

Measuring and assessing the biological health of soils

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E-CHAPTER FROM THIS BOOK



Macrofauna as indicators of soil health: earthworms and enchytraeids

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1 Introduction

Reports highlighting the degradation of soils in Europe and worldwide are flourishing (Akça et al., 2024; Pennock et al., 2015; Smith et al., 2024). These reports emphasize that 33% of soils are moderately to highly degraded and face significant threats, including biodiversity loss (Pennock et al., 2015). This is particularly concerning as soils support 59% of all life on Earth (Anthony et al., 2023). In this context, developing biological indicators for soil health is essential for identifying strategies for soil monitoring and improvement. Soil

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fauna, almost exclusively consisting of invertebrates, represent a substantial portion of life in soils, i.e., around 23% of total species number (Decaëns et al., 2006), and play a critical role in maintaining and enhancing soil quality and providing ecosystem services (Lavelle et al., 2006). This chapter focuses on two key soil faunal groups, earthworms and enchytraeids, as potential soil health indicators.

Earthworms and enchytraeids both belong to the phylum Annelida and the class Oligochaeta, and both are considered as ecosystem engineers that play a crucial role in soil functioning and provide numerous ecosystem services (Blouin et al., 2013; Conti & Mulder, 2022). Earthworm species are often classified according to their feeding behavior and habitat in three main ecological categories: *epigeics* that feed on litter at the soil surface, *endogeics* that feed on soil organic matter, and form non-permanent burrows, and *anecics* that feed on litter at the soil surface and live in permanent vertical burrows (Bouché, 1972; Lee, 1985). Enchytraeids, also known as 'potworms,' are often classified into two groups according to their reproduction strategy: *r strategists* that have a high reproduction rate but high juvenile mortality, and *K strategists* that have slower reproduction rates but longer life span (Graefe & Schmelz, 1999). The main difference between earthworms and enchytraeids is their size; earthworms are classified as macrofauna (diameter > 2 mm) while enchytraeids belong to the mesofauna (diameter: 200 µm to 2 mm) (Potapov et al., 2022). Earthworms and enchytraeids are typically considered to have similar functions in soils, albeit at different orders of magnitude and scale given their difference in size, making it logical to treat both groups within the same chapter. While the role of earthworms on soil functions has been extensively studied and multiple high-quality reviews are available (Blouin et al., 2013; Lavelle et al., 2006; Vidal et al., 2023), enchytraeids are particularly understudied (Pelosi & Römbke, 2016).

For earthworms and enchytraeids to impact soil functions, they must be present in the soil in sufficient amounts. Overall, earthworms and enchytraeids are widely distributed in soils with abundances often reaching 500 and 100 000 ind. m⁻², respectively (Potapov et al., 2022). Yet, many agricultural management practices and climatic conditions adversely affect earthworms and enchytraeids, with populations often varying dramatically even in similar soil types and climate conditions. The ubiquitous presence of earthworms and enchytraeids in soils in combination with their sensitivity to anthropogenic and climatic factors make them good candidates for soil health indicators (Brussaard et al., 2004; Creamer et al., 2022; Turbé et al., 2010), the topic of this chapter. We chose to focus primarily on agricultural soils, where concerns for soil degradation and biodiversity loss are particularly pertinent, also given their role in ensuring food security (Kopittke et al., 2019). However, we do not

exclude instructive examples from forest and urban soils, where earthworms and enchytraeids also play important roles.

Figure 1 illustrates the structure of the chapter. It focuses on the impact of land use, agricultural management practices and climate on earthworms (Section 2) and enchytraeids (Section 3), as well as the interactions between these two faunal groups (Section 4). Our ultimate goal is to discuss their potential as indicators of soil health (Section 7). However, this is conditional on the capacity to sample and quantify them efficiently (Section 5). It is also important to emphasize that soil biota presence does not equate soil biota being very active. Thus, we also present some methods to assess the activity of earthworms and enchytraeids in soils (Section 6).

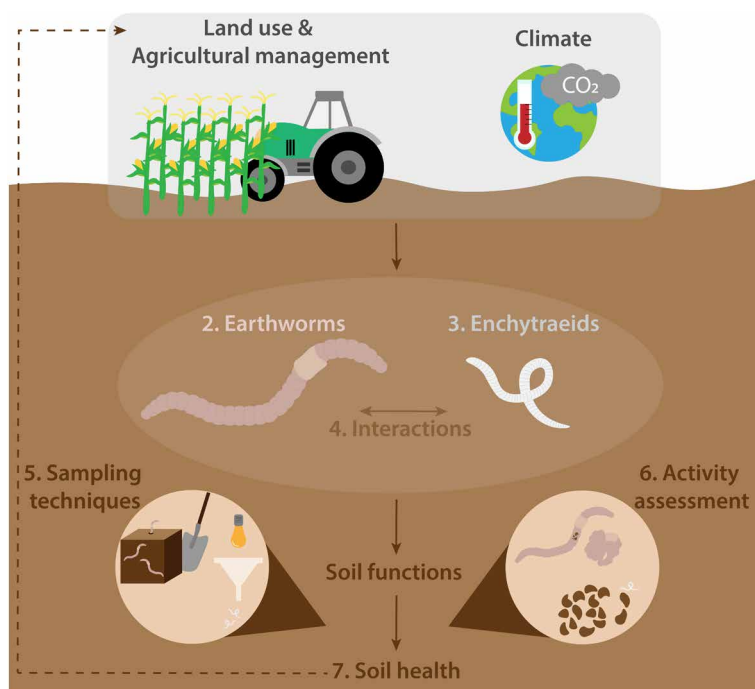


Figure 1 Structure of this chapter, which focuses on the role of earthworms and enchytraeids as indicators of soil health. It examines the impact of land use, agricultural management practices and climate on earthworms (Section 2) and enchytraeids (Section 3), as well as the potential interactions between these two soil organisms (Section 4). For their effective use as soil indicators, it is essential to sample and quantify earthworms and enchytraeids using efficient techniques (Section 5) and evaluate their activity in the soil, as their mere presence does not guarantee activity (Section 6). Finally, the chapter highlights the opportunities and challenges of utilizing earthworms and enchytraeids as reliable indicators of soil health (Section 7).

2 Effect of land use, agricultural management, and climate on earthworm communities

Earthworms serve as valuable indicators of soil health due to their sensitivity to environmental changes, with land use, management practices, and climatic conditions all being important. In terms of land use, this section primarily compares grasslands and croplands. We subsequently explore management practices, in particular those that increase or decrease earthworm density and diversity by modifying the physical and chemical soil properties, as well as the organic matter availability as food for earthworms (Fig. 2). The impact of these management practices on earthworm populations may be exacerbated by climate change, particularly through increases in droughts and flooding events (Fig. 3), which are also examined in this section. The increase in atmospheric CO₂

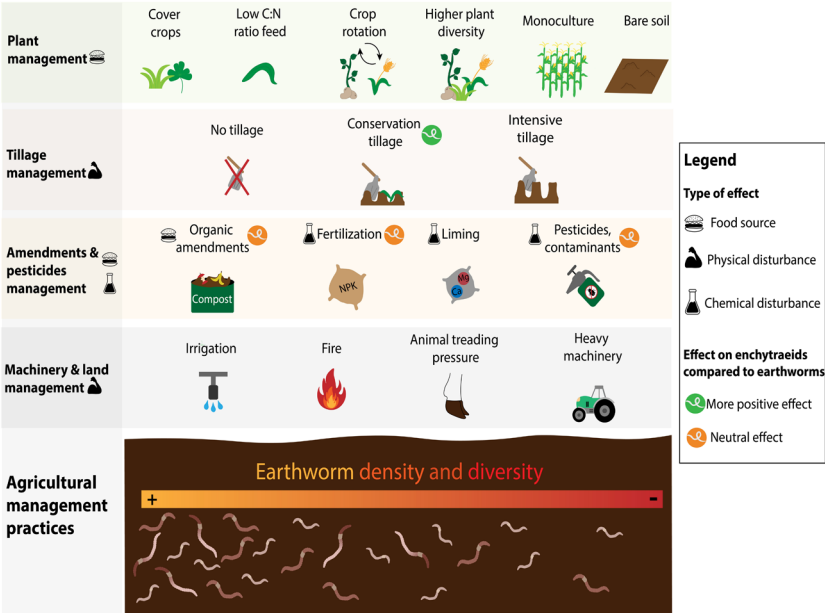


Figure 2 Potential impact of various agricultural management practices on earthworm density and diversity is categorized based on management type, with a primary focus on croplands and grasslands. These effects are further classified into three categories: chemical disturbance, physical disturbance, and the availability of food source. The impact of some practices is also highlighted for enchytraeids, with the color of the circle indicating the relative response compared with earthworms. However, studies on enchytraeids are limited and less abundant compared to research on earthworms. It is important to note that this figure is conceptual, designed to represent average effects of practices, while substantial variability in responses has been observed depending on the specific context and species studied. The initial idea of this figure is inspired from Brown et al. (2006).

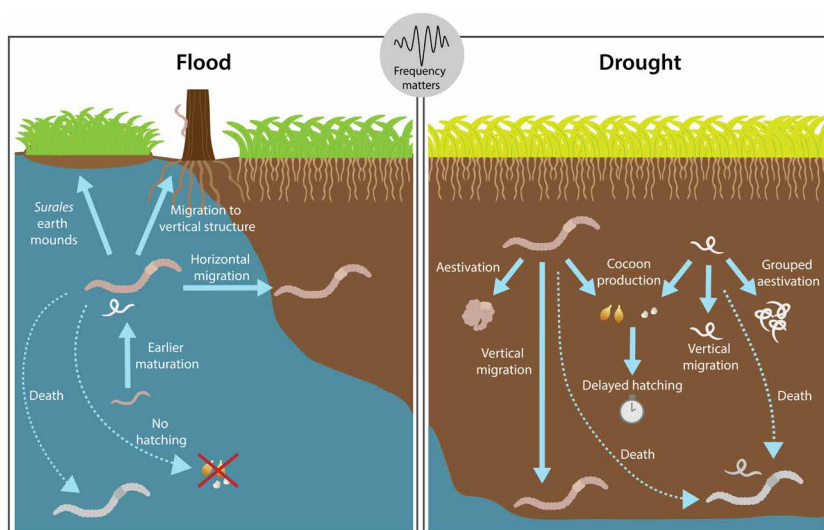


Figure 3 Effects of flooding and drought conditions on earthworms and enchytraeids. Frequent flood and drought events can lead to mortality in earthworms and enchytraeids and halt cocoon hatching (dashed arrows), ultimately causing a decline in their abundance and diversity. However, these organisms can also exhibit adaptive responses (solid arrows) to extreme climatic conditions, such as horizontal or vertical migration, aestivation, or alterations in reproductive dynamics. It is important to note that this figure is conceptual, intended to illustrate average effects of floods and droughts, while considerable variability in responses has been observed depending on the specific context and species studied.

concentrations is not expected to directly affect earthworms and enchytraeid populations, as these organisms are adapted to significantly higher CO_2 levels within the soil (Blankinship et al., 2011; Goncharov et al., 2023). Potential indirect effects, such as those influencing plant primary production and soil microbial communities, and consequently habitat quality for earthworms and enchytraeids, are not addressed in this chapter.

2.1 Temperate and continental grasslands and croplands

Earthworms are widely distributed across temperate and continental areas and often dominate invertebrate biomass (Curry, 2004; Turbé et al., 2010). The most abundant earthworm populations are typically found in managed grasslands, with lower abundances found in croplands, forests, vineyards and native pastures (Curry, 1993; King & Hutchinson, 2007; Lavelle, 1983; Rutgers et al., 2016). Earthworm abundance and ecological diversity are both impacted by land use and management. Even when earthworms are present in significant quantities, one or two of the three ecological categories can be

absent or lacking, as widely observed with anecic species across grasslands and croplands (Stroud, 2019; van de Logt et al., 2023b).

Agricultural soils in temperate and continental regions across the world are dominated by earthworm species originating from Europe. Earthworms are common across Europe and include Lumbricidae species, such as *Aporrectodea caliginosa*, *Allolobophora chlorotica* and *Lumbricus rubellus* (Ashwood et al., 2024; Rutgers et al., 2016). These lumbricid species have inadvertently or purposely spread to many other temperate and continental regions. In northern forests of North America, where indigenous earthworms are lacking (Hendrix et al., 1986), the spread of invasive lumbricids (e.g. *Lumbricus terrestris*) and Asian Megascolecids (e.g., *Amyntas* spp.) is impacting the structure and function of temperate forest ecosystems through the removal of litter on the forest floor (Bohlen et al., 2004; Chang et al., 2021). In other temperate regions (e.g., Australia and New Zealand), indigenous earthworms such as *Anisochaeta gigantea* are found in native forests but have not adapted to managed grasslands and croplands (Dalby et al., 1998; Lee, 1961). In these agricultural systems, the introduction of *A. caliginosa* improved pasture productivity by 28–113% (Stockdill, 1982).

Earthworm populations of over 1200 ind. m⁻² have been observed in managed temperate grasslands although lower abundances are more common (Curry, 1993; Rutgers et al., 2016). A positive relationship between pasture production and earthworm abundance has been observed, with earthworm numbers increasing in response to both the quantity and quality of the plant biomass available to soil fauna. The increased earthworm activity in turn improves soil quality and pasture productivity. Increases in earthworm populations as a result of increased pasture productivity have also been reported in systems amended with synthetic fertilisers (Curry et al., 2008; Schon et al., 2008). In both grasslands and croplands, larger increases in earthworm populations are often observed with the combined application of synthetic fertiliser and organic amendments (Curry, 1987; Leroy et al., 2008). Improvements in pasture quality through the addition of legumes can also benefit earthworm populations (Van Eekeren et al., 2009) (Fig. 2).

Conversely, the application of some fertilisers can contribute to soil acidification, which is detrimental to earthworm populations (Pelosi et al., 2020) as they prefer soils of neutral pH. The long-term Park Grass Experiment at Rothamsted, running since 1856, showed that earthworms were absent in soils with a pH < 4 (Edwards & Lofty, 1974), resulting in an accumulation of undecomposed organic matter forming a layer on the soil surface (Silvertown et al., 2006). However, soil acidification can be remediated with the application of lime, and liming is known to increase earthworm populations (Holland et al., 2018; Springett & Syers, 1984) (Fig. 2).

Typically, increased pasture production also leads to increases in livestock numbers, liveweight loading and treading pressure. Increased treading pressure can lead to soil compaction, especially on vulnerable and/or heavier soil types when wet. These conditions make the soil physical environment more challenging for earthworm presence (Schon et al., 2012). Surface-dwelling epigeic earthworms are most sensitive to the treading pressures of livestock (Cluzeau et al., 1992; de Bruyn & Kingston, 1997; Schon et al., 2011, 2012). With cattle treading pressure greater than that of sheep (Drewry, 2006), earthworm populations are more abundant under the latter (Schon et al., 2011). Rotational grazing practices appear to benefit earthworm populations under pastures compared to continuous grazing (Alvarez et al., 2024; Voisin, 1960).

The disruption of the soil physical environment and food supply through cultivation can have major detrimental impacts on earthworms. Hence, earthworm populations are generally less abundant in annual cropping systems in comparison to grasslands (Fraser et al., 1996; van Eekeren et al., 2008) (Fig. 4). The intensity of cultivation (e.g., frequency of interventions, length of rotations) is an important factor. Practices such as no-till, strip-till, conservation and minimum tillage reduce the level of soil disturbance (Fig. 2). No-tillage and conservation tillage systems have been observed to sustain higher earthworm abundances (+137%) than conventional ploughing (Briones & Schmidt, 2017). However, even a one tillage event during pasture renewal can have a

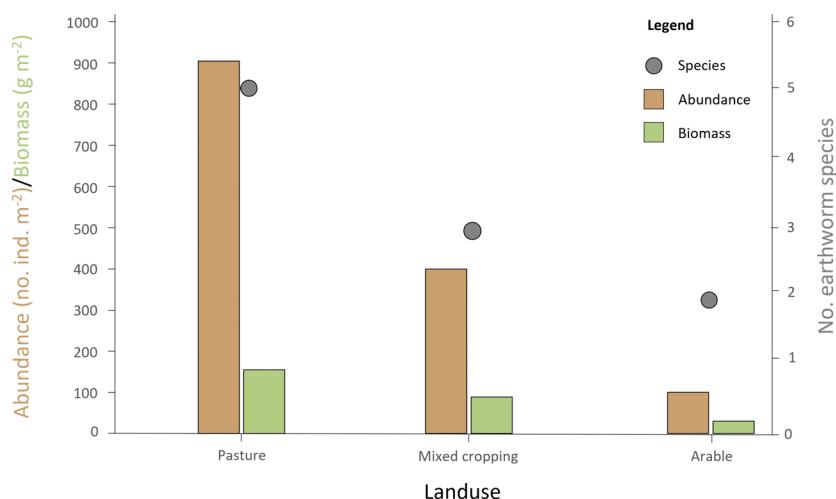


Figure 4 Changes in earthworm abundance, biomass, and species diversity under improved pasture, mixed cropping, and continuous arable use in the Canterbury Plains of New Zealand, which has a temperate climate. Abundance is expressed as number of individuals per meter square and biomass as gram per meter square. Source: Adapted from: Fraser et al. (1996).

detrimental impact on earthworms, taking more than a year to recover to pre-cultivation levels (Bell et al., 2009).

Decreases in earthworm abundance in cropping systems often coincide with reduced species diversity (Briones & Schmidt, 2017; Fraser et al., 1996) (Fig. 4). In particular, anecic earthworms, with their (semi-)permanent burrows that are vulnerable to cultivation, are often found at low densities or are completely absent from arable fields (Edwards, 1983; van Eekeren et al., 2008). A global meta-analysis reports also epigeic earthworms to be sensitive to cultivation (Briones & Schmidt, 2017). The reduction in two of the three earthworm ecological groups under cropping systems has obvious implications for soil functions mediated by earthworms, including decomposition of organic material and maintenance of soil structure (Blouin et al., 2013).

It is not only the physical disturbance of cultivation in cropping systems that has a negative impact on earthworm populations. Edwards and Lofty (1982) reported a continuous decline in earthworm populations under no-till treatments during 8 years of continuous cereal cropping. Similar declines in earthworm populations under conventional tillage were reported where corn was continually cropped, although the decline was slowed by the addition of manure (Whalen et al., 1998). Other practices that can mitigate the impacts of cropping systems on earthworm communities include the management of crop residues, the use of cover crops and the addition of organic amendments (Briones & Schmidt, 2017). D'Hose et al. (2018) reported increases in earthworm abundance when applying either farmyard manure (+151%), slurry (+103%) or compost (+63%), in comparison to synthetic fertiliser addition. Often, tillage treatments and crop residue inputs change simultaneously between systems, making it difficult to determine the role of either factor. For example, Blanco-Canqui (2022) found that the combination of cover crops with low C/N ratios (e.g., *Pisum sativum* L.) promote earthworm abundance under no-till or reduced-till systems, as compared to a combination of lower quality cover crops (e.g., *Sinapis alba* L.) under conventionally tilled systems.

Pesticides have been reported to alter the growth, reproduction, behavior, essential enzymes and DNA of earthworms (Yatoo et al., 2022). In a review by Pelosi et al. (2014), insecticides and fungicides used in agricultural systems were found to have the greatest detrimental impact on survival and reproduction of earthworms. No significant effect of glyphosate was observed on earthworm populations in cropping systems (Briones & Schmidt, 2017). However, a recent comprehensive review on the subject highlighted that glyphosate and glyphosate-based herbicides can have negative effects on earthworms at the recommended application rate. These effects may not always manifest themselves after a single application or when focusing solely on adult mortality. However, when evaluating sensitive endpoints such as reproduction and growth, and considering field-relevant species subjected to multiple applications per

year, negative effects were observed at sub-individual, individual, population and community levels (de Lima E Silva & Pelosi, 2024).

Since earthworms breathe through their skin, they need to always keep it moist, and the availability of water in the soil plays a fundamental role in their activity, life cycle, reproduction and abundance. Earthworms are therefore most abundant in the upper soil profile when soil moisture is not limiting. When irrigation is used to overcome seasonal soil moisture deficits, higher earthworm populations during the drier summer period are expected (Fraser et al., 2012). Drought or flooding conditions can affect earthworm population negatively for several years (Curry, 1993; Kiss et al., 2021; Plum & Filser, 2005). They have developed mechanisms to survive dry conditions, moving deeper into the soil profile and entering a state of aestivation (Fig. 3). For instance, *A. caliginosa* is known to be particularly sensitive to drought, responding by entering aestivation, drastically decreasing its metabolic rates (Bayley et al., 2010). For species such as *L. rubellus*, laying cocoons that hatch when conditions are more favorable is another adaptive response (Edwards & Bohlen, 1996). When soil moisture is not limiting, increasing temperatures in cooler temperate regions may benefit earthworm activity, with earthworm burrowing increasing from 15°C to 20°C. During flooding events, earthworms may migrate horizontally to find unflooded areas or vertical structures (e.g. trees or poles) (Singh et al., 2019). The success of these adaptations depends on the scale and frequency of the weather events. As the frequency and intensity of extreme climatic conditions will increase as a result of climate change, the ability of earthworm populations to recover may be reduced, especially if the time interval between two extreme events is less than the development time from cocoon to the adult stage of the earthworm life cycle (i.e., about 6 months for many lumbricid earthworm species) (Plum & Filser, 2005). For instance, at sites subject to frequent flooding, earthworms matured at a lower weight and at a younger age, and cocoons were unable to hatch (Klok et al., 2006; Thonon & Klok, 2007). Managed grasslands which have a higher earthworm abundance and diversity may be better placed to buffer adverse environmental conditions than croplands (Kiss et al., 2021; Liu et al., 2025). These results emphasize the importance of examining the interactive effects of climate factors, land use and management practices on earthworms to improve system resilience, an area that remains largely understudied (Singh et al., 2019).

2.2 Tropical grasslands and croplands

In tropical regions, native species have high endemism levels with limited geographical distributions, mainly due to habitat variability and restricted dispersal ability (Lavelle & Lapied, 2003). Preferences for particular soil conditions are commonplace in earthworms, and some have very restrictive

distributions, such as *Glossoscolex ibira*, a large species found only in a low pH sandy Acrisol, near the town of Ibirá, in São Paulo state, Brazil (Caballero, 1976). On the other hand, very successful pantropical species like *Pontoscolex corethrurus* display a very wide tolerance for soil types, as well as chemical and physical conditions (Taheri et al., 2018), attributes also found in several other widespread earthworm species, such as those in the *Amyntas* genus (Steffen, 2012). Very few of the 2000 or more tropical earthworm species have been the object of detailed studies. Nevertheless, earthworms have been proposed as bioindicators of land use disturbance and/or change in several tropical countries including Ivory Coast, India, Mexico, Peru and Brazil (Fragoso et al., 1997; Guéi & Tondoh, 2012; Tondoh et al., 2007). Furthermore, they have been used as indicators of soil management practices, such as no-tillage systems, particularly in Brazil (Bartz et al., 2014).

Earthworms are particularly affected by land use and management practices. As an example of the potential differences between earthworm populations in various agricultural and natural habitats in the tropics, Fig. 5

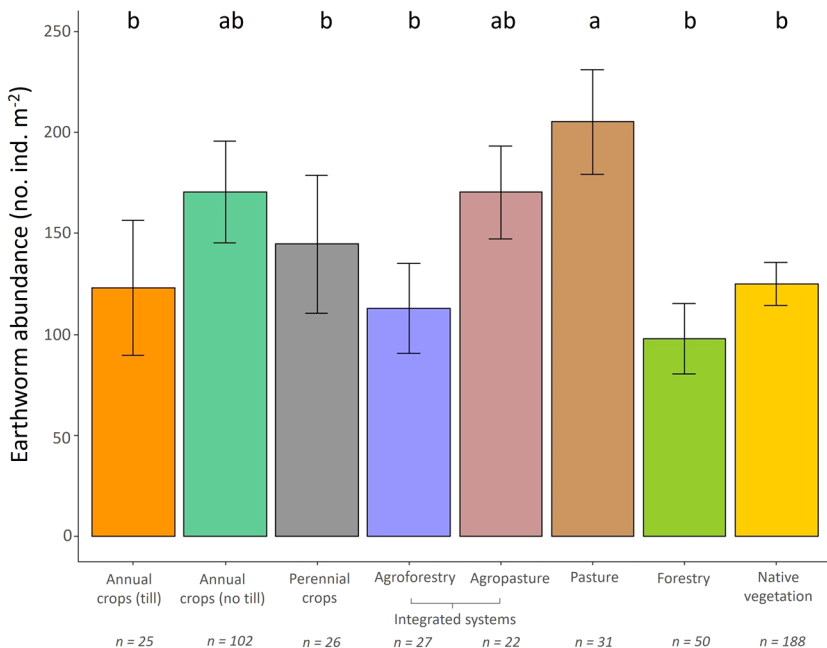


Figure 5 Earthworm abundance was evaluated across 468 sites in Brazil under various land-use systems. Abundance is reported as the number of individuals per meter square. Significant differences between land uses are indicated by different letters. Details of species composition are provided in Fig. 6. Significant differences between land uses are indicated by different letters as a result of a Kruskal-Wallis test followed by a post-hoc Dunn test. Values represent the mean and bars the standard deviation.

summarizes the content of an unpublished database of one of the authors (G. Brown) on the total earthworm abundance and species richness across 468 sites in Brazil. Land use included annual and perennial crops, pastures, and integrated production (agroforestry and agropasture) systems, as well as native vegetation and forestry plantations. Earthworm abundance was the highest in pastures (Fig. 5). The species most commonly encountered in these Brazilian agroecosystems were in the genus *Dichogaster*, representing small, exotic earthworms native to Africa; and *P. corethrurus*, the most abundant species encountered (Fig. 6). Only one of the ubiquitous species may be native to Latin America: a small and thin earthworm in the Ocnerodrilidae family (*Nematogenia panamaensis*), commonly associated with annual cropping systems.

There are only a few publications describing potential impacts of pesticides on tropical earthworms in the laboratory, and even fewer reporting field studies. Most studies focused on vermicomposting species like *Perionyx excavatus*, which are not the aim of this chapter. Some common ubiquitous endogeic species, such as *P. corethrurus* and *Amyntas gracilis*, were evaluated

Land use systems	Earthworm species	No. sites (%)	Abundance (ind. m ⁻²)	Range (min - max ind. m ⁻²)
Annual crops including tillage and no-tillage systems (n = 127) 	<i>Dichogaster saliens</i>	37 (30)	16 ± 3	3 - 225
	<i>Dichogaster gracilis</i>	33 (26)	13 ± 2	5 - 100
	<i>Nematogenia panamaensis</i> ?	32 (26)	15 ± 3	5 - 220
	<i>Pontoscolex corethrurus</i>	25 (20)	60 ± 12	5 - 320
	<i>Dichogaster affinis</i>	24 (19)	11 ± 2	3 - 65
	<i>Dichogaster bolaii</i>	22 (18)	15 ± 3	5 - 208
Integrated systems including agroforestry and agropastoral systems (n = 49) 	<i>Pontoscolex corethrurus</i>	29 (59)	170 ± 12	1 - 300
Perennial crops (n = 26) 	<i>Pontoscolex corethrurus</i>	21 (81)	144 ± 30	4 - 765
Pastures (n = 31) 	<i>Pontoscolex corethrurus</i>	25 (80)	155 ± 29	4 - 419

Figure 6 Mean abundance (individuals m⁻²) of the most frequently encountered earthworm species across various land-use systems (i.e. species present at more than 15% of all sampled sites; percentage occurrence is indicated in parentheses), along with the range of abundance (minimum and maximum values) observed across 468 sites in Brazil.

in the lab (Awaknavar & Karabhantanal, 2004, 2005; Buch et al., 2013; Cantelli, 2011; Chang & Bruno, 1970; Khalil, 2013, 2015; Morowati, 2000; Mostert, 2001; Mostert et al., 2002; Parelho et al., 2018). Unfortunately, very few studies have addressed impacts of pesticides on native earthworm species. Observed effects ranged from almost absent (Brazil; insecticide lambda-cyhalothrin and the fungicide carbendazim (Garcia, 2004)) to slightly negative (India; insecticide malathion; Panda & Sahu, 2000; Senapati et al., 1992, 1994) or strongly negative (Mexico, Glyphos®, Classical Faena®, and Faena Fuerte®) (García-Pérez et al., 2014). Garcia-Perez et al. (2020) emphasized the growing evidence that epigeic, endogeic and anecic earthworms are vulnerable to repeated applications of glyphosate. More detailed and, at the same time, broader field tests, which would help us understand the potential short- and long-term effects of pesticides on tropical earthworm communities are still largely missing. There is also a need for studies comparing different species under identical test conditions and a range of contaminants. Finally, very little is known about the effects of mixtures of pesticides (Pelosi et al., 2021b).

The impact of other agricultural management practices such as soil tillage have been reviewed globally, but always with few results from tropical countries (Briones & Schmidt, 2017). Two recent reviews (Bartz et al., 2024; Demetrio et al., 2020) clearly showed higher populations in no-tillage sites although the type and frequency of the soil management employed is critical: periodic tillage can be very detrimental, and the lack of crop rotation was also highlighted as a limiting factor (Fig. 2). Nonetheless, few experiments have addressed crop rotation effects, particularly the inclusion of legumes in cropping systems. Oluko et al. (2014) and Guéi et al. (2019) highlighted the importance of external N inputs into the system for increasing earthworm populations and optimizing their roles in crop production. Long-term no-tillage can cause major soil compaction when there is too much traffic or no adequate cover cropping, and both have been associated with lower earthworm populations in Southern and Southeastern Brazil (Dudas et al., 2020).

Organic matter additions via manure deposition on the surface or incorporated into the soil have helped increase earthworm populations in several locations in the tropics (Oliveira Filho et al., 2018; Senapati et al., 1999) (Fig. 2). However, the long-term impacts of high heavy metal concentrations (particularly Cu, Ni or Cd) brought with these wastes is a concern and must be monitored to avoid a decrease in earthworm populations (Cotton DCF & Curry JP, 1980). Similar concerns are associated with antibiotics in some wastes (such as ivermectin), as high concentrations of this acaricide can lower reproduction rates (Ma et al., 2023), though other studies have shown little to no non-target effects (Kaneda et al., 2006; Scheffczyk et al., 2016). Further, many highly weathered tropical soils, particularly in the wetter regions, are highly acidic and require liming in order to be useful and productive for agricultural purposes.

Similar to temperate soils, acidification is expected to negatively impact earthworm populations and liming likely remediates this effect (Fig. 2), but very few studies on tropical soils exist.

As noted earlier (Section 2.1), earthworms are particularly sensitive to climatic factors, and especially moisture levels. Among the 40 species collected in the Manaus region of the Amazon (database G. Brown), 33 lived strictly in areas close to watercourses, while four inhabited soils with large moisture variations. The remainder lived in rotting tree trunks (Ayres & Guerra, 1981). In environments with seasonal rainfall, such as tropical Savannas, many species enter aestivation and/or seek deeper soil layers with higher moisture contents (Fig. 3). For instance, *Rhinodrilus alatus* enters aestivation for more than 6 months, at an average depth of 30 cm (Drumond et al., 2015), while *Glossoscolex paulistus* is normally active in 30 cm deep U-shaped burrows but aestivates in chambers at 50 cm depth (Abe & Buck, 1985). An Amazonian species *Chibui bari* undergoes diapause for around 6 months at approximately 1 m depth (Guerra, 1988).

Earthworms also have evolved responses to flooding events. When the tropical grassland plains of Colombia (Orinoco Llanos) are flooded, earthworms, primarily *Andiorrhinus* species, construct *surales*. These are large mounds composed mainly of casts, built by earthworms searching for aeration (Zangerlé et al., 2016b). Interestingly, similar structures have also been observed in a solar park located on temperate flooded grasslands in the Netherlands. These mounds appear to be primarily constructed by *Aporrectodea caliginosa* (Ron de Goede, personal communication, 01-09-2024). Given the increasing frequency of rainfall events due to climate change, these mounds could play a growing role in both temperate and tropical regions.

The potential impact of climate change on tropical earthworms has not yet been adequately determined. Two recent literature reviews, for instance, did not contain any data on tropical climates and earthworm species (Ghosh, 2021; Singh et al., 2019). Only one study was found, which evaluated the impact of predicted climate change on the distribution of a widely used fish-bait species, *R. alatus* (Hughes et al., 2018). The authors concluded that, under a realistic scenario of climate change for 2070, the distribution of this earthworm species would become restricted, and its habitat fragmented. This would lead to a decline in earthworm populations, the collapse of harvesting activities and severe impacts on the local community that relies on this traditional practice for subsistence. The global analysis by Phillips et al. (2019), though based on limited data from tropical regions, revealed that climate is one of the most significant factors influencing earthworm abundance, biomass and species richness worldwide. It may also further contribute to earthworm invasion. This finding suggests that any potential changes in global climate could have substantial impacts on these parameters.

3 Effect of land use, agricultural management, and climate on enchytraeid communities

Enchytraeids are regarded as valuable indicators of land use and management practices, particularly in agriculture (Pelosi & Römcke, 2016, 2018) due to their abundance across various ecosystems, their essential role in ecosystem functioning and their sensitivity to a wide range of environmental stresses. The first section focuses on the effect of different land uses on enchytraeid communities, comparing forests, grasslands and arable soils. A next section is dedicated to agricultural practices, highlighting how population size and species composition are affected by ploughing, pesticides, and other factors (Fig. 2). In a final section, we review how climate parameters influence enchytraeids, which, in turn, significantly affects ecosystem processes.

3.1 Land use and enchytraeid communities

Enchytraeids are often considered typical forest-dwelling organisms, but they are also commonly found in agroecosystems. Their abundance – often dominated by *Cognettia sphagnetorum* – is generally higher in forest than in grasslands and croplands, likely due to the low pH levels of forest soils, which enchytraeids tend to prefer (Beylich & Graefe, 2009; Pelosi & Römcke, 2018). However, this pattern does not always hold. For instance, Springett et al. (1996) found higher enchytraeid abundance in kiwifruit orchards and hill pastures than in a dairy pasture and native forest. As microbivorous and saproverous organisms (Didden W A M, 1993), enchytraeids often find greater food availability and encounter fewer disturbances in grasslands, which generally results in higher populations compared to arable fields (Barbercheck et al., 2009). Yet, some studies suggested that land use tends to affect species composition more strongly than total abundance (Beylich & Graefe, 2010; Nowak, 2004).

3.2 Agricultural management practices and enchytraeid communities

In grasslands, enchytraeids are influenced by livestock grazing and mowing, with grazing having a more negative effect than mowing, likely due to soil compaction induced by animal trampling (Maraldo et al., 2015). In arable fields, most studies have focused on the effects of soil tillage, particularly ploughing, on enchytraeid communities. Ploughing alters the vertical distribution and composition of enchytraeid community, but the overall impact is unclear due to contrasting findings. Some positive effects of ploughing on enchytraeids may offset the mechanical damage caused by conventional tillage. For instance, the incorporation of crop residues within the soil profile can provide enchytraeids with food (Lagerlöf et al., 1989; Manetti et al., 2010; Severon et al., 2010);

promote bacterial growth, which favors bacterial-feeding organisms with high metabolic activity like enchytraeids (Hendrix et al., 1986); and increase pore space, which facilitates enchytraeid movement through the soil (Lagerlöf et al., 1989). As a result intermediate disturbance, such as non-inversion tillage, has been reported to favor enchytraeids (Chan & Heenan, 1995) (Fig. 2).

As with earthworms, many laboratory studies report harmful effects of pesticides on enchytraeids (Römbke et al., 2017). However, these controlled tests often lack ecological relevance due to factors like test duration, use of artificial soils, model species and single-species tests. The response of enchytraeids to pesticides at the community level can be studied using semi-field methods, such as Terrestrial Model Ecosystems (Burrows & Edwards, 2004; Scholz-Starke et al., 2013) or by directly sampling communities in the field. Harmful effects of pesticides on enchytraeids were reported in both field and semi-field studies, though rarely at the recommended application rate (Pelosi & Römbke, 2016). Results vary due to numerous interacting factors, and more studies are needed on the long-term effects of pesticide mixtures applied at agronomically recommended doses.

Other practices, such as inorganic fertilization and organic matter inputs, also affect enchytraeid community abundance and composition, though data on these effects remain limited. Generally, organic matter inputs appear beneficial to enchytraeid communities (Andrén & Lagerlöf, 1983; Mitchell et al., 1978). The effects of inorganic fertilization are more variable and may be negative (Birkhofer et al., 2008) possibly due to changes in soil pH and electrical conductivity following fertilizer applications (Lagerlöf et al., 1989) (Fig. 2). Contrasting results when assessing effects of land use and management on enchytraeids may also arise from annual climatic variations in enchytraeid communities (Maraldo et al., 2015).

3.3 Climate and enchytraeid communities

Enchytraeids are soft-bodied organisms highly dependent of soil moisture for survival, reproduction and activity. Vulnerable to drought, they are typically confined to moist habitats (Didden, 1991). Severe droughts can dramatically alter enchytraeid water content, reproduction and survival, affecting their abundance, diversity and composition (Beylich & Achazi, 1999; Coyle et al., 2017; Maraldo & Holmstrup, 2010). Like earthworms, enchytraeids have different strategies to cope with drought (Fig. 3). Studies from over 50 years ago (Dózsa-Farkas, 1973, 1977; Willard, 1972) reported that enchytraeids, such as *Stercutus niveus*, enter aestivation during dry summer periods. Dózsa-Farkas (1973) observed in laboratory conditions that enchytraeids cluster in small, dense, inactive groups in response to dry soil conditions, a phenomenon that remains largely overlooked in the literature. When conditions are unfavorable,

enchytraeids can also survive in a cocoon stage (Christensen, 1956; Lagerlöf & Strandh, 1997) or migrate to more humid microhabitats (Didden, 1991; Maraldo, 2009; Springett et al., 1970). However, due to their small size, enchytraeids cannot migrate as deep as earthworms. Maraldo and Holmstrup (2009) identified *Cognettia sphagnetorum* in 5–10 cm deep layers below the surface, during dry periods, whereas *Lumbricus terrestris* can reach depths of up to 2 m under similar conditions (van de Logt et al., 2023a).

Optimal conditions of 20% gravimetric water content (−2.57 kPa) were found for *E. albidus*, supporting high survival, feeding activity and reproductive rates. As for earthworms, overly moist soil conditions may reduce enchytraeid reproduction by preventing cocoons laying (Cécile Serbource, personal communication, 01-09-2024) (Fig. 3). Temperature also influences enchytraeid activity, productivity and reproduction (Briones et al., 2007; Dial et al., 2016; Maraldo et al., 2010; Patricio Silva et al., 2014). For instance, freeze tolerance in the enchytraeid *Fridericia ratzeli* relies on glucose accumulation, a mechanism similar to that of freeze-tolerant earthworm species (Holmstrup & Sjørnsen, 2001). Optimal temperatures for enchytraeids, such as model species *Enchytraeus* sp., are around 18°C. In a meta-analysis, Briones et al. (2007) found that a mean annual temperature above 16°C can limit the presence of *C. sphagnetorum*. Some enchytraeid species can live in areas with very dry summers and severe winters, indicating distinct physiological or behavioral adaptations (Grongroft & Miehlisch, 1983; Pedersen & Holmstrup, 2003; Willard, 1974). Other species, such as *Fridericia galba* and *Enchytraeus buchholzi*, can tolerate dry conditions as long as temperatures remain moderate (Abrahamsen, 1971; Dózsa-Farkas, 1977).

In conclusion, enchytraeids in agricultural fields are sensitive to both management practices and climatic variability. Climate change is expected to increase the frequency and intensity of heavy rainfall events and extend drought periods, posing challenges for enchytraeid populations (Holmstrup et al., 2012). These effects may be subtle at the level of total abundance, making genus- or species-level indicators more informative.

4 The interaction between earthworms and enchytraeids

4.1 An unclear relationship

Enchytraeids and earthworms can provide similar benefits to the soil, but at different scales. However, there is still limited data on interactions between these two groups under natural conditions. Some studies revealed a competitive relationship, as both inhabit the same soil horizon and consume similar food sources (Gajda et al., 2017; Larsen et al., 2016). Beylich and Graefe

(2010) highlighted that enchytraeid populations tend to increase in areas with low earthworm activity, suggesting a potential exclusion relationship. The authors also demonstrated that smaller earthworm species or juveniles of medium-sized species (belonging to endogeic or epigeic groups) exhibit more antagonistic relationships with enchytraeids compared to larger anecic species. The presence of invasive earthworm species has also been shown to decrease the enchytraeid densities (Schlaghamerský et al., 2014). However, earthworms and enchytraeids may also display positive relationships. For instance, Schlaghamerský et al. (2014) and Nuutinen et al. (2017) demonstrated that the presence of *Lumbricus terrestris* may facilitate the presence of enchytraeids by increasing macroporosity. Schrader and Seibel (2001) and Beylich and Graefe (2009) suggested that the casting of anecic earthworms near the soil surface may locally improve conditions for enchytraeids and other soil organisms. Karaban and Uvarov (2014) observed a positive influence of *Aporrectodea caliginosa* on enchytraeid abundance, attributing this to its non-trophic activities such as burrowing, cast deposition and mucus release. Several authors underlined that, in the absence of resource limitation, earthworms and enchytraeids can coexist without competitive exclusion (Beylich & Graefe, 2010; Makulec & Pilipiuk, 2000; Ricci et al., 2015).

4.2 Diverging responses to external factors

Very little is known about the factors driving the interactions between earthworms and enchytraeids, including climate, food resources and agroecological practices. Few studies have documented differing responses between earthworms and enchytraeids to external factors. For instance, Bart et al. (2017) and Kobetičová et al. (2010) demonstrated that earthworms are more sensitive to contaminated soils and pesticides exposure than enchytraeids, using avoidance tests. However, Serbource et al. (2024) compared the sensitivity of earthworms and enchytraeids to different stressors under similar test conditions and found them to be equally sensitive to chemical stressors regardless of the studied endpoint (mortality or reproduction). This study also underlined the lack of studies (1) on environmentally relevant (i.e. representative of natural soils) enchytraeid and earthworm species and (2) on other driving factors than chemicals such as agricultural practices and climate change. Topoliantz et al. (2000) found that after tillage, the activity of enchytraeids increased when earthworm activity declined (Fig. 2). Further, while this has not been tested, enchytraeids' preference for acidic soils suggests they may be less affected by fertilizer-induced soil acidification than earthworms. These few studies point toward the need to quantify both earthworms and enchytraeids when assessing soil health, as enchytraeids could partially maintain the soil functions performed by earthworms.

5 How to sample and monitor earthworm and enchytraeid populations

Sampling earthworms and enchytraeids in an efficient, reliable and reproducible way is a crucial step in assessing the effects of land use, management practices and climate on these soil organisms and for developing reliable soil health indicators. Below, we summarize the most common methods for sampling earthworms and enchytraeids. We also direct readers to key references for further information.

5.1 How to sample earthworms

There is a wide diversity of earthworm sampling methods, which often makes comparing studies challenging. This variation is partly due to the fact that not every sampling method is suitable for all soil conditions or earthworm species. We can broadly distinguish two main groups of methods to systematically sample earthworms: the *ethological methods* that mainly rely on the earthworms being stimulated to come out of the soil themselves, and the *excavation methods* followed by hand sorting approaches with or without wet sieving (Bouche, 1969; Satchell, 1969; Singh et al., 2016) (Fig. 7). Ethological approaches include the use of electricity, i.e., the octet method (Eisenhauer et al., 2008; Schmidt, 2001a; Weyers et al., 2008) and the use of chemicals such as formaldehyde (Raw, 1959), hot mustard (Gronstol et al., 2000; Lawrence & Bowers, 2002), onion solution (Steffen et al., 2013) and allyl isothiocyanate (AITC) (Pelosi et al., 2009; Zaborski, 2003). Another less well-known approach involves actively searching for earthworms within specific habitats, such as beneath dead logs in forests, within and under dung pats in pastures, or in wetter environments like stream margins, alongside or inside marshes, in bromeliads and in suspended soils (Bartz et al., 2014; Decaens et al., 2016; James, 1996). If needed, these specific niches should be considered in addition to soil sampling.

The effectiveness of each method varies between ecological categories of earthworms. Hand sorting is more effective in detecting small individuals, including endogeics and juvenile anecics, which are often underestimated with ethological methods due to their lower mobility (Bartlett et al., 2006; Callaham Jr & Hendrix, 1997; Chan & Munro, 2001). Larger anecics with deeper burrowing strategies are often missed with hand sorting. Among ethological methods, the octet approach has the advantage of not disrupting the soil biogeochemistry, which can be a significant advantage in urban areas where the use of chemicals and excavation may not be viable options (Pelosi et al., 2021a) or in manipulative experiments where imposed treatments should not be disturbed. The downside of this method is that it requires specialized equipment (Schmidt, 2001a), and it is highly dependent on adequate soil water content to transmit the electric signal. When a chemical approach is used, Pelosi

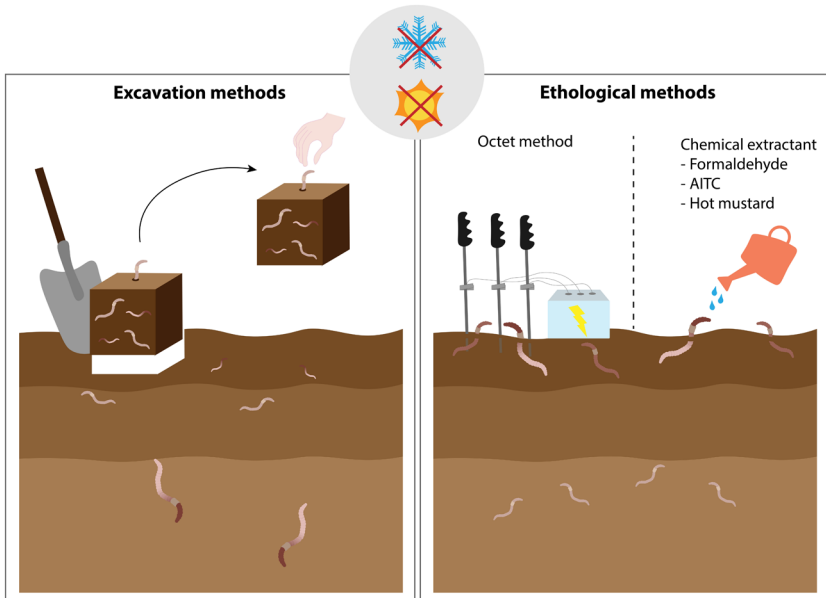


Figure 7 Overview of earthworm sampling methods, divided into two main categories: excavation methods (left) and ethological methods (right). Excavation methods involve removing a block of soil and hand-sorting earthworms. Ethological methods utilize external stimuli, such as electricity (e.g. the octet method) or chemical extractants applied to the soil surface, including formaldehyde, allyl isothiocyanate (AITC) and hot mustard. Excavation methods tend to favor the collection of smaller individuals, such as juveniles and endogeic earthworms but often miss species that burrow deeper. Conversely, ethological methods are more effective for collecting epigeic and anecic species, while underestimating smaller species due to their lower mobility. Field sampling is generally discouraged during very cold or very dry weather conditions. We do not aim to provide an exhaustive list of sampling methods; instead, we direct readers to key references in the text for further information.

et al. (2009) advocate the use of AITC, which is not as toxic as formaldehyde and is easier to standardize than hot mustard. Although considered to be the most reliable approach, hand sorting is very labor intensive. To overcome the challenges related to hand-sorting, Schmidt (2001b) suggests a time-limited (40 minutes per 25 cm × 25 cm × 25 cm block) hand-sorting approach for large and long-term monitoring campaigns. In Fig. 8, we provide a brief description of the main methods used for earthworm sampling, together with their pros and cons. Providing a detailed analysis of these approaches is beyond the scope of this review. We refer readers to Singh et al. (2016) who performed a thorough review of sampling methods.

Given all the pros and cons of each methods, the most reliable approach might be to combine hand sorting with chemical extraction. In this line, the

	Excavation methods	Brief description	Soil disturbance	Time	Efficiency			Toxicity	Cocoon extraction	Earthworm injuries
					Adult anecic	Juvenile anecic	Endogeic			
	Hand-sorting	A block of soil is excavated and earthworms are hand sorted	Soil extraction		Migrate deeper					Some earthworms cut in two with spade
	Hand-sorting with wet-sieving	A block of soil is hand sorted for earthworms and washed with mesh sieve	Soil extraction		Migrate deeper					Some earthworms cut in two with spade
	Formaldehyd	A formaline solution is applied to a determined soil surface	Pollution			Low mobility	Low mobility	Carcinogenic		Die if not washed under water
	ATC	A allyl isothiocyanate solution is applied to a determined soil surface				Low mobility	Low mobility			
	Mustard	A hot mustard solution is applied to a determined soil surface				Low mobility	Low mobility			
	Octet	Electroshocks are sent to the soil				Low mobility	Low mobility			

Figure 8 A brief description of the main methods used for earthworm sampling, along with their pros and cons. The color scale provides a relative comparison of methods based on key factors to consider during sampling, ranging from yellow (positive) to red (negative). A detailed analysis of these approaches is beyond the scope of this review. Readers are directed to key references in the text for further information.

latest ISO norm 23611-1:2018(E) (ISO, 2018) recognizes the human and ecosystem toxicity of formaldehyde and proposes hand sorting followed by AITC extraction when deep burrowing earthworm species are present.

Regardless of the sampling method chosen, climatic conditions should be considered when sampling earthworms, with a special focus on soil moisture and temperature (Eggleton et al., 2009). Periods when earthworms are inactive or suffering stressful conditions, i.e. winter and summer, should be avoided (Section 2). In temperate regions, the activity of earthworms drastically decreases when the soil temperature is below 5°C in winter and when the soil moisture content is below the wilting point in summer (Curry, 2004; Daugbjerg, 1988). In tropical regions, sampling is advised during the wet season, when temperatures are relatively high without drought stress (Fragoso et al., 1999; Fragoso & Lavelle, 1992; Singh et al., 2019).

5.2 How to sample enchytraeids

Enchytraeids are typically sampled using a soil corer with a diameter between 3 cm and 6 cm (Fig. 9). In agricultural soils, it is common to collect samples for

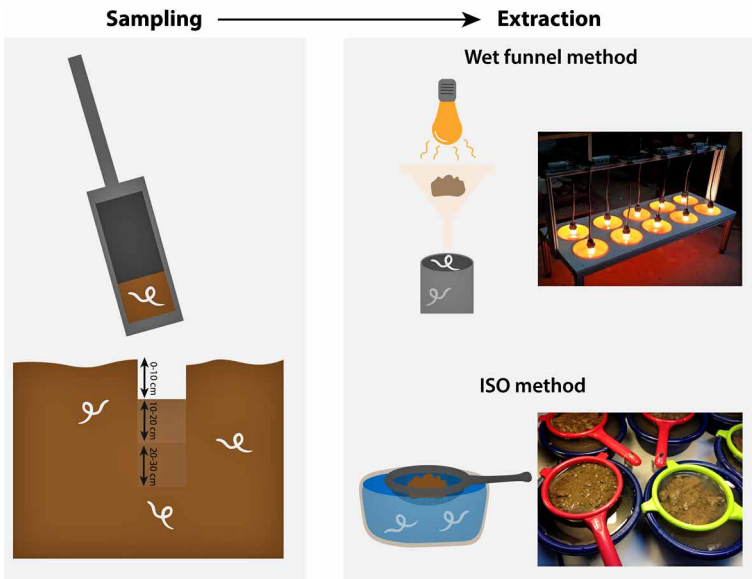


Figure 9 Different stages of enchytraeid sampling, from field collection. Sampling is typically performed at a depth of 0–10 cm but can also include other depths where enchytraeids are found, such as 10–20 cm and 20–30 cm. Two main methods are available for extraction: the wet funnel method, which requires a heat source, and the ISO method, which involves submerging samples in water and does not necessarily require heat. Counting and identification are usually carried out using a petri dish placed under the microscope when the enchytraeids are still alive.

enchytraeid extraction up to 30 cm where most of the enchytraeids are thriving. Enchytraeids are more abundant in the upper layers (0–10 cm) in plots under reduced or no-tillage while under conventional tillage, they are more equally distributed over the soil profile and therefore generally sampled at a soil depth 0–20 cm (Pelosi & Römbke, 2016).

After collection, soil samples can be kept refrigerated at 4–6°C up to 2 weeks after collection (ISO, 2019). The ISO norm 23611-3 recommends to extract enchytraeids using a wet extraction approach which consists of submerging the soil samples in water on a sieve (mesh size approximatively 1 mm) for 2–7 days and collecting the sinking enchytraeids. Some variations of this approach exist, notably the wet funnel method that uses a light bulb to create a source of heat in order to increase the extraction efficiency and reduce the extraction time (Fig. 9) (Kobetičová & Schlaghamerský, 2003; O’connor, 1955). In contrast to earthworms, enchytraeids can only be identified alive as their transparent body becomes opaque after death, which makes identification impossible (Schmelz & Collado, 2010). Similar to earthworms, we strongly recommend sampling enchytraeids at multiple times throughout the year (e.g. in autumn and spring), in order to effectively evaluate the impacts of agricultural management on enchytraeids, alongside natural climatic fluctuations (Maraldo & Holmstrup, 2009).

6 How to assess earthworm and enchytraeid activity

It is often overlooked that earthworms and enchytraeids, in order to influence soil functions, not only need to be present but also to be active. In this section, we therefore want to discuss approaches specifically focused on assessing the activity of these soil biota (Fig. 10). While abundant earthworm populations are likely to reflect conditions where earthworms are active and reproducing, more direct measurements of earthworm activity can help us to better understand the effects of agricultural management on earthworms.

Quantifying bioturbation is particularly challenging due to the opaque nature of the soil matrix and the dynamic nature of bioturbation (Vidal et al., 2023). This might partly explain why directly assessing earthworm and enchytraeid activity have not yet been considered as indicators of soil health. Here, we argue that some methods could be quick and efficient enough to serve as biological indicators for soil health in the future.

6.1 How to assess earthworm activity

Ecotoxicological approaches – Earthworms have long been used as bioindicators in ecotoxicological studies due to their widespread presence in soil, sensitivity to contaminants and ease of handling (Sanchez-Hernandez,

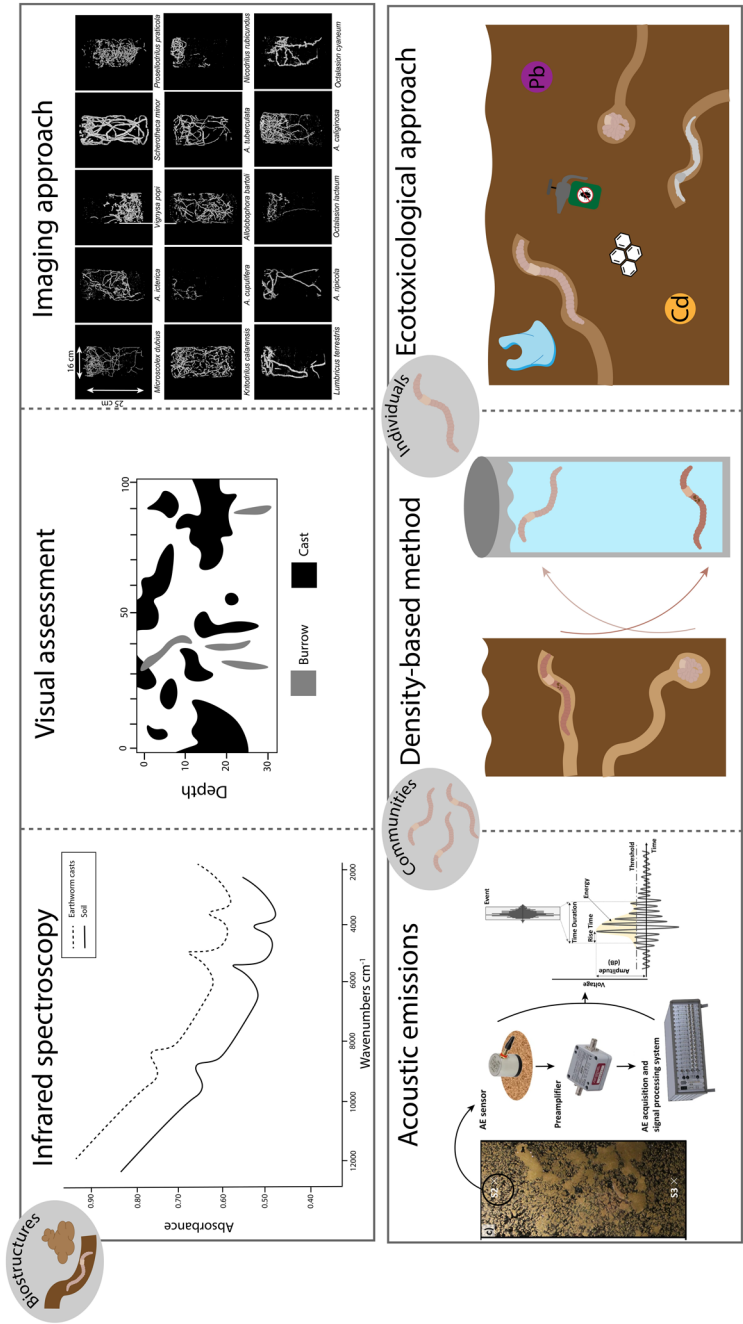


Figure 10 Different approaches used to quantify earthworm activity, classified based on their object of quantification: biostuctures, earthworm communities and individual earthworms. The infrared spectroscopy and the visual assessment figures were created to depict hypothetical results; the imaging approach figure is from Vidal et al. (2023); the acoustic emissions figure is adapted from Lacoste et al. (2018) by combining parts of Fig. 1 and Fig. 4 from the original paper, which is licensed under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

2006; Velki & Ečimović, 2017). In standardized testing protocols, both acute (e.g. LC50 tests) and chronic (e.g. reproduction tests) effects on earthworms can be assessed (ISO, 2023; OECD, 2016). For these tests, earthworms are exposed to either artificial or natural soils for 2 weeks in acute tests or for several weeks to months in chronic tests. Ecotoxicological assays typically focus on a few model species, with *Eisenia fetida*, *Eisenia andrei* and *Lumbricus terrestris* being the most frequently studied (e.g., Chelinho et al., 2011). These assays primarily assess the risks of soil pollution as an indicator of soil health, under controlled laboratory conditions. However, these tests can also be used to assess the habitat function of a soil using non-spiked soils. Native or ubiquitous earthworm species of interest can be kept in 500 g soil following the recommendations of ISO (2023). Growth and reproduction is assessed using juvenile or adult individuals, respectively, providing valuable information on their ability to survive in and colonize a particular habitat. Tests like this have been done using natural soils and several non-standard earthworm species like *A. caliginosa* in the temperate region (Bart et al., 2018a) and *P. corethrurus* in Brazil (Buch et al., 2017), though the duration of the test with the latter species had to be expanded to 90 days in order to ensure reproduction. Nonetheless, this approach does of course not fully capture the range of ecosystem functions that earthworms perform as a community in soil, such as their substantial influence on soil structure (Bartlett et al., 2010). Alternatively, the methods described below emphasize evaluating the impact of earthworm activity on soil through their bioturbation effects.

Visual assessment – Most existing methods for assessing the activity of earthworms focus on assessing earthworm-made structures including casts (Chevallier et al., 2006; Gerard, 1967; Perreault & Whalen, 2006) and burrows (Capowiez et al., 2021; Perreault & Whalen, 2006). Quantifying these structures can be done in the field using visual assessment of burrows and cast deposits on the soil surface (Mueller et al., 2009; Peigné et al., 2013; Pérès et al., 1998). A major drawback of this approach is that it fails to account for species that rarely produce surface casts, such as endogeic species (Capowiez et al., 2021) or for middens formed by anecics species in semi-permanent locations (Rossi & Nuutinen, 2004). Some studies have attempted to assess earthworm bioturbation at the profile scale, e.g., using the Soil-Structure-Pattern (SPP) method (Piron et al., 2012), but this method has proven too complex for larger monitoring streams or for providing practical management advice. Consequently, it has been proposed to add a 'earthworm bioturbation' item within the more widely used Visual Soil Structure Assessment (VSSA). This includes measuring the density and distribution of cast deposits, counting burrow openings and assessing the freshness of cast aggregates. This would result in a classification including four levels of bioturbation, from low to high (Piron et al., 2017).

Imaging approaches – To capture the activity of earthworms in soils, several imaging approaches with various degree of sophistication have been used to visually and quantitatively assess earthworm behavior, movement and their effect on soil structure. Image capturing technologies such as digital cameras or scanners have been used to monitor the temporal dynamics of soil biota, including earthworms. These methods include imaging devices placed directly in the field (Belaud et al., 2024), imaging within mesocosms (Djerdj et al., 2020; Jangorzo et al., 2015) or imaging after sample collection and preparation (Sauzet et al., 2023). X-ray tomography has often been used to create 3D images depicting how earthworms influence soil porosity and structure, allowing for monitoring burrow formation dynamics over time (Capowiez et al., 2011). A key drawback of this approach, however, is that it requires destructive sampling and access to advanced instrumentation.

Infrared spectroscopy – Approaches such as near infrared spectroscopy (NIRS) (Bottinelli et al., 2013; Zangerlé et al., 2014, 2016a) and mid-infrared spectroscopy (MIRS) (Bottinelli et al., 2021) show promise for rapidly and cost-effectively dating certain biostructures and linking their composition to specific earthworm species. In this approach, structures of interest can be collected from the field and exposed to an infrared light while intensity of adsorption is measured. The information extracted from the spectra enables to differentiate earthworm-processed soil from surrounding soil. While these approaches provide valuable insights into earthworm activity, they have not yet been adopted as direct indicators of soil health and require substantial calibration measures. A more promising use of these infrared spectroscopic approaches as a soil health indicator may be to assess general soil quality and specific biological characteristics, such as soil microbial biomass or soil respiration (Cécillon et al., 2009).

Acoustic emissions – A few recent studies have explored the acoustic signatures of earthworms to monitor their activity (Keen et al., 2022; Lacoste et al., 2018; Robinson et al., 2024). Under controlled laboratory conditions, Lacoste et al. (2018) found a positive correlation between acoustic emissions and earthworm burrow length. More recently, Keen et al. (2022) were able to detect the acoustic emissions generated by invasive earthworm species in Tundra soils during a field mesocosm experiment. Although still in initial stages of development, this approach appears to be a promising, low-cost and non-invasive method to assess the bioturbation induced by earthworms, and possibly also other soil biota (Robinson et al., 2024).

Density-based method – Garamszegi et al. (2025) recently developed a density-based method to quantify earthworm activity. This promising, easy and quick method uses the fact that earthworms empty their gut when they enter in aestivation. As a result, active earthworms can be separated from inactive ones using a 1.08 g cm^{-3} glucose solution, with active earthworms sinking

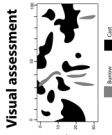
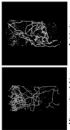
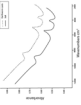
Brief description		Object of quantification	Soil disturbance	Time	Realistic conditions	Equipment	Population representativity	Ethics
Ecotoxicological methods 	Acute tests	Individual earthworms	Destructive			Laboratory	Few species	Earthworms exposed to toxic substance
	Chronic tests	Individual earthworms	Destructive			Laboratory	Few species	Earthworms exposed to toxic substance
Visual assessment 	Soil surface	Biostructures	Non-destructive				Surface casting species	
	Profile scale	Biostructures	Non-destructive				Entire population	
Imaging 	Cameras or scanners	Biostructures	Non-destructive		Often, mesocosms experiments		Entire population	
	X-Ray (micro) tomography	Biostructures	Destructive				Entire population	Destructive sampling
Infrared spectroscopy 		Biostructures	Mostly destructive				Entire population	
Acoustic emissions 		Earthworm communities	Non-destructive				Entire population	
Densit-based method 		Individual earthworms	Destructive				Entire population	Destructive sampling, earthworms exposed to a harmless glucose solution

Figure 11 A brief description of the main methods used to assess earthworm activity, along with their pros and cons. The color scale provides a relative comparison of methods based on key factors for assessing activity, ranging from yellow (positive) to red (negative). A detailed analysis of these approaches is beyond the scope of this review. Readers are directed to key references in the text for further information. The infrared spectroscopy and the visual assessment figures were created to depict hypothetical results; the imaging approach figure is from Vidal et al. (2023); the acoustic emissions figure is adapted from Lacoste et al. (2018) by combining parts of Figs 1 and 4 from the original paper, which is licensed under a Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>).

and inactive earthworm with empty guts floating. In contrast to the previously mentioned approaches, it has the advantage of capturing the current activity of earthworms at the individual level, while other methods, when performed at the field scale, reflect the presence of semi-permanent structures mostly at the population level.

In conclusion, each method for assessing earthworm activity has its advantages and disadvantages (Fig. 11). The primary criterion for a soil health indicator is that it should be easy to implement in large-scale sampling campaigns, meaning that the method used should not be overly time-consuming or expensive while providing valuable information for practical management decisions.

6.2 How to assess enchytraeid activity?

Ecotoxicological approaches – Enchytraeids have been used as models in terrestrial ecotoxicology since the early 2000s as they were recognized as indicator organisms for chemical stress in terrestrial ecosystems (Didden & Römbke, 2001). Standardized protocols exist to assess survival and reproduction of enchytraeids when exposed to chemicals (ASTM, 2000; OECD, 2004). A few ecotoxicological studies deal with enchytraeid activity through the assessment of their feeding activity or avoidance behavior. For feeding behavior, the bait lamina method (ISO, 2016) can be used both under field (Amossé et al., 2018) and laboratory conditions (Bart et al., 2018b) as enchytraeids are considered to be among the main consumers of the bait in the topsoil (Helling et al., 1998). Moreover, avoidance test can be used to evaluate a specific locomotor response of enchytraeids when exposed to a chemical (Amorim et al., 2008; Kobetičová et al., 2010). These methods are informative and easy to implement but do not allow studying physical consequences of enchytraeid activity in soils.

Visual assessment and imaging approaches – Similar to endogeic earthworms, enchytraeids have low assimilation efficiencies which they compensate by high ingestion rates (Didden, 1993; Scheu, 1991). Van Vliet et al. (1995) calculated that every year, the enchytraeid community present at an agricultural site ingested and transported more than 2 kg of mineral soil per square meter, thereby considerably contributing to the evolution of soil structure through bioturbation and production of fecal pellets (Sandor & Schrader, 2012; Van Vliet et al., 1993). Some species such as *Enchytraeus lacteus* also contribute to the modification of soil surface roughness due to the production of casts (Schrader et al., 1997). Didden (1991) described the physical remnant of enchytraeids as a 'spongy' structure (Fig. 12a). The physical activity of enchytraeids in soils can be assessed through photographs (Van Vliet et al., 1993), determination of aggregate stability (Carrera et al., 2011) or using

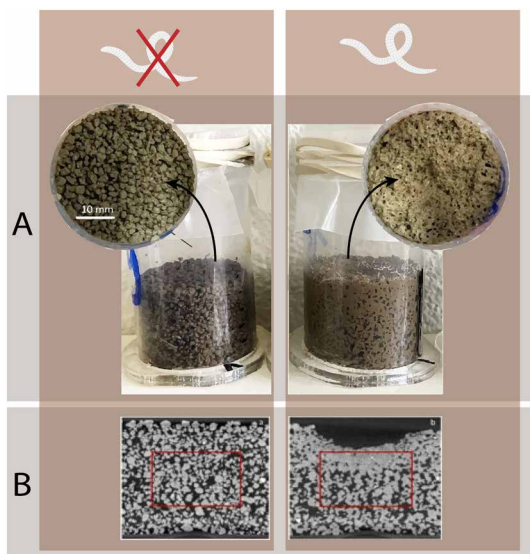


Figure 12 Effect of enchytraeids on soil structure. (a) Side and top views of a column experiment showing soil sieved to 2 mm, with a bulk density of 0.8 g cm^{-3} , incubated for 1 month without (left) and with (right) enchytraeids. The soil was inoculated with *Enchytraeus crypticus* (biomass equivalent to 240 000 individuals per m^2). Note the juveniles visible along the edges of the column in the side view. Source: Adapted from: Serbource et al. (2024). (b) X-ray microtomography images from another experiment showing soil cross-sections. Soil was incubated for 40 days with *Enchytraeus albidus* and *Enchytraeus crypticus*. Red squares represent the zones used to calculate indicators in Serbource et al. (2025).

a laser relief meter for measuring surface roughness due to enchytraeids fecal pellets (Schrader et al., 1997). Otherwise, thin soil sections have been used *in situ* to study the small aggregates made by enchytraeids (Carrera et al., 2011; Topoliantz et al., 2000). However, these structures can in turn be consumed by other soil invertebrates (e.g., earthworms, collembola), strongly limiting their visibility on thin sections. Another imaging approach that could, in principle, be used to assess enchytraeid activity is X-ray microtomography, a non-invasive and non-destructive imaging technique. So far, we are aware of only two studies that used this approach to analyze the enchytraeid pore network (Porre et al., 2016; Serbource et al., 2025) (Fig. 12b).

In conclusion, efforts to quantify the activity of enchytraeids in soils remain very limited. Most studies use model species, though wild enchytraeid species would provide more ecologically relevant insights. A major limitation remains that, unlike earthworms, many enchytraeid species remain challenging to breed due to the limited understanding of their specific needs.

7 Earthworms and enchytraeids as soil health indicators

7.1 Biological indicators, a recent history

Until recently, most soil health monitoring campaigns have primarily relied on chemical indicators, often overlooking physical and even more biological indicators (Bünemann et al., 2018; van Leeuwen et al., 2017). Soil organic carbon was the main biological indicator used until the late twentieth century. Early in the twenty-first century, however, some studies began to introduce more specific biological indicators (Bonilla-Bedoya et al., 2023), including earthworm-related ones and, to a lesser extent, enchytraeids (Pulleman et al., 2012). These soil animals, especially earthworms, were thus increasingly integrated within large programs to monitor soil quality (Fründ et al., 2010) (Section 7.3).

7.2 Earthworms and enchytraeids, good indicators of soil health?

A good indicator of soil health should (1) be sensitive to changes in land use, management and climate; (2) reflect general soil functioning by integrating its physical, chemical, and biological properties; and (3) be accessible and useful for stakeholders, such as farmers and policymakers (Doran & Parkin, 1997). The sensitivity of earthworms and enchytraeids to changes in land use, management and climate has been summarized in Sections 2 and 3, while the contributions of earthworms, and to a lesser extent enchytraeids, to soil functioning have been detailed in several reviews (Blouin et al., 2013; Briones, 2014; Coleman et al., 2024; Conti & Mulder, 2022; Vidal et al., 2023). However, while it is clear that earthworms and enchytraeids are sensitive to external factors and play essential roles in soil ecosystems, converting their functions into a practical and accessible indicator for stakeholders remains a challenge (Fig. 13). One reason for this is that effects on earthworms and enchytraeids are generally obvious at the genus or species level rather than at the level of total abundance, prohibiting easy access by non-specialists. Another challenge for stakeholders is to choose the most relevant among all the existing biological indicators. For instance, Zwetsloot et al. (2022) identified as many as 289 soil biology methods for assessing soil multifunctionality. Among these, it has been suggested that, for practical insights, measuring the key organisms (in this case, earthworms and enchytraeids) is often easier than measuring the processes they perform (Creamer et al., 2022). Based on this, Zwetsloot et al. (2022) recommend four methods each for assessing earthworms and enchytraeids, including morphological identification (Bouché, 1972; Schmelz & Collado,

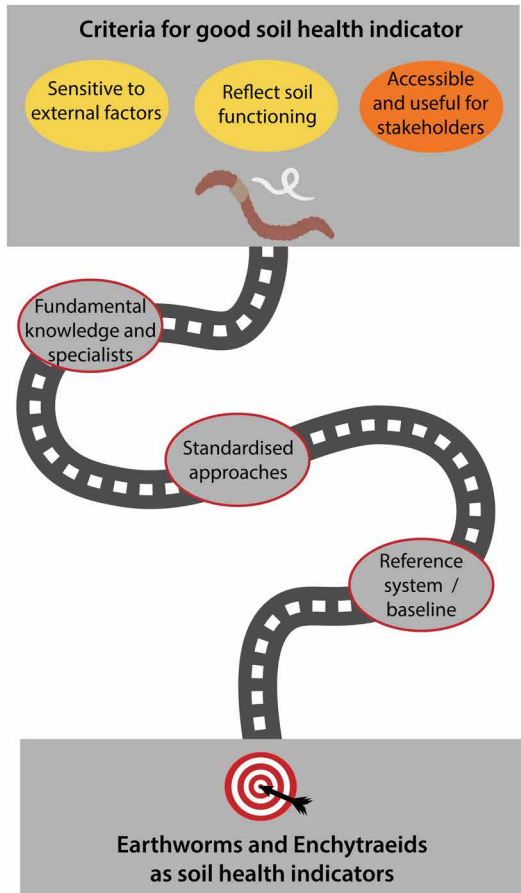


Figure 13 Opportunities and challenges of using earthworms and enchytraeids as indicators of soil health. Although earthworms and enchytraeids are sensitive to external factors and play essential roles in soil ecosystems (yellow circles), translating their functions into practical and accessible indicators for stakeholders remains a challenge (orange circle). To tackle this challenge, various aspects need to be considered (gray circles with red borders).

2010) counting/biomass or metabarcoding (Bienert et al., 2012; Creer et al., 2016; Pansu et al., 2015).

7.3 When to use earthworms and enchytraeids as indicators?

There is growing recognition that the selection of soil health indicators should be context-specific (Creamer et al., 2022; Schreefel et al., 2024), and that biological indicators alone are not sufficient to assess soil health and should be combined

with physical and chemical indicators in order to capture soil multifunctionality (Coyne et al., 2022). Consequently, earthworms and enchytraeids should be incorporated as indicators only if they provide relevant insights for a specific purpose. So, when are earthworms and enchytraeids valuable as indicators? Creamer et al. (2022) note that earthworms and enchytraeids directly contribute to six and five key soil processes (out of 25), respectively, and play active roles in three of the four primary soil functions: ‘water regulation and purification,’ ‘nutrient cycling,’ and ‘carbon and climate regulation’; without direct effect on ‘disease and pest regulation’ (Fig. 14). Earthworms, in particular, are considered essential for assessing soil functions, especially in relation to biodiversity (Griffiths et al., 2016). Although enchytraeids are less often considered, they contribute to soil biodiversity (van Leeuwen et al., 2017) and are recommended as soil quality indicators in cases where earthworms are absent (Pulleman et al., 2012). In addition, combining data on these two annelids can provide complementary information, as earthworms and enchytraeids do not necessarily respond the same way to stress in terms of abundance and diversity (Section 4) (Beylich &

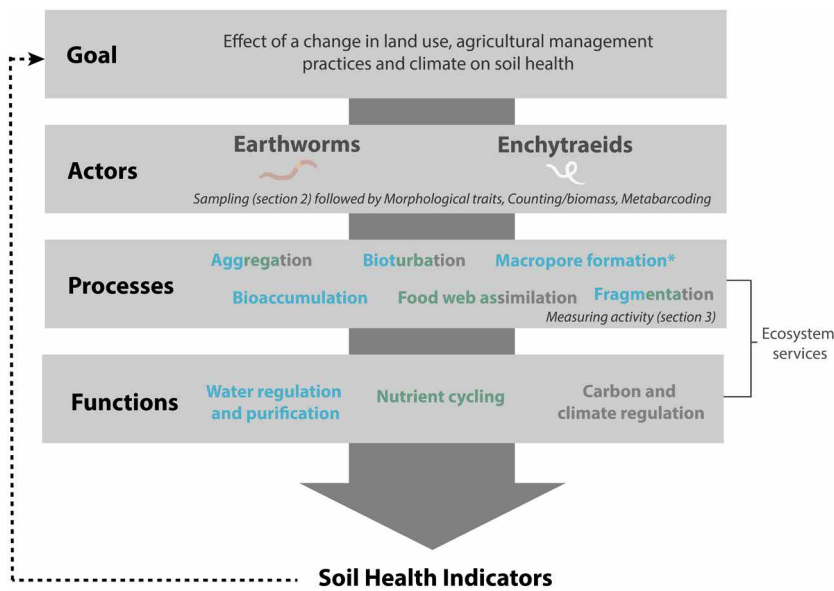


Figure 14 Why use earthworms and enchytraeids as soil health indicators? Main processes in which earthworm and enchytraeids are involved, determining their role on three key soil functions: water regulation and purification, nutrient cycling, and carbon and climate regulation. An asterisk (*) indicates a process carried out exclusively by earthworms, not enchytraeids. This classification is adapted from Creamer et al. (2022) and Zwetsloot et al. (2022); with a special focus on earthworms and enchytraeids. The function delivered thanks to one or more processes have the same color code. Processes that deliver more than one function are multi-colored according to the functions they deliver. The delivery of soil functions contributes to the provision of ecosystem services.

Graefe, 2009; Fründ et al., 2010). Although earthworms and enchytraeids are involved in fewer soil processes than microorganisms (Creamer et al., 2022), Delgado-Baquerizo et al. (2020) emphasize that larger invertebrates help keep to *multiple soil functions operating near peak capacity* by regulating the flow of resources to smaller organisms that operate at lower functional levels.

As a result, earthworms, and to a lesser extent enchytraeids, are being incorporated in large frameworks to monitor soil health, as summarized in Fründ et al. (2010). For instance, the Biological Indicator system for Soil Quality (BISQ) of the Netherlands Soil Monitoring Network (NSMN) has been monitoring several biological indicators for 300 locations, including the abundance and diversity of earthworms and enchytraeids, from 1997 to 2014, every 6 years (Rutgers et al., 2009). In Germany, several federal states are involved in the long-term monitoring of earthworms and enchytraeids in some of the 800 permanent soil monitoring sites (Römbke et al., 2013). The French Soil Quality Monitoring Network has been monitoring earthworms in 109 locations in Britany through the RMQS Biodiv from 2006 to 2008 (Cluzeau et al., 2012). Yet, most of these initiatives take place in Europe, while there is still a strong data gap in, e.g., the Americas, North Australia, Asia, Russia and Africa (Phillips et al., 2019). To tackle this challenge, among others, the recent initiative 'Soil BON earthworm' aims at gathering the community of earthworm experts to improve the monitoring of earthworm distribution globally (Ganault et al., 2024).

7.4 Remaining challenges

7.4.1 The need for fundamental knowledge and specialists

To advance the development of biological indicators, it is essential to deepen scientific knowledge about the ecology and functional roles of earthworms and enchytraeids. For instance, only about 20% of the estimated 30 000 existing earthworm species have been identified (Decaëns et al., 2024) and the most useful ways to classify them are still debated (Bottinelli & Capowiez, 2021). Moreover, despite available identification keys (Schmelz and Collado, 2010), morphological identification of enchytraeids is challenging as they must be identified while alive, under a microscope. While the estimated diversity of enchytraeids is at least ten times lower than that of earthworms (Anthony et al., 2023), a significant share of these species remains unclassified (Decaëns et al., 2006). Traditional identification of earthworms and enchytraeids rely on dichotomous keys (Bouché, 1972; Schmelz & Collado, 2010; Sims & Gerard, 1999) which require specialist taxonomists – professionals who are increasingly rare (Andre et al., 2001). New DNA-based methods, such as barcoding, are increasingly used to assess biological diversity in soil samples (Dozsa-Farkas et al., 2012; Epp et al., 2012). Although these molecular identification methods

offer promising alternatives, they are still in development and not yet sufficiently refined for widespread use (Decaëns et al., 2013; Dupont, 2009; Marchán et al., 2022). In the context of agroecology in which agriculture will have to rely on biodiversity to provide ecosystem services, a better quantification of the role of the different species or categories of earthworms and enchytraeids under different conditions is crucial. Moreover, understanding how land use, management practices and climate factors impact this soil biota (Sections 2 and 3), and thus soil functions and ecosystem services will enable the development of more sustainable agricultural systems that are adapted or resilient to future climate scenarios.

7.4.2 The need for standardized sampling and analytical approaches

Soil health cannot be effectively assessed using a single, standardized indicator; instead, choosing the right indicators requires a clear understanding of specific goals and context (Schreefel et al., 2024). When earthworms and enchytraeids are selected as indicators to address particular research questions, it is essential to define an appropriate measurement strategy for data collection. There is a strong consensus on the need to harmonize sampling and analysis methods across Europe and ideally worldwide (Ganault et al., 2024; Griffiths et al., 2016; van Leeuwen et al., 2017). Of particular importance is the spatial and temporal resolution of earthworm and enchytraeid sampling, which determines the reliability of the data. The distribution of earthworms and enchytraeids at field scale strongly varies between seasons (Section 5), but it is also strongly spatially clustered (Rossi, 2003; Van Vliet, 2000). Rossi (2003) showed that two earthworm species within a 45 × 45 m plot in a grass savanna in Côte d'Ivoire were clearly distributed in distinct patches within this plot. Valckx et al. (2009) showed that the distribution of several juvenile and adult earthworm species in a Belgium arable field was either overlapping or segregating. Rossi and Nuutinen (2004) demonstrated that sampling unit size was key in modelling the distribution of *L. terrestris* in a Finnish forest. While we fully support these harmonization efforts, it is important to recognize that sampling and analytical approaches for earthworms and enchytraeids may need adjustment based on specific context, the spatial and temporal resolution required, and research objectives (Section 4).

7.4.3 The need for reference systems/baseline/normal values

Once earthworm and/or enchytraeid indicators are chosen and implemented, it needs to be compared to a reference system, a baseline or normal values (Blair et al., 1997). For instance, once a management practice is applied, outcome

indicators are used to illustrate the potential success of a change over time compared to a baseline (Schreefel et al., 2024). As trivial as this might sound, these types of values are often not available, with the high variability across seasons, land uses and soil types as a key constraint. The reference system should thus be well adapted to the context and goals of the study. Considering these needs, Krüger et al. (2018) laid the groundwork for establishing a reference system for biological indicators, including earthworms, in Wallonia, Belgium. To achieve this, the authors collected data on the number and biomass of earthworms at four different times throughout the year from 60 sites with varied land uses and soil types. Reference ranges were established by combining variances and calculating cumulative distribution functions. In France, the ongoing LANDWORM project aims to quantify the current and past (less than 50 years) effects of land use and management on earthworm communities. The project takes into account the diverse soil and climatic conditions to better understand and predict earthworm community assembly and to identify land management practices that support their population. LANDWORM also aims to produce reference and threshold values to contribute to the bio-monitoring of the French territory, which could be used later at the European level. Ultimately, to efficiently use earthworms as soil health indicators, it is also crucial to link the reference values obtained in the types of projects mentioned above to their significance in terms of functions and ecosystem services.

8 Conclusion

To effectively use earthworms and enchytraeids as soil health indicators, several questions still need to be addressed in future research. Below, we conclude this chapter by highlighting key challenges that need to be addressed for advancing this field:

- *Understanding combined effects of management practices, land use, and climatic factors on earthworm and enchytraeid populations in order to mitigate climate change effects.* Specific management practices or land uses that promote greater abundance and diversity of these organisms are likely to enhance ecosystem resilience to adverse climatic conditions. However, this area remains largely understudied (Section 2).
- *Improving the accessibility and usefulness of indicators for stakeholders.* Stakeholders face a wide range of potential biological indicators to choose from. Identifying earthworms and enchytraeids to the genus or species level is challenging for non-specialists, despite being critical for evaluating the effects of land use, management practices and climate on

soil health. Enhancing the user-friendliness of these indicators is therefore essential to their success (Section 7).

- *Developing methods to assess activity of earthworms and enchytraeids.* The presence of soil biota does not necessarily indicate high biological activity. In order to improve earthworm- and enchytraeid-based indicators, we therefore recommend the further development and adoption of methods to measure activity levels of earthworms and enchytraeids. These methods may be based on various approaches, such as density methods, visual assessments or acoustic approaches (Section 6).
- *Identifying unknown species of earthworms and enchytraeids.* The functionality of indicators is still severely hampered by lacks in the knowledge of earthworm and enchytraeid species. The identification of new species requires the expertise of specialist taxonomists, who are becoming increasingly rare. The development of new DNA-based methods, such as barcoding, offers promising support for species identification. However, this approach still needs further refinement (Section 7.4).
- *Studying interactions between earthworms and enchytraeids.* Both groups of soil biota coexist in natural environments but may respond differently to changes in land use, management and climate. There is still much knowledge on soil health to be gained by studying their interactions and complementary roles in the soil (Section 4).
- *Breeding more representative and relevant model species of earthworms and enchytraeids for laboratory testing.* Many studies on the effects of earthworms and enchytraeids on soil properties rely on a very limited number of model species. This is particularly true for enchytraeids, which are challenging to breed due to limited knowledge of their specific requirements. Developing better breeding techniques for various species of these faunal groups is essential for more representative laboratory testing (Section 6).
- *Testing effect of pesticides on earthworms and enchytraeids under realistic conditions, at ecologically relevant dosages and accounting for interactions between compounds.* Controlled tests assessing the impact of pesticides on these organisms often lack ecological relevance due to factors such as short test durations, the use of artificial soils, reliance on model species and single-species testing. More realistic test conditions are necessary for relevant indicators (Sections 2 and 3).

9 Where to look for further information

9.1 Key book chapters, articles, and guides

- Fründ, H.-C., et al. (2010). Earthworms as bioindicators of soil quality. In C. A. Edwards & J. R. Lofly (Eds.), *Biology of earthworms* (pp. 261–278). Springer.

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9.2 International conferences

- The International Symposium on Earthworm Ecology – this conference is held every 4 years and provide updates on all aspects of earthworm research, as well as citizen science initiatives. The 13th edition of this symposium will be held in Wageningen University and Research, the Netherlands, in August 2026.
- The International Colloquium on Soil Zoology is held every 4 years and is one of the key scientific meetings on earthworms, enchytraeids as well as other soil faunal groups. The most recent colloquium was held in Cape town, South Africa, in August 2024.

9.3 Initiatives

- The Soil BON Earthworm – a global initiative aimed at gathering global data and information on earthworms. Initiated by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Soil BON Earthworm – A global initiative on earthworm distribution, traits, and spatiotemporal diversity patterns | Soil Organisms.

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