Soil biodiversity accounts for a major share of global biodiversity, but its drivers, threats, and possible future changes are still under-explored and not well understood (Geisen, Wall, & van der Putten, 2019). While the biogeography of aboveground organisms has been the basis for fundamental rules in ecology and has helped inform decision makers about priority conservation habitats for decades, the global distribution of soil biodiversity has only recently seen a surge of scientific interest and synthesis work (Cameron et al., 2018). In this issue of *Molecular Ecology*, Bastida et al. (2020) publish the first global maps of soil invertebrate diversity that have been sampled at 83 locations, across six continents, using standardised methods and DNA sequencing. Using data from nematodes, arachnids and rotifers, and structural equation models, they find that diversity of these taxa is primarily driven by vegetation and climate. Given the anthropogenic changes that are occurring, and are projected to continue, this study provides important baseline information for future soil biodiversity and function monitoring, as well as exciting working hypotheses for targeted experiments.

**KEYWORDS**
aboveground-belowground interactions, amplicon sequencing, climate change, invertebrates, macroecology, soil biodiversity

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**Perspective**

**Putting soil invertebrate diversity on the map**

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Ecologists have had a very good foundational knowledge of the global distribution of plants and aboveground animals for many decades. But despite the immense diversity of soil organisms, our knowledge of the global distribution, drivers and threats to soil biodiversity is very limited. In this issue of *Molecular Ecology*, Bastida et al. (2020) produce the first global maps of soil invertebrate diversity that have been sampled at 83 locations, across six continents, using standardised methods and DNA sequencing. Using data from nematodes, arachnids and rotifers, and structural equation models, they find that diversity of these taxa is primarily driven by vegetation and climate. Given the anthropogenic changes that are occurring, and are projected to continue, this study provides important baseline information for future soil biodiversity and function monitoring, as well as exciting working hypotheses for targeted experiments.

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properties as potential explanatory variables, and uniform amplicon sequencing. Such standardised sampling is typically not possible in global studies of soil invertebrates, which usually rely on data sampled with a variety of methods (e.g., Phillips et al., 2019; van den Hoogen et al., 2019). Moreover, structural equation modelling is used to account for, and explore, the relative importance of dependent (groups of) variables.

This study reveals that soil invertebrate diversity, as assessed here based on 18S rRNA, is dominated by phylotypes of Nematoda, Arachnida (mostly soil mites), and Rotifera (Figure 1), with a much lower number representing Insecta, Annelida, Platyhelminthes and others. In subsequent analyses, the authors focus on the most diverse taxa, although estimates are potentially lower than what would be expected from traditional sampling techniques. They find that their diversity is consistently determined by aridity and plant community properties, including forest cover, plant diversity, and plant productivity. In addition to direct effects of water limitation, part of the detrimental aridity effect on soil invertebrate diversity is mediated by reduced plant productivity. Moreover, plant species richness turns out to increase the diversity of soil nematodes and rotifers, stressing the observation that biodiversity decline at one trophic level or group of organisms may have significant cascading effects on other taxa (Eisenhauer et al., 2013).

Using Cubist models, regression tree models suitable for predictions, Bastida et al. (2020) produce global maps of soil biodiversity distribution, which show unique biodiversity hotspots for the different groups of soil invertebrates, confirming earlier studies on potential mismatches of biodiversity hotspots among taxa (e.g., Phillips et al., 2019; Tedersoo et al., 2014; van den Hoogen et al., 2019). Another novel advance in comparison to previous studies is the analysis and identification of ecological clusters of soil invertebrates that share similar environmental preferences. While such global soil biodiversity clusters have already been reported for bacteria (Delgado-Baquerizo et al., 2018), this is the first study on soil invertebrate diversity clusters that is likely to inspire more future work, e.g., on the functional aspects of these communities as well as on ecosystem consequences of soil invertebrate diversity change.

Although a one-time sampling campaign can create an important biodiversity baseline, the information that could be obtained from repeated monitoring of soil biodiversity would be exceptional. Given that this study used standardized methods, the ability to repeat and extend to underrepresented regions of the globe is increased. Repeated measures can provide insights into how soil biodiversity is changing in relation to its drivers, specifically forest cover, plant diversity, and aspects of climate, which are all likely to change with anthropogenic impacts. More benefits could also be gained by increasing spatial coverage (Cameron et al., 2018). Thus, any global biodiversity monitoring should be initiated in a way that reduces spatial gaps in sampling (Cameron et al., 2018), using general calls for participation and/or more targeted communication.

Bastida et al. (2020) use molecular methods that are common in microbial studies, and going forward it is likely that molecular methods will increasingly be used for soil invertebrate sampling, especially in relation to such global monitoring. There are a number of advantages to validating such data. While the methodology is still in the early stages, most commonly used assays suffer from either low taxonomic resolution within, or biases against, some groups of soil invertebrates (Drummond et al., 2015). Bastida et al. (2020) stress that phylotype diversity should not be equated to species richness; however, phylotypes differentiated by the markers used can vary from a subspecies level to genera from different families. Naturally, the extent of this problem varies for the different organisms, for example, with nematodes being more accurately represented than mites. We should be looking at establishing improved molecular assays within global monitoring, potentially using multiple and group-specific marker genes to ensure uniform taxonomic resolution. Likewise, validation of these assays and populating molecular databases present ongoing challenges.

**FIGURE 1** Examples of Arachnida (Euphthiracaridae; left), nematodes (middle) and rotifer (right). These groups of soil invertebrates dominated the 18S rRNA sequences in Bastida et al. (2020). Images provided by Andy Murray (left and middle) and JRC Global Soil Biodiversity Atlas (right; H. Segers, Proyecto Agua, R. Moreno)
Due to the limitations of amplicon sequencing, phylotype diversity is the only measure that can be reliably retained from the data. If by combining molecular with some standard sampling and identification, the quantitative abundances of the taxa were able to be captured, then a variety of other follow-up studies could be undertaken. One such example would be investigating food web structure and energy fluxes, based on abundances and biomasses of soil invertebrates. Using energy fluxes, it would be possible to infer ecosystem functions, such as decomposition, belowground herbivory and predation (Barnes et al., 2018)—encompassing heretofore hidden soil processes with high relevance for the functioning of ecosystems. Given the link found by Bastida et al. (2020) between soil invertebrate communities and plant community structure as well as climate, future approaches could provide interesting insights into potential environmental change-induced shifts in ecosystem functioning.

Taken together, significant recent advances in soil biogeography have shed light on the global distribution and main drivers of, as well as potential threats to, soil biodiversity. Nevertheless, the observed relationships need to be backed up by experimental results to infer causality. Bastida et al. (2020) provide exciting working hypotheses for such future experiments to study causal relationships and the mechanisms underlying such relationships. Global experimental networks of ecological experiments can be used to explore the generality and context-dependencies of driver effects. Moreover, evidence is accumulating that interactions among multiple, co-occurring processes with high relevance for the functioning of ecosystems.

Causality. Bastida et al. (2020) provide exciting working hypotheses for such future experiments to study causal relationships and the mechanisms underlying such relationships. Global experimental networks of ecological experiments can be used to explore the generality and context-dependencies of driver effects. Moreover, evidence is accumulating that interactions among multiple, co-occurring processes with high relevance for the functioning of ecosystems.

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