)	EarthStat	Mueller et al. (2012); West et al. (2014)	Total calculated by taking the sum of the total applied fertilizer (N, P and K) values for 17 crops	Kilograms (over each 5 arcmin grid cell)	0–2,314,226
Distance to dense forest	Global Forest Watch	Hansen et al. (2013)	Calculated as the minimum distance to any cell that contained $\geq 80\%$ of dense forest	Kilometres	0–324.47
Number of land-cover types	Kehoe et al. (2017)	Kehoe et al. (2017)	Calculated as the number of land-cover types within a 5 km buffer zone around each site	Number of land-cover types	1–10
Homogeneity metric	Tuanmu and Jetz (2015)	Tuanmu and Jetz (2015)	Calculated as the mean homogeneity value within a 5 km buffer zone around each site	Homogeneity value between zero and one	0.15–0.67
Percentage of natural habitat	Hoskins et al. (2016)	Hoskins et al. (2016)	Re-projected proportions of major natural habitats at a 1 km ² resolution	Percentage	0.99–99.99

Notes: The "range in dataset" column presents the range of values for each explanatory variable across the sampled PREDICTS sites used in the analysis, not the complete possible range of the variable.

Information Figures S5.6-S5.9). Model output tables are presented in the Supporting Information (Appendix S4).

To compare the relative magnitudes of change in biodiversity with variation in all variables, we predicted the percentage difference in both total abundance and species richness across the range of each of the explanatory variables at the sites included in the analyses. All other variables were held constant, at median values for continuous predictors, and for cropland and intense use for land use and use intensity, respectively. Depending on the realm of interest, the forest biome was set to either “Tropical & Subtropical Moist Broadleaf Forests” or “Temperate Broadleaf & Mixed Forests”. Predictions of abundance and species richness were generated by sampling 10,000 estimates based on the variance-covariance matrix. The percentage difference between the extremes of each explanatory variable was calculated for each random sample and summarized in terms of the median and 95% confidence intervals (not prediction intervals). These results are presented in the Supporting Information (Table S6.5) and Figure 3. Note that not all of the effects shown in Figure 3

were significant alone but are included in the figure if they showed a significant interaction with land use or use intensity. The percentage changes in biodiversity as a result of these significant interactions are presented in Figures 4 and 5.

3 | RESULTS

The relative importance of the local and landscape variables assessed differed depending on the realm and the biodiversity metric considered. Nevertheless, in almost all cases, landscape-scale variables were associated with stronger variation in total abundance and species richness than local-scale land use and land-use intensity (Supporting Information Table S6.5). Despite generally having a smaller effect on biodiversity, the main effects of local-scale land use and land use intensity, and the interaction between these variables, were often associated with substantial changes in total abundance and species richness (Figure 2; Supporting Information Tables

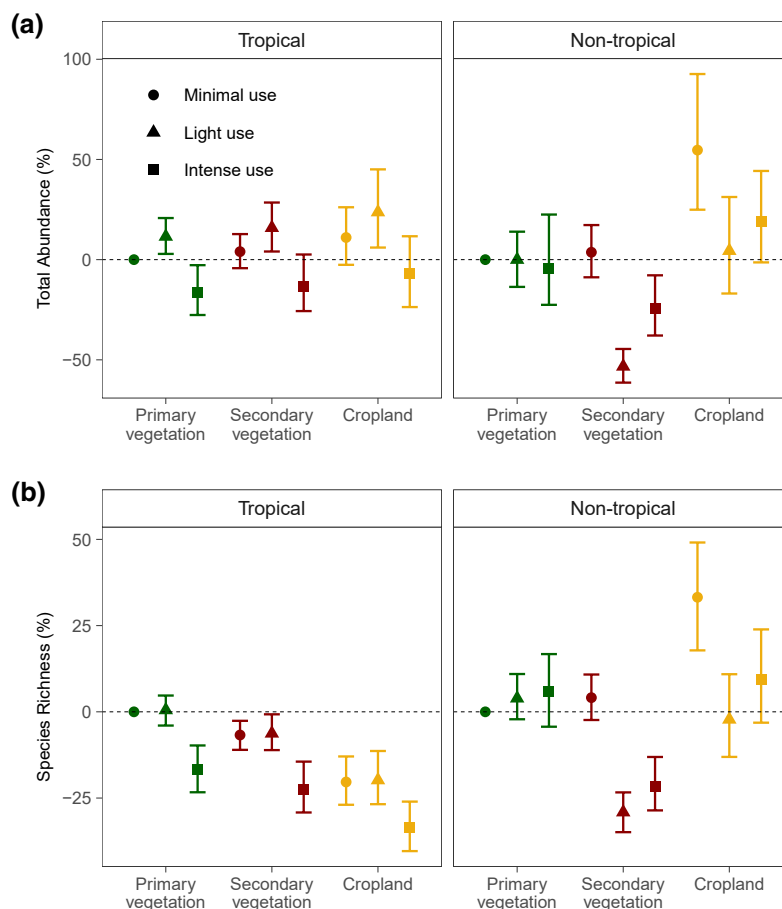


FIGURE 2 Difference in (a) total abundance and (b) species richness associated with the interaction between land use and use intensity. The percentage change of each biodiversity variable was determined by sampling the fixed effects 1000 times based on the variance-covariance matrix, then calculating the median value (points) and the 2.5th and 97.5th percentiles (error bars). Values are expressed as a percentage of the value in primary vegetation with minimal use intensity. Main effect of land use: tropical abundance, $\chi^2_{2,14} = 1, p = .594$; non-tropical abundance, $\chi^2_{2,18} = 44, p < .001$; tropical richness, $\chi^2_{2,12} = 77, p < .001$; and non-tropical richness, $\chi^2_{2,18} = 67, p < .001$. Main effect of use intensity: tropical abundance, $\chi^2_{2,9} = 75, p < .001$; non-tropical abundance, $\chi^2_{2,18} = 25, p < .001$; tropical richness, $\chi^2_{2,12} = 38, p < .001$; and non-tropical richness, $\chi^2_{2,18} = 13, p < .01$. Interaction between land use and use intensity: tropical abundance, $\chi^2_{4,33} = 6, p = .171$; non-tropical abundance, $\chi^2_{4,25} = 80, p < .001$; tropical richness, $\chi^2_{4,33} = 4, p = .360$; and non-tropical richness, $\chi^2_{4,29} = 114, p < .001$.

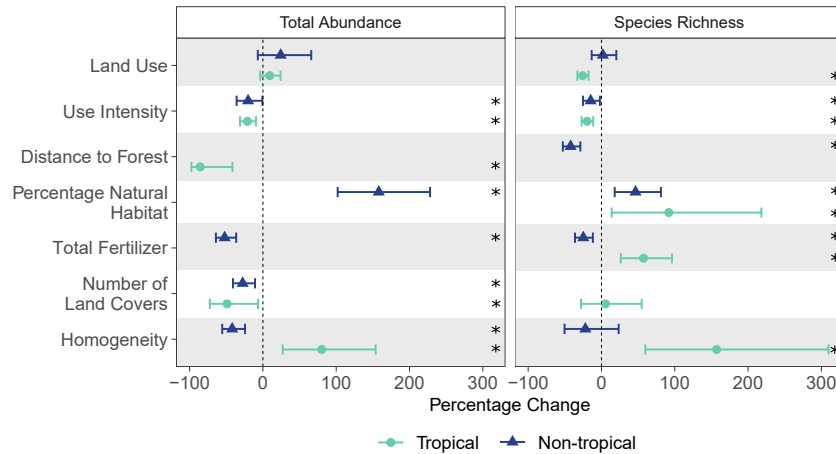


FIGURE 3 Percentage difference in model-estimated total abundance (left) and species richness (right) associated with variation in each of the local- and landscape-scale variables in tropical and non-tropical sites. Differences are shown for the range of values of each explanatory variable across the sites included in the analysis. Blank cells indicate that the fixed effect (either alone or in interaction with land use or use intensity) was not selected as significant in the model-selection process (for final model structures, see Supporting Information Appendix S3). Non-focal explanatory variables were held constant: predominant land use was set to “cropland”; use intensity was set to “intense use”; and all continuous variables were set to the median value across sampled sites. Predicted biodiversity values were obtained by randomly drawing 10,000 estimates based on the variance–covariance matrix. We present median values as points, with error bars representing the 95% confidence intervals of the model-estimated mean biodiversity difference (i.e., not prediction intervals). Asterisks indicate effects where the confidence intervals do not cross zero. Note that significance in this sense can differ from significance inferred by backward stepwise model selection, as presented in the text.

S6.3 and S6.4). This is particularly evident in tropical croplands, where species richness was reduced by 33% in the most intensively used areas.

Local intensification of cropland (comparing minimal-use and intense-use cropland) was associated with a reduction in both richness and abundance of c. 20% in both tropical and non-tropical sites (Figure 3; Supporting Information Table S6.5). Differences between intensively used primary vegetation and intensively used cropland were non-significant, except for species richness in the tropics, where richness was almost 26% lower in intensively used cropland compared with intensively used primary vegetation (Figure 3; Supporting Information Table S6.5).

Of the landscape-scale variables, distance to forest and percentage of natural habitat had the most consistent associations with biodiversity, although their relative importance varied among biodiversity metrics and regions (Figure 3; Supporting Information Table S6.5; Figures S5.10 and S5.11). An increased percentage of natural habitat in the surrounding landscape was consistently associated with increases in both species richness and total abundance of between 47 and 158% across a range of 1–99% natural habitat availability, although not significantly so in all cases (Figure 3; Supporting Information Table S6.5; main effect of percentage of natural habitat: tropical abundance, $\chi^2_{1,12} = 0.3$, $p = .58$; non-tropical abundance, $\chi^2_{1,18} = 75$, $p < .001$; tropical richness, $\chi^2_{1,13} = 2$, $p = .193$; and non-tropical richness, $\chi^2_{1,18} = 60$, $p < .001$). The significant interactions between the percentage of natural habitat and both land use and use intensity for species richness in the tropics showed that the positive association with natural habitat was observed primarily in cropland sites (Figure 4; interaction between land use and percentage natural

habitat: $\chi^2_{2,25} = 8$, $p < .05$) and in intensively used land (Figure 5; interaction between use intensity and percentage natural habitat, $\chi^2_{2,25} = 6$, $p < .05$). Likewise, at the greatest sampled distances from forest (325 km), total abundance in tropical croplands was reduced by 86% and non-tropical richness by 42% in comparison to sites adjacent to forest (Figure 3; Supporting Information Table S6.5; main effect of distance to forest: tropical abundance, $\chi^2_{1,10} = 3$, $p = .07$; non-tropical abundance, $\chi^2_{1,19} = 3$, $p = .07$; tropical richness, $\chi^2_{1,15} = 0.4$, $p = .55$; and non-tropical richness, $\chi^2_{1,18} = 25$, $p < .001$). Although distance to forest had a marginally non-significant association with tropical abundance on its own, a significant interaction with land use showed that reductions in abundance with increasing distance to forest were primarily observed in croplands (Figure 4; interaction between land use and distance to forest: $\chi^2_{2,19} = 18$, $p < .001$).

For tropical sites, landscape homogeneity had the strongest association with species richness and second-strongest association with total abundance (Supporting Information Table S6.5; main effect of homogeneity: tropical abundance, $\chi^2_{1,9} = 14$, $p < .001$; and tropical richness, $\chi^2_{1,12} = 17$, $p < .001$). Abundance was 80% higher and richness 157% higher at the most homogeneous sites compared with the least homogeneous sites (Figure 3). For species richness in the tropics, a significant interaction with land use revealed a stronger positive association in croplands than in natural habitats (Figure 4; Supporting Information Figure S5.12; interaction between land use and homogeneity: tropical richness, $\chi^2_{2,25} = 11$, $p < .05$). Conversely, for non-tropical sites, landscape homogeneity was less important and, in contrast to tropical sites, was associated with reductions in both abundance and richness (although the confidence intervals for richness crossed zero; Figure 3; Supporting Information Table S6.5;

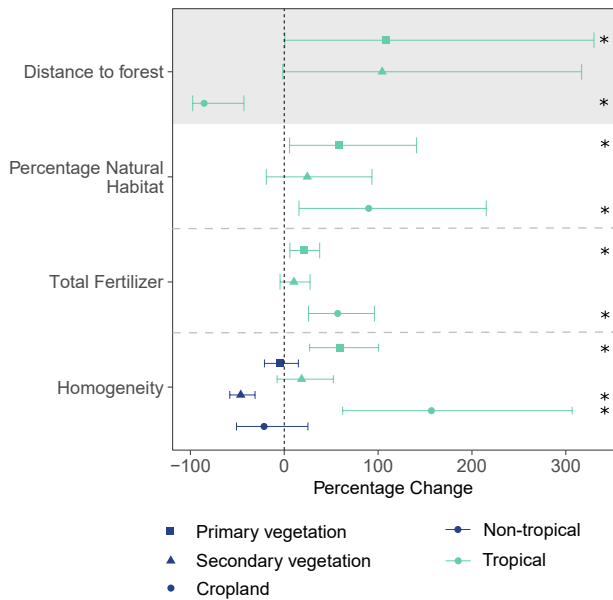


FIGURE 4 Percentage difference in model-estimated total abundance (shaded area) and species richness associated with variation in each landscape-scale variable in interaction with land use in tropical and non-tropical sites. Differences are shown for the range of values of each explanatory variable across the sites included in the analysis. Blank cells indicate that the interaction with land use was not selected as significant in the model-selection process (for final model structures, see Supporting Information Appendix S3). The only non-tropical results are shown in blue (homogeneity), and the only total abundance results are shaded (distance to forest). Non-focal explanatory variables were held constant: use intensity was set to “intense use”; and all continuous variables were set to the median value across sampled sites. Predicted biodiversity values were obtained by drawing 10,000 estimates at random based on the variance–covariance matrix. We present median values as points, while error bars represent the 95% confidence intervals of the model-estimated mean biodiversity difference (not prediction intervals). Asterisks indicate effects where the confidence intervals do not cross zero. Note that significance in this sense can differ from significance inferred by backward stepwise model selection, as presented in the text.

main effect of homogeneity: non-tropical abundance, $\chi^2_{1,18} = 26$, $p < .001$; and non-tropical richness, $\chi^2_{1,18} = 18$, $p < .001$).

Fertilizer also showed a clear association with biodiversity in most cases (main effect of fertilizer application: tropical abundance, $\chi^2_{1,11} = 0.6$, $p = .45$; non-tropical abundance, $\chi^2_{1,18} = 7$, $p < .01$; tropical richness, $\chi^2_{1,12} = 7$, $p < .05$; and non-tropical richness, $\chi^2_{1,18} = 5$, $p < .05$). Non-tropical abundance and richness were 52% and 25% lower, respectively, in sites with the highest in comparison to the lowest rates of fertilizer application. However, there was a positive difference in tropical richness (an increase of 58% at the highest compared with lowest fertilizer application rates; Figure 3). Changes in biodiversity, however, were seen only across very low levels of fertilizer application, and only for certain land uses or land-use intensities, with biodiversity remaining largely stable at higher rates of fertilizer application (Supporting Information Figure S5.13). A significant interaction with use

intensity revealed that in the non-tropical realm, reductions in abundance and species richness were associated with intensively used land (Figure 5; interaction between use intensity and fertilizer application: non-tropical abundance, $\chi^2_{2,25} = 20$, $p < .001$; and non-tropical richness, $\chi^2_{2,29} = 14$, $p < .01$).

The association between the number of land covers and biodiversity varied in importance depending on the biodiversity metric and realm in question, but was in no case the variable most strongly associated with biodiversity differences (Figure 3; Supporting Information Table S6.5; main effect of number of land covers: tropical abundance, $\chi^2_{1,15} = 0.2$, $p = .67$; non-tropical abundance, $\chi^2_{1,18} = 10$, $p < .01$; tropical richness, $\chi^2_{1,14} = 0.3$, $p = .56$; and non-tropical richness, $\chi^2_{1,19} = 2$, $p = .19$). No difference was seen for tropical species richness, but reductions of 28% in non-tropical abundance were seen in landscapes with the most compared with the fewest land covers (Figure 3; Supporting Information Table S6.5). A significant interaction with use intensity for tropical abundance and richness revealed some differences in responses across sites of varying use intensity (Figure 5; Supporting Information Figure S5.14; interaction between use intensity and number of land covers: tropical abundance, $\chi^2_{2,19} = 12$, $p < .05$; and tropical richness, $\chi^2_{2,25} = 10$, $p < .01$).

The variation explained by the fixed effects in the models was low (Table 2). However, such low pseudo- R^2 values associated with fixed effects are similar to or better than previous analyses based on the PREDICTS database (Newbold et al., 2015, 2020) and on similar heterogeneous biodiversity databases (Spooner et al., 2018; Williams et al., 2022), where the majority of the variation is often explained by the random effects.

4 | DISCUSSION

Overall, landscape-scale measures of land-use intensity are consistently associated with stronger variation in biodiversity than local land use and use intensity, although the latter still emerge as important correlates of biodiversity patterns. As in previous local and regional studies (e.g., Garibaldi et al., 2011; Martin et al., 2019; Redlich, Martin, & Steffan-Dewenter, 2018), we show that landscape characteristics play a key role in shaping local biodiversity, although their effects differ in magnitude and even direction between the tropical and non-tropical realms.

The availability of natural habitat (distance to dense forest and proportion of natural habitat in the surrounding landscape) was almost always the strongest correlate of biodiversity differences. The importance of natural habitat for maintaining biodiversity is well known at smaller scales (Carvalho et al., 2010; Kohler et al., 2007; Öckinger & Smith, 2007; Plath et al., 2021); however, its relative importance in comparison to other variables at the global scale has not been shown before. This finding highlights the biodiversity benefits of land-management strategies that integrate natural habitat within agricultural landscapes, such as agroforestry and certain elements of sustainable intensification (Garnett et al., 2013; Torralba

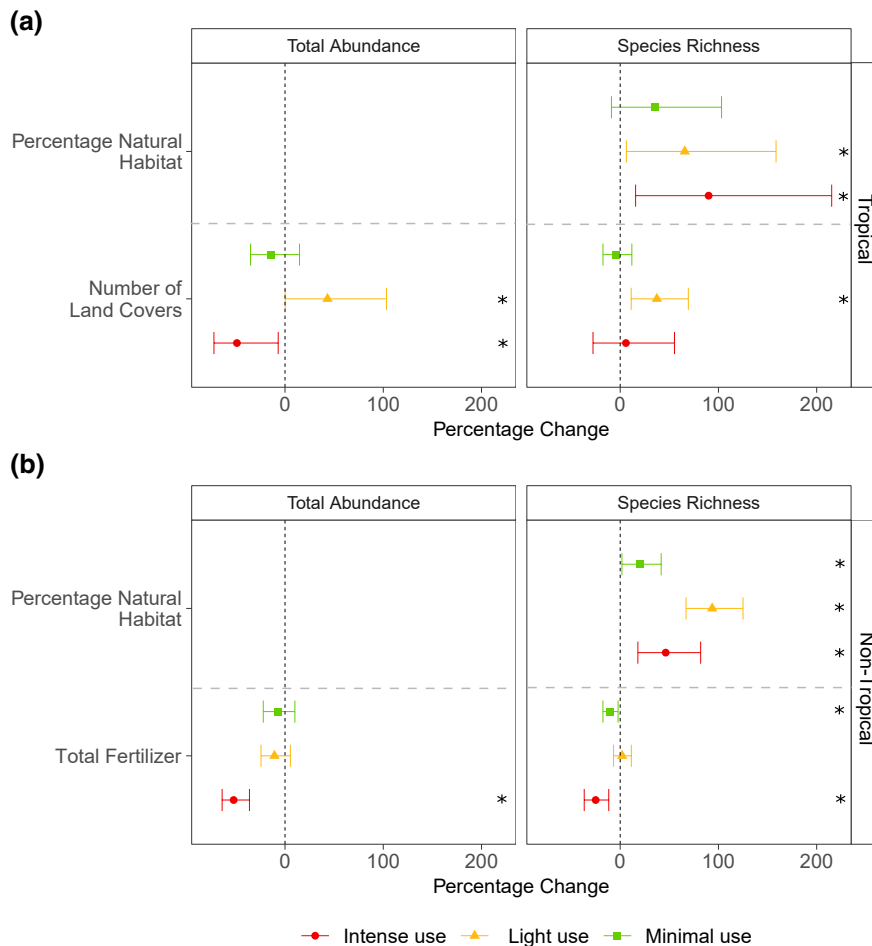


FIGURE 5 Percentage difference in model-estimated total abundance (left) and species richness (right) associated with variation in each of the landscape-scale variables in interaction with use intensity in (a) tropical and (b) non-tropical sites. Differences are shown for the range of values of each explanatory variable across the sites included in the analysis. Blank cells indicate that the interaction with use intensity was not selected as significant in the model-selection process (for final model structures, see Supporting Information Appendix S3). Non-focal explanatory variables were held constant: land use was set to “cropland”; and all continuous variables were set to the median value across sampled sites. Predicted biodiversity values were obtained by drawing 10,000 estimates at random based on the variance-covariance matrix. We present median values as points, while error bars represent the 95% confidence intervals of the model-estimated mean biodiversity difference (not prediction intervals). Asterisks indicate effects where the confidence intervals do not cross zero. Note that significance in this sense can differ from significance inferred by backward stepwise model selection, as presented in the text.

Biodiversity metric and realm	Conditional R^2	Marginal R^2	Proportion of residual variance explained by fixed effects
Species richness, tropical	0.62	0.01	0.03
Species richness, non-tropical	0.65	0.03	0.08
Total abundance, tropical	0.90	0.01	0.10
Total abundance, non-tropical	0.92	0.05	0.39

TABLE 2 Variation explained by biodiversity models

Notes: Shown here are the conditional and marginal pseudo- R^2 values, calculated according to the methods of Nakagawa and Schielzeth (2013), and the percentage of residual variance unexplained by the random effects that is explained by the fixed effects [i.e., $\text{marginal}/1 - (\text{conditional} - \text{marginal})$]. All values are shown to two decimal places. Marginal R^2 describes the variance explained by fixed effects only, whereas the conditional R^2 is the variance explained by both fixed and random effects.

et al., 2016). Distance to forest showed somewhat weaker effects in non-tropical regions, possibly because grasslands rather than forest are often more diverse in this region (Feurdean et al., 2018).

Homogeneity was also an important variable, and its relationship with biodiversity metrics differed between realms, with a positive relationship in the tropics and a negative relationship in the non-tropics. This difference might reflect the difficulty in differentiating, using remotely sensed data, between homogeneity of natural habitats, which might be beneficial for biodiversity, versus homogeneity of human-dominated land uses, which is more likely to be detrimental. With non-tropical regions having larger agricultural fields on average (Lesiv et al., 2019), particularly in the Northern Hemisphere, it is possible that increases in homogeneity in these areas reflect an increase in homogeneous human-dominated landscapes, whereas increases in homogeneity in the tropics are more likely to reflect increases in homogeneous natural vegetation. The relationships we observe might also reflect differences in the composition of communities between realms. The non-tropics have experienced a long history of human land-use conversion and intensification, which has resulted in the filtering out of many species that depend on natural habitats (Balmford, 1996; Le Provost et al., 2020; Sullivan et al., 2016). Indeed, generalist species have been shown to respond positively to landscape heterogeneity (Katayama et al., 2014; Redlich, Martin, Wende, et al., 2018), and differences in the levels of historical disturbance experienced have been shown to affect how species respond to habitat fragmentation (Betts et al., 2019).

The number of land-cover types had a generally weaker relationship with biodiversity, although significant relationships were negative. This was surprising, given that land-cover diversity has previously been shown to have a positive relationship with biodiversity (Redlich, Martin, Wende, et al., 2018). However, with the measure of land-cover diversity we used here, we were unable to distinguish between the number of natural land-cover types within a landscape, which is likely to be beneficial for biodiversity, and an increase in agricultural land cover, leading to a reduction of nearby natural habitat, which is likely to have a negative impact. Indeed, six of the 12 land-cover types considered represent human-dominated areas (Kehoe et al., 2017).

Differences in biodiversity responses between realms and across multiple landscape variables are not often considered within research. The divergent responses to landscape-scale habitat and land management that we show here might help to explain results seen in previous studies showing that tropical and Mediterranean biodiversity respond more strongly to changes in land use than biodiversity in other terrestrial areas (Martins & Pereira, 2017; Newbold et al., 2020) and highlight the importance of investigating differences between tropical and non-tropical regions.

4.1 | Scale issues

Fertilizer application had relatively strong associations with biodiversity; however, the direction of the association differed

between tropical and non-tropical regions. Also, differences were seen only at very low levels of fertilizer application (Supporting Information Figure S5.13). It is important to note that the fertilizer estimates used here are at a very coarse spatial scale (c. 100 km² grid cells). Biodiversity responses would be likely to differ if fertilizer application was measured at the fine scales at which species experience the impacts of chemical pollutants. The fact that the thematically coarse but spatially specific measure of land-use intensity captured within the PREDICTS database retains a good deal of explanatory power could indicate that a broad suite of local land-use intensity factors (for many of which there are no global maps) are more relevant than landscape-level fertilizer application for the measures of biodiversity considered here. There is a clear need for fine-resolution but large-extent data on land-use intensity for better integration of this important driver of biodiversity change (Dullinger et al., 2021).

This issue of scale might also apply to the other landscape characteristics assessed. It is possible that if alternative spatial scales were considered, the observed relationships with biodiversity might change. It is also likely that different taxonomic groups respond at different spatial scales. For example, birds will be likely to respond to changes in landscapes across larger scales than, for example, insects (Gonthier et al., 2014). Nevertheless, despite the coarse grain of the landscape-scale variables we included in our analysis, biodiversity varied more strongly with these variables than with local measures of land use or land-use intensity.

4.2 | Limitations

As a global-scale assessment of biodiversity responses, our study inevitably had limitations. First, given that this analysis looks at differences in biodiversity across space, we cannot infer how biodiversity has changed over time. Second, the biodiversity data in the PREDICTS database, as with all biodiversity data, are biased in several ways. For example, rare species might be undersampled owing to their lower detectability in comparison to more common species. This bias will probably be more pronounced in tropical regions, where data are sparser. Third, other factors besides those we considered might play important roles in moderating biodiversity, and the inclusion of additional factors will be likely to improve the amount of biodiversity variation the models are able to explain. Field size and pesticide applications have been shown to be important in previous small-scale studies (Fahrig et al., 2015; Geiger et al., 2010; Ricciardi et al., 2021). At the time of analysis, global maps of these factors were not available, but new maps have recently been developed (e.g., Lesiv et al., 2019; Maggi et al., 2019). Fourth, the role of natural habitat within the landscape is likely to be driven by a complex interaction of the proximity, size and density of forest patches. For the purposes of this analysis, we used one simple measure of proximity to dense forest, including a fixed threshold for what was considered "dense". Likewise, alternative natural habitat types, such as semi-natural grassland, are also likely

to have a role, as indicated by the importance of natural habitat explored here. However, our focus on forest biomes should ensure that we are detecting the effect of the main sources of natural habitat in this system. Future work should investigate additional factors as our understanding and the availability of data improve.

5 | CONCLUSIONS

The increasing need to expand and intensify cropland systems is going to place biodiversity under greater threat as the human population continues to increase (Kehoe et al., 2017; Zabel et al., 2019). Our results highlight that the availability of natural habitat, in both tropical and non-tropical regions, is likely to play an important role in maintaining biodiversity within cropland systems. The integration of natural habitat into cropland systems should be prioritized in future land-use planning, although differences in patterns between tropical and non-tropical realms show the need for locally specific measures.

ACKNOWLEDGMENTS

This work was supported by a UK Natural Environment Research Council (NERC) grant (NE/R010811/1), a NERC Independent Research Fellowship to C.D. (NE/N01524X/1) and a Royal Society University Research Fellowship to T.N.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Input dataset is available via Figshare <https://doi.org/10.6084/m9.figshare.19649688.v1>. Code to carry out the analyses presented in this paper is available from GitHub: https://github.com/CharlotteOuthwaite/PREDICTS_landscape_variables.

ORCID

Charlotte L. Outhwaite  <https://orcid.org/0000-0001-9997-6780>

REFERENCES

- Balmford, A. (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, 11, 193–196.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Bellemare, M. F., & Wichman, C. J. (2020). Elasticities and the inverse hyperbolic sine transformation. *Oxford Bulletin of Economics and Statistics*, 82, 50–61.
- Betts, M. G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D. B., Barlow, J., Eigenbrod, F., Faria, D., Fletcher, R. J., Hadley, A. S., Hawes, J. E., Holt, R. D., Klingbeil, B., Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Melles, S. L., ... Ewers, R. M. (2019). Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*, 366, 1236–1239.
- Carvalho, L. G., Seymour, C. L., Veldtman, R., & Nicolson, S. W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, 47, 810–820.
- Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, 8, 148–159.
- Crouzeilles, R., & Curran, M. (2016). Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *Journal of Applied Ecology*, 53, 440–448.
- Dainese, M., Luna, D. I., Sitzia, T., & Marini, L. (2015). Testing scale-dependent effects of seminatural habitats on farmland biodiversity. *Ecological Applications*, 25, 1681–1690.
- Dullinger, I., Essl, F., Moser, D., Erb, K., Haberl, H., & Dullinger, S. (2021). Biodiversity models need to represent land-use intensity more comprehensively. *Global Ecology and Biogeography*, 30, 924–932.
- Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, 118, e2023483118.
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K. F., Mitchell, S., & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, 200, 219–234.
- Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biological Conservation*, 228, 224–232.
- Garibaldi, L. A., Gemmill-Herren, B., D'Annolfo, R., Graeb, B. E., Cunningham, S. A., & Breeze, T. D. (2017). Farming approaches for greater biodiversity, livelihoods, and food security. *Trends in Ecology & Evolution*, 32, 68–80.
- Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., ... Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14, 1062–1072.
- Garnett, T., Appleby, M. C., Balmford, A., Bateman, I. J., Benton, T. G., Bloomer, P., Burlingame, B., Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P. K., Toulmin, C., Vermeulen, S. J., & Godfray, H. C. J. (2013). Sustainable intensification in agriculture: Premises and policies. *Science*, 341, 33–34.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L. W., Dennis, C., Palmer, C., Oñate, J. J., ... Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11, 97–105.
- Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H. Y., Iverson, A. L., Batáry, P., Rudolphi, J., Tschardtke, T., Cardinale, B. J., & Perfecto, I. (2014). Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141358.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853.
- Hijmans, R. J. (2018). *raster: Geographic data analysis and modeling*. R package version 2.8-4. <https://CRAN.R-project.org/package=raster>
- Hoskins, A. J., Bush, A., Gilmore, J., Harwood, T., Hudson, L. N., Ware, C., Williams, K. J., & Ferrier, S. (2016). Downscaling land-use data to provide global 30" estimates of five land-use classes. *Ecology and Evolution*, 6, 3040–3055.

- Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Alhusseini, T. I., Bedford, F. E., Bennett, D. J., Booth, H., Burton, V. J., Chng, C. W. T., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londoño, S., Emerson, S. R., Gao, D., ... Purvis, A. (2017). The database of the PREDICTS (projecting responses of ecological diversity in changing terrestrial systems) project. *Ecology and Evolution*, 7, 145–188.
- Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A., Phillips, H.R.P., Alhusseini, T.I., Bedford, F.E., Bennett, D.J., Booth, H., Burton, V.J., Chng, C.W.T., Choimes, A., Correia, D.L.P., Day, J., Echeverría-Londoño, S., Emerson, S.R., Gao, D., Garon, M., ... Purvis, A. (2016). *Dataset: The 2016 release of the PREDICTS database*. Natural History Museum data Portal (data.nhm.ac.uk). <https://doi.org/10.5519/0066354>
- Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Senior, R. A., Bennett, D. J., Booth, H., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londoño, S., Garon, M., Harrison, M. L. K., Ingram, D. J., Jung, M., Kemp, V., ... Purvis, A. (2014). The PREDICTS database: A global database of how local terrestrial biodiversity responds to human impacts. *Ecology and Evolution*, 4(24), 4701–4735.
- Katayama, N., Amano, T., Naoe, S., Yamakita, T., Komatsu, I., Takagawa, S., Sato, N., Ueta, M., & Miyashita, T. (2014). Landscape heterogeneity–biodiversity relationship: Effect of range size. *PLoS One*, 9, e93359.
- Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., & Kueemmerle, T. (2017). Biodiversity at risk under future cropland expansion and intensification. *Nature Ecology & Evolution*, 1, 1129–1135.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E. J., Tscharrntke, T., & Verhulst, J. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 276, 903–909.
- Kohler, F., Verhulst, J., Van Klink, R., & Kleijn, D. (2007). At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *Journal of Applied Ecology*, 45, 753–762.
- Le Provost, G., Badenhausser, I., Le Bagousse-Pinguet, Y., Clough, Y., Henckel, L., Violle, C., Bretagnolle, V., Roncoroni, M., Manning, P., & Gross, N. (2020). Land-use history impacts functional diversity across multiple trophic groups. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 1573–1579.
- Lesiv, M., Laso Bayas, J. C., See, L., Duerauer, M., Dahlia, D., Durando, N., Hazarika, R., Kumar Sahariah, P., Vakolyuk, M., Blyshchuk, V., Bilous, A., Perez-Hoyos, A., Gengler, S., Prestele, R., Bilous, S., Akhtar, I. U. H., Singha, K., Choudhury, S. B., Chetri, T., ... Fritz, S. (2019). Estimating the global distribution of field size using crowdsourcing. *Global Change Biology*, 25, 174–186.
- Maggi, F., Tang, F. H. M., la Cecilia, D., & McBratney, A. (2019). PEST-CHEMGRIDS, global gridded maps of the top 20 crop-specific pesticide application rates from 2015 to 2025. *Scientific Data*, 6, 170.
- Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., ... Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22, 1083–1094.
- Martins, I. S., & Pereira, H. M. (2017). Improving extinction projections across scales and habitats using the countryside species-area relationship. *Scientific Reports*, 7, 1–7.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, 536, 143–145.
- Mehrabi, Z., Ellis, E. C., & Ramankutty, N. (2018). The challenge of feeding the world while conserving half the planet. *Nature Sustainability*, 1, 409–412.
- Millard, J., Outhwaite, C. L., Kinnersley, R., Freeman, R., Gregory, R. D., Adedaja, O., Gavini, S., Kioko, E., Kuhlmann, M., Ollerton, J., Ren, Z.-X., & Newbold, T. (2021). Global effects of land-use intensity on local pollinator biodiversity. *Nature Communications*, 12, 2902.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Biodiversity synthesis*. World Resources Institute, Washington, DC.
- Monfreda, C., Ramankutty, N., & Foley, J. A. (2008). Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles*, 22, n/a–n/a.
- Mueller, N. D., Gerber, J. S., Johnston, M., Ray, D. K., Ramankutty, N., & Foley, J. A. (2012). Closing yield gaps through nutrient and water management. *Nature*, 490, 254.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Gray, C. L., Scharlemann, J. P. W., Börger, L., Phillips, H. R. P., Sheil, D., Lysenko, I., & Purvis, A. (2016). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, 39, 1151–1163.
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverría-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.
- Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology & Evolution*, 4(12), 1630–1638.
- Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44, 50–59.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience*, 51, 933.
- Plath, E., Rischen, T., Mohr, T., & Fischer, K. (2021). Biodiversity in agricultural landscapes: Grassy field margins and semi-natural fragments both foster spider diversity and body size. *Agriculture, Ecosystems & Environment*, 316, 107457.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353.
- R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Redlich, S., Martin, E. A., & Steffan-Dewenter, I. (2018). Landscape-level crop diversity benefits biological pest control. *Journal of Applied Ecology*, 55, 2419–2428.
- Redlich, S., Martin, E. A., Wende, B., & Steffan-Dewenter, I. (2018). Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLoS One*, 13, e0200438.
- Ricciardi, V., Mehrabi, Z., Wittman, H., James, D., & Ramankutty, N. (2021). Higher yields and more biodiversity on smaller farms. *Nature Sustainability*, 4, 651–657.
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng, A., Potts, S. G., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, 11, 499–515.

- Rigby, R. A., Stasinopoulos, D. M., & Akantziliotou, C. (2008). A framework for modelling overdispersed count data, including the Poisson-shifted generalized inverse gaussian distribution. *Computational Statistics & Data Analysis*, *53*, 381–393.
- Spooner, F. E. B., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*, *24*, 4521–4531.
- Sullivan, M. J. P., Newson, S. E., & Pearce-Higgins, J. W. (2016). Changing densities of generalist species underlie apparent homogenization of UKbird communities. *Ibis*, *158*, 645–655.
- Torralba, M., Fagerholm, N., Burgess, P. J., Moreno, G., & Plieninger, T. (2016). Do European agroforestry systems enhance biodiversity and ecosystem services? A meta-analysis. *Agriculture, Ecosystems and Environment*, *230*, 150–161.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity—Ecosystem service management. *Ecology Letters*, *8*, 857–874.
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biological Reviews*, *87*, 661–685.
- Tuanmu, M. N., & Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, *24*, 1329–1339.
- Watling, J. I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L. M., Fang, R., Hamel-Leigues, A. C., Lachat, T., Leal, I. R., Lens, L., Possingham, H. P., Raheem, D. C., Ribeiro, D. B., Slade, E. M., Urbina-Cardona, J. N., Wood, E. M., & Fahrig, L. (2020). Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecology Letters*, *23*, 674–681.
- West, P. C., Gerber, J. S., Engstrom, P. M., Mueller, N. D., Brauman, K. A., Carlson, K. M., Cassidy, E. S., Johnston, M., MacDonald, G. K., Ray, D. K., & Siebert, S. (2014). Leverage points for improving global food security and the environment. *Science*, *345*, 325–328.
- Williams, J. J., Freeman, R., Spooner, F., & Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology*, *28*, 797–815.
- Zabel, F., Delzeit, R., Schneider, J. M., Seppelt, R., Mauser, W., & Václavík, T. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*, *10*, 2844.

BIOSKETCH

All authors are contributors to the BIOTA project (www.biota-ucl.org), a NERC-funded project that is focused on determining the interactions, trade-offs and synergies between biodiversity, food production and trade globally.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Outhwaite, C. L., Ortiz, A. M. D., Spooner, F. E. B., Dalin, C., & Newbold, T. (2022). Availability and proximity of natural habitat influence cropland biodiversity in forest biomes globally. *Global Ecology and Biogeography*, *31*, 1589–1602. <https://doi.org/10.1111/geb.13532>