WORKSHOP REPORT

# sOilFauna - a global synthesis effort on the drivers of soil macrofauna communities and functioning

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## Abstract

Understanding global biodiversity change, its drivers, and the ecosystem consequences requires a better appreciation of both the factors that shape soil macrofauna communities and the ecosystem effects of these organisms. The project "sOilFauna" was funded by the synthesis center sDiv (Germany) to address this major gap by forming a community of soil ecologists, identifying the most pressing research questions and hypotheses, as well as conducting a series of workshops to foster the global synthesis and hypothesis testing of soil macrofauna. The overarching goal is to analyze the most comprehensive soil macrofauna database - the MACROFAUNA database - which collates abundance data of 17 soil invertebrate groups assessed with a standardized method at 7180 sites around the world, and seeks to foster the collection of future data. In a recent kick-off workshop in May 2022, the first research priorities and collaboration guidelines were determined. Here, we summarize the main outcomes of this workshop and highlight the benefits of creating an open global community of soil ecologists providing standardized soil macrofauna data for future research, evaluation of ecosystem health, and nature protection.

## 1.    Background

Global change is pushing ecosystems towards novel environmental conditions that may threaten their integrity and stability. The extent to which ecosystems are resilient to these alterations strongly depends on the response of their biological components to external stressors. Soil macrofauna communities are a critical component of ecosystems' functioning and resilience (Bardgett & van der Putten 2014, Lavelle et al. 2022), owing to their major role in fluxes of carbon and energy (Wardle et al. 2004, Jochum & Eisenhauer 2022). They contribute a substantial part of total biodiversity (including insects), one of the largest pools in belowground animal biomass (Decaëns et al. 2006, Bar-On et al. 2018, Tuma et al. 2020), and often live at the interface of above- and belowground worlds, connecting soils to aboveground invertebrate and vertebrate food webs (Jochum & Eisenhauer 2022).

Despite these critical roles, the global distribution and main drivers of soil macrofauna communities are poorly understood and the subject of ongoing research (e.g. Decaëns 2010, Tsiafouli et al. 2015, Phillips et al. 2019a, Lavelle et al. 2022, Potapov et al. 2022a). Anticipating the response of ecosystems to global change requires a general framework depicting and predicting the response of soil macrofauna communities to environmental changes (Phillips et al. 2019a) and the implications for ecosystem functioning (Eisenhauer et al. 2017). Although empirical studies are accumulating, general predictions have yet to emerge. This impedes concrete management recommendations for soil fauna diversity to mitigate the effect of global change on ecosystems.

One of the reasons for this lack of knowledge is the diversity of environmental conditions and the versatility of the responses of soil macrofauna communities to global changes (Blankinship et al. 2011, Phillips et al. 2019a). To circumvent this challenge, we need to synthesize previous results and novel data, which takes into account and explains the discrepancy between previous studies, using standardized global datasets that represent major environmental gradients around the globe. In the context of the sOilFauna working group, we propose to start from general ecological theories elaborated on aboveground organisms to develop a general framework that links global drivers and environmental change to soil macrofauna communities and their functional roles in ecosystems. Our approach is to develop a reference database - MACROFAUNA - collating data from studies that address the link between environmental conditions, soil macrofauna biodiversity, and ecosystem functioning. We focus on data that assessed the abundance per unit of surface of 17 soil taxa with soil monolith and litter

sampling according to the TSBF sampling method. Data can originate from both natural and anthropized ecosystems, provided that metadata follows our data report template. The dataset presently covers 7180 transects across all continents and will be extended in the future. The database will be regularly updated, and we propose to develop an open community of researchers in soil ecology that are willing to share such data and participate in synthesis efforts. The database will be released on open access and made interoperable with other information facilities such as GBIF. We will use the database to explore critical questions that need to be addressed to elaborate a general framework.

In this kick-off workshop report, we present the main research objectives and questions, how we plan to approach our goals and invite external researchers to join our effort and contribute to the MACROFAUNA database as well as future syntheses. We plan to investigate macroecological patterns of soil macrofauna abundance, diversity, and community composition in relation to global drivers (sections 3.1.1–3.1.2) and more local factors such as landscape effects or land use (section 3.1.3–3.1.4). We also plan to assess community stability (section 3.1.5) and drivers of body size variation (section 3.1.6), estimate energy fluxes (section 3.2.1), quantify the macrofaunal influence on various ecosystem processes and functions (section 3.2.2), including temporal/seasonal aspects (section 3.3) as well as methodological aspects (section 3.4).

## 2.    The MACROFAUNA database

We will first describe the database 'MACROFAUNA' on which most of the analysis will be based.

### 2.1    The present state of the database

The database gathers data originating mostly from a standardized method called TSBF (ISO 2011), which entails excavating soil monoliths and surface litter on an area of 25 x 25 cm and a depth of 30 cm. Then the soil fauna is manually extracted by hand-sorting. This method provides estimates of density (ind $m^{-2}$) and biomass (g $m^{-2}$). An early version of the database was already published and explored (Lavelle et al. 2022) (https://datadryad.org/stash/dataset/doi:10.5061/dryad.r2280gbc2).

Since its earlier release, the database evolved and now gathers three types of data:

1.   The abundance and biomass of the 17 main large (> 1.5 mm) soil invertebrate groups (Table 1);

2. Associated land cover and management, agricultural practices, and primary productivity;
3. Associated soil properties, such as soil type, soil texture, soil pH, nutrient content.

Most soil fauna data come from transects of five soil monoliths taken within a plot. However, the database includes data reported at different levels of sampling resolution: at layer, monolith, and transect levels. Taking advantage of the different resolutions will allow us to test the significance of spatial scaling of soil biodiversity indicators and hypotheses. We will also select data resolution for each specific question. For example, monolith level data are better suited than transect level data to estimate local variability, sampling effort, and interactions between taxa.

In order to address the quality of the sub datasets and the uncertainty of the different georeferencing practices in the database, we operate in several steps. First, we review manually each dataset to assess its quality. We check with the data providers the metadata and the location of the points by checking the position on an interactive map. Based on this step, we flag datasets with insufficient metadata or location certainty (> 1 km), in order to be able to remove them in downstream analyses that need precise metadata or coordinates, such as mapping procedures or land use intensity analysis. Second, we use metadata and coordinate certainty of data

as weight in the cross-validation procedures while fitting and evaluating the models. With this robust procedure, data with more uncertainty are kept, which preserves power, but are given less weight and are resampled less frequently in the modeling procedure, and hence have less influence in the model.

The database presently holds 15380 records spread across the globe (Fig. 1). These records represent 7180 transects, among which 5489 records are at the monolith level, including 970 monoliths with separate soil layers.

## 2.2 Future development of the MACROFAUNA database - call for contributions

The MACROFAUNA database is evolving and will be regularly updated in the future. We plan to release a new version each year at the beginning of June. We are inviting researchers to contribute to the database with their own data. Sharing their data will give them the opportunity to be involved in papers that would use their data, as explained in the 'Composition of the working group' section. We will develop a system that would allow us to separately publish each independent dataset provided to MACROFAUNA with a unique DOI. Below, we present how we intend to develop the database in the future and how people can contribute.

**Table 1.** List of the 17 taxa covered by the MACROFAUNA database

| Common name | Scientific name |
| --- | --- |
| Earthworms | Crassiclitellata (except microdriles) |
| Ants | Formicidae |
| Termites | Termitidae and Rhinotermitidae |
| Coleoptera | Coleoptera |
| Spiders and scorpions | Arachnida |
| Millipedes | diplopoda |
| Centipedes | Chilopoda |
| Woodlices | Isopoda |
| Mosquitoes and flies (larvae) | Diptera |
| Coackroaches | Blattidae and Corydiidae |
| Bugs | Hemiptera |
| Earwings | Dermaptera |
| Butterflies (larvae) | Lepidoptera |
| Grasshopers, crickets | Orthoptera |
| Gastropoda | Gastropoda |
| Diplura | Diplura |
| Thysanoptera | Thysanoptera |

### 2.2.1 Development of the core database: abundance and biomass of soil macrofauna taxa

To develop the core of the MACROFAUNA database, we invite people to share their data using our template, which can be found here: https://doi.org/10.5281/zenodo.4543852. Because we plan to improve this template, we recommend future data providers to double-check that they use the latest version of the template. As a general rule, we recommend to provide data at the highest possible detail, and to put extra effort to fill in the metadata, in particular the date and the geographical coordinates together with their accuracy. Data from high latitudes and altitudes, North America, Africa, Australia, deserts, and urban areas are particularly welcomed.

### 2.2.2 Development of a sister database at species and morphospecies level

In a second step, we intend to build a sister database with a higher taxonomic resolution, at species or morphospecies level. The present taxonomic resolution in the MACROFAUNA database is typically at the order level. Increasing the taxonomic resolution will allow us to explore several additional topics. In particular, we could compare patterns of community structure at both taxonomic resolutions (order and morphospecies, Kaspari 2001, Ganault et al. 2021), which would be instrumental for identifying the mechanisms shaping biodiversity patterns. Similar patterns would suggest high niche conservation along evolution, and would imply that broad taxonomic data can be used as indicators of species-level patterns. On the opposite, contrasting patterns would suggest that species interactions, which are averaged at low taxonomic resolution, play a significant role at the macroecological scale, a point that is still hotly debated. Higher taxonomic resolution would also allow us to explore in greater depth patterns and drivers of functional and food-web structures. At the moment, we have a limited number of datasets at the species or morphospecies level, and we warmly encourage researchers to contribute with their own data.

### 2.3 Complementary data sources

We will use machine-learning techniques to model and map taxa distribution (Norberg et al. 2019). Because this kind of approach works better with large training datasets, we will complement the MACROFAUNA database for the mapping module with two additional datasets. Firstly, we will retrieve abundance data of earthworms, Chilopoda, Diplopoda, and Isopoda from the Edaphobase Portal https://portal.edaphobase.org/. This database is open access and contains data across 1315 localities for these four groups. Secondly, we have extracted 179836 separate occurrence data points for the 17 taxonomic groups from GBIF https://www.gbif.org/fr/, a large open database for an early step of the mapping process. These points may be used to complement the dataset and/or for specific purposes such as comparing different techniques and validating predictions. We will perform several analytical experiments to see if and how these datasets should be harmonized to produce distribution maps with the highest accuracy and certainty.

## 2.4 Future release of the database and derived products

We plan to release the MACROFAUNA database and static maps of macrofauna on open access. We will publish metadata on iDiv's data portal to increase findability. The interactive maps of macrofauna abundance will be hosted by OpenGeoHub. Overall, the project will release:

- The living MACROFAUNA database, with georeferenced data of soil macrofauna abundance, soil properties, human practices, and vegetation productivity.
- Global 1000 x 1000 m high-resolution interactive maps of abundance and biomass for the 17 soil taxa, together with macrofauna taxonomic richness and functional diversity.

## 3. Conceptual ideas and main goals of the working group

### 3.1 Patterns and drivers of soil macrofauna communities

A global perspective is needed regarding how soil macrofauna communities are structured across biomes and latitudes, to get a better understanding of the drivers of soil biodiversity and its functions (energy fluxes through trophic interactions, primary productivity, decomposition, nutrient cycling, air, and water fluxes). In order to develop a structured framework with clearly delineated approaches, we will address this topic from different angles and will plot the results in a series of maps.

### 3.1.1 Global patterns of soil macrofauna community abundance and diversity

Starting from the existing theory, we intend to assess to what extent soil macrofauna communities mirror
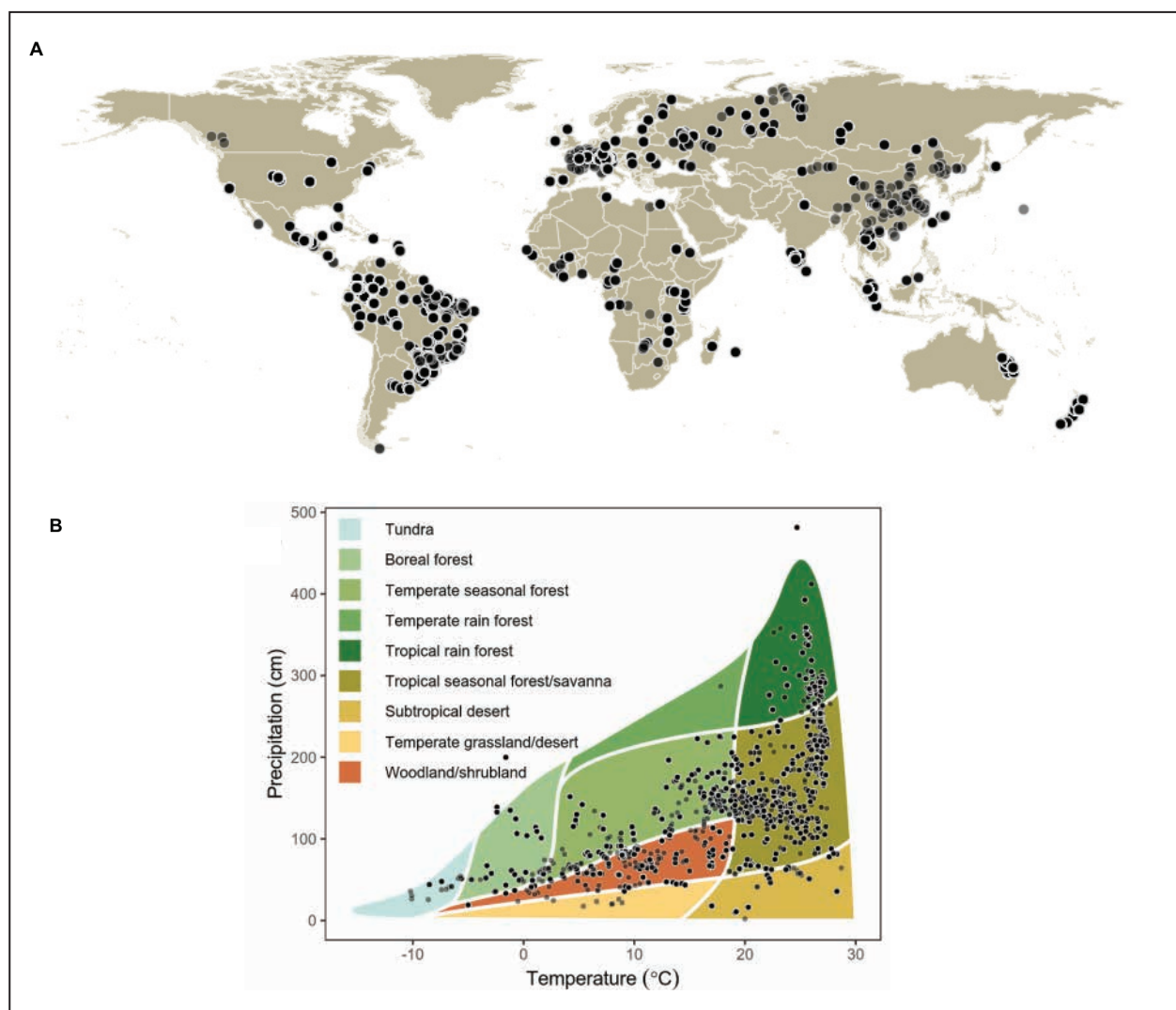
**Figure 1.** Location of the transects in the present version of the MACROFAUNA database (**A**) Map of the data (**B**) Location of the data in relation to the biomes.

latitudinal patterns and other general macroecological laws reported on aboveground organisms. For instance, we will explore if we find the traditional latitudinal gradient of biodiversity, with an increase in abundance and taxa number towards the tropics (Willig et al. 2003), or if we rather find alternative patterns such as those observed for other soil fauna (e.g., oribatids in Maraun et al. 2007). Describing the global patterns as a function of environmental variation will also allow us to identify the main environmental drivers of this variation. Latitudinal gradients of biodiversity have been mostly related to the increase in energy and resource availability in the tropics. Ecological theory states that a larger amount of energy might increase the abundance (More-Individuals Hypothesis, Wright 1983) and the diversity of species/taxa (Energy-diversity hypothesis, Wright 1983). Yet, different energetic resources for soil communities could lead to contrasting patterns for different taxa (Calderón-Sanou et al. 2022). For example, while the abundance of soil organisms directly linked to plants follows the latitudinal variation of their host (e.g., a higher diversity of ectomycorrhizal fungi in temperate ecosystems where the area of host vegetation is greater, Tedersoo et al. 2012), soil organisms consuming organic matter respond to changes in soil organic matter availability and thus show different latitudinal patterns (e.g. Oribatida diversity increased through northern latitudes, Caruso et al. 2019) (Fig. 2). Moreover, harsh abiotic conditions (e.g, frost events, acid soils, presence of pesticides) might also limit the abundance and diversity of soil macrofauna and influence their global patterns (Fig. 2) (Physiological Tolerance hypothesis, Currie et al. 2004; Beaumelle et al. 2020). We will use random
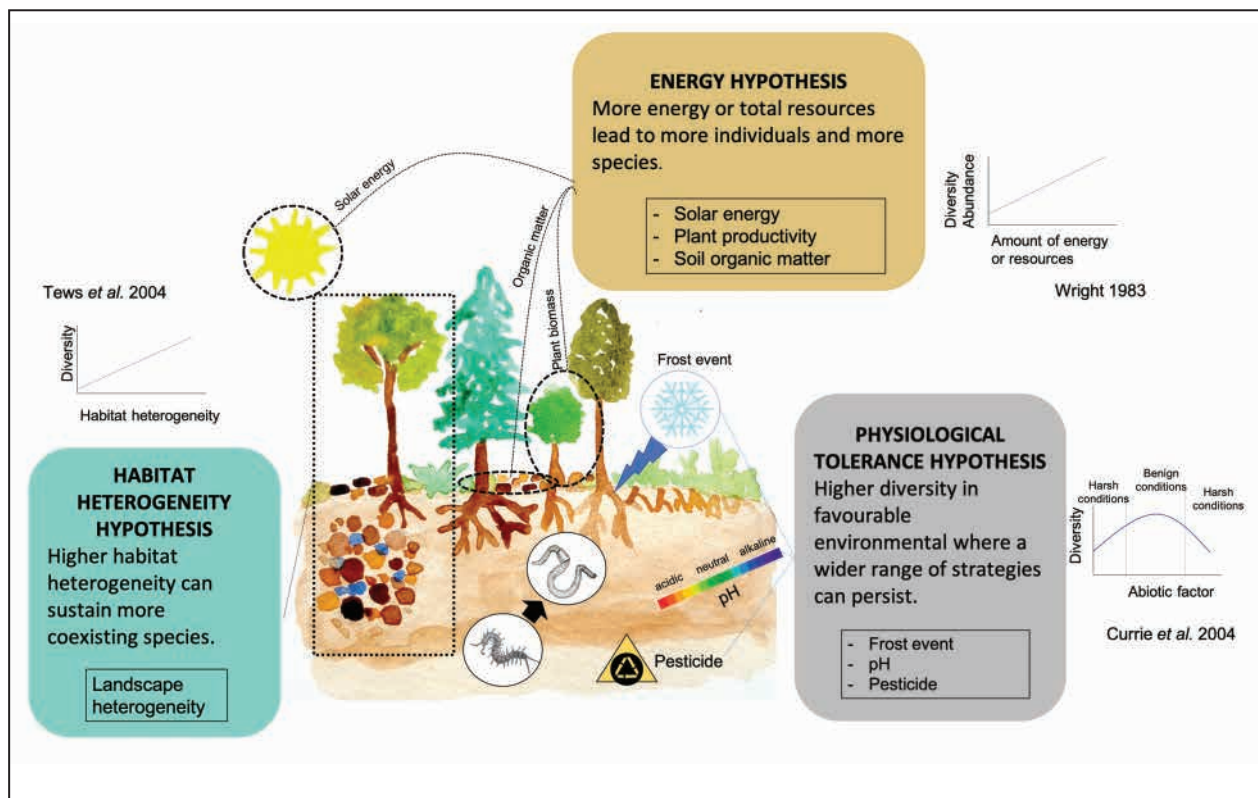
**Figure 2.** Main hypotheses of soil biodiversity drivers. Adapted from (Calderón-Sanou et al. 2022).

forest models (Breiman 2001), as we did in Calderón-Sanou et al. (2022), to evaluate the relative importance of several environmental factors in explaining soil macrofauna diversity. This method is particularly suited when nonlinear relationships are expected, which is typically the case in data with large spatial extent such as ours. It is also powerful to include data uncertainty by putting weights on observations depending on their quality. Relating these factors to different hypotheses will allow us to identify the main drivers and explain the observed latitudinal patterns for each taxa based on ecological theory. Finally, we will be able to discuss the similarities or discrepancies found across taxa and in comparison to aboveground organisms. Latitudinal gradients of soil macrofauna might also be dependent on the spatial grain of the analysis, as already shown for earthworms (Mathieu & Davies 2014, Phillips et al. 2019b). Finally, we will also compare the variation in abundance and diversity of soil macrofauna taxa between natural and anthropogenic land uses to assess how human activity modulates the expected macroecological trends. This will be achieved by comparing the response of soil macrofauna community structure along large environmental gradients in both natural and anthropized systems. This will allow us to quantify the effects of human activity at a global scale.

### 3.1.2 Global patterns of soil macrofauna community composition

Here, we will ask how soil macrofauna communities are structured at the global scale. Can we identify different 'community types' in the different biomes across the globe? We can expect a gradient from simplified communities in harsh environments (extreme conditions such as high perturbation levels or extreme soil conditions) to more complex communities where net primary productivity is high, with the highest complexity at intermediate disturbance level (Moi et al. 2020). We will also explore if communities from anthropogenic systems are subsets of natural ones (nestedness), or if alternatively, there is a strong composition turnover (replacement) and habitat specialization. The organization of vegetation in biomes globally has been a major discovery that frames ecosystem ecology in general. However, the extent to which soil macrofauna communities are also organized in clusters at the global scale, as found recently in aboveground communities (Mendoza & Araújo 2019), and how they relate to climatic conditions and vegetation biomes is still elusive. We will explore this pattern in natural and anthropogenic ecosystems, in order to assess if human activities have homogenized soil macrofauna communities at the global scale, and if they push local soil community composition away from macroecological

expectations. To do so, we will use multivariate analysis such as non-supervised ordination and clustering (e.g. PCA and k-means). Taking advantage of the fact that soil macrofauna communities encompass taxa with a diversity of traits, functional roles, and trophic guilds, we will also explore questions that have received little attention so far for aboveground organisms, because of a lack of data on the global scale. For instance, we will explore how food-web chain length (see section 3.2.1 for the methodology) and functional diversity vary with latitude and resource availability (Baiser et al. 2019). We will also relate the relative strength of predation, decomposition, and ecosystem engineering to global environmental gradients. Another question is whether macrofauna community structure follows the same pattern with depth, through the soil profile, independently of the biogeographical location, or if its distribution follows specific patterns in each region or soil type.

### 3.1.3 The effects of landscape heterogeneity on soil macrofauna communities

Landscape ecosystem heterogeneity effects on biodiversity are well studied in several fields of ecology, but evidence of these effects on soil organisms remains scarce, in particular for soil fauna (Ettema and Wardle, 2002). While it is expected that higher ecosystem heterogeneity drives higher local diversity (Fig. 2), at the landscape scale this is often related to the increased number of niches and diverse conditions (Tews et al. 2004). Typically, more homogeneous landscapes are associated with larger patch sizes and lower local ecosystem and environmental complexity (Fahrig et al. 2011, Ryser et al. 2021). This, in turn, relates to lower biodiversity, especially in modified systems (e.g., agriculture) where local impacts such as tillage can add up with landscape-scale effects. Though, evidence of the opposite can also be found in aboveground systems (e.g., tropical forests). It is now well established that soil organisms are affected by environmental features at multiple smaller scales because of their specific dispersal capacities (Bonte et al. 2004, Mathieu et al. 2004, 2009, Caro et al. 2013, Dupont et al. 2017, Thakur et al. 2020), but there is still no strong evidence of the direct effects of landscape heterogeneity on the diversification of soil conditions and soil biodiversity (but see Bonte et al. 2004, Mathieu et al. 2004, Aviron et al. 2005). The response of the taxa is most likely driven by their dispersal capacity, which is generally thought to be low but could actually be underestimated (Dupont et al. 2015, Le Provost et al. 2021). Here, we will test if ecosystem heterogeneity (e.g., given by multiple landscape metrics using land cover/ use as the basis for calculation, such as mesh size, patch connectivity, and patch size) is a good predictor of local soil macrofauna diversity while considering the effects of multiple landscape sizes. This will be achieved by multivariate linear regression and random forest. The goal is not only to understand how landscape heterogeneity is directly related to local soil biodiversity patterns but also to estimate at which spatial scale (here determined by landscape size) these effects are more significant.

### 3.1.4 The effect of land-use intensity on soil macrofauna communities

Land-use and agricultural management practices are key drivers of soil biodiversity and of ecological functions regulated by the activity of these organisms. The diversity of agricultural practices and environmental conditions (climate, landscape, soil type) creates a complex multivariate environmental gradient from which it is difficult to build a unique intensity index and to test general hypotheses such as the intermediate disturbance hypothesis. However, building a land-use intensification index and matching it with soil macrofauna data would be very valuable to establish baselines to which farmers and managers could refer. We will use the land management information data from the database (e.g., fertilizers, pesticides, tillage, inputs, irrigation) and existing indexes of land-use intensity (Fischer et al. 2010, Blüthgen et al. 2012) to build a multivariate index reflecting the major management options: tillage, inputs, fertilizers, irrigation, taking into account the nature, the amount and the frequency of the management (Decaëns & Jiménez 2002, Phillips et al. 2021). Because management options differ strongly from one land-use type to the other, we will first build separate land-use intensity gradients for the different land-use systems, and as a second step, see how they can be combined in one unified index.

We will explore the effect of land-use intensity on all taxa together, but also on the abundance of the separate 17 macrofauna taxa (typically at the order level). We expect that the different taxa will be affected specifically by different management interventions. For example, tillage is known to affect more large-bodied organisms than smaller ones through direct mortality (Phillips et al. 2019a), while organic matter additions may enrich whole communities, as energy is transferred from detritivores to higher trophic levels (Kelly et al. 2021, Olayemi et al. 2022). By comparing the response of the different taxa, we will be able to identify which taxa and functional groups are the most sensitive to land-use intensification.

Exploring the different dimensions of the index will allow us to identify the most influential management aspects and the ones that can support or degrade soil macrofauna communities. This will allow us to identify the potential leverages to manage soil macrofauna and explore the tradeoffs between the different dimensions

of management and seek a hypothetical multivariate optimal level of land-use intensity.

### 3.1.5 Stability of soil macrofauna communities

In the context of global change, soil communities will face an increased frequency and intensity of perturbations. We aim to estimate the ability of soil communities to cope with different types of perturbations, be it a single event (pulse perturbation, such as a forest clearcut) or changes that are repeated over time (multiple events, press perturbation, such as pesticides). By using the different ecological gradients of our dataset, and the index built in 3.1.4, we aim to investigate a general model predicting how the local abiotic (i.e., land use) and biotic (i.e., local diversity) context determine the fragility of communities that can thereafter be used to identify specific endangered ecosystems. To do so, we will look at the variations in community stability and relate them to environmental features. Since MACROFAUNA data allows estimating quantitative food webs thanks to energy flux estimations (see section 3.2.1), to estimate stability, we will follow the approach of de Ruiter et al. (1995) and use the quantitative food webs to parameterize Jacobian matrices (i.e., community matrices sensu May, 1972) that are central to stability analysis. Taking advantage of recently developed mathematical methods, we will also assess long- and short-term stability and the effect of disturbance on specific taxa (Haegeman et al. 2016, Arnoldi et al. 2019). In order to disentangle the respective effects of the different environmental gradients, which are correlated, we plan to start from ecological theory and build appropriate null models to test our hypothesis. We might also need to subset the database to isolate factors in case of strong bias in favor or certain range of the predictors.

### 3.1.6 Global drivers of body size of soil macrofauna

Understanding how macrofauna body size varies along environmental gradients is of major concern, as body size is strongly linked to both an organism's capacity to withstand adverse conditions and to its role in the ecosystem. Being able to predict taxa body size variation in response to environmental gradients is thus an important step towards understanding the effect of the environment on soil macrofauna communities and on their effect on ecosystem functioning. It has been suggested that body size of some organisms should increase with latitude (Bergmann' rule, Bergmann 1847), and Net Primary Productivity (Primary Productivity hypothesis, Aava, 2001, Morales-Castilla et al., 2012) but decrease with disturbance (Gibb et al. 2018) and temperature

(Gardner et al. 2011). However, these hypotheses were mostly developed on endotherms and the relevance for ectotherms is debated, because more complex or opposite trends have been observed, in particular for soil taxa (Shelomi 2012, Mathieu & Davies 2014, Karagkouni et al. 2016). We will test whether similar patterns are observed at a higher taxonomic resolution, typically order level, in soil macrofauna. With the data available, we will investigate the relationship between abundance, biomass, and average body size (biomass/abundance ratio) of the whole macrofauna communities, and of specific taxa. Modeling these relationships and identifying the main driving factors will allow us to estimate macrofauna biomass body size in sites where it was not measured. This will improve our approach to analyze food-web and energy fluxes reconstruction, which requires body size estimation. To predict body size, we will build separate models of body size distribution for each taxa in response to environmental conditions, and use this model to make predictions. We plan to use machine learning (e.g. random forests, Breiman 2001) and check afterward for spatial correlation in the residuals. If there is too much spatial correlation, then we will use generalized additive mixed model (GAMM, Wood 2006), which allows the modeling of nonlinear relationships with spatially correlated predictors.

## 3.2 Soil macrofauna diversity and ecosystem functioning

Soil macrofauna is involved in many ecosystem processes including primary productivity, soil structure formation and regulation, carbon and nutrient cycling, water and air fluxes regulation (de Graaff et al. 2015, Brown et al. 2018). However, precise quantification of the various effects of soil macrofauna taxa on ecosystem processes are lacking, and unbalanced, with a large proportion of studies investigating the role of earthworms (as ecosystem engineers) on primary productivity (van Groenigen et al. 2014), decomposition (Huang et al. 2020), soil aggregation (Lehman et al. 2017), bulk aggregation (Lehman et al. 2017) or nitrogen cycling (Xue et al. 2022). This knowledge gap can be explained by the tremendous diversity of macrofauna in terms of species, traits, and ecology, and therefore in terms of ecosystem processes impacted (Potapov et al. 2022a). Additionally, macrofauna effects depend on climate and soil conditions, making it even more difficult to set up experiments able to disentangle the effects of several taxa, their combination (e.g., diversity), in interaction with climate and soil properties. Although challenging, it is important to describe and quantify the relationship

between macrofauna (community and trophic structure, presence of specific taxa) and ecosystem processes, which we plan to address in two ways, first by quantifying fluxes of energy in soil food webs (Schwarz et al. 2017, Jochum & Eisenhauer 2022), and second by performing a meta-analysis on experiments that manipulated broad macrofauna groups and quantified the effect on ecosystem functions (primary productivity, decomposition, nutrient cycling, air, and water fluxes, Beaumelle et al. 2020).

### 3.2.1 Fluxes of energy in networks

Food webs are among the most comprehensive biodiversity analytical frameworks that account for interactions among different organism groups. Soil food webs are typically analyzed as quantitative networks, and energy fluxes therein were related to stability (Rooney & McCann 2012), biodiversity (Barnes et al. 2014), and multifunctionality (Potapov 2022b) of communities and ecosystems. This approach opens exciting perspectives to test macroecological patterns regarding the functioning of soil macrofauna communities. Thus far, no global-scale quantitative analyses of energy fluxes in soil food webs have been possible due to a lack of appropriate data. Since the MACROFAUNA database includes biomass data on multiple trophic groups including detritivores (e.g. earthworms, diplopods, isopods, termites, cockroaches), herbivores (e.g. hemipterans, homopterans, some beetle and butterfly larvae), predators (e.g. spiders, centipedes, some beetles, and flies), and omnivores (e.g. ants, earwigs, some beetles), it is possible to reconstruct the macrofauna compartment of soil food webs (Potapov et al. 2021) and analyze energy fluxes at a global scale using environmental temperature data. The energy flux approach quantifies all energetic transactions in the food web and can be used to quantify specific trophic functions: detritivory, herbivory, and predation (Barnes et al. 2014). We will build on the recent studies that used energy flux to estimate top-down pressure of herbivores on plants (Barnes et al. 2020) and top-down pressure of predators across trophic levels (Potapov et al. 2019). However, we will go further and test the following hypotheses at the global scale: (1) **climate hypothesis**: temperature and moisture are the two main drivers of energy fluxes in macrofauna food webs that increase total flux (Wall et al. 2008), total flux-to-biomass ratio, relative predation (Roslin et al. 2017), and herbivory-to-detritivory balance; (2) **productivity hypothesis**: ecosystem productivity increases total energy flux (Fig. 2, energy hypothesis), but decreases the relative predation pressure (Hatton et al. 2015, Jochum and Eisenhauer 2022) and the herbivory-to-detritivory balance; (3) **biodiversity hypothesis**: plant species richness increases total flux and relative predation pressure (Barnes et al. 2020); (4) **disturbance hypothesis**: disturbed ecosystems (croplands, plantations, densely human-populated areas) decrease relative predation pressure and multifunctionality, while increasing inequality in energy distribution among macrofauna groups (Potapov 2022b). In addition, we will explore how disturbance affects the slope between energy flux and taxonomic diversity in macrofauna communities (Barnes et al. 2014, Potapov et al. 2019).

### 3.2.2 Soil macrofauna and ecosystem processes

To quantify the contribution of different macrofauna taxa to different ecosystem processes, we propose a two-step approach. First, we will use the global database MACROFAUNA to assess the correlation between soil macrofauna community structure (taxa richness, dominance indexes, trophic length) and primary productivity. For this, we will use piecewise structural equation modeling (Lefcheck 2016), which allows us to test complex relationships between interacting variables. In order to go beyond correlation, we will develop in a second step a meta-analysis of studies that tested experimentally the effect of soil fauna on ecosystems processes (decomposition, nutrient cycling air and water fluxes) by manipulating soil fauna (addition or exclusion) in a controlled way (Bradford et al. 2002, Heemsbergen et al. 2004, Eisenhauer et al. 2012). We will prioritize field studies, but will also consider greenhouse and laboratory experiments, and use this information as moderator in the meta-analysis. This method has already proven useful to study the effect of earthworms on plant productivity (van Groenigen et al. 2014), of detritivorous macrofauna on litter mass loss (Frouz et al. 2015, Chassain et al. 2021), or predaceous macrofauna on pest control (Diehl et al. 2013, Greenop et al. 2018). Here, we propose to run a meta-analysis encompassing all macrofauna groups and ecosystem processes to assess which taxa-process relationships are studied or missing, and then we will quantify macrofauna effects on various ecosystem processes based on available data.

## 3.3 Towards a temporal and seasonal framework

Although seasonality is a fundamental feature of the environment (Mellard et al. 2019), in terrestrial ecosystems, studies encompassing the seasonality of organisms and ecosystem processes are highly biased towards the aboveground compartment (e.g. plant shoots, above-ground insects), and birds (Eisenhauer

et al. 2018). Concomitantly, it is widely known that the above and the belowground compartments interact and affect each other (Wardle et al. 2004, Eisenhauer et al. 2018). For instance, the timing of leaf fall, which represents an increase in resource availability for litter-dwelling organisms, especially in deciduous forests, determines when and how decomposition and nutrient cycling happen, which are primarily dependent on soil macrofauna activity (Guo et al. 2020). Moreover, it has been proposed that roots and root exudates, which present a strong seasonal trend, contribute substantially to the nutrition of soil animals (Albers et al. 2006, Pollierer et al. 2007). Seasonality also directly drives soil fauna activity through variations in temperature and humidity. It is well known that taxa such as earthworms, ants, and millipedes are not active during unfavorable conditions and can enter in quiescence until favorable conditions.

Two main energy channels can be differentiated in the soil: the green and the brown energy channels. Trophic interactions based on live organic matter, e.g. live leaves and roots, are called 'green', while interactions based on dead organic matter, e.g. litter, are called 'brown' (Odum 1969). The relative contribution of the green and brown channels for soil food webs may then vary along the year, according to climatic and plant seasonality. In more seasonal ecosystems (for instance, temperate ecosystems), roots follow a clear phenological pattern and grow mainly in spring and summer. However, in fall and winter, roots senesce and die, decreasing their availability as an energy source for soil macrofauna. In the same way, flowers and leaves also senesce during the colder periods, but this increases litterfall and the subsequent availability of detritus-based energy sources. Consequently, soil macrofauna food webs may shift resource use seasonally, following the seasonality of resource availability. In this project, we aim to test whether the energy source (green *vs*. brown channels) changes over the year in temperate and tropical ecosystems. To do so, we will use soil macrofauna data sampled in different seasons, which are available in the MACROFAUNA database, to estimate quantitative food webs (see section 3.2.1) and compare the relative importance of green to brown channels in soil food webs across seasons in different ecosystems. We hypothesize that in seasonal climates the balance between green and brown channels changes over the season, with a dominant green channel in spring and summer, and a dominant brown channel in fall and winter. We also expect that the ratio between green and brown channels will be different between temperate and tropical climates because of the higher litter recycling rate and lower soil nutrient content in the tropics.

### 3.4 Merging and scaling up data: methodological aspects

The biodiversity and abundance of soil macrofauna can be efficiently compared across sites using the Tropical Soil Biology and Fertility (TSBF) method (Lavelle 1988, Anderson & Ingram 1993, Lavelle et al. 2022). However, there are variations around this method, for instance, regarding the size of the samples, their depth, and the extraction method (hand-sorting in the field or in the lab, or extraction with a special apparatus in the lab). These methodological variations are likely to generate biases that need to be taken into account to produce better estimates of soil macrofauna abundance and diversity. We will build a statistical model that will allow us to rescale the data in a standardized way, and to combine datasets produced with variations around the official TSBF method. To do so, we will explore several sources of variation:

1. Depth of sampling. We will use data points with data by horizons to explore how soil macrofauna is distributed along the monolith profile (depth) in different climates and land uses. This will allow us to estimate the efficiency of shallow sampling, typically 0–10 cm depth samples, to capture the main and most abundant taxa, and the possible limitations of not considering deeper layers. We will also identify conditions (e.g., drier areas, or even under native vegetation like some forests) under which soil macrofauna is typically present below 10 cm, and should be sampled in deeper layers.

2. Intensity of sampling. In the official TSBF method, five or preferably ten samples (soil monoliths) along a transect are recommended to adequately sample the community at a given location (Anderson & Ingram 1993, Lavelle 1998). However, this sampling effort and spatial arrangement of the samples are major constraints and may not be achievable in some situations. As a consequence, many studies have used fewer samples or alternative spatial designs. Proposals for a minimum of three samples have been made recently (e.g., for FAO assessments on-farm, NETSOB and GLOSOB), but previous simulations estimated that a minimum of five samples per transect were required to compare abundance and diversity between land uses (Rossi et al 2006). Here, we will use a resampling approach to explore the effect of within-transect sampling effort and spatial arrangement to provide recommendations to take into account sampling intensity and spatial design in analyses.

3. Sampling date. We will explore how to take into account the sampling date during the year, as it is well known - but poorly documented - that organisms may be more abundant or diverse at different times of the year, due to seasonality. This will also allow us to determine the 'best sampling date or season' per ecosystem type and per region, to assess the full soil macrofauna community in different situations.

4. Presence of social insects. The absolute abundance and diversity of soil-dwelling social insects - ants and termites - is difficult to assess with the TSBF method, because the TSBF sampling design is not optimized to tackle the patchy distribution (both of individuals for a given species, and of species within a community) of these social insects. To assess the efficiency of the TSBF method for social insect abundance and biomass, we will compare data from TSBF samples with those from social insect specific sampling methods.

## 4. Composition and working mode of the group

The project is composed of a mix of young and senior scientists (see author's list of present paper for the composition). We believe that diversity breeds complementarity and performance also in work and science-related contexts. Therefore, we actively implemented measures to increase professional and cultural backgrounds and complementarity. The mix of expertise covers soil ecology, agronomy, interaction networks, phenology, macroecology, food webs, data management, GIS computing, and statistical modeling, acquired from experimental and theoretical approaches. Geographically, participants' origins cover North and South America, Europe, Asia, and Russia.

The sOilFauna project is funded by sDiv (grant SFW9.02) for three years, from 2022 to 2024, and will include three in-person workshops at sDiv (Leipzig, Germany), with regular additional online meetings. New collaborations are welcomed. Please approach the project leaders if interested: J. Mathieu and N. Eisenhauer. In order to clarify the terms of collaboration, we present here how we intend to include collaborators:

**Collaboration guidelines**
- We value the contribution of all data providers – the basis for any synthesis effort. We offer co-authorship to any data provider and associated workers that contributed to the data. Data providers will be co-author of the papers that use their data and will be ranked by contribution.
- We will create a *living database* that will grow over time to improve global coverage.
- We will form a global community of scientists (#GlobalSoilMacrofauna, http://www.globalsoil macrofauna.com) that will be informed about any scientific plans using the MACROFAUNA database.
- The first set of papers will follow an *opt-out approach*, where all workshop participants, data providers, and contributors will be listed and invited to contribute as authors.
- In the second set of papers, we will follow an *opt-in approach*, where all project members will be informed about proposed synthesis work and can actively engage in case of interest and significant contribution.
- Ideally, all contributed datasets will be released in the MACROFAUNA database to foster reproducibility. However, this can be modulated for specific datasets, based on data providers' constraints. We plan to develop a system with individual DOI for each subset, to increase data providers' credit and also to allow updates of the subdatasets.

## 5. Conclusions and outlook

To fully appreciate and address the biodiversity crisis and issues related to the sustainability of human activities such as agriculture, the community of soil ecologists is growing together to synthesize global datasets on soil biodiversity (e.g. Tedersoo et al. 2014, Delgado-Baquerizo et al. 2018, Phillips et al. 2019b, Smith et al. 2019, van den Hoogen et al. 2019, Guerra et al. 2020, 2021a). In many cases, this has become a very inclusive initiative with open calls for standardized data contribution, participation, co-authorship of subsequent products, as well as data storage and sharing (e.g. Maestre & Eisenhauer, 2019, Smith et al. 2019, Lembrechts et al. 2020, Ochoa-Hueso et al. 2020, Guerra et al. 2021b, Potapov et al. 2022a). With these numerous activities on the way, there is a special obligation to be globally representative and inclusive (Maestre & Eisenhauer 2019). Clear, inexpensive, and easily-repeatable methods are required and benefits for all partners have to be generated (Maestre a Eisenhauer 2019). Following this rationale, the #GlobalSoilMacrofauna consortium is collecting global soil macrofauna data in a standardized way to answer pressing questions in ecology. Soil

macrofauna is the most visible and accessible component of highly-diverse soil foodwebs, and may thus be of high interest to many researchers and land managers. Here, we present the first steps towards global syntheses, main research objectives and hypotheses, as well as collaboration guidelines to guide subsequent work. Given many similar interests at the moment, it will be important to create synergies between parallel initiatives like Soil BON (Guerra et al. 2021b, Potapov et al. 2022a), FAO (NETSOB and GLOSOB - methods and global observations activities), SoilFaUNa (Phillips et al., *in preparation*), etc. to harmonize approaches as much as possible. While the primary goal of this paper is to inform and encourage potential collaborators and data contributors, the main research questions and collaboration principles may also inspire other working groups and initiatives. We hope that this initiative will provide the required standardized soil macrofauna data for future research, as well as evaluation of ecosystem health and nature protection status. As such, our results should produce critical knowledge for developing evidence-based strategies in order to succeed in the agro-ecological transition of managed landscapes and will thus constitute a major milestone in the general understanding of soil ecology and ecosystem functioning.

## 6.  Acknowledgements

## 7.  References

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