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Faeces traits as unifying predictors of detritivore effects on organic matter turnover

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Abstract

In the last decade, our understanding of plant litter decomposition and soil organic matter formation substantially improved but critical blind spots remain. Particularly, the role of detritivores, i.e. soil animals that feed on litter and soil, is poorly understood and notoriously missing from biogeochemical models. This major gap results from methodological difficulties to isolate their effect and from the astonishing diversity of detritivorous organisms~~, that vary in shape, size, anatomy, taxonomy, organic matter processing,~~ with few common features, thereby hampering the identification of general patterns. In this viewpoint~~Here~~, we propose that the characteristics of their faeces can predict detritivore effects on soil processes related to organic matter turnover across the large detritivore diversity. Indeed, ~~these~~ faeces are common to all detritivores, and a large part of organic matter is transformed into faeces in many ecosystems. T~~and t~~wo recent studies presented here showed that faeces characteristics are powerful predictors of the fate and turnover of this transformed organic matter. We suggest~~We thus suggest~~ that faeces characteristics, such as water-holding capacity, size and spatial organisation of the faecal pellets and of their constituting particles, particulate organic matter connectivity, as well as the characteristics of dissolved organic matter in faecal pellets, are promising ~~such as water-holding capacity, size and spatial organization of feacal pellets and of their constituting particles, particulate organic matter connectivity, as well as the characteristics of dissolved organic matter in faecal pellets, are promising~~ ~~be considered as~~ ‘effect traits’. By focussing on similar features rather than differences, this approach has the potential to break down barriers of this highly fragmented soil animal group, in particular between earthworms that are often studied as ecosystem engineers and classical litter transformers such as millipedes, woodlice, or snails. We discuss ways of tackling the complexity of using such traits, particularly regarding the composite determinism of faeces characteristics that are driven both by the detritivore identity and the ingested organic matter. Rigorous and hypothesis-based use of faeces characteristics as effect traits, including clear identification of studied processes, could allow integrating detritivores in our current understanding of organic matter turnover.

Key-words

Macroarthropods ; Soil functioning ; Soil invertebrates ; Soil processes ; Trait-based approaches

1. Introduction

Plant litter decomposition and the subsequent formation of soil organic matter (SOM) are key ecosystem processes that control biogeochemical cycling and the ability of soils to store large amounts of carbon (Lehmann and Kleber, 2015). In the last decade, a new understanding of litter decomposition and SOM formation has emerged (Basile-Doelsch et al., 2020; Dignac et al., 2017; Schmidt et al., 2011), through (i) a renewed characterization of the chemical nature and protection mechanisms of SOM (Kögel-Knabner and Rumpel, 2018; Lehman and Kleber, 2015), (ii) a growing recognition that interactions between plant litter, microbial communities and minerals rather than litter recalcitrance control SOM formation (Cotrufo et al., 2013, 2015; Dynarski et al., 2020), and (iii) the recognition of the important role roots play in SOM formation (Adamczyk et al., 2019, Clemmensen et al., 2013; Rasse et al., 2005; Sokol et al., 2019a). In contrast, while the importance of soil invertebrates in soil processes is often acknowledged (Briones, 2018; Griffith et al., 2021), our understanding of their roles in SOM dynamics is still poor (Filser et al., 2016; Prescott and Vesterdal, 2021). Detritivores in particular, i.e., soil invertebrates that feed on dead organic matter, importantly contribute to organic matter turnover (Prescott and Vesterdal, 2021). They do so by ingesting large amounts of organic matter, assimilating a part of it and rejecting the main part as faeces (David, 2014). This processing greatly affects the organic matter physicochemical characteristics (e.g., Coulis et al., 2009, 2016; Hedde et al., 2005; Joly et al., 2018; Le Mer et al., 2020; Vidal et al., 2016) and its contribution to SOM formation (Angst et al., 2019, Vidal et al., 2019). Despite clear evidence that in many ecosystems detritivores process large amounts of organic matter, we lack a general understanding of their ~~global~~ role in its turnover.

One of the main obstacles to understanding the detritivores' influence on organic matter turnover is the difficulty to isolate these effects experimentally. Traditionally, the role of soil invertebrates in decomposition processes has been studied using litterbags of different mesh sizes (0.1 mm, 2 mm, 4 to 8 mm), sequentially excluding soil invertebrates based on their body width (e.g., Handa et al., 2014; Wall et al., 2008). A meta-analysis of such studies reported that micro- and mesofauna (body width < 2 mm) presence increased litter mass loss by 37% on average across biomes (Garcia-Palacios et al., 2013). This figure emphasises the importance of soil invertebrates in decomposition, but has several limitations. The focus on body width means that the measured effect includes not only the effect of soil invertebrates feeding on plant litter (detritivores), but also of other functional groups with potential top-down effects such as microbivores and predators (Koltz et al., 2018; Lenoir et al., 2007). Moreover, the large mesh sizes used for treatments allowing faunal access entail that the litter consumed by detritivores but returned to soil as faeces is not retrieved in litterbags and considered as lost mass. The decomposition of these faeces and their contribution to SOM formation is a major unknown (Prescott, 2010). Studies on decomposition in reconstructed detritivore communities in microcosms (e.g., Hattenschwiler and Gasser, 2005; Joly et al., 2021; Vidal et al., 2019), or on the detritivore faeces fate (e.g., Coulis et al. 2016; Decaëns, 2000; Joly et al., 2020) contributed to overcoming the limitations of the litterbag technique. Yet, the complexity of such studies limited the number of detritivore species considered and thus the identification of general patterns across the diversity of detritivores.

The extreme diversity of detritivores is~~represents~~ the other dominant obstacle towards identifying general principles of detritivore effects on organic matter turnover. Detritivores include millipedes, woodlice, earthworms, snails, and insect larvae, which greatly differ in their morphologies, behaviours, and the ways they process organic matter. Historically, the role of these animals on soil processes was studied considering separate broad functional groups and subgroups. Specialists of millipedes (e.g., David and Gillon, 2002), woodlice (Zimmer, 2002), or snails (Astor et al., 2015) often studied the role of a few species on litter decomposition separately. In addition, since earthworms also modify their environment through their burrowing activities, most earthworm studies focussed on their global role as ‘ecosystem engineers’ (Lavelle and Spain, 2001; Wardle, 2002) rather than ‘detritivores’. Clearly, the separate study of the various groups of detritivores have limited the identification of general principles of detritivore effects on soil processes. ~~Earthworms were classified in ecological categories (epigeic, anecic, and endogeic) based on morphological, anatomical, and ecological attributes (Bouché, 1972), but the morphoanatomical criteria used do not necessarily reflect their functional roles (e.g., feeding characteristics, burrowing activity; Bottinelli and Capowiez, 2021). The lack of a common framework to study detritivores is accentuated by the use of non-mutually exclusive terminologies amongst studies, almost interchangeably referring to animals, fauna, invertebrates, or arthropods. Most studies further discriminate these groups by size (macro-, meso-, micro-) without clear links between size classes and functional roles. Faeces are also referred to using different terminologies between subgroups or studies, including feces/faeces, fecal/faecal pellets, casts, dejections, excrements, excreta, egesta. These contrastinged terminologies may have limited the identification of general principles of detritivore effects on soil processes.~~

Trait-based approaches allow moving beyond broad categorical characterisation of organisms based on their assumed differences in ecosystem function, to more precise continuous characterisation based on characteristics that relate to their differences in ecosystem function, known as *effect traits* (Garnier et al., 2016; Violle et al., 2007). In plant studies, effect traits have proved very useful for upscaling from organisms to ecosystems, whether aboveground traits (Lavorel and Garnier, 2002; Violle et al. 2007) or belowground ones (Freschet et al., 2021), particularly as predictors of litter decomposition (Cornwell et al., 2008; Rosenfield et al., 2020). For example, plant litter with high specific leaf area and leaf nitrogen and phosphorus concentrations generally decomposes rapidly, while high dry matter content and tannin concentrations of leaves are associated with slow decomposition (Cortez et al., 2007; de la Riva et al., 2019; Kazakou et al., 2006). ~~These traits are therefore well- defined effect traits with relatively predictable impacts on specific ecosystem processes.~~ To better integrate detritivores into the current framework of SOM dynamics, we ~~urgently~~ need to identify effect traits that link the activity of these animals to processes controlling SOM dynamics, but this challenge lags behind. In the European invertebrate trait database BETSI (https://portail.betsi.cnrs.fr/, Pey et al., 2014), out of 76 traits recorded, only 11 can be considered as effect traits according to Brousseau et al. (2018), and only two of these have direct links to ecosystem function (i.e. burrowing strategy and feeding traits). This calls for a common effort to identify effect traits of detritivores relevant to organic matter turnover that enable meaningful comparisons amongst taxa. Such traits should (i) be measurable on all kinds of detritivores and (ii) have a demonstrated link to the studied function. This point is crucial as current applications of trait-based approaches often lack such a clear link (Brousseau et al., 2018; Shipley et al., 2016).

In this viewpoint paper~~Here~~, we argue that detritivore faeces are a promising yet overlooked part of their phenotype, which characteristics, measurable on all soil fauna, can predict their effect on key soil processes related to organic matter turnover. First, we show that detritivore faeces represent important by-products of detritivore activity and that their characteristics are directly related to organic matter turnover. Then, with two selected recent case studies, focusing on litter-feeding and soil-feeding detritivores respectively, we show that characteristics of faeces can predict their fate~~that faeces characteristics across detritivores species can predict the fate of species-specific faeces~~, and thus predict the effect of these detritivores species on litter decomposition and SOM formation. We thus advocate for the consideration of faeces characteristics as detritivore effect traits. Such traits ~~, that~~ could be powerful unifying traits across~~for~~ the large diversity of detritivores that otherwise share few common features with little link to ecosystem function.

2. Faeces as key by-products of detritivory

Detritivores are soil animals that feed on dead organic matter, either on leaf litter (arthropods, snails, epigeic earthworms), on soil and root litter (endogeic earthworms), or both (anecic earthworms). Since these food sources are rather nutrient-depleted and hard to digest (Sterner and Elser, 2002), detritivores typically have low assimilation efficiencies and high consumption rates (Crossley et al.,1971; Curry and Schmidt 2007; David, 2014). Thus, they ingest a lot of dead organic matter, assimilate a small part of it, and ~~r~~eg~~j~~es~~c~~t most of it to soils as faeces (Fig. 1). ~~Local Ss~~tudies from temperate (Schaefer et al., 1990), Mediterranean (David and Gillon, 2002), arid (Sagi et al., 2019), and tropical ecosystems (Dangerfield and Milner, 1996) estimated that in these ecosystems, 40-50% of the annual litterfall is consumed by detritivores and returned to soils as faeces. In ecosystems where detritivores are abundant, these faeces thus represent a substantial part of the soil profile, e.g., in temperate (Zanella, 2018) or tropical ecosystems (Bottinelli et al., 2021). Undeniably, in many ecosystems, large quantities of organic matter originating from litter are decomposed and stabilised only after conversion into faeces.

Determining the physicochemical characteristics of these faeces and how they affect their fate is thus critical to understand detritivore effects on organic matter turnover (Prescott and Vesterdal, 2021).

The conversion of plant litter and/or soil into detritivore faeces leads to profound physicochemical changes that can affect the fate of organic matter in soils. For detritivores that preferentially feed on plant litter (e.g. millipedes, woodlice, snails), faeces ~~were found to~~ have ~~a~~ higher concentrations of dissolved organic carbon and nitrogen, water-holding capacity and surface area available for microbial colonisation, and lower C:N ratio and tannins content compared to the plant litter from which they are derived (Coulis et al., 2009, 2016; Ganault et al., 2022; Joly et al., 2018, 2020). Because these physicochemical characteristics are known to influence~~drive~~ decomposition rates (Makkonen et al., 2012) and the contribution of litter to SOM formation (Cotrufo et al., 2013), their changes during gut passage are likely to drive the fate of the egested organic matter. In fact, faeces of detritivores such as millipedes typically decompose faster than the litter from which they are derived - an acceleration previously linked to the higher lability of the faeces compared to the ingested litter (Coulis et al., 2016; Joly et al., 2018). Similar to the physicochemical characteristics of leaf litter, those of faeces from distinct detritivore species could thus predict their fate.

F~~In turn, f~~or detritivores such as endogeic earthworms that feed on mineral soil, ingestion of soil and its incorporation into earthworm faeces (known as ‘casts’) also lead to major changes in soil physicochemical characteristics. Compared to bulk soil, the faeces are richer in organic carbon, total and mineral nitrogen, total and available phosphorus, and exhibit higher cation-exchange capacity, base saturation and pH (van Groenigen et al., 2019). Similar to litter, these characteristics are known to relate to further microbial degradation and organic matter decomposition (Jouquet et al., 2008), so their changes following gut passage can affect the formation and stabilisation of SOM (Clause et al., 2014). For instance, increased ~~changes in~~ soil compaction and reduced pore size distribution that allow air and water circulation can limit~~alter~~ the accessibility of microbial communities to organic matter, and thus physically protect SOM (Angst et al., 2017). Recently, Barthod et al. (2020, 2021) reported that faeces produced by *Eisenia* sp. fed with different clay minerals have a contrasting composition, which in turn differently affected the microbial decomposition of organic matter occluded in these faeces incubated in the soil. This demonstrates a clear link between earthworm faeces characteristics and their fate.

Generally, there is thus growing evidence that detritivore faeces are important decomposition by-products and that their characteristics can be linked to their fate in soils. This suggests that faeces characteristics of different detritivore species could predict the species-specific effect on organic matter turnover. Recently, two studies, each focusing on multiple detritivore species, used this approach to predict their effects on organic matter turnover.

3. Case studies using faeces traits to predict detritivore effects on organic matter turnover

3.1 *Case study 1: Detritivore faeces traits as predictors of organic matter turnover*

The potential of faeces traits as predictors of organic matter turnover was recently illustrated in a study on the role of detritivores on litter decomposition (Joly et al., 2020). The authors explored how detritivores affect litter decomposition, by converting litter into faeces, and how this effect varies across six phylogenetically-diverse invertebrates species. To do so, they collected faeces from six detritivore species (three millipede, two woodlouse and one snail species) feeding on litter of six tree species, separately, resulting in 36 faeces types (Fig. 2). Then, they measured physicochemical characteristics on the 36 faeces types and on the six intact litter types as controls. They then placed all substrates to decompose on top of soil to study the detritivore effect on organic matter turnover. Faeces varied in colour depending on the nature of ingested litter, and in shape depending on detritivore identity (Fig. 2), whereas their physicochemical characteristics (e.g., elemental composition, surface area, water-holding capacity) were driven both by the nature of the ingested litter and the animal identity. Importantly, these faeces traits were tightly correlated with faeces decomposition. Indeed, faeces C and N losses correlated with faeces concentration in dissolved organic carbon and total dissolved nitrogen, respectively. This shows that faeces traits may be predictors of organic matter turnover across detritivore species as different as millipedes and snails, suggesting that extending trait measures to detritivore faeces may allow predicting their effects on soil processes.

Another major finding of this study was that the detritivore effect – that is, the difference in organic matter quality or element cycling rate between faeces and intact litter – depended on the ingested litter species, with larger positive effects for low-quality and slow-cycling litter, and small or negative effects for high-quality and fast cycling litter (Fig. 3). This general pattern was consistent across detritivore species, suggesting that diverse detritivores play a similar role in organic matter turnover. Yet, the magnitude of the effect, and its relationship with the intact litter characteristics were detritivore species-specific. The parameters of the relationship between litter quality/cycling and the change in quality/cycling following litter conversion into faeces, could thus be used as powerful effect traits. The intercept describes the extent to which a given detritivore species increases organic matter quality/cycling. The slope, in turn, describes the extent to which the effect of this detritivore species varies depending on the initial quality/cycling rate of the ingested litter.

3.2 *Case study 2: Microstructural organisation of earthworm faeces as predictor of earthworm effect on organic matter turnover*

The potential use of earthworm faeces properties as predictors of organic matter turnover was also recently investigated for six earthworm species (Le Mer et al., 2022). In this study, the authors explored how earthworms affect SOM stability by occluding fresh organic matter within their faeces, and how this effect varies between different earthworm species. To do so, they collected six earthworm species, from three ecological categories (epigeic, anecic, and endogeic), fed the earthworms with the same organic matter and soil and collected the resulting six faeces types. They then incubated each faeces type individually under optimal conditions and measured CO_2 respiration rates after 7, 42 and 140 days of incubation as indicators of SOM stability. Finally, they measured the characteristics and physical organisation of the six faeces types and the control soil without earthworm activity. To characterise the SOM occluded by earthworms in their faeces, the authors measured several faeces traits such as organic C content and organic matter stability by Rock-Eval 6 analysis. Moreover, thanks to x-ray microtomography and image analyses, the spatial organisation between pore and POM structures at micro-scale (9.5 µm) was also characterised. For each faeces sample, the authors computed the (i) pore and (ii) POM volumes, as well as the (iii) pore subvolumes directly connected to the air outside the faeces and the (iv) POM subvolumes connected, directly or indirectly (through the connected pores), to the outside of the faeces. The contribution to the faeces volume (%) and the mean volume of individualised pores and organic matter fragments (mm^3) was computed for each of these faeces pores and POM compartments (total, connected and unconnected ones).

Despite deriving from the same soil and same plant litter, the physicochemical characteristics of fresh faeces, such as elemental content and physical cast organisation (content of particulate organic matter and pores) varied amongst earthworm species (Fig. 4a and 4b). SOM stability in faeces depended on the identity of earthworms that produced the faeces, and at least half of the variation in respiration rates amongst faeces of different earthworm species could be explained by species-specific variations of the microstructural traits of faeces (Fig. 4).

One of the major findings of this study was that, regardless of the earthworm species or the stage of faeces decomposition considered, a substantial part of the variability in faeces mineralisation rates observed could be explained by the physical organisation of these faeces. These included volume contribution of POM, and especially its connection with the microporosity, which possibly favoured the accessibility of SOM to microorganisms (Fig. 4c). This study therefore suggests that earthworm faeces traits can ultimately contribute to determining the effect of different earthworm species on SOM dynamics.

4. Discussion, challenges and perspectives

The two case studies highlight the pertinence of using faeces characteristics to predict the effects of the myriad of detritivore species on soil processes. Despite major differences in morphology, and feeding and behavioural habits, diverse detritivore species share faeces as a common feature. We believe that measuring characteristics on detritivore faeces is a promising research avenue to unify research areas so far compartmentalised into subgroups of soil fauna (Fig. 5). In the following sections, we discuss key aspects related to the use of faeces characteristics as predictors of soil processes, including potential difficulties and precautions, research directions and integration within current frameworks.

4.1. Which faeces traits for which soil processes?

A pertinent use of effect traits requires (i) a clear identification of the process of interest and (ii) the formulation of clear hypotheses on the link between the measured traits and the process of interest. In a literature review, Brousseau et al. (2018) identified a detrimental lack of such clarification in 39% of the reviewed studies on arthropod effect traits. This is especially important for organic matter turnover, which results from multiple processes including leaching of water-soluble compounds, enzymatic degradation by microorganisms, physical and physico-chemical protection, that can all contribute to the stabilisation and destabilisation of SOM (Fig. 5, right panel). Because of the strong control of physicochemical characteristics on these processes, detritivore faeces traits may be linked to organic matter turnover through their effect on specific processes, but to varying degrees depending on the process considered and the temporal scale. In the two aforementioned case studies, such links between processes and faeces traits were hypothesised. For example, Joly et al. (2020) hypothesised that the link between concentrations of DOC in faeces and faeces C loss over time was due to an increased leaching of water-soluble compounds following litter conversion into detritivore faeces, which would facilitate decomposition and increase the amount of organic matter transferred to the underlying soil ~~facilitatethus accelerate decomposition~~. Similarly, Le Mer et al. (2022) hypothesised that increasing volume~~connectivity~~ of POM in earthworm faeces, connected with the pore space presenting an uninterrupted path to the edge of the cast, ~~with the outside of the faeces in earthworm faeces~~ facilitates microbial activity and thus SOM mineralisation. In the long term, however, it remains unknown if faeces traits related to organic matter C loss (Joly et al., 2020) or CO_2 emissions (Le Mer et al., 2022) translate into changes in the persistence of SOM. Because both leaching and microbial activity can favour the production of microbial biomass and thus necromass, and~~, they may~~ ultimately affect the formation of mineral-associated organic matter (Sokol et al. 2019b), faeces DOC concentrations or POM connectivity may predict the contribution of faeces to SOM formation~~, the most persistent SOM form (Cotrufo et al., 2015)~~. However, once the easily degradable compounds are leached or used by microorganisms, the remaining fragments that compose the faeces may contribute to the formation of a partly decomposed POM pool, which is not necessarily subject to stabilisation processes. The formation of this kind of POM may be linked to different faeces traits, such as the average faeces particle size (Joly et al., 2020) or its location within the pore structure of the faeces (Le Mer et al., 2022). The feeding of detritivores on faeces (known as coprophagy), either on their own (e.g., Kautz et al., 2002), or that of other species (e.g., Bonkowski et al., 1998), could further affect the fate of organic matter. Faeces characteristics determining their palatability to detritivores may thus also be considered as faeces traits.

Future use of detritivore faeces traits should thus carefully consider the mechanistic links between the traits and soil processes/ parameters considered, and the timescale at which the traits are relevant as predictor of soil processes. The study of faeces characteristics is still in its infancy and characteristics not yet considered may prove useful in the future. As starting points, we recommend that future studies should consider physical traits such as water-holding capacity, faecal pellets specific area and density, faeces particle size, pore structure, and POM connectivity, as well as chemical characteristics such as elemental composition and DOC or TDN concentrations, as predictor of faeces decomposition, mineralisation, and contribution to SOM formation. These faeces characteristics could also possibly explain detritivore-species specific effects on aggregate size distribution and stability. Such characteristics are easily measurable and on relatively small amounts of faeces (see. Joly et al., 2018, 2020, Le Mer et al., 2022). We encourage future studies to explore relationships between faeces traits and soil processes in order to build a conceptual framework linking detritivores and organic matter turnover.

4.2. Bridging research between litter- and soil-feeding detritivores

While the two case studies presented here focused on different groups of detritivores with different food sources (feeding on leaf litter in Joly et al. (2020), and feeding on soil and litter in Le Mer et al. (2022)) and considered different soil processes (organic matter C and N loss in Joly et al., 2020; soil C mineralisation in Le Mer et al., 2022), we argue that their respective approaches could be combined by considering similar faeces characteristics and processes (leaching, microbial degradation, stabilisation) across a diversity of organisms feeding on plant litter and mineral soil (Fig. 5, left panel). Notably, earthworms do not solely feed on mineral soil but also, depending on species, ingest varying quantities of litter at various stages of decomposition~~depending on species~~. Simultaneously, litter-feeding detritivores also integrate substantial amounts of soil as part of their diet (David, 2014). Yet, most earthworm studies compared earthworm faeces to the bulk soil often ignoring the ingestion and fate of litter, and in turn the faeces of litter-feeding detritivores was mostly compared to the intact litter ignoring the ingestion of soil and its fate. Because both groups ingest and mix soil and litter to some extent, they may affect similar soil processes to varying degrees. We thus suggest that these groups be placed along gradients of litter-soil ingestion, and that their faeces be compared to the average characteristics and fate of their food source (soil and litter).

The depth at which produced faeces are returned to the soil may also be an important faeces trait to predict detritivore effects of organic matter turnover and combine the roles of litter and soil feeding detritivores. Although many detritivore species live and feed in the litter layer, some live deeper in the soil and most at least move through the soil, as recently illustrated with 3D image analyses of soil burrows in mesocosms occupied by earthworms and millipedes (Mele et al., 2021). The creation of biopores by millipedes, well-known by soil zoologists, has been rarely considered by ecologists. A direct consequence of this is that faeces may also be deposited deeper than the ingested food in the soil, thus possibly changing decomposition rate. Indeed, Coulis et al. (2016) showed that faeces decomposition was faster than intact litter at soil surface, and that this decomposition was even faster when faeces were buried. Instead, an isopod species in the Negev desert that lives in deep burrows deposits its faeces at the soil surface (Sagi et al., 2019; Yair and Rutin, 1981). The average depth at which a given detritivore species typically deposits its faeces, and the proportion of buried faeces compared to surface ones, may thus be important factors for the fate of the faeces, and could place detritivore species along a continuous axis rather than categorise detritivore into soil-dwelling and litter-dwelling groups.

4.3. The composite determinism of detritivore faeces traits

A main difficulty in the use of faeces traits as predictors of organic matter turnover is that these traits have a composite determinism, originating both from the identity of the detritivore and from the quality of its resources (Fig. 5). We argue that this feature does not contradict the consideration that faeces characteristics are relevant effect traits. The composite determinism of faeces traits does not prevent identifying which traits are powerful predictors of organic matter turnover. For example, in the case studies presented above, the authors identified faeces DOC concentrations as a good predictor of faeces C loss (Joly et al., 2020), and Le Mer et al. (2022) similarly demonstrated that microstructural traits predicted CO_2 emissions from earthworm faeces. The composite determinism of faeces traits, however, clearly makes it more challenging to use species-specific trait values to upscale to the community and ecosystem levels. For example, the use of community-weighed means is based on measurements of the local community structure and on taxon-specific trait values, averaged from local measurements or from databases. While some traits are mainly determined by the detritivore species (e.g., size, shape and location of faeces), for traits related to chemical characteristics, the attribution of a trait value to a detritivore species is not straightforward. Indeed, their value depends on the ingested resource and its interaction with the detritivore species. For such traits, the approach presented in the case study 1 (Joly et al., 2020) might be a promising solution: the relevant trait is not the faeces trait per se, but the change in trait value between the food and the produced faeces. Building relationships between the quality of the ingested organic matter and relevant faeces traits, for major groups of detritivores or even for individual species as proposed in Fig. 3, appears as a relevant way to overcome the difficulties arising from the composite determinism of faeces traits. With this framework, the knowledge of litter quality and of the local community of detritivores could allow a reasonable prediction of the effect of litter transformation into faeces.

4.4. Integration into current frameworks of trait-based ecology

While studying detritivore faeces characteristics appears as a promising way to better understand and integrate the role of detritivore in organic matter dynamics, we must also ask whether they can be considered as *traits*. Traits are defined as “any morphological, physiological, or phenological heritable feature measurable at the individual level, from the cell to the whole organism, without reference to the environment or any other level of organization" (Pey et al., 2014; Violle et al., 2007). If applied rigorously, faeces characteristics do not fit to this definition, since faeces are not part of the individual, strictly speaking. Yet, because they are largely shaped by the identity of the detritivore, faeces characteristics can to a large extent be conceptualised and analysed~~analyzed~~ as traits. Similar extensions of the use of traits beyond the living organisms is commonly applied, for example for plant litter traits as an extension of plant traits (e.g., Fujii et al., 2020; Garcia-Palacios et al., 2016; Makkonen et al., 2012) or enzymatic production as microbial trait (Piton et al., 2020; Weimann, 2016). Thus, we argue that including faeces characteristics as traits of the detritivores that produced them is a reasonable and fruitful option.

We then must answer: can faeces traits be considered as *functional* traits? Defining what makes a trait functional is far from trivial, because several definitions of functions have been used in ecology (Malaterre et al., 2019). From a selectionist approach, the functions of a trait of biological entities are "the effect for which those entities were favoured under past natural selection" (Malaterre et al., 2019). This definition bears similarity with the functional trait definition proposed by Violle et al. (2007) or Garnier et al. (2016), as traits "indirectly influencing the fitness of an individual via its effects on growth, reproduction, or survival". Response traits, which vary in response to changes in environmental conditions, fit well with these selectionist approaches. The question to answer to determine if faeces characteristics fit this selectionist definition is therefore: do the characteristics of faeces feed back to the fitness of the organisms producing the faeces? This question was explored for soil engineers by Jouquet et al. (2006) who differentiated, following Jones et al. (1994, 1997), between 'extended phenotype engineers' as organisms creating biogenic structures that directly influence the fitness of the organism producing it, and ‘accidental engineers’ for which no such positive effect is recorded. It was recently shown that earthworm activity in European forests could increase soil pH, thereby making soil conditions more favourable for themselves ~~alter the soil characteristics~~ and~~in a way that~~ reinforcing~~es~~ earthworm abundance (Desie et al., 2020). This suggests that the feeding activity of soil fauna and transformation of organic matter can alter soil properties in a way that affects soil fauna fitness. For other detritivores, we are not aware of studies demonstrating that faeces properties modify environmental conditions in a way that benefits fitness, and the answer might depend on the studied species. When the term *functional* is used in a selectionist meaning, faeces traits are thus not unequivocally functional. However, other authors proposed non-selectionist, alternative definitions of function, and therefore of functional traits (Dussault, 2018, Malaterre et al. 2019). In this approach, traits are functional when they enable the organism to achieve particular contribution to ecosystem processes (Dussault, 2018). Following this alternative definition of function, they can also be considered functional traits. Regardless of the definition of function and functional traits, faeces traits are unambiguously *effect trait*, which influences ecosystem properties (Garnier and Navas, 2012).

5. Conclusions

In conceptual and mechanistic biogeochemical models, soil fauna are the ‘*elephant in the room*’ (Briones, 2018; Filser et al., 2016; Griffiths et al., 2021, Prescott and Vesterdal, 2021), likely because of the difficulty of studying and synthesising such a diverse group of organisms, which roles are difficult to isolate. As a first step towards bridging this gap, our viewpoint proposes a way to integrate detritivorous soil animals by focu~~s~~sing on their faeces, which is a common feature amongst detritivores and represents a key decomposition by-product in detritivore-rich ecosystems. Faeces characteristics of distinct detritivore species were recently shown to predict relatively well processes involved in organic matter turnover, and we thus formalised faeces characteristics as *effect traits*. This appears as a promising way to deal with the astonishing diversity of detritivores in soils, which may in particular unify historical soil fauna groups such as soil engineers and litter transformers. This approach could overall contribute to the inclusion of detritivores in biogeochemical models, thereby improving our understanding and modelling of carbon cycling.

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Figure captions

Figure 1: A sample of the diversity of detritivores and their faeces.

Figure 2: Diversity of detritivore faeces resulting from leaf litter of six tree species eaten by six detritivore species. From Joly et al., 2020.

Figure 3: Schematic representation of the relationships between the detritivore effect (i.e. changes in litter characteristics following detritivore conversion of litter into faeces) and intact litter characteristics, as observed in Joly et al., 2020. Changes in the magnitude of the detritivore effect following litter conversion into faeces are described by the intercept (e.g. **m** for species 1 and **n** species 2). Changes in the interaction between the detritivore effect and the intact litter characteristics are described by the slope (e.g. **a** for species 2 and **b** for species 3). The intercept and slope value for each species can then be used to determine the change in organic matter characteristics following conversion into detritivore faeces.

Figure 4: Microstructural traits as predictors of carbon mineralization rates in faeces. a) Multidimensional representation of earthworm faeces microstructures during decomposition. For

all species, porosity increases through time, while POM and fresh organic matter decreases. b) Mineralization rates of faeces produced by six earthworm species belonging to three ecological categories, measured after 7, 42 and 140 days of incubation. Mineralisation rates depend on earthworm species and faeces age. c) Respective importance of faeces traits as predictors of C mineralisation. Altogether, these microstructural traits explain more than 50% of the variability in faeces CO_2 emissions.

Figure 5: Conceptual framework formalising faeces traits as unifying predictors of detritivore effects on organic matter turnover. Amongst the diversity of detritivore, each individual can be placed along a gradient of litter and soil ingestion. Detritivores produce faeces whose traits are governed by the composite determinism of the identity of the detritivore, the characteristics of its ressource and the interactions between both factors. These faeces traits are related to the several processes that contribute to organic matter turnover in soils.

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To: Editorial Board of *Geoderma* Montpellier, 21/04/2022

Manuscript Coq *et al.*

Please find herewith a revision of our manuscript entitled « Faeces traits as unifying predictors of detritivore effects on organic matter turnover » which we would like you to consider for publication in *Geoderma*.

We are pleased with the generally positive assessment of our work and welcome the constructive feedback from both reviewers. We revised our manuscript accordingly. We believe that the revised version has significantly improved in quality, and we hope that the changes made in the manuscript, as well as our responses to the queries of the reviewers will be satisfying.

In particular, we modified the abstract and shortened the introduction. We also proposed a list of faeces traits we expect to be particularly relevant to predict their fate.

Specific answers to each of the reviewers' comments is provided below.

Thank you very much for your consideration.

Yours sincerely,

Sylvain COQ

We declare that none of the material presented in this manuscript has been published or is considered for publication elsewhere.

Response to reviewer comments:

Reviewer #1: This is an interesting thought piece on an important topic. The authors correctly posit that the characteristics of detritivore faeces will influence their rate of decomposition and thereby influence organic matter turnover. It follows that faeces should have functional effect traits. This suggestion should provoke research to identify the characteristics that most strongly influence decomposition rate and if these can be considered to be functional traits. It would therefore be beneficial for the field for the manuscript to be published.

> *We are grateful to the reviewer for taking the time to review our manuscript, for the positive assessment of our work and the constructive comments. We considered them all carefully and revised our manuscript accordingly.*

I have only one major suggestion for improvement, and that is for more thinking be provided around what characteristics of faeces are most likely to influence their decomposition or, conversely their contribution to soil organic matter. Few scientists will have given more thought to this than the authors of this paper, so they should have some great insights as to what characteristics they think influence the fate of faeces. For example, I see little reference to the size of particles within the faeces, despite some of the authors demonstrating the importance of this factor. It would seem that how tightly packed the particles are within the pellets would be important as small particles should be more susceptible to decay than large particles or faeces that remain intact. In the current manuscript they stay very close to statistical results from the few previous papers, rather than positing what factors should be important. For example, the finding that C losses correlated with DOC and N losses correlated with TDN is neither surprising nor is it very helpful for identifying traits that determine the fate of the faecal matter. The paper would advance the field more by presenting ideas about the characteristics of faeces most likely to influence their fate, how these might be measured, and some hypotheses that could be tested to advance our understanding of this topic.

> *Thanks for this advice. We initially decided to stick to the evidence from the two case studies, to illustrate that faeces characteristics can predict processes of organic matter turnover. However, we agree that further insights could give directions for future studies. We now more specifically discuss which faeces characteristics should be considered in future studies (lines 32-35 in the abstract and 296- 306 in the main text).*
>
> *On the correlation between DOC and C losses, we do believe that it may determine the fate of faecal matter. Indeed, leachates can form mineral-associated organic matter (MAOM), either through direct adsorption to mineral particles or through incorporation into microbial biomass. The quantity of DOC in faeces may thus predict the contribution of faeces to MAOM formation. We now more specifically describe this point (L272 – 276 and 302-304).*

Minor comments:

Line 61: organic matter characteristics such as ?

> *Here, we referred to multiple physicochemical characteristics. We clarified this point.*

65: not sure what global means in this context. Sentence makes sense without this word.

> *We removed "global" from the sentence.*

85: is rather than represents

We modified this accordingly.

104: contrasting

Thank you - we corrected this.

116: "These are well-defined effect traits"

Thank you - we corrected this.

118: remove 'urgently' - more suitable for grant proposal

We removed “urgently” from the sentence.

133: "that characteristics of faeces can predict their fate"

Thank you - we modified this accordingly.

135-137: this sentence is cumbersome

We split this sentence in two to make it more understandable.

144: eject

Thank you - we corrected this.

145: 'local' not needed

We removed “local” from the sentence.

157: "faeces have higher"

Thank you - we corrected this.

161: 'influence' rather than 'drive'

We modified this accordingly.

163 and 175: what changes are you referring to? During gut passage?

Yes, exactly. We clarified this point in both sentences.

169: remove 'in turn'

We removed “In turn” from the sentence.

177: something funny about this sentence. Wouldn't air and water circulation increase decomposition rather than physical protection?

> *We rewrote this sentence to avoid this confusion.*

253: does this influence how easily the faeces fragment into particles?

> *Indeed, these faeces traits could likely influence the stability of these faeces or the stability of soil aggregates, which could feedback to organic matter turnover. However, the authors of the study presented in the case study 2 did not explore this effect. We acknowledge that it is an interesting perspective, and we now mention this point in the discussion (lines 301 - 302).*

281: increased leaching of DOC probably only influences early rates of mass loss of faeces, as for litter

> *This is likely true (although remains to be tested), but this could still reduce the overall amount of litter that remains undecomposed and increase the transfer of OM to the soil. Indeed, detritivores preferentially feed on litter that has already undergone the early mass loss due to leaching. By transforming litter into faeces, detritivores thus allow further leaching. We clarified this aspect (L272 – 276 and 302-304).*

283: the meaning of "increasing connectivity of POM with the outside of the faeces" is not clear to me

> *We clarified this sentence (lines 276 - 278).*

388: the meaning of "reinforces earthworm abundance" is not clear to me. I think you mean that earthworms create conditions conducive to earthworms and so their abundance increases once they get a foothold? Same species or other species too?

> *Here, we refer to the paper by Desie et al. 2020 where the authors showed, using structural equations modelling, that in several studied forests across Europe, earthworms (no species in particular) can alter soil conditions and pH in particular and thus create suitable living conditions for themselves. We reworded this section to make this clearer (L 394 - 397).*

Final thoughts:

Re: 'composite determinism'. Maybe this could be addressed with reference to context-dependency. So the characteristics of faeces probably depend mostly on the animal but this can be adjusted somewhat by the nature of this litter eg high quality vs low quality - maybe an example could be presented in the format we used to think through context dependency of decomposition (Fig 7 of Prescott & Vesterdal 2021).

We can see that there is a similarity between the ‘composite determinism’ that we put forward here and the often-used concept of ‘context-dependency’ in ecology. This concept is highly relevant for plant litter decomposition, as illustrated in the recent review by Prescott & Vesterdal 2021, to point out the key role of environmental conditions on this complex process.

However, we believe that the composite determinism of faeces characteristics is not perfectly expressed by the concept of context-dependency. Faeces traits are co-constructed by the characteristics of the two organisms involved (plants and detritivores), and none of them can be considered as an environmental condition, nor can we hierarchise their role in determining faeces traits. As explained in the discussion, some faeces traits are mainly determined by the detritivore identity while others are determined by the identity of the consumed litter. This is noteworthy as this case of composite determinism has not been previously described in trait-based ecology to our knowledge. Through this term, we hope to conceptualise this composite-determinism and spark a new interest into the potential use of traits for structures that are formed by multiple organisms. We acknowledge that this is not an easy question though. A discussion of the similarities/differences between context-dependency and composite determinism would require a longer development, and we prefer not to complexify the discussion.

Finally, what about coprophagy. I expect the tendency for the species to consume their own faeces or the palatability of their faeces to other organisms would influence its fate - would this be a functional trait?

Absolutely, this is a valid point. We now mention this aspect in the discussion (lines 298-292).

Very interesting paper, I enjoyed reading it.

Many thanks!

Reviewer #2: The paper with reference GEODER-D-21-02589 entitled "Faeces traits as unifying predictors of detritivore effects on organic matter turnover" by Coq and colleagues addresses the use of faeces' (dejections) characteristics of different groups of soil invertebrates' fauna as traits to improve our understanding for a functional classification of the so-called group of detritivores or litter transformers.

By using the characteristics of their faeces the authors aim at predicting the effect of the large diversity of detritivores on soil processes related to organic matter turnover. Faeces characteristics can be considered within the group of "effect traits" since those are powerful predictors of the fate and turnover of this transformed organic matter.

The contribution is very important and timely relevant as in the very last years some initiatives related to soil biota characterization in many sites and on the effects of their processes in the soil have been put in place, bringing the attention to the accepted classification of ecosystem engineers like earthworms and classical litter transformers such as millipedes. Sometimes the boundaries are not clear as some of the litter transformers can also be considered as ecosystem engineers (autogenic type according to the seminal work of Jones et al. 1994) as the they transform a resource (litter) into another physical material, matching the concept of soil ecosystem engineering. In my opinion there is no clear boundaries for this classification and its use depends on the objectives of the study but I sincerely welcome this contribution that will add to the ongoing general debate of the effect of soil fauna on soil organic matter dynamics.

My recommendation is that this manuscript should be accepted in Geoderma journal after minor revision.

I have included some minor comments that hopefully authors will gently take into consideration.

> *We thank the reviewer for taking the time to review our work and provide us with constructive comment to further improve our manuscript. We considered all suggestions carefully and revised our manuscript accordingly.*

Minor comments

Abstract: The abstract should be rewritten. There are neither data provided in this section nor results of the two case studies included in this manuscript.

> *Thanks for sharing your view on this. We now make it clearer that this work is a viewpoint paper, and we also rewrote parts of the abstract to better present the results of the case-studies highlighted here, also in line with comments from reviewer 1 (lines 32-35).*

Introduction: This section is too long. I recommend to shorten it. Also, include what your main hypothesis and objectives of this contribution are. It seems that your main objective was to perform a directed review by selecting a couple of case studies and infer a framework of soil functioning by combining both approaches; this needs to be clarified.

> *Thank you for this view. We streamlined parts of the introduction when possible, significantly shortening the introduction. We also now clarify that this article is a viewpoint paper that highlights results of recent selected studies to put forward a new approach to studying the role of soil fauna on soil processes (lines 27 in the abstract and 120 in the introduction).*

Line 179. Please, remove italics in sp.

> *Thank you - this was corrected accordingly.*

Line 302. … focused … .

> *Thank you - we corrected this spelling at this line and a few other instances.*

Line 309. It is not only that earthworms feed on different quantities of litter, but in different state or degree of decomposing material; in other words, organic matter in different stages of decomposition, less or more fragmented and decomposed material.

> *This is a good point. We clarified this sentence.*

Line 322. See also recent work by Wieland et al. (2021).

Wieland, R., Ukawa, C, Joschko, M., Krolzcyk, A., Fritsch, G., Schmidt, O., Filser, J., Jiménez, J.J. Use of Deep Learning for structural analysis of CT-images of soil samples. Royal Society Open Science 8(3):201275 (doi:10.1098/rsos.201275)

> *Thank you for bringing this work to our attention. This is indeed an interesting paper on the use of deep learning to decipher the structure of soil samples analysed with CT-scans. However, the role of soil fauna on soil structure is not discussed at all in this paper, so its relevance at this point of our manuscript is not clear.*

Line 328. Please, let me suggest these two earlier references on desert isopods. Not only recent papers are worthy to include in the list of references.

M. Shachak, E.A. Chapman, and Y. Steinberger. 1976. Feeding, Energy Flow and Soil Turnover in the Desert Isopod, Hemilepistus reaumuri. Oeocologia, 24, 57-69

and

Yair, A., and J. Rutin. 1981. Some aspects of the regional variation in the amount of available sediment produced by isopods and porcupines, northern Negev, Israel. Earth Surface Processes and Landforms 6:221-234.

> *Again, thank you for bringing this work to our attention. We knew of the work by Shachak et al 1976, but not the study by Yair and Rutin, which is indeed very interesting with perhaps some of the first ever published photos of detritivore faeces. We included this reference to our manuscript. Instead, since Shachak et al 1976 conducted their study in the lab, its connection to our discussion is less clear and we decided not to include it.*

Figures are OK and no changes are suggested.

Highlights

- Detritivores are diverse animals which role in soil processes is difficult to predict
- We argue that detritivore faeces characteristics may be promising effect traits
- Two case studies show that faeces traits predict organic matter turnover
- This could unify groups of animals so far separated between soil- and litter-feeding

Faeces traits as unifying predictors of detritivore effects on organic matter turnover

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Viewpoint paper for **Geoderma**

Special Issue **“Assessing soil functioning through invertebrate trait-based approaches”**

Abstract

In the last decade, our understanding of plant litter decomposition and soil organic matter formation substantially improved but critical blind spots remain. Particularly, the role of detritivores, i.e. soil animals that feed on litter and soil, is poorly understood and notoriously missing from biogeochemical models. This major gap results from methodological difficulties to isolate their effect and from the astonishing diversity of detritivorous organisms with few common features, thereby hampering the identification of general patterns. In this viewpoint, we propose that the characteristics of their faeces can predict detritivore effects on soil processes related to organic matter turnover across the large detritivore diversity. Indeed, faeces are common to all detritivores, and a large part of organic matter is transformed into faeces in many ecosystems. Two recent studies presented here showed that faeces characteristics are powerful predictors of the fate and turnover of this transformed organic matter. We suggest that faeces characteristics, such as water-holding capacity, size and spatial organisation of the faecal pellets and of their constituting particles, particulate organic matter connectivity, as well as the characteristics of dissolved organic matter in faecal pellets, are promising ‘effect traits’. By focusing on similar features rather than differences, this approach has the potential to break down barriers of this highly fragmented soil animal group, in particular between earthworms that are often studied as ecosystem engineers and classical litter transformers such as millipedes, woodlice, or snails. We discuss ways of tackling the complexity of using such traits, particularly regarding the composite determinism of faeces characteristics that are driven both by the detritivore identity and the ingested organic matter. Rigorous and hypothesis-based use of faeces characteristics as effect traits, including clear identification of studied processes, could allow integrating detritivores in our current understanding of organic matter turnover.

Key-words

Macroarthropods ; Soil functioning ; Soil invertebrates ; Soil processes ; Trait-based approaches

1. Introduction

Plant litter decomposition and the subsequent formation of soil organic matter (SOM) are key ecosystem processes that control biogeochemical cycling and the ability of soils to store large amounts of carbon (Lehmann and Kleber, 2015). In the last decade, a new understanding of litter decomposition and SOM formation has emerged (Basile-Doelsch et al., 2020; Dignac et al., 2017; Schmidt et al., 2011), through (i) a renewed characterization of the chemical nature and protection mechanisms of SOM (Kögel-Knabner and Rumpel, 2018; Lehman and Kleber, 2015), (ii) a growing recognition that interactions between plant litter, microbial communities and minerals rather than litter recalcitrance control SOM formation (Cotrufo et al., 2013, 2015; Dynarski et al., 2020), and (iii) the recognition of the important role roots play in SOM formation (Adamczyk et al., 2019, Clemmensen et al., 2013; Rasse et al., 2005; Sokol et al., 2019a). In contrast, while the importance of soil invertebrates in soil processes is often acknowledged (Briones, 2018; Griffith et al., 2021), our understanding of their roles in SOM dynamics is still poor (Filser et al., 2016; Prescott and Vesterdal, 2021). Detritivores in particular, i.e., soil invertebrates that feed on dead organic matter, importantly contribute to organic matter turnover (Prescott and Vesterdal, 2021). They do so by ingesting large amounts of organic matter, assimilating a part of it and rejecting the main part as faeces (David, 2014). This processing greatly affects the organic matter physicochemical characteristics (e.g., Coulis et al., 2009, 2016; Hedde et al., 2005; Joly et al., 2018; Le Mer et al., 2020; Vidal et al., 2016) and its contribution to SOM formation (Angst et al., 2019, Vidal et al., 2019). Despite clear evidence that in many ecosystems detritivores process large amounts of organic matter, we lack a general understanding of their role in its turnover.

One of the main obstacles to understanding the detritivores' influence on organic matter turnover is the difficulty to isolate these effects experimentally. Traditionally, the role of soil invertebrates in decomposition processes has been studied using litterbags of different mesh sizes (0.1 mm, 2 mm, 4 to 8 mm), sequentially excluding soil invertebrates based on their body width (e.g., Handa et al., 2014; Wall et al., 2008). A meta-analysis of such studies reported that micro- and mesofauna (body width < 2 mm) presence increased litter mass loss by 37% on average across biomes (Garcia-Palacios et al., 2013). This figure emphasises the importance of soil invertebrates in decomposition, but has several limitations. The focus on body width means that the measured effect includes not only the effect of soil invertebrates feeding on plant litter (detritivores), but also of other functional groups with potential top-down effects such as microbivores and predators (Koltz et al., 2018; Lenoir et al., 2007). Moreover, the large mesh sizes used for treatments allowing faunal access entail that the litter consumed by detritivores but returned to soil as faeces is not retrieved in litterbags and considered as lost mass. The decomposition of these faeces and their contribution to SOM formation is a major unknown (Prescott, 2010). Studies on decomposition in reconstructed detritivore communities in microcosms (e.g., Hattenschwiler and Gasser, 2005; Joly et al., 2021; Vidal et al., 2019), or on the detritivore faeces fate (e.g., Coulis et al. 2016; Decaëns, 2000; Joly et al., 2020) contributed to overcoming the limitations of the litterbag technique. Yet, the complexity of such studies limited the number of detritivore species considered and thus the identification of general patterns across the diversity of detritivores.

The extreme diversity of detritivores is the other dominant obstacle towards identifying general principles of detritivore effects on organic matter turnover. Detritivores include millipedes, woodlice, earthworms, snails, and insect larvae, which greatly differ in their morphologies, behaviours, and the ways they process organic matter. Historically, the role of these animals on soil processes was studied considering separate broad functional groups and subgroups. Specialists of millipedes (e.g., David and Gillon, 2002), woodlice (Zimmer, 2002), or snails (Astor et al., 2015) often studied the role of a few species on litter decomposition separately. In addition, since earthworms also modify their environment through their burrowing activities, most earthworm studies focussed on their global role as ‘ecosystem engineers’ (Lavelle and Spain, 2001; Wardle, 2002) rather than ‘detritivores’. Clearly, the separate study of the various groups of detritivores have limited the identification of general principles of detritivore effects on soil processes. Trait-based approaches allow moving beyond broad categorical characterisation of organisms based on their assumed differences in ecosystem function, to more precise continuous characterisation based on characteristics that relate to their differences in ecosystem function, known as *effect traits* (Garnier et al., 2016; Violle et al., 2007). In plant studies, effect traits have proved very useful for upscaling from organisms to ecosystems, whether aboveground traits (Lavorel and Garnier, 2002; Violle et al. 2007) or belowground ones (Freschet et al., 2021), particularly as predictors of litter decomposition (Cornwell et al., 2008; Rosenfield et al., 2020). For example, plant litter with high specific leaf area and leaf nitrogen and phosphorus concentrations generally decomposes rapidly, while high dry matter content and tannin concentrations of leaves are associated with slow decomposition (Cortez et al., 2007; de la Riva et al., 2019; Kazakou et al., 2006).To better integrate detritivores into the current framework of SOM dynamics, we need to identify effect traits that link the activity of these animals to processes controlling SOM dynamics, but this challenge lags behind. In the European invertebrate trait database BETSI (https://portail.betsi.cnrs.fr/, Pey et al., 2014), out of 76 traits recorded, only 11 can be considered as effect traits according to Brousseau et al.

(2018), and only two of these have direct links to ecosystem function (i.e. burrowing strategy and feeding traits). This calls for a common effort to identify effect traits of detritivores relevant to organic matter turnover that enable meaningful comparisons amongst taxa. Such traits should (i) be measurable on all kinds of detritivores and (ii) have a demonstrated link to the studied function. This point is crucial as current applications of trait-based approaches often lack such a clear link (Brousseau et al., 2018; Shipley et al., 2016).

In this viewpoint paper, we argue that detritivore faeces are a promising yet overlooked part of their phenotype, which characteristics, measurable on all soil fauna, can predict their effect on key soil processes related to organic matter turnover. First, we show that detritivore faeces represent important by-products of detritivore activity and that their characteristics are directly related to organic matter turnover. Then, with two selected recent case studies, focusing on litter-feeding and soil-feeding detritivores respectively, we show that characteristics of faeces can predict their fate, and thus predict the effect of these detritivores species on litter decomposition and SOM formation. We thus advocate for the consideration of faeces characteristics as detritivore effect traits. Such traits could be powerful unifying traits across the large diversity of detritivores that otherwise share few common features with little link to ecosystem function.

2. Faeces as key by-products of detritivory

Detritivores are soil animals that feed on dead organic matter, either on leaf litter (arthropods, snails, epigeic earthworms), on soil and root litter (endogeic earthworms), or both (anecic earthworms). Since these food sources are rather nutrient-depleted and hard to digest (Sterner and Elser, 2002), detritivores typically have low assimilation efficiencies and high consumption rates (Crossley et al.,1971; Curry and Schmidt 2007; David, 2014). Thus, they ingest a lot of dead organic matter, assimilate a small part of it, and egest most of it to soils as faeces (Fig. 1). Studies from temperate (Schaefer et al., 1990), Mediterranean (David and Gillon, 2002), arid (Sagi et al., 2019), and tropical ecosystems (Dangerfield and Milner, 1996) estimated that in these ecosystems, 40-50% of the annual litterfall is consumed by detritivores and returned to soils as faeces. In ecosystems where detritivores are abundant, these faeces thus represent a substantial part of the soil profile, e.g., in temperate (Zanella, 2018) or tropical ecosystems (Bottinelli et al., 2021). Undeniably, in many ecosystems, large quantities of organic matter originating from litter are decomposed and stabilised only after conversion into faeces. Determining the physicochemical characteristics of these faeces and how they affect their fate is thus critical to understand detritivore effects on organic matter turnover (Prescott and Vesterdal, 2021).

The conversion of plant litter and/or soil into detritivore faeces leads to profound physicochemical changes that can affect the fate of organic matter in soils. For detritivores that preferentially feed on plant litter (e.g. millipedes, woodlice, snails), faeces have higher concentrations of dissolved organic carbon and nitrogen, water-holding capacity and surface area available for microbial colonisation, and lower C:N ratio and tannins content compared to the plant litter from which they are derived (Coulis et al., 2009, 2016; Ganault et al., 2022; Joly et al., 2018, 2020). Because these physicochemical characteristics are known to influence decomposition rates (Makkonen et al., 2012) and the contribution of litter to SOM formation (Cotrufo et al., 2013), their changes during gut passage are likely to drive the fate of the egested organic matter. In fact, faeces of detritivores such as millipedes typically decompose faster than the litter from which they are derived - an acceleration previously linked to the higher lability of the faeces compared to the ingested litter (Coulis et al., 2016; Joly et al., 2018). Similar to the physicochemical characteristics of leaf litter, those of faeces from distinct detritivore species could thus predict their fate.

For detritivores such as endogeic earthworms that feed on mineral soil, ingestion of soil and its incorporation into earthworm faeces (known as ‘casts’) also lead to major changes in soil physicochemical characteristics. Compared to bulk soil, the faeces are richer in organic carbon, total and mineral nitrogen, total and available phosphorus, and exhibit higher cation-exchange capacity, base saturation and pH (van Groenigen et al., 2019). Similar to litter, these characteristics are known to relate to further microbial degradation and organic matter decomposition (Jouquet et al., 2008), so their changes following gut passage can affect the formation and stabilisation of SOM (Clause et al., 2014). For instance, increased soil compaction and reduced pore size distribution that allow air and water circulation can limit the accessibility of microbial communities to organic matter, and thus physically protect SOM (Angst et al., 2017). Recently, Barthod et al. (2020, 2021) reported that faeces produced by *Eisenia* sp. fed with different clay minerals have a contrasting composition, which in turn differently affected the microbial decomposition of organic matter occluded in these faeces incubated in the soil. This demonstrates a clear link between earthworm faeces characteristics and their fate.

Generally, there is thus growing evidence that detritivore faeces are important decomposition by-products and that their characteristics can be linked to their fate in soils. This suggests that faeces characteristics of different detritivore species could predict the species-specific effect on organic matter turnover. Recently, two studies, each focusing on multiple detritivore species, used this approach to predict their effects on organic matter turnover.

3. Case studies using faeces traits to predict detritivore effects on organic matter turnover

3.1 *Case study 1: Detritivore faeces traits as predictors of organic matter turnover*

The potential of faeces traits as predictors of organic matter turnover was recently illustrated in a study on the role of detritivores on litter decomposition (Joly et al., 2020). The authors explored how detritivores affect litter decomposition, by converting litter into faeces, and how this effect varies across six phylogenetically-diverse invertebrates species. To do so, they collected faeces from six detritivore species (three millipede, two woodlouse and one snail species) feeding on litter of six tree species, separately, resulting in 36 faeces types (Fig. 2). Then, they measured physicochemical characteristics on the 36 faeces types and on the six intact litter types as controls. They then placed all substrates to decompose on top of soil to study the detritivore effect on organic matter turnover. Faeces varied in colour depending on the nature of ingested litter, and in shape depending on detritivore identity (Fig. 2), whereas their physicochemical characteristics (e.g., elemental composition, surface area, water-holding capacity) were driven both by the nature of the ingested litter and the animal identity. Importantly, these faeces traits were tightly correlated with faeces decomposition. Indeed, faeces C and N losses correlated with faeces concentration in dissolved organic carbon and total dissolved nitrogen, respectively. This shows that faeces traits may be predictors of organic matter turnover across detritivore species as different as millipedes and snails, suggesting that extending trait measures to detritivore faeces may allow predicting their effects on soil processes.

Another major finding of this study was that the detritivore effect – that is, the difference in organic matter quality or element cycling rate between faeces and intact litter – depended on the ingested litter species, with larger positive effects for low-quality and slow-cycling litter, and small or negative effects for high-quality and fast cycling litter (Fig. 3). This general pattern was consistent across detritivore species, suggesting that diverse detritivores play a similar role in organic matter turnover. Yet, the magnitude of the effect, and its relationship with the intact litter characteristics were detritivore species-specific. The parameters of the relationship between litter quality/cycling and the change in quality/cycling following litter conversion into faeces, could thus be used as powerful effect traits. The intercept describes the extent to which a given detritivore species increases organic matter quality/cycling. The slope, in turn, describes the extent to which the effect of this detritivore species varies depending on the initial quality/cycling rate of the ingested litter.

3.2 *Case study 2: Microstructural organisation of earthworm faeces as predictor of earthworm effect on organic matter turnover*

The potential use of earthworm faeces properties as predictors of organic matter turnover was also recently investigated for six earthworm species (Le Mer et al., 2022). In this study, the authors explored how earthworms affect SOM stability by occluding fresh organic matter within their faeces, and how this effect varies between different earthworm species. To do so, they collected six earthworm species, from three ecological categories (epigeic, anecic, and endogeic), fed the earthworms with the same organic matter and soil and collected the resulting six faeces types. They then incubated each faeces type individually under optimal conditions and measured CO_2 respiration rates after 7, 42 and 140 days of incubation as indicators of SOM stability. Finally, they measured the characteristics and physical organisation of the six faeces types and the control soil without earthworm activity. To characterise the SOM occluded by earthworms in their faeces, the authors measured several faeces traits such as organic C content and organic matter stability by Rock-Eval 6 analysis. Moreover, thanks to x-ray microtomography and image analyses, the spatial organisation between pore and POM structures at micro-scale (9.5 µm) was also characterised. For each faeces sample, the authors computed the (i) pore and (ii) POM volumes, as well as the (iii) pore subvolumes directly connected to the air outside the faeces and the (iv) POM subvolumes connected, directly or indirectly (through the connected pores), to the outside of the faeces. The contribution to the faeces volume (%) and the mean volume of individualised pores and organic matter fragments (mm^3) was computed for each of these faeces pores and POM compartments (total, connected and unconnected ones).

Despite deriving from the same soil and same plant litter, the physicochemical characteristics of fresh faeces, such as elemental content and physical cast organisation (content of particulate organic matter and pores) varied amongst earthworm species (Fig. 4a and 4b). SOM stability in faeces depended on the identity of earthworms that produced the faeces, and at least half of the variation in respiration rates amongst faeces of different earthworm species could be explained by species-specific variations of the microstructural traits of faeces (Fig. 4).

One of the major findings of this study was that, regardless of the earthworm species or the stage of faeces decomposition considered, a substantial part of the variability in faeces mineralisation rates observed could be explained by the physical organisation of these faeces. These included volume contribution of POM, and especially its connection with the microporosity, which possibly favoured the accessibility of SOM to microorganisms (Fig. 4c). This study therefore suggests that earthworm faeces traits can ultimately contribute to determining the effect of different earthworm species on SOM dynamics.

4. Discussion, challenges and perspectives

The two case studies highlight the pertinence of using faeces characteristics to predict the effects of the myriad of detritivore species on soil processes. Despite major differences in morphology, and feeding and behavioural habits, diverse detritivore species share faeces as a common feature. We believe that measuring characteristics on detritivore faeces is a promising research avenue to unify research areas so far compartmentalised into subgroups of soil fauna (Fig. 5). In the following sections, we discuss key aspects related to the use of faeces characteristics as predictors of soil processes, including potential difficulties and precautions, research directions and integration within current frameworks.

4.1. Which faeces traits for which soil processes?

A pertinent use of effect traits requires (i) a clear identification of the process of interest and (ii) the formulation of clear hypotheses on the link between the measured traits and the process of interest. In a literature review, Brousseau et al. (2018) identified a detrimental lack of such clarification in 39% of the reviewed studies on arthropod effect traits. This is especially important for organic matter turnover, which results from multiple processes including leaching of water-soluble compounds, enzymatic degradation by microorganisms, physical and physico-chemical protection, that can all contribute to the stabilisation and destabilisation of SOM (Fig. 5, right panel). Because of the strong control of physicochemical characteristics on these processes, detritivore faeces traits may be linked to organic matter turnover through their effect on specific processes, but to varying degrees depending on the process considered and the temporal scale. In the two aforementioned case studies, such links between processes and faeces traits were hypothesised. For example, Joly et al. (2020) hypothesised that the link between concentrations of DOC in faeces and faeces C loss over time was due to an increased leaching of water-soluble compounds following litter conversion into detritivore faeces, which would facilitate decomposition and increase the amount of organic matter transferred to the underlying soil. Similarly, Le Mer et al. (2022) hypothesised that increasing volume of POM in earthworm faeces, connected with the pore space presenting an uninterrupted path to the edge of the cast, facilitates microbial activity and thus SOM mineralisation. In the long term, however, it remains unknown if faeces traits related to organic matter C loss (Joly et al., 2020) or CO_2 emissions (Le Mer et al., 2022) translate into changes in the persistence of SOM. Because both leaching and microbial activity can favour the production of microbial biomass and thus necromass, and ultimately affect the formation of mineral-associated organic matter (Sokol et al. 2019b), faeces DOC concentrations or POM connectivity may predict the contribution of faeces to SOM formation. However, once the easily degradable compounds are leached or used by microorganisms, the remaining fragments that compose the faeces may contribute to the formation of a partly decomposed POM pool, which is not necessarily subject to stabilisation processes. The formation of this kind of POM may be linked to different faeces traits, such as the average faeces particle size (Joly et al., 2020) or its location within the pore structure of the faeces (Le Mer et al., 2022). The feeding of detritivores on faeces (known as coprophagy), either on their own (e.g., Kautz et al., 2002), or that of other species (e.g., Bonkowski et al., 1998), could further affect the fate of organic matter. Faeces characteristics determining their palatability to detritivores may thus also be considered as faeces traits.

Future use of detritivore faeces traits should thus carefully consider the mechanistic links between the traits and soil processes/ parameters considered, and the timescale at which the traits are relevant as predictor of soil processes. The study of faeces characteristics is still in its infancy and characteristics not yet considered may prove useful in the future. As starting points, we recommend that future studies should consider physical traits such as water-holding capacity, faecal pellets specific area and density, faeces particle size, pore structure, and POM connectivity, as well as chemical characteristics such as elemental composition and DOC or TDN concentrations, as predictor of faeces decomposition, mineralisation, and contribution to SOM formation. These faeces characteristics could also possibly explain detritivore-species specific effects on aggregate size distribution and stability. Such characteristics are easily measurable and on relatively small amounts of faeces (see. Joly et al., 2018, 2020, Le Mer et al., 2022). We encourage future studies to explore relationships between faeces traits and soil processes in order to build a conceptual framework linking detritivores and organic matter turnover.

4.2. Bridging research between litter- and soil-feeding detritivores

While the two case studies presented here focused on different groups of detritivores with different food sources (feeding on leaf litter in Joly et al. (2020), and feeding on soil and litter in Le Mer et al. (2022)) and considered different soil processes (organic matter C and N loss in Joly et al., 2020; soil C mineralisation in Le Mer et al., 2022), we argue that their respective approaches could be combined by considering similar faeces characteristics and processes (leaching, microbial degradation, stabilisation) across a diversity of organisms feeding on plant litter and mineral soil (Fig. 5, left panel). Notably, earthworms do not solely feed on mineral soil but also, depending on species, ingest varying quantities of litter at various stages of decomposition. Simultaneously, litter-feeding detritivores also integrate substantial amounts of soil as part of their diet (David, 2014). Yet, most earthworm studies compared earthworm faeces to the bulk soil often ignoring the ingestion and fate of litter, and in turn the faeces of litter-feeding detritivores was mostly compared to the intact litter ignoring the ingestion of soil and its fate. Because both groups ingest and mix soil and litter to some extent, they may affect similar soil processes to varying degrees. We thus suggest that these groups be placed along gradients of litter-soil ingestion, and that their faeces be compared to the average characteristics and fate of their food source (soil and litter).

The depth at which produced faeces are returned to the soil may also be an important faeces trait to predict detritivore effects of organic matter turnover and combine the roles of litter and soil feeding detritivores. Although many detritivore species live and feed in the litter layer, some live deeper in the soil and most at least move through the soil, as recently illustrated with 3D image analyses of soil burrows in mesocosms occupied by earthworms and millipedes (Mele et al., 2021). The creation of biopores by millipedes, well-known by soil zoologists, has been rarely considered by ecologists. A direct consequence of this is that faeces may also be deposited deeper than the ingested food in the soil, thus possibly changing decomposition rate. Indeed, Coulis et al. (2016) showed that faeces decomposition was faster than intact litter at soil surface, and that this decomposition was even faster when faeces were buried. Instead, an isopod species in the Negev desert that lives in deep burrows deposits its faeces at the soil surface (Sagi et al., 2019; Yair and Rutin, 1981). The average depth at which a given detritivore species typically deposits its faeces, and the proportion of buried faeces compared to surface ones, may thus be important factors for the fate of the faeces, and could place detritivore species along a continuous axis rather than categorise detritivore into soil-dwelling and litter-dwelling groups.

4.3. The composite determinism of detritivore faeces traits

A main difficulty in the use of faeces traits as predictors of organic matter turnover is that these traits have a composite determinism, originating both from the identity of the detritivore and from the quality of its resources (Fig. 5). We argue that this feature does not contradict the consideration that faeces characteristics are relevant effect traits. The composite determinism of faeces traits does not prevent identifying which traits are powerful predictors of organic matter turnover. For example, in the case studies presented above, the authors identified faeces DOC concentrations as a good predictor of faeces C loss (Joly et al., 2020), and Le Mer et al. (2022) similarly demonstrated that microstructural traits predicted CO_2 emissions from earthworm faeces. The composite determinism of faeces traits, however, clearly makes it more challenging to use species-specific trait values to upscale to the community and ecosystem levels. For example, the use of community-weighed means is based on measurements of the local community structure and on taxon-specific trait values, averaged from local measurements or from databases. While some traits are mainly determined by the detritivore species (e.g., size, shape and location of faeces), for traits related to chemical characteristics, the attribution of a trait value to a detritivore species is not straightforward. Indeed, their value depends on the ingested resource and its interaction with the detritivore species. For such traits, the approach presented in the case study 1 (Joly et al., 2020) might be a promising solution: the relevant trait is not the faeces trait per se, but the change in trait value between the food and the produced faeces. Building relationships between the quality of the ingested organic matter and relevant faeces traits, for major groups of detritivores or even for individual species as proposed in Fig. 3, appears as a relevant way to overcome the difficulties arising from the composite determinism of faeces traits. With this framework, the knowledge of litter quality and of the local community of detritivores could allow a reasonable prediction of the effect of litter transformation into faeces.

4.4. Integration into current frameworks of trait-based ecology

While studying detritivore faeces characteristics appears as a promising way to better understand and integrate the role of detritivore in organic matter dynamics, we must also ask whether they can be considered as *traits*. Traits are defined as "any morphological, physiological, or phenological heritable feature measurable at the individual level, from the cell to the whole organism, without reference to the environment or any other level of organization" (Pey et al., 2014; Violle et al., 2007). If applied rigorously, faeces characteristics do not fit to this definition, since faeces are not part of the individual, strictly speaking. Yet, because they are largely shaped by the identity of the detritivore, faeces characteristics can to a large extent be conceptualised and analysed as traits. Similar extensions of the use of traits beyond the living organisms is commonly applied, for example for plant litter traits as an extension of plant traits (e.g., Fujii et al., 2020; Garcia-Palacios et al., 2016; Makkonen et al., 2012) or enzymatic production as microbial trait (Piton et al., 2020; Weimann, 2016). Thus, we argue that including faeces characteristics as traits of the detritivores that produced them is a reasonable and fruitful option.

We then must answer: can faeces traits be considered as *functional* traits? Defining what makes a trait functional is far from trivial, because several definitions of functions have been used in ecology (Malaterre et al., 2019). From a selectionist approach, the functions of a trait of biological entities are "the effect for which those entities were favoured under past natural selection" (Malaterre et al., 2019). This definition bears similarity with the functional trait definition proposed by Violle et al. (2007) or Garnier et al. (2016), as traits “indirectly influencing the fitness of an individual via its effects on growth, reproduction, or survival”. Response traits, which vary in response to changes in environmental conditions, fit well with these selectionist approaches. The question to answer to determine if faeces characteristics fit this selectionist definition is therefore: do the characteristics of faeces feed back to the fitness of the organisms producing the faeces? This question was explored for soil engineers by Jouquet et al. (2006) who differentiated, following Jones et al. (1994, 1997), between ‘extended phenotype engineers’ as organisms creating biogenic structures that directly influence the fitness of the organism producing it, and ‘accidental engineers’ for which no such positive effect is recorded. It was recently shown that earthworm activity in European forests could increase soil pH, thereby making soil conditions more favourable for themselves and reinforcing earthworm abundance (Desie et al., 2020). This suggests that the feeding activity of soil fauna and transformation of organic matter can alter soil properties in a way that affects soil fauna fitness. For other detritivores, we are not aware of studies demonstrating that faeces properties modify environmental conditions in a way that benefits fitness, and the answer might depend on the studied species. When the term *functional* is used in a selectionist meaning, faeces traits are thus not unequivocally functional. However, other authors proposed non-selectionist, alternative definitions of function, and therefore of functional traits (Dussault, 2018, Malaterre et al. 2019). In this approach, traits are functional when they enable the organism to achieve particular contribution to ecosystem processes (Dussault, 2018). Following this alternative definition of function, they can also be considered functional traits. Regardless of the definition of function and functional traits, faeces traits are unambiguously *effect trait*, which influences ecosystem properties (Garnier and Navas, 2012).

5. Conclusions

In conceptual and mechanistic biogeochemical models, soil fauna are the ‘*elephant in the room*’ (Briones, 2018; Filser et al., 2016; Griffiths et al., 2021, Prescott and Vesterdal, 2021), likely because of the difficulty of studying and synthesising such a diverse group of organisms, which roles are difficult to isolate. As a first step towards bridging this gap, our viewpoint proposes a way to integrate detritivorous soil animals by focusing on their faeces, which is a common feature amongst detritivores and represents a key decomposition by-product in detritivore-rich ecosystems. Faeces characteristics of distinct detritivore species were recently shown to predict relatively well processes involved in organic matter turnover, and we thus formalised faeces characteristics as *effect traits*. This appears as a promising way to deal with the astonishing diversity of detritivores in soils, which may in particular unify historical soil fauna groups such as soil engineers and litter transformers. This approach could overall contribute to the inclusion of detritivores in biogeochemical models, thereby improving our understanding and modelling of carbon cycling.

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Figure captions

Figure 1: A sample of the diversity of detritivores and their faeces.

Figure 2: Diversity of detritivore faeces resulting from leaf litter of six tree species eaten by six detritivore species. From Joly et al., 2020.

Figure 3: Schematic representation of the relationships between the detritivore effect (i.e. changes in litter characteristics following detritivore conversion of litter into faeces) and intact litter characteristics, as observed in Joly et al., 2020. Changes in the magnitude of the detritivore effect following litter conversion into faeces are described by the intercept (e.g. **m** for species 1 and **n** species 2). Changes in the interaction between the detritivore effect and the intact litter characteristics are described by the slope (e.g. **a** for species 2 and **b** for species 3). The intercept and slope value for each species can then be used to determine the change in organic matter characteristics following conversion into detritivore faeces.

Figure 4: Microstructural traits as predictors of carbon mineralization rates in faeces. a) Multidimensional representation of earthworm faeces microstructures during decomposition. For

all species, porosity increases through time, while POM and fresh organic matter decreases. b) Mineralization rates of faeces produced by six earthworm species belonging to three ecological categories, measured after 7, 42 and 140 days of incubation. Mineralisation rates depend on earthworm species and faeces age. c) Respective importance of faeces traits as predictors of C mineralisation. Altogether, these microstructural traits explain more than 50% of the variability in faeces CO_2 emissions.

Figure 5: Conceptual framework formalising faeces traits as unifying predictors of detritivore effects on organic matter turnover. Amongst the diversity of detritivore, each individual can be placed along a gradient of litter and soil ingestion. Detritivores produce faeces whose traits are governed by the composite determinism of the identity of the detritivore, the characteristics of its ressource and the interactions between both factors. These faeces traits are related to the several processes that contribute to organic matter turnover in soils.

Figure 1

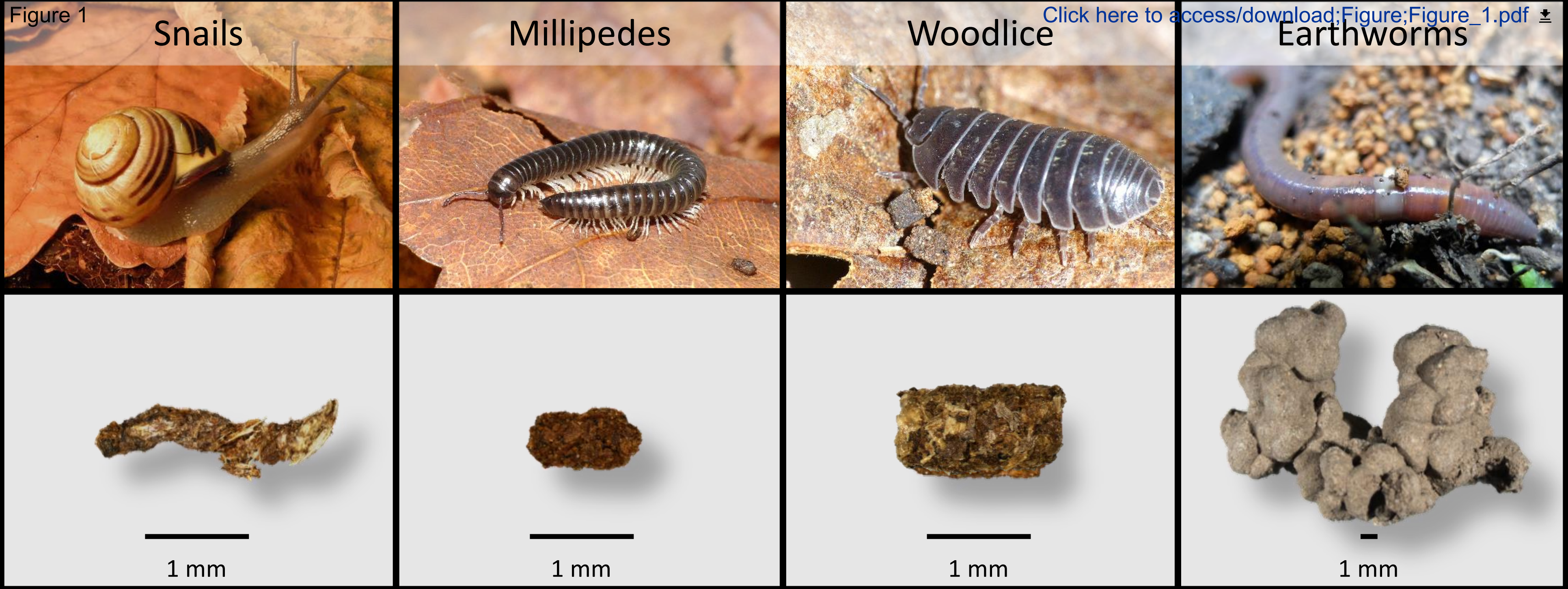


Figure 2

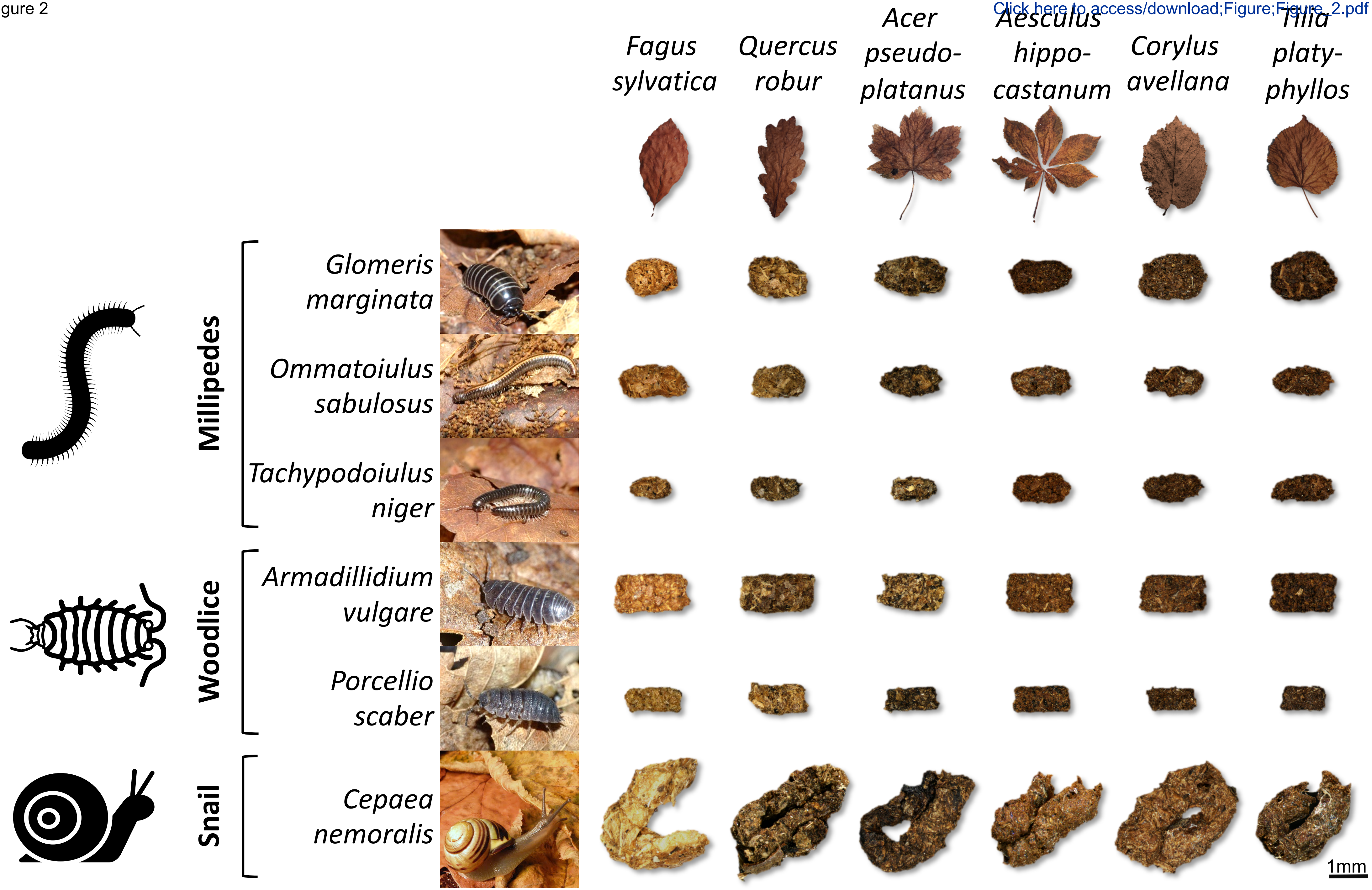
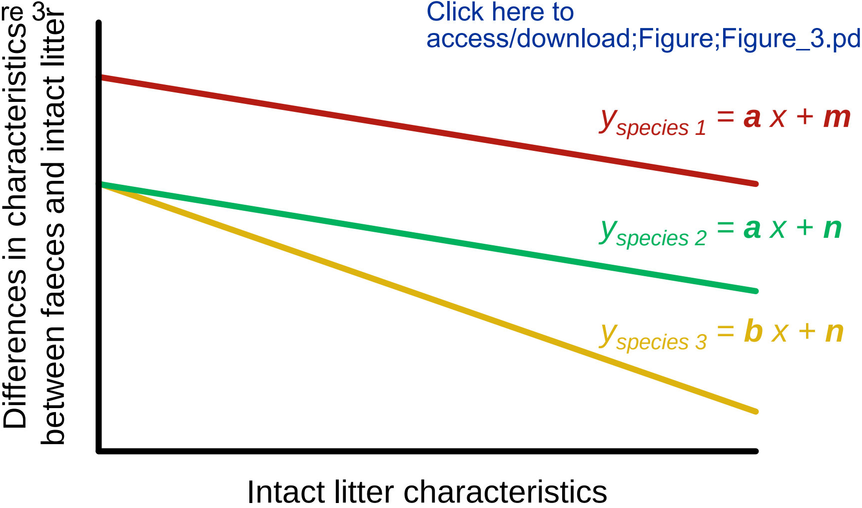
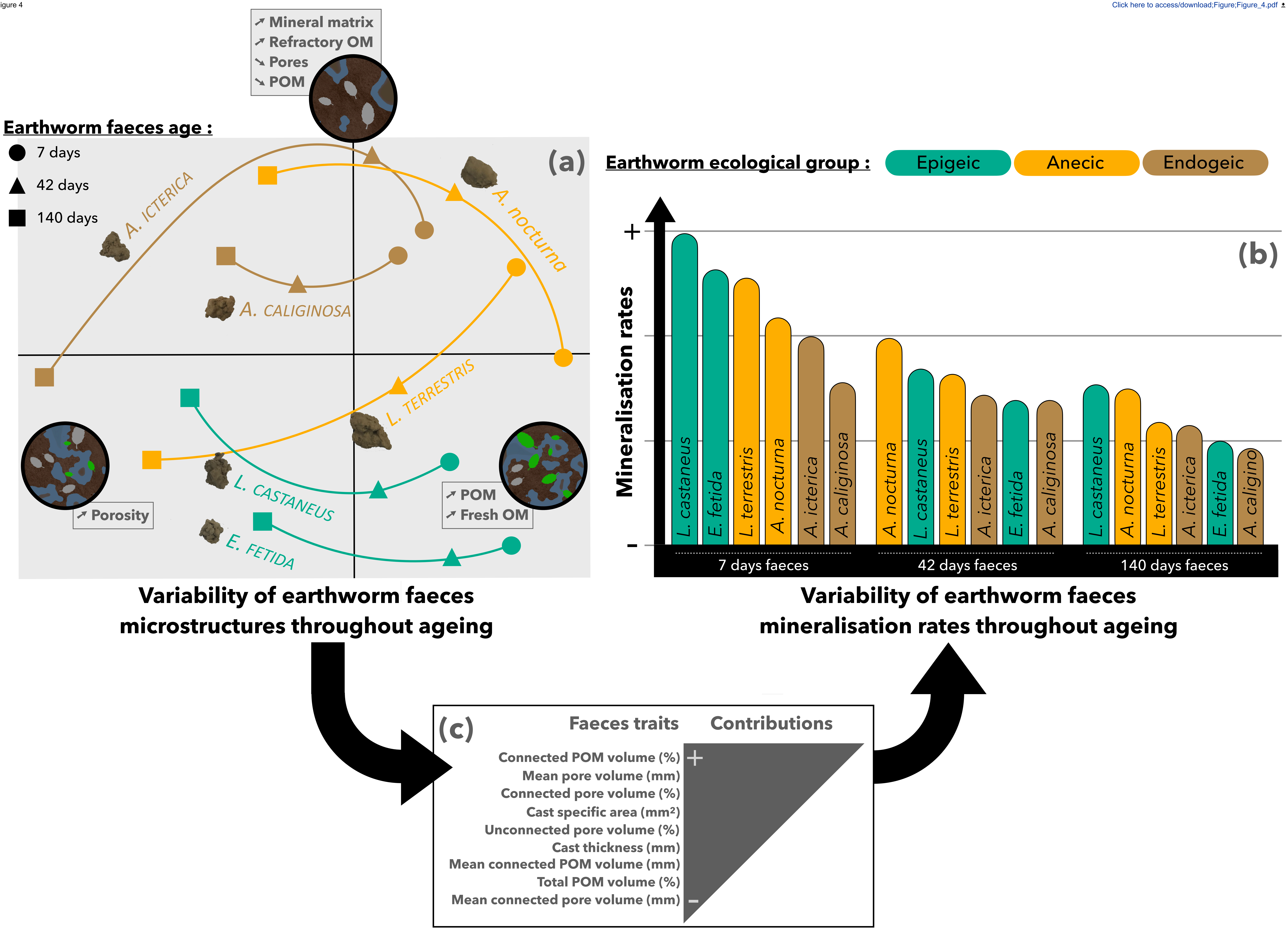

Fagus sylvatica
Quercus robur
Acer pseudo-platanus
Aesculus hippo-castanum
Corylus avellana
Tilia platy-phyllos
Millipedes
Glomeris marginata
Ommatoiulus sabulosus
Tachypodoiulus niger
Woodlice
Armadillidium vulgare
Porcellio scaber
Snail
Cepaea nemoralis
1mm

Figure 3

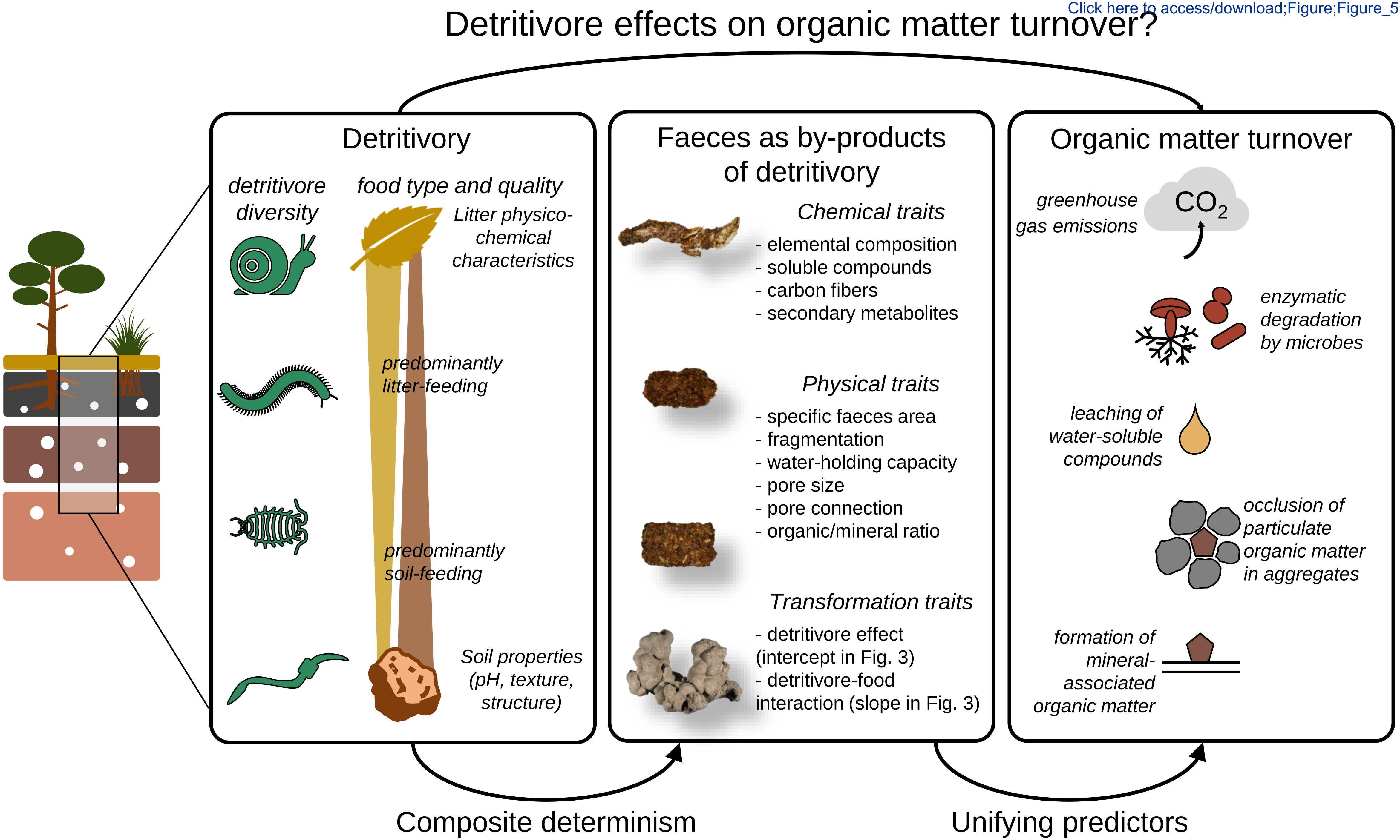

Differences in characteristics
between faeces and intact litter
$y_{species\ 1} = \boldsymbol{a}\ x + \boldsymbol{m}$
$y_{species\ 2} = \boldsymbol{a}\ x + \boldsymbol{n}$
$y_{species\ 3} = \boldsymbol{b}\ x + \boldsymbol{n}$
Intact litter characteristics



Variability of earthworm faeces microstructures throughout ageing

Variability of earthworm faeces mineralisation rates throughout ageing

Figure 5



Detritivore effects on organic matter turnover?

Detritivory

detritivore diversity

food type and quality

Litter physico-chemical characteristics

predominantly litter-feeding

predominantly soil-feeding

Soil properties (pH, texture, structure)

Faeces as by-products of detritivory

Chemical traits

- elemental composition
- soluble compounds
- carbon fibers
- secondary metabolites

Physical traits

- specific faeces area
- fragmentation
- water-holding capacity
- pore size
- pore connection
- organic/mineral ratio

Transformation traits

- detritivore effect (intercept in Fig. 3)
- detritivore-food interaction (slope in Fig. 3)

Organic matter turnover

greenhouse gas emissions

enzymatic degradation by microbes

leaching of water-soluble compounds

occlusion of particulate organic matter in aggregates

formation of mineral-associated organic matter

Composite determinism

Unifying predictors

Declaration of interests

☐The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Cornelia Rumpel reports financial support was provided by ANR.