Global distribution of earthworm diversity

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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" (habitat cover and some soil variables were measured in the field; the remaining variables were extracted from global data layers based on the geographic coordinates of the sites (14)). Within each theme, each model contained interactions between the variables. After model simplification, all models retained most of the original variables, but some interactions were removed (table S3).

Consistent with previous results (20), local earthworm diversity predictions based on global climate data match the species richness pattern reported in the literature (21).
environmental data layers resulted in estimates of between 0 and 4 species per site across most of the terrestrial surface (Fig. 1B) (mean, 0.95 species; SD, 0.96). Most of the boreal and subarctic regions were predicted to have low values of species richness, which is in line with aboveground biodiversity patterns (21, 22). However, local diversity also occurred in subtropical and tropical areas, such as Brazil, India, and Indonesia, in contrast to commonly observed aboveground patterns, such as the latitudinal gradient in plant diversity (22). This pattern could be due to different relationships with climate variables. For example, although plant diversity increases with potential evapotranspiration (PET) (22), earthworm diversity tended to decrease with increasing PET (table S3). In addition, soil properties, which are typically not included in models of aboveground diversity, can play a role in determining earthworm communities (11, 15, 23). For instance, litter availability and soil nutrient content are important regulators of earthworm diversity, with oligotrophic forest soils having more epigeic species, and eutrophic soils more endogeics (23). Furthermore, tropical regions with higher decomposition rates have fewer soil organic resources and lower local earthworm diversity (Fig. 1B and table S3), dominated by endogeic species, which have specific digestion systems that allow them to feed on low-quality soil organic matter (11, 14, 20).

High local species richness was typically found at mid-latitudes, such as the southern tip of South America, the southern regions of Australia and New Zealand, and Europe (particularly the United Kingdom, France, and Germany). However, there were some exceptions, such as central Africa. Although this pattern contrasts with latitudinal diversity patterns found in many aboveground organisms (6, 24), it is consistent with patterns found in some belowground organisms [ectomycorrhizal fungi (3), bacteria (5)], but not all [arbuscular mycorrhizal fungi (25), oribatid mites (26)]. Such mismatches between above- and belowground biodiversity have been predicted (1, 7) but not shown across the globe for soil fauna at the local scale.

The patterns seen here could in part be a result of glaciation in the last ice age, as well as human activities. Temperate regions (mid- to high latitudes) that were previously glaciated were likely recolonized by earthworm species with high dispersal capabilities and large geographic ranges (19) and through human-mediated dispersal [“anthropochorous” earthworms (16)]. Thus, temperate communities could have high local diversity, as seen here, but those species would be widely distributed, resulting in lower regional diversity relative to local diversity. In the tropics, which did not experience glaciation, the opposite may be true. Specific locations may have individual species that are highly endemic, but these species are not widely distributed (table S4). This high local endemism would result in low local diversity (as found here) and high regional diversity (as suggested by (10)) relative to that low local diversity. When the numbers of unique species within latitudinal zones that had equal numbers of sites were calculated (i.e., a regional richness that accounted for sampling effort), there appeared to be a regional latitudinal diversity gradient (Fig. 2).

Even with a sampling bias (table S4), regional richness in the tropics was greater than in the temperate regions, despite low local diversity. These results should be interpreted with caution, given the latitude span of the tropical zones. However, the underlying data suggest that endemism of earthworms and β-diversity within the tropics (27) may be considerably higher than within the well-sampled temperate region (table S4). Therefore, it is likely that the tropics harbor more species overall.

The predicted total abundance of the local community of earthworms typically ranged between 1 and 50 individuals per m² across the globe, in line with other estimates (28) (Fig. 1C; mean, 20.59 individuals per m²; SD, 24.84). There was a slight tendency for areas of higher total abundance to be in temperate areas, such as Europe (particularly the United Kingdom and France), New Zealand, and part
of the Pampas and surrounding region (South America), rather than the tropics. Lower total abundance occurred in some of the tropical and subtropical regions of Brazil and central Africa, and in parts of India. Given the positive relationship between total abundance and ecosystem function (29), in regions with lower earthworm abundance, such functions may be reduced or carried out by other soil taxa (1).

The predicted total biomass of the local earthworm community (adults and juveniles) across the globe showed extreme values (>2 kg) in 0.12% of pixels, but biomass typically ranged (97.3% of pixels) between 1 g and 150 g per m² [Fig. 1D; median, 6.16; mean, 51.18; SD, 488.12; see (14) for additional discussion of extreme values]. The areas of high total biomass were concentrated in East Asia [although it should be noted that data points in this region were limited (Fig. 1A) and thus predictions may not be reliable (fig. SIC)]. The majority of the globe showed low total biomass. In northern North America, where there are no native earthworms (33), the slightly higher density and, in some regions, higher biomass of earthworms likely reflects the earthworm invasion of these regions. The small invasive European earthworm species encounter an enormous unused resource pool, which leads to high population sizes (30). On the basis of previous suggestions (28), we expected that earthworms would decrease in body size toward the poles, showing low biomass relative to the total abundance in temperate or boreal regions. In contrast, in tropical regions (e.g., Brazil and Indonesia) that are dominated by giant earthworms that normally occur at low densities and low species richness (31), we expected high biomass but low abundance. However, these patterns were not found. This could be due to the relatively small number of sample points for the biomass model (n = 4167) compared to the diversity (n = 7386) and total abundance models (n = 8677), reducing the predictive ability of the model (fig. SIC), most notably in large regions of Asia and in areas of Africa, particularly the boundaries of the Sahara Desert and the southern regions (which coincides with sites where samples are lacking). Additionally, the difficulty in consistently capturing such large earthworms in every sample may increase data variability, reducing the ability of the model to predict.

Overall, the three community metric models performed well in cross-validation (Table 1 and figs. S3 and S4) [see (14) for further details and caveats]. 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 (32).

For all three community metric models, climatic variables were the most important drivers (the “precipitation” theme being the most important for both species richness and total abundance models, and “temperature” and “precipitation” being some of the most important variables for the total biomass model; Fig. 3). The importance of climatic variables in shaping diversity and distribution patterns at large scales is consistent with many above-ground taxa [e.g., plants (22), reptiles, amphibians, and mammals (32)] and belowground taxa [bacteria and fungi (3, 35), nematodes (33)]. This suggests that climate-related methods and data, which are typically used by macroecologists to estimate 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 (34). Our findings further highlight that changes in temperature and precipitation are likely to influence earthworm diversity (35) and distributions (15), with implications for the functions that they provide (12). 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 (33). However, a change in climate will most likely affect abundance and biomass of the earthworm communities before it affects diversity, as shifts in the latter depend on dispersal capabilities, which are relatively low in earthworms.

We expected that soil properties would be the most important driver of earthworm communities, but this was not the case (Fig. 3), likely because of the scale of the study. First, the importance of drivers could change at different spatial scales. Climate is driving patterns at global scales, but within climatic regions (or at the local scale), other variables may become more important (36). Thus, one or more soil properties may be the most important drivers of earthworm communities within each of the primary studies, rather than across them all. Second, for soil properties, the mismatch in scale between community metrics and the soil properties taken from global layers [for sites where sampled soil properties were missing (14)] potentially reduced the apparent importance of the theme. Habitat cover directly influenced the earthworm community, particularly the abundance and biomass of the community (Fig. 3 and fig. S5, A and B) and the composition of the three ecological groups (epigeics, endogeics, and anecics) (fig. S6) (14). 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 (37) and standardized data]. However, our habitat cover variable did not directly consider local management (such as land use or intensity).

Our findings suggest that climate change might have substantial effects on earthworm communities and the functioning of ecosystems; any climate change–induced alteration in earthworm communities is likely to have
Fig. 3. The importance of the six variable themes from the three biodiversity models. Rows show the results of each model (top, species richness; middle, abundance; bottom, biomass). Columns represent the variable themes that are present in the simplified biodiversity model. The most important variable group has the largest circle. Within each row, the circle size of the other variable themes is proportional to the relative change in importance. The circle size should only be compared within a row.

cascading effects on other species in these ecosystems (13, 28). Despite earthworm communities being controlled by environmental drivers similar to those that affect above-ground communities (22, 37), these relationships result in different patterns of diversity. We highlight the need to integrate below-ground organisms into biodiversity research, despite differences in the scale of sampling, if we are to fully understand large-scale patterns of biodiversity and their underlying drivers (7, 8, 98), especially if processes underlying macroecological patterns differ between above-ground and belowground diversity (38). The inclusion of soil taxa may alter the distribution of biodiversity hotspots and conservation priorities. For example, protected areas (7) may not be protecting earthworms (7), despite their importance as ecosystem function providers (12) and soil ecosystem engineers for other organisms (11). By modeling both realms, aboveground/belowground comparisons are possible, potentially allowing a clearer view of the biodiversity distribution of whole ecosystems.

REFERENCES AND NOTES

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SUPPLEMENTARY MATERIALS

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Earthworm distribution in global soils

Earthworms are key components of soil ecological communities, performing vital functions in decomposition and nutrient cycling through ecosystems. Using data from more than 7000 sites, Phillips et al. developed global maps of the distribution of earthworm diversity, abundance, and biomass (see the Perspective by Fierer). The patterns differ from those typically found in aboveground taxa; there are peaks of diversity and abundance in the mid-latitude regions and peaks of biomass in the tropics. Climate variables strongly influence these patterns, and changes are likely to have cascading effects on other soil organisms and wider ecosystem functions.

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