REVIEW

BRITISH ECOLOGICAL SOCIETY | **Functional Ecology**

Linking effect traits of soil fauna to processes of organic matter transformation

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Abstract

1. Soil organic matter (SOM) transformation processes are regulated by the activities of plants, microbes, and fauna. Compared with plants and microbes, effects of soil fauna are less understood because of their high taxonomic and functional diversity, and mix of direct and indirect effect mechanisms. Trait-based approaches offer a generic perspective to quantify mechanistic relationships between soil fauna and SOM transformations, including decomposition, translocation, and stabilisation of organic carbon. Yet, at present, we lack a consensus concerning relevant key effect traits of soil fauna (i.e. those affecting ecosystem functioning).

2. Here, we address this knowledge gap by focusing on relationships between soil fauna effect traits and SOM transformations. Based on existing literature, we identify key processes linked to SOM transformations, and fauna effect traits universally applicable across taxa and soil types, and discuss the process-trait links.

3. We define eight SOM transformation processes that are directly affected by soil fauna: (i) litter mass loss, (ii) litter fragmentation, (iii) SOM aggregation in faeces, (iv) SOM aggregation in soil mineral particles, (v) decomposition of faeces, (vi) SOM and mineral translocation, (vii) pore space creation and maintenance and (viii) SOM stabilisation. We link these processes to general effect traits classified into four categories: (a) food selection and ingestion, (b), digestion and excretion, (c) mobility, and (d) body mass and metabolic rate. We also propose proxies when effect trait measurements are laborious.

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4. The proposed links between effect traits and SOM transformation processes need to be validated in targeted experiments. We urge researchers to obtain quantitative experimental data, together with metabolic approaches, to integratively quantify soil fauna contributions to soil functioning.

1 | INTRODUCTION

1.1 | Soil organic matter and soil biota

Photosynthesis and decomposition are the two main processes determining most terrestrial life. Approximately, 90% of primary production enters the soil organic matter (SOM) pool in the form of plant litter (Cebrian, 1999). Further transformation of SOM is determined by an interplay between organic matter physico-chemical properties, decomposer and detritivore community, and local environmental conditions (Hättenschwiler et al., 2005; Joly et al., 2023). A large part of SOM is decomposed by an array of soil organisms, that is, microbes and soil fauna, which transform organically bound carbon and nutrients to inorganic compounds, thereby making them available for plant uptake, released to the atmosphere, or sequestered in soil. This makes SOM transformation one of the key soil functions in terrestrial ecosystems, which is linked to several supporting and regulating ecosystem services, and underpinned by multiple interrelated soil processes (Greiner et al., 2017). Land use change and management intensification, in combination with an increase in the frequency, duration, and amplitude of extreme climatic events put pressure on organisms inhabiting soils and the ecosystem functions they perform. As soil fauna (from nematodes to earthworms) is involved in many soil processes related to SOM transformation (Angst et al., 2024; Frouz, 2018), such as the production of faeces, grazing on microbes, or mixing of organic matter and mineral soil, a shift in their community composition due to fluctuating environmental factors will impact many of these functions. However, our ability to predict the consequences of a shift in soil fauna species composition for ecosystem processes is very limited. We therefore urgently need an integrated predictive framework that allows us to study how changes in the composition of soil fauna communities impact the transformation of SOM.

1.2 | The Raunkiærian shortfall in soil fauna ecology

One basic premise of ecology is to provide predictions on what will happen to communities and ecosystems when environmental conditions are changing. We have made great progress in mapping the distribution of soil fauna across spatial scales (e.g. Delgado-Baquerizo et al., 2020; Phillips et al., 2019; Potapov et al., 2023; Van Den Hoogen et al., 2019), predicting their vulnerability to environmental change, and changes over space (Calderón-Sanou et al., 2024) and time (Zeiss et al., 2024). Currently, most of these mappings are based on taxonomic approaches, limiting our understanding of the mechanisms behind the observed patterns. There is an increasing body of evidence showing that the use of trait-based approaches provides not only a mechanistic understanding of community change but also enhances our ability to predict which type of species will respond positively or negatively to altered stress levels (McGill et al., 2006). Traits are here defined as morphological, physiological, phenological, and behavioural features measurable in an individual (sensu Pey, Nahmani, et al., 2014; Violle et al., 2007). Examples are predictable shifts in terrestrial isopod community composition across rural–urban land use gradients (Dias et al., 2013) or across soil moisture levels (Ooms et al., 2020) based on species-specific water loss rates. Our knowledge about traits in soil organisms has been rapidly growing over the last decades (Brousseau et al., 2018a, 2018b; Wong et al., 2018), and the construction of trait databases dedicated to soil fauna following standardised trait measurement protocols has been strengthening this research line (deCastro-Arrazola et al., 2023; Moretti et al., 2017; Pey, Laporte, et al., 2014). However, our limited knowledge on how and how strong traits of soil fauna affect soil processes – compared with for example, plants or vertebrates (Gonçalves-Souza et al., 2023) – evidences the so-called Raunkiærian shortfall regarding the lack of trait knowledge in soil fauna ecology (Hortal et al., 2015). Although several works study the impacts of single or multiple species on soil processes related to SOM transformation (e.g. Coulis et al., 2015; Hedde et al., 2007; Heděnec et al., 2022; Heemsbergen et al., 2004; Lavelle, 1996), our knowledge on how a shift in community-level trait composition affects SOM transformation remains rudimentary.

1.3 | Response and effect traits

If the taxonomic, and correspondingly, trait composition of the soil community is modified due to a change in land use management or climate, how do we quantify the associated change in the rate of key soil ecosystem functions? What are the most promising tools to measure it? One theoretical concept connecting the response of communities to environmental change with their impact on ecosystem functions is the so-called response-to-effect (R-to-E) trait framework, which was first proposed by Lavorel and Garnier (2002). The

basic premises of the framework are that: (i) if an ecosystem process of interest is selected, (ii) if the group of organisms that delivers this process is identified, and (iii) if the stressor at play to which this group of organisms has to respond is known, then (iv) the consequences of fluctuations in environmental factors on ecosystem functions can be linked via species-specific traits (Lavorel et al., 2013). Response traits of organisms relate directly to the environmental drivers of their occurrence and can inform us of the response of biotic assemblages to changes in these drivers through shifts in the species trait composition. Effect traits provide insight into how changes in species composition alter the ecosystem processes the community drives. When a linkage exists between response and effect traits, that is, if both are correlated or if they show a trade-off, the reaction of the ecosystem to a change in species composition (based on effect traits) due to environmental filtering (based on response traits) can be deduced (Lavorel et al., 2013). Multiple studies have used trait approaches across soil fauna taxa to study their responses to the environment (Luza et al., 2023; McGill et al., 2006; Schleuning et al., 2023; Warnke et al., 2023; Winemiller et al., 2015). Fewer studies, however, targeted general effect traits linked to ecosystem processes that soil fauna drive (see e.g. Hedde et al., 2022). Here, we follow the 'effect trait' facet of the framework to link specific soil fauna traits to distinct soil processes with the long-term goal of quantifying the contribution of soil fauna to SOM transformation processes. For this purpose, we here particularly focus on soil micro-, meso-, and macro- fauna, spanning several phyla that mainly belong to 'soil invertebrates', that is, nematodes, arthropods, annelids, and molluscs (Decaëns, 2010).

1.4 | Identifying fauna effect traits that link to soil processes

First, we identify key candidate traits based on the four biological processes that influence the main activities (see Winemiller et al., 2015)

performed by soil fauna during consumption, translocation, and transformation of plant-derived dead organic matter (i.e. saprophagy/detritivory in a broad sense; Le Guillarme et al., 2023): (1) food preferences, (2) internal food processing, (3) animal movement and (4) metabolic rate. Each of these categories results from the interactions of several traits that we aim to list in an integrated manner among soil fauna taxa involved in SOM transformation. Since 'hard' mechanistically specific traits are often difficult and laborious to measure, we identify proxies that are commonly measured as a substitute for some traits in ecological research (e.g. body mass as a proxy for consumption rate; Figure 1). Second, we distinguish the main ecological processes of SOM transformation possibly mediated by soil fauna traits: (1) litter mass loss, (2) subsequent litter chemical and physical transformation, and (3) translocation and stabilisation in the soil matrix. For each individual process, we list the associated traits of soil fauna. Our goal is to identify effect traits that allow us to predict how changes in species composition and abundance (community structure) affect ecosystem processes. Finally, we briefly describe perspectives in quantitative integration of the effect trait facet of the framework into the modelling of soil ecosystem functioning and highlight remaining gaps and frontiers on this path.

2 | KEY TRAITS OF SOIL INVERTEBRATES RELATED TO SOM TRANSFORMATION

Many soil invertebrates are microbivores, detritivores, or saprophages in a broad sense, feeding on microorganisms and dead plant material or soil organic matter (SOM; Le Guillarme et al., 2023; Potapov et al., 2022). Through their feeding and burrowing activities, soil invertebrates transform and translocate organic matter, affecting its physical and chemical characteristics and its interactions with microorganisms (Griffiths et al., 2021; Lavelle et al., 2006). The traits that are linked to these activities include food consumption

ORGANISM

ECOSYSTEM

What can we measure/estimate?

What do we want to know about the organism?

What do we want to know about the ecosystem?

Trait proxies

Effect traits

Processes of organic matter transformation

E.g. Body mass → E.g. Consumption rate → E.g. Litter mass loss

FIGURE 1 Conceptual link between effect traits of soil invertebrates and soil processes. In this example, decomposition (litter mass loss) is the process of interest and the unit of expression is the mass loss rate, which can be measured. Mass loss is affected by the litter consumption rate of a species (the key effect trait). Litter consumption rate, that is, the amount of litter consumed per unit of time, is causally related to the species' body size, as large organisms consume more litter than small organisms. As litter consumption rate measurements are time-consuming, body size can be used as a proxy for consumption rate.

('What and how much is consumed?'), digestion ('What is assimilated?') and excretion ('What is discarded?'; Figure 2). Next to the amount of SOM that is processed, characteristics of SOM that are left behind as faeces also affect soil processes (Coq et al., 2022) ('environment' and 'extended phenotype'; Figure 2). Furthermore, soil fauna can actively move across the soil and along the soil profile, carrying SOM inside and outside their bodies, and mixing different organic and mineral matter pools in the soil ('mobility'). Finally, we consider metabolic rate, body mass, and phenology of organisms as overarching scaling coefficients ('quantifiers') of invertebrate effects on soil processes—because the activity of organisms, and thus the amount of organic matter they can transform or carry, is directly related to these quantifiers. Below, we describe these main universal (i.e. applicable across taxa) soil invertebrate traits, grouped into four effect trait categories.

2.1 | Food preference and selection

Soil fauna exhibits a wide variability in feeding preferences, ranging from detritivores, microbivores, and herbivores to omnivores and carnivores. Based on previous research, we can roughly assign the feeding preferences of different invertebrate taxa to single or multiple organic substrates, such as microorganisms, living and decaying plant material, SOM, and other invertebrates (Potapov et al., 2022). Universal feeding preferences can be assigned across different invertebrate groups and can be linked to organic matter transformation processes. For example, invertebrates feeding on leaf litter affect litter mass loss (Patoine et al., 2017; Zhou et al., 2020). However, a high number of species can feed on different trophic levels (Digel et al., 2014) and the overall ability to feed selectivity could depend on the mode of ingestion (e.g. earthworms presumably ingest less selectively than springtails which can choose particular fungi on a substrate). Moreover, food selection depends on the availability of food sources, which may result in potential flexibility, that is, varying proportions of different resources in the diet when the most preferred food is limited (Briones, 2018; Briones et al., 2010). Thus, feeding preferences are the main universal effect trait to consider in this respect, and as a proxy for these preferences, classifying organisms into broad feeding guilds can be proposed (Hedde et al., 2022).

2.2 | Food ingestion, digestion, assimilation, and excretion

Ingested food is digested, partly assimilated, and partly excreted. Detritivores have a relatively low assimilation efficiency, typically ranging from 10% to 30% (Jochum et al., 2017; Winsome, 2005). Assimilation efficiencies that exceed 50% are very rare (e.g. for some termite species with complex microbial gut communities Wood & Sands, 1978). The low assimilation efficiencies of many soil invertebrates are assumed to be the result of the lack of the ability to produce endogenous cellulases (van der Drift, 1951). However, recently, cellulase-encoding genes have been isolated in various soil invertebrates (Griffiths et al., 2021; Muelbaier et al., 2024; Nozaki et al., 2009; Sade et al., 2018) and the explanation for low assimilation efficiencies may lay in the ratio between carbon and nitrogen in the consumed detritus (Jochum et al., 2017). Irrespective of specific causalities, repeatedly observed low assimilation efficiencies of detritivores have two important consequences: (1) most organic matter consumed by animals is not assimilated/respired, but is returned to the system in the form of faeces and (2) invertebrates need to ingest disproportionally high amounts of food to meet their metabolic demands. The physical and chemical properties of detritivore faeces are distinctly different from those of the substrate ingested especially when the organic matter ingested was initially of poor quality (Joly et al., 2020). In most cases, we observe a higher lability of organic matter in faeces (lower C:N ratio, increased dissolved organic carbon) that links directly to litter mass loss through leaching and microbial biomass production (Joly et al., 2020) and SOM aggregation (Bossuyt et al., 2005). Overall, invertebrate communities process relatively large quantities of detritus, changing its chemical and physical properties. In this context, digestive and assimilation capabilities (e.g. gut enzymatic activities and absorptive capacities) and substrate-to-faeces change in physical and chemical properties are important universal effect traits that are linked to organic matter dynamics in soil.

2.3 | Mobility

Soil invertebrates, especially large-sized ones, can actively move through the soil profile in the search for shelter or food, egg deposition, or avoiding predators or unfavourable environmental conditions. For example, detritivores can consume litter on the soil surface, but then move down the soil profile and deposit faeces in lower soil layers, redistributing organic matter across different horizons (Frouz, 2018). A remarkable example is anecic earthworms that live in semi-permanent rather deep vertical burrows and feed on leaf litter from the soil surface and drag it down in their burrow while ingesting soil from deeper layer before depositing casts on the surface which enhances SOM vertical redistribution. Invertebrate mobility may result in the translocation of microorganisms, thus modulating the activity of the latter on SOM dynamics (Lavelle et al., 2005). The vertical distribution of soil invertebrates could also be an indication of their association with different stages of decomposition (from fresh plant litter to SOM), hence different food qualities (Berg & Bengtsson, 2007). However, several manipulation studies demonstrated that environmental conditions (i.e. temperature and moisture) can exert a stronger influence than the substrate quality and drive downward movements that are related to ecomorphological traits of fauna (Briones et al., 2020; Juan-Ovejero et al., 2019; Krab et al., 2010). These vertical movements in response to environmental stress can be rapid, even for small animals such as meso- and micro-fauna (Briones et al., 1997; Whitford et al., 1981).

Movement and bioturbation behaviour of invertebrates—that are realised notably within the home range of the organism—also
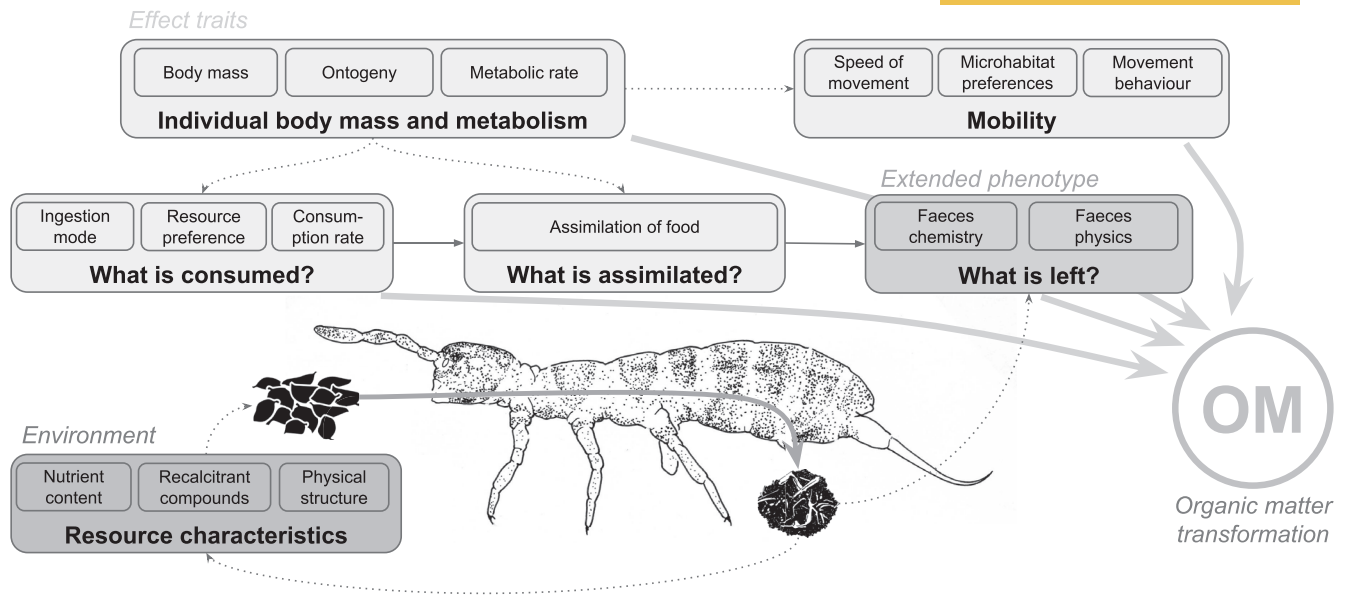
FIGURE 2 Main categories of effect traits of soil invertebrates potentially influencing SOM transformation and stabilisation. The effect trait categories are selected according to the main actions performed by fauna and their impacts on detritus parameters.

represent universal traits linked to redistribution of SOM and influencing its dynamics. The spatial home range, that is, its spatio-temporal habitat use, will determine the spatial direction and amount of material translocated, as well as the quality and type of the translocated resource (Auclerc et al., 2022). The home range can be approximated via descriptors of moving behaviour, such as the vertical and horizontal distribution (sometimes mentioned as an ecological preference, i.e., 'vertical stratification'), or moving speed and burrowing capacity (e.g. the body diameter and the appendages morphology).

2.4 | Body size, mass, and metabolic rate

Feeding and mobility-related traits can be assigned across various soil invertebrate taxa, but the final functional impact of an individual organism on ecosystem processes will depend on how much food it will consume/assimilate/excrete, how much material gets mixed, and how far and how much organic material it can carry to other places. All of those are closely linked to the metabolic rate and body mass of this organism. These two traits are interconnected and are often seen as key traits since they are related to most of the responses and the ecosystem effects of an organism (Moretti et al., 2017). Since soil invertebrates span over eight orders of magnitude in body mass, from less than a microgram to dozens of grams (Potapov, Rozanova, et al., 2021), body mass is a very informative effect trait in cross-taxa studies. Metabolic rate is the amount of energy needed to sustain an organism per unit of time and it scales closely with body mass and environmental temperature (Brown et al., 2004). Meta-analyses of metabolic rate estimates derived from numerous laboratory measurements showed taxon-dependent variation in metabolic rates across the biologically relevant temperature ranges (−2 to 40°C;

Ehnes et al., 2011; Meehan, 2006). Metabolic rate (that depends on the body size and mass of the organism) influences the overall consumption rate (Hendriks & Mulder, 2008; Petersen & Luxton, 1982), as well as the rate and temporal dynamics of several activities of an organism (Ulrich et al., 2015), which make it among the most important effect traits to consider in SOM transformations.

The feeding preferences of soil fauna encompass a broad spectrum. Invertebrates feeding on leaf litter, for instance, influence litter mass loss. However, many species can feed on different sources. This flexibility is influenced by the mode of ingestion and the varying food source availability and leads to different proportions of resources in the diet. Thus, classifying organisms into broad feeding guilds (e.g. detritivores, microbivores to carnivores, omnivores) is proposed as a proxy for feeding preferences. Ingested food is partly digested, assimilated, and excreted with detritivores exhibiting relatively low assimilation efficiencies. This results in the return of most organic matter as faeces, impacting SOM aggregation. Mobility in soil invertebrates—influenced by environmental conditions—affects the redistribution of organic matter across soil horizons. The metabolic rate and body mass of soil invertebrates—linked to each other and to environmental temperature—are critical for determining their functional impact on ecosystem processes, notably SOM transformations.

3 | LINKING INVERTEBRATE TRAITS TO THE PROCESSES OF SOM TRANSFORMATION

In our approach, we focus mainly on the role of invertebrates in SOM transformation via the consumption of plant-derived detritus, but it is inevitably interlinked with feeding on microbial and animal residues.

Based on existing reviews (e.g. Frouz, 2018) and literature included in the following sections, we identified the following critical processes related to SOM transformation that are affected by soil fauna: (i) litter mass loss, (ii) litter fragmentation, (iii) mixing of organic and mineral materials in invertebrate faeces, (iv) aggregation of particles, (v) microbial decomposition of faeces, (vi) particle translocation, (vii) pore space regulation, and (viii) SOM pools stabilisation. Below, we discuss each of these processes with specific reference to effect traits of soil invertebrates that play important roles therein and thereby differentiate respective proxies for such traits (Figure 3). Taken together, the established relationships between effect traits, their proxies, and the related soil processes provide a conceptual framework to better understand, explore, and predict the role of soil invertebrates in decomposition processes and SOM formation.

3.1 | Litter mass loss

Litter mass loss is one of the most important variables that describe the decomposition of dead plant material. Many soil animals use litter and the associated microorganisms as their main food resource (Potapov et al., 2022). Detritivores ingest small litter fragments, which are partly assimilated and transformed into biomass or respired. Undigested materials are expelled out as faeces (see below) and usually form a part of the litter fragmentation layer (Frouz, 2018; Prescott & Vesterdal, 2021), continuing in soil in the form of aggregates or in association with mineral soil. The more an animal consumes, the more mass is lost from the litter. Therefore, the effect trait that directly links to litter mass loss and that can be used across soil fauna taxonomic groups is litter consumption rate. Litter consumption rate is defined as the amount of ingested litter per unit of body mass and unit of time by animal(s). If multiplied by the biomass, this measure provides the absolute amount of litter lost due to ingestion by soil fauna (see e.g. cross-ecosystem calculations in Heděnec et al., 2022). This makes litter consumption rate a key trait in understanding, for example, how a change in litter-consuming species composition affects litter decomposition. However, measurement of this trait for individual species requires many laboratory experiments. One way to circumvent this time investment is using body mass as a substitute, making body mass a potential proxy of consumption rate. Within taxonomic groups, inter- as well as intraspecific consumption rate scales allometrically with the body size of species, via a log–log relationship. The larger the body is, the more litter absolutely speaking usually will be consumed. This holds across taxa with different body plans, such as insect larvae, earthworms, millipedes, and isopods. Body size can therefore be used as a scalable proxy for litter consumption rate that is more easily accessible via databases, literature, or direct measurements. Complementary to body mass, metabolic rate can be used as a proxy for consumption rate. This measure accounts for the temperature-related changes in the feeding activity of ectothermic consumers (Rall et al., 2012). The higher the temperature, the more substrate per unit of time is consumed if no severe limitations in water availability are
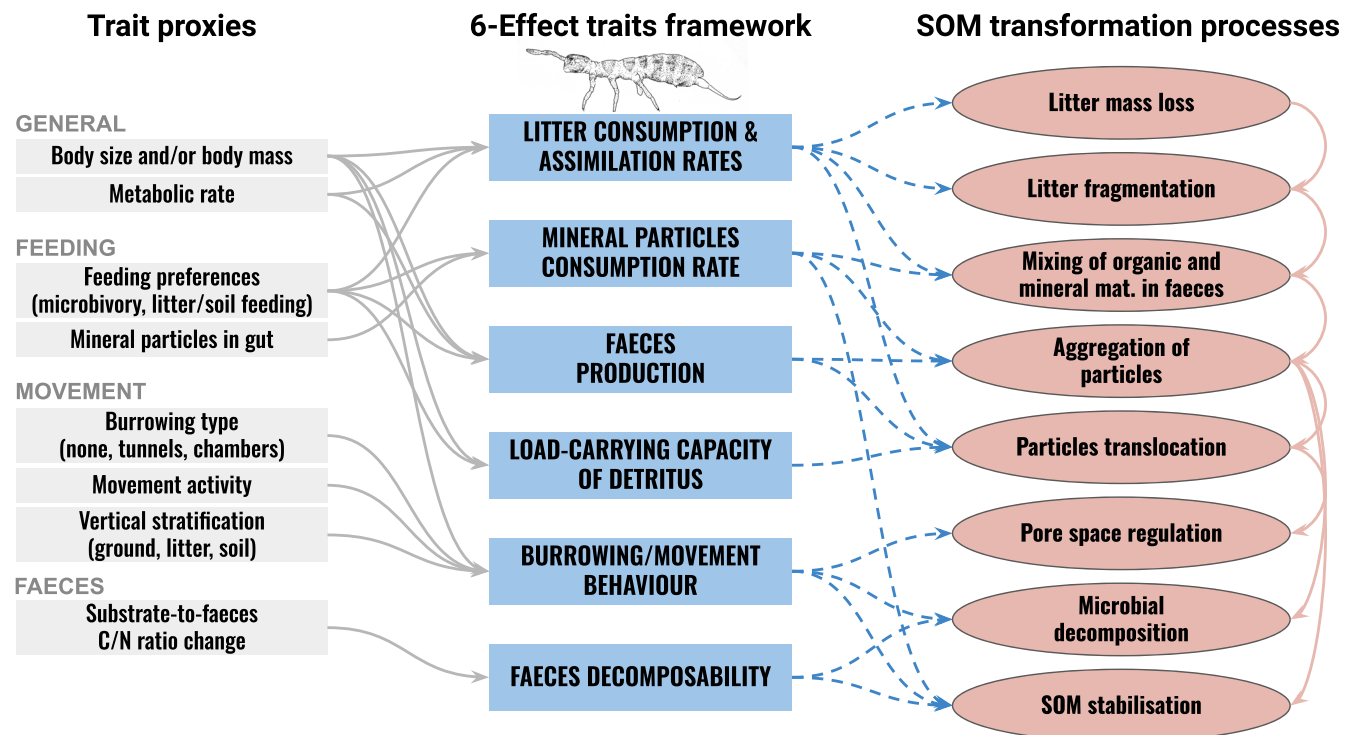
FIGURE 3 Six effect traits framework, highlighting how soil invertebrates activities affect soil organic matter transformation processes. Trait proxies (grey) are examples of functional traits that are considered appropriate candidates to estimate the key effect traits (blue). Effect traits (that also include extended phenotype, i.e. faeces) relate to soil fauna activities that influence the sequence of eight key SOM transformation processes (pink) through hypothetical trait–processes relationships (see Sections 3.1–3.8).

present. However, similar-sized species that belong to very different taxonomic groups, for example, an earthworm and a large beetle larva, can differ substantially in litter consumption rate. This might be due to differences in ingestion and/or assimilation rates or in resource use efficiency. Differences in ingestion rate between species that differ in body plan can be related to their mouthpart and digestive-tract morphology, and therefore, ingestion mode (Figure 3), at least qualitatively. Across taxa, different allometric coefficients (Ehnes et al., 2011) and feeding preferences (Potapov et al., 2022) should be accounted for.

3.2 | Litter fragmentation

Litter fragmentation is a major step in the decomposition process and is defined as the physical breakdown of leaf litter into smaller fragments (Giweta, 2020). Fragmentation increases the surface-to-volume ratio of the organic matter, which facilitates access to this resource by other soil biota, especially microorganisms, and thereby enhances decomposition and mineralisation (David, 2014; Frouz et al., 2015). Litter fragmentation is typically performed by soil-detritivorous invertebrates, such as millipedes, isopods, litter-feeding earthworms, and some insect larvae. The universal, and probably most relevant trait of soil invertebrates related to litter fragmentation is again litter consumption rate. Consumption rate defines the extent of litter fragmentation by assuming that the more an animal consumes, the more material it detaches from the leaf, and the smaller the litter fragments produced. As described above, body size and metabolic rate can be used as proxies of consumption rate, and thus are also linked to litter fragmentation. Besides, fragmentation depends on the ingestion mode of the animal, whether they feed selectively on soft plant tissues or also cut and graze on coarse detritus, consequently affecting the type of litter fragments produced. Ingestion mode (which can be expressed as a categorical trait) is related to mouthpart morphology across taxa, for example, the radula of gastropods, the chewing structures and gnathochilarium of millipedes, or the buccal apparatus of nematodes on the microscale. Also, within these groups, morphology strongly differs, for example, in terms of form and strength. Measurement protocols for arthropod mouthpart morphology such as mandible type (categorical) and mandible biting force (continuous) are available for across- and within-group comparisons (Ang et al., 2024; Brousseau et al., 2018a, 2018b; Raymond-Léonard et al., 2019), but such data collection usually involves extensive dissection and microscopy work. Currently, the mouthpart morphology data for soil invertebrates are scarce and mainly defined at a coarse taxonomic resolution.

3.3 | Mixing of organic and mineral materials in faeces

Animals consuming plant material and mineral soil particles mix both inside their gut. This process can be performed, for example, by earthworms or other macro- and mesofauna that feed on partly decomposed litter or SOM. This mixing directly affects the physical and chemical composition of faeces. For example, if litter is mixed with clay during passage through the earthworm gut, this physically reduces microbial access to organic matter and creates additional nutrient limitations (Frouz, 2018). To assess this process, the consumption rate of organic and mineral particles is probably the most informative trait. To estimate the consumption rate of mineral particles, proxies such as fraction of mineral particles in the gut or faeces can be used. This proportion may be associated with litter palatability (i.e. litter traits) that drives the feeding preference of detritivores between fresh litter and SOM (Sterner & Elser, 2002). Food selection may be important as well since unselective feeding may result in more mineral particles being ingested (e.g. some earthworms consume large quantities of SOM), which should also vary with the overall percentage of mineral particles in the soil. It can be expected that invertebrates burrowing deeper in soil ingest more mineral particles (because plant inputs to soil commonly decrease with depth) and thus the vertical distribution across the soil profile can also be used to predict the process of animal-driven mixing of organic and mineral materials. However, there is no solid empirical evidence supporting this. In fact, studies on springtails show that lower-soil-dwelling species do not have more amorphous material/hemorganic humus in their guts than upper-soil and litter-dwelling species (Ponge, 2000; Potapov, Pollierer, et al., 2021). Overall, we suggest measuring the fraction of mineral particles in the gut or faeces as the most informative trait and ingestion mode as a potential proxy for the organo-mineral mixing process via fauna ingestion.

3.4 | SOM aggregation in soil particles

Soil aggregation is the process by which organic and organo-mineral aggregates of different sizes are joined and sticked together (Lavelle et al., 2020; Mataix-Solera et al., 2011). Along with many other biotic agents, such as bacterial-produced oligosaccharides (Chotte, 2005), plant exudates (Baumert et al., 2018; Habib et al., 1990), or fungal mycelium (Lehmann, Leifheit, et al., 2017), soil fauna participate in glueing of various soil particles together (Lehmann, Zheng, et al., 2017). The aggregates of different sizes, shapes, and content contribute to the soil structure, including pore space (Statescu et al., 2013; Yudina et al., 2022), and reduce the access of decomposers to particulate organic matter occluded within aggregates (see also Section 3.8), thus stabilising carbon in soils. Overall, high soil aggregation is essential for preserving a number of core soil parameters, such as productivity, soil water and air regimes, resistance to erosion, degradation, and pollution (Mataix-Solera et al., 2011; Rabot et al., 2018). Soil aggregation is notably impacted by the activity of earthworms (Guhra et al., 2020; Zhang & Schrader, 1993) and mesofauna (Dos Santos Nascimento et al., 2021; Maaß et al., 2015; Siddiky et al., 2012). It is driven by faeces production, which can stabilise SOM and forms aggregates (Angst et al., 2024; Swaby, 1949), joints microaggregates and binds them with organic-enriched gut secretions (Zhang

& Schrader, 1993). Additionally, some taxa present building behaviours that lead them to bind faeces together to form macrostructures (e.g. Diplopoda, or Collembola in Poinsot, 1966). We suggest focusing on aggregation processes via faeces-driven mechanisms. The contribution of soil fauna to soil aggregation may be estimated by calculating the consumption and assimilation rate of detritus (i.e. affecting faeces production), and characterising faeces traits (size, stability, mineral fraction). These faeces traits need to be quantified in experiments measuring aggregation in the presence of specific animals during a certain period of time. Such an experimental approach would allow one to measure the direct participation of soil fauna in aggregate formation, which may include many mechanical and biochemical interactions.

In addition, the external excretion and egg-laying of arthropods also constitutes an input of SOM which binds microaggregates to the soil (Maaß et al., 2015). Further indirect effects are expected via interaction with plant roots and fungal mycelium (Erktan et al., 2020). Another positive effect on soil aggregation is provided by the external excretion of various biochemically rich products (Danladi & Ohaeri, 2020), which are well-known, for example, for earthworms ('mucus') (Guhra et al., 2020) and snails/slugs ('slime'). The liquid, enzyme-enriched fraction of excrement should also be considered. Via chemical assemblages with mineral compounds of soil (McCook, 1884), those excretions bind microaggregates and primary particles together, forming new meso- and macroaggregates ('repackaging', Joly et al., 2018). The effect of excreta-driven mechanisms on soil aggregation can be quantified via excretion rates, but these data are scarce, and future mesocosm experiments are needed to test the trait-process links.

3.5 | Degradation of faeces

Upon litter conversion into faeces by soil invertebrates, numerous physical, chemical, and biological transformations occur due to altered microbial activity and/or abundance (Coq et al., 2022) and to carbon and nutrient leaching (Joly et al., 2020). Recent studies showed that faeces C:N ratio, tannin content, water saturation capacity, specific area of the faeces, or of the particles within the faeces are important predictors of faeces mass loss and microbial activity (Coq et al., 2022; Joly et al., 2015, 2018, 2020). Typically, conversion into faeces leads to reduction in C:N ratio of up to 60% (Bastow, 2011; Ganault et al., 2022; Joly et al., 2018), improving the bioavailability of OM for microbial use. Therefore, we recommend the measurement of faeces C:N ratio as an easily measurable characteristic that correlates well with faeces mass, C, and N loss (Joly et al., 2020). Faeces characteristics are partially determined by litter's initial properties, that is, changes in C:N ratio upon litter conversion into faeces are higher for low-quality litter. Hence, we recommend to report the change in C:N from leaf litter to faeces by measuring both faeces and litter C:N ratio (Coq et al., 2022; Joly et al., 2020). Because of the low assimilation rates, faeces still contain many nutrients and are re-ingested or ingested by other fauna as a source

of nutrients (Briones, 2018). This mechanism adds a further trophic level to soil–plant–animal interactions (Zimmer & Topp, 2002) and makes it challenging to quantify mechanisms driving the net effect of litter-to-faeces conversion on microbial decomposition processes.

3.6 | SOM and mineral particle translocation

Particle translocation by soil fauna includes the redistribution of organic (or mineral) components within the soil matrix from one location to another (Auclerc et al., 2022; Eisenhauer et al., 2007; Wilkinson et al., 2009). It is complementary to physical transport of particles, for example, by water or gravity. Particle translocation modifies soil physical structure (Blouin et al., 2013; Lehmann, Zheng, et al., 2017), redistributes organic matter pools (Kononova, 2013), and changes nutrient availability for decomposer biota (Bottinelli et al., 2015; deCastro-Arrazola et al., 2023; Ferlian et al., 2022; Lavelle, 1996). A remarkable example of ecosystem-level consequences of these processes is the pronounced effect of invasive earthworms on soil properties and functions in previously earthworm-free ecosystems (Ferlian et al., 2020). An intuitive trait to assess fauna translocation activity is the individual load-carrying capacity that we define here as the capacity to transport and distribute matter (similar to that estimated for pollinators or leaf-cutting ants). This capacity results from a combination of morphological and anatomical (external and internal) traits on which we can hypothesise: (i) the animal's body shape and size/volume, complemented by the volume of its appendages, (ii) the adherence of particles to its cuticle (although some taxa like Collembola present strong anti-adhesive properties, see Helbig et al., 2011) and of its setae, and (iii) its movement behaviour expressed, for example, with locomotion traits such as the strength of its movement muscles or specific burrowing limbs, (iv) gut passage time of ingested material. In the perspective of a quantitative estimation of the translocation process, this load-carrying capacity of the individual is modulated by the home range of the animal.

3.7 | Pore space regulation: Creation and maintenance

Soil fauna may affect soil physical structure—thus SOM—by creating and maintaining pore space. This space causes modification of the microhabitat conditions, supports water infiltration, gas exchange (Bouché & Al-Addan, 1997; Lee & Foster, 1991), and the activity of small-bodied organisms as well as plant roots (Andriuzzi et al., 2016; Erktan et al., 2020; Medina-Sauza et al., 2019). These mechanisms interact in return with SOM. The traits involved in pore space creation are in relation with the burrowing and digging activities of soil fauna. These activities concern primarily earthworms, ants and termites, and secondarily dung beetles, insect larvae, springtails and spiders, soil-nesting bees and wasps, and mole crickets. The burrowing capacity of the animal (see Section 3.6) is related to morphological traits such as body diameter (even though social insects

may build tunnels much larger than themselves), while the burrowing behaviour (Blanchart et al., 2009; Meurer et al., 2020) varies across taxa and within a taxa along with its ontogeny (e.g. between a larva and an adult). The traits involved in pore space maintenance are related to the movement behaviour of the animal, such as enchytraeids that remove pore necks/blockages, thereby maintaining the openness and connectivity of macropores (Porre et al., 2016). Quantifying the burrowing behaviour of taxa needs standardised laboratory experiments. Although the burrowing rate has previously been measured for different species or functional groups of earthworms (e.g. Capowiez et al., 2015, 2024; Ruiz et al., 2017), the information remains scarce for other taxa (but see e.g. Bryson, 1939; Mele et al., 2021; Kravchenko, 2022). A first approximation to estimate the importance of this process across soil invertebrate taxa and ecosystems could be done by measuring the contributions of different taxa to soil porosity using X-ray CT scanning and linking it with water infiltration measurements. By doing so, Capowiez et al. (2015) showed that water infiltration rates were largely explained by total volume of bioturbation which corresponds to macropores totally or partially refilled with casts or casts crushed along the burrow walls. More recently, Pham et al. (2023) were able to relate three main traits (body weight, circular and longitudinal muscle thickness) to earthworms' influence on soil water infiltration. The use of such traits provides a mechanistic understanding of how soil fauna affect soil porosity and ecosystem processes.

3.8 | SOM pool stabilisation

The stability of SOM in soil is of paramount importance for soil fertility and climate change mitigation (Angst et al., 2023; Lavallee et al., 2020). SOM stability is often determined by separating SOM into two functionally different pools, of which the formation can be strongly affected by soil fauna (Angst et al., 2024): particulate organic matter (POM) and mineral-associated organic matter (MAOM). POM is composed of partly decomposed plant fragments and has relatively short residence times in soil (up to several years), if not occluded within aggregates (see Section 3.4; Mueller & Koegel-Knabner, 2009). The major process by which POM enters mineral soils is via the physical transfer of organic particles from aboveground litter or organic horizons. This transfer is mostly driven by soil fauna (see Section 3.6). Taxa with an intense vertical movement between litter/organic and mineral horizons can be expected to increase the amount of POM in soil (e.g. anecic earthworms; Ma et al., 2014) via mixing of organic particles and mineral soil (see Section 3.3). Accumulation of POM could be further fostered if such taxa have high excretion rates, as faeces can represent POM themselves and/or constitute the nucleus for the formation of aggregates (Angst et al., 2024), in which POM is protected against microbial decay (see Sections 3.4 and 3.5). Correspondingly, traits relevant to the accumulation of POM could be inferred from movement behaviour, such as temporal changes in the vertical distribution, moving speed, and burrowing capacity of fauna (see Sections 3.3–3.6)

combined with measurements of consumption and assimilation rates (see Section 3.1).

MAOM represents intimate associations of SOM with mineral surfaces that can persist in soil on centennial to millennial timescales (Lehmann et al., 2020). MAOM is considered to form via two major pathways: (i) sorption of dissolved OM or depolymerized plant compounds to mineral surfaces; and (ii) sorption of microbial residues or necromass to mineral surfaces after microbial death (Liang et al., 2017). These pathways can be directly or indirectly affected by certain soil fauna traits. For example, ingestion mode and feeding preferences (i.e. when involving the consumption of microbes in mineral soil, or direct microbivory) can affect microbial community composition, activity, and biomass (Jiang et al., 2018; Niu et al., 2024; Rosenberg et al., 2009), and in turn emergent microbial traits such as carbon use efficiency, with potentially strong effects on microbial necromass production and MAOM formation (Tao et al., 2023). Likewise, biochemical substances excreted by soil fauna or dissolved organic matter released from faeces could adsorb on reactive mineral surfaces or boost efficient growth of microorganisms and thus MAOM formation (see Section 3.4; Angst et al., 2022, 2024; Kou et al., 2023). As the main traits and their proxies to measure, we suggest feeding preferences for microbes, consumption rate, the proportion of mineral particles in faeces, and movement behaviour.

Research on the effects of soil fauna traits on POM or MAOM formation is extremely scarce (Coq et al., 2022; Le Mer et al., 2022). We thus see a clear need for mechanistic studies, at both laboratory and field scales, that tackle this vast research gap.

4 | APPLICATION AND PERSPECTIVES

The integration of effect traits and their links to an organism's role in a specific SOM transformation process can serve to improve existing models of soil functioning in terms of (i) generality across soil fauna taxa, that is, combined actions of different taxonomic groups, and (ii) dimensionality through the use of the six effect traits. For example, in a nutrient fluxes model such as the one presented by Barot et al. (2007), the six effect traits information could inform the single information block used for taxa (here, earthworms). Since trophic interactions among soil taxa also impact soil processes, the proposed effect traits can also be integrated into soil food-web modelling, and hence, would help in defining edges (interactions and their strength) between different pools of SOM and functional groups (see also Fry et al., 2019) via specific soil processes (Figure 4; Brousseau et al., 2018a, 2018b; Potapov, 2022). Our approach can, for example, bring dimensionality to the 'detritivores' compartment of the KEYLINK (Flores et al., 2021) or Romul-hum models (Chertov et al., 2017). In such models, authors mainly use the quantitative flux of matter or energy transferred between compartments per unit of time to estimate the processes. The generic six trait information can be used to obtain a more accurate estimation of fluxes whatever the taxonomic identity of the detrivore is considered. For example, the energy flux from litter to litter-feeding invertebrates can be a
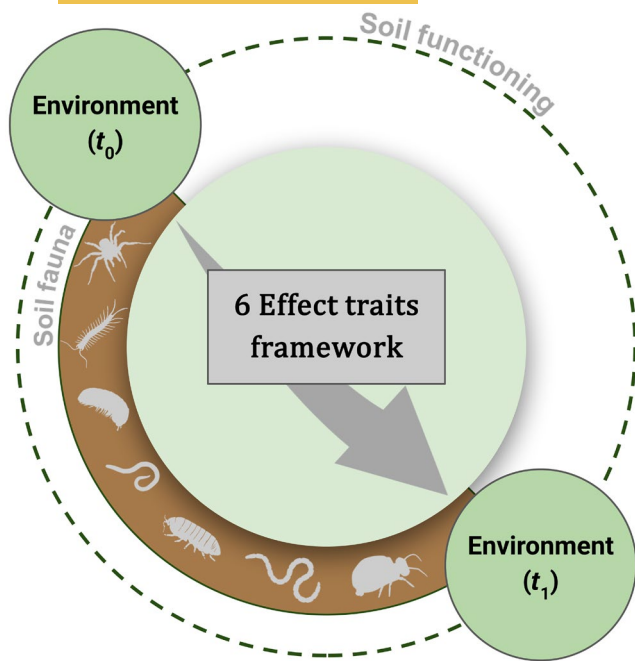
FIGURE 4 Conceptual integration of effect traits of soil invertebrates in dynamic modelling of soil processes.

quantitative proxy of the litter mass loss, litter fragmentation, and faeces production (if assimilation efficiency is taken into account; Potapov, 2022). Our trait-based approach—which focuses on soil invertebrates—is also theoretically generalisable to all soil fauna taxa (Anthony et al., 2023) and could, for example, encompass megafaunal vertebrates or the soil-dwelling larval stages of various flying insects.

Our framework can also be projected in space and time, that is, at small scales to study, for example, the heterogeneity of soil properties, and at larger scales informing functional biogeography of soil fauna. To this end, the spatio-temporal variability of organism communities, their trait values (e.g. changing consumption rates and associated efficiencies with litter quality), and universal quantifiers (e.g. changing metabolic rate due to variation in environmental temperature with day, season, or climate) need to be taken into account: some of the effect traits are also response traits. Temperature is a strong modulator of metabolic and feeding rates at different time scales, which have important implications for soil functioning (Briones, 2018; Thakur et al., 2018). Climatic and seasonal rhythms may interfere with individual traits related to ontogeny and phenology, which also drive fauna-mediated soil functions such as decomposition (Sagi & Hawlena, 2024). This implies that both individual values and community-level mean values of each trait vary with the environment at different time frames. The former also impacts the latter through the concept of intraspecific trait variability, on which knowledge is still growing in soil fauna studies, but trait databases can handle different levels of organisation (see e.g. regional and continental values in Bonfanti et al., 2018).

Overall, we call for a joint effort to collect effect traits of soil invertebrates to create mechanistic soil functioning models. Such

models would allow us to predict how changes in community composition will impact ecological functions and processes in the future biosphere. Soil fauna trait-based ecology has emerged in the past two decades, yet there have been few attempts for standardised trait data collection. Standardised protocols have been developed (Moretti et al., 2017) and databases mostly filled with literature-based species-level data across soil taxa have been made available, for example, BETSI (Pey, Laporte, et al., 2014) or Ecotaxonomy (Potapov et al., 2019). These collections represent an important resource for a first attempt in obtaining data of our proposed six effect traits (or for their trait proxies, that are more likely to be available for a wide array of taxa) when measuring traits in situ is not feasible. Now, we call for more targeted collections of soil fauna effect traits that are directly linked to soil processes, as identified in our conceptual framework. This should be based on open communication among researchers and by applying standard protocols. We also highlight the value of standardised mesocosm experiments to validate trait-process links (e.g. KEYSOM Cost Action in Jiménez et al., 2020). Ultimately, the exchange between trait databases and soil biodiversity occurrence (community) databases will allow for an upscaling of the effect of soil communities on ecosystem functioning through the present effect trait framework. Initiatives such as COST Action EUdaphobase (https://www.cost.eu/actions/CA182 37/) embraced this dialogue as one of their major goals.

AUTHOR CONTRIBUTIONS

Anton M. Potapov, Jonathan Bonfanti, Gerrit Angst, Pierre Ganault and Matty P. Berg conceived the ideas, designed methodology, and analysed the literature; Anton M. Potapov and Jonathan Bonfanti led the writing of the manuscript; Jonathan Bonfanti, Anton M. Potapov, Gerrit Angst, Pierre Ganault, Maria J. I. Briones, Irene Calderón-Sanou, Ting-Wen Chen, Erminia Conti, Florine Degrune, Nico Eisenhauer, Olga Ferlian, Davorka Hackenberger, Amelie Hauer, Mickaël Hedde, Karin Hohberg, Paul Henning Krogh, Christian Mulder, Camila Perez-Roig, David Russell, Oren Shelef, Zheng Zhou, Andrey G. Zuev, and Matty P. Berg participated in collecting the literature, contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare. Maria J. I. Briones is an Associate Editor of *Functional Ecology* but took no part in the peer review process of this article.

DATA AVAILABILITY STATEMENT

No data are used in the study.

STATEMENT ON INCLUSION

Our study consists of a narrative review, that is, a secondary analysis and interpretation of a body of knowledge resulting from a literature review on which no geographical restriction was applied. The majority of authors are affiliated with institutions across various European countries, with additional representation from South America and Southeast Asia. Approximately, one-third of the authors are early career researchers. All authors were equally encouraged to contribute throughout various stages of the entire study process.

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REFERENCES

Andriuzzi, W. S., Ngo, P.-T., Geisen, S., Keith, A. M., Dumack, K., Bolger, T., Bonkowski, M., Brussaard, L., Faber, J. H., Chabbi, A., Rumpel, C., & Schmidt, O. (2016). Organic matter composition and the protist and nematode communities around anecic earthworm burrows. *Biology and Fertility of Soils*, 52(1), 91–100. https://doi.org/10.1007/s00374-015-1056-6

Ang, S. B. H., Lam, W. N., Png, G. K., Tan, S. K. B., Lee, B. P. Y.-H., Khoo, M., Luskin, M. S., Wardle, D. A., & Slade, E. M. (2024). Isopod mouthpart traits respond to a tropical forest recovery gradient. *Oecologia*, 204(1), 147–159. https://doi.org/10.1007/s00442-023-05494-8

Angst, G., Frouz, J., Van Groenigen, J. W., Scheu, S., Kögel-Knabner, I., & Eisenhauer, N. (2022). Earthworms as catalysts in the formation and stabilization of soil microbial necromass. *Global Change Biology*, 28(16), 4775–4782. https://doi.org/10.1111/gcb.16208

Angst, G., Mueller, K. E., Castellano, M. J., Vogel, C., Wiesmeier, M., & Mueller, C. W. (2023). Unlocking complex soil systems as carbon sinks: Multi-pool management as the key. *Nature Communications*, 14(1), 2967. https://doi.org/10.1038/s41467-023-38700-5

Angst, G., Potapov, A., Joly, F.-X., Angst, Š., Frouz, J., Ganault, P., & Eisenhauer, N. (2024). Conceptualizing soil fauna effects on labile and stabilized soil organic matter. *Nature Communications*, 15(1), 5005. https://doi.org/10.1038/s41467-024-49240-x

Anthony, M. A., Bender, S. F., & Van Der Heijden, M. G. A. (2023). Enumerating soil biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 120(33), e2304663120. https://doi.org/10.1073/pnas.2304663120

Auclerc, A., Beaumelle, L., Barantal, S., Chauvat, M., Cortet, J., De Almeida, T., Dulaurent, A.-M., Dutoit, T., Joimel, S., Séré, G., & Blight, O. (2022). Fostering the use of soil invertebrate traits to restore ecosystem functioning. *Geoderma*, 424, 116019. https://doi.org/10.1016/j.geoderma.2022.116019

Barot, S., Ugolini, A., & Brikci, F. B. (2007). Nutrient cycling efficiency explains the long-term effect of ecosystem engineers on primary production. *Functional Ecology*, 21(1), 1–10. https://doi.org/10.1111/j.1365-2435.2006.01225.x

Bastow, J. L. (2011). Facilitation and predation structure a grassland detrital food web: The responses of soil nematodes to isopod processing of litter: Facilitation and predation structure a soil food web.

Journal of Animal Ecology, 80(5), 947–957. https://doi.org/10.1111/j.1365-2656.2011.01853.x

Baumert, V. L., Vasilyeva, N. A., Vladimirov, A. A., Meier, I. C., Kögel-Knabner, I., & Mueller, C. W. (2018). Root exudates induce soil macroaggregation facilitated by fungi in subsoil. *Frontiers in Environmental Science*, 6, 140. https://doi.org/10.3389/fenvs.2018.00140

Berg, M. P., & Bengtsson, J. (2007). Temporal and spatial variability in soil food web structure. *Oikos*, 116(11), 1789–1804. https://doi.org/10.1111/j.2007.0030-1299.15748.x

Blanchart, E., Marilleau, N., Chotte, J.-L., Drogoul, A., Perrier, E., & Cambier, C. (2009). SWORM: An agent-based model to simulate the effect of earthworms on soil structure. *European Journal of Soil Science*, 60(1), 13–21. https://doi.org/10.1111/j.1365-2389.2008.01091.x

Blouin, M., Hodson, M. E., Delgado, E. A., Baker, G., Brussaard, L., Butt, K. R., Dai, J., Dendooven, L., Peres, G., Tondoh, J. E., Cluzeau, D., & Brun, J.-J. (2013). A review of earthworm impact on soil function and ecosystem services: Earthworm impact on ecosystem services. *European Journal of Soil Science*, 64(2), 161–182. https://doi.org/10.1111/ejss.12025

Bonfanti, J., Hedde, M., Joimel, S., Krogh, P. H., Violle, C., Nahmani, J., & Cortet, J. (2018). Intraspecific body size variability in soil organisms at a European scale: Implications for functional biogeography. *Functional Ecology*, 32(11), 2562–2570. https://doi.org/10.1111/1365-2435.13194

Bossuyt, H., Six, J., & Hendrix, P. F. (2005). Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology and Biochemistry*, 37(2), 251–258. https://doi.org/10.1016/j.soilbio.2004.07.035

Bottinelli, N., Jouquet, P., Capowiez, Y., Podwojewski, P., Grimaldi, M., & Peng, X. (2015). Why is the influence of soil macrofauna on soil structure only considered by soil ecologists? *Soil and Tillage Research*, 146, 118–124. https://doi.org/10.1016/j.still.2014.01.007

Bouché, M. B., & Al-Addan, F. (1997). Earthworms, water infiltration and soil stability: Some new assessments. *Soil Biology and Biochemistry*, 29(3–4), 441–452. https://doi.org/10.1016/S0038-0717(96)00272-6

Briones, M. J. I. (2018). The serendipitous value of soil Fauna in ecosystem functioning: The unexplained explained. *Frontiers in Environmental Science*, 6, 149. https://doi.org/10.3389/fenvs.2018.00149

Briones, M. J. I., Carrera, N., Huang, J., Barreal, M. E., Schmelz, R. M., & Garnett, M. H. (2020). Substrate quality and not dominant plant community determines the vertical distribution and C assimilation of enchytraeids in peatlands. *Functional Ecology*, 34(6), 1280–1290. https://doi.org/10.1111/1365-2435.13537

Briones, M. J. I., Garnett, M. H., & Ineson, P. (2010). Soil biology and warming play a key role in the release of 'old C' from organic soils. *Soil Biology and Biochemistry*, 42(6), 960–967. https://doi.org/10.1016/j.soilbio.2010.02.013

Briones, M. J. I., Ineson, P., & Piearce, T. G. (1997). Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. *Applied Soil Ecology*, 6(2), 117–134. https://doi.org/10.1016/S0929-1393(97)00004-8

Brousseau, P., Gravel, D., & Handa, I. T. (2018a). Trait matching and phylogeny as predictors of predator–prey interactions involving ground beetles. *Functional Ecology*, 32(1), 192–202. https://doi.org/10.1111/1365-2435.12943

Brousseau, P.-M., Gravel, D., & Handa, I. T. (2018b). On the development of a predictive functional trait approach for studying terrestrial arthropods. *Journal of Animal Ecology*, 87(5), 1209–1220. https://doi.org/10.1111/1365-2656.12834

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. https://doi.org/10.1890/03-9000

Bryson, H. R. (1939). The identification of soil insects by their burrow characteristics. *Transactions of the Kansas Academy of Science (1903-)*, 42, 245–253.

Calderón-Sanou, I., Ohlmann, M., Münkemüller, T., Zinger, L., Hedde, M., Lionnet, C., Martinez-Almoyna, C., Saillard, A., Renaud, J., Le Guillarme, N., Gielly, L., Consortium, O., & Thuiller, W. (2024). Mountain soil multitrophic networks shaped by the interplay between habitat and pedoclimatic conditions. *Soil Biology and Biochemistry*, 190, 109282. https://doi.org/10.1016/j.soilbio.2023.109282

Capowiez, Y., Bottinelli, N., Sammartino, S., Michel, E., & Jouquet, P. (2015). Morphological and functional characterisation of the burrow systems of six earthworm species (Lumbricidae). *Biology and Fertility of Soils*, 51(7), 869–877. https://doi.org/10.1007/s00374-015-1036-x

Capowiez, Y., Marchán, D., Decaëns, T., Hedde, M., & Bottinelli, N. (2024). Let earthworms be functional—Definition of new functional groups based on their bioturbation behavior. *Soil Biology and Biochemistry*, 188, 109209. https://doi.org/10.1016/j.soilbio.2023.109209

Cebrian, J. (1999). Patterns in the fate of production in plant communities. *The American Naturalist*, 154(4), 449–468. https://doi.org/10.1086/303244

Chertov, O., Komarov, A., Shaw, C., Bykhovets, S., Frolov, P., Shanin, V., Grabarnik, P., Priputina, I., Zubkova, E., & Shashkov, M. (2017). Romul_Hum—A model of soil organic matter formation coupling with soil biota activity. II. Parameterisation of the soil food web biota activity. *Ecological Modelling*, 345, 125–139. https://doi.org/10.1016/j.ecolmodel.2016.10.024

Chotte, J.-L. (2005). Importance of microorganisms for soil aggregation. In A. Varma & F. Buscot (Eds.), *Microorganisms in soils: Roles in genesis and functions* (Vol. 3, pp. 107–119). Springer-Verlag. https://doi.org/10.1007/3-540-26609-7_5

Coq, S., Ganault, P., Le Mer, G., Nahmani, J., Capowiez, Y., Dignac, M.-F., Rumpel, C., & Joly, F.-X. (2022). Faeces traits as unifying predictors of detritivore effects on organic matter turnover. *Geoderma*, 422, 115940. https://doi.org/10.1016/j.geoderma.2022.115940

Coulis, M., Fromin, N., David, J., Gavinet, J., Clet, A., Devidal, S., Roy, J., & Hättenschwiler, S. (2015). Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels. *Oikos*, 124(10), 1304–1316. https://doi.org/10.1111/oik.01917

Danladi, J. G., & Ohaeri, O. C. (2020). Proximate and mineral composition of snail slime (*Achatina marginata*). *World Journal of Pharmacy and Pharmaceutical Sciences*, 9(11), 2304–2512.

David, J. F. (2014). The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views. *Soil Biology and Biochemistry*, 76, 109–118. https://doi.org/10.1016/j.soilbio.2014.05.009

Decaëns, T. (2010). Macroecological patterns in soil communities. *Global Ecology and Biogeography*, 19(3), 287–302. https://doi.org/10.1111/j.1466-8238.2009.00517.x

deCastro-Arrazola, I., Andrew, N. R., Berg, M. P., Curtsdotter, A., Lumaret, J., Menéndez, R., Moretti, M., Nervo, B., Nichols, E. S., Sánchez-Piñero, F., Santos, A. M. C., Sheldon, K. S., Slade, E. M., & Hortal, J. (2023). A trait-based framework for dung beetle functional ecology. *Journal of Animal Ecology*, 92(1), 44–65. https://doi.org/10.1111/1365-2656.13829

Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., Bastida, F., Berhe, A. A., Cutler, N. A., Gallardo, A., García-Velázquez, L., Hart, S. C., Hayes, P. E., He, J.-Z., Hseu, Z.-Y., Hu, H.-W., Kirchmair, M., Neuhauser, S., Pérez, C. A., ... Singh, B. K. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, 4(2), 210–220. https://doi.org/10.1038/s41559-019-1084-y

Dias, A. T. C., Krab, E. J., Mariën, J., Zimmer, M., Cornelissen, J. H. C., Ellers, J., Wardle, D. A., & Berg, M. P. (2013). Traits underpinning

desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia*, *172*(3), 667–677. https://doi.org/10.1007/s00442-012-2541-3

Digel, C., Curtsdotter, A., Riede, J., Klarner, B., & Brose, U. (2014). Unravelling the complex structure of forest soil food webs: Higher omnivory and more trophic levels. *Oikos*, *123*(10), 1157–1172. https://doi.org/10.1111/oik.00865

Dos Santos Nascimento, M., Anjos Bittencourt Barreto-Garcia, P., Henrique Marques Monroe, P., Nogueira Scoriza, R., & De Souza Gomes, V. (2021). Interaction between edaphic mesofauna and organic carbon within water-stable aggregates in forestry systems: A case study in northeastern Brazil. *Catena*, *202*, 105269. https://doi.org/10.1016/j.catena.2021.105269

Ehnes, R. B., Rall, B. C., & Brose, U. (2011). Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates: Invertebrate metabolism. *Ecology Letters*, *14*(10), 993–1000. https://doi.org/10.1111/j.1461-0248.2011.01660.x

Eisenhauer, N., Partsch, S., Parkinson, D., & Scheu, S. (2007). Invasion of a deciduous forest by earthworms: Changes in soil chemistry, microflora, microarthropods and vegetation. *Soil Biology and Biochemistry*, *39*(5), 1099–1110. https://doi.org/10.1016/j.soilbio.2006.12.019

Erktan, A., Rillig, M. C., Carminati, A., Jousset, A., & Scheu, S. (2020). Protists and collembolans alter microbial community composition, C dynamics and soil aggregation in simplified consumer–prey systems. *Biogeosciences*, *17*(20), 4961–4980. https://doi.org/10.5194/bg-17-4961-2020

Ferlian, O., Cesarz, S., Lochner, A., Potapov, A., Thouvenot, L., & Eisenhauer, N. (2022). Earthworm invasion shifts trophic niches of ground-dwelling invertebrates in a North American forest. *Soil Biology and Biochemistry*, *171*, 108730. https://doi.org/10.1016/j.soilbio.2022.108730

Ferlian, O., Thakur, M. P., Castañeda González, A., San Emeterio, L. M., Marr, S., Da Silva Rocha, B., & Eisenhauer, N. (2020). Soil chemistry turned upside down: A meta-analysis of invasive earthworm effects on soil chemical properties. *Ecology*, *101*(3), e02936. https://doi.org/10.1002/ecy.2936

Flores, O., Deckmyn, G., Curiel Yuste, J., Javaux, M., Uvarov, A., Van Der Linde, S., De Vos, B., Vereecken, H., Jiménez, J., Vinduskova, O., & Schnepf, A. (2021). KEYLINK: Towards a more integrative soil representation for inclusion in ecosystem scale models—II: Model description, implementation and testing. *PeerJ*, *9*, e10707. https://doi.org/10.7717/peerj.10707

Frouz, J. (2018). Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma*, *332*, 161–172. https://doi.org/10.1016/j.geoderma.2017.08.039

Frouz, J., Roubíčková, A., Heděnec, P., & Tajovský, K. (2015). Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. *European Journal of Soil Biology*, *68*, 18–24. https://doi.org/10.1016/j.ejsobi.2015.03.002

Fry, E. L., De Long, J. R., Álvarez Garrido, L., Alvarez, N., Carrillo, Y., Castañeda-Gómez, L., Chomel, M., Dondini, M., Drake, J. E., Hasegawa, S., Hortal, S., Jackson, B. G., Jiang, M., Lavallee, J. M., Medlyn, B. E., Rhymes, J., Singh, B. K., Smith, P., Anderson, I. C., … Johnson, D. (2019). Using plant, microbe, and soil fauna traits to improve the predictive power of biogeochemical models. *Methods in Ecology and Evolution*, *10*(1), 146–157. https://doi.org/10.1111/2041-210X.13092

Ganault, P., Barantal, S., Coq, S., Hättenschwiler, S., Lucas, S., Decaëns, T., & Nahmani, J. (2022). Leaf litter morphological traits, invertebrate body mass and phylogenetic affiliation explain the feeding and feces properties of saprophagous macroarthropods. *European Journal of Soil Biology*, *109*, 103383. https://doi.org/10.1016/j.ejsobi.2021.103383

Giweta, M. (2020). Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: A review. *Journal of Ecology and Environment*, *44*(1), 11. https://doi.org/10.1186/s41610-020-0151-2

Gonçalves-Souza, T., Chaves, L. S., Boldorini, G. X., Ferreira, N., Gusmão, R. A. F., Perônico, P. B., Sanders, N. J., & Teresa, F. B. (2023). Bringing light onto the Raunkiæran shortfall: A comprehensive review of traits used in functional animal ecology. *Ecology and Evolution*, *13*(4), e10016. https://doi.org/10.1002/ece3.10016

Greiner, L., Keller, A., Grêt-Regamey, A., & Papritz, A. (2017). Soil function assessment: Review of methods for quantifying the contributions of soils to ecosystem services. *Land Use Policy*, *69*, 224–237. https://doi.org/10.1016/j.landusepol.2017.06.025

Griffiths, H. M., Ashton, L. A., Parr, C. L., & Eggleton, P. (2021). The impact of invertebrate decomposers on plants and soil. *New Phytologist*, *231*(6), 2142–2149. https://doi.org/10.1111/nph.17553

Guhra, T., Stolze, K., Schweizer, S., & Totsche, K. U. (2020). Earthworm mucus contributes to the formation of organo-mineral associations in soil. *Soil Biology and Biochemistry*, *145*, 107785. https://doi.org/10.1016/j.soilbio.2020.107785

Habib, L., Morel, J. L., Guckert, A., Plantureux, S., & Chenu, C. (1990). Influence of root exudates on soil aggregation. *Symbiosis*, *9*, 87–91.

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hedde, M., Blight, O., Briones, M. J. I., Bonfanti, J., Brauman, A., Brondani, M., Calderón Sanou, I., Clause, J., Conti, E., Cortet, J., Decaëns, T., Erktan, A., Gérard, S., Goulpeau, A., Iannelli, M., Joimel-Boulanger, S., Jouquet, P., Le Guillarme, N., Marsden, C., … Capowiez, Y. (2022). A common framework for developing robust soil fauna classifications. *Geoderma*, *426*, 116073. https://doi.org/10.1016/j.geoderma.2022.116073

Hedde, M., Bureau, F., Akpa-Vinceslas, M., Aubert, M., & Decaëns, T. (2007). Beech leaf degradation in laboratory experiments: Effects of eight detritivorous invertebrate species. *Applied Soil Ecology*, *35*(2), 291–301. https://doi.org/10.1016/j.apsoil.2006.08.002

Heděnec, P., Jiménez, J. J., Moradi, J., Domene, X., Hackenberger, D., Barot, S., Frossard, A., Oktaba, L., Filser, J., Kindlmann, P., & Frouz, J. (2022). Global distribution of soil fauna functional groups and their estimated litter consumption across biomes. *Scientific Reports*, *12*(1), 17362. https://doi.org/10.1038/s41598-022-21563-z

Heemsbergen, D. A., Berg, M. P., Loreau, M., van Hal, J. R., Faber, J. H., & Verhoef, H. A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, *306*(5698), 1019–1020. https://doi.org/10.1126/science.1101865

Helbig, R., Nickerl, J., Neinhuis, C., & Werner, C. (2011). Smart skin patterns protect springtails. *PLoS One*, *6*(9), e25105. https://doi.org/10.1371/journal.pone.0025105

Hendriks, A. J., & Mulder, C. (2008). Scaling of offspring number and mass to plant and animal size: Model and meta-analysis. *Oecologia*, *155*(4), 705–716. https://doi.org/10.1007/s00442-007-0952-3

Hortal, J., De Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Jiang, Y., Qian, H., Wang, X., Chen, L., Liu, M., Li, H., & Sun, B. (2018). Nematodes and microbial community affect the sizes and turnover rates of organic carbon pools in soil aggregates. *Soil Biology and Biochemistry*, *119*, 22–31. https://doi.org/10.1016/j.soilbio.2018.01.001

Jiménez, J. J., Filser, J., & The KEYSOM Team. (2020). Soil fauna: Key to soil organic matter dynamics and modelling. handbook of methods. COST Action ES1406.

Jochum, M., Barnes, A. D., Ott, D., Lang, B., Klarner, B., Farajallah, A., Scheu, S., & Brose, U. (2017). Decreasing stoichiometric resource quality drives compensatory feeding across trophic levels in

tropical litter invertebrate communities. *The American Naturalist*, *190*(1), 131–143. https://doi.org/10.1086/691790

Joly, F.-X., Coq, S., Coulis, M., David, J.-F., Hättenschwiler, S., Mueller, C. W., Prater, I., & Subke, J.-A. (2020). Detritivore conversion of litter into faeces accelerates organic matter turnover. *Communications Biology*, *3*(1), 660. https://doi.org/10.1038/s42003-020-01392-4

Joly, F.-X., Coq, S., Coulis, M., Nahmani, J., & Hättenschwiler, S. (2018). Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition. *Functional Ecology*, *32*(11), 2605–2614. https://doi.org/10.1111/1365-2435.13178

Joly, F.-X., Coulis, M., Gérard, A., Fromin, N., & Hättenschwiler, S. (2015). Litter-type specific microbial responses to the transformation of leaf litter into millipede feces. *Soil Biology and Biochemistry*, *86*, 17–23. https://doi.org/10.1016/j.soilbio.2015.03.014

Joly, F.-X., Scherer-Lorenzen, M., & Hättenschwiler, S. (2023). Resolving the intricate role of climate in litter decomposition. *Nature Ecology & Evolution*, *7*, 214–223. https://doi.org/10.1038/s41559-022-01948-z

Juan-Ovejero, R., Benito, E., Barreal, M. E., Rodeiro, J., & Briones, M. J. I. (2019). Tolerance to fluctuating water regimes drives changes in mesofauna community structure and vertical stratification in peatlands. *Pedobiologia*, *76*, 150571. https://doi.org/10.1016/j.pedobi.2019.150571

Kononova, M. M. (2013). *Soil organic matter: Its nature, its role in soil formation and in soil fertility* (2nd ed.). Elsevier Science.

Kou, X., Morriën, E., Tian, Y., Zhang, X., Lu, C., Xie, H., Liang, W., Li, Q., & Liang, C. (2023). Exogenous carbon turnover within the soil food web strengthens soil carbon sequestration through microbial necromass accumulation. *Global Change Biology*, *29*(14), 4069–4080. https://doi.org/10.1111/gcb.16749

Krab, E. J., Oorsprong, H., Berg, M. P., & Cornelissen, J. H. C. (2010). Turning northern peatlands upside down: Disentangling microclimate and substrate quality effects on vertical distribution of Collembola. *Functional Ecology*, *24*(6), 1362–1369. https://doi.org/10.1111/j.1365-2435.2010.01754.x

Kravchenko, S. (2022). X-ray computed tomography imaging & soil biology. In S. Jon Mooney, I. M. Young, R. J. Heck, & S. Peth (Eds.), *X-ray imaging of the soil porous architecture* (pp. 159–182). Springer International Publishing. https://doi.org/10.1007/978-3-031-12176-0_10

Lavallee, J. M., Soong, J. L., & Cotrufo, M. F. (2020). Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology*, *26*(1), 261–273. https://doi.org/10.1111/gcb.14859

Lavelle, P. (1996). Diversity of soil fauna and ecosystem function. *Biology International*, *33*, 3–16.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., & Rossi, J.-P. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, *42*, S3–S15. https://doi.org/10.1016/j.ejsobi.2006.10.002

Lavelle, P., Rouland, C., Diouf, M., Binet, F., & Kersanté, A. (2005). Regulation of microbial activities in functional domains of roots and invertebrates. In A. Varma & F. Buscot (Eds.), *Microorganisms in soils: Roles in genesis and functions* (Vol. 3, pp. 291–305). Springer Berlin Heidelberg. https://doi.org/10.1007/3-540-26609-7_14

Lavelle, P., Spain, A., Fonte, S., Bedano, J. C., Blanchart, E., Galindo, V., Grimaldi, M., Jimenez, J. J., Velasquez, E., & Zangerlé, A. (2020). Soil aggregation, ecosystem engineers and the C cycle. *Acta Oecologica*, *105*, 103561. https://doi.org/10.1016/j.actao.2020.103561

Lavorel, S., & Garnier, É. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556.

Lavorel, S., Storkey, J., Bardgett, R. D., De Bello, F., Berg, M. P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R. J., Díaz, S., & Harrington, R. (2013). A novel framework for linking functional diversity of plants

with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, *24*(5), 942–948. https://doi.org/10.1111/jvs.12083

Le Guillarme, N., Hedde, M., Potapov, A. M., Martínez-Muñoz, C. A., Berg, M. P., Briones, M. J. I., Calderón-Sanou, I., Degrune, F., Hohberg, K., Martinez-Almoyna, C., Pey, B., Russell, D. J., & Thuiller, W. (2023). The soil food web ontology: Aligning trophic groups, processes, resources, and dietary traits to support food-web research. *Ecological Informatics*, *78*, 102360. https://doi.org/10.1016/j.ecoinf.2023.102360

Le Mer, G., Bottinelli, N., Dignac, M.-F., Capowiez, Y., Jouquet, P., Mazurier, A., Baudin, F., Caner, L., & Rumpel, C. (2022). Exploring the control of earthworm cast macro- and micro-scale features on soil organic carbon mineralization across species and ecological categories. *Geoderma*, *427*, 116151. https://doi.org/10.1016/j.geoderma.2022.116151

Lee, K., & Foster, R. (1991). Soil fauna and soil structure. *Soil Research*, *29*(6), 745. https://doi.org/10.1071/SR9910745

Lehmann, A., Leifheit, E. F., & Rillig, M. C. (2017). Mycorrhizas and soil aggregation. In *Mycorrhizal mediation of soil* (pp. 241–262). Elsevier. https://doi.org/10.1016/B978-0-12-804312-7.00014-0

Lehmann, A., Zheng, W., & Rillig, M. C. (2017). Soil biota contributions to soil aggregation. *Nature Ecology & Evolution*, *1*(12), 1828–1835.

Lehmann, J., Hansel, C. M., Kaiser, C., Kleber, M., Maher, K., Manzoni, S., Nunan, N., Reichstein, M., Schimel, J. P., Torn, M. S., Wieder, W. R., & Kögel-Knabner, I. (2020). Persistence of soil organic carbon caused by functional complexity. *Nature Geoscience*, *13*(8), 529–534. https://doi.org/10.1038/s41561-020-0612-3

Liang, C., Schimel, J. P., & Jastrow, J. D. (2017). The importance of anabolism in microbial control over soil carbon storage. *Nature Microbiology*, *2*(8), 17105. https://doi.org/10.1038/nmicrobiol.2017.105

Luza, A. L., Barneche, D. R., Cordeiro, C. A. M. M., Dambros, C. S., Ferreira, C. E. L., Floeter, S. R., Giglio, V. J., Luiz, O. J., Mendes, T. C., Picolotto, V. A. P., Quimbayo, J. P., Silva, F. C., Waechter, L., Longo, G. O., & Bender, M. G. (2023). Going across taxa in functional ecology: Review and perspectives of an emerging field. *Functional Ecology*, *37*(12), 3091–3110. https://doi.org/10.1111/1365-2435.14442

Ma, Y., Filley, T. R., Szlavecz, K., & McCormick, M. K. (2014). Controls on wood and leaf litter incorporation into soil fractions in forests at different successional stages. *Soil Biology and Biochemistry*, *69*, 212–222. https://doi.org/10.1016/j.soilbio.2013.10.043

Maaß, S., Caruso, T., & Rillig, M. C. (2015). Functional role of microarthropods in soil aggregation. *Pedobiologia*, *58*, 59–63. https://doi.org/10.1016/j.pedobi.2015.03.001

Mataix-Solera, J., Cerdà, A., Arcenegui, V., Jordán, A., & Zavala, L. M. (2011). Fire effects on soil aggregation: A review. *Earth-Science Reviews*, *109*(1–2), 44–60. https://doi.org/10.1016/j.earscirev.2011.08.002

McCook, H. C. (1884). A spider that makes a spherical mud-daub cocoon. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *36*, 151–153.

McGill, B., Enquist, B., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Medina-Sauza, R. M., Álvarez-Jiménez, M., Delhal, A., Reverchon, F., Blouin, M., Guerrero-Analco, J. A., Cerdán, C. R., Guevara, R., Villain, L., & Barois, I. (2019). Earthworms building up soil microbiota, a review. *Frontiers in Environmental Science*, *7*, 81. https://doi.org/10.3389/fenvs.2019.00081

Meehan, T. D. (2006). Mass and temperature dependence of metabolic rate in litter and soil invertebrates. *Physiological and Biochemical Zoology*, *79*(5), 878–884. https://doi.org/10.1086/505997

Mele, G., Buscemi, G., Gargiulo, L., & Terribile, F. (2021). Soil burrow characterization by 3D image analysis: Prediction of

macroinvertebrate groups from biopore size distribution parameters. *Geoderma*, 404, 115292. https://doi.org/10.1016/j.geoderma.2021.115292

Meurer, K., Barron, J., Chenu, C., Coucheney, E., Fielding, M., Hallett, P., Herrmann, A. M., Keller, T., Koestel, J., Larsbo, M., Lewan, E., Or, D., Parsons, D., Parvin, N., Taylor, A., Vereecken, H., & Jarvis, N. (2020). A framework for modelling soil structure dynamics induced by biological activity. *Global Change Biology*, 26(10), 5382–5403. https://doi.org/10.1111/gcb.15289

Moretti, M., Dias, A. T. C., De Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, 31(3), 558–567. https://doi.org/10.1111/1365-2435.12776

Muelbaier, H., Arthen, F., Collins, G., Hickler, T., Hohberg, K., Lehmitz, R., Pauchet, Y., Pfenninger, M., Potapov, A., Romahn, J., Schaefer, I., Scheu, S., Schneider, C., Ebersberger, I., & Bálint, M. (2024). Genomic evidence for the widespread presence of GH45 cellulases among soil invertebrates. *Molecular Ecology*, 33, e17351. https://doi.org/10.1111/mec.17351

Mueller, C. W., & Koegel-Knabner, I. (2009). Soil organic carbon stocks, distribution, and composition affected by historic land use changes on adjacent sites. *Biology and Fertility of Soils*, 45(4), 347–359. https://doi.org/10.1007/s00374-008-0336-9

Niu, G., Liu, T., Zhao, Z., Zhang, X., Guan, H., He, X., & Lu, X. (2024). Subtropical forest macro-decomposers rapidly transfer litter carbon and nitrogen into soil mineral-associated organic matter. *Forest Ecosystems*, 11, 100172. https://doi.org/10.1016/j.fecs.2024.100172

Nozaki, M., Miura, C., Tozawa, Y., & Miura, T. (2009). The contribution of endogenous cellulase to the cellulose digestion in the gut of earthworm (*Pheretima hilgendorfi*: Megascolecidae). *Soil Biology and Biochemistry*, 41(4), 762–769. https://doi.org/10.1016/j.soilbio.2009.01.016

Ooms, A., Dias, A. T. C., Van Oosten, A. R., Cornelissen, J. H. C., Ellers, J., & Berg, M. P. (2020). Species richness and functional diversity of isopod communities vary across an urbanisation gradient, but the direction and strength depend on soil type. *Soil Biology and Biochemistry*, 148, 107851. https://doi.org/10.1016/j.soilbio.2020.107851

Patoine, G., Thakur, M. P., Friese, J., Nock, C., Hönig, L., Haase, J., Scherer-Lorenzen, M., & Eisenhauer, N. (2017). Plant litter functional diversity effects on litter mass loss depend on the macro-detritivore community. *Pedobiologia*, 65, 29–42. https://doi.org/10.1016/j.pedobi.2017.07.003

Petersen, H., & Luxton, M. (1982). A comparative analysis of soil Fauna populations and their role in decomposition processes. *Oikos*, 39(3), 288. https://doi.org/10.2307/3544689

Pey, B., Laporte, M.-A., Nahmani, J., Auclerc, A., Capowiez, Y., Caro, G., Cluzeau, D., Cortet, J., Decaëns, T., Dubs, F., Joimel, S., Guernion, M., Briard, C., Grumiaux, F., Laporte, B., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., ... Hedde, M. (2014). A thesaurus for soil invertebrate trait-based approaches. *PLoS One*, 9(10), e108985. https://doi.org/10.1371/journal.pone.0108985

Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaëns, T., Deharveng, L., Dubs, F., Joimel, S., Briard, C., Grumiaux, F., Laporte, M.-A., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufo, L., & Hedde, M. (2014). Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic and Applied Ecology*, 15(3), 194–206. https://doi.org/10.1016/j.baae.2014.03.007

Pham, Q. V., Nguyen, T. T., Lam, D. H., Capowiez, Y., Nguyen, A. D., Jouquet, P., Tran, T. M., & Bottinelli, N. (2023). Using morpho-anatomical traits to predict the effect of earthworms on soil water

infiltration. *Geoderma*, 429, 116245. https://doi.org/10.1016/j.geoderma.2022.116245

Phillips, H. R. P., Guerra, C. A., Bartz, M. L. C., Briones, M. J. I., Brown, G., Crowther, T. W., Ferlian, O., Gongalsky, K. B., Van Den Hoogen, J., Krebs, J., Orgiazzi, A., Routh, D., Schwarz, B., Bach, E. M., Bennett, J. M., Brose, U., Decaëns, T., König-Ries, B., Loreau, M., ... Eisenhauer, N. (2019). Global distribution of earthworm diversity. *Science*, 366(6464), 480–485. https://doi.org/10.1126/science.aax4851

Poinsot, N. (1966). Existence d'un comportement constructeur chez un Collembole Isotomidae Subisotoma variabilis (Gisin, 1949). *Revue d'Écologie et de Biologie du Sol*, 3, 173–178.

Ponge, J.-F. (2000). Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. *Biology and Fertility of Soils*, 32(6), 508–522.

Porre, R. J., Van Groenigen, J. W., De Deyn, G. B., De Goede, R. G. M., & Lubbers, I. M. (2016). Exploring the relationship between soil mesofauna, soil structure and N_2O emissions. *Soil Biology and Biochemistry*, 96, 55–64. https://doi.org/10.1016/j.soilbio.2016.01.018

Potapov, A., Sandmann, D., & Scheu, S. (2019). Ecotaxonomy: Linking traits, taxa, individuals and samples in a flexible virtual research environment for ecological studies. *Biodiversity Information Science and Standards*, 3, e37166. https://doi.org/10.3897/biss.3.37166

Potapov, A. M. (2022). Multifunctionality of belowground food webs: Resource, size and spatial energy channels. *Biological Reviews*, 97(4), 1691–1711. https://doi.org/10.1111/brv.12857

Potapov, A. M., Beaulieu, F., Birkhofer, K., Bluhm, S. L., Degtyarev, M. I., Devetter, M., Goncharov, A. A., Gongalsky, K. B., Klarner, B., Korobushkin, D. I., Liebke, D. F., Maraun, M., Mc Donnell, R. J., Pollierer, M. M., Schaefer, I., Shrubovych, J., Semenyuk, I. I., Sendra, A., Tuma, J., ... Scheu, S. (2022). Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biological Reviews*, 97(3), 1057–1117. https://doi.org/10.1111/brv.12832

Potapov, A. M., Guerra, C. A., Van Den Hoogen, J., Babenko, A., Bellini, B. C., Berg, M. P., Chown, S. L., Deharveng, L., Kováč, Ľ., Kuznetsova, N. A., Ponge, J.-F., Potapov, M. B., Russell, D. J., Alexandre, D., Alatalo, J. M., Arbea, J. I., Bandyopadhyaya, I., Bernava, V., Bokhorst, S., ... Scheu, S. (2023). Globally invariant metabolism but density-diversity mismatch in springtails. *Nature Communications*, 14(1), 674. https://doi.org/10.1038/s41467-023-36216-6

Potapov, A. M., Pollierer, M. M., Salmon, S., Šustr, V., & Chen, T. (2021). Multidimensional trophic niche revealed by complementary approaches: Gut content, digestive enzymes, fatty acids and stable isotopes in Collembola. *Journal of Animal Ecology*, 90(8), 1919–1933. https://doi.org/10.1111/1365-2656.13511

Potapov, A. M., Rozanova, O. L., Semenina, E. E., Leonov, V. D., Belyakova, O. I., Bogatyreva, V. Y., Degtyarev, M. I., Esaulov, A. S., Korotkevich, A. Y., Kudrin, A. A., Malysheva, E. A., Mazei, Y. A., Tsurikov, S. M., Zuev, A. G., & Tiunov, A. V. (2021). Size compartmentalization of energy channeling in terrestrial belowground food webs. *Ecology*, 102(8), e03421. https://doi.org/10.1002/ecy.3421

Prescott, C. E., & Vesterdal, L. (2021). Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. *Forest Ecology and Management*, 498, 119522. https://doi.org/10.1016/j.foreco.2021.119522

Rabot, E., Wiesmeier, M., Schlüter, S., & Vogel, H.-J. (2018). Soil structure as an indicator of soil functions: A review. *Geoderma*, 314, 122–137. https://doi.org/10.1016/j.geoderma.2017.11.009

Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 367(1605), 2923–2934. https://doi.org/10.1098/rstb.2012.0242

Raymond-Léonard, L. J., Gravel, D., & Handa, I. T. (2019). A novel set of traits to describe Collembola mouthparts: Taking a bite out of the broad chewing mandible classification. *Soil Biology and Biochemistry*, *138*, 107608. https://doi.org/10.1016/j.soilbio.2019.107608

Rosenberg, K., Bertaux, J., Krome, K., Hartmann, A., Scheu, S., & Bonkowski, M. (2009). Soil amoebae rapidly change bacterial community composition in the rhizosphere of *Arabidopsis thaliana*. *The ISME Journal*, *3*(6), 675–684. https://doi.org/10.1038/ismej.2009.11

Ruiz, S., Schymanski, S. J., & Or, D. (2017). Mechanics and energetics of soil penetration by earthworms and plant roots: Higher rates Cost More. *Vadose Zone Journal*, *16*(8), 1–16. https://doi.org/10.2136/vzj2017.01.0021

Sade, Y. B., de Moraes, D. T., Beltrão, P. J., & Vicentim, M. P. (2018). Cellulases from invertebrate animals. In M. Brienzo (Ed.), *Bioethanol and beyond: Advances in production process and future directions* (pp. 261–284). Nova Science Publishers.

Sagi, N., & Hawlena, D. (2024). Climate dependence of the macro-faunal effect on litter decomposition—A global meta-regression analysis. *Ecology Letters*, *27*(1), e14333. https://doi.org/10.1111/ele.14333

Schleuning, M., García, D., & Tobias, J. A. (2023). Animal functional traits: Towards a trait-based ecology for whole ecosystems. *Functional Ecology*, *37*(1), 4–12. https://doi.org/10.1111/1365-2435.14246

Siddiky, M. R. K., Schaller, J., Caruso, T., & Rillig, M. C. (2012). Arbuscular mycorrhizal fungi and collembola non-additively increase soil aggregation. *Soil Biology and Biochemistry*, *47*, 93–99. https://doi.org/10.1016/j.soilbio.2011.12.022

Statescu, F., Zauca, D. C., & Pavel, L. V. (2013). Soil structure and water-stable aggregates. *Environmental Engineering and Management Journal*, *12*(4), 741–746. https://doi.org/10.30638/eemj.2013.091

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press.

Swaby, R. J. (1949). The influence of earthworms on soil aggregation. *Journal of Soil Science*, *1*(2), 195–196. https://doi.org/10.1111/j.1365-2389.1950.tb00730.x

Tao, F., Huang, Y., Hungate, B. A., Manzoni, S., Frey, S. D., Schmidt, M. W. I., Reichstein, M., Carvalhais, N., Ciais, P., Jiang, L., Lehmann, J., Wang, Y.-P., Houlton, B. Z., Ahrens, B., Mishra, U., Hugelius, G., Hocking, T. D., Lu, X., Shi, Z., … Luo, Y. (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, *618*(7967), 981–985. https://doi.org/10.1038/s41586-023-06042-3

Thakur, M. P., Reich, P. B., Hobbie, S. E., Stefanski, A., Rich, R., Rice, K. E., Eddy, W. C., & Eisenhauer, N. (2018). Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nature Climate Change*, *8*(1), 75–78. https://doi.org/10.1038/s41558-017-0032-6

Ulrich, W., Hoste-Danyłow, A., Faleńczyk-Koziróg, K., Hajdamowicz, I., Ilieva-Makulec, K., Olejniczak, I., Stańska, M., & Wytwer, J. (2015). Temporal patterns of energy equivalence in temperate soil invertebrates. *Oecologia*, *179*(1), 271–280. https://doi.org/10.1007/s00442-015-3317-3

Van Den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., De Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., De Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., … Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, *572*(7768), 194–198. https://doi.org/10.1038/s41586-019-1418-6

van der Drift, J. (1951). Analysis of the animal community in a beech forest floor. *Tijdschrift voor Entomologie*, *94*, 1–168.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Warnke, L., Hertel, D., Scheu, S., & Maraun, M. (2023). Opening up new niche dimensions: The stoichiometry of soil microarthropods in European beech and Norway spruce forests. *Ecology and Evolution*, *13*(5), e10122. https://doi.org/10.1002/ece3.10122

Whitford, W. G., Freckman, D. W., Elkins, N. Z., Parker, L. W., Parmalee, R., Phillips, J., & Tucker, S. (1981). Diurnal migration and responses to simulated rainfall in desert soil microarthropods and nematodes. *Soil Biology and Biochemistry*, *13*(5), 417–425. https://doi.org/10.1016/0038-0717(81)90087-0

Wilkinson, M. T., Richards, P. J., & Humphreys, G. S. (2009). Breaking ground: Pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews*, *97*(1–4), 257–272. https://doi.org/10.1016/j.earscirev.2009.09.005

Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, *18*(8), 737–751. https://doi.org/10.1111/ele.12462

Winsome, T. (2005). Fauna. In I. D. I. Hillel & J. L. Hatfield (Eds.), *Encyclopedia of soils in the environment* (1st ed., pp. 539–548). Elsevier/Academic Press.

Wong, M. K. L., Guénard, B., & Lewis, O. T. (2018). Trait-based ecology of terrestrial arthropods. *Biological Reviews*, *94*, 999–1022. https://doi.org/10.1111/brv.12488

Wood, T., & Sands, W. (1978). The role of termites in ecosystems. In M. Brian (Ed.), *Production ecology of ants and termites* (pp. 245–292). Cambridge University Press.

Yudina, A. V., Klyueva, V. V., Romanenko, K. A., & Fomin, D. S. (2022). Micro- within macro: How micro-aggregation shapes the soil pore space and water-stability. *Geoderma*, *415*, 115771. https://doi.org/10.1016/j.geoderma.2022.115771

Zeiss, R., Briones, M. J. I., Mathieu, J., Lomba, A., Dahlke, J., Heptner, L., Salako, G., Eisenhauer, N., & Guerra, C. A. (2024). Effects of climate on the distribution and conservation of commonly observed European earthworms. *Conservation Biology*, *38*(2), e14187. https://doi.org/10.1111/cobi.14187

Zhang, H., & Schrader, S. (1993). Earthworm effects on selected physical and chemical properties of soil aggregates. *Biology and Fertility of Soils*, *15*(3), 229–234. https://doi.org/10.1007/BF00361617

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., Aerts, R., Berg, M. P., McKie, B., Van Ruijven, J., Hättenschwiler, S., & Scheu, S. (2020). Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. *Journal of Ecology*, *108*(6), 2283–2297. https://doi.org/10.1111/1365-2745.13452

Zimmer, M., & Topp, W. (2002). The role of coprophagy in nutrient release from feces of phytophagous insects. *Soil Biology and Biochemistry*, *34*(8), 1093–1099. https://doi.org/10.1016/S0038-0717(02)00044-5