Global distribution of earthworm diversity

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Abstract

Soil organisms provide crucial ecosystem services that support human life. However, little is known about their diversity, distribution, and the threats affecting them. Here, we compiled a global dataset of sampled earthworm communities from over 7000 sites in 56 countries to predict patterns in earthworm diversity, abundance, and biomass. We identify the environmental drivers shaping these patterns. Local species richness and abundance typically peaked at higher latitudes, while biomass peaked in the tropics, patterns opposite to those observed in aboveground organisms. Similar to many aboveground taxa, climate variables were more important in shaping earthworm communities than soil properties or habitat cover. These findings highlight that, while the environmental drivers are similar, conservation strategies to conserve aboveground biodiversity might not be appropriate for earthworm diversity, especially in a changing climate.

One sentence summary: Global patterns of earthworm diversity, abundance and biomass are driven by climate but patterns differ from many aboveground taxa.

Main Text

Soils harbour high biodiversity, and are responsible for a large number of ecosystem functions and services that we rely upon for our well-being (*1*). Despite calls for large-scale biogeographic studies of soil organisms (*2*), global biodiversity patterns remain relatively unknown, with most efforts focused on soil microbes (*3*, *4*), the smallest of the soil organisms. Consequently, the drivers of soil biodiversity, particularly soil fauna, remain unknown at the global scale.

Further, our ecological understanding of global biodiversity patterns (e.g., latitudinal diversity gradients *9*) is largely based on the distribution of aboveground taxa. For many aboveground taxa, variables relating to climate (*10*, *11*) or energy (e.g., primary productivity *12*) are often the most important predictors of diversity across large scales. At large scales, climatic drivers also shape belowground communities (*3*, *13–15*), but the response to these drivers in belowground communities may differ from those seen aboveground (*3*, *16*). For example, mean annual temperature correlates positively with aboveground diversity (*17*), but negatively correlates with the diversity of many classes of fungi (*3*), likely due to the optimum temperature of the latter being exceeded (*18*).

Here we analyse global patterns in earthworm diversity, abundance, and biomass (hereafter 'community metrics'). Earthworms are considered ecosystem engineers (*5*) in many habitats, and increase soil quality (e.g., nutrient availability through decomposition *5*). They also provide a variety of vital ecosystem functions and services (*6*). Whereas most biodiversity-ecosystem functioning studies focus on species richness as a diversity measure (*7*), the provisioning of ecosystem functions by earthworms is likely to vary depending on the abundance, biomass, and ecological group of the earthworm species (*8*) (see Supplementary Materials and Methods). Consequently, understanding global patterns in community

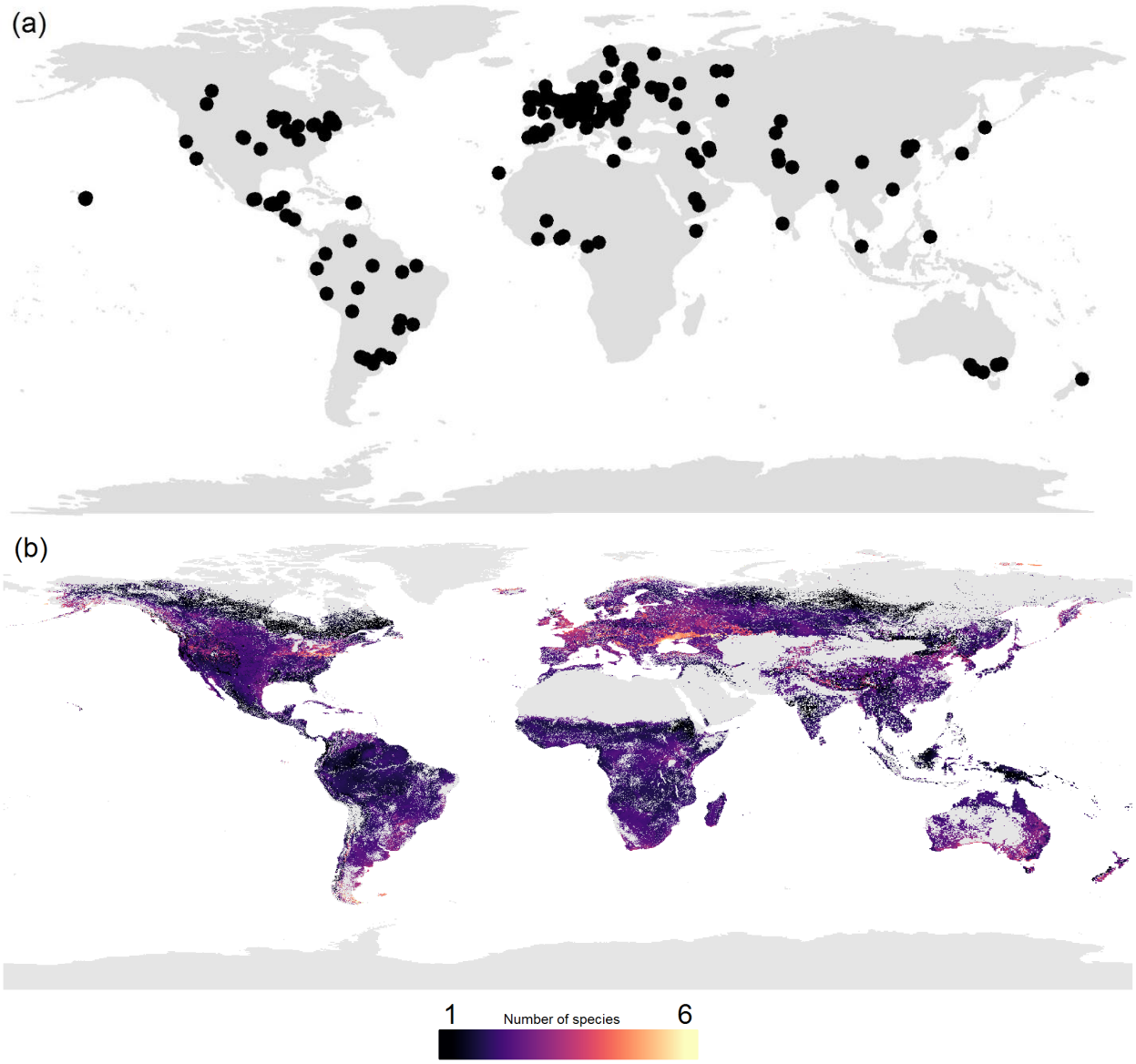
metrics for earthworms is critical for predicting how community changes may alter ecosystem functioning.

From small-scale field studies we know that soil properties such as pH and soil carbon influence earthworm diversity (*14*, *19*, *20*). For example, lower pH values constrain the diversity of earthworms by reducing calcium availability (*21*), and soil carbon provides resources that sustain earthworm diversity (*19*). Alongside the many interacting soil properties (*14*), a variety of other drivers can shape earthworm diversity, such as climate and habitat cover (*19*, *22*, *23*). However, to date, no framework has integrated a comprehensive set of environmental drivers of earthworm communities to identify the most important ones at a global scale.

Many soil organisms have shown global diversity patterns that differ from aboveground organisms (*3*, *16*, *24*). Therefore, we anticipate that earthworm community metrics (particularly diversity) will not follow global patterns seen aboveground. This would be consistent with previous studies at smaller scales, which have shown that the species richness of earthworms increases with latitude (*14*, *23*). Because of the relationship between earthworm communities, habitat cover, and soil properties on local scales, we furthermore expect soil properties (e.g., pH and soil organic carbon) to be key environmental drivers of earthworm communities.

Here, we present the first global maps predicting earthworm biodiversity, distilled into three earthworm community metrics: diversity, abundance, and biomass. We collated 181 earthworm diversity datasets from the literature and unpublished field studies (162 and 19, respectively) to create a dataset spanning 56 countries (all continents except Antarctica) and 7048 sites (Fig. 1a). We used these raw data to explore key characteristics of earthworm communities, and determine the environmental drivers that shape earthworm biodiversity. We then used the relationships between earthworm community metrics and environmental drivers (Table S1) to predict local earthworm communities across the globe.

Three mixed effects models were constructed, one for each of the three community metrics; species richness (calculated within a site, ~1m^2), abundance per m^2, and biomass per m^2. Each model contained 12 environmental variables as main effects (Table S2), which were grouped into six themes; ‘soil’, ‘precipitation’, ‘temperature’, ‘water retention’, ‘habitat cover’, and ‘elevation’ (see Supplementary Materials and Methods). Within each theme, each model contained interactions between the variables. Following model simplification, all models retained most of the original variables, but some interactions were removed (Table S3).


(a)
(b)
1
Number of species
6

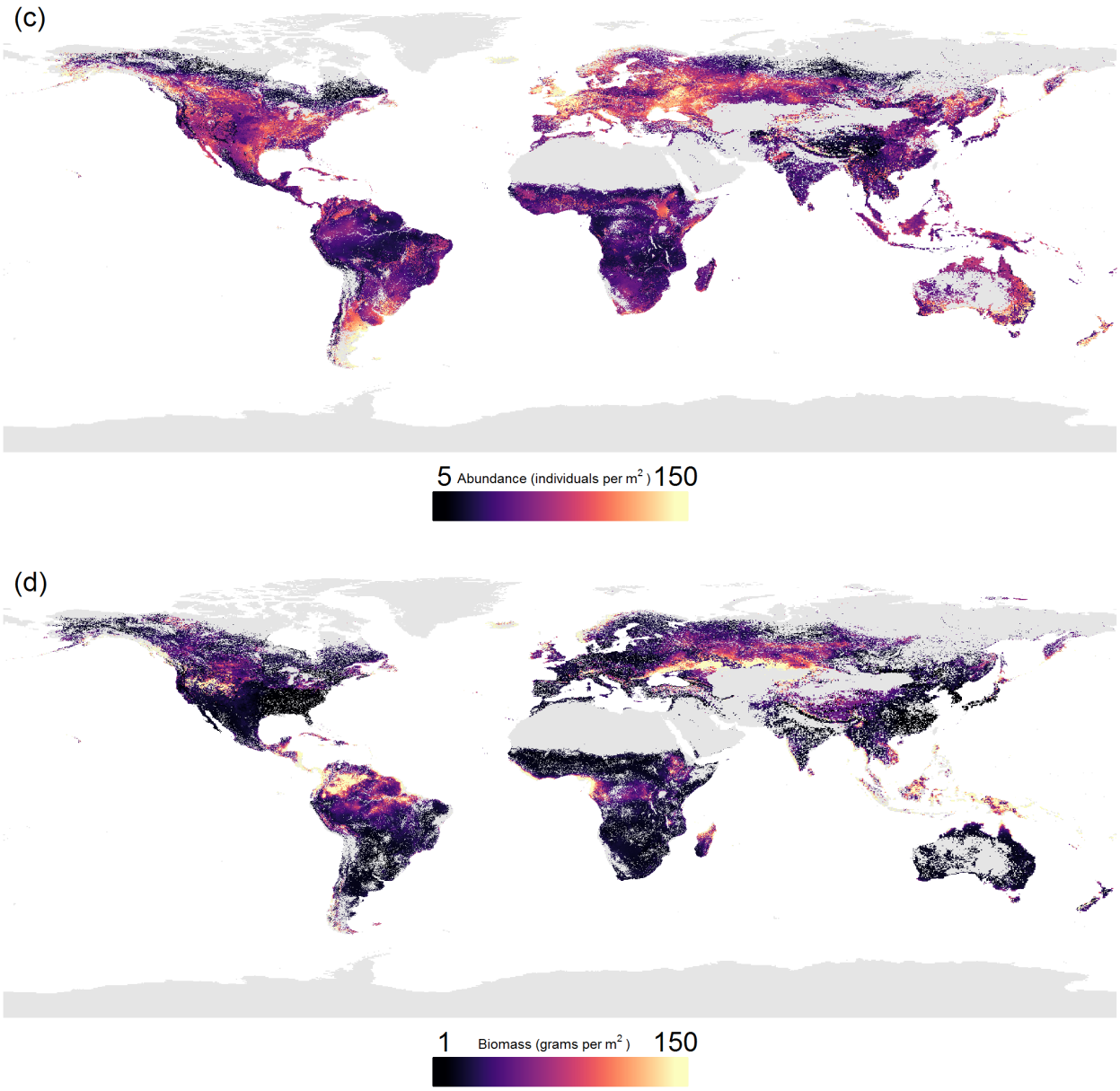


Fig. 1. (a) Map of the distribution of data, showing any record that was used in at least one of the three models (species richness, abundance, and biomass). Each black dot represents the centre of a 'study' (i.e., a set of data with consistent methodology, see Supplementary Materials and Methods). In total, 229 studies were included (from 181 datasets), which equated to 7048 sites across 56 countries. (b-d): The globally predicted values from the three biodiversity models, species richness (within site, ~1m^2; panel b), abundance (panel c; individuals per m^2), and biomass (panel d; grams per m^2). Areas of high diversity are shown in yellow colours, and areas of low diversity are shown in dark purple colours. Grey areas are habitat cover categories which lacked samples of earthworm communities, thus lack predictions. To prevent outliers skewing the visualization of results, the colour of maps were curtailed at the extreme low and high values. Curtailing was based on where the majority of values laid. Thus, values lower or higher than that number marked on the scale are coloured the same but may represent a large range of values.

Predicting based on global environmental data layers, local diversity of earthworms was estimated to range between 1 and 4 species across most of the terrestrial globe (Fig. 1b) (mean: 1.98 species; SD: 0.55). These values are in line with previous suggestions (*20*). The lowest values of species richness occurred across the boreal/subarctic regions, which was expected based on aboveground biodiversity patterns. However, low diversity also occurred in subtropical and tropical areas, such as India and Indonesia, in contrast with commonly observed aboveground patterns, such as the latitudinal gradient in plant diversity. This low earthworm diversity could be due to these regions typically being outside of the optimal temperature range (12-20˚C) for earthworms (*25*).

Areas of high local species richness were at mid-latitudes, such as the southern tip of South America, and the southern regions of Australia and New Zealand. Europe (particularly north of the Black Sea) and northeastern USA also had particularly high local species richness. While this pattern seems to contrast with the latitudinal diversity patterns found in many aboveground organisms (*9*, *26*), it is consistent with patterns found in some belowground organisms (ectomycorrhizal fungi *3*, bacteria *15*, *27*), but not all (arbuscular mycorrhizal fungus *13*, oribatid mites *28*). Such mismatches between above- and belowground biodiversity have been predicted (*1*, *24*), but not shown for different soil fauna diversity metrics at the global scale. This work further highlights that it is important that soil organism diversity patterns are examined in concert with those of aboveground taxa if we are to fully understand large-scale patterns of biodiversity and their underlying drivers (*16*, *24*, *29*). Moreover, conservation strategies that are designed for aboveground organisms may not protect earthworms (*24*), despite their importance as ecosystem function providers (*6*) and soil ecosystem engineers (*5*).

The patterns seen here could be a result of past climates, in particular glaciation in the last ice age. Regions in the mid- to high latitudes that were previously glaciated were likely re-colonised by earthworm species with high dispersal capabilities and large geographic ranges (*23*). Thus, mid-latitude communities would have high local diversity but minimal beta-diversity, i.e., low regional diversity, and the opposite would be true in tropical regions. When the number of unique species within each 5-degree latitude band was calculated (i.e., regional richness, Fig. 2a) there was no evidence of a latitudinal diversity gradient once sampling effects had been accounted for (Fig. 2b). Given that regional richness of the tropics was on par with the temperate region, despite low local diversity and relatively low sampling effort (Fig. 2a), endemism of earthworms and beta diversity within the region (*30*) must be considerably higher than within the well-sampled temperate region.

Across the globe, the predicted total abundance of the local community of earthworms typically ranged between 5 and 150 individuals per m^2 , in line with other estimates (*31*) (Fig. 1c; mean: 57 individuals per m^2; SD: 43.59). There was a slight tendency for areas of higher community abundance to be in temperate areas, such as Europe (particularly the UK, France and Ukraine), New Zealand, and part of the Pampas and surrounding region (South America), rather than the tropics. Lower community abundance occurred in many of the tropical and sub-tropical regions, such as Brazil, central Africa, and parts of China. Given the positive relationship between community abundance and ecosystem function (*32*), in regions of lower earthworm abundance there may be implications for provisioning of the ecosystem services performed by these organisms. Further research is needed to disentangle whether these functions are reduced or whether they are carried out by other soil taxa (*1*).

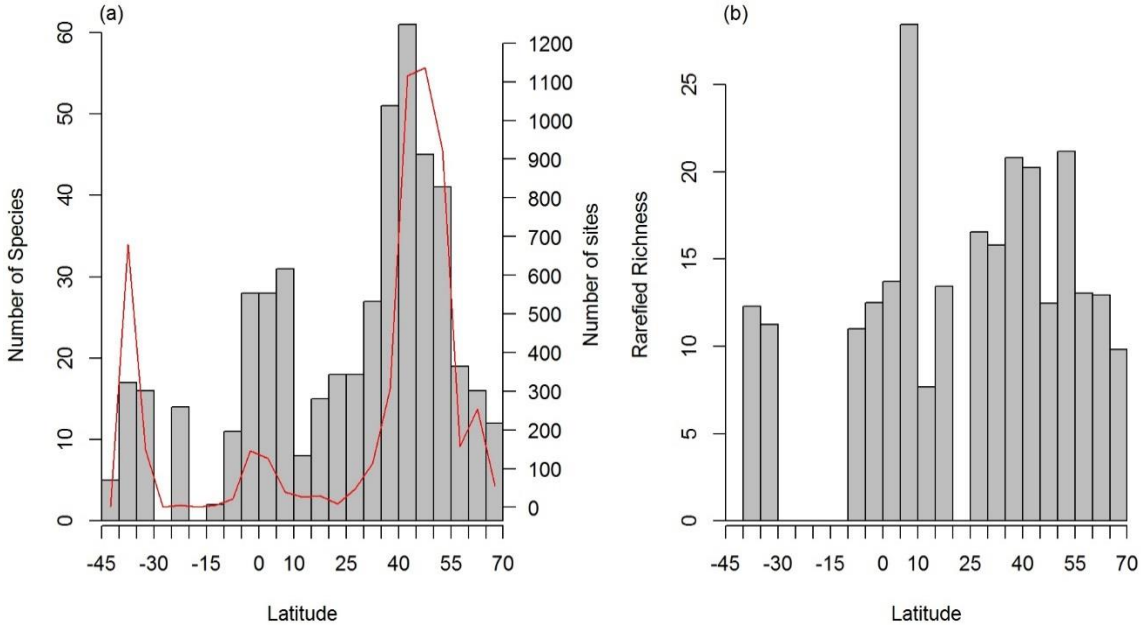


Fig. 2 (a) The number of unique species within each 5 degree latitude band (grey bars) and the number of sampled sites within the same latitude band (red line). (b) Sampled-based rarefied species richness within each 5 degree latitude band. Latitude bands with less than 22 sites were not included in the analysis.

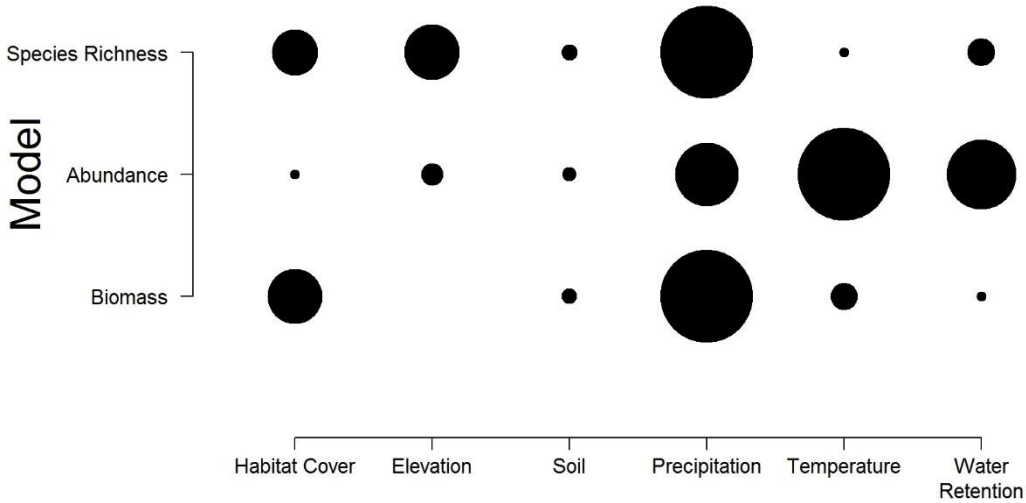


Fig. 3: Based on RandomForest models, the importance of the six variable themes from the three biodiversity models. Each row shows the results of each model (top: species richness, middle: abundance, bottom: biomass). Each column represents a theme of variables that was present in the simplified biodiversity model. In the main plot area, the most important variable group has the largest circle. Within each row, the circle size of the other variable themes are scaled in size depending on the relative change in importance. Thus, the circle size should only be compared within a row. Variable theme importance, calculated from the node impurity, was the weighted average of all variables within each theme, following simplification.

The predicted total biomass of the local earthworm community across the globe typically ranged between 1 g and 150 g per m^2 (Fig. 1d; mean: 380.86g; SD: 47684.3; median: 18.54, see Supplementary Materials and Methods for discussion in regard to extreme values). The areas of high earthworm biomass were spread across the globe, but concentrated in the tropics (particularly Indonesia, parts of coastal West Africa, Southern Central America, much of Colombia and Western Venezuela), some regions of North America, and the Eurasian Steppe. In some regions, this was almost the inverse of the abundance patterns (Fig. 1c); thus, these results may relate to the fact that earthworms decrease in body size towards the poles (*31*), unlike other animals (*33*). This decrease in earthworm body size might be due to smaller-bodied earthworms with greater dispersal capabilities recolonising northern regions following deglaciation post-ice age (*23*). In northern North America, where there are no native earthworms (*8*), high density and, in some regions, high biomass of earthworms likely reflects the earthworm invasion of these regions. The invasive smaller European earthworm species encounter an enormous unused resource pool, which leads to exceptionally high population sizes (*34*). In contrast, in Brazil, where we had a relatively higher sampling density (Fig. 1a), patterns of abundance and biomass corresponded with the earthworm species that have been documented there. There are a number of giant earthworm species within Brazil (and other countries in the tropics, such as Indonesia, where a similar pattern is shown) (*35*). These giant earthworms normally occur at low densities and low species richness (*35*), causing the high biomass but low abundance.

Overall, the three community metric models performed well in cross-validation (Fig. S2) with relatively high R^2 values (Table S4 a and c; see Supplementary Material for further details and caveats discussion). But, given the nature of such analyses, models and maps should only be used to explore broad patterns in earthworm communities and not at the fine scale, especially in relation to conservation practices (*12*).

For all three of the community metric models (species richness, abundance, and biomass), climatic variables were the most important drivers (‘precipitation’ theme being the most important for both species richness and total biomass models, and ‘temperature’ theme for the community abundance model; Fig. 3). The importance of climatic variables is consistent with many aboveground taxa (e.g., plants *10*, reptiles/amphibians/mammals *12*) and belowground taxa (bacteria and fungi *3*, *15*, nematodes *27*) when examined at large scales. This suggests that climate-related methods and data, which are typically used by macroecologists for the estimation of aboveground biodiversity, may also be suitable for estimating earthworm communities. However, the strong link between climatic variables and earthworm community metrics is cause for concern, as climate will continue to change due to anthropogenic activities over the coming decades (*36*). Our findings further highlight that changes in temperature and precipitation are likely to influence earthworm diversity (*37*) and their distributions (*14*), with implications for the functions that they provide (*6*). The expansion or shifts in distributions may be particularly problematic in the case of invasive earthworms, such as in areas of North America, where they can considerably change the ecosystem (*8*). However, a change in climate will most likely affect abundance and biomass of the earthworm communities before diversity as shifts in the latter depend upon dispersal capabilities, which are relatively low in earthworms. This underscores the need to study earthworms in terms of multiple community metrics in order to accurately assess responses of communities to climate change.

We expected that soil properties would be the most important driver of earthworm communities, but this was not the case (Fig. 3). However, soil properties and habitat cover did influence the earthworm community (Fig. S3 a and b). This was especially true in the case of habitat cover, which altered the composition of the three ecological groups (epigeic, endogeics, and anecics, see Supplementary Methods and Materials and Fig. S4) within the earthworm community. Across larger scales, climate influences both habitat cover and soil properties, all of which affect earthworm communities. Being able to account for this indirect effect with appropriate methods and data may alter the perceived importance of soil properties and habitat cover (e.g., with pathway analysis *11* and standardised data). In addition, the importance of drivers could change at different spatial scales, with climate driving patterns at global

scales but within climatic regions (or at the local scale) other variables may become more important (*38*). Finally, for soil properties, the mismatch in scale between community metrics and soil properties taken from global layers (for sites where sampled soil properties were missing; see Supplementary Methods and Materials) could also reduce the apparent importance of the theme.

By compiling a global dataset of earthworm communities we show, for the first time, the global distribution of earthworm diversity, abundance, and biomass, and identify key environmental drivers responsible for these patterns. Our findings suggest that climate change might have significant and serious effects on earthworm communities and the functioning of ecosystems. These findings are of particular relevance given the role of earthworms as ecosystem engineers that structure the environment for other soil organisms; thus, any climate change-induced alteration in earthworm communities is likely to have cascading effects on other species in these ecosystems (*8*, *31*). Despite earthworm communities being driven by similar environmental drivers as aboveground communities (*10*, *11*), these relationships result in different patterns of diversity. We highlight the need to integrate belowground organisms into the biodiversity paradigm to fully understand global patterns of biodiversity. This is especially true if the inclusion of soil taxa changes the location of biodiversity hotspots and thus conservation priorities (*24*) or if processes underlying macroecological patterns differ between aboveground and belowground diversity (*29*). Our study creates an avenue for future research: given that climate was the most important predictor of earthworm communities, it is possible for ecologists who have previously focused on modelling aboveground diversity to use similar methods belowground. By modelling both realms, aboveground/belowground comparisons are possible, potentially allowing a clearer view of the biodiversity distribution of whole ecosystems.

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Supplementary Materials

Materials and methods
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