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Response to Comment on “Global distribution of earthworm diversity”

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James *et al.* claim that there are areas of concern in our work. We believe that they have misunderstood the methods behind our paper and that differences in scale have been overlooked. Once those misunderstandings have been resolved, their remaining criticisms are either not sustained or agree with our statements. To advance the field, we recommend additional sampling using comparable methodologies in underrepresented areas.

Criticisms of our paper (1) by James *et al.* (2) can be broken into three main areas: (i) criticisms of the conclusions, (ii) criticisms of the data used, and (iii) criticisms of including anthropogenic habitats.

James *et al.* incorrectly claim that we “conclude that tropical earthworm communities are less diverse and abundant than temperate communities.” In fact, we conclude that “it is likely that the tropics harbor more species overall,” as shown by figure 2 of (1). However, we want to draw attention to other global distribution studies that also found lower local soil biodiversity in tropical soils relative to temperate or arctic regions [e.g., microbes (3), nematodes (4)]. James *et al.* also claim that using local or site-level estimates of diversity to understand global patterns is not appropriate (2). This is not true, as different scales of diversity can be used to test ecological principles, such as the latitudinal diversity gradient (5). Our modeled outputs provide a general pattern, and discrepancies are expected to occur if it were to be ground-truthed.

We applied transparent inclusion criteria [see “Literature search” in supplementary materials of (1)] for papers screened, which is a required method in synthesis studies (6) and is necessary when data have been collected using different methodologies. This resulted in removal of 92.3% of papers, which is not an exceptionally large proportion. For example, a highly cited ecological meta-analysis (7) removed 90.6% of papers during the screening process. However, we stress that it was not mandatory for datasets to include species-level identification, as stated in (2).

James *et al.* provide a list of publications that appear to

contradict our results. These papers are highly informative in terms of earthworm inventories, but their results are not directly comparable to our study. Most of the papers listed in (2) do not give α -level (local-level) estimates of earthworm diversity that are adequate to allow a quantitative analysis, such as ours, to be carried out. In (1), we defined “local” in terms of site-level data, where a “site” was defined as “a location of one or more samples that adequately captured the earthworm community.” In a number of the listed papers, such as (8) [their reference 5; note that the values reported in (2) do not match the actual values in this publication], the values given are totals of several sampling sites (using our definition), and hence not α -diversity, but rather overall diversity within a larger region. The literature presented does not contradict our conclusion, but instead reinforces that there are likely high levels of β -diversity of earthworms in the tropics.

James *et al.* also discuss the sampling curves of earthworm species within temperate and tropical biomes. Unfortunately, as no citation was provided, we are unable to establish the foundation of these claims. However, given our findings in figure 2 of (1) (high regional diversity, implying high β -diversity when local diversity is low), we would not argue against this point.

In (2) the spatial biases in our data were also discussed. We had already highlighted in (1) that we need more sampling in the tropics and other underrepresented areas. Figure 2 of (1) was not intended to show where future sampling should occur (as longitude should also be taken into ac-

count for such recommendations), but rather to account for the fact that there was less sampling across certain broad latitudinal zones. Thus, we reiterate our call, adding to comments in (2), for more sampling not only in the tropics but also in many other places, including underrepresented temperate zones such as Russia [see figure 1A of (1)].

The taxonomic expertise of our data contributors was also called into question by James *et al.* We had already highlighted the high percentage of unidentified species in the tropics in our text as well as in table S4 of (1). However, we do disagree with (2) regarding identification expertise needed for the temperate realm, as there are also many species in temperate regions that cannot be identified by external features alone. In addition, the taxonomy presented in (1) was checked by multiple earthworm taxonomists, and thus we stand by its reliability. But we wholeheartedly agree that more taxonomists are needed globally to help improve current knowledge of earthworm geographic patterns.

Throughout (2), additional ways of sampling earthworm communities were suggested. Although we agree with these methods, we stress that they are suitable only in certain instances. Qualitative methods (e.g., a free search for earthworms at a site) are often used for species inventories, and we agree with (2) that this would give higher numbers of earthworm species in an area. However, owing to a lack of a standardized sample effort and area, qualitative methods are not comparable across studies. Conversely, quantitative approaches (e.g., hand-sorting through soil within a 50 cm × 50 cm quadrat) typically use standardized methods that are comparable across studies but are unlikely to detect every species that could be present at a particular habitat or site (in particular, those associated with certain microhabitats or microsites, such as dead logs or compost piles). In (1) we needed comparable results to allow us to analyze a large set of standardized quantitative data and to decrease the total variation associated with the collated datasets. Thus, typically taxonomic literature (e.g., reporting species' presence or absence using qualitative approaches) was excluded, and as a result, there will be a bias toward less rare species. Although DNA barcoding would be useful for future global synthesis studies, there are not yet enough data for such studies. Furthermore, several studies [e.g., (9)] have reported the existence of cryptic species in the temperate realm, so diversity outside the tropics is also expected to increase as a result of using molecular methods.

In a world undisturbed by anthropogenic activities, we would predict large-scale biogeographic patterns using only data from natural habitats. However, because human impacts are causing unprecedented amounts of land use change (10) and because there are relatively few areas of natural habitats in parts of the world (e.g., Europe), anthropogenic habitats need to be considered in biodiversity stud-

ies. To present the most realistic view possible of current earthworm communities, we included a global layer on habitat cover within our models [see figures S5 and S6 of (1)]. If these habitats contain fewer species, we felt it was important to show the impact of this across a global scale, rather than excluding these expanding systems [e.g., agriculture covers 37% of Earth's land (11)] from our analysis. The distribution of each category of habitat cover was relatively even across temperate and tropical regions in (1), although some disparity existed (e.g., 22.2% of sites in the tropics, but only 14.9% of sites in the temperate region, were identified as "cropland").

Finally, we would like to highlight again that with more data, the reliability of conclusions can only be improved, and we welcome any additional sampling using comparable methodologies in underrepresented areas. However, it is crucial that these data are made freely available, either in original publications or in online repositories.

This response has been submitted on behalf of all co-authors of (1), with their knowledge.

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