Title: Two distinct ecological behaviours within anecic earthworm species in temperate climates

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Abstract

Earthworm species in temperate climates have usually been classified into three main ecological categories according to their morpho-anatomical, physiological and ecological traits: epigeic, endogeic and anecic. However, since these ecological categories were first defined, many studies on the ecological traits of widespread anecic species: *Lumbricus centralis* (Bouché, 1972), *Lumbricus terrestris* (Linnaeus, 1758), *Aporrectodea longa longa* (Ude, 1885) and *Aporrectodea giardi* (Ribaucourt, 1901) have revealed two distinct feeding behaviours, as well as differences in their growth rates and burrowing behaviour. In this review we highlight that within anecic earthworms, *Lumbricus* anecic species (here after "LAS") mainly consume fresh plant-derived materials on the soil surface modifying the quantity and spatial organisation of said materials. In contrast, *Aporrectodea* anecic species (here after "AAS") consume mainly aged plant-derived materials already incorporated into the soil and only a small proportion of surface-available plant-derived materials. Furthermore, the AAS have a denser and more complex burrow network than LAS. This suggests that AAS burrow into the soil to search for soil organic matter incorporated in the soil whereas the LAS essentially focus on burying the surface litter into their burrow. Consequently, LAS seem to benefit from easily assimilated substrates, grow faster and reach maturity in a shorter time span than AAS species. This distinction between anecic *Lumbricus* and *Aporrectodea* earthworms is expected to have different consequences for soil trophic network and soil functioning such as carbon and nutrient cyclings, water regulation and soil structure maintenance.

Keywords

Burrow; feeding guild; growth; plant-derived material; soil organic matter

1. Introduction

During the last half century, earthworm species in temperate climates have usually been classified into three main ecological categories (i.e. epigeic, anecic and endogeic; [1]) given their general distinct contribution to soil processes [2–4]. However, these studies highlighted that, within ecological categories, species contribution to soil processes is highly heterogeneous, underlining that the ecological categories are not sufficient to assess the functional role of earthworms [5].

Earthworm species were first qualitatively categorized into ecological categories using morpho-anatomical, physiological and ecological traits by Bouché [1,6]. Bottinelli et al. [7] quantitatively revised these ecological categories, but did not include ecological traits explicitly in consideration of the anecic group, although several reports are available on the ecological traits of anecic species [8–11]. Usually, it is assumed that anecic earthworms feed on surface plant litter, and bury this material into their vertical or near vertical burrows [12–14] to accelerate the decomposition processes performed by soil microorganisms [15,16]. The plant litter ingested and digested during gut transit is assimilated by anecic earthworms, allocated to maintenance, growth and reproduction [17,18]. However, under a temperate climate, two widespread eartworms genera are classified within the anecic ecological categories *Lumbricus* and *Aporrectodea* anecic species (hereafter “LAS” and “AAS” respectively) and have been grouped together until now [1,7]. A large body of evidence supports the idea that these two anecic genera have distinct ecological traits and should be distinguished according to their feeding and burrowing behaviours, as well as growth rate [19,10,20].

Here, we present a comprehensive review of the scientific literature and synthesize the relationships between anecic earthworms and plant-derived materials in temperate climates, focusing on the distinctions between *Lumbricus centralis* (Bouché, 1972), *Lumbricus terrestris*

(Linnaeus, 1758), *Aporrectodea longa longa* (Ude, 1885) and *Aporrectodea giardi* (Ribaucourt, 1901), four of the most widespread and studied anecic species. We focus on their feeding behaviour and possible consequences on their growth rates and burrowing behaviour, given the relevant relationships between these traits [18,9,13].

2. Procedure

A literature review of the feeding behaviour (location and age preference of plant-derived materials consumed), growth rate and burrowing behaviour (shape of the burrow network) of four anecic species (*L. centralis, L. terrestris, A. longa longa* and *A. giardi*) used the ISI-Web of Science research database. These anecic species are widespread [1,21] where many studies refer to *L. centralis* [22–24], *L. terrestris* [23,25,26], *A. longa* [25–27] and *A. giardi* [22,25,28,29] and were recorded in agricultural, natural and urban fields, although it is not possible yet to distinguish preferences of one or another for a specific land use. In addition, we selected these anecic species due to their morphological and anatomical similarity within LAS (between *L. centralis* and *L. terrestris*) and within AAS (between *A. longa* and *A. giardi*) [1]. The following combinations of keywords were used in Topics: ((“lumbricus centralis” OR “lumbricus terrestris” OR “aporrectodea longa” OR “aporrectodea giardi”) AND (feed* OR plant* OR organic matter* OR mass* OR weight* OR growth* OR burrow* OR gallery*)) which returned 1272 publications. After carefully checking all generated results, 102 references published between 1963 and 2022 were selected (Supplementary material 1). To complete the review, peer-reviewed publications in the references of the selected publications were also studied when they fitted our selection criteria.

3. *Lumbricus* anecic species consume more surface plant litter than *Aporrectodea* anecic species

Both LAS and AAS ingest either living or dead plant-derived materials, microorganisms and mineral soil (Table 1). Nevertheless, several qualitative and quantitative differences exist between the two anecic genera *Lumbricus* and *Aporrectodea* and are summarized below.

Under controlled conditions, *L. centralis* and *L. terrestris* contributed significantly to surface litter mass loss, at rates varying from 2.4 [30] to 84 mg g^{-1} day^{-1} [31]. In line with these results, several studies observed that the digestive tract of *L. terrestris* contained high amounts of plant-derived materials, ranging from 39 % [32] to 80 % [33,34] of the total gut content. The well recognized enrichment of *L. terrestris* casts in C content compared with surrounding soil is due to the presence of plant-derived materials [35,36,19,37,38] which is not observed in the absence of such materials on the soil surface [39–43]. Additionally, few authors have observed that *L. terrestris* and *L. centralis* only consume plant-derived materials located on the soil surface and not when buried in the soil profile [44,45]. Indirectly, this was also observed in other studies in which the growth of *L. terrestris* was likely limited by the absence of surface litter [46,47,41,48,49]. The soil surface feeding behaviour of LAS could hamper their feeding when litter is buried through arable ploughing or soil engineering in artificial soils. In sum, these observations indicate that LAS seem to be sapro-geophagous, consuming preferentially plant-derived materials on the soil surface.

The few studies that focused on *A. longa longa* and *A. giardi*, quantified rates of surface litter mass loss under controlled conditions varying from 0.0 mg g^{-1} day^{-1} [10,20,28,50] to 57 mg g^{-1} day^{-1} [51]. It has thus been observed that even when litter was available on the soil surface, AAS did not feed upon it [10,20,28,50]. Moreover, studies that involved both *Lumbricus* and *Aporrectodea* consistently showed that LAS consumed more plant-derived materials than AAS [52,10,20,50]. This suggests that AAS species either have a lower metabolism compared to LAS or that there are other food sources, besides plant-derived surface material suitable for these species, most likely native and incorporated soil organic matter. In line with the latter, the digestive tract of *A. longa longa* showed a lower content of plant-derived material compared with *L. terrestris* [8], by as much as 38% [32]. The effect on C-litter enrichment in casts of AAS was either not observed or was lower than for LAS [36,19]. The C content in the casts of *Aporrectodea* does not seem to depend on the presence of litter at the soil surface. Alekseeva et al. [53] observed that when no litter was provided on the soil surface, the C content of *A. giardi* casts was still higher than the bulk soil (5.3% for *A. giardi* casts, 3.8 % for soil at 0-20 cm and 1.2% for soil at 40-60 cm). Similarly, Jégou et al. [9] observed that, compared with the surrounding soil, casts of *A. giardi* were not significantly enriched in C when litter was available on the soil surface. Thus, AAS seem to be geo-saprophagous, consuming a high proportion of plant-derived materials already incorporated into the soil with a slight proportion of plant-derived materials from the soil surface.

4. Fresh *vs.* aged plant-derived materials: two distinct food resources for *Lumbricus* and *Aporrectodea* anecic species

Plant-derived materials within the digestive tract of *L. terrestris* consisted of 50% [32,33] to 65% [8] of fresh (i.e. still recognizable) plant litter or roots. Martin et al. [54], using isotopic markers, also observed that the C assimilated by *L. terrestris* originates in fresh fractions of plant-derived materials, with a turnover time in soil of a few years. This observation was also confirmed for *L. centralis* [56]. Moreover, using isotopic markers, the source of C and nitrogen (N) in the casts of *L. terrestris* was found to originate from fresh plant-derived materials [9,57]. Thus, LAS seem to mainly consume fresh plant-derived materials on the soil surface and thus contribute to the burial of organic matter from the surface into the soil profile. Consequently, LAS are highly involved in modifying the quantity and spatial organisation of plant-derived material once deposited on the soil surface [58,14,59]. Interestingly, among anecic species, only *Lumbricus* species were observed to select or consume living plants [6,60,61,48], but the authors did not quantify the importance of these observations, which suggests that it represented a minor part of their diet.

Aged, plant-derived materials are common in the digestive tract of *A. longa longa*, i.e., vegetal matter that is no longer recognisable as a particular plant organ or tissue [8,34]. Accordingly, Larsen et al. [16] observed that *A. longa longa* fed preferentially on aged soil C sources with an assimilated C of between five and seven years old [62] which supported findings of previous studies performed on *A. giardi* [28,63,64]. Moreover, Cortez et al. [28], using isotopic markers, observed that C and N in the casts of *A. giardi* originated mainly from incorporated soil organic matter and little from the litter provided on the soil surface. Andriuzzi et al. [56], using isotopic markers, observed that *A. longa longa* incorporated less fresh C into its burrows than *L. centralis*. Several studies with isotopic markers [65–68,62,16] have shown that the resource spectrum of AAS is located between those of endogeic species (e.g., *Allolobophora chlorotica*, *Aporrectodea caliginosa* and *Allolobophora rosea*) and LAS species, while the resource spectrum of LAS seems to be more restricted. Overall, AAS consume a high proportion of aged plant-derived materials requiring a fairly advanced state of decomposition.

Since fresh plant-derived materials are richer in C and N than aged plant-derived material from the soil, it can be assumed that the C and N contents in the casts of LAS are likely to be higher than those of AAS. This was confirmed by Jégou et al. [9,19] who observed that the C and N enrichment in the casts compared with the bulk/surrounding soil was higher for *L. terrestris* than for *A. giardi*. Similarly, Vos et al. [69] observed that the dissolved C content in the casts of *L. terrestris* was higher than in those produced by *A.giardi*, however, the total C content in the casts of *L. terrestris* and *A. longa longa* were similar. Thus, we speculate that the aged C content in the casts of AAS is deeply incorporated and not easily available for organic matter decomposition by soil microorganisms.

5. Faster growth of *Lumbricus* anecic species compared to *Aporrectodea* anecic species

Lumbricus anecic species, by preferentially feeding on fresh plant-derived materials, can therefore benefit from easily assimilated nutrients compared with AAS that prefer to feed on aged plant-derived materials. These distinctive feeding behaviours lead us to speculate that growth rate or time to maturity (days to reach full clitellum development) are respectively slower and longer for AAS than for LAS. This was confirmed by several studies under controlled conditions [70,71], and, for example, Lowe and Butt [72] observed that the growth rate of *L. terrestris* was 2.2 times faster than that of *A. longa longa* (0.15 and 0.07 g worm^{-1} week^{-1}, respectively), and Butt [73] observed that the time to maturity was longer for *A. longa longa* than for *L. terrestris* under identical conditions (4 and 3 months, respectively).

6. Denser and more complex burrow networks for *Aporrectodea* anecic species

Although their burrow networks are more or less vertical, *L. terrestris* normally has one to two main galleries, with very little branchings, whereas the burrow networks of *A. longa longa* and *A. giardi* are much denser, and tortuous with branched burrows [74–76,19,12,77,78,13,79]. As an illustration, under controlled conditions, Bastardie et al. [12] observed that the total length of the burrow network of *A. giardi* was 3.2 times greater than that of *L. terrestris* (52 and 168 cm, respectively). Accordingly, Briones and Álvarez-Otero [80] observed a thicker tegument in *A. longa longa* than in *L. terrestris*, suggesting a better resistance to abrasion for AAS and consequently a higher burrowing behaviour. In the light of this review, these results may suggest that AAS burrow into the soil searching for native and aged soil organic matter, whereas LAS essentially focus on burying the surface litter in their burrow. Interestingly, it is well known that *L. centralis* and *L. terrestris* form middens at the entrance of their burrows [81,14] which are a surface structure made up of a mix of soil, casts, mucus and buried plant-derived materials but this has never been reported for *A. longa longa* and *A. giardi*. In addition, the permanent burrow systems of *L. centralis* and *L. terrestris* lead to a high and constant enrichment of the entire burrow network by fresh plant-derived materials, whereas the denser system of burrows developed by *A. longa longa* and *A. giardi* result in C-litter dilution in the complex and numerous structures formed [36,82,57,83,56].

7. Knowledge gaps

Differences in feeding behaviour between AAS and LAS could be supported by further studies focussing on morpho-anatomical, histological and physiological traits [1,7]. For example, in the digestive tract, the typhlosole (dorsal involution of the intestine wall) increases the epithelial area without increasing the gut volume [84,85]. Thus the shape of typhlosole could indicate the efficiency to absorb nutrients, with a more complex shaped typhlosole increasing the ability to absorb nutrients [86,87]. Thus, it could be speculated that the typhlosole of AAS is much more developed than that of LAS. Unfortunately, the shape of thyphlosole within anecic earthworms is poorly described, and if so, not often quantitatively [1,26]. Gates [21] observed that the typhlosole of *A. longa longa* is much more developed, complex and with more branches than that of *L. terrestris*, but this remains to be quantified. Another example of some anatomical differences between the two anecic genera demonstrated by Bolton [88] is that *L. terrestris* have very active calciferous glands, while those of *A. longa longa* are very poorly developed. Piearce [89] formulated several hypotheses to explain this differentiation of calciferous glands between both genera, such as the neutralization of dietary acids, the fixation of respiratory carbon dioxide or the excretion of excess calcium in the diet. Although it remains speculative, these anatomical differences could be interpreted as an adaptation to a distinct feeding behaviour. Thereafter, if differences in feeding behaviour and consequences on growth or burrowing behaviour are confirmed, further studies are warranted on the consequences of soil functioning (e.g. decomposition of organic matter, primary production, water regulation...) as they are sorely lacking especially for AAS.

Finally, differences in feeding behaviour, growth rate and burrowing behaviour highlighted in this review have often been observed using the same anecic earthworm species of *Lumbricus* (i.e., *L. centralis*, *L. terrestris*) or *Aporrectodea* (i.e., *A. longa longa*, *A. giardi*) genera. Further studies with other *Lumbricus* and *Aporrectodea* species in addition to other anecic genera, such as *Scherotheca*, *Octodrilus*, *Fitzingeria*, could be useful to confirm distinct ecological behaviours within the anecics. It would allow us to investigate whether this distinction is genus-related or whether other genera of anecic earthworms may cluster together to form an ecological sub-category.

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References

[1] M.B. Bouché, Lombriciens de France: écologie et systématique, INRA-Annales de Zoologie Ecologie Animale, INRA, France, 1972.

[2] J.W. Van Groenigen, K.J. Van Groenigen, G.F. Koopmans, L. Stokkermans, H.M.J. Vos, I.M. Lubbers, How fertile are earthworm casts? A meta-analysis, Geoderma. 338 (2019) 525–535.

[3] W. Huang, G. González, X. Zou, Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global meta-analysis, Appl. Soil Ecol. 150 (2020) 103473.

[4] O. Ferlian, M.P. Thakur, A. Castañeda González, L.M. San Emeterio, S. Marr, B. da Silva Rocha, N. Eisenhauer, Soil chemistry turned upside down: a meta-analysis of invasive earthworm effects on soil chemical properties, Ecology. 101 (2020) e02936.

[5] N. Bottinelli, Y. Capowiez, Earthworm ecological categories are not functional groups, Biol. Fertil. Soils. 57 (2021) 329–331.

[6] M.B. Bouché, Strategies lombriciennes, Ecol. Bull. 25 (1977) 122–132.

[7] N. Bottinelli, M. Hedde, P. Jouquet, Y. Capowiez, An explicit definition of earthworm ecological categories – Marcel Bouché's triangle revisited, Geoderma. 372 (2020) 114361.

[8] G. Ferrière, Fonctions des Lombriciens. VII. Une méthode d'analyse de la matière organique végétale ingérée, Pedobiologia. 20 (1980) 263–273.

[9] D. Jégou, D. Cluzeau, J. Balesdent, P. Tréhen, Effects of four ecological categories of earthworms on carbon transfer in soil, Appl. Soil Ecol. 9 (1998) 249–255.

[10] N. Eisenhauer, S. Marhan, S. Scheu, Assessment of anecic behavior in selected earthworm species: Effects on wheat seed burial, seedling establishment, wheat growth and litter incorporation, Appl. Soil Ecol. 38 (2008) 79–82.

[11] W.S. Andriuzzi, O. Schmidt, L. Brussaard, J.H. Faber, T. Bolger, Earthworm functional traits and interspecific interactions affect plant nitrogen acquisition and primary production, Appl. Soil Ecol. 104 (2016) 148–156.

[12] F. Bastardie, Y. Capowiez, J.-R. de Dreuzy, D. Cluzeau, X-ray tomographic and hydraulic characterization of burrowing by three earthworm species in repacked soil cores, Appl. Soil Ecol. 24 (2003) 3–16.

[13] Y. Capowiez, N. Bottinelli, S. Sammartino, E. Michel, P. Jouquet, Morphological and functional characterisation of the burrow systems of six earthworm species (Lumbricidae), Biol. Fertil. Soils. 51 (2015) 869–877.

[14] V. Nuutinen, K.R. Butt, Earthworm dispersal of plant litter across the surface of agricultural soils, Ecology. 100 (2019) e02669.

[15] G.G. Brown, I. Barois, P. Lavelle, Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains, Eur. J. Soil Biol. 36 (2000) 177–198.

[16] T. Larsen, M.M. Pollierer, M. Holmstrup, A. D'Annibale, K. Maraldo, N. Andersen, J. Eriksen, Substantial nutritional contribution of bacterial amino acids to earthworms and enchytraeids: A case study from organic grasslands, Soil Biol. Biochem. 99 (2016) 21–27.

[17] M.S. Laverack, The physiology of earthworms, Pergamon Press, Oxford, England, 1963.

[18] O. Daniel, L. Kohli, M. Bieri, Weight gain and weight loss of the earthworm *Lumbricus terrestris* L. at different temperatures and body weights, Soil Biol. Biochem. 28 (1996) 1235–1240.

[19] D. Jégou, S. Schrader, H. Diestel, D. Cluzeau, Morphological, physical and biochemical characteristics of burrow walls formed by earthworms, Appl. Soil Ecol. 17 (2001) 165–174.
[20] K. Hoeffner, M. Santonja, D. Cluzeau, C. Monard, Epi-anecic rather than strict-anecic earthworms enhance soil enzymatic activities, Soil Biol. Biochem. 132 (2019) 93–100.
[21] G.E. Gates, Burmese earthworms: An introduction to the systematics and biology of megadrile oligochaetes with special reference to Southeast Asia, Trans. Am. Philos. Soc. 62 (1972) 1–326.
[22] J.-F. David, J.-F. Ponge, P. Arpin, G. Vannier, Reactions of the macrofauna of a forest mull to experimental perturbations of litter supply, Oikos. 61 (1991) 316–326.
[23] S.W. James, D. Porco, T. Decaëns, B. Richard, R. Rougerie, C. Erséus, DNA barcoding reveals cryptic diversity in *Lumbricus terrestris* L., 1758 (Clitellata): Resurrection of *L. herculeus* (Savigny, 1826), PLOS ONE. 5 (2010) e15629.
[24] A. Vergnes, M. Blouin, A. Muratet, T.Z. Lerch, M. Mendez-Millan, M. Rouelle-Castrec, F. Dubs, Initial conditions during Technosol implementation shape earthworms and ants diversity, Landsc. Urban Plan. 159 (2017) 32–41.
[25] T. Decaëns, P. Margerie, M. Aubert, M. Hedde, F. Bureau, Assembly rules within earthworm communities in North-Western France - A regional analysis, Appl. Soil Ecol. 39 (2008) 321–335.
[26] C. Pelosi, B. Pey, M. Hedde, G. Caro, Y. Capowiez, M. Guernion, J. Peigné, D. Piron, M. Bertrand, D. Cluzeau, Reducing tillage in cultivated fields increases earthworm functional diversity, Appl. Soil Ecol. 83 (2014) 79–87.
[27] D. Cluzeau, M. Lebouvier, P. Trehen, M.B. Bouché, C. Badour, A. Perraud, Relations between earthworms and agricultural practices in the vineyards of Champagne. Preliminary results, Earthworms Mucchi Modena. (1987) 465–484.
[28] J. Cortez, R. Hameed, M.B. Bouché, C and N transfer in soil with or without earthworms fed with 14C- and 15N-labelled wheat straw, Soil Biol. Biochem. 21 (1989) 491–497.
[29] A. Auclerc, Y. Capowiez, F. Guérold, J. Nahmani, Application of X-ray tomography to evaluate liming impact on earthworm burrowing activity in an acidic forest soil under laboratory conditions, Geoderma. 202–203 (2013) 45–50.
[30] F. Binet, P. Trehen, Experimental microcosm study of the role of *Lumbricus terrestris* (Oligochaeta : Lumbricidae) on nitrogen dynamics in cultivated soils, Soil Biol. Biochem. 24 (1992) 1501–1506.
[31] J. Cortez, R. Hameed, Effects of maturation of Rye-Grass (*Lolium perenne* L) litter in soil on its consumption and assimilation by earthworms, *Lumbricus terrestris* L, Rev. Ecol. Biol. Sol. 25 (1988) 397–412.
[32] M.B. Bouché, A. Kretzschmar, Fonctions des lombriciens II. Recherches méthodologiques pour l’analyse qualitative de la matière organique végétale ingéré (étude du peuplement de la station RCP-165/PBI), Rev. Ecol. Biol. Sol. 11 (1974) 127–139.
[33] M. Judas, Gut content-analysis of earthworms (lumbricidae) in a beechwood, Soil Biol. Biochem. 24 (1992) 1413–1417.
[34] N. Bernier, Earthworm feeding activity and development of the humus profile, Biol. Fertil. Soils. 26 (1998) 215–223.
[35] A. Farenhorst, B.T. Bowman, Sorption of atrazine and metolachlor by earthworm surface castings and soil, J. Environ. Sci. Health Part B. 35 (2000) 157–173.
[36] D. Jégou, D. Cluzeau, V. Hallaire, J. Balesdent, P. Tréhen, Burrowing activity of the earthworms *Lumbricus terrestris* and *Aporrectodea giardi* and consequences on C transfers in soil, Eur. J. Soil Biol. 36 (2000) 27–34.

[37] A. Vidal, K. Quenea, M. Alexis, S. Derenne, Molecular fate of root and shoot litter on incorporation and decomposition in earthworm casts, Org. Geochem. 101 (2016) 1–10.
[38] A. Vidal, K. Quenea, M. Alexis, T.T. Nguyen Tu, J. Mathieu, V. Vaury, S. Derenne, Fate of 13C labelled root and shoot residues in soil and anecic earthworm casts: A mesocosm experiment, Geoderma. 285 (2017) 9–18.
[39] M.J. Shipitalo, R. Protz, A.D. Tomlin, Effect of diet on the feeding and casting activity of *Lumbricus terrestris* and *L. rubellus* in laboratory culture, Soil Biol. Biochem. 20 (1988) 233–237.
[40] J.H. Görres, M.C. Savin, J.A. Amador, Soil micropore structure and carbon mineralization in burrows and casts of an anecic earthworm (*Lumbricus terrestris*), Soil Biol. Biochem. 33 (2001) 1881–1887.
[41] S. Marhan, S. Scheu, Effects of sand and litter availability on organic matter decomposition in soil and in casts of *Lumbricus terrestris* L., Geoderma. 128 (2005) 155–166.
[42] S. Marhan, E. Kandeler, S. Scheu, Phospholipid fatty acid profiles and xylanase activity in particle size fractions of forest soil and casts of *Lumbricus terrestris* L. (Oligochaeta, Lumbricidae), Appl. Soil Ecol. 35 (2007) 412–422.
[43] J. Clause, S. Barot, B. Richard, T. Decaëns, E. Forey, The interactions between soil type and earthworm species determine the properties of earthworm casts, Appl. Soil Ecol. 83 (2014) 149–158.
[44] M. Sauvadet, M. Chauvat, D. Cluzeau, P.-A. Maron, C. Villenave, I. Bertrand, The dynamics of soil micro-food web structure and functions vary according to litter quality, Soil Biol. Biochem. 95 (2016) 262–274.
[45] K. Hoeffner, C. Monard, M. Santonja, D. Cluzeau, Feeding behaviour of epi-anecic earthworm species and their impacts on soil microbial communities, Soil Biol. Biochem. 125 (2018) 1–9.
[46] J.K. Whalen, R.W. Parmelee, Growth of *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L. under laboratory and field conditions, Pedobiologia. 43 (1999) 1–10.
[47] C.N. Lowe, K.R. Butt, Influence of organic matter on earthworm production and behaviour: a laboratory-based approach with applications for soil restoration, Eur. J. Soil Biol. 38 (2002) 173–176.
[48] J. Kirchberger, N. Eisenhauer, W.W. Weisser, M. Türke, Experimental evaluation of herbivory on live plant seedlings by the earthworm *Lumbricus terrestris* L. in the presence and absence of Soil surface litter, PLoS ONE. 10 (2015) e0123465.
[49] J. Frazão, R.G.M. de Goede, Y. Capowiez, M.M. Pulleman, Soil structure formation and organic matter distribution as affected by earthworm species interactions and crop residue placement, Geoderma. 338 (2019) 453–463.
[50] G. Jorge-Escudero, C.A. Pérez, H. Friberg, S. Söderlund, S. Vero, G. Garmendia, J. Lagerlöf, Contribution of anecic and epigeic earthworms to biological control of *Fusarium graminearum* in wheat straw, Appl. Soil Ecol. 166 (2021) 103997.
[51] J.A. Van Rhee, Earthworm activities and the breakdown of organic matter in agricultural soils, in: Soil Org. Proc. Colloq. Soil Fauna Soil Microflora Their Relatsh., North-Holland Publishing Company, 1963: pp. 55–59.
[52] S.A. Moody, M.J.I. Briones, T.G. Piearce, J. Dighton, Selective consumption of decomposing wheat straw by earthworms, Soil Biol. Biochem. 27 (1995) 1209–1213.
[53] T. Alekseeva, P. Besse, F. Binet, A.M. Delort, C. Forano, N. Josselin, M. Sancelme, C. Tixier, Effect of earthworm activity (*Aporrectodea giardi*) on atrazine adsorption and biodegradation, Eur. J. Soil Sci. 57 (2006) 295–307.

[54] A. Martin, J. Balesdent, A. Mariotti, Earthworm diet related to soil organic matter dynamics through 13C measurements, Oecologia. 91 (1992) 23–29.
[55] Q.L. Zhang, P.F. Hendrix, Earthworm (*Lumbricus rubellus* and *Aporrectodea caliginosa*) effects on carbon flux in soil, Soil Sci. Soc. Am. J. 59 (1995) 816–823.
[56] W.S. Andriuzzi, P.-T. Ngo, S. Geisen, A.M. Keith, K. Dumack, T. Bolger, M. Bonkowski, L. Brussaard, J.H. Faber, A. Chabbi, C. Rumpel, O. Schmidt, Organic matter composition and the protist and nematode communities around anecic earthworm burrows, Biol. Fertil. Soils. 52 (2015) 91–100.
[57] A. Don, B. Steinberg, I. Schöning, K. Pritsch, M. Joschko, G. Gleixner, E.-D. Schulze, Organic carbon sequestration in earthworm burrows, Soil Biol. Biochem. 40 (2008) 1803–1812.
[58] K.R. Butt, V. Nuutinen, T. Sirén, Resource distribution and surface activity of adult *Lumbricus terrestris* L. in an experimental system, Pedobiologia. 47 (2003) 548–553.
[59] M.J. McTavish, S.D. Murphy, Rapid redistribution and long-term aggregation of mulch residues by earthworms (*Lumbricus terrestris*), Appl. Soil Ecol. 169 (2022) 104195.
[60] R.W. Sims, B.M. Gerard, Earthworms. Synopses of the British Fauna No. 31 (revised) The Linnean Society and the Brackish-Water Sciences Association, Field Studies Council, Shrewsbury, 1999.
[61] B. Griffith, M. Türke, W.W. Weisser, N. Eisenhauer, Herbivore behavior in the anecic earthworm species *Lumbricus terrestris* L.?, Eur. J. Soil Biol. 55 (2013) 62–65.
[62] M.J.I. Briones, M.H. Garnett, T.G. Piearce, Earthworm ecological groupings based on 14C analysis, Soil Biol. Biochem. 37 (2005) 2145–2149.
[63] O. Schmidt, Intrapopulation variation in carbon and nitrogen stable isotope ratios in the earthworm *Aporrectodea longa*, Ecol. Res. 14 (1999) 317–328.
[64] O. Schmidt, N.J. Ostle, Tracing nitrogen derived from slurry in earthworms using 15N/14N stable isotope ratios at natural abundances, Appl. Soil Ecol. 12 (1999) 7–13.
[65] O. Schmidt, C.M. Scrimgeour, L.L. Handley, Natural abundance of 15N and 13C in earthworms from a wheat and a wheat-clover field, Soil Biol. Biochem. 29 (1997) 1301–1308.
[66] M.J.I. Briones, R. Bol, D. Sleep, L. Sampedro, D. Allen, A dynamic study of earthworm feeding ecology using stable isotopes, Rapid Commun. Mass Spectrom. 13 (1999) 1300–1304.
[67] M.J.I. Briones, R. Bol, D. Sleep, D. Allen, L. Sampedro, Spatio-temporal variation of stable isotope ratios in earthworms under grassland and maize cropping systems, Soil Biol. Biochem. 33 (2001) 1673–1682.
[68] M.J.I. Briones, R. Bol, Natural abundance of 13C and 15N in earthworms from different cropping treatments: The 7th international symposium on earthworm ecology · Cardiff · Wales · 2002, Pedobiologia. 47 (2003) 560–567.
[69] H.M.J. Vos, G.F. Koopmans, L. Beezemer, R.G.M. de Goede, T. Hiemstra, J.W. van Groenigen, Large variations in readily-available phosphorus in casts of eight earthworm species are linked to cast properties, Soil Biol. Biochem. 138 (2019) 107583.
[70] K.R. Butt, Interactions between selected earthworm species: A preliminary, laboratory-based study, Appl. Soil Ecol. 9 (1998) 75–79.
[71] C.N. Lowe, K.R. Butt, Growth of hatchling earthworms in the presence of adults: interactions in laboratory culture, Biol. Fertil. Soils. 35 (2002) 204–209.
[72] C.N. Lowe, K.R. Butt, Interspecific interactions between earthworms: A laboratory-based investigation, Pedobiologia. 43 (1999) 808–817.

[73] K.R. Butt, Reproduction and growth of three deep-burrowing earthworms (Lumbricidae) in laboratory culture in order to assess production for soil restoration, Biol. Fertil. Soils. 16 (1993) 135–138.
[74] J. Pitkänen, V. Nuutinen, Distribution and abundance of burrows formed by *Lumbricus terrestris* L. and *Aporrectodea caliginosa* Sav. in the soil profile, Soil Biol. Biochem. 29 (1997) 463–467.
[75] D. Jégou, D. Cluzeau, H.J. Wolf, Y. Gandon, P. Tréhen, Assessment of the burrow system of *Lumbricus terrestris*, *Aporrectodea giardi*, and *Aporrectodea caliginosa* using X-ray computed tomography, Biol. Fertil. Soils. 26 (1997) 116–121.
[76] D. Jégou, V. Hallaire, D. Cluzeau, P. Tréhen, Characterization of the burrow system of the earthworms *Lumbricus terrestris* and *Aporrectodea giardi* using X-ray computed tomography and image analysis, Biol. Fertil. Soils. 29 (1999) 314–318.
[77] F. Bastardie, Y. Capowiez, P. Renault, D. Cluzeau, A radio-labelled study of earthworm behaviour in artificial soil cores in term of ecological types, Biol. Fertil. Soils. 41 (2005) 320–327.
[78] D. Felten, C. Emmerling, Earthworm burrowing behaviour in 2D terraria with single- and multi-species assemblages, Biol. Fertil. Soils. 45 (2009) 789–797.
[79] Y. Capowiez, F. Gilbert, A. Vallat, J.-C. Poggiale, J.-M. Bonzom, Depth distribution of soil organic matter and burrowing activity of earthworms—mesocosm study using X-ray tomography and luminophores, Biol. Fertil. Soils. 57 (2021) 337–346.
[80] M.J.I. Briones, R. Álvarez-Otero, Body wall thickness as a potential functional trait for assigning earthworm species to ecological categories, Pedobiologia. 67 (2018) 26–34.
[81] G.A. Nielsen, F.D. Hole, Earthworms and the development of coprogenous A1 horizons in forest soils of Wisconsin, Soil Sci. Soc. Am. J. 28 (1964) 426–430.
[82] W.D. Shuster, S. Subler, E.L. McCoy, Deep-burrowing earthworm additions changed the distribution of soil organic carbon in a chisel-tilled soil, Soil Biol. Biochem. 33 (2001) 983–996.
[83] B. Pey, J. Cortet, F. Watteau, K. Cheynier, C. Schwartz, Structure of earthworm burrows related to organic matter of a constructed Technosol, Geoderma. 202–203 (2013) 103–111.
[84] L.M. Semenova, Relation of the structure of digestive tract in earthworms (Lumbricidae) to their feeding habits, Zool Zh. 45 (1966) 986–997.
[85] M. Florkin, Chemical Zoology V4: Annelida, Echiuria, And Sipuncula, Elsevier, 2012.
[86] T.S. Perel, Differences in Lumbricid organization connected with ecological properties, Ecol. Bull. 25 (1977) 56–63.
[87] C.E. Stevens, I.D. Hume, Comparative physiology of the vertebrate digestive system, Cambridge University Press, 2004.
[88] P.J. Bolton, Studies in the general ecology, physiology and bioenergetics of woodland lumbricidae, Doctoral, Durham University, 1969.
[89] T.G. Piearce, The calcium relations of selected Lumbricidae, J. Anim. Ecol. 41 (1972) 167.
[90] M.A. Wright, Factors' governing ingestion by the earthworm *Lumbricus terrestris* (L.), with special reference to apple leaves, Ann. Appl. Biol. 70 (1972) 175–188.
[91] T. Piearce, Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils, Pedobiologia. 33 (1989) 91–100.
[92] B.M. Doube, O. Schmidt, K. Killham, R. Correll, Influence of mineral soil on the palatability of organic matter for lumbricid earthworms: A simple food preference study, Soil Biol. Biochem. 29 (1997) 569–575.

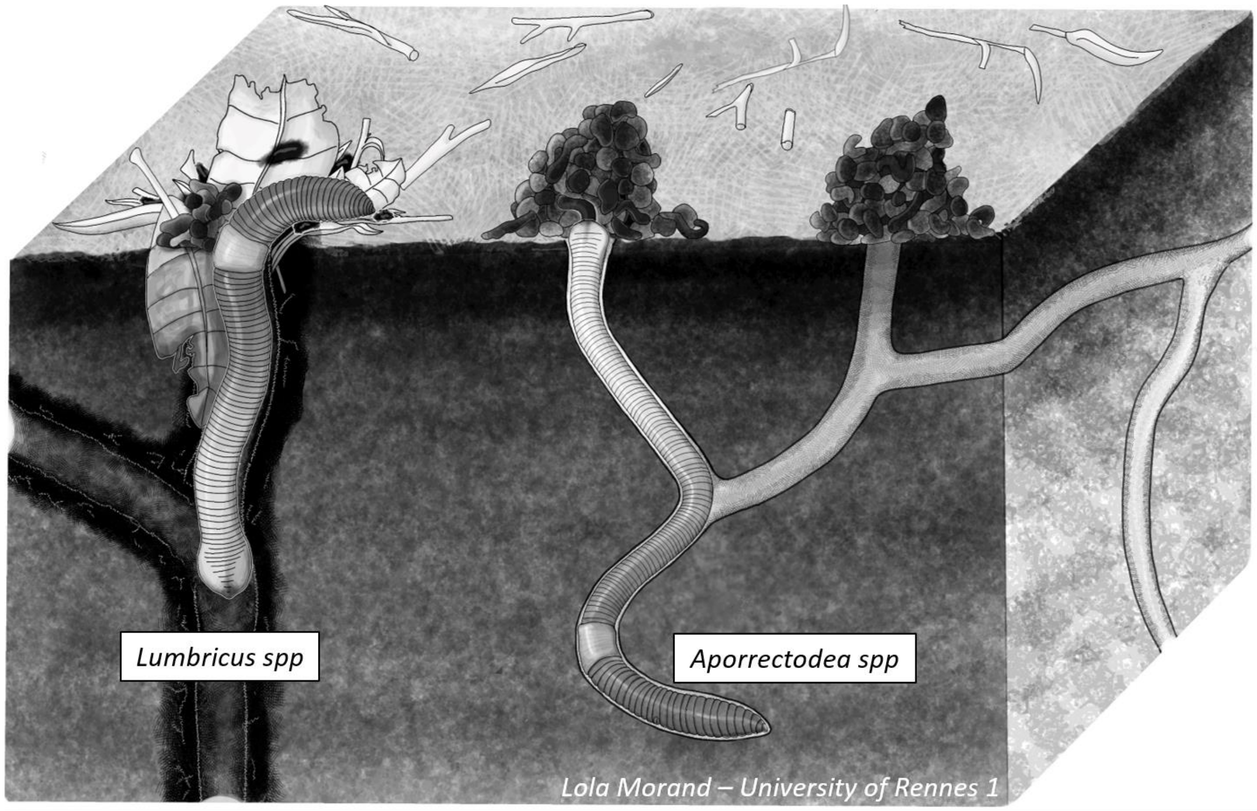
[93] R. Neilson, B. Boag, Feeding preferences of some earthworm species common to upland pastures in Scotland, Pedobiologia. 47 (2003) 1–8.
[94] N.S.S. Rajapaksha, K.R. Butt, E.I. Vanguelova, A.J. Moffat, Earthworm selection of Short Rotation Forestry leaf litter assessed through preference testing and direct observation, Soil Biol. Biochem. 67 (2013) 12–19.
[95] T.G. Piearce, Gut contents of some lumbricid earthworms, Pedobiologia. 18 (1978) 153–157.
[96] F. Ashwood, K.R. Butt, K.J. Doick, E.I. Vanguelova, Investigating tree foliar preference by the earthworms *Aporrectodea longa* and *Allolobophora chlorotica* in reclaimed and loam soil, Appl. Soil Ecol. 110 (2017) 109–117.
[97] J. Cortez, M.B. Bouché, Do earthworms eat living roots?, Soil Biol. Biochem. 24 (1992) 913–915.
[98] P. Euteneuer, H. Wagentristl, S. Steinkellner, M. Fuchs, J.G. Zaller, H.-P. Piepho, K.R. Butt, Contrasting effects of cover crops on earthworms: Results from field monitoring and laboratory experiments on growth, reproduction and food choice, Eur. J. Soil Biol. 100 (2020) 103225.
[99] M. Mcrill, G.R. Sagar, Earthworms and Seeds, Nature. 243 (1973) 482.
[100] D.L. Shumway, R.T. Koide, Seed preferences of *Lumbricus terrestris* L., Appl. Soil Ecol. 1 (1994) 11–15.
[101] J. Clause, P. Margerie, E. Langlois, T. Decaëns, E. Forey, Fat but slim: Criteria of seed attractiveness for earthworms, Pedobiologia. 54, Supplement (2011) S159–S165.
[102] P.M. Quackenbush, R.A. Butler, N.C. Emery, M.A. Jenkins, E.J. Kladivko, K.D. Gibson, *Lumbricus terrestris* prefers to consume garlic mustard (*Alliaria petiolata*) seeds, Invasive Plant Sci. Manag. 5 (2012) 148–154.
[103] J. Clause, S. Barot, E. Forey, Effects of cast properties and passage through the earthworm gut on seed germination and seedling growth, Appl. Soil Ecol. 96 (2015) 108–113.
[104] J. Clause, E. Forey, N. Eisenhauer, C.E. Seal, A. Soudey, L. Colville, S. Barot, Seed selection by earthworms: chemical seed properties matter more than morphological traits, Plant Soil. 413 (2017) 97–110.
[105] K.R. Butt, Food quality affects production of *Lumbricus terrestris* (L.) under controlled environmental conditions, Soil Biol. Biochem. 43 (2011) 2169–2175.
[106] T.S. Svendsen, G.H. Baker, Survival and growth of *Aporrectodea longa* (Lumbricidae) fed on sheep and cow dung with and without moxidectin residues, Aust. J. Agric. Res. 53 (2002) 447–451.
[107] N.L. Schon, A.D. Mackay, R.A. Gray, C. van Koten, Establishment of *Aporrectodea longa* and measurement of dung carbon incorporation in soils under permanent pasture, Eur. J. Soil Biol. 75 (2016) 174–179.
[108] O.P. Schulmann, A.V. Tiunov, Leaf litter fragmentation by the earthworm *Lumbricus terrestris* L., Pedobiologia. 43 (1999) 453–458.
[109] A. Cooke, M. Luxton, others, Effect of microbes on food selection by *Lumbricus terrestris*., Rev. Ecol. Biol. Sol. 17 (1980) 365–370.
[110] J. Cooke, The effects of fungi on food selection by *Lumbricus terrestris* L., in: J.E. Satchell (Ed.), Earthworm Ecol., Springer Netherlands, 1983: pp. 365–373.
[111] M. Bonkowski, B.S. Griffiths, K. Ritz, Food preferences of earthworms for soil fungi, Pedobiologia. 44 (2000) 666–676.
[112] K.R. Butt, Utilisation of solid paper-mill sludge and spent brewery yeast as a feed for soil-dwelling earthworms, Bioresour. Technol. 44 (1993) 105–107.

[113] K.R. Butt, J. Frederickson, R.M. Morris, Effect of earthworm density on the growth and reproduction, Pedobiologia. 38 (1994) 254–261.
[114] W.E. Hamilton, D.L. Dindal, C.M. Parkinson, M.J. Mitchell, Interaction of earthworm species in sewage sludge-amended soil microcosms: *Lumbricus terrestris* and *Eisenia fetida*, J. Appl. Ecol. 25 (1988) 847–852.
[115] B.M. Doube, P.M. Stephens, C.W. Davoren, M.H. Ryder, Interactions between earthworms, beneficial soil microorganisms and root pathogens, Appl. Soil Ecol. 1 (1994) 3–10.
[116] P.R. Dalby, G.H. Baker, S.E. Smith, Competition and cocoon consumption by the earthworm *Aporrectodea longa*, Appl. Soil Ecol. 10 (1998) 127–136.

TABLE

Table 1: Resource spectrum of the selected temperate anecic earthworm species (*Lumbricus centralis*, *Lumbricus terrestris*, *Aporrectodea longa longa* and *Aporrectodea giardi*) found in this review (non-exhaustive table, useful for illustrative purposes).

Resource spectrum		***Lumbricus* anecic species**	***Aporrectodea* anecic species**
PLANTS	Shoots	**Dead:** [90,91,33,52,92,34,93,10,94,11,45,20] **Alive:** [6,60,61,48]	**Either dead or alive:** [95,52,28,92–94,11,96]
PLANTS	Roots	**Either dead or alive:** [32,95,8,34,37] **Alive:** [97]	**Either dead or alive:** [95,98]
PLANTS	Seeds	[99,95,100,10,101–104]	[95,10]
PLANTS	Other	**Pollen and moss:** [34]	
Dung		[92,70,72,47,71,105]	[92,70,72,106,47,71,107]
Soil		[95,92,34,108,93,41]	[95,28,92,93]
Micro-organisms		**Fungi:** [109,110,34,52,111,16] **Bacteria:** [90,16] **Algae:** [34]	**Fungi:** [95,52,16] **Bacteria:** [16] **Protozoa:** [95] **Algae:** [95]
Others materials		**Paper sludge:** [73,112,113] **Sewage sludges:** [114,115]	**Earthworm cocoons:** [116] **Nodes and arthropod cuticle:** [95]



SUPPLEMENTARY MATERIAL

TITLE: TWO DISTINCT ECOLOGICAL BEHAVIOURS WITHIN ANECIC EARTHWORM SPECIES IN TEMPERATE CLIMATES

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Supplementary material 1: Papers found in ISI Web of Knowledge database published between 1963 and 2021, dealing with the feeding behaviour, growth rate and burrowing behaviour of one or further selected temperate anecic species (*Lumbricus centralis, Lumbricus terrestris, Aporrectodea longa longa* and *Aporrectodea giardi*).

Alekseeva, T., Besse, P., Binet, F., Delort, A.M., Forano, C., Josselin, N., Sancelme, M., Tixier, C., 2006. Effect of earthworm activity (*Aporrectodea giardi*) on atrazine adsorption and biodegradation. Eur. J. Soil Sci. 57, 295–307.

Andriuzzi, W.S., Ngo, P.-T., Geisen, S., Keith, A.M., Dumack, K., Bolger, T., Bonkowski, M., Brussaard, L., Faber, J.H., Chabbi, A., Rumpel, C., Schmidt, O., 2015. Organic matter composition and the protist and nematode communities around anecic earthworm burrows. Biol. Fertil. Soils 52, 91–100.

Andriuzzi, W.S., Schmidt, O., Brussaard, L., Faber, J.H., Bolger, T., 2016. Earthworm functional traits and interspecific interactions affect plant nitrogen acquisition and primary production. Appl. Soil Ecol. 104, 148–156.

Ashwood, F., Butt, K.R., Doick, K.J., Vanguelova, E.I., 2017. Investigating tree foliar preference by the earthworms *Aporrectodea longa* and *Allolobophora chlorotica* in reclaimed and loam soil. Appl. Soil Ecol. 110, 109–117.

Bastardie, F., Capowiez, Y., de Dreuzy, J.-R., Cluzeau, D., 2003. X-ray tomographic and hydraulic characterization of burrowing by three earthworm species in repacked soil cores. Appl. Soil Ecol. 24, 3–16.

Bastardie, F., Capowiez, Y., Renault, P., Cluzeau, D., 2005. A radio-labelled study of earthworm behaviour in artificial soil cores in term of ecological types. Biol. Fertil. Soils 41, 320–327.

Bernier, N., 1998. Earthworm feeding activity and development of the humus profile. Biol. Fertil. Soils 26, 215–223.

Binet, F., Trehen, P., 1992. Experimental microcosm study of the role of *Lumbricus terrestris* (Oligochaeta : Lumbricidae) on nitrogen dynamics in cultivated soils. Soil Biol. Biochem. 24, 1501–1506.

Bolton, P.J., 1969. Studies in the general ecology, physiology and bioenergetics of woodland lumbricidae (Doctoral). Durham University.

Bonkowski, M., Griffiths, B.S., Ritz, K., 2000. Food preferences of earthworms for soil fungi. Pedobiologia 44, 666–676.

Bottinelli, N., Hedde, M., Jouquet, P., Capowiez, Y., 2020. An explicit definition of earthworm ecological categories – Marcel Bouché's triangle revisited. Geoderma 372, 114361.

Bouché, M.B., 1977. Strategies lombriciennes. Ecol. Bull., Soil Organisms as Components of Ecosystems 25, 122–132.

Bouché, M.B., 1972. Lombriciens de France: écologie et systématique, INRA-Annales de Zoologie Ecologie Animale. ed. INRA, France.

Bouché, M.B., Kretzschmar, A., 1974. Fonctions des lombriciens II. Recherches méthodologiques pour l'analyse qualitative de la matière organique végétale ingéré (étude du peuplement de la station RCP-165/PBI). Rev. Ecol. Biol. Sol 11, 127–139.

Briones, M.J.I., Álvarez-Otero, R., 2018. Body wall thickness as a potential functional trait for assigning earthworm species to ecological categories. Pedobiologia 67, 26–34.
Briones, M.J.I., Bol, R., 2003. Natural abundance of 13C and 15N in earthworms from different cropping treatments: The 7th international symposium on earthworm ecology · Cardiff · Wales · 2002. Pedobiologia 47, 560–567.
Briones, M.J.I., Bol, R., Sleep, D., Allen, D., Sampedro, L., 2001. Spatio-temporal variation of stable isotope ratios in earthworms under grassland and maize cropping systems. Soil Biol. Biochem. 33, 1673–1682.
Briones, M.J.I., Bol, R., Sleep, D., Sampedro, L., Allen, D., 1999. A dynamic study of earthworm feeding ecology using stable isotopes. Rapid Commun. Mass Spectrom. 13, 1300–1304.
Briones, M.J.I., Garnett, M.H., Piearce, T.G., 2005. Earthworm ecological groupings based on 14C analysis. Soil Biol. Biochem. 37, 2145–2149.
Butt, K.R., 2011. Food quality affects production of *Lumbricus terrestris* (L.) under controlled environmental conditions. Soil Biol. Biochem. 43, 2169–2175.
Butt, K.R., 1998. Interactions between selected earthworm species: A preliminary, laboratory-based study. Appl. Soil Ecol. 9, 75–79.
Butt, K.R., 1993a. Reproduction and growth of three deep-burrowing earthworms (Lumbricidae) in laboratory culture in order to assess production for soil restoration. Biol. Fertil. Soils 16, 135–138.
Butt, K.R., 1993b. Utilisation of solid paper-mill sludge and spent brewery yeast as a feed for soil-dwelling earthworms. Bioresour. Technol. 44, 105–107.
Butt, K.R., Frederickson, J., Morris, R.M., 1994. Effect of earthworm density on the growth and reproduction. Pedobiologia 38, 254–261.
Butt, K.R., Nuutinen, V., Sirén, T., 2003. Resource distribution and surface activity of adult *Lumbricus terrestris* L. in an experimental system. Pedobiologia, 7th International Symposium on Earthworm Ecology 47, 548–553.
Capowiez, Y., Bottinelli, N., Sammartino, S., Michel, E., Jouquet, P., 2015. Morphological and functional characterisation of the burrow systems of six earthworm species (Lumbricidae). Biol. Fertil. Soils 51, 869–877.
Capowiez, Y., Gilbert, F., Vallat, A., Poggiale, J.-C., Bonzom, J.-M., 2021. Depth distribution of soil organic matter and burrowing activity of earthworms—mesocosm study using X-ray tomography and luminophores. Biol. Fertil. Soils 57, 337–346.
Clause, J., Barot, S., Forey, E., 2015. Effects of cast properties and passage through the earthworm gut on seed germination and seedling growth. Appl. Soil Ecol. 96, 108–113.
Clause, J., Barot, S., Richard, B., Decaëns, T., Forey, E., 2014. The interactions between soil type and earthworm species determine the properties of earthworm casts. Appl. Soil Ecol. 83, 149–158.
Clause, J., Forey, E., Eisenhauer, N., Seal, C.E., Soudey, A., Colville, L., Barot, S., 2017. Seed selection by earthworms: chemical seed properties matter more than morphological traits. Plant Soil 413, 97–110.
Clause, J., Margerie, P., Langlois, E., Decaëns, T., Forey, E., 2011. Fat but slim: Criteria of seed attractiveness for earthworms. Pedobiologia 54, Supplement, S159–S165.
Cooke, A., Luxton, M., others, 1980. Effect of microbes on food selection by *Lumbricus terrestris*. Rev. Ecol. Biol. Sol 17, 365–370.
Cooke, J., 1983. The effects of fungi on food selection by *Lumbricus terrestris* L., in: Satchell, J.E. (Ed.), Earthworm Ecology. Springer Netherlands, pp. 365–373.
Cortez, J., Bouché, M.B., 1992. Do earthworms eat living roots? Soil Biol. Biochem. 24, 913–915.

Cortez, J., Hameed, R., 1988. Effects of maturation of Rye-Grass (*Lolium perenne* L) litter in soil on its consumption and assimilation by earthworms, *Lumbricus terrestris* L. Rev. Ecol. Biol. Sol 25, 397–412.

Cortez, J., Hameed, R., Bouché, M.B., 1989. C and N transfer in soil with or without earthworms fed with 14C- and 15N-labelled wheat straw. Soil Biol. Biochem. 21, 491–497.

Dalby, P.R., Baker, G.H., Smith, S.E., 1998. Competition and cocoon consumption by the earthworm *Aporrectodea longa*. Appl. Soil Ecol. 10, 127–136.

Don, A., Steinberg, B., Schöning, I., Pritsch, K., Joschko, M., Gleixner, G., Schulze, E.-D., 2008. Organic carbon sequestration in earthworm burrows. Soil Biol. Biochem. 40, 1803–1812.

Doube, B.M., Schmidt, O., Killham, K., Correll, R., 1997. Influence of mineral soil on the palatability of organic matter for lumbricid earthworms: A simple food preference study. Soil Biol. Biochem., 5th International Symposium on Earthworm Ecology 29, 569–575.

Doube, B.M., Stephens, P.M., Davoren, C.W., Ryder, M.H., 1994. Interactions between earthworms, beneficial soil microorganisms and root pathogens. Appl. Soil Ecol. 1, 3–10.

Eisenhauer, N., Marhan, S., Scheu, S., 2008. Assessment of anecic behavior in selected earthworm species: Effects on wheat seed burial, seedling establishment, wheat growth and litter incorporation. Appl. Soil Ecol. 38, 79–82.

Euteneuer, P., Wagentristl, H., Steinkellner, S., Fuchs, M., Zaller, J.G., Piepho, H.-P., Butt, K.R., 2020. Contrasting effects of cover crops on earthworms: Results from field monitoring and laboratory experiments on growth, reproduction and food choice. Eur. J. Soil Biol. 100, 103225.

Farenhorst, A., Bowman, B.T., 2000. Sorption of atrazine and metolachlor by earthworm surface castings and soil. J. Environ. Sci. Health Part B 35, 157–173.

Felten, D., Emmerling, C., 2009. Earthworm burrowing behaviour in 2D terraria with single- and multi-species assemblages. Biol. Fertil. Soils 45, 789–797.

Ferrière, G., 1980. Fonctions des Lombriciens. VII. Une méthode d'analyse de la matière organique végétale ingérée. Pedobiologia 20, 263–273.

Florkin, M., 2012. Chemical Zoology V4: Annelida, Echiuria, And Sipuncula. Elsevier.

Frazão, J., de Goede, R.G.M., Capowiez, Y., Pulleman, M.M., 2019. Soil structure formation and organic matter distribution as affected by earthworm species interactions and crop residue placement. Geoderma 338, 453–463.

Gates, G.E., 1972. Burmese earthworms: An introduction to the systematics and biology of megadrile oligochaetes with special reference to Southeast Asia. Trans. Am. Philos. Soc. 62, 1–326.

Görres, J.H., Savin, M.C., Amador, J.A., 2001. Soil micropore structure and carbon mineralization in burrows and casts of an anecic earthworm (*Lumbricus terrestris*). Soil Biol. Biochem. 33, 1881–1887.

Griffith, B., Türke, M., Weisser, W.W., Eisenhauer, N., 2013. Herbivore behavior in the anecic earthworm species *Lumbricus terrestris* L.? Eur. J. Soil Biol. 55, 62–65.

Hamilton, W.E., Dindal, D.L., Parkinson, C.M., Mitchell, M.J., 1988. Interaction of earthworm species in sewage sludge-amended soil microcosms: *Lumbricus terrestris* and *Eisenia fetida*. J. Appl. Ecol. 25, 847–852.

Hoeffner, K., Monard, C., Santonja, M., Cluzeau, D., 2018. Feeding behaviour of epi-anecic earthworm species and their impacts on soil microbial communities. Soil Biol. Biochem. 125, 1–9.

Hoeffner, K., Santonja, M., Cluzeau, D., Monard, C., 2019. Epi-anecic rather than strict-anecic earthworms enhance soil enzymatic activities. Soil Biol. Biochem. 132, 93–100.

Jégou, D., Cluzeau, D., Balesdent, J., Tréhen, P., 1998. Effects of four ecological categories of earthworms on carbon transfer in soil. Appl. Soil Ecol. 9, 249–255.
Jégou, D., Cluzeau, D., Hallaire, V., Balesdent, J., Tréhen, P., 2000. Burrowing activity of the earthworms *Lumbricus terrestris* and *Aporrectodea giardi* and consequences on C transfers in soil. Eur. J. Soil Biol. 36, 27–34.
Jégou, D., Cluzeau, D., Wolf, H.J., Gandon, Y., Tréhen, P., 1997. Assessment of the burrow system of *Lumbricus terrestris*, *Aporrectodea giardi*, and *Aporrectodea caliginosa* using X-ray computed tomography. Biol. Fertil. Soils 26, 116–121.
Jégou, D., Hallaire, V., Cluzeau, D., Tréhen, P., 1999. Characterization of the burrow system of the earthworms *Lumbricus terrestris* and *Aporrectodea giardi* using X-ray computed tomography and image analysis. Biol. Fertil. Soils 29, 314–318.
Jégou, D., Schrader, S., Diestel, H., Cluzeau, D., 2001. Morphological, physical and biochemical characteristics of burrow walls formed by earthworms. Appl. Soil Ecol. 17, 165–174.
Jorge-Escudero, G., Pérez, C.A., Friberg, H., Söderlund, S., Vero, S., Garmendia, G., Lagerlöf, J., 2021. Contribution of anecic and epigeic earthworms to biological control of *Fusarium graminearum* in wheat straw. Appl. Soil Ecol. 166, 103997.
Judas, M., 1992. Gut content-analysis of earthworms (lumbricidae) in a beechwood. Soil Biol. Biochem. 24, 1413–1417.
Kirchberger, J., Eisenhauer, N., Weisser, W.W., Türke, M., 2015. Experimental evaluation of herbivory on live plant seedlings by the earthworm *Lumbricus terrestris* L. in the presence and absence of Soil surface litter. PLoS ONE 10, e0123465.
Larsen, T., Pollierer, M.M., Holmstrup, M., D'Annibale, A., Maraldo, K., Andersen, N., Eriksen, J., 2016. Substantial nutritional contribution of bacterial amino acids to earthworms and enchytraeids: A case study from organic grasslands. Soil Biol. Biochem. 99, 21–27.
Lowe, C.N., Butt, K.R., 2002a. Influence of organic matter on earthworm production and behaviour: a laboratory-based approach with applications for soil restoration. Eur. J. Soil Biol. 38, 173–176.
Lowe, C.N., Butt, K.R., 2002b. Growth of hatchling earthworms in the presence of adults: interactions in laboratory culture. Biol. Fertil. Soils 35, 204–209.
Lowe, C.N., Butt, K.R., 1999. Interspecific interactions between earthworms: A laboratory-based investigation. Pedobiologia 43, 808–817.
Marhan, S., Kandeler, E., Scheu, S., 2007. Phospholipid fatty acid profiles and xylanase activity in particle size fractions of forest soil and casts of *Lumbricus terrestris* L. (Oligochaeta, Lumbricidae). Appl. Soil Ecol. 35, 412–422.
Marhan, S., Scheu, S., 2005. Effects of sand and litter availability on organic matter decomposition in soil and in casts of *Lumbricus terrestris* L. Geoderma, Mechanisms and regulation of organic matter stabilisation in soils 128, 155–166.
Martin, A., Balesdent, J., Mariotti, A., 1992. Earthworm diet related to soil organic matter dynamics through 13C measurements. Oecologia 91, 23–29.
Mcrill, M., Sagar, G.R., 1973. Earthworms and Seeds. Nature 243, 482.
McTavish, M.J., Murphy, S.D., 2022. Rapid redistribution and long-term aggregation of mulch residues by earthworms (*Lumbricus terrestris*). Appl. Soil Ecol. 169, 104195.
Moody, S.A., Briones, M.J.I., Piearce, T.G., Dighton, J., 1995. Selective consumption of decomposing wheat straw by earthworms. Soil Biol. Biochem. 27, 1209–1213.
Neilson, R., Boag, B., 2003. Feeding preferences of some earthworm species common to upland pastures in Scotland. Pedobiologia 47, 1–8.

Nielsen, G.A., Hole, F.D., 1964. Earthworms and the development of coprogenous A1 horizons in forest soils of Wisconsin. Soil Sci. Soc. Am. J. 28, 426–430.

Nuutinen, V., Butt, K.R., 2019. Earthworm dispersal of plant litter across the surface of agricultural soils. Ecology 100, e02669.

Pelosi, C., Pey, B., Hedde, M., Caro, G., Capowiez, Y., Guernion, M., Peigné, J., Piron, D., Bertrand, M., Cluzeau, D., 2014. Reducing tillage in cultivated fields increases earthworm functional diversity. Appl. Soil Ecol., XVI International Colloquium on Soil Zoology & XIII International Colloquium on Apterygota, Coimbra, 2012 – Selected papers 83, 79–87.

Perel, T.S., 1977. Differences in Lumbricid organization connected with ecological properties. Ecol. Bull. 25, 56–63.

Pey, B., Cortet, J., Watteau, F., Cheynier, K., Schwartz, C., 2013. Structure of earthworm burrows related to organic matter of a constructed Technosol. Geoderma 202–203, 103–111.

Piearce, T., 1989. Acceptability of pteridophyte litters to *Lumbricus terrestris* and *Oniscus asellus*, and implications for the nature of ancient soils. Pedobiologia 33, 91–100.

Piearce, T.G., 1978. Gut contents of some lumbricid earthworms. Pedobiologia.

Pitkänen, J., Nuutinen, V., 1997. Distribution and abundance of burrows formed by Lumbricus terrestris L. and Aporrectodea caliginosa Sav. in the soil profile. Soil Biol. Biochem., 5th International Symposium on Earthworm Ecology 29, 463–467.

Quackenbush, P.M., Butler, R.A., Emery, N.C., Jenkins, M.A., Kladivko, E.J., Gibson, K.D., 2012. *Lumbricus terrestris* prefers to consume garlic mustard (*Alliaria petiolata*) seeds. Invasive Plant Sci. Manag. 5, 148–154.

Rajapaksha, N.S.S., Butt, K.R., Vanguelova, E.I., Moffat, A.J., 2013. Earthworm selection of Short Rotation Forestry leaf litter assessed through preference testing and direct observation. Soil Biol. Biochem. 67, 12–19.

Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.-A., Villenave, C., Bertrand, I., 2016. The dynamics of soil micro-food web structure and functions vary according to litter quality. Soil Biol. Biochem. 95, 262–274.

Schmidt, O., 1999. Intrapopulation variation in carbon and nitrogen stable isotope ratios in the earthworm *Aporrectodea longa*. Ecol. Res. 14, 317–328.

Schmidt, O., Ostle, N.J., 1999. Tracing nitrogen derived from slurry in earthworms using 15N/14N stable isotope ratios at natural abundances. Appl. Soil Ecol. 12, 7–13.

Schmidt, O., Scrimgeour, C.M., Handley, L.L., 1997. Natural abundance of 15N and 13C in earthworms from a wheat and a wheat-clover field. Soil Biol. Biochem. 29, 1301–1308.

Schon, N.L., Mackay, A.D., Gray, R.A., van Koten, C., 2016. Establishment of *Aporrectodea longa* and measurement of dung carbon incorporation in soils under permanent pasture. Eur. J. Soil Biol. 75, 174–179.

Schulmann, O.P., Tiunov, A.V., 1999. Leaf litter fragmentation by the earthworm *Lumbricus terrestris* L. Pedobiologia 43, 453–458.

Semenova, L.M., 1966. Relation of the structure of digestive tract in earthworms (Lumbricidae) to their feeding habits. Zool Zh 45, 986–997.

Shipitalo, M.J., Protz, R., Tomlin, A.D., 1988. Effect of diet on the feeding and casting activity of *Lumbricus terrestris* and *L. rubellus* in laboratory culture. Soil Biol. Biochem. 20, 233–237.

Shumway, D.L., Koide, R.T., 1994. Seed preferences of *Lumbricus terrestris* L. Appl. Soil Ecol. 1, 11–15.

Shuster, W.D., Subler, S., McCoy, E.L., 2001. Deep-burrowing earthworm additions changed the distribution of soil organic carbon in a chisel-tilled soil. Soil Biol. Biochem. 33, 983–996.

Sims, R.W., Gerard, B.M., 1999. Earthworms. Synopses of the British Fauna No. 31 (revised) The Linnean Society and the Brackish-Water Sciences Association. Field Studies Council, Shrewsbury.

Stevens, C.E., Hume, I.D., 2004. Comparative physiology of the vertebrate digestive system. Cambridge University Press.

Svendsen, T.S., Baker, G.H., 2002. Survival and growth of *Aporrectodea longa* (Lumbricidae) fed on sheep and cow dung with and without moxidectin residues. Aust. J. Agric. Res. 53, 447–451.

Van Rhee, J.A., 1963. Earthworm activities and the breakdown of organic matter in agricultural soils, in: Soil Microflora and Their Relationships. Presented at the Soil organisms: proceedings of the colloquium on soil fauna, J. Doeksen, J. van der Drift, Amsterdam.

Vidal, A., Quenea, K., Alexis, M., Derenne, S., 2016. Molecular fate of root and shoot litter on incorporation and decomposition in earthworm casts. Org. Geochem. 101, 1–10.

Vidal, A., Quenea, K., Alexis, M., Nguyen Tu, T.T., Mathieu, J., Vaury, V., Derenne, S., 2017. Fate of 13C labelled root and shoot residues in soil and anecic earthworm casts: A mesocosm experiment. Geoderma 285, 9–18.

Vos, H.M.J., Koopmans, G.F., Beezemer, L., de Goede, R.G.M., Hiemstra, T., van Groenigen, J.W., 2019. Large variations in readily-available phosphorus in casts of eight earthworm species are linked to cast properties. Soil Biol. Biochem. 138, 107583.

Whalen, J.K., Parmelee, R.W., 1999. Growth of *Aporrectodea tuberculata* (Eisen) and *Lumbricus terrestris* L. under laboratory and field conditions. Pedobiologia 43, 1–10.

Wright, M.A., 1972. Factors' governing ingestion by the earthworm *Lumbricus terrestris* (L.), with special reference to apple leaves. Ann. Appl. Biol. 70, 175–188.