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Effects of land use and soil properties on taxon richness and abundance of soil assemblages

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Abstract

Land-use change and habitat degradation are among the biggest drivers of aboveground biodiversity worldwide but their effects on soil biodiversity are less well known, despite the importance of soil organisms in developing soil structure, nutrient cycling and water drainage. Combining a global compilation of biodiversity data from soil assemblages collated as part of the PREDICTS project with global data on soil characteristics, we modelled how taxon richness and total abundance of soil organisms have responded to land use. We also estimated the global Biodiversity Intactness Index (BII)—the average abundance and compositional similarity of taxa that remain in an area, compared to a minimally impacted baseline, for soil biodiversity. This is the first time the BII has been calculated for soil biodiversity. Relative to undisturbed vegetation, soil organism total abundance and taxon richness were reduced in all land uses except pasture. Soil properties mediated the response of soil biota, but not in a consistent way across land uses. The global soil BII in cropland is, on average, a third of that originally present. However, in grazed sites the decline is less severe. The BII of secondary vegetation depends on age, with sites with younger growth showing a lower BII than mature vegetation. We conclude that land-use change has reduced local soil biodiversity worldwide, and this further supports the proposition that soil biota should be considered explicitly when using global models to estimate the state of biodiversity.

KEYWORDS

belowground biodiversity, Biodiversity Intactness Index, community composition, global, use intensity

1 | INTRODUCTION

Although there has been increasing work on the patterns of soil biodiversity, these studies tend to be delimited by taxonomy (Guerra, Bardgett, et al., 2021; Guerra, Delgado-Baquerizo, et al., 2021; Phillips et al., 2019; Tedersoo et al., 2014; van den Hoogen et al., 2019), size (e.g., macrofauna—Lavelle et al., 2022) or region (Burkhardt et al., 2014). Global syntheses of biodiversity loss are still based mostly on aboveground biodiversity (Phillips et al., 2017), despite soil communities showing different responses (Burton et al., 2022; Cameron et al., 2019) and their importance for ecosystem functioning and human well-being (FAO et al., 2020). Land-use change has been highlighted as among the most important recent drivers (Díaz et al., 2019; Jaureguiberry et al., 2022) of biodiversity loss but its global effect on soil communities has not been well assessed. Both species diversity and overall organismal abundance can influence ecosystem functionality, for example, reducing decomposer diversity can slow decomposition (Hooper et al., 2012), while higher earthworm density can increase both plant productivity (van Groenigen et al., 2014) and soil water infiltration (Andriuzzi et al., 2015).

Converting natural ecosystems to production landscapes often reduces numbers of species of soil organisms found in ecological samples (henceforth, taxon richness) across a range of taxa including ants, scarab beetles and termites (Alroy, 2017; Luke et al., 2014). One possible mechanism is a reduction in micro-habitat diversity, given that habitat heterogeneity apparently promotes soil biota diversity (Burton & Eggleton, 2016; Ettema & Wardle, 2002; Frouz et al., 2011). The higher leaf-litter input in forested sites, whether natural or planted, compared with grassland and agricultural sites, provides both a food source and habitat, and the more closed canopy of such sites mitigates microclimatic extremes (Martius et al., 2004). Sites in more homogeneous, open land uses where the canopy has been removed (i.e., most agriculture) are therefore expected to host fewer soil species than nearby forested sites (Lavelle et al., 2022), especially if they are subjected to practices that physically affect the soil, such as tillage (Briones & Schmidt, 2017; Tsiafouli et al., 2015).

The impacts of land-use change on soil biodiversity may vary depending on physicochemical properties of the soil, as these have a strong influence on the assemblages living on and in the soil. pH is known to be one of the strongest drivers of soil animal communities (Johnston & Sibly, 2020). A neutral to alkaline pH, common in agricultural landscapes, tends to favour bacteria-based communities over fungal ones (Frey et al., 2004; Manning, 2012), so it is likely to enhance the diversity and abundance of bacterial feeders such as earthworms (Decaëns, 2010). By contrast, systems such as forests where pH is typically slightly acidic and nitrogen content is low tend to have higher fungal (especially mycorrhizal) diversity, and support more litter-feeding arthropods (Manning, 2012). Soil organisms are generally less abundant where total soil organic carbon is low, including where it has been removed by intensive agriculture (Blakemore, 2018), although the quality of the organic matter and physical availability are also important (Le Couteulx et al., 2015; Schmidt et al., 2011), but global data on these properties are lacking. Soil compaction, reflected in bulk density, reduces both the abundance and species richness of a wide range of soil taxa (Blasi et al., 2013; Larsen et al., 2004; Röhrig et al., 1998). The effect of soil texture is harder to predict; soils with a high proportion of clay particles generally have better water and nutrient, retention than soils with a high sand content (Coleman et al., 2001), which could mitigate the drying effect of conversion to agriculture, but clay soils also have high bulk density so are more prone to compaction. However, soil texture is less coupled to land use as, unlike pH, organic carbon content and bulk density, it is not affected by soil management.

Highlights

- Land-use change is an important driver of biodiversity loss, but soil communities are understudied.
- We modelled how soil biota responds to land use and soil properties using global databases.
- Globally, local soil biodiversity is reduced in all land uses compared with an undisturbed baseline.
- Soil biota should be included in biodiversity frameworks to ensure targets are also met belowground.

Here, we combine global data on soil characteristics (Hengl et al., 2017) with biodiversity data from soil and epigean assemblages in different land uses worldwide to test two main hypotheses: (1) conversion to human-dominated land use reduces the abundance and taxon richness of soil biota; and (2) some or all the physicochemical properties of soil outlined above mediate these effects. Because taxon richness might not reflect all types of biodiversity impacts, for example, species lost may be replaced by others (Hillebrand et al., 2018; Stork et al., 2017), we also model how land use affects compositional similarity (Baselga, 2013) and thereby estimate the Biodiversity Intactness Index (BII) (De Palma, Hoskins, et al., 2021; De Palma, Sanchez-Ortiz, et al., 2021; Scholes & Biggs, 2005) for soil biodiversity for the first time. The BII is a measure of the average state of local biodiversity relative to an unimpacted baseline condition (Scholes & Biggs, 2005). The Index shows how local biodiversity responds to human pressures such as land use, combining abundance and community similarity data for a wide range of animals, plants and fungi. It is one of the two measures of biodiversity included in the Planetary Boundaries Framework (Steffen et al., 2015), and unlike most indicators can be modelled under future scenarios. The first global estimate of terrestrial BII, which used data overwhelmingly from aboveground assemblages, found it had already fallen below the proposed 'safe limit' of 90% (Newbold et al., 2016); we assess whether biotic integrity has been similarly eroded in soil assemblages.

2 | MATERIALS AND METHODS

2.1 | Soil assemblage data

Given there is no well-developed catalogue or official definition of global soil biodiversity (Orgiazzi, 2021; Ramirez et al., 2015), we extracted surveys from the PREDICTS database (Hudson et al., 2014) as of 5 July 2022 that sampled communities within the soil, at the soil surface or in the leaf litter. The PREDICTS database is a global compilation of biodiversity survey data, each of which made spatial comparisons between ecological assemblages at multiple sampling points facing different land use and related pressures. We rely on the accuracy of the data provided by authors, including taxon identifications, but most sources are from peer-reviewed papers. The database uses a tiered data structure, the highest level being sources, which typically represent a single paper. Each source contains one or more studies, defined as data collected using the same sampling method. Each study may or may not be split into spatial blocks but will always have two or more sites at which biodiversity was sampled. For further detail on the structure, construction and data cleaning of the database see Hudson et al., 2014.

2.2 | Site-level explanatory variables

Each site had already been classified into one of six land-use classes based on Hurtt et al. (2011): primary vegetation (land with no evidence of vegetation destruction), secondary vegetation (recovering after destruction of primary vegetation), plantation forest (trees planted for fruit or timber in previously cleared areas), cropland (land planted with herbaceous crops), pasture (land where livestock is grazed regularly or permanently) and urban (areas of human habitation). Sites were also classified into one of three use-intensity classes: minimal (disturbance minor and/or limited in scope), light (moderate disturbance e.g., selective logging, medium intensity farming, pasture with significant inputs or high-stock density) or intense (recent clear felling, high-intensity monoculture farming, pasture with significant inputs and stock density) based on descriptions of the habitat and its management in the original paper (see Hudson et al., 2014 for details of use intensity classifications). For the models estimating the BII we used Land Use Harmonisation 2 classes (Hurtt et al., 2020), to permit future work to project BII over time and future land-use scenarios. Site-specific soil properties were insufficiently reported in the original papers, so instead six soil properties (percentage clay, silt, sand, pH in water, soil organic carbon [SOC] and bulk density) widely reported to influence soil biodiversity were obtained from the SoilGrids250m database (Hengl et al., 2017) for the geographic coordinates of each biodiversity sample. SoilGrids provides global predictions for soil properties at seven depths using machine learning methods based on remote sensed soil covariates and a training data set of soil profiles. The weighted mean of soil properties at depths 0–5 cm and 5–15 cm was used in modelling as no biodiversity data sources sampled deeper than 15 cm. Because collinearity was likely, generalised variance inflation factors (GVIFs) were calculated (Zuur et al., 2009) before modelling began. Among the soil-texture variables, the percentage of clay had the lowest GVIF so was preferred to silt and sand; all remaining variables had GVIFs below five. Soil properties were scaled and centred before modelling. All analyses were carried out in R version 4.2.0 (R Core Team, 2022).

2.3 | Model construction

We used mixed-effects models (as implemented in *lme4* version 1.1.29; Bates et al., 2015) to accommodate the heterogeneity arising from the wide range of sampling methods, temporal differences and macroecological gradients among the studies in the PREDICTS database. The most complex fixed-effects structure we considered included land use and intensity as main effects, the four soil properties as linear main effects and each soil property's interaction with land use. The most complex random-effects structure tested included Spatial Block (SSB) nested within Study (SS) as random intercepts, and random slopes, with respect to SS, of each soil property and land use intensity. Akaike's Information Criterion (AIC) values were compared among models in order to select the optimal random-effects structure. This comparison was conducted across a set of models, each with the different possible random-effects structure, while maintaining the maximal fixed-effects structure. Thus, the maximal model was:

$$\begin{aligned} Y_i = {} & \text{Land Use Intensity} + \text{pH} + \text{clay}_{\%} + \text{SOC} \\ & + \text{BulkDensity} + \text{pH} : \text{Land Use} + \text{clay}_{\%} : \text{Land Use} \\ & + \text{SOC} : \text{Land Use} + \text{BulkDensity} \\ & : \text{Land Use} + (1 + \text{SS}|\text{SSB}), \end{aligned}$$

where Y_i was either taxonomic richness or total abundance (described below). Fixed effects were selected using backwards stepwise selection with likelihood-ratio tests; interaction terms were tested first, and the significance of terms was assessed using Type III Wald Tests with Satterthwaite's method using *lmerTest* (Kuznetsova et al., 2015) and were removed when $p > 0.05$. Main effects were removed when $p > 0.05$ unless they were part of significant interaction terms.

2.4 | Taxon-richness model

Within-sample richness was calculated as the number of differently named taxa at each site. Taxon richness at each site was then $\log(x + 1)$ transformed and modelled with a Gaussian error structure, as models with quasi-poisson errors (Rigby et al., 2008) did not converge.

2.5 | Abundance model

Total organismal abundance at each site was the sum of the abundances of all taxa sampled. In a small minority of studies, sampling effort varied among sites and abundances were reported in effort-sensitive metrics (e.g., counts, rather than counts per unit effort). When this occurred, we rescaled the abundances by the sampling effort to make all abundance values comparable within the study. Note that such corrections do not make values directly comparable among different studies, because they reported sampling effort in different units; the study-level random intercept accommodates this heterogeneity. Finally, total abundance values were rescaled within each study; this was done by dividing each site's total abundance by the maximum abundance found across all sites within the study, resulting in sites within each study varying between 0 and 1. To reduce among-study heterogeneity and thereby aid with model convergence, rescaled abundance was square-root transformed before modelling with Gaussian errors. Modelling then proceeded as with species-richness.

2.6 | Compositional similarity model

Many changes in ecological assemblages can be missed by metrics such as species richness and overall abundance (Hillebrand et al., 2018). To capture such changes, we also modelled how land use affects compositional similarity compared with a natural assemblage, which also was part of the process for estimating the BII. In the absence of historical baseline data on soil biodiversity, we used the community composition of Primary Vegetation as a proxy for the baseline condition. Within each study, we calculated a measure of compositional similarity between each baseline site and each other site in turn, using the *bray.part* function in the *betapart* package (Baselga, 2013). Simply, for each pairwise comparison of sites, the following equation was used:

$$d_{\mathrm{BC\_bal}} = 1 - \frac{\min(B,C)}{A + \min(B,C)},$$

where

$$A = \sum \min(x_{ij}, x_{ik}),$$

$$B = \sum ij - \min(x_{ij}, x_{ik}),$$

$$C = \sum ik - \min(x_{ij}, x_{ik}),$$

where x_{ij} is the abundance of species i at site j, and x_{ik} is the abundance of species i at site k (Baselga., 2013). $d_{\mathrm{BC\text{-}bal}}$ is the balanced variation component of the (corrected) abundance-based Bray–Curtis dissimilarity metric (Baselga, 2013); this measure can most easily be visualised as the overlap in the species abundance distribution between the two sites being compared. If either site in the comparison had no individuals, compositional similarity was set as 0. Because compositional similarity is biased upwards in data sets having poor taxonomic resolution, we included a study-level measure of taxonomic resolution in the model. Briefly, within each study, each taxon's resolution was scored on a 5-point scale (0 = above Order; 1 = above Family; 2 = above Genus; 3 = above Species; 4 = Species-level), taxonomic imprecision was then calculated as 4—taxonomic precision (given that 4 is the maximum value for precision) and included as an additive fixed effect. Mean taxonomic precision was similar in each land use transition (Table S3).

Because compositional similarity is calculated pairwise, it can be affected by imbalances in study size. To prevent large studies from having too much influence in the analysis, the data were thinned so that each study contributed no more than 1% of the total data. Site weights were calculated by land-use type and site identity so that less frequent land uses or sites were given greater weight. All sites from studies that made up less than 1% of the data set were kept. Where studies contributed more than 1% of the data set, the contribution was capped at 1% by taking a random sample of sites within that study, weighted by land-use type and site identity. Compositional similarity was logit transformed (*car* package, version 2.1-61; John et al., 2020 prior to analysis; an adjustment of 0.01 was used to account for values of 0 and 1).

To account for decays in compositional similarity with geographic distance between sites we included geographic distance (log transformed), divided by the average size of a sampling plot in the data set. We also accounted for the decay in compositional similarity with environmental distances and soil-property distance. These were calculated as Gower's dissimilarity (cube-root transformed) using the *gower* package (van der Loo, 2022) based on three WorldClim (Fick & Hijmans, 2017) variables, minimum temperature of the coldest month, precipitation of the wettest month and precipitation of the driest month, as well as elevation and the four soil-property variables. These variables were gathered using the site's geographic coordinates. Climatic information could have been incorporated in a more detailed and granular way, for example, by including the temperature and rainfall immediately prior to sampling, but sampling dates were not always sufficiently precise for this. The land-use contrast between the two sites (e.g., primary vegetation—primary vegetation, or primary vegetation—cropland) was included as a fixed effect along with its interactions with the continuous variables. We included Study as a random intercept and assessed whether a random slope was supported by using the same framework as the earlier models, choosing the random structure with the lowest AIC value among the models that converged successfully; the identity of the second site (S_2) was also included as a random intercept to remove the pseudoreplication that would otherwise arise from comparing each baseline site to every other site within the study. Backwards stepwise model simplification was performed to simplify the fixed effects structure of the model fit using Maximum Likelihood. The final model was:

$$\begin{aligned}\text{Compositional Similarity} = {} & \text{Land Use Contrast} \\ & + \text{Gower's Dissimilarity (climate)} \\ & + \text{Geographic distance} \\ & + \text{Gower's Dissimilarity (soil)} \\ & + \text{Taxonomic Imprecision} \\ & + (1|S_2) + (1|\text{SS}).\end{aligned}$$

2.7 | Biodiversity Intactness Index

For total abundance, the modelled responses were back-transformed (squared) and expressed relative to the modelled estimate of a baseline of Primary Vegetation. For compositional similarity, the modelled responses were back-transformed (inverse-logit) and expressed relative to the modelled estimate for the baseline, that is, the compositional similarity between two Primary Vegetation sites, with the same geographic distance, environment and soil properties (i.e., zero environmental distance between the sites). We then multiplied these back-transformed and relative abundance and compositional similarity values together to calculate the BII.

3 | RESULTS

The full data set used for analysis contained 5195 sites from 81 sources and 105 studies worldwide, representing 31 countries and 12 biomes. Around half the sites were sampled belowground, 40% at the soil surface and the rest from both strata (Table S1). The taxa included were primarily arthropods, fungi, nematodes and annelids (Figure 1). Sites were spread globally, although Africa, Oceania and Pacific Islands and some land-use types in Asia were deficient, and pasture and temperate biome sites were overrepresented (Table S2, Figures S1 and S2). Sites in the reduced data set used for the compositional similarity models were also spread globally, but only Europe, South America and Southeast Asia were well represented (Figure S4).

3.1 | Taxon richness model

Relative to assemblages in primary vegetation, soil assemblages were less diverse in secondary vegetation (except minimal use), plantation and cropland sites, but close to the baseline in pasture (Figure 2). Of the soil properties, all were retained as additive fixed effects and all except pH were retained as interactive effects with land use in the Minimally Adequate Model (Table 1). The interaction between land use and soil properties did not statistically differ been land uses (Figure S3).

3.2 | Abundance model

Relative to assemblages in primary vegetation, the overall abundance of soil biota is lower in secondary vegetation (except minimal use intensity), much lower in plantation light and intense sites, and cropland sites, but comparable to baseline levels in pasture (Figure 3). There was little difference in response to intensity, except for in light use plantation which showed the greatest decrease in diversity compared with the baseline. Soil organic carbon was the only soil property significant as an additive effect, but all soil properties except pH had significant interactions with land use (Table 1). The interaction between soil properties and land use was not significantly different for most land uses, except cropland showed different responses to other land-use types (Figure 4).

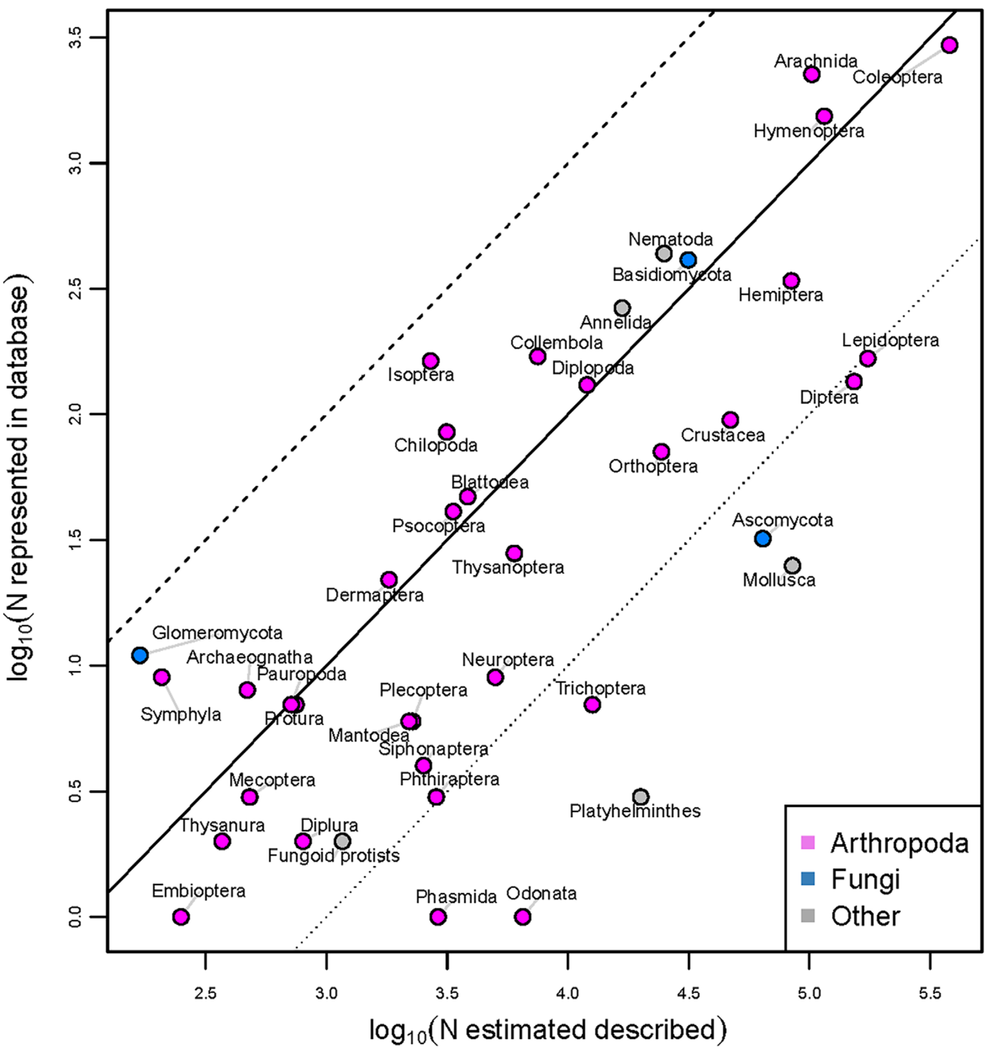

FIGURE 1 The number of species represented in our data and the number estimated to have been described (Chapman, 2009) on a logarithmic scale (base 10) for major taxonomic groups. Lines show (from bottom to top) 0.1%, 1% and 10% representation of described species in our data set; magenta, arthropods; blue, fungi and grey, other invertebrates. This figure is an update of Hudson et al. (2016), Figure 4, including only studies that sampled soil and leaf-litter communities.

3.3 | Biodiversity Intactness Index

In the abundance part of the soil BII all soil properties interacted significantly with land use. Soil organism total abundance was not significantly different from the baseline primary vegetation except for cropland (Figure S5). The compositional similarity part of BII was significantly reduced in all land uses, relative to primary vegetation, particularly in grazed and cropland sites (Figure S6). The soil BII in mature and intermediate vegetation was the same as the baseline of primary vegetation, with young secondary vegetation having a lower BII of 0.76, grazed sites had a BII of 0.59 and cropland sites 0.35.

4 | DISCUSSION

4.1 | Land use

The taxon richness of soil assemblages differed between land uses, but a decline was not seen in all human-dominated land uses compared with more natural ones as in hypothesis (1). The first global model of data in the PREDICTS database, which at that time was strongly biased towards aboveground assemblages, found that secondary vegetation approached primary vegetation in terms of both taxon richness and abundance (Newbold et al., 2015). By contrast, in our models of a greatly expanded set of solely soil assemblage data, taxon richness was markedly lower in secondary vegetation than in primary vegetation, except for minimally used secondary vegetation, which had a similar richness to primary vegetation (Figure 2). Two processes are likely to contribute to this effect. First, most soil organisms have low mobility and can require decades to recover from disturbance (Adl et al., 2006; Chang et al., 2017), so recovery may take longer than for other taxa. Second, secondary vegetation tends to be more open than primary vegetation, with warmer, drier microclimates (Chen et al., 1993; Didham & Lawton, 1999) that are consistently associated with reduced soil community diversity (Collison et al., 2013; Hamberg et al., 2008),

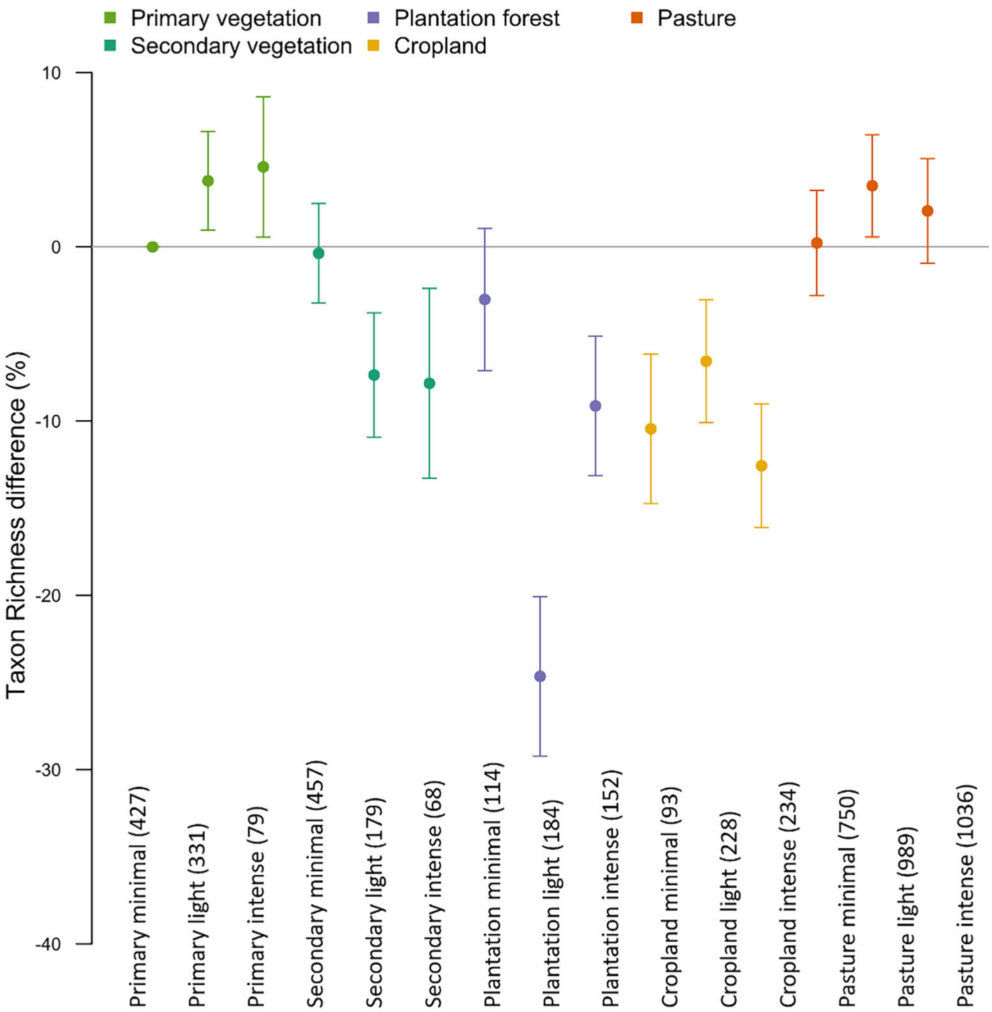

FIGURE 2 Response of (back-transformed) taxon richness to land-use type and intensity (from minimal—disturbance minor and/or limited in scope, light—moderate disturbance, to intense disturbance), relative to minimally used primary vegetation (shown here as a baseline). The effects are shown here with soil properties set to their median values. Error bars show 95% confidence intervals. Numbers in parentheses are the number of data points.

TABLE 1 ANOVA for minimally adequate model of taxon richness and abundance.

		Taxon richness		Abundance	
Term	**df**	***F* value**	***p*-value**	***F* value**	***p*-value**
Land use intensity	14	11.54	<0.001***	19.00	<0.001***
pH	1	2.35	0.13	1.48	0.23
Organic carbon	1	1.00	0.32	1.38	0.24
Clay %	1	4.07	0.04*	0.004	0.95
Bulk density	1	7.44	0.01**	8.25	0.004**
pH * Land use	4			7.84	<0.001***
Organic carbon * Land use	4	19.85	<0.001***	10.61	<0.001***
Clay % * Land use	4			7.98	<0.001***
Bulk density * Land use	4	4.54	0.002**	5.47	<0.001***

Note: Missing values indicate terms dropped from the models. Asterisks indicate the level of significance calculated using Type III Wald Tests with Satterthwaite's method: *≤0.05; **<0.01 and ***<0.001.

potentially limiting the extent of recovery that is possible.

In another strong contrast to the first global model of PREDICTS data, soil organisms in pasture attain similar taxon richness and abundance as in primary vegetation. This agrees with other studies that found high soil fauna biomass in temperate grasslands (Hedĕnec et al., 2022). Pastoral management practices cause less physical disruption of the soil structure than many arable farming practices (Aksoy et al., 2017). However, compositional

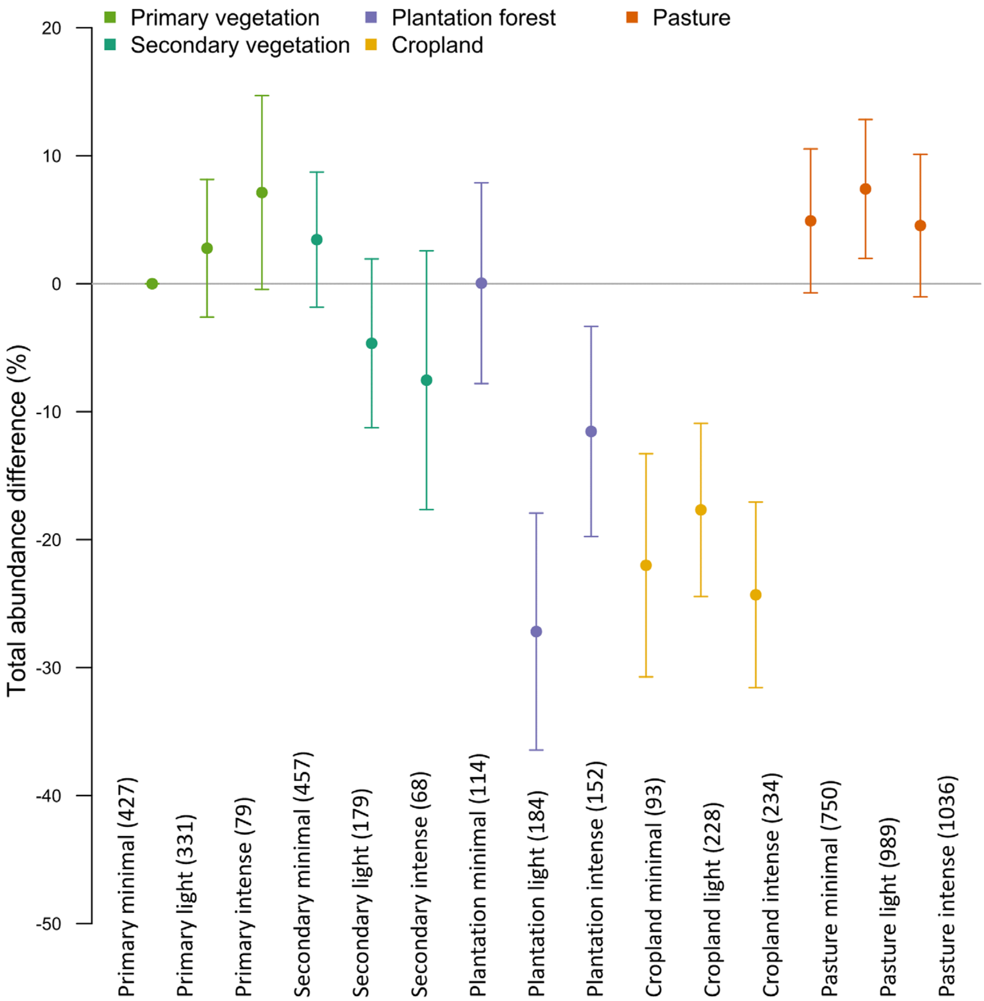

FIGURE 3 Response of (back-transformed) total organism abundance to land-use intensity (from minimal—disturbance minor and/or limited in scope, light—moderate disturbance, to intense disturbance), with minimally used primary vegetation used as a baseline for comparison. Land-use intensity effects are shown with soil properties set to their median values. Error bars show 95% confidence intervals. Numbers in parentheses are the number of data points.

similarity in grazed land uses was significantly lower than the baseline, comparable with cropland (Figure S6), so this could be driven by differences in response between taxonomic groups. In keeping with other studies (Lavelle et al., 2022), cropland sites had much lower abundance and taxon richness than matched sites in primary vegetation, consistent with evidence that the use of tillage, pesticides and fertilisers disturbs soil biodiversity (Kladivko, 2001; Postma-Blaauw et al., 2013; Tsiafouli et al., 2015). The similarly low abundance and taxon richness in all but minimally used plantation forest was more unexpected. The identity of tree species strongly influences quality and quantity of leaf litter (Muys & Lust, 1992; Neirynck et al., 2000; Reich et al., 2005), and most of the plantation sites in this data set are either from conifer plantations, which are known to acidify the soil (Alfredsson et al., 1998; Augusto et al., 1998) making it less hospitable to many soil organisms, or oil-palm, which has previously been shown to harbour a particularly low-species diversity (Phillips et al., 2017). Reduced vegetation density and richness of the understory in many plantations, especially in light and intense uses, may also lead to drier soils and lower quality and quantity leaf-litter input, and hence fewer soil animals (Cakir & Makineci, 2013; Collison et al., 2013).

The response of soil biodiversity to use intensity varies with land use but generally not statistically significantly. The decrease in soil biodiversity with increasing use intensity in secondary vegetation may reflect the increasing openness and warmer drier habitats with disturbance. For most land uses there was no clear pattern with either metric with use intensity, which probably reflects the qualitative nature of these classes. Future models could incorporate quantitative measures of intensity, for example, relative stocking density for grazed land (Piipponen et al., 2022) which may give more informative results.

4.2 | Soil properties

Supporting hypothesis (2), soil properties mediated the responses of both taxon richness and abundance of belowground assemblages to land use, but in variable

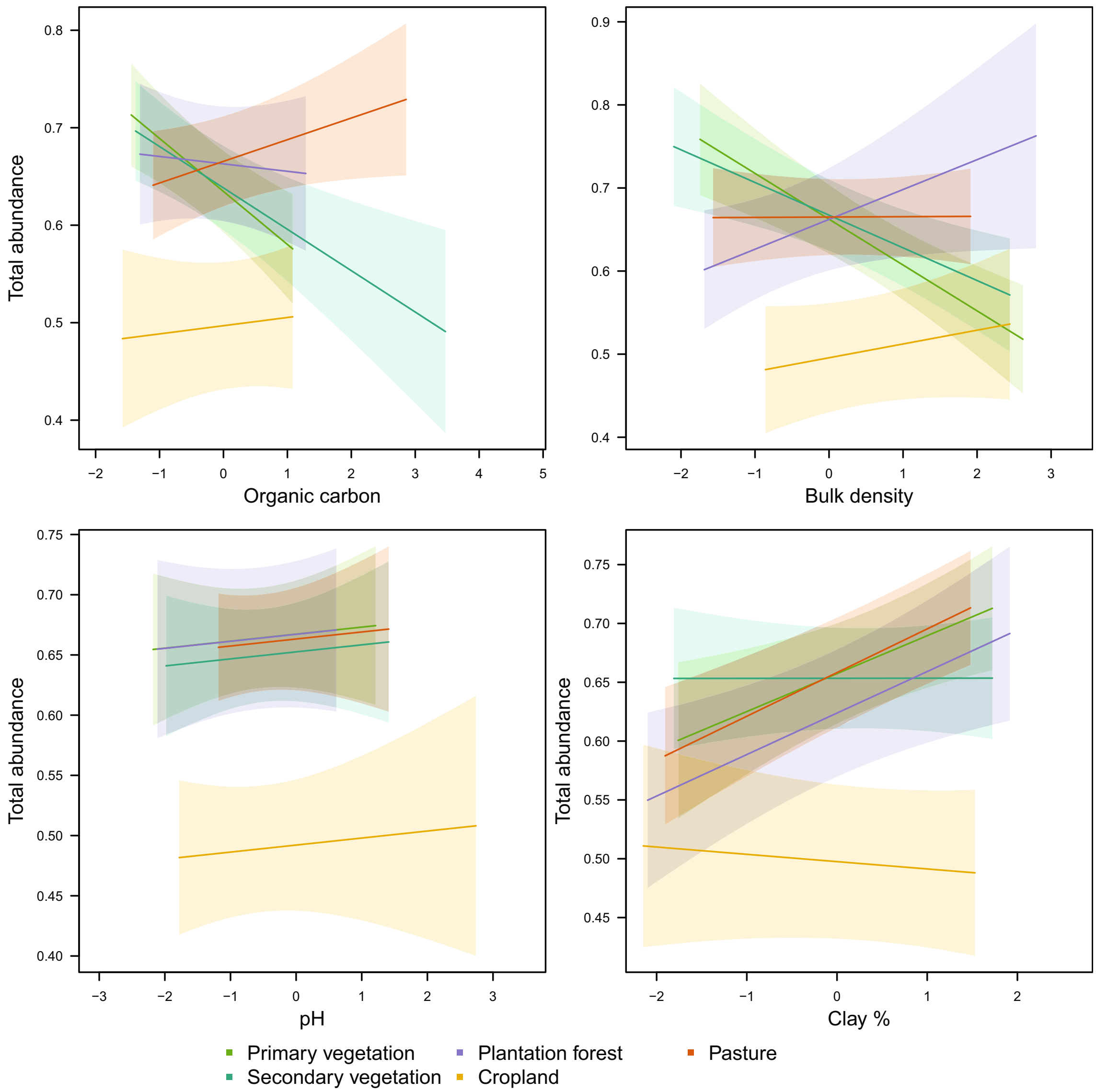

FIGURE 4 The (back-transformed) response of abundance to each of four (scaled) soil properties, in each of five land uses. These effects are shown with other fixed effects set to their median values. Colours represent land uses. Shading spans ±0.5 standard errors.

ways. Abundance increased with soil organic carbon in pasture sites, but not in other land uses. A positive relationship might be expected since organic carbon stimulates soil organism biomass production (Lavelle et al., 2006). As the effect was not seen on other land uses, we speculate that it was driven by competitive species (r-strategists), which thrive in high-nutrient, human-dominated land uses (Bongers & Bongers, 1998). Taxon richness was lower when organic carbon was higher for most land uses, except in pasture and cropland.

All land uses showed higher organismal abundance in clay-rich soils, perhaps because such soils are generally more nutrient-rich and retain water better (Coleman et al., 2001), resulting in an environment commonly preferred by many soil organisms (Jones & Eggleton, 2014; Nielsen et al., 2014). Taxon richness tended to decline with pH in all land uses. Taxon-specific effects of pH have often been reported, with a higher pH associated with higher abundances of earthworms (Edwards & Bohlen, 1996; Jones & Eggleton, 2014) and free-living nematodes (Mulder et al., 2005) which can have a negative effect on abundance and species richness of other soil organisms (Hågvar, 1990; Raty & Huhta, 2003). Such taxonomic differences and competitive effects may explain the inconsistencies seen.

Global syntheses inevitably hide taxonomic and regional patterns, with the goal of gaining generality to allow spatial and temporal projections and estimation of the status and trend of indicators. Biases are ubiquitous in biodiversity databases (Tydecks et al., 2018) and although this is one of the most taxonomically representative analysed so far, it still lacks data from certain taxonomic groups, regions and biomes. Notably, except for fungi, microorganisms are unrepresented, despite them being a major part of biodiversity in soils (Decaëns, 2010), and some meiofaunal groups may be underestimated. The data set is biased towards pasture and temperate ecosystems, and there was insufficient data to model the effects of urban land use on soil biodiversity. As with other data sets (Lavelle et al., 2022), dry habitats such as deserts are underrepresented. These data biases may propagate through to analytical results because species' responses to land use, use intensity and soil properties may vary due to their taxonomy, eco-morphology, other traits and biome (Decaëns, 2010; Lavelle et al., 2022; Mulder et al., 2005). Representativeness could be improved further by incorporating additional biodiversity data harmonised from other data sets (Burkhardt et al., 2014; Guerra, Bardgett, et al., 2021; Guerra, Delgado-Baquerizo, et al., 2021; Lavelle et al., 2022) and data collection efforts (Potapov et al., 2022). Although the mixed-effects methods used are robust to unbalanced data sets, further work to explore these differences, such as the use of taxonomic weights (McRae et al., 2017), or by level of adaptation to soil environments (e.g., eco-morphological index, EMI, Parisi et al., 2005; Yan et al., 2012), would be valuable.

Although the soil data we used has a nominal spatial resolution of 250 m, which is not very different from the typical spatial scale and proximity of the sites in the PREDICTS database (Newbold et al., 2015), they were interpolated from much sparser samples (Hengl et al., 2017); therefore, they may not accurately reflect the soil properties experienced by the biota at our sites. Furthermore, important soil properties including soil moisture and temperature were not included. Site-specific soil property data were available for some studies included in the analysis but were insufficient and too inconsistent to be included. These limitations may explain the unclear and sometimes unexpected relationships between soil properties and soil organism abundance and taxon richness. However, despite their limitations, the data show that soil properties did influence soil biota, and in ways that differed between land-use types.

Species richness does not reflect all types of compositional changes, as species lost may be replaced by others leaving richness unchanged (Hillebrand et al., 2018; Stork et al., 2017). At a local scale, species composition and loss of particular species may be more important for ecosystem functioning than the total number of species. Additionally, the functional diversity of organisms may be more important than taxonomic diversity for ecosystem function (Díaz et al., 2006). The BII provides a more informative measure of changes in biological assemblages than taxon richness and abundance. Compared with primary vegetation, cropland had the lowest BII, with around a third of original biodiversity remaining, while biodiversity was less depleted in grazed sites, with a BII of 0.59. Our results suggest that while mature and intermediate age secondary vegetation has a comparable BII to primary sites, this is not the case with young secondary vegetation, which is consistent with soil biodiversity taking time to reestablish after removal of vegetation.

Along with the depressed abundance and taxon richness of local soil biodiversity in land uses other than primary vegetation and pasture, this supports that soil biota should be considered explicitly when using global models to estimate the state of biodiversity (Guerra, Bardgett, et al., 2021; Guerra, Delgado-Baquerizo, et al., 2021). For example, given that our models show that both soil organism abundance and taxon richness were markedly lower in most intensities of secondary vegetation than in primary vegetation, evaluation of restoration of degraded ecosystems (per Target 15 of the Aichi Targets 'restoration of at least 15 per cent of the world's degraded ecosystems'; CBD, 2011) would need specific assessment of soil biota as well as the (more commonly monitored) aboveground biota.

The BII is designed to be projected using different land-use scenarios and can be back projected to estimate changes in BII over time; these, and regional and national models can be explored in future analyses. Additionally, important soil properties such as temperature and moisture are not currently included, along with the effects of climate change and the projected changes of climate change on soil properties. Interactions between land use and climate change are likely to have greater impacts than these drivers alone (Outhwaite et al., 2022), so urgent work is needed to consider both threats on soil biotas. A further important future step will be to incorporate uncertainty measures from the two biodiversity models that comprise the BII and the drivers to provide uncertainty estimates. Validation of the soil BII from comparing model outputs with observational data would also be valuable. These limitations are common in all global biodiversity indicators (Watermeyer et al., 2021) and do not detract from our main findings.

5 | CONCLUSIONS

Relative to assemblages in primary vegetation, the local abundance and taxon richness of soil biota are decreased in secondary vegetation, plantation and cropland sites worldwide, but not in pasture. Soil physicochemical properties mediated the responses of both taxon richness and abundance of belowground assemblages to land use but in variable ways. Globally, the average soil BII of cropland is a third that of intact ecosystems, however, grazed sites show less decline. The soil BII of secondary sites depends on age, being similar to primary vegetation in mature sites, but lower in young sites. Implementation of the Convention on Biological Diversity's forthcoming global biodiversity framework needs to explicitly include soil biodiversity to ensure that restoration of degraded ecosystems has positive outcomes for soil as well as aboveground biota.

AUTHOR CONTRIBUTIONS

Victoria Burton: Data curation; formal analysis; visualization; writing – review and editing; writing – original draft; investigation; conceptualization. **Andrés Baselga:** Software; methodology; writing – review and editing. **Adriana De Palma:** Writing – review and editing; data curation; methodology; investigation; conceptualization. **Helen R. P. Phillips:** Data curation; investigation; writing – review and editing. **Christian Mulder:** Data curation; investigation; writing – review and editing. **Paul Eggleton:** Writing – review and editing; funding acquisition; investigation; supervision; conceptualization. **Andy Purvis:** Conceptualization; investigation; funding acquisition; writing – review and editing; methodology; supervision.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NHM Data Portal at https://data.nhm.ac.uk/dataset/release-of-data-added-to-the-predicts-database-november-2022, reference number https://doi.org/10.5519/jg7i52dg.

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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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