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Advances in Agronomy

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https://doi.org/10.1016/bs.agron.2023.05.001

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CHAPTER ONE

The role of earthworms in agronomy: Consensus, novel insights and remaining challenges

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Advances in Agronomy, Volume 181
ISSN 0065-2113
https://doi.org/10.1016/bs.agron.2023.05.001

Abstract

Earthworms have a prominent role in supporting soil functioning and thus in providing key services to humanity. Their beneficial role relates to effects on soil structure, carbon and nutrient cycling as well as the soil microbial community. Optimizing the role of earthworms in agricultural systems is therefore crucial for maintaining or improving soil quality and supporting a more sustainable, circular agriculture. Here, we summarize established knowledge on the role of earthworms in agronomy; present novel insights from the past decades; and identify key knowledge gaps to be addressed in the future to fully benefit from earthworms in our agricultural soils. We start by discussing how earthworms affect basic soil processes through their effects on soil structure, microbial communities and biogeochemical cycles. Further, we show how as a result of these changes, earthworms indirectly affect plant growth, the soil greenhouse gas balance and play a role in remediation of contaminated arable soils. We further address one of the paradoxes of earthworm ecology: that they are often not present in the soils where they are most needed. We subsequently discuss potential solutions to this paradox. Finally, we identify 10 key questions that need to be addressed in the near future. In our view, recognizing that earthworms are not a stand-alone solution to improving the sustainability of cropping systems, but an essential piece of the puzzle is crucial for optimizing the benefits they offer in agronomic systems. By managing our earthworm populations well, we manage our soils well.

1. Introduction

Around 540 million years ago, the Earth experienced a "burrowing revolution," with the evolution of large numbers of ecosystem engineers. This bioturbation of substrate drastically changed the structure of the ocean floor and created new habitats. It promoted the "Cambrian explosion" of life forms and led to a fundamental change in global biogeochemical cycles (Meysman et al., 2006). Today, descendants of these early ecosystem engineers still have a pivotal role in the functioning of ocean sediments as well as terrestrial soils. In the soil, earthworms are probably the most important faunal ecosystem engineers. With a worldwide average density of approx. 20 individuals per m^2 (excluding Antarctica) (Phillips et al., 2021), they provide vital soil functions and services to humanity.

If we define agronomy as "*the relationships between crops, soils, climates and agricultural practices, and between agriculture and the environment*" (European Society for Agronomy, https://european-agronomy.org/), then earthworms should clearly be considered important actors. Their effects on structure and microbiology strongly affect the physical and chemical properties of soils as well as plant growth; their actions can lead to both increases and decreases of fluxes of pollutants to surface water and the atmosphere. Because of these key roles in agronomic functions, managing earthworm populations in arable soils could be a promising strategy toward a more sustainable and circular agriculture. Here, we review our current knowledge on the role of earthworms in agronomy and discuss new concepts and challenges to better integrate earthworms in the management of arable soils.

The most important quality of earthworms is to ingest, fragment, mix and transport both organic (plant residues, soil organic matter (SOM) and microorganisms) and inorganic (soil particles) material in ways that differ among species. Therefore, earthworms are traditionally classified according to their feeding and burrowing behavior. Three main ecological categories (guilds) are usually distinguished: *epigeics* that mainly feed on litter at the soil surface with activities limited to a few centimeters below the soil-litter interface; *endogeics* that mainly feed on SOM and form non-permanent burrows without preferential orientation; and *anecics* that mainly feed on litter at the soil surface and live in permanent vertical burrows (Bouché, 1972; Lee, 1985). While below we discuss the limits of using these categories and present some emerging views on more function-based categories, we will generally use this framework to align with the main body of literature to date.

After a short sketch of the history of earthworm research from antiquity up till modern times (Section 2), the structure of the present review is guided by our view of the role of earthworms in agronomy (Fig. 1). In this view, the effect of earthworms on soil biogeochemical processes and plant growth is primarily driven by their effects on soil structure (Section 3) and their interactions with microorganisms (Section 4). By shaping soil structure and soil biotic communities, earthworms affect the biogeochemical cycling of carbon (Section 5) and nutrients (Section 6) both directly and indirectly. Their combined influence on soil biological, chemical and physical processes affects plant growth (Section 7), soil-derived greenhouse gas emissions (Section 8), and the remediation potential of polluted soils (Section 9). Toward the end of the review, we ask ourselves to what extent the beneficial effects of earthworms are limited by poor habitat quality, as it sometimes seems like earthworms may have the largest benefits in soils where they

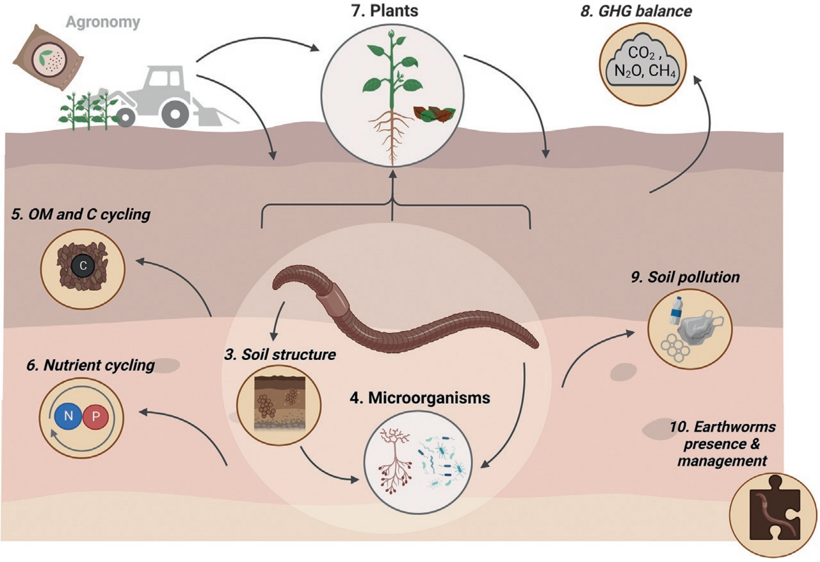

Fig. 1 Structure of the present review, guided by our view of the role of earthworms in agronomy, which is primarily driven by their effects on soil structure (Section 3) and their interaction with microorganisms (Section 4). As a result, earthworms affect the biogeochemical cycling of carbon (Section 5) and nutrients (Section 6), ultimately affecting plant growth (Section 7), the soil greenhouse gas balance (Section 8), and the remediation potential of polluted soils (Section 9). Finally, this review addresses how we can potentially manage the presence and the effect of earthworms in arable soils (Section 10). Numbers correspond to section numbers in the present review. *The figure is created with BioRender.com.*

are least likely to occur. How can we manage the presence and the effects of earthworms in such soils (Section 10)? We end with 10 pertinent questions that we think need to be addressed to fully understand and reach earthworms' potential in agricultural systems.

2. Earthworms in agronomy, a long history

2.1 Earthworms in classical and Hellenistic times: Myths and mistranslations

Scientists love to tell stories about the origins of their field of study, and earthworm scientists can draw from a particularly impressive list of these "origin myths." Two of these, especially, are often repeated: namely, that "Cleopatra declared earthworms sacred and killing them punishable by death," and that "Aristotle called earthworms the intestines of the earth." Combined, these stories suggest a deep appreciation of the importance of earthworms in agriculture in classical times. However, both stories have not passed the test of scientific scrutiny.

The origin of the story of Cleopatra VII Philopator (69–30 BCE), the last ruler of the Ptolemaic Kingdom of Egypt and nowadays commonly referred to as "Cleopatra," is particularly obscure. It seems to appear first in Minnich (1977), who does not provide a source. After studying classical texts and interviewing prominent Egyptologists, Professor Emilia Rota of the Università degli Studi di Siena in Italy has concluded that this story is very likely not authentic, and originates from classical authors and translators taxonomically confusing earthworms with eels; eels being sacred to the Nile (Herodotus, Historiae 2, 72, as cited by (Rota, 2011) and E. Rota (personal communication)).

Even further back in time, the story about Aristotle is not so much apocryphal as it is a misinterpretation of what he meant when he stated that earthworms were γήςέντερα (ges entera, "*the intestines of the earth*"). Although it has been suggested that this statement indicates knowledge of their role in decomposition (Lavelle, 1997), it is much more likely that it was based on their superficial resemblance to animal guts (Theon of Alexandria, as cited in Buhle (1793)). Also in later classical times, the medieval period, and even in early modern times, observations about earthworms were mainly focussed on their supposed relationships with eels and snakes, their procreation, and about their behavior rather than their role in soil fertility.

For a fascinating overview of historical earthworm tales, we recommend Rota (2011).

In conclusion: it seems there was no general appreciation of the positive effects of earthworms on soil fertility in antiquity or medieval times. It took one of the giants of modern science to point out their special role in agronomy.

2.2 Renewed appreciation for earthworms at the dawn of modern science

It can be considered both a blessing and a curse that the first modern scientist to seriously study earthworms was such an icon as Charles Darwin. On the one hand, the insights in his *"The formation of vegetable mould through the action of earthworms with observations on their habits"* (Darwin, 1881) benefit from his unequalled powers of observation and deduction. On the other hand, compared to his main work on evolution, this book was considered marginal and was often derisively referred to as Darwin's "worm book" (Gould, 1985). This book, where for the first time he describes bioturbation (although the term was coined much later) and biosorting as fundamental soil forming processes, was largely ignored by the founding father of soil science, Vasily Dokuchaev, who was rather dismissive about Darwins' work (Johnson and Schaetzl, 2015). It is rather ironic that recent research suggests that the formation of Chernozems, the soils which Dokuchaev studied most intensively (Dokuchaev, 1883), is strongly affected by the activity of earthworms (Dreibrodt et al., 2022).

Even though Darwin's "worm book" seemed like a slightly eccentric trifle at the time, the American paleontologist Stephen Jay Gould has most eloquently and convincingly argued that the "worm book" is actually a logical and integral part of his scientific work. Darwin's work is characterized by his unparalleled ability to observe seemingly unimportant processes, to combine this with the power of imagination, and to understand how important these processes could be, multiplied over millions of years and billions of individuals. This is certainly true for his work on evolution, but equally so for his work on the formation of coral atolls and, indeed, for his work on earthworms (Darwin, 1842, 1859, 1881). In Goulds' words: Darwin was keenly aware that *"Nature's mills, like Gods', grind slowly and exceedingly small."*

Without a doubt, it is the description of bioturbation as well as many detailed observations on the habits of earthworms that are the most important contributions of Darwin to the earthworm literature (Fig. 2). His book is still very much worth reading and includes creative experiments involving filter paper cut in different shapes and his children playing various

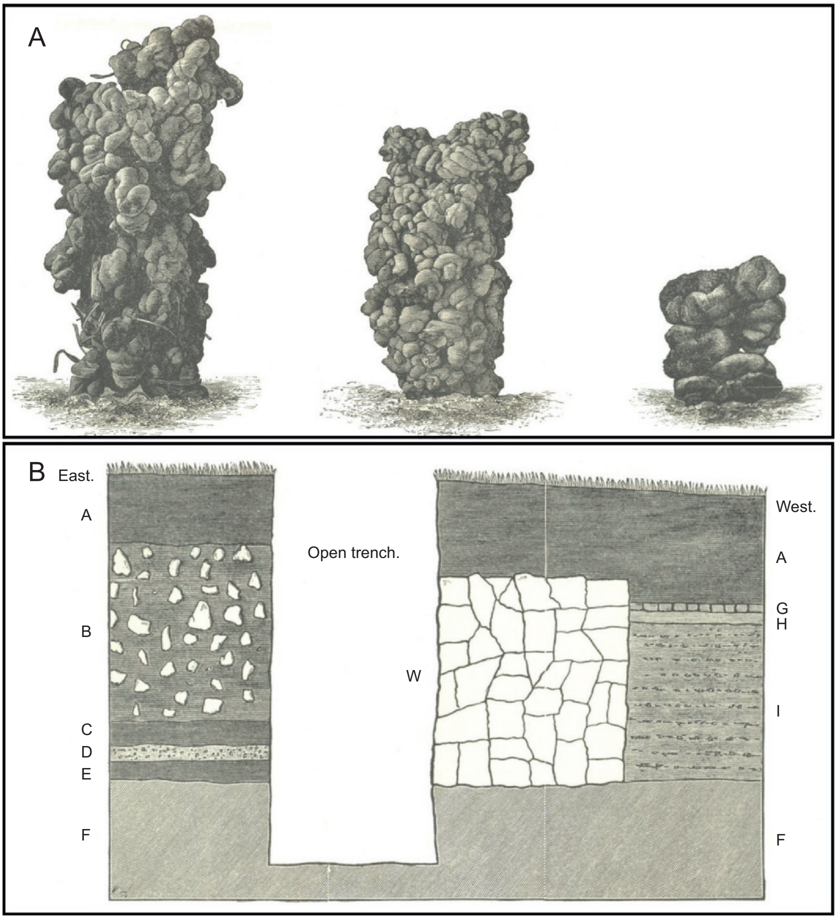

Fig. 2 Pictures from Darwin's last book (Darwin, 1881), devoted entirely to earthworms. Without using the term, this is the first description of the role of earthworms in bioturbation. (A) Very detailed depictions of earthworm casts. (B) A buried Roman ruin illustrating how earthworms process the soil at the profile scale.

music instruments, as well as extensive descriptions of buried Roman ruins, and painstaking depictions of earthworm casts (Fig. 2). For all his wonderful observations and reasoning, his work only fleetingly touches upon the effects of earthworms on soil fertility.

2.3 Toward current earthworm research in agronomy

There is little doubt that current research programs on earthworms started with the ground-breaking work of Marcel Bouché, most famously his

"Stratégies lombriciennes" (Bouché, 1977). With this well-known work, Bouché first defined three ecological categories (epigeic, endogeic and anecic) that determined feeding and burrowing behavior, and positioned individual species on a triangle depicting their distance to these three category axes. Although refinements to this subdivision have been proposed (e.g., Lavelle, 1981), and even alternatives have recently been suggested (e.g., Bottinelli et al., 2020a) (see Section 3.1), this subdivision has proven to be immensely important in linking different earthworm species to their behavior and influence on soil functioning. It remains one of the great ironies of earthworm science that this seminal work of Bouché has never been translated into English, making it only a secondary source to non-native speakers.

Based on the groundwork laid down by Bouché and others, the research on earthworms and their various functions in the soil has exploded over the last 50 years. The direction of this research has been highlighted by Blouin et al. (2013a) who gave an overview of the "paradigmatic proximity" between earthworms and several ecosystem services that they provide. For the present review, we have updated this analysis for the last 10 years, showing trends over the last 55 years (Fig. 3). Interestingly, the link between earthworms and soil structure and nutrient cycling already peaked in the

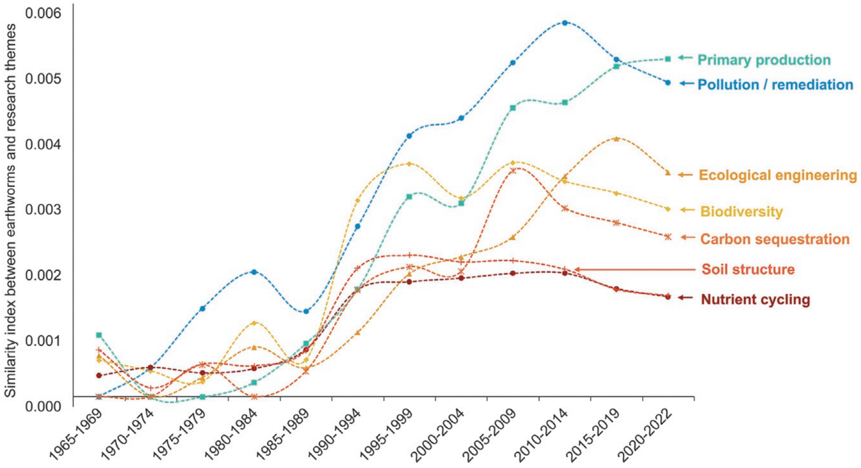

Fig. 3 Timeline highlighting the association in the scientific literature between earthworms and the ecosystem services they provide over the last 55 years. The association between earthworms and soil structure and nutrient cycling increased in the 1990s, while the link between earthworms and primary production is still increasing to the present day. Further details on the approach can be found in Blouin et al. (2013a). The dotted lines have been smoothed for aesthetic purposes.

1990s, and its association with biodiversity, carbon sequestration and ecosystem engineering in the decades after. Yet, the relationship between earthworms and primary production (the ecosystem service mostly associated with agronomy) is still increasing up to this day. Therefore, there is still a need to integrate all the different effects earthworms have on plant production into one coherent framework, despite earlier landmark papers on the topic (Brown et al., 1999; Scheu, 2003; Van Groenigen et al., 2014).

3. Earthworms and soil structure

3.1 How earthworms influence soil structure

Soil structure, i.e., the spatial arrangement of mineral and organic components, is a key characteristic that determines the physical quality of soils and thus its ability to sustain agronomic production (Rabot et al., 2018). With the rise of agroecology and the need for more sustainable production systems, earthworms, as physical ecosystem engineers are increasingly recognized as important agents to improve soil structure. While burrowing, earthworms consume soil and displace soil particles to both feed and facilitate their movement underground (Arrázola-Vásquez et al., 2022; Capowiez et al., 2014). Rates and modes of burrowing differ between earthworm species (Arrázola-Vásquez et al., 2022; Capowiez et al., 2014) as well as depend on environmental conditions (Rushton, 1986). The ingested soil is partly egested as casts at the soil surface or within burrows (Capowiez et al., 2014). For long, the opacity and heterogeneity of soils made the study of earthworm's burrowing behavior a serious methodological challenge. This changed in the early 1990s, when the development of X-ray computed tomography made it possible to characterize macroporosity inside soil cores (Joschko et al., 1993). This methodology has considerably improved our understanding of earthworm bioturbation, i.e., the formation, transformation and destruction of burrows and casts (Capowiez et al., 2011). Despite these advances, the amount of data available is still limited and there is a strong knowledge bias toward two main species, *Lumbricus terrestris* and *Aporrectodea caliginosa,* which are often used as representatives of the two main burrowing ecological categories, anecic and endogeic, respectively.

3.1.1 Earthworm burrows: Morphology and turnover

The morphology of earthworm burrows is highly variable between species (Capowiez et al., 2015). Different environmental conditions and agricultural management practices can modify earthworm burrowing systems by affecting the earthworm community structure (Capowiez et al., 2021; Frazão et al., 2019). For example, tillage decreases the ratio between anecic and endogeic earthworms (Chan, 2001), whereas the use of organic residues increases the abundance of all species and particularly those of epigeics if applied at the soil surface as a mulch (Lee, 1985). The historical view of earthworm science has emphasized a strong dichotomy between burrows made by endogeic and anecic earthworms (Bertrand et al., 2015; Blouin et al., 2013b; Edwards and Arancon, 2022; Lavelle and Spain, 2001). In this view, anecics build permanent, vertical and continuous burrows up to a few meters depth, while endogeics create non-permanent, discontinuous burrows without preferential orientation in the upper 30 cm. This vision has recently been challenged by Bottinelli and Capowiez (2021) who concluded that no straightforward link can be made between categories and burrow morphology. The authors analyzed the morphology of burrows produced by more than 80 earthworm species under controlled conditions and highlighted the great diversity of burrow system in terms of diameter, depth, continuity and branching intensity (Fig. 4A). Species such as *Aporrectodea icterica* and *Octalasion cyaneum* burrowed mainly in the lower part of soil cores even if the organic matter (OM) concentration was homogeneously distributed.

While these findings have improved our understanding of the burrowing behavior of individual earthworm species, extrapolating to the field scale in arable soils remains challenging. Indeed, studies exploring the relationship between a given earthworm community and its burrow system have either pictured oversimplified systems (Pérès et al., 2010) or did not find a significant correlation (Capowiez et al., 1998; Lamandé et al., 2011). The reason is probably that, although the burrowing rate is known for most of the species, the lifespan of these structures is largely ignored (Le Mer et al., 2021). The destruction of burrows, whether caused by the earthworm activity, climate-related factors (swelling, freezing and rapid inundation), or agricultural practices (e.g., tillage, compaction) exerts an equally significant impact on the overall burrow system as the rate of creation, at any point in time. Pelosi et al. (2017) tested the effect of earthworms on soil structure after tillage compared to non-tillage. They showed that the soil macroporosity remained relatively stable with time in the two systems (from 3.75% to 5% of the bulk soil, respectively, without significant differences between dates), despite earthworms being more abundant in the non-tilled system. These results demonstrate the transient nature of most burrows and that burrow creation and destruction are in balance.

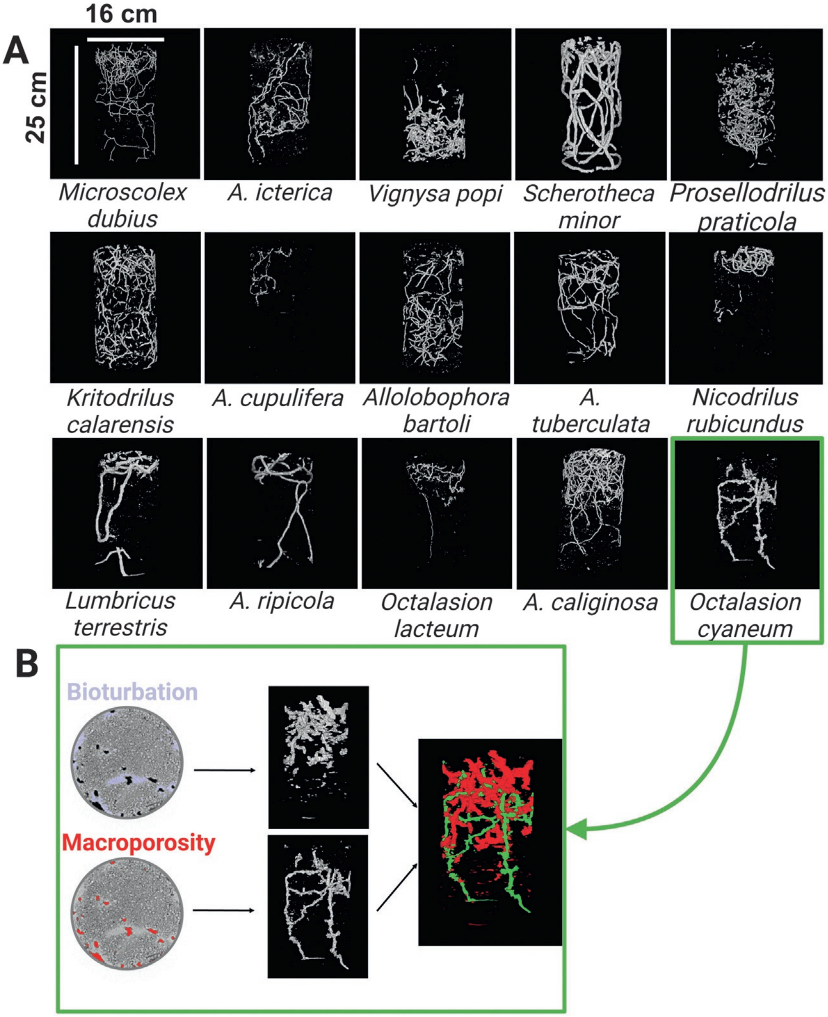

Fig. 4 Earthworm burrow systems and bioturbation. (A) Examples of 3D reconstruction of earthworm burrow systems (macropores) made by different species in a repacked soil core after 1 month of incubation. (B) A focus on the earthworm species *Octalasion cyaneum* depicting macropores and bioturbated areas using an X-ray computed imaging approach.

3.1.2 Both surface and belowground casts count

Casts are biogenic organo-mineral aggregates egested by earthworms that come in various shapes (e.g., granular vs pasty), are of different size and are deposited in different locations (on the soil surface or belowground).

Some surface casts have distinct features. For example, *L. terrestris* creates "middens" at the opening of its main burrow that consists of casts mixed with litter (Nuutinen and Butt, 2019). The structure of casts evolves rapidly after their production from unstable and water-rich, to water-stable aggregates. These structural changes come along with a modification of the biogeochemical composition (see Sections 5 and 6) (Mariani et al., 2007).

Most earthworm scientists focus on surface casts for practical sampling reasons, while they represent less than 50% of the casts deposited (Decaëns, 2000) and are exclusively produced by anecic or epi-anecic earthworms (Edwards and Arancon, 2022). A few studies only have investigated belowground casts using visual assessment in soil profiles (Piron et al., 2017) or using X-ray tomography for earthworms incubated in repacked soils cores. Using the latter approach (Fig. 4B), Capowiez et al. (2014, 2015) showed that burrows made by epi-anecics and anecics (macroporosity on Fig. 4B) were less refilled (bioturbation on Fig. 4B) than those made by endogeics.

3.2 Hydro-physical functions of burrows and casts

Unravelling the functions of earthworm biostructures in arable soils requires more collaborations between the fields of soil physics and soil biology, two scientific domains with distinct aims and approaches (Bottinelli et al., 2015). Soil physicists mostly study the effects of macroporosity (including earthworm burrows) on preferential flow without considering the origin of the macroporosity. Conversely, most soil biologists consider only earthworm burrows, neglecting the rest of the soil structure (meso- and microporosity) and typically have a simplified view of burrows as endless pipes through which water can flow freely. Obviously, soil biologist should learn from recent advances in soil physics to avoid *a priori* statements such as "*the more burrow there is, the higher water infiltration will be*" which neglect how and when preferential flow is taking play (McCoy et al., 1994; Nimmo, 2012).

3.2.1 Functional effects associated with soil transfer properties

Even though earthworm burrows rarely occupy more than 5% of the total porosity, they can play a key role in water infiltration due to their continuity and general vertical orientation. This contributes to preferential flow that can occur in water saturated and non-saturated soils (Nimmo, 2012). Knowledge on the effect of burrows on water infiltration in soil is mostly limited to a few species, especially *L. terrestris*. However, this epi-anecic species behaves very differently from most other anecics. For instance, it creates one main vertical burrow with occasionally a few lateral branches connecting to the surface, forming a Y-shaped burrow (Shipitalo and Butt, 1999). This species generally does not enter diapause in summer and thus creates burrows that can be several meters deep. In addition, *L. terrestris* exhibits territorial behavior because adult competes for food at the soil surface and therefore mean abundances are low in crop lands (rarely more than 10 earthworms m^{-2}). Obviously, such deep vertical burrows can have a huge effect on water infiltration when soils are flooded during rain events (Andriuzzi et al., 2015; Willoughby and Kladivko, 2002).

Most anecic species create rather vertical and continuous burrows that are connected to the surface and atmosphere, but the resulting burrow systems are usually more extended (laterally) and branched than those of *L. terrestris* (Capowiez et al., 2015). Even though the maximal depth of anecic burrow systems is still unknown, the efficiency of anecic burrows regarding water infiltration is considered to be similar to that of epi-anecic burrows. However, anecic burrow systems are understudied with only lab studies published so far (Trojan and Linden, 1992). Endogeic burrow systems, which are typically not connected to the surface and regularly refilled with casts, raise doubt on their functioning in a similar manner to those of *L. terrestris*. Experimental evidence has shown that even discontinuous burrows can contribute to preferential flow (Allaire-Leung et al., 2000) and enhance water infiltration (Trojan and Linden, 1992), with the length of burrows positively correlating with the rate of water infiltration, particularly for *A. icterica* (Capowiez et al., 2015).

Regardless of the ecological strategy considered, it remains challenging to link earthworm burrow creation to water infiltration due to the complex interaction between burrows and soil, and the numerous confounding factors at the field scale (e.g., management practices, climatic conditions). Schneider et al. (2018) conducted a unique field study investigating the links between earthworm abundance, burrows and water flow at large spatial (catchment) and temporal scale (1 year). While showing a good correlation between both earthworm abundance and burrow system and hydrology, the main driving force remained the soil moisture, and thus seasonal effects. Despite the lack of robust field data, we can realistically expect that in regions with intense rain events, burrows of epi-anecic species are of primary importance, followed by those of anecic earthworms. Even so, anecics form more compacted burrow walls (due to their reuse of the burrows), which might limit water infiltration (Bastardie et al., 2002). When rain events are less severe and soils are not flooded, burrow connectivity becomes of the utmost importance and the entire burrow system can improve the efficiency of water infiltration. Interestingly, Sammartino et al. (2012, 2015) were able to directly observe water flow within active macroporosity, which refers to the network of macropores where preferential water flow takes place, including earthworm burrows. They accomplished this by utilizing a rain simulator situated within a medical scanner and conducting repeated scans of a natural soil core. Sammartino et al. (2012, 2015) demonstrated that despite the active macropores in the form of earthworm burrows represented less than 10% of the soil porosity, the vertical continuity of these connected structures enabled a high contribution to the water infiltration (as rivulets along the burrow walls).

In addition to the effect of burrows on water infiltration, casts also have a higher water holding capacity than the surrounding soil. This can be explained by the preference of earthworms for fine mineral particles and OM (McDaniel et al., 2015) as well as the specific porosity of casts (Hallam et al., 2021; Stockdill and Cossens, 1969). Soil water retention is classically assessed using small soil cylinders (100 cm^3) and the values cannot be easily extrapolated to the soil profile, which limits its use in an agronomic context. Fig. 5 shows the results of a unique experiment testing the effect of

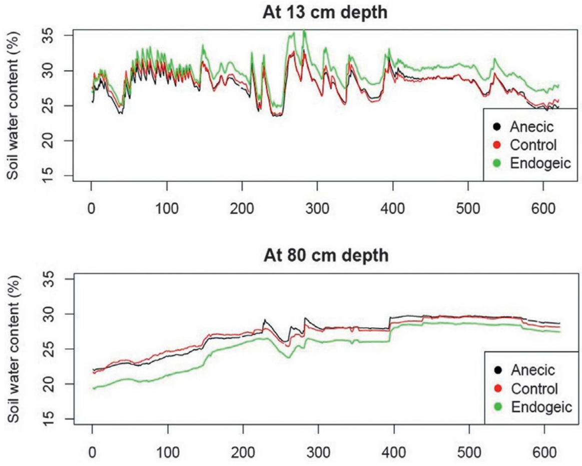

Fig. 5 Effect of earthworms on soil water content. The soil water content was measured daily at two depths (13 and 80 cm) in soil macrocosms (5 m^3 each, height = 2 m) of the Ecotron facility containing with either anecics, endogeics or without earthworms (control). Climate (rain and temperature) was simulated according to the data recorded in Rennes (France) a year before.

earthworms on soil water content. Twelve macrocosms (5 m^3 each, height = 2 m) were incubated for 3 years with three wheat cycles at the Montpellier Ecotron facility (https://www.ecotron.cnrs.fr/) with either anecics (100 g m^{-2}), endogeics (55 g m^{-2}) or without earthworms. Soil water content was recorded every hour using TDR sensors at two depths (13 and 80 cm). The results showed that endogeic species had the greatest influence on soil water content: an increasing effect at 13 cm depth and a decreasing effect at 80 cm. Anecic species had a limited effect. From this study it may be concluded that endogeic species have a beneficial effect on the water distribution in the soil profile, leading to a greater water availability to plants in the topsoil.

3.2.2 Soil aeration, compaction and erosion

Contrary to water infiltration and retention, the effect of earthworms on soil aeration has received less attention, perhaps because this is not often limiting crop growth (exceptions being compacted or anoxic soils; Kretzschmar and Ladd, 1993). Yet, it is an emerging topic in the debate on earthworms' impact on GHG emissions (see Section 8). In essence, the factors influencing soil aeration and water infiltration are the same, i.e., burrow continuity and connectivity to the atmosphere. Shipitalo and Gibbs (2000) demonstrated that *L. terrestris* burrows were connected to tile drains by using smoke under field conditions. Capowiez et al. (2006) showed that applying the insecticide imidacloprid at environmentally realistic concentrations resulted in decreases in the length and continuity of burrows of *A. nocturna* and *A. icterica*. In turn, this reduced gas diffusion through the soil by approximatively 40%.

Soil compaction (an increasing threat for agricultural soils; Keller and Or, 2022) can limit both the abundance (Chan and Barchia, 2007) and activity (Capowiez et al., 2021) of earthworms. However, earthworms are also among the most important de-compacting agents (Drewry, 2006). For example, Capowiez et al. (2012) showed that earthworms were able to rapidly recolonize a highly compacted wheat field (1.6 g cm^{-3}), reaching the initial abundance of burrows and water infiltration rate after 2 years.

Finally, earthworms can have both positive and negative effects on soil erosion, mainly through the activity of epi-anecic and anecic species. On the one hand, they can limit erosion by promoting water infiltration and thus limit surface runoff. Bottinelli et al. (2021) recently demonstrated that the production of surface casts by anecic earthworms (dominated by *Amynthas adexilis)* in a Vietnamese catchment (35 t ha^{-1}) mainly contributed to the topsoil formation rather than erosion (3 t ha^{-1}). On the other hand, surface casts may be eroded in relatively steep areas or may play a role in surface sealing (crust formation) (Blanchart et al., 2004; Jouquet et al., 2008a; Le Bayon and Binet, 2001).

To conclude, earthworm bioturbation plays a central role in soil hydrophysical processes. By shaping soil structure earthworms also contribute to the creation and destruction of habitats for microorganisms, as discussed in the next section.

4. Earthworms and microbial communities

To analyze the effect of earthworms on microbial communities, it is possible to examine specific microsites such as the earthworm gut, casts, burrows, the entire drilosphere (i.e., the earthworm-affected soil) or by considering a composite sample comprised of multiple microsites. Given the focus of this review, this section will not consider the earthworm gut but the other microsites which have a considerable impact on soil microbial communities. Among these microsites, casts are the most extensively studied, as they can represent up to one-third of the soil volume (Lavelle, 1978) with a turnover rate of 1 or 2 months (Zangerlé et al., 2014).

4.1 Contrasting effects on microbial biomass and abundance

The effect of earthworms on microbial biomass is a long-lasting debate in soil ecology. Depending on the nature of the interaction between earthworms and microbes, a negative or positive effect can be hypothesized. Since earthworms are relatively large soil organisms, they can be considered potential predators of smaller ones, especially microbes. Therefore, they are considered as higher-level consumers in detritivorous trophic networks (De Ruiter et al., 1994; Hunt et al., 1987) and could be expected to decrease microbial biomass. Note that a decreased biomass is not in contradiction with an increased microbial production, as the recycling rate may be increased (Barot et al., 2007). In contrast to this view, earthworms can feed thanks to a close association with microbes, on which they sometimes rely for several enzymes required to degrade a given compound (Lattaud et al., 1998, 1999). Consequently, earthworm-microbe interactions have also been described as mutualistic (Lavelle et al., 1995).

A recent review of earthworm impact on microbial communities concluded that all the three ecological categories (epigeic, endogeic and anecic earthworms) can have either a positive, neutral or negative effect on microbial community biomass and abundance (Medina-Sauza et al., 2019) (Fig. 6A). The main difference between the different categories was that

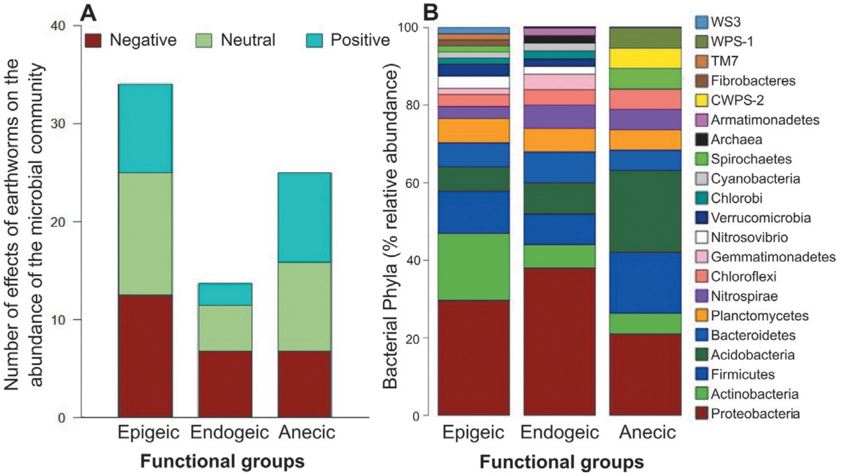

Fig. 6 Effect of earthworms on microbial abundance, according to their ecological category. (A) Number of publications depicting a negative, neutral or positive effect of earthworms on the abundance of microbial communities, considering 31 studies from 1986 to 2018. (B) Effect of earthworms on the relative abundance of microbial phyla, considering 11 peer-reviewed publications. *The figures were reproduced from Medina-Sauza, R.M., Álvarez-Jiménez, M., Delhal, A., Reverchon, F., Blouin, M., Guerrero-Analco, J.A., Cerdán, C.R., Guevara, R., Villain, L., Barois, I., 2019. Earthworms building up soil microbiota, a review. Front. Environ. Sci. 7, 81, are licensed under CC BY4.0 (Creative Commons—Attribution 4.0 International—CC BY 4.0).*

the proportion of studies reporting a positive (and neutral) effect of endogeic earthworms was lower than for epigeic and anecic earthworms. As the ecological categories do therefore not determine the direction of earthworm effect, species-specific bioturbation patterns could be a better predictor. In an experiment with a supply of litter at the top of the mesocosm, the microbial biomass was higher in the top 7 cm of the soil at low earthworm densities. However, at high earthworm density the microbial biomass was highest in the lower layer (7–14 cm) (Sheehan et al., 2008). In another experiment, lettuce was supplied at the top of the soil in the presence of *L. terrestris*, whereas it was mixed into the soil in the control treatment (Devliegher and Verstraete, 1997). The number of colony-forming units (CFUs) was 60–320 times higher in the casts and burrow walls than in the uningested soil in the 0–5 cm layer, whereas it was "only" 6–32 times higher in the deeper layer (5–22 cm), with intermediate bacterial counts for the control soil. When wheat straw compost was mixed into the soil, earthworms were responsible for a 130 mg C g^{-1} soil decrease in microbial biomass and a concomitant increase of available nutrients

(Zhang et al., 2000). By studying soils invaded by earthworms at contrasting intensities, Jang et al. (2022) found a homogenization of the upper soil layers in terms of abundance of bacteria and fungi (by qPCR on 16S rRNA gene and fungal ITS2 region, respectively): microbial abundances were as high in intermediate layers (2–10 cm) as in the upper layer of the soil (0–2 cm) in the presence of earthworms, but the deeper layer (10–20 cm) was not affected.

The reduction of microbial biomass in the presence of earthworms suggests that earthworms are first consuming microbial biomass. However, by subsequently putting copiotroph microbial taxa into close contact with degradable substrates, they might lead to an increase in microbial biomass in their casts and burrows. Interestingly, the effect of earthworms on microbial abundance extends beyond casts into the bulk soil. A higher abundance (measured by qPCR) was observed for bacteria and fungi in the bulk soil surrounding the cast compared to the bulk soil without earthworms (Blouin and Jacquiod, 2020). The drilosphere therefore extends beyond the physical aggregates produced by earthworms, likely due to the diffusion of labile compounds or the dispersal of microorganisms away from the cast.

4.2 Diversity and composition

The relationship between earthworm presence and microbial diversity is difficult to determine. This is partly due to the diversity of methods used to quantify microbial diversity: the number of cultivable species, the number of DGGE or T-RFLP fragments (fingerprint methods), DNA sequencing to get Operational Taxonomic Units (OTUs), and more recently Amplicon Sequence Variants. Similar to microbial biomass, there is no general trend in microbial diversity as a result of earthworm presence: positive, neutral and negative effects have all been observed (Medina-Sauza et al., 2019). As with microbial biomass, depth is an important factor. Jang et al. (2022) described an earthworm invasion where the richness of OTUs for archaea/bacteria at intermediate depth (2–10 cm) was similar to the richness in the upper layer (0–2 cm) in the presence of earthworms. However, in their absence richness was decreasing with depth.

The effect of earthworms on different taxa is clearer than that on microbial diversity. Fast growing species are over-represented in earthworm casts and burrows, for example members of the phyla Actinobacteria, Firmicutes, Proteobacteria, and especially members of the genus Pseudomonas known as Plant Growth Promoting Bacteria (see Section 7.2.4). By averaging the results of 11 peer-reviewed publications, Medina-Sauza et al. (2019)

concluded that among the dominant bacterial phyla (representing 70% of the taxa), endogeic, epigeic and anecic earthworms were particularly efficient in stimulating Proteobacteria, Actinobacteria and Firmicutes/Acidobacteria, respectively (Fig. 6B). Unfortunately, these variations in microbial species abundance are typically analyzed at only one single date, while temporal changes are likely to occur, e.g., during cast aging. In this regard, research on vermicompost is at the forefront in microbiota response to earthworms, since it is straightforward to study the succession of microbial communities during the composting process with earthworms, from fresh wastes up to the mature vermicompost. Gopal et al. (2017) reported that alpha diversity of bacteria (diversity within one entity) increased up to the 75th day of vermicomposting, and then decreased. Beta diversity (diversity across entities) and the distribution of the most abundant OTUs showed a different temporal trend. During the first half of the process (0–75 days), Acidobacteria, Actinobacteria, Chloroflexi, Gemmatimonadetes, Nitrospirae, Planctomycetes, TM7 and WS3 groups increased in relative importance, with Bacteroidetes and Proteobacteria decreasing. After the 75th day, the pattern reversed for Bacteroidetes and Proteobacteria, and Acidobacteria and Actinobacteria as well as others decreased. Some phyla such as the Firmicutes increased throughout the 105-day vermicomposting process (Gopal et al., 2017).

4.3 An earthworm core microbiota?

There are different ways to consider the association between a macroorganism, such as an earthworm, human or plant, and its microbial community. The holobiont has been defined as the macroorganism (plant or animal) together with its associated microbiota (Hammer et al., 2019), and has been proposed as *the* unit of selection in evolution (Theis et al., 2016; Zilber-Rosenberg and Rosenberg, 2008). Yet, many scientists disagree with this evolutionary interpretation (Moran and Sloan, 2015). One empirical piece of evidence which could help to decide between these views would be the presence of a *core microbiota*, i.e., a subset of the whole microbial community found in a host, which is faithfully associated with its host regardless of the environment in which the host lives. In this regard, a core microbiota has been found in humans (Turnbaugh et al., 2009) and plants (Lundberg et al., 2012). For animals, including earthworms, the picture looks less straightforward (Hammer et al., 2019). Looking for specific associations between nine earthworm species and the microbiota of their casts under controlled conditions, Aira et al. (2022) found that the cast microbiome was mainly composed of native bacteria (different from those of the diet) and were significantly different in structure among host species, supporting the idea that earthworms possess a core cast microbiota. In terms of taxa, Bacteroidetes, Actinobacteria and Proteobacteria were more abundant than in the diet of all the earthworm species, while Firmicutes varied among species. In a laboratory experiment looking at microbial communities in earthworm casts and the plant rhizosphere in three contrasting soils, 136 OTUs were systematically found in earthworm cast irrespective of the soil. This again supports the existence of a core microbiota, with a strong phylogenetic signal for Actinobacteria and Proteobacteria (Jacquiod et al., 2020). The authors also found a core microbiota for the plant-earthworm interaction, consisting of 106 OTUs that were different from those of the core microbiota of the earthworm or the plant alone. Building on the concept of niche construction (Odling-Smee et al., 1996) and extended phenotype (Dawkins, 1999), these results open new research questions about the possibility to consider the soil as a niche co-constructed by many macro- and microorganisms (see Section 11).

5. Earthworms, soil organic matter and carbon cycling

5.1 From food to cast: An adventurous route for the organic carbon

The main effect of earthworms in agricultural soils comes from their capacity to shape the soil structure (see Section 3) and stimulate certain microbial communities (see Section 4). This is mostly initiated by the feeding habit of earthworms that are semi-detrivores, i.e., feeding both on plant residues, other organic residues (detrivore), and soil (geophagus) (Fig. 7). The earthworm ingestion rate of organic residues can range from 2.6 to 80 mg dry matter g fresh mass^{-1} day^{-1}, regardless of the OM source and the earthworm species (Curry and Schmidt, 2007). When earthworms feed on plant residues from agricultural crops (i.e., corn leaves, alfalfa and clover), the ingestion rate narrows down to 6–13 mg dry matter g fresh mass^{-1} day^{-1} for *L. terrestris* and 18–52 mg dry matter g fresh mass^{-1} day^{-1} for *L. rubellus* (Shipitalo et al., 1988). As a result, it has been estimated that the litter mass loss is increased twofold in the presence of earthworms, at the global scale (Huang et al., 2020). However, due to the limited number of studies considering cropping systems in this meta-analysis, this conclusion may not necessarily be applicable to agricultural systems. As detailed in Curry and Schmidt (2007), the litter

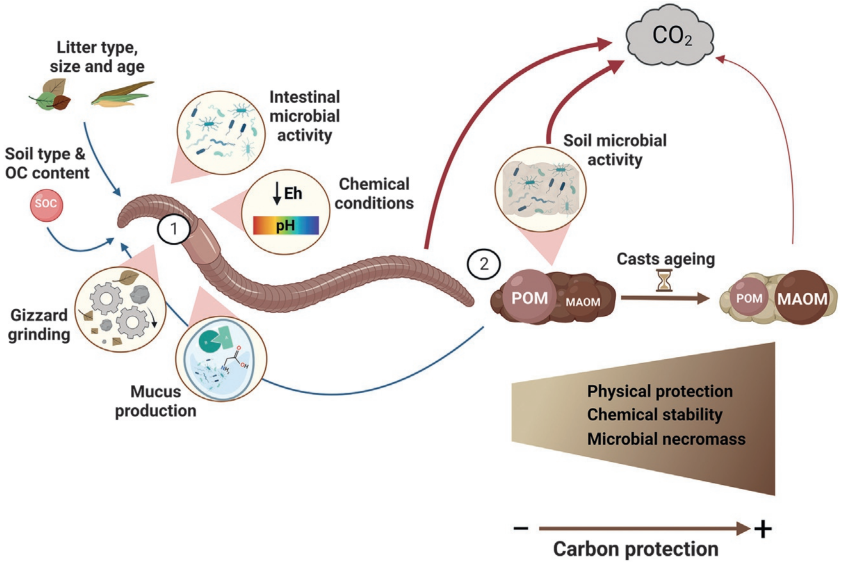

Fig. 7 Main mechanisms driving the effect of earthworms on the organic carbon (OC) cycling and carbon stabilization. The effect of earthworms on the OC cycling is driven by (1) processes occurring within the earthworm body and (2) processes happening within the earthworm-affected soil. (1) Internal processes include intestinal microbial activity, grinding within the gizzard, specific chemical conditions and production of mucus within the gut. (2) External processes include the microbial activity and the aging of the casts, which lead to a shift from a particulate organic matter (POM) to a mineral-associated organic matter (MAOM) dominated system. The enhanced protection of OC resulting from casts aging can be attributed to physical, chemical and biological mechanisms. Blue arrows represent specific ingestion habits of earthworms that can influence the effect of earthworms on OC protection. These include litter type, size and age, soil type and soil organic carbon (SOC) content and the capacity of some earthworm species to re-process casts. Red arrows represent carbon losses in the form of carbon dioxide (CO_2), regulated by earthworm respiration and microbial mineralization. *The figure is created with BioRender.com.*

ingestion rate by earthworms is strongly dependent on litter quality and palatability, together with environmental conditions driving the activity of earthworms. Earthworms tend to prefer organic residues that are rich in proteins and carbohydrates (Edwards et al., 2013), low in phenolic compounds, with relatively low C:N ratio (Hendriksen, 1990), relatively fine particle size (<1 mm) (Lowe and Butt, 2003) and colonized with microorganisms (Cooke, 1983; Moody et al., 1995; Wright, 1972).

The effect of earthworms on litter decomposition is mediated by their capacity to ingest soil, stimulating the fragmentation of litter in the gut.

In temperate arable soils, the amount of soil ingested by earthworm ranges between 0.7 and 3.3 g dry soil g fresh mass day^{-1} (Angst et al., 2022; Curry and Schmidt, 2007; Curry et al., 1995; Lavelle, 1988).

While the material ingested by the earthworm rapidly passes through the gut (1–20 h, depending on the species) (Barois et al., 1993; Brown, 1995; Brown et al., 2000), soil structures are ground in the gizzard and organic residues are fragmented (Barois et al., 1993) . The fragmentation of organic residues increases their surface area and thus their vulnerability to microbial decomposition (Lavelle and Martin, 1992). The activity of selected microbial communities is further enhanced by the specific chemical conditions in the gut (e.g., anoxic, pH close to neutral) and the presence of intestinal mucus in the earthworm gut that is made of readily degradable organic carbon (Drake and Horn, 2007; Martin et al., 1987). This results in high OC mineralization rates in the earthworm gut and in fresh casts (Binet et al., 1998; Lubbers et al., 2013a, 2017; Speratti and Whalen, 2008). Despite thorough food processing, the amount of carbon assimilated by earthworms is relatively low, with an estimated carbon assimilation rate ranging from 1% to 6% (Bohlen et al., 2004; Bolton and Phillipson, 1976; Cortez et al., 1989), although higher values (up to 19% of the OM) have been suggested for some species (e.g., *Pontoscolex corethrurus*), especially when found in tropical regions (Lavelle, 1988). Thus, most of the carbon ingested by earthworms is found back in their feces. According to Cortez et al. (1989), who performed an incubation experiment for 31 days with wheat straw and the earthworm *Nicodrilus giardi giardi*, more than 90% of the carbon ingested by earthworms is found back in the earthworm casts. While most of the carbon ingested by the earthworm is egested back in casts, the form and stability of the OM is altered compared to its initial status and evolve during cast aging.

5.2 Do earthworms decrease or increase organic carbon stability?

Do earthworms decrease or increase organic carbon stability? This question has animated debates in the earthworm research community in the last decade(s) (Lubbers et al., 2013a; Zhang et al., 2013). One promising way to disentangle the effect of earthworm on soil carbon cycling is to look at the feces they produce and compare their composition and structure to a soil that is not affected by earthworms (Bossuyt et al., 2005; Haynes and Fraser, 1998; Jégou et al., 2000; Jouquet et al., 2008b). Building on this concept, Coq et al. (2022) have recently proposed to use feces traits of detritivores, including earthworms, as a mean to predict their effect on OM turnover.

As earthworms feed on organic residues and soil with higher organic carbon (OC) contents (Curry and Schmidt, 2007), it is not surprising that the OC content in casts is higher compared with the surrounding soil (Brown et al., 2000), 48% higher according to the metanalysis by Van Groenigen et al. (2019). But is this OC stable in time? Despite the debates about earthworms and OC stability, there is a consensus on the fact that the time after cast production is a key parameter to disentangle the mechanisms driving OC stability within casts.

Earthworms increase litter decomposition and the mineralization of indigenous SOM due to the intense grinding of organic residues and soil, and the enhanced microbial activity. The OC mineralization that starts in the earthworm gut continues in fresh casts that have been produced for a few days or weeks (Lavelle and Martin, 1992; Mariani et al., 2007), at varying rates according to species-specific microstructural traits (Le Mer et al., 2022). Carbon mineralization in fresh casts is favored by the high water and mucus contents which promotes microbial activity (Martin et al., 1987), as well as the relatively low structural stability (Marinissen and Dexter, 1990) that prevents the physical protection of carbon against decomposition.

The stabilization of OC mainly occurs while casts are aging a few months or years after their production (Bottinelli et al., 2020b; Brown et al., 2000; Martin, 1991), assuming casts are not degraded or re-processed (Bottinelli et al., 2021; Le Mer et al., 2021). The routes resulting in a potential increase of soil carbon persistence can be physical (i), chemical (ii) and biological (iii) (Fig. 7).

(i) As casts are aging and drying, clay-polyvalent cation-OM linkages increase (Shipitalo and Protz, 1989) and soil particles are attracted as a result of the tension produced by water menisci and the rise of water matric potential (Marinissen and Dexter, 1990). These physical processes promote the formation of stronger organo-mineral and mineral-mineral bonds (Marinissen and Dexter, 1990; Shipitalo and Protz, 1989). Vidal et al. (2019) showed that the OC contribution to mineral-associated organic matter (MAOM) increased from 58% to 85% during cast aging (8–54 weeks) of *L. terrestris* (Fig. 8A, B). As a result, the protection of carbon within macroaggregates and microaggregates could be enhanced (Bossuyt et al., 2005; Fonte et al., 2007; Pulleman et al., 2005; Vidal et al., 2019), leading to a substantial reduction in carbon mineralization (Brown et al., 2000; Zhang et al., 2013). According to multiple studies, carbon is primarily incorporated and stabilized within macroaggregates (Bossuyt et al., 2006; Fahey et al., 2013; Lubbers et al., 2017; Zhang et al., 2013). Additionally, after

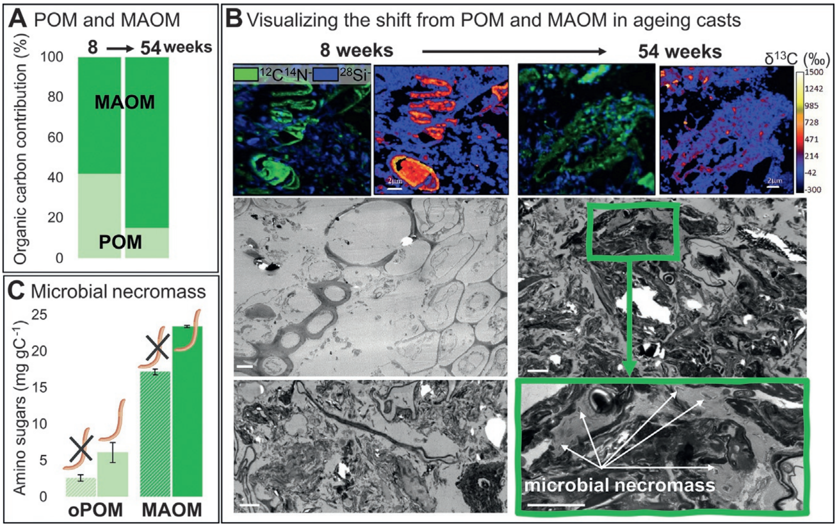

Fig. 8 Drivers of carbon stabilization within earthworm casts. (A, B) The shift from particulate organic matter (POM) to mineral-associated organic matter (MAOM) in aging casts (from 8 to 54 weeks) as depicted using (A) a density fractionation approach and (B) nano and microscale imaging approaches with nanoscale secondary ion mass spectroscopy (NanoSIMS) (colored measurements) and scanning electron microscopy (SEM) (black and white measurements). Microbial necromass could be identified on the SEM measurements of aging casts at 54 weeks. (C) Earthworms increase microbial-derived amino-sugars (biomarkers used as a proxy for microbial necromass) in MAOM and small occluded POM (oPOM), two SOM pools that are considered to be particularly stable. (B) The scale corresponds to 2 µm. (C) Bars indicate standard error. *Panels (A) and (B) are adapted from Vidal, A., Watteau, F., Remusat, L., Mueller, C.W., Nguyen Tu, T.-T., Buegger, F., Derenne, S., Quenea, K., 2019. Earthworm cast formation and development: a shift from plant litter to mineral associated organic matter. Front. Environ. Sci. 7, with TEM and NanoSIMS figures merged, are licensed under CC BY 4.0 (Creative Commons—Attribution 4.0 International—CC BY 4.0). Panel (C) is adapted from Angst, G., Mueller, C.W., Prater, I., Angst, Š., Frouz, J., Jílková, V., Peterse, F., Nierop, K.G., 2019. Earthworms act as biochemical reactors to convert labile plant compounds into stabilized soil microbial necromass. Commun. Biol. 2, 1–7, with the amino sugars from macroaggregates and microaggregates being summed and with modified colors, is licensed under CC BY 4.0 (Creative Commons—Attribution 4.0 International—CC BY 4.0).*

the destruction of existing microstructure in the earthworm gut (Shipitalo and Protz, 1989; Six et al., 2004), the combined effect of microbial activity and mineral properties in casts may also serve as nuclei for the formation of new microaggregates, effectively trapping carbon (Angst et al., 2019; Vidal et al., 2019).

(ii) Organic molecules are also subject to chemical changes while casts are aging. While fresh casts primarily consist of easily decomposable OM (Bottinelli et al., 2020b; Guggenberger et al., 1996; Vidal et al., 2016a), the OM in aging casts is thermally more stable (Bottinelli et al., 2020b) and organic compounds present higher degree of oxidation (Vidal et al., 2016a) that could promote their stabilization in casts by adsorbing on mineral surfaces (Chefetz and Xing, 2009; Eusterhues et al., 2003; Rumpel et al., 2004). However, it also appears that the chemical characteristics of old casts (produced for more the 2.5 years) resembles non-biogenic aggregates (Angst et al., 2017). Therefore, while the chemical composition of the OM ingested by earthworms tends to control the fate of OC in fresh casts (Vidal et al., 2019), the long-term stabilization of OC in casts seems mainly connected to physical protection (Angst et al., 2017).

(iii) While aging, casts can also be rapidly colonized by microorganisms that were not necessarily favored during the gut transit (e.g., fungi) (Brown, 1995; Tiwari and Mishra, 1993; Vidal et al., 2016b), which can also participate to further enhance the physical stability of casts (Marinissen and Dexter, 1990). For example, the hyphae of fungi can enhance soil structure formation through enmeshment and pressure exerted on soil particles (Baumert et al., 2018; Rillig and Mummey, 2006; Vidal et al., 2018). Microorganisms also produce extracellular polymeric substances (EPS) that can serve as binding agents for the build-up of MAOM and the formation of aggregates (Costa et al., 2018; Kopittke et al., 2020). While living microbial biomass plays an essential role in the cycling of carbon in earthworm casts, recent studies have also highlighted the key contribution of microbial necromass in aging earthworm casts (Angst et al., 2019, 2022; Nguyen Tu et al., 2020; Vidal et al., 2019). Microbial necromass is increasingly recognized as a key SOC pool (approx. 50%) in arable soils (Angst et al., 2021; Kallenbach et al., 2015; Liang et al., 2019; Miltner et al., 2012; Sokol et al., 2022). Experimental evidence shows that earthworms could increase microbial-derived amino-sugars (biomarkers used as a proxy for microbial necromass) by 37–143% (Angst et al., 2019, 2022; Mora et al., 2003). Angst et al. (2019) demonstrated that the activity of earthworms favored the build of microbial necromass in MAOM and small occluded particulate organic matter (oPOM) (Fig. 8C). These two SOM pools (MAOM and oPOM) are considered to be particularly stable (Cotrufo and Lavallee, 2022; Lehmann and Kleber, 2015;

Witzgall et al., 2021), leading authors conclude that earthworms foster the formation of persistent carbon (Angst et al., 2019). The increase of MAOM during cast aging coincides with the replacement of particulate organic matter (POM) by porosity, and thus oxygen that provide favorable conditions for microbial activity (Kravchenko et al., 2015; Le Mer et al., 2022; Puche et al., 2022), which will produce microbial necromass with time. Thus, a more thorough understanding of the mechanisms driving carbon stabilization within casts emerges by investigating the distribution of carbon within different SOM pools (and not exclusively within aggregates) and tracking the build-up and fate of microbial necromass within these pools.

5.3 What about the net effect of earthworms on OC at larger scale?

From the previous section, it appears clear that earthworms create OC hotspots in soils and that this carbon could be persistent in time. Yet, to understand the effect of earthworms on OC cycling from an agronomical perspective, we need to associate mechanistic approaches to holistic/large scale and longer-term approaches (Andrén et al., 2001; Coq et al., 2007; Lavelle and Martin, 1992). For that, we should investigate the net effect of earthworms on OC, being the result of both mineralization and protection mechanisms, at the soil profile and field scale. At the field scale and/or longer term, earthworms have no effect or even decrease SOC content and stocks (Alban and Berry, 1994; Chevallier et al., 2001; Desjardins et al., 2003; Don et al., 2008; Pashanasi et al., 1996; Zhang et al., 2013). In addition, most earthworm effects on OC dynamics tend to be concentrated in the topsoil, with no or limited effects in the subsoil (Andrén et al., 2001; Fahey et al., 2013; Lubbers et al., 2017; Vidal et al., 2017). Certain deep-burrowing earthworm species can still affect subsoil OC by digging burrows that form preferential flow for the transfer of fresh OC in the subsoil, without significantly affecting stocks (Don et al., 2008).

The fact that earthworms do not affect SOC stocks in arable soils does not mean that earthworms could not play a key role in increasing or maintaining soil carbon stability. Indeed, earthworms have the capacity to change the stability of OC in soils (see Section 5.2), which affects the persistence of carbon at longer time scales. Yet, the magnitude of earthworm-induced carbon stabilization is particularly challenging to quantify at the field scale, especially in the presence of growing plants. Indeed, earthworms have been shown to increase plant growth (see Section 7), and thus organic carbon inputs in the form of litter and rhizodeposits. This indirect plant-induced effect of earthworms on soil carbon is poorly understood. To conclude, elucidating the net role of earthworms on carbon cycling at the field scale first requires some efforts to tackle the interactive plant-microorganism-earthworm effects on stable OC pools (MAOM, oPOM, microbial necromass), in topsoil and subsoil.

6. Earthworms and nutrient cycling

Earthworms have a substantial effect on carbon cycling through the ingestion and transformation of OM (see Section 5). Given that OM consist not only of carbon but also of macro- and micronutrients, it is not surprising that earthworms also affect nutrient cycling. Due to their feeding behavior, earthworms concentrate nutrient-rich material into their casts, thus creating hotspots of soil fertility with higher total nutrient content (+40–46% for total N and P in casts) (Fig. 9). This nutrient concentration effect is coupled

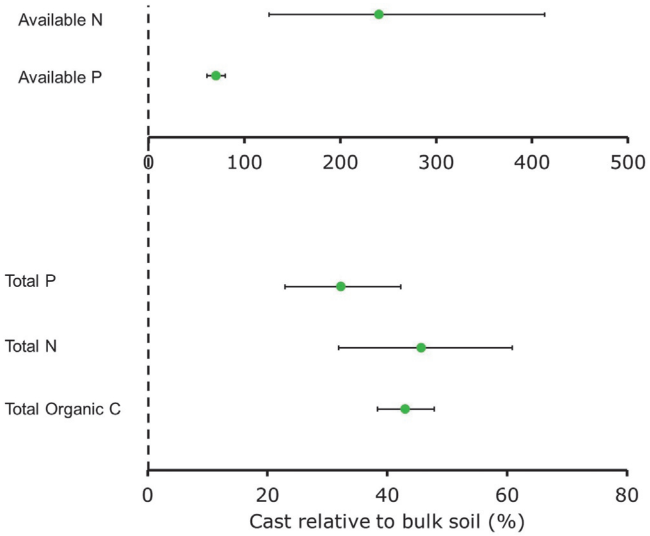

Fig. 9 Earthworm cast fertility, results of a meta-analysis. The earthworm effect is expressed relative to the surrounding bulk-soil. As earthworms cannot create carbon (C), nitrogen (N) and phosphorus (P), the increase in total concentrations is the result of preferential feeding on nutrient-rich organic matter. The increase in available N and P mostly reflects the biochemical transformations occurring in the earthworm gut. *This figure is adapted from Van Groenigen, J.W., Van Groenigen, K.J., Koopmans, G.F., Stokkermans, L., Vos, H.M., Lubbers, I.M., 2019. How fertile are earthworm casts? A meta-analysis. Geoderma 338, 525–535.*

to a transformation effect in the gut and casts of earthworms that mainly results in increasing nutrient availability (Van Groenigen et al., 2019). While we can anticipate most nutrients to undergo concentration and transformation through the action of earthworms, the pathways leading to this outcome differ between nutrients such as nitrogen (N) and phosphorus (P).

6.1 Earthworms create transient hotspots for mineral nitrogen

Mineral N content is typically higher in the earthworm gut and earthworm-affected soil as compared to the surrounding soil (Decaëns et al., 1999; Parkin and Berry, 1994; Parle, 1963; Wilcox et al., 2002). A meta-analysis showed that this content is on average 241% higher in casts than in the surrounding soil (Fig. 9) (Van Groenigen et al., 2019). The origin of these increased mineral N levels can be a direct result of mineralization of organic N (Parkin and Berry, 1994; Syers et al., 1979) and an indirect result through earthworm urine and mucus (Needham, 1957; Whalen and Parmelee, 1999), or the tissue of dead earthworms (Curry and Byrne, 1992; Hill et al., 2019; Schmidt and Curry, 2001). The mineralization rate of organic N within the earthworm gut varies according to the earthworm species (Postma-Blaauw et al., 2006; Sheehan et al., 2006), the food sources (Parkin and Berry, 1994; Sheehan et al., 2006), the soil types (Brown, 1995; Marhan and Scheu, 2006), and the agriculture management practices (e.g., nutrient amendments) (Helling and Larink, 1998; Subler et al., 1998), with estimates of earthworm-induced N mineralization ranging between <30 to $90\,\mathrm{kg\,N\,ha^{-1}\,year^{-1}}$ (Anderson et al., 1983; Curry et al., 1995; Willems et al., 1996). The mineral N produced will be partly assimilated by earthworms, with a N assimilation efficiency reaching 10–30% (Binet and Trehen, 1992; Bouché et al., 1997; Whalen and Parmelee, 1999), which is substantially higher compared to carbon assimilation rates (see Section 5.1). The N assimilated by earthworms is rapidly turned over (1–1.7% of earthworm tissue N per day) (Barois et al., 1987; Curry et al., 1995; Hameed et al., 1994; Whalen and Parmelee, 1999) through the excretion of mucus and urine that corresponds to $88\text{–}328\,\mu\mathrm{g\,N\,g}$ live $\mathrm{worm^{-1}\,day^{-1}}$, depending on the species (Needham, 1957; Whalen and Parmelee, 1999). The amount of N mineralized from dead earthworms can also be significant, and has been estimated to be around $7.5\,\mathrm{kg\,N\,ha^{-1}\,year^{-1}}$ at the field scale (Curry and Byrne, 1992; Schmidt and Curry, 2001).

These mechanisms lead initially to higher ammonium (NH_4^+) content in earthworm-affected soil (Subler et al., 1998). For example, fresh casts of the tropical anecic earthworm *Martiodrilus carimaguensis* contained ten times more NH_4^+ than the surrounding soil (Decaëns et al., 1999). Ammonium is generally rapidly converted to nitrate (NO_3^-) through nitrification during the first week after cast production, and diffuses into the surrounding soil during the following weeks (Decaëns et al., 1999; Xue et al., 2022). In a system with low N inputs, the produced N could be immobilized and remain potentially stable within aggregates (Fonte et al., 2007; Sheehy et al., 2019). Yet, the higher N mineralization rates together with the formation of water preferential flows in the presence of earthworms could increase N leaching in arable soils, particularly when managed conventionally (Amador et al., 2006; Domínguez et al., 2004; Fonte et al., 2007; Subler et al., 1997; Wang et al., 2005). The presence of earthworms can also significantly reduce these losses by promoting increased N uptake by plants (see Section 7), if mineralization coincides with periods of active plant growth (Curry et al., 1995). For example, Shutenko et al. (2022) have recently proposed, based on a lab and field experiment using a ^{15}N enrichment approach, that the N contained in earthworm mucus could be directly and quickly (<72 h) taken up by plants, possibly in the form of organic N. The importance of this rapid transfer of nutrients from earthworm-products to plants still needs to be determined. To conclude, casts are a short-term hotspot for mineral N, and a significant share of the mineral N released in cast can rapidly be mineralized, taken up by the plant, immobilized with the microbial communities, entrapped within aggregates and/or leached out (Lavelle and Martin, 1992; Van Groenigen et al., 2019).

6.2 Earthworms increase phosphorus availability through multiple pathways

Phosphorus is the most limiting nutrient for plant growth after N, but is less mobile and available in the soil (Hinsinger, 2001). Given that earthworms influence several factors that determine P availability (e.g., pH, metal concentration, microbial activity), it is not surprising that they play a role in increasing soil P availability (Le Bayon and Milleret, 2009), especially in low-P arable soils. Similar as for N, potentially available P content is higher in casts compared to the surrounding soil (Brossard et al., 1996; Sharpley and Syers, 1976), on average 84% higher (Van Groenigen et al., 2019) (Fig. 9), with variations among earthworm species (Vos et al., 2019).

There are several biochemical pathways through which earthworms can affect P availability to the plant (Fig. 10). As for the N cycling, the effect of earthworms on the microbial activity can increase P availability through

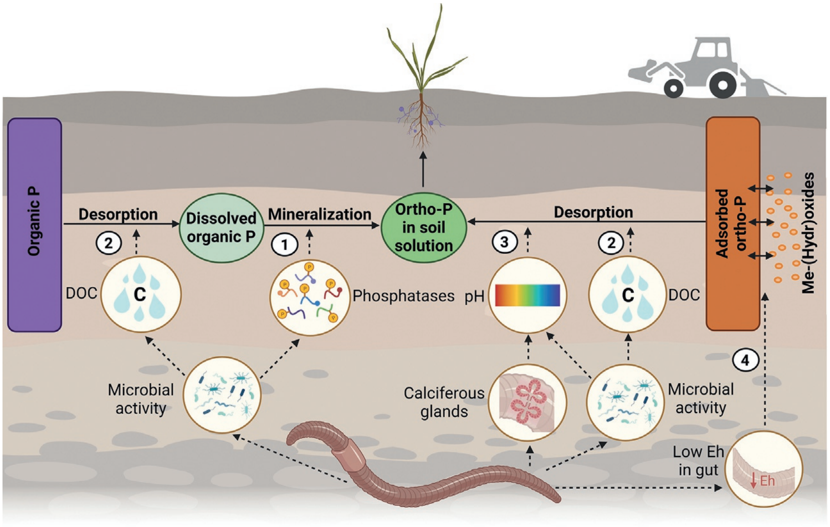

Fig. 10 Earthworms can affect phosphorus (P) availability to the plant (defined as orthophosphates, ortho-P, in soil solution) through several biochemical pathways. (1) Their stimulation of microbial activity can lead to increased production of phosphatases and subsequent mineralization of organic P. (2) Microbial stimulation may also lead to increases in DOC in the soil, leading to competitive desorption of organic as well as inorganic P adsorbed to the soil solid phase. (3) Strong changes in pH in earthworm casts will affect P speciation and adsorption. Finally, (4) the low redox potential in the earthworm gut may lead to a decrease of the reactive surface area of metal(Me) (hydr) oxides, including iron-(hydr)oxides and thereby a decrease in adsorbed ortho-P. *The figure is created with BioRender.com.*

stimulation of the production of phosphatases, i.e., enzymes specialized in P mineralization. Several studies have highlighted higher phosphatase concentrations in the earthworm gut and in earthworm-affected soil or wastes (Buck et al., 1999; Cao et al., 2015; Flegel and Schrader, 2000; Hoang et al., 2016, 2020; Hoeffner et al., 2019; Le Bayon and Binet, 2006; Satchell and Martin, 1984; Tao et al., 2009), resulting in temporarily higher available P content (Le Bayon and Binet, 2006).

However, the effects of earthworms on P availability go further than direct mineralization. Earthworms can also increase the amount of dissolved organic carbon (DOC) in soil by stimulating microbial activity, OM mineralization and excreting mucus (Barois and Lavelle, 1986; Ros et al., 2017; Vos et al., 2014). As organic/inorganic P and DOC compete for the same binding sites, particularly the reactive surfaces of soil metal (hydr)oxides (Morel et al., 2000; Schoumans and Groenendijk, 2000), the increase of DOC content can promote the temporal desorption of the P previously adsorbed on the soil solid phase (Ros et al., 2017). The change in chemical sorption equilibria induced by higher pH in the presence of earthworms will also affect the rate of competitive desorption (Ros et al., 2017; Vos et al., 2014).

Vos et al. (2022a) have recently proposed a new pathway for earthworm-induced increased P availability. In iron(Fe)-(hydr)oxide-dominated soils, earthworms decrease the reactive surface area of metal-(hydr)oxides and thus reduce the binding capacity of orthophosphate-P at the surface of these minerals (Fig. 11). This could be initiated by the formation of Fe^{2+} under the anoxic conditions of the earthworm gut, acting as a catalyst for the aging

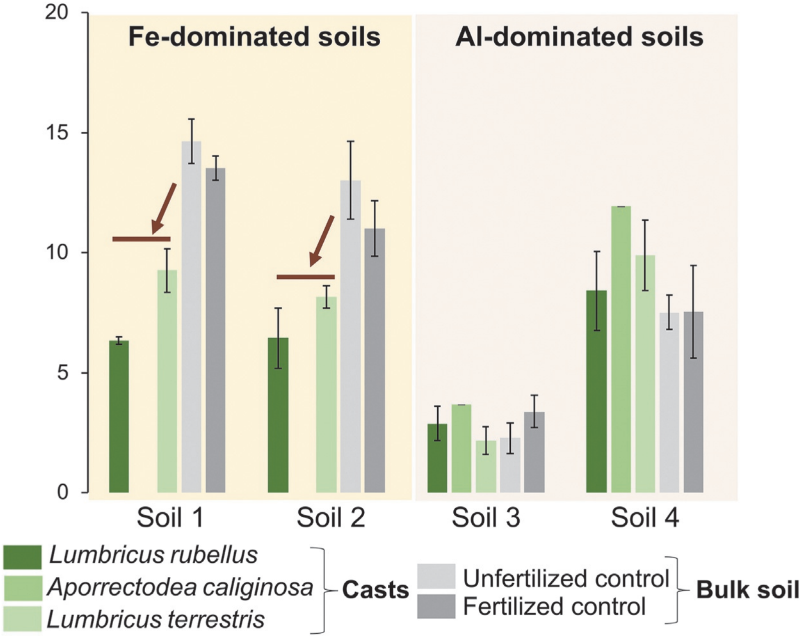

Fig. 11 Reduced reactive surface area in earthworm casts in iron-(hydr)oxide dominated soils (Fe-dominated soils, soils 1 and 2). The reduced conditions in the earthworm gut promote the aging of iron-(hydr)oxide particles, increasing their size and decreasing their reactive surface area. In aluminium-(hydr)oxide dominated soils (Al-dominated soils, soils 3 and 4), which are not redox-sensitive, this effect does not occur. The reduction in reactive surface area leads to a decrease in the amount of adsorbed orthophosphates and thereby to an increase in phosphorus availability. *This figure is adapted from Vos, H.M., Hiemstra, T., Lopez, M.P., van Groenigen, J.W., Voegelin, A., Mangold, S., Koopmans, G.F., 2022. Earthworms affect reactive surface area and thereby phosphate solubility in iron-(hydr) oxide dominated soils. Geoderma 428, 116212, only showing data for reactive surface with additional arrows indicating the decrease in reactive surface area and with modified colors, is licensed under CC BY 4.0 (Creative Commons—Attribution 4.0 International—CC BY 4.0).*

process of Fe-(hydr)oxides, resulting in the decrease of their reactive surface area (Drake and Horn, 2007; Zhou et al., 2019). This mechanism emerged as one of the main pathways for earthworm-induced P availability, together with mineralization within the earthworm gut (and more important than pH effects or competitive desorption with DOC). This new pathway was not observed in Al-dominated soils (Al not being redox sensitive) where the increase of available P was mainly determined by the mineralization of OM (Vos et al., 2022a). The pathway could be of utmost importance for soils that combine a high phosphorus retention, and thus a strong shortage of available P, with a substantial Fe-(hydr)oxide content, as it is the case in some tropical arable soils (Batjes, 2011; Sanchez et al., 2003).

As for nitrogen, the earthworm-induced increase of available P is time and space dependent (Le Bayon and Milleret, 2009), and could eventually result in increased P losses (Le Bayon et al., 2002; Sharpley and Syers, 1976), especially in arable soils that have reached P saturation (Cordell et al., 2009; Elser and Bennett, 2011). Earthworm-induced phosphorus availability decreases rapidly, i.e., within a few days or weeks depending on the earthworm species and food source (Le Bayon and Binet, 2006; Lopez-Hernandez et al., 1993), making it crucial for plant roots and/or mycorrhizal fungi to reach these transient hotspots in time to benefit from the increase in P availability.

6.3 Earthworms and the cycling other elements

Studies investigating the effect of earthworms on the cycling of elements other than nitrogen and phosphorus are scarce. There are indications that the content and availability of other macronutrients including potassium, calcium and magnesium also increases within earthworm gut and earthworm-affected soil (Adejuyigbe et al., 2006; Asawalam and Johnson, 2007; Basker et al., 1992, 1993; Carpenter et al., 2007; Ganeshamurthy et al., 1998; Jouquet et al., 2008a). These nutrients could be released through the decomposition of OM (Basker et al., 1993) and/or the weathering of soil minerals during the passage within the earthworm gut (Carpenter et al., 2007). For calcium, the higher content could also be associated to the production of calcium carbonate granules from calciferous glands of earthworms (Brinza et al., 2014; Canti and Piearce, 2003; Versteegh et al., 2014; Wiecek and Messenger, 1972), although the biological function of this process remains unclear (Briones et al., 2008). There is also increasing evidence that earthworms could increase soil silicon availability, a non-essential nutrient with beneficial effects on plant stress resistance (Bityutskii et al., 2016; Hu et al., 2018). Indeed, earthworm guts have been shown to shelter substantial and diverse communities of silicate solubilizing bacteria that participate in silicon weathering and dissolution (Hu et al., 2018). Earthworms can also increase the availability of essential micronutrients such as zinc, manganese and/or iron in soil (Bityutskii et al., 2012; Dehghanian et al., 2018). The pH being important for the speciation of many micronutrients such as zinc and copper, it can be expected that the earthworm-mediated change of pH is an important pathway to explain this increase. If earthworms have the potential to increase the availability of essential or beneficial nutrients in the soil, they can also increase the availability of potentially toxic non-essential heavy metals, such as cadmium, lead or chromium (Sizmur and Richardson, 2020; Wen et al., 2004). Interestingly, arsenic being a toxic anion with similar chemical properties as P, the earthworm-mediated pathways promoting P availability (see Section 6.2) could also be true for arsenic. Increasing the availability of toxic elements could be seen as an advantage in the context of remediation (see Section 9) but could also represent a risk for agricultural crops in certain circumstances, e.g., in soils with high contents of potentially available non-essential heavy metals.

7. Earthworms and plants

7.1 Earthworms enhance plant growth

The insight that earthworms are good for soil fertility and therefore plant growth is already old (see Section 2). To add to the historical sources already mentioned before, in 1789 the English naturalist Gilbert White stated that:

> "… worms seem to be the great promotors of vegetation, which would proceed but lamely without them…."
>
> ***White (1789)***

The main pathways through which earthworms increase plant growth have been known for a long time as well. Gilbert White continues:

> "… [worms promote vegetation] …by boring, perforating, and loosening the soil, and rendering it pervious to rains and the fibers of plants; by drawing straw and stalks and twits into it; and, most of all by throwing up such infinite numbers of lumps of earth called worm casts, which being their excrement, is a fine manure for grain and grass."
>
> ***White (1789); underlining added***

In modern terms, we would say: they improve soil structure, and they improve soil fertility through mineralization of OM. Without a doubt, these are still the main pathways discussed today (see Sections 3 resp. Sections 4 and 6), with new mechanisms still being discovered (see for example the shift in the chemical adsorption of phosphorus in earthworm casts, Fig. 11, Section 6.2). However, more recently it has been recognized that there are other pathways as well, relying more on interactions between soil organisms (Fig. 12). The landmark papers by Brown et al. (1999, 2004) and Scheu (2003) list five pathways through which earthworms can positively affect plant growth:

1. their consumption of OM and other organisms such as bacteria or fungi results in the mineralization of different nutrients;
2. their effect on soil structure associated with the building of burrows and casts, which affects the porosity and modifies the equilibrium between water and air in pore space;
3. the control of pathogens and parasites;

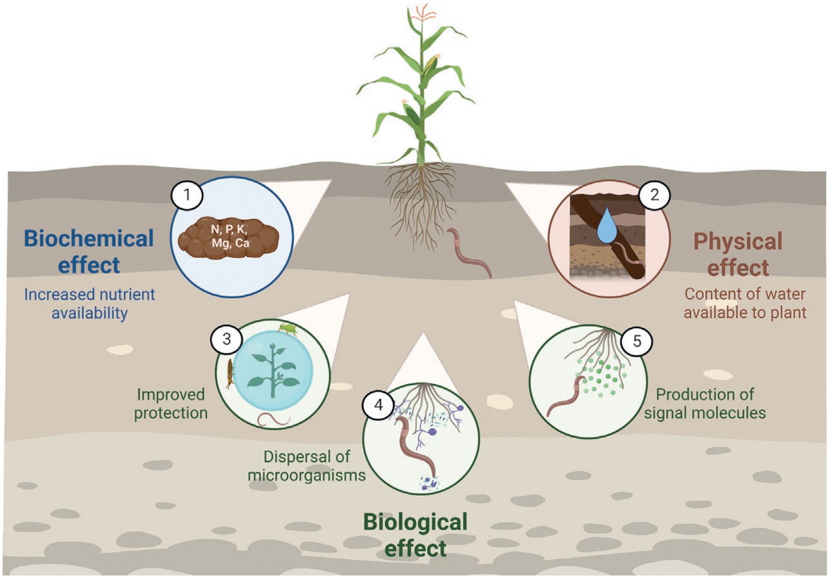

Fig. 12 Possible biochemical, physical and biological pathways explaining the effect of earthworms on plant growth. Earthworms can (1) increase the mineralization of nutrients and therefore enhance their availability; (2) affect the soil structure through their burrowing and casting activities, consequently affecting e.g., the soil water content, water flow and root growth; (3) improve plant protection against parasites and pathogens; (4) feed on and disperse beneficial microorganisms; (5) produce signal molecules. *The figure is created with BioRender.com.*

4. the dispersal of symbionts or other beneficial microorganisms;
5. the production of hormone-like compounds, which could directly interfere with plant growth, development and immunity

Although the first two points mostly align with the pathways that were already highlighted centuries ago, the last three pathways are mostly the result of painstaking research over the last decennia. Of course, to some extent isolating these pathways creates an artificial construct as they are likely to interact. For example, the effect of earthworms on soil structure (see Section 3) is very likely to have an effect on the composition of the microbial community (see Section 4). In turn, this will have consequences for SOM composition (see Section 5), nutrient cycling (see Section 6) and hormone-like compounds production. Yet, optimizing the use of earthworms in agriculture necessarily requires having an idea on the relative importance of these mechanisms, or no predictive model could ever be developed. Below, we will shortly discuss all five pathways.

7.2 Five pathways

7.2.1 Nutrient availability

Based on the "all minus one" approach, where only one factor is removed to study the effect of earthworms on it, Blouin et al. (2006) explored the effect of earthworms along a gradient of mineral N availability. If enhanced N mineralization would be the main mechanism involved in the stimulatory effect of earthworms on plant growth, the earthworm effect should be most pronounced when the N availability in soil is low. Conversely, the beneficial earthworm effect should disappear when the soil has an excess of mineral N, since the extra N provided by earthworms would not lead to additional benefits. However, they found using non-linear regression that a significant positive earthworm effect was observed along the whole gradient, supporting the idea that the main mechanism involved in earthworm effect on plant growth was not N mineralization. This observation was confirmed in a study involving two earthworm species (one anecic and one endogeic), three plant species, two soils (one poor and one rich) and two N fertilization levels (presence and absence) (Laossi et al., 2009), which also showed a constant effect of earthworms regardless of N fertilization. Meta-analyses showed that the beneficial effect on plant growth due to earthworms was no longer significant when N supply exceeds 30 kg N ha^{-1} $year^{-1}$ (Van Groenigen et al., 2014) or was reduced in the presence of vermicompost (compost produced by epigeic earthworms), from +38% when fertilizer was applied as compared with +14% when it was not (Blouin et al., 2019).

7.2.2 Soil structure

By comparing the effect of earthworms on plants grown under conditions of adequate water supply compared to drought, it is possible to evaluate if water availability plays a role in the positive effect of earthworms on plant growth. For example, a recent study by Hodson et al. (2023) observed a positive effect of earthworms on plants under conditions of drought. However, the opposite can also be true: Blouin et al. (2007) describe an experiment where an endogeic earthworm that had a positive effect in conditions of adequate water supply induced a negative effect on plant under drought conditions. Because of a reduced soil water storage capacity in the presence of earthworms, plants grown with earthworms showed an earlier stomatal closure and decrease in photosynthetic CO_2 assimilation, resulting in a lower biomass than plant under drought conditions without earthworms. Under very different conditions, i.e., during extreme rainfall events which tend to saturate the soil and remove the air necessary for root respiration, anecic earthworms helped alleviating the negative effect of water logging on plant growth (Andriuzzi et al., 2015). This was likely due to a faster drop in soil moisture content made possible by the increased continuous vertical macropores which favor drainage. The contrasting effects described above call for an in-depth analysis of the effect of earthworms on soil structure (see Section 3) to predict the effect of earthworms on the water available for plant growth.

7.2.3 Control of parasites and pathogens

Earthworms have been found to be particularly beneficial to plant growth in situations where plants are exposed to pathogens or parasites. Earthworms can influence plant–herbivore interactions, for both aboveground and belowground herbivores (Wurst, 2010). For above-ground herbivores such as aphids, a first hypothesis was that earthworms increased nutrient availability to the plant, leading to more palatable and rich plant tissues for the herbivores. However, negative effects of earthworms on aphid populations were also observed (Wurst et al., 2003). This was explained by the fact that earthworms did not only affect nutrient uptake, but also the amount of defensive compounds produced by the plant, such as phytosteroles (Wurst et al., 2004a) and iridoid glycosides (Wurst et al., 2004b). For belowground herbivores such as plant-parasitic nematodes, several studies showed a decreased population of parasites (Boyer et al., 2013; Dash et al., 1980; Senapati, 1992; Yeates, 1981) in the presence of earthworms, initially interpreted as predation of nematodes by earthworms. However, the alleviation of the negative effect of nematodes by earthworms has also been observed when the actual nematode density was higher in the presence of earthworms (Blouin et al., 2005). The modulation of the expression of the gene coding for a phospholipase D, a precursor of jasmonic acid which is a plant hormone involved in defence mechanisms, was observed in the presence of earthworms, suggesting that aside from the predation effect, earthworms could improve plant tolerance to parasitic nematodes (see Section 7.2.5). Furthermore, several studies investigated the effect of earthworm extracts as antimicrobial agents. Earthworm polysaccharides were found to have broad-spectrum antibacterial activities on plant-pathogen microbes in vitro (Wang et al., 2007).

7.2.4 Dispersal and stimulation of symbionts and other beneficial microorganisms

Mycorrhizal fungi are well known for their influence on plant productivity. These fungi form a network belowground, which allows the exchange of nutrients or signals among coexisting plants (Van Der Heijden et al., 2015). Intact spores of arbuscular mycorrhizal fungi (AMF) have been found in the casts of 13 earthworm species, with a higher concentration than in the surrounding soil (Reddell and Spain, 1991). These spores were viable and able to infect *Sorghum bicolor*. Even if the transport of these spores by earthworms is likely to occur at short distance, it could be of great ecological importance since anecic earthworms could increase the concentration of spores at soil surface, making them able to disperse further by the wind, water and other vectors. All three earthworm guilds are likely to have a major ecological role in plant-mycorrhiza interactions (Reddell and Spain, 1991). Anecics deposit their casts in burrows/soil cracks where plant roots are known to preferentially grow. Epigeic and endogeic deposit their feces respectively at soil surface where seeds are germinating, or in the bulk soil where plants develop their root system. Earthworms have indeed been observed to increase mycorrhizal colonization of maize roots (Li et al., 2012) and increase hyphal length density (Li et al., 2013a), with a consecutive increase in plant growth. Increases in many enzymatic activities are also observed when earthworms and mycorrhiza are present simultaneously (Li et al., 2013b; Zhang et al., 2016). The beneficial effect of the interaction between earthworm and arbuscular mycorrhizae could be dependent on the dominant N-form in the soil (He et al., 2018) and plant preference for this form (Boudsocq et al., 2012).

Plant Growth Promoting Bacteria (PGPB) are known for facilitating N fixation, P solubilization, production of hormones (see Section 7.2.5), as well as antimicrobial activities with biocontrol effects (Bashan and Holguin, 1998). The interaction between earthworms and PGPBs is not well documented, with only a few studies reporting results. For example, Wu et al. (2012) reported earthworm-induced increases in the abundance of three PGPR species (N-fixing, phosphate-solubilizing and K-solubilizing bacteria) (Wu et al., 2012). Regarding the availability of nutrients, a simultaneous inoculation of earthworms and PGPR can act synergistically to increase the concentrations of available N, P, and potassium to a larger extent than those of single inoculation of earthworms or PGPB (Wu et al., 2012, 2013).

7.2.5 Signal molecules

Puga-Freitas et al. (2012a) reported an *in vitro* study where they compared the effect of a cast isolated in a nylon membrane on the growth of *Lolium perenne* and *Oryza sativa* with that of an equivalent amount of non-ingested soil. This setup excluded the possibility of a physical effect of earthworms as they were not present. In addition, no increased mineralization was likely to play a role as agar gel was providing all required nutrients *ad libitum*. Finally, no effects on pathogen control or symbiont dispersal could occur due to the absence of earthworms. This meant that the only mechanism potentially responsible for an effect on plant growth was the diffusion of molecules other than nutrients from the cast. A positive effect of earthworm cast was observed on *L. perenne*, whereas a negative effect was observed on *O. sativa*, with a respective +30% and −30% effect on total dry biomass. This (plant) species dependent effect is typical for the effect of signal molecules, and difficult to explain by a nutrient effect. The study of Puga-Freitas et al. (2012a) also highlighted the importance of signal molecules and hormone-like compounds by transcriptomic analysis of plant shoots. It showed that the presence of earthworms did not modify the expression of genes involved in nutrient uptake and assimilation, but rather of genes involved in the response to pathogens and exogenous hormone applications, in line with another recent transcriptomic study (Hodson et al., 2023). Finally, in an experiment comparing the growth of a wild *Arabidopsis thaliana* genotype and a mutant for auxin production and transport (Aux1-Axr4.2) in the presence and absence of earthworms, it has been observed that the dwarf phenotype of the mutant was reverted to the wild phenotype in the presence of earthworms, with a sevenfold increase in plant total biomass (Fig. 13). Since the mutant was differing from the wild type only by its altered auxin pathway, the authors deduced that auxin level in the soil was increased in the presence of earthworms, diffused up to the roots

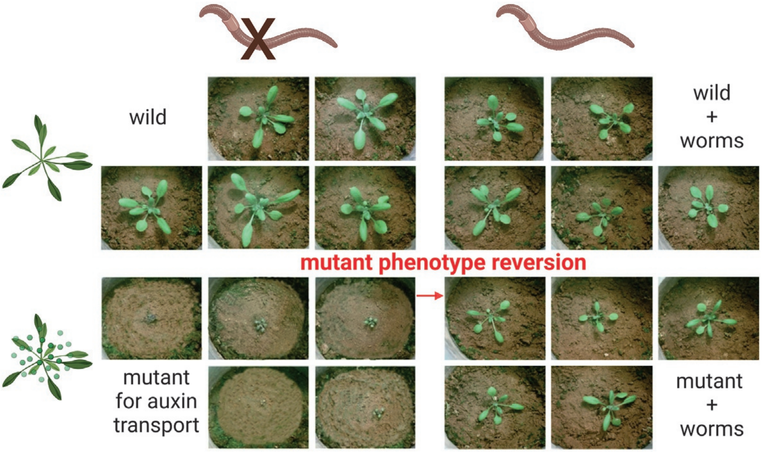

Fig. 13 Earthworms may partly affect plant growth through the production of signal molecules. Here, photographs are presented depicting wild type and mutant *Arabidopsis thaliana* plants with and without earthworms, taken 3 weeks after sowing. The mutant plant exhibits impaired auxin transport, which significantly hampers its growth. Earthworms help alleviate the deficiency of auxin pathways in plants. *Photographs are adapted from Puga-Freitas, R., Barot, S., Taconnat, L., Renou, J.P., Blouin, M. (2012). Signal molecules mediate the impact of the earthworm* Aporrectodea caliginosa *on growth, development and defence of the plant* A. thaliana. *PLoS One 7 (12), e49504, with the addition of more detailed images.*

and re-established the auxin level in root cells at the level required for cell elongation (Puga-Freitas et al., 2012b). Previous studies already showed that auxin-like compounds were present in "humic substances" (Muscolo et al., 1998) or earthworm compost (Canellas et al., 2002), which could have important consequences for nitrate uptake and N transfer to the shoot and plant growth (Quaggiotti et al., 2004). There are thus many pieces of a puzzle that strongly suggests that the effect of earthworms on plant growth is at least partially due to signal molecules.

7.3 How large is the beneficial effect of earthworms on plant growth?

Despite all the new insights on the pathways through which earthworms enhance plant growth, it is still difficult to quantify how large this effect is, and how it is affected by environmental conditions. In a meta-analysis encompassing 58 published studies, Van Groenigen et al. (2014) found an average yield increase of 25% in the presence of earthworms, and an increase in total aboveground biomass of 23% across a range of climates, crops and soils. Although very impressive, this does not mean that earthworms increase yields with these large amounts in all systems, or even in many realistic systems. Meta-analyses are constrained by the published studies that can be found, and there are several reasons why published effects of earthworms on plant growth are generally over-optimistic and sometimes biased toward one pathway:

(i) *The geographic origin of most studies.* Published studies on the effects of earthworms on plant growth are dominated by countries such as Great Britain, France, Germany, the Netherlands and the United States, leading to a strong bias toward temperate or continental climates (66% of the studies included), to the detriment of (sub)tropical systems. It is therefore perhaps not surprising that N rather than, e.g., P, was identified as the most important nutrient through which earthworms can contribute to plant growth. In those cases where studies identified temperate soils with a low P status and N was applied in sufficient amounts, a significant effect of earthworms on P supply was often identified (e.g., Vos et al., 2022a).

(ii) *(Lack of) fertilized treatments.* In the meta-analysis of Van Groenigen et al. (2014), only 12% of the studies applied N fertilizer and/or manure at rates exceeding 30 kg N ha^{-1} year^{-1} (roughly the rate of N deposition in industrialized regions). In other words: most published studies are not realistic for most agricultural systems in developed regions in terms of N input, leading to an overestimation of the N supply effect of earthworms under realistic agricultural conditions (a similar argument can probably be made for other nutrients).

(iii) *Pre-treatment of soil.* Any good experiment assessing the effects of earthworms on plant yield will need to compare an earthworm treatment with a control without earthworms. Unfortunately, this means that most published articles with a reliable control consisted of disturbed and repacked soil in order to remove any native worms, with only very few studies finding other ways of removing earthworms from control treatments (e.g., Callaham et al., 2001; Zaller and Arnone, 1999). In the meta-analysis of Van Groenigen et al. (2014), approximately 75% of studies were performed on disturbed soil. This repacking of soil inevitably leads to easier rootability for plants (at least on the short term) and therefore to underestimation of "soil structure" pathway through which earthworms may benefit plant growth.

(iv) *Unrealistically high numbers of earthworms and residue application rates.* Earthworm densities higher than 600 individuals m^{-2} (Kreuzer et al., 2004; Noguera et al., 2010) or even exceeding than 5000 individuals m^{-2} have been used in some incubation studies (e.g., Barrion and Litsinger, 1997; Stevens and Warren, 2000; Van Rhee, 1965). Likewise, some studies applied residue as food for earthworms exceeding 6000 kg ha^{-1} (Scheu et al., 1999; Stephens et al., 1994), even reaching rates of 17,000 kg ha^{-1} (Atlaviny et al., 1968). These represent highly optimistic and sometimes even unrealistically beneficial conditions for earthworms to increase plant growth—especially since earthworms are most likely to show a strong effect under conditions of low soil fertility (see point 2)—conditions where high residues production and large earthworm populations are not likely to occur.

(v) *Large numbers of earthworms dying during experiments.* Related to the previous point, earthworms added to experimental treatments also comprise a significant amount of N in their body tissue (see Section 6.1), which may become available relatively fast for plant growth if they die during the experiment. It was already recognized early on that this effect may obfuscate other effects of earthworms on plant growth, with the addition of a control treatment with dead earthworms as a useful safeguard (Russell, 1910) which unfortunately is not often included nowadays. Regrettably, Van Groenigen et al. (2014) did not report earthworm survival rates in the studies with exceedingly large earthworm populations. However, data from a more realistic experimental setup can demonstrate the potential isignificance of this effect. Kreuzer et al. (2004) reported a density of 764 individuals m^{-2} (mostly *A. caliginosa*) with a survival rate of 62.5%. This translates into 286.5 individuals m^{-2} dying, and with a few assumptions (0.6 g fresh weight per individual, 15% dry matter content, N content of 4%) it can be calculated that this represents approximately 1 g of N m^{-2}, or 10 kg N ha^{-1}—an amount large enough to have significant effects on plant productivity, especially in soils with low fertility.

Perhaps not surprising then, although it is very clear that earthworms significantly and beneficially affect plant growth through a variety of mechanisms, it remains challenging to give an answer to the question to what extent, and through what mechanisms, earthworms affect plant growth. Experimental conditions are crucial, and the enormous challenges of designing an experiment with controlled earthworm populations (including a control without earthworms) complicate things dramatically (see Section 11).

8. Earthworms and the soil GHG balance

8.1 Why would earthworms affect soil-derived GHG emissions?

The greenhouse gas balance of the soil, i.e., the balance between stabilizing new carbon on the one hand and emitting greenhouse gases such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) on the other hand, is not a standalone topic. In previous sections, we have seen that earthworms affect carbon cycling (see Section 5), as well as soil structure which in turn affects both the availability of C and N, and redox conditions (see Section 3). Ultimately, earthworms exert a strong effect on microbial activity (see Section 4), altering nutrient cycling processes such as denitrification (see Section 6.1). Given the profound effects of earthworms on all these controlling factors, it would be miraculous if earthworms did not dramatically affect the soil GHG balance.

Fig. 14 summarizes what we know so far about the effects of earthworms on the soil GHG balance. In general, carbon cycles faster in systems containing earthworms. Decomposition is quicker (see Section 5), but as earthworms may increase plant growth, the input of carbon into the soil may also increase due to rhizodeposition and crop residue. For N, the picture is more complex. Nitrous oxide is produced through various microbial transformation processes, with nitrification and denitrification as the most well-known processes, but other processes such as nitrifier denitrification are also potentially important (Kool et al., 2011; Wrage et al., 2001). Although these different pathways all differ in the conditions that drive them, it is possible to identify a few proximate soil factors that strongly affect N_2O emissions from soil, i.e., soil redox conditions (often approximated by moisture content), temperature, pH, available C, and available N (Granli and Bøckman, 1994). Out of these factors, earthworms increase available C and N, and in general decrease redox potential in their gut (Horn et al., 2003). This leads in general to emissions of nitrous oxide and even dinitrogen from earthworms across most species (Depkat-Jakob et al., 2013; Horn et al., 2006). Interesting as those direct emissions are, they are relatively minor. Typical rates are around 2.5×10^{-9} g N_2O-N h^{-1} g^{-1} fresh weight (Bertora et al., 2007; Matthies et al., 1999), translating perhaps to maximally a few grams of N_2O-N produced per ha per day. Although these amounts could potentially be significant as emissions, earthworms are producing this N_2O mostly in the soil. Nitrous oxide concentrations in the soil are typically high,

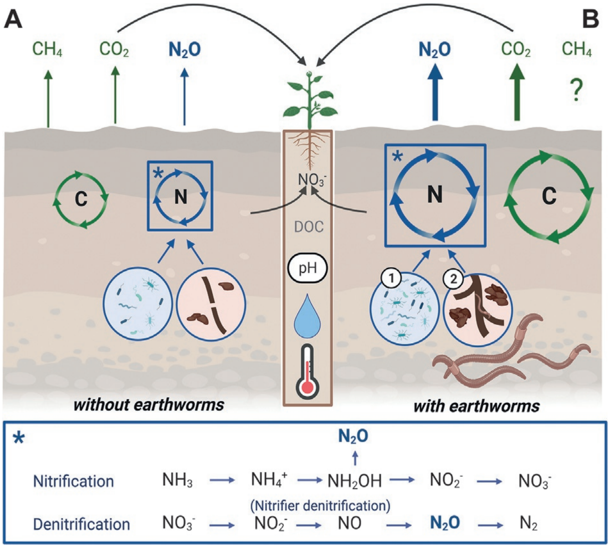

Fig. 14 Effects of earthworms on the soil GHG balance with particular focus on N_2O. In the absence of earthworms (A), N_2O emissions are mainly affected by pH, soil moisture content, temperature, available carbon (C) and nitrogen (N) and microbial transformation processes. The presence of earthworms (B), besides increasing available C and N and modifying soil moisture content, affects N_2O emissions by (1) enhancing microbial activity and (2) by producing casts and creating burrows, which represent respectively an important source of N_2O and an easy way for this gas to reach the atmosphere. It has to be noted that effects of earthworms on the soil GHG balance could be altered in the presence of growing plants that fix carbon dioxide (CO_2) and take up N e.g., in the form of nitrate (NO_3^-). *The figure is created with BioRender.com.*

easily exceeding 10 ppm or more, and relatively little N_2O is being emitted into the atmosphere as most of it is further reduced to dinitrogen (Clough et al., 2005).

Instead, earthworm-induced N_2O emissions seem to be an effect of earthworm-induced changes to the soil rather than emissions from earthworms themselves. Casts and burrows represent an important source of N_2O emissions before denitrification is fully completed (Paul et al., 2012) as they have high denitrification rates (Elliott et al., 1991; Parkin and Berry, 1994, 1999) and are generally relatively well-connected to the atmosphere.

Out of the three major greenhouse gases, by far least is known about the interactions of earthworms with methane. Although it has been shown that some species of earthworms can emit methane from their body, like N_2O (Depkat-Jakob et al., 2012), quantitative data on their effects on soil-derived emissions are mostly lacking. Given the fact that methanogenesis requires much lower redox potential than N_2O production (Serrano-Silva et al., 2014), and that earthworms can increase aeration of the soil through their burrowing activity, it is possible that earthworms stimulate methanotrophy rather than methanogenesis in relatively wet systems, leading to net decreases in topsoil CH_4 emissions to the atmosphere (e.g., John et al., 2020; Kernecker et al., 2015).

8.2 What do we know about the effect of earthworms on the soil GHG balance?

Quantitative studies on soil-derived GHG emissions as a direct effect of earthworm activity started relatively late. A decade has now passed since the available studies to date were first summarized in Lubbers et al. (2013b). This meta-analysis of all published studies on the overall effect of earthworms on the soil's GHG balance showed that earthworm presence on average increase CO_2 and N_2O emissions by 33% and 42%, respectively. Even though these increases are a clear and significant summary of studies published at that time, a meta-analysis is always limited by the scope of the available studies (see Section 7.1). Therefore, the nature of the studies included in the meta-analysis of Lubbers et al. (2013b) deserve additional scrutiny.

The meta-analysis focused on quantitative studies published up to and including 2011. As with the meta-analysis on earthworm effects on plant growth (see Section 7.1), only studies were included where an earthworm treatment could be compared to a similar treatment that was demonstrable without any earthworms. This strongly restricted the number of studies in the meta-analysis and led to an emphasis on studies that were relatively artificial in their set-up, as it is notoriously difficult to maintain realistic conditions without having the possibility of earthworms entering or cocoons hatching. Many of the included studies were therefore so-called proof of principle studies, meaning that only one aspect of the soil GHG balance-earthworm interaction was investigated without consideration of other aspects. These included, for example, very short-term studies, studies without plants present, laboratory incubations with unrealistically high earthworm densities, or where unrealistically high amounts of residue or fertilizer was applied. Even though the meta-analyses also included field experiments with realistic management and realistic earthworm densities (e.g., Lubbers et al., 2013b), it is likely that the nature of the papers included in the meta-analysis could have led to an overestimation of the earthworm effect on GHG emissions under realistic conditions.

Since the publication of Lubbers et al. (2013a) (and probably partly because of it), the number of publications on earthworms and the GHG balance of the soil has increased dramatically. Table 1 shows the result of a literature query, showing that for the 10 years since the publication of Lubbers et al. (2013b), more studies have been published on various aspects of the soil GHG balance than in the 20 years before (the period covered by the original meta-analysis). These include experimental studies challenging the conclusions of Lubbers et al. (2013b) and Zhang et al. (2013), but also studies offering a more multifunctional perspective (Liu et al., 2019). Much progress has been made on various aspects of earthworm–GHG interactions such as effects of moisture, temperature, texture, pH, crop management, etc. Lubbers et al. (2020) recently linked the effects of earthworms to those of other important groups of soil fauna, showing that whereas earthworm-induced CO_2 emissions increased with increased functional faunal diversity, N_2O emissions decreased, possibly due to a more complete denitrification process, leading to N_2 rather than N_2O being produced.

What are the remaining questions with respect to the effects of earthworms on the soil GHG balance? We see a few:

1. There have been many studies focused only on measuring effects of earthworms on N_2O and/or CO_2 emissions, and even more on effects of earthworms on various C and N pools in the soil. However, it is very difficult to combine results from different experiments in one coherent picture. What is needed are experiments where both C stabilization and GHG emissions are measured in the same system, allowing for a full C and N budget and therefore a much better insight in the shifts earthworms bring to the soil GHG balance.

Table 1 Numbers of published articles found on the relation between earthworms and the soil GHG balance in the period 1990–2011 vs 2011-present.

Query	# Of articles, 1990–2011	# Of articles, 2012–2022
Earthworm* carbon dioxide (CO_2) emission	14	27
Earthworm* methane (CH_4) emission	13	18
Earthworm* nitrous oxide (N_2O) emission	32	70
Earthworm* total soil C	625	804

Results from Web of Science query (on title, abstract and keywords).

2. In addition, more realistic systems will need to be measured over longer periods of time. In particular, effects of growing plants should be included, as earthworm-induced increases in plant growth (see Section 7.1) may provide positive feedbacks to the amount of C entering the soil, and thereby to the amount of C stabilized. Unfortunately, it would be excessively difficult to measure CO_2 emissions in such a system, because of root respiration obfuscating heterotrophic CO_2 production. Finally, it has proven extremely difficult to maintain different communities of earthworms (and systems without any earthworms) in different experimental plots under realistic conditions for longer periods of time (e.g., Vos et al., 2022b).
3. A single experimental study will not be able to change the broad conclusions of a meta-analysis encompassing 57 of published studies, such as the one of Lubbers et al. (2013b). With the large number of studies published since 2011, there seems to be an opportunity for a new meta-analysis, allowing for more detailed analyses of effects of environmental conditions on earthworm-induced shifts in the GHG balance. Such a meta-analysis could probably also consider effects of earthworms on CH_4 emissions—something for which in 2013 there were too few studies to be included in the meta-analysis.

9. Earthworms and soil remediation

Agriculture, including organic farming, may contaminate soils via the application of sewage sludges, manure, (plastic-contaminated) composts, agrochemicals, crop irrigation with reclaimed wastewater, and the use of plastic materials (Ng et al., 2018; Scopetani et al., 2022). A wide variety of pollutants are detected in agricultural soils, such as pesticides, metals, polycyclic aromatic hydrocarbons, polyhalogenated hydrocarbons, pharmaceutical active compounds, flame retardants, phthalates, and microplastics (<5 mm plastic fragments).

Among preventive and mitigating strategies to reduce soil contamination, *in situ* bioremediation is a viable option for recovering soil fertility and increase its resilience potential. Among the wide range of engineered and biological remediation methodologies (Megharaj et al., 2011), bio-based strategies are preferred because of the minimum negative impact on soil structure, and chemical and biological properties (Megharaj et al., 2011; Morillo and Villaverde, 2017). Notably, the use of earthworms as biological vectors of bioremediation, i.e., vermiremediation, is gaining scientific attention because of their key role on soil structure (see Section 3) and chemical-biological properties (see Sections 4–6) that impact the fate of pollutants.

9.1 Basic mechanisms of earthworm-assisted remediation

Earthworms facilitate the degradation and the immobilization of pollutants via three major interconnected processes (Fig. 15): (i) stimulation of soil microorganisms able to co-metabolize pollutants (Liu et al., 2011; Rodriguez-Campos et al., 2014), (ii) alteration of SOM dynamics, thereby modulating the mobility and bioavailability of pollutants (Morillo and Villaverde, 2017), and (iii) the earthworm's capacity to bioaccumulate and detoxify pollutants (Katagi and Ose, 2015; Wu et al., 2022).

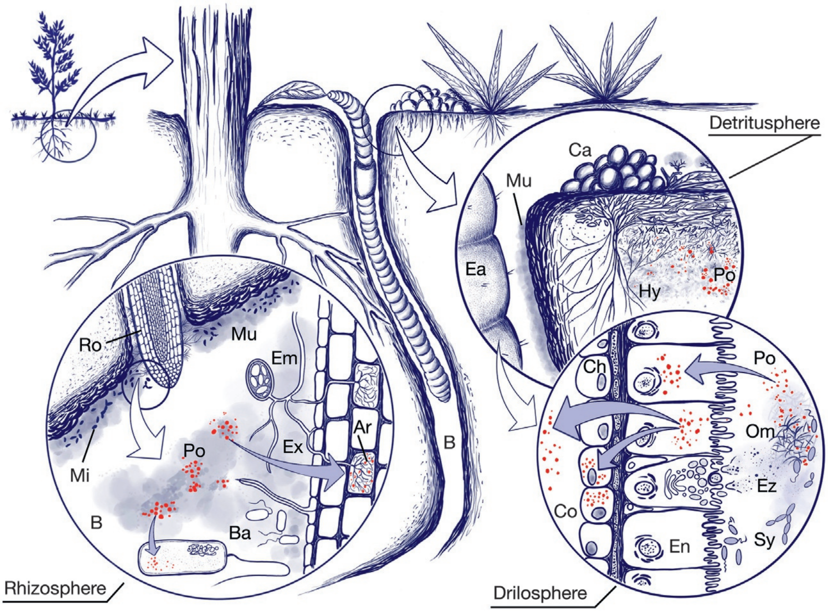

Fig. 15 The key processes induced by earthworms that contribute to pollutant biodegradation and immobilization occur in the rhizosphere (soil surrounding a living root), detritusphere (soil surrounding plants and animals at different stages of decomposition) and drilosphere (earthworm-affected soil). These processes include the stimulation of microbial pollutant degraders, the modification of organic matter dynamics, and the bioaccumulation and degradation of pollutants. *Ar*, arbuscule; *B*, burrow; *Ba*, bacteria; *Ca*, casts; *Ch*, chloragogen cells; *Co*, coelomic cavity; *Ea*, earthworm; *Em*, endomycorrhiza; *En*, enterocytes; *Ex*, exudates; *Ez*, enzymes; *Hy*, hyphae; *Mi*, microorganisms; *Mu*, mucus; *Om*, organic matter; *Po*, pollutants, indicated with red spots; *Ro*, root; *Sy*, symbionts.

There is substantial knowledge about earthworm-derived impacts on soil microbial activity, biomass, and community structure (see Section 4). The development of high-throughput molecular biology techniques ("omics" methods) has facilitated the identification of the main earthworm-induced microbial degraders. For example, the inoculation of acetochlor-spiked agricultural soils with *Eisenia fetida* (vs earthworm-free soils) promoted the degradation rate of the herbicide, with *Lysobacter*, *Kaistobacter*, *Flavobacterium*, *Arenimonas*, *Aquicell, Aeromonas,* and *Algoriphagus* being the potential herbicide degraders (Han et al., 2021). In a similar study, metolachlor was significantly degraded in agricultural soils in the presence of *E. fetida*, which stimulated preferentially soil fungi (*Fusarium*, *Metarhizium*, *Trichoderma*, and *Stachybotrys*) (Sun et al., 2020). The microorganisms present in the earthworm gut can also participate in degrading organic pollutants. For example, two (*Cupriavidus* and *Pseudomonas*) and one gut symbionts (*Flavobacterium*) were identified as atrazine degraders in herbicide (10 mg/kg, dry mass)-spiked agricultural soils incubated with the endogeic earthworm *Amynthas robustus* and *E. fetida*, respectively (Lin et al., 2018).

The use of earthworm-microorganism interactions as a phytoremediation strategy has intensified in the last decade, and focused particularly on AMF (Meng et al., 2021). For example, the co-application of *E. fetida* and the AMF *Rhizophagus intraradius* enhanced the cadmium accumulation by *Solanum nigrum* (Wang et al., 2020), while copper phytoextraction by *Canavalia ensiformis* increased in the presence of *Eisenia andrei* and the AMF *Rhizoglomus clarum* (Santana et al., 2019). Similarly, the phytoremediation of lead-contaminated soils using the Bermude grass (*Cynodon dactylon*) was significantly higher in soils treated with *E. fetida*, AMF and rhizobacteria (plant growth promoters) compared to earthworm-free soils (Mahohi and Raiesi, 2021). This integrated bioremediation strategy has proven successful in soils contaminated with organic pollutants. The co-application of *E. fetida*, two bacteria strains with upgraded catalytic potential and alfalfa (*Medicago sativa*) was the best option to remove 50–70% of dieldrin, and 20–25% of benzo(a)pyrene and heavy metals from historically-contaminated soils (Urionabarrenetxea et al., 2021). Collectively, these studies suggest that integrating a bioremediation scheme that combines earthworms, microorganisms, and plants represents a viable strategy for increasing metal removal and degradation of organic contaminants, while improving soil quality.

Earthworms also contribute to plant litter decomposition and SOM dynamics (see Section 5), thus altering the bioavailability of pollutants. Particularly, earthworm casts are stable reservoirs of MAOM (Vidal et al., 2019) unless they disintegrate (Bottinelli et al., 2020b), so pollutants sequestered in these microstructures could have limited mobility and bioavailability, which could increase their environmental persistence (Hickman and Reid, 2008). Likewise, the co-application of earthworms and AMF in metal-contaminated soils may result in metal immobilization in the rhizosphere as a consequence of mucus secretion by earthworms, and hyphae and root exudates, which can serve as binding agents for metals (Sizmur et al., 2010; Wang et al., 2022a).

The earthworm's sensitivity to pollutants is a critical factor in vermiremediation, in front of environmental factors such as SOM and N contents, soil texture, or pH (Chao et al., 2022). Sensitivity differs among earthworm species and is generally related to the efficiency of their xenobiotic detoxification system (Lu et al., 2017). For example, the epigeic *Eisenia* species seem more tolerant to pesticides compared to anecic and endogeic species (Robinson et al., 2021). Thus, both toxicity of organic contaminants and the detoxification capacity of earthworms should be considered before using these organisms as drivers of contaminant dissipation.

9.2 Vermiremediation of emerging contaminants

Emerging pollutants such as pharmaceutical active ingredients, brominated flame retardants, and microplastics are being increasingly detected in agricultural soils (Carter et al., 2014; Ng et al., 2018), with detrimental effects on plants and soil microorganisms (Bartrons and Peñuelas, 2017; De Souza Machado et al., 2019). Most studies dealing with the interaction between emerging pollutants and earthworms have exclusively examined toxic effects and bioaccumulation, providing first evidence for the potential of vermiremediation. For example, *E. fetida* can accumulate carbamazepine, diclofenac, fluoxetine, and orlistat, and although they quickly eliminate the four pharmaceuticals when transferred to a clean soil, 20–60% of accumulated drugs still remained in earthworm tissues (Carter et al., 2016a). The same earthworm species efficiently accumulated polybrominated diphenyl ether (PBDE) after 28 days of exposition to diverse PBDE-contaminated substrates (soil, biosolids, polyurethane microplastics, and compost) (Gaylor et al., 2013). The bioaccumulation of these emerging pollutants is species-specific. The bioaccumulation factor values for fluoxetine and orlistat in *E. fetida* were more than twofold those observed in *L. terrestris* (Carter et al., 2016b). Similarly, *E. fetida* showed a higher bioaccumulation of tetrabromobisphenol A (TBBPA) (Chen et al., 2017) and hexabromocyclododecane isomers (Li et al., 2016) than the anecic earthworm *Metaphire guillelmi*, probably because of the higher lipid and protein contents of the former. Despite this high bioaccumulation potential, the metabolic capability of *E. fetida* against polybrominated chemicals such as PBDE is very limited (Jiang et al., 2021; Qiao et al., 2022). Indeed, Chen et al. (2017) showed that, although *E. fetida* and *M. guillelmi* were able to metabolize TBBPA, *M. guillelmi* broke down faster and almost entirely the TBBPA into the dimethyl ether metabolite. These results suggest that earthworms, particularly anecic species, can probably remove and biodegrade PBDEs such as TBBPA with the gut symbiont intervention, which is promising for the remediation of soils contaminated with brominated flame retardants (Feng et al., 2016).

Soil microplastic pollution has recently raised the interest of the scientific community. Excessive accumulation of micro- and nanoplastics in soil may cause adverse effects on soil communities (Ng et al., 2018), on plant growth (De Souza Machado et al., 2018; Qi et al., 2018) and potentially on human health if contaminated plants are ingested (Abdolahpul Monikh et al., 2022). Despite these environmental and health risks, little attention has been paid to plastic biodegradation in soil, and how we can facilitate microplastic degradation, including biodegradable polymers (Sanchez-Hernandez et al., 2020; Wang et al., 2022b). Nonetheless, the inoculation of plastic-contaminated soils with earthworms seems to be a viable option to mitigate microplastic-derived adverse effects on plants (Qi et al., 2018). Some studies have shown that earthworms such as *L. terrestris* could transport and accumulate plastic fragments, microplastics and/or nanoplastics in subsoil by dragging them along burrows within cast or on their skin (Heinze et al., 2021; Rillig et al., 2017). Given the enhanced microbial and enzymatic activity in burrows and casts (see Section 4), these microplastics, especially biodegradable polymers, could be biodegraded (Sanchez-Hernandez et al., 2020). Likewise, there is some evidence that the earthworm gut of, e.g., *L. terrestris* may harbor microbial degraders capable of depolymerizing polyethylene (Lwanga et al., 2018). This study opens not only an exciting field in biotechnology for plastic polymer degradation but also in the vermiremediation of microplastic-contaminated soil.

9.3 Earthworm-based preventive measures against agricultural soil contamination

Many environmental stressors such as climate change-derived impacts, the decline of OM, the loss of biodiversity or the soil contamination threaten soil health and resilience. Soil resilience is defined as "the ability of soil to resist or recover from an anthropogenic or natural perturbation" (Lal, 1997). Therefore, it is theoretically viable to increase soil resilience by acting on soil physicochemical and biological properties. In case of pollution, soil resilience can be enhanced by long-term stimulation of potential biological degraders or by increasing the presence of soil organo-mineral complexes to favor pollutant immobilization. In this regard, the biochar technology emerges as an attractive option because of its exceptional capacity for adsorbing environmental pollutants, its stimulating effect on soil microorganisms (Beesley et al., 2011; Han et al., 2016), and compatibility with earthworms (Sanchez-Hernandez et al., 2019).

Biochar is formed during the pyrolysis or thermochemical conversion of biomass at high temperatures (300–650 °C) and anoxic atmosphere (Kambo and Dutta, 2015). The use of biochar is considered as a carbon sequestration strategy with direct applications in soil for fertilization and pollutant removal. The incorporation of biochar into soil has led to the coining of a new sphere of soil functioning, i.e., "charosphere" which is defined as the soil surrounding the biochar that is influenced by the physicochemical properties of biochar, ultimately affecting soil-plant-microorganism interactions (Quilliam et al., 2013). Additionally, the joint application of biochar and earthworms may significantly alter the charosphere with potential benefits for pollutant dissipation (Fig. 16). Earthworms may facilitate the retention of enzymes and microorganisms on biochar surface, probably because earthworm mucus acts as a cross-linking agent that can increase the adsorption capacity of biochar (Sanchez-Hernandez et al., 2019). Furthermore, biochar may promote the growth of microbial communities in both the soil and the gut microenvironment of earthworms (Jin et al., 2022). Altogether these studies suggest that the earthworm-biochar interaction may favor the stabilization and augmentation of contaminant-detoxification enzymes. For example, the incubation of biochar in agricultural soils inoculated with *L. terrestris* and *A. caliginosa* facilitated the coating of biochar by carboxylesterase enzymes, which inactivated organophosphorus pesticides (Sanchez-Hernandez, 2018) (Fig. 16A, B). These findings present a promising avenue in the field of biotechnology for soil bioremediation with potential benefits in agronomy.

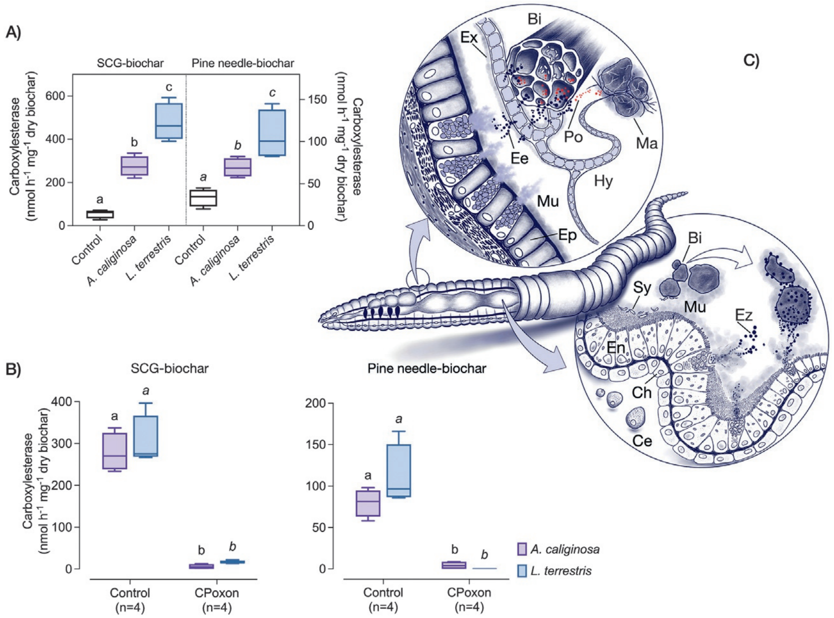

Fig. 16 The effect of co-application of biochar and earthworms on potential pollutant dissipation. (A) Carboxylesterase activity in soils incubated with biochars of spent coffee ground (SCG)- and pine needles after 2 months of incubation together with earthworms (*Aporrectodea caliginosa* or *Lumbricus terrestris*). The two biochar were incubated in earthworm-free soils to serve as control. (B) Biochar particles were extracted from the soil described in (A) and the carboxylesterase activity was measured after 30-min incubation of biochar in the presence of the organophosphate chlorpyrifos-oxon (CPoxon, 1.5×10^{-5} M). In (B) controls represent the biochar particles incubated with pesticide-free buffer, which serves as a baseline for enzyme activity. Significant differences between treatment groups are indicated by different letters (Kruskal-Wallis test followed by post hoc Mann-Whitney test, $P < 0.05$). A pictorial conceptual model illustrating the biological activation of biochar with enzymes derived from microorganisms (e.g., fungal hyphae) or earthworm gut epithelium. Epidermic and gut mucus would act as a cross-linker in the enzyme binding to the biochar surface (C). *Bi*, biochar; *Ch*, chloragogen cells; *Ce*, coelomocytes; *Ee*, exoenzymes; *En*, enterocytes; *Ep*, epidermis; *Ex*, exudates; *Ez*, enzymes; *Hy*, hyphae; *Ma*, microaggregates; *Mu*, mucus; *Po*, pollutants; *Sy*, symbionts. Pollutants are indicated with red spots. *This figure is reused and adapted with permission from Sanchez-Hernandez, J.C. (2018). Biochar activation with exoenzymes induced by earthworms: a novel functional strategy for soil quality promotion. J. Hazard. Mater. 350, 136–143.*

10. Distribution of earthworms in agricultural soil, the chicken or egg dilemma

10.1 A paradox

Earthworms can stimulate plant growth through a variety of pathways (see Section 7) and can therefore contribute to productivity and sustainability of agroecosystems. However, most studies demonstrating these relationships have been conducted under relatively artificial conditions, with earthworm communities artificially manipulated to create "treatments" that can be compared with each other. To assess how beneficial earthworms may be in real-world agroecosystems, it is also important to consider how many earthworms there are likely to be; i.e., it is important to consider the quality of the habitat for earthworms in various agroecosystems. When the results of meta-analyses on the effects of earthworms on soil fertility and plant growth (e.g., Van Groenigen et al., 2014, 2019) are compared to studies on factors regulating earthworm community composition (Hackenberger and Hackenberger, 2014; Phillips et al., 2019; Rutgers et al., 2016), then a paradox arises: *earthworms seem to have the most beneficial effect on plant growth in systems where they are least likely to occur or in systems that cannot realistically exist*. For example, Van Groenigen et al. (2014) showed that earthworms had the greatest effects on plant growth in agroecosystems that (i) received little or no N fertilization; have earthworm communities exceeding 400 individuals m^{-2}; and (ii) return more than 5000 kg ha^{-1} of residue to the soil. However, it is extremely unlikely that systems that do not receive any N would be so productive (with the possible exception of extensively managed pastures) or would be able to sustain such high numbers of earthworms for any extended periods of time. In addition, the size and structure of earthworm communities in agroecosystems is to a large extent determined by temperature and precipitation rather than by soil properties or management (Rutgers et al., 2016). Unfavorable climatic factors lead to much lower earthworm abundances in parts of the arid tropics and subtropics (Phillips et al., 2019), strongly limiting their possible contributions to plant growth and other ecosystem services. Therefore, the potential beneficial role of earthworms across different agroecosystems should be calibrated against their likely community size in these systems. Below, we make a first effort to do so.

10.2 The potential role of earthworms in different systems

Fig. 17 conceptually explores the relationship between the potential beneficial effects of earthworms and the likelihood that earthworms occur in those systems. Different agroecosystems are positioned along an axis depicting external nutrient (N and P) input on the one hand (e.g., fertilizer, manure, compost, etc.) and total C input on the other hand (e.g., crop residue, rhizodeposition, manure, compost). Please note that this figure is conceptual, that the various systems depicted in it are only a small subsample from the wide variety of agroecosystems that exist, and that the descriptions below will inevitably be relatively rough.

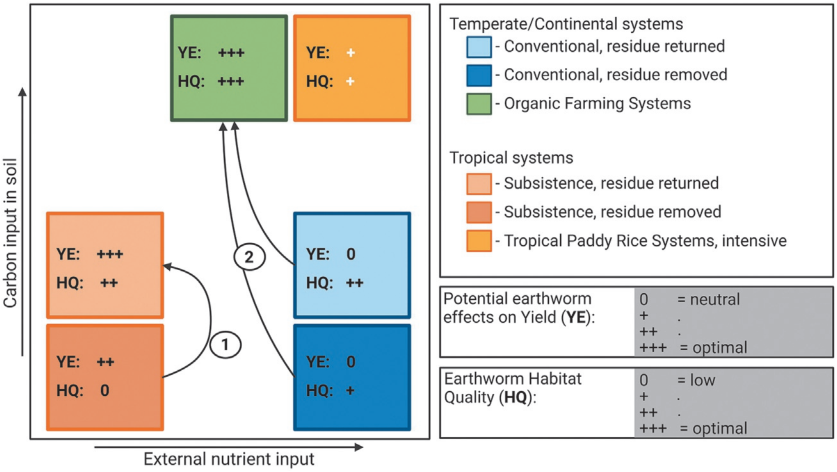

Fig. 17 A conceptual overview of potential effect of earthworms on yield across arable cropping systems. Effects are based on hypothetically high earthworm densities. Actual earthworm densities typically encountered in these systems are indicated as well. Black font indicates relative certainty about the effects; white font indicates relatively little experimental evidence and/or speculated effects by the authors. (1) indicates the conversion from a system where residues are removed to a system where residues are returned to the soil, while (2) indicates the conversion from a conventional system to an organic system. *The figure is created with BioRender.com.*

Among the systems considered, we expect the smallest effect of earthworms on yields in conventionally managed crop systems in temperate or continental climates (Fig. 17). In these systems, large amounts of external nutrient inputs (fertilizers), as well as regular and intensive tillage of the soil, are likely to overrule the most important benefits that earthworms offer to plant growth: mineralization of nutrients and improvement of soil structure (see Section 7). Due to relatively small amounts of carbon entering the soil (little manure or compost added, and a large part of primary production removed due to high harvest indices), these systems generally don't offer a particularly good habitat (Crittenden et al., 2014, 2015; Rutgers et al., 2016). Pesticide application have also been shown to decrease earthworm abundance by 40% and 60% for *Allolobophora chlorotica* and *L. terrestris* respectively in cereal crop soils (Pelosi et al., 2013).

(Sub-)tropical subsistence farming systems are typically characterized by little or no external nutrient input, and by very high proportions of the (relatively low) primary production being removed for food, fuel, feed and building material. Whereas earthworms, when present, could probably have a very positive effect on plant growth in these marginal soils, the absence of significant amounts of carbon inputs into the soil, as well as dry periods in some areas result in relatively low habitat quality.

Tropical paddy rice systems are among the most important systems in the world for staple food production, but we do not know much about the beneficial effects of earthworms in these systems. Although some positive results on crop growth are reported in the literature, these are typically from aerobic rice rather than paddy rice (e.g., Blouin et al., 2006; Noguera et al., 2010; Ratsiatosika et al., 2021). For paddy rice, negative effects as well as positive effects have been reported (e.g., Barrion and Litsinger, 1997; Owa et al., 2003) and very little information is available on the size and structure of earthworm communities, especially in continuous rice cropping systems. Much more study is needed on the potential benefits of earthworms to such systems under realistic conditions.

10.3 How to break the paradox?

What should we do to increase the benefits of earthworms in plant production systems? If we look through the prism of the two axis of Fig. 17, increasing the amount of carbon input to the soil would be an obvious strategy, as it both improves habitat quality and provides the opportunity for mineralization of nutrients. For the conventional cropping system depicted in Fig. 17, a first step would be to return crop residue to the soil as much as possible. However, as these systems often receive large amounts of external nutrients in the form of mineral fertilizers, this improved habitat quality might not lead to increased earthworm effects on plant production. A more radical change would constitute a switch to an organic system. For example, in organic farming systems in temperate regions, external nutrient inputs are typically not too high and mostly in the form of organic amendments (e.g., through manure or compost). Nutrient supply to the plants therefore hinges on timely mineralization of nutrients from SOM and external organic soil supplements—something which earthworms can significantly increase. Due to large inputs of OM as well as the general absence of intensive tillage and the use of pesticides, habitat quality of organic farming systems is potentially quite high (e.g., Crittenden et al., 2014). For tropical subsistence farming systems, increasing the amount of residue returned to the soil might also be key to improving habitat quality (e.g., Blanco-Canqui and Lal, 2009; Tian et al., 1993). Obviously, this is often not easy as crop residues are used for meaningful purposes such as fuel or feed for livestock. It will require a serious shift in the management of such systems to take full advantage of the benefits earthworms can bring. In the end, we cannot see earthworms as a stand-alone solution to improving the sustainability of cropping systems. Rather, they are one essential piece of the puzzle. By managing our earthworm populations well, we manage our soils well.

11. Ten questions and challenges for future earthworm research in agriculture

Below, we will end our review by formulating ten pertinent questions that need to be answered in order to bring earthworm science forward.

1. *How can we control the abundance and effects of earthworms in arable soils?*

Our review presents the current knowledge on the (mostly beneficial) role of earthworms in agronomy. Yet, for earthworms to affect agricultural soils, they need to be present and active. In certain systems, especially in arable soils, establishing diverse earthworm population remains a key challenge (see Section 10). Earthworm inoculation has not always been successful, especially in highly degraded soils, and the key to promote the colonization of earthworms is to adopt changes in management (likely toward more organic farming practices).

2. *What is the long-term effect of earthworms in agricultural soils?*

The effect of earthworms on soil is highly time dependent. Earthworms create transient hotspots of energy and nutrients (see Sections 5 and 6) that require good timing and spatial distribution to efficiently benefit plant growth, without ultimately increasing GHG emissions (see Section 8). Earthworms also create burrows and casts that are submitted to aging, transformation or destruction. Yet, due to budgetary and practical constraints the large majority of earthworm research is done in short term experiments under often artificial conditions. The challenge for earthworm scientists is to devise experiments that can characterize the long-term effect of earthworms and compare it to a treatment without earthworms present.

3. *How can we efficiently measure earthworm bioturbation?*

Bioturbation is the driving force through which earthworms support soil functions. However, measuring and monitoring bioturbation *in situ* at the field scale remains a big methodological challenge (see Section 3). Several novel and promising approaches are being developed. Methodologies such as near infrared spectroscopy (NIRS) and mid-infrared spectroscopy (MIRS) spectroscopy, for instance, are able to rapidly and cheaply assign biostructures to earthworm species. Capturing the activity of earthworms in such a way would enable the design of simulation models to assess relationships between earthworm communities, created biostructures and the physical functioning of agricultural soils.

4. *How do earthworms, microorganisms and plants interact and communicate?*

Despite not being necessarily physically connected, strong interactions exist between earthworms and plants resulting, for example, in the buildup of specific microbial communities that can have feedback effects on plants. Mounting evidence indicates that earthworms may partly increase plant growth by emitting (or stimulating microorganisms that emit) signal molecules that interfere with plant hormonal pathways. This three-way interaction could potentially increase plant tolerance to parasitic organisms and guide plant roots toward nutrient-rich casts (see Section 7.2). This line of earthworm research is still in its infancy and will benefit from the use of transcriptomic analyses and of plant mutants that are impaired in certain hormone pathways.

5. *How important are interactions between earthworms and macro/mesofauna?*

In the present review, we mainly consider the interaction between earthworms, microorganisms and plants. However, it is clear that the ecosystem engineering activities will dramatically affect the habitat of most soil fauna and that interactions are bound to occur. Recent studies indicate that this may indeed lead to significant changes in soil functioning. For example, recent studies show that not only growing plants decrease earthworm-induced N_2O emissions but that increasing the functional faunal diversity might do something similar (see Section 8.2). This calls for integrating other important groups of soil fauna in order to fully tackle the role of earthworms in agronomy.

6. *To what extent do earthworm-root interactions affect soil biogeochemical cycling?*

We have highlighted numerous direct and indirect pathways through which earthworms can affect plant growth (see Section 7) and plants can mitigate effects induced by earthworms (e.g., nutrients, GHG emissions) (see Sections 6 and 8). Yet, for practical reasons, many studies are still conducted without *in situ* growing plants, potentially leading to unrealistic conclusions. Future earthworm research should aim to systematically include living plants and pay particular attention to earthworm-root interactions.

7. *What is the contribution of earthworms in stabilizing organic carbon in the drilosphere?*

The living microorganisms stimulated by earthworms ultimately die, forming a potentially stable pool of carbon in the soil as mineral-associated organic matter or occluded particulate organic matter (see Section 5). While microbial necromass has been recognized to contribute to roughly half of the organic carbon in soils, we are only starting to understand the role of earthworms in forming and maintaining this necromass—something we need to know in order to understand the dynamics of soil carbon sequestration.

8. *What are the main pathways driving the effect of earthworms on phosphorus availability?*

Earthworms could be of primary importance to increase the availability of phosphorus in arable soils, particularly where phosphorus is limiting plant growth and in low input systems. We have shown that the pathways for such an effect go further than the "traditional" assumed pathways of increased mineralization (see Section 6.2). Yet, the contribution of these different pathways is still largely unknown, and we need intensive cooperation with, among others, soil mineralogists and inorganic chemists to understand them.

9. *What is the role of earthworms in the cycling of other soil elements?*

Nitrogen and phosphorus are worldwide the most limiting macronutrients. Therefore, it is logical that most earthworm studies have focused on those two elements. Yet, many described pathways through which earthworms affect nitrogen and phosphorus cycling are also valid, *mutatis mutandis*, for other elements, both beneficial (e.g., micronutrient, beneficial trace elements) or not (toxic elements) for plant growth (see Section 6.3). For example, the novel pathways of earthworm-induced P availability might very well apply as well to elements whose bioavailability is strongly affected by soil chemical and—mineralogical parameters. While most studies to date on this topic are mainly descriptive, mechanistic research on the topic is necessary.

10. *Can we efficiently remediate polluted arable soils using earthworms?*

Earthworms have the capacity to degrade and/or to immobilize a wide range of soil pollutants (see Section 9). Among these are emerging contaminants that represent an increasing threat on agricultural soils, which could be partly tackled by vermiremediation. While it was shown that earthworms could bioaccumulate large amounts of pollutants without resulting in toxic effects as well as incorporate pollutants within biostructures, the full potential and efficiency of vermiremediation at field scale remains unclear.

Acknowledgments

Authors acknowledge Donald L. Sparks for the invitation to write this review. We also thank Gerrit Angst for sharing data on earthworm abundance and microbial necromass in Fig. 8C. We would like to thank Alex Milcu and the Montpellier Ecotron facility for their support in obtaining the data of Fig. 5.

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