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Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains[§]

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Abstract – The moment the soil enters into contact with an earthworm, both superficially and internally, physicochemical and biological changes take place. The drilosphere represents the whole soil volume under earthworm influence. Thus it includes the body surfaces, the gut and all the internal features of the worm that are in contact with the ingested soil, as well as the external structures (casts, burrows, middens) created by earthworm activities. The extent of the drilosphere and its particular characteristics depend on the species and ecological categories of the earthworm community present as well as the spatial and temporal scale of interest. Spatially, the drilosphere can interact with other soil functional domains and lead to significant changes in the litter system or detritusphere (generally decreasing litter stocks) and the rhizosphere (affecting both root biomass and density), the two main sources of organic matter (OM) additions to the soil, as well as in the aggregatusphere and the porosphere. Drilosphere effects on microbial activity and OM decomposition can be completely different (and opposite) depending on the spatio-temporal scale of observation. At the level of the gut, microbial activity is dramatically stimulated in a matter of a few hours via a mutualistic digestion system. In this process, water and soluble-C in the form of intestinal mucus (the Kiss) produced by the earthworm (Prince Charming) awakens the dormant microflora (Sleeping Beauties), thereby increasing decomposition of the stable forms of soil OM ingested. During gut passage populations of other organisms (e.g. protozoa, nematodes, fungi) may decline with digestion, although these organisms probably form a minor component of the earthworm's energy needs. In the casts and on the burrow walls, the abundant nutrient resources for soil microflora continue the priming effect of the gut, increasing over a short time period mineralization rates and plant nutrient bio-availability. However as castings, particularly of the 'compacting group', and burrow walls begin to dry and stabilize with age (days to weeks), OM decomposition, nutrient mineralization and microbial activity decrease, often reaching levels lower than uningested soil due to 'protection'. Finally at the scale of years to decades and soil profile, it appears that the drilosphere can exert an important regulation on OM incorporation and turnover rates, and soil C stocks. © 2000 Éditions scientifiques et médicales Elsevier SAS

drilosphere / earthworms / soil properties / micro-organisms / organic matter dynamics

1. INTRODUCTION

Researching the interactions between soil macrofauna and micro-organisms is like finding one's way through a maze of below-ground processes in which the path sometimes leads in one direction and then another, back along the same or another track, and then finally forward again. These shifts in direction, exemplified by the large number of publications showing apparently conflicting results in this subject, are very likely due to the different approaches used to investigate soil interactive phenomena, as well as to the great diversity of species and functions performed by soil organisms and their effects on soil organic matter (SOM) dynamics and microbial activity at different scales of space and time. An example of this is the role that earthworms may play in both acceleration of decomposition and mineralization processes (C loss) and in carbon storage or protection from decomposition (C accumulation) in stable aggregates.

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This paper attempts to find the various paths through this maze by dissecting the interactions between earthworms, a dominant component of the soil faunal biomass with important influence on soil function, and two essential soil processes: SOM dynamics and microbial activity. There are several ways to approach this complex issue; we have chosen to first identify the forces or spheres governing and involved in these processes, and then assess the effect of earthworms on these forces (spheres).

1.1. Functional spheres of soil regulation

Seven main spheres of influence (functional domains) in soil have been identified according to their origin and significance in regulating major soil processes and functions such as aggregation, organic matter (OM) decomposition, nutrient cycling, microbial populations and activity and plant production [13, 14, 94]. These are: (1) the litter system or detritusphere; (2) rhizosphere; (3) porosphere; (4) aggregatusphere; (5) the drilosphere; (6) termitosphere; and (7) myrmecosphere. The first two spheres represent the two main sources of OM additions to soil, being plant and animal remains on the soil surface (litter system) and plant roots. The type, quality (e.g. C:N ratio, lignin, polyphenol contents), quantity (production, biomass) and spatio-temporal distribution of these inputs is key to the rate of decomposition and mineralization as well as to the abundance, biomass and distribution of litter- and soil-inhabiting organisms [14]. The porosphere consists of the arrangement of voids and solids of various sizes (macro, meso, micro) in the soil. These pores, filled with air and water, can be occupied by bacteria, protozoa and nematodes inhabiting water films and fungal mycelia, roots, micro-arthropods and other organisms inhabiting the aerial portions. The amount and size of pores are determinant in their ability to retain water, and provide O_2 and other gases for soil metabolism. Soil aggregates (aggregatusphere) are groups of soil particles bound together forming a stronger unit than the surrounding particles. These aggregates can range in size from micro (50–250 μm) to macro (> 250 μm diam.) and are often associated with OM and microbial (esp. bacteria; fungi) and faunal activities [127]. Soil C and N cycles are intimately dependent on aggregate status of soil; the stability of these aggregates is a key in protecting (occluding) OM from decay. The oxygen status of these aggregates is also important; aeration is necessary for nitrification and water saturation may lead to denitrification (N loss). Soil animal-created spheres form important habitats that differ from unaltered soil. Ant and termite nests and mounds and earthworm casts and galleries incorporate (aggregates, pores) and transform (litter, roots) features of the other functional spheres and thus are not completely independent from them, although they can usually be distinguished by their origin. When taken separately, these animal-induced spheres can significantly affect microbial activity and SOM dynamics; yet because these organisms are moving in, and producing their structures within the soil, on its surface and in the root zone, they can overlap considerably with other functional domains in soil (*figure 1*; drilosphere). The resulting interactions can often dramatically modify the functional role of these other domains, depending on the organism's (in this case the earthworm's) ecological role, category and behaviour. For example, feeding, burrowing and casting activities can affect the dynamics of root growth and penetration through soil (rhizosphere), aggregation (aggregatusphere), porosity (porosphere) and the amount of litter present on the soil surface (litter system). Given these interactions, it is important to first characterize and define the drilosphere, highlighting its importance as a major soil constituent and its role in biological regulation within the soil, and then discuss how the drilosphere affects SOM dynamics and microbial activity at different spatio-temporal scales through its interactions with other soil functional domains. This is achieved by focusing at first on the interactions with the rhizosphere and the litter system and then ending with the two pedo-physical zones, the aggregatusphere and the porosphere.

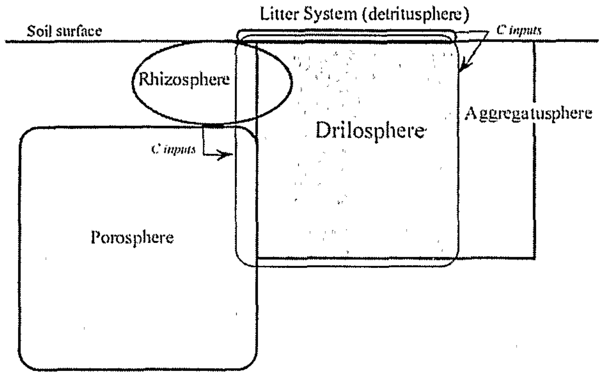

Figure 1. Overlap of the drilosphere (shaded box) with the other edaphic biological regulation spheres (rhizosphere, porosphere, litter system and aggregatusphere). The size of each sphere roughly represents its hypothetical contribution to total soil volume (aggregatusphere 45 %; porosphere 45 %; rhizosphere 7 %; litter system 2 %). The amount of overlap represented graphically is for a hypothetical drilosphere and is explained in the text. Non-overlapped portions represent the earthworms themselves (< 1 %).

2. THE DRILOSPHERE

2.1. Definition

The concept of an earthworm 'sphere' of influence is relatively recent and, despite the fact that earthworms have been modifying soil characteristics for millennia wherever they are found world-wide, it has only been recently that soil scientists described vermic horizons and even Vermisols, where earthworm influence on soils reaches dramatic proportions [29, 88, 136]. The term 'zoosphere' was first used by Joffe [79], in reference to the soil modified by soil animals and Jenny [77] highlighted the role of biota (organisms) in the soil formation process. The 'drilosphere' was coined by Bouché [21], originally to describe the zone 2-mm thick around earthworm burrow walls, while the term 'vermisphere' was used by Hamilton and Dindal [64] in reference to the soil volume within and under (along the longitudinal burrow axis) the anecic earthworm (*Lumbricus terrestris*) created structure called the 'midden' [125–126].

Lavelle [95] expanded the meaning of the 'drilosphere' to include earthworm populations and all the soil volume, microbial and invertebrate populations affected by their activities. This broader definition included five main components, going from smaller to larger spatial (and temporal) scales: the earthworm itself as an individual, including (1) the internal micro-environment of the earthworm gut and (2) the earthworm surface in contact with soil; and the externally produced earthworm structures, i.e. (3) surface and below-ground casts, (4) middens and (5) burrows, galleries or diapause chambers (open and closed) (*figure* 2). Each of these components can have contrasting effects on microbial activity and OM dynamics depending on the temporal scale, as observed in *figure 3* (see section 7.2).

2.2. Drilosphere components

The earthworm body, both internally and externally, is the site of metabolic processes such as external and internal mucus production, respiration, gut passage and nitrogenous excretion (*figure* 2). At this level, microbial activity is enhanced in the gut via a mutualistic digestion system that enhances the ability of the worm to use ingested organic resources (see section 3). Similarly, externally secreted mucus can also act as a microbial 'primer'.

Castings, the by-products of gut passage (*figure 3*), are egested in two main forms: globular and granular. These casts have different sizes, stabilities and durations, and often nutrient contents, and their effects on OM dynamics and microbial activity can be very different. Globular casts are large and produced by 'compacting' earthworm species, and therefore tend to be more stable and longer lasting than the granular casts, produced by 'de-compacting' species [18]. There can be interesting interactions between these aggregates in that de-compacting species may ingest casts of compacting species, and vice versa [17, 18, 37, 78]. The former opens the way for mineralization of physically-protected C, and the latter 'protects' potentially-mineralizable C.

Middens, created by anecic earthworms (see section 4.2), consist of an accumulation of surface castings, leaves and other organic materials buried into and surrounding a burrow opening at the soil surface (*figure* 2). These structures can be considered hot-spots of microbial and faunal activity and accelerated OM decomposition.

Burrows, produced as the earthworm works its way through the soil, can be permanent (and several years old) or temporary, open or cast-filled, are mostly important in water and gaseous exchange and movement into the soil, and can serve as preferential pathways for plant root expansion (see section 5.3; *figure* 2).

2.3. The effect of ecological categories

The drilospheres resulting from the activity of the different earthworm ecological categories (epigeic, anecic and endogeic; *figure* 2) vary greatly from each other. Epigeic earthworms live in and consume plant litter and litter inhabiting organisms (rarely ingesting soil), thus their direct effects are primarily confined to the litter system, although indirect effects on the soil environment may also be important (see section 4.1). Anecics feed on particulate OM mixed with soil particles and bury surface litter, often forming middens (*figure* 2) and deep primarily vertical burrows (see section 4.2), while endogeics are mostly SOM feeders and burrow extensively both horizontally and vertically within the soil (*figure* 2). An ordination of the different earthworm species and their respective ecological category along the latitudinal gradient [93], showed that epigeic and anecic earthworms were more abundant in temperate regions, while in tropical regions endogeic earthworms were predominant. Since endogeics feed on SOM, a diversification of this category into three sub-categories (poly-, meso- and oligo-humic; *figure* 2) allows them to enlarge their ecological niche and feed on different pools (qualities) of SOM of varying assimilability [93].

2.4. 'Ecosystem engineering' and soil functional regulation

Anecic and endogeic earthworms produce structures which have effects on soil properties and processes that go beyond their body size and life-time, up to the landscape level and decades of time and their activities can significantly modify the availability of resources to other soil organisms. Therefore, these earthworms can be considered 'ecosystem engineers' [80, 103]. As earthworms colonize new (still unaltered) soils or re-alter soil previously processed by other earthworms at different times in the past, or soil from within or around other functional edaphic spheres, soil properties and processes (physical, chemical and biological) are modified.

The drilosphere is thus a dynamic sphere of earthworm influence on soil which is constantly changing in space and in time. The temporal dynamics are dependent on the periods of activity of an earthworm community, how long it has been in place and the duration of the different structures created, while the spatial dynamics are controlled by the horizontal and vertical distribution of the community, and the biotic and abiotic factors that determine this distribution. However, drilosphere interactions with state soil prop-

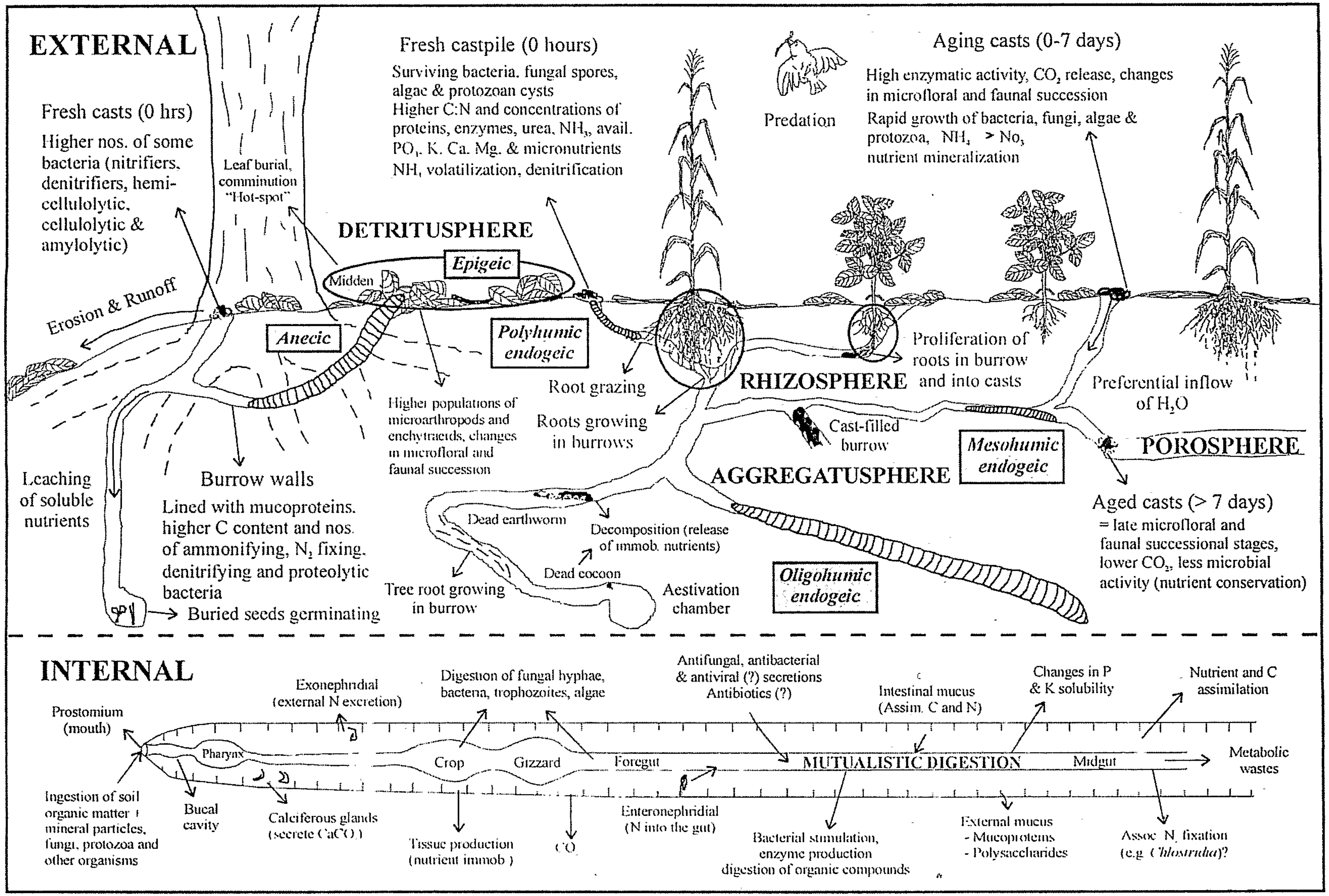

Figure 2. Diagrammatic representation of the external (burrows, casts, middens) and internal (associated with the earthworm body) components of the drilosphere and their overlap with other functional domains in soil affecting organic matter dynamics and microbial activity (drawing by G. Brown).

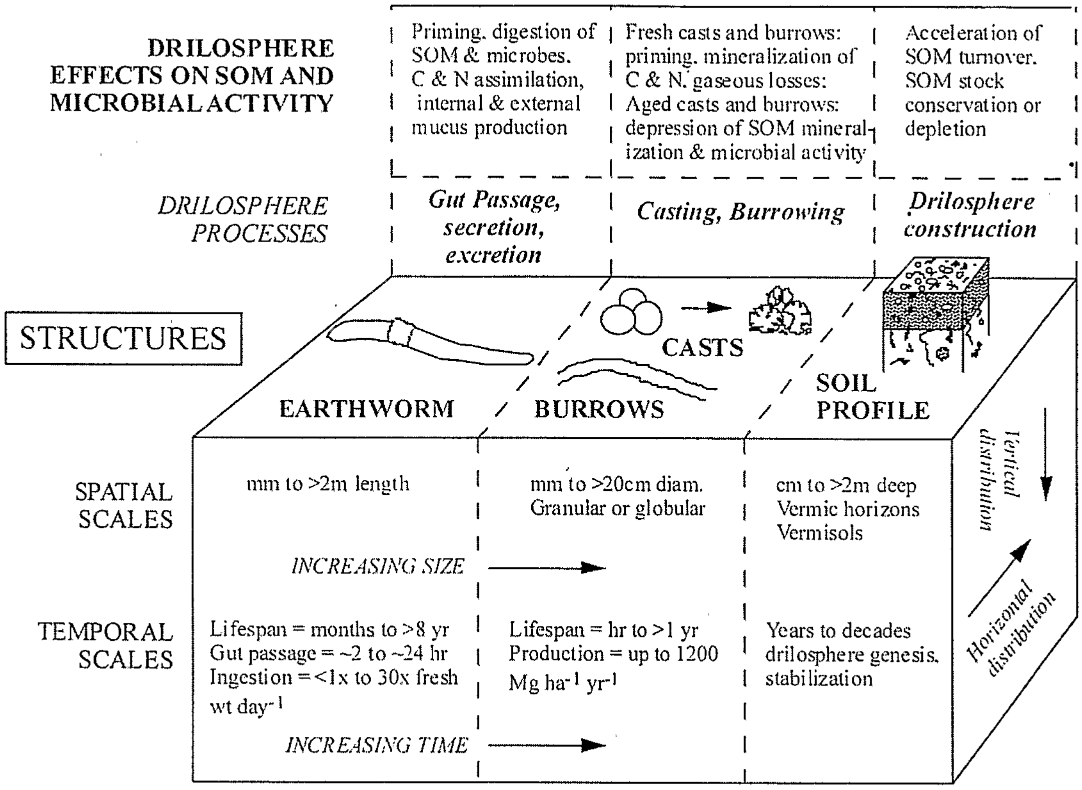

Figure 3. The effect of drilosphere structures and processes (internal and external) on soil organic matter dynamics and microbial activity at different scales of space and time, from the earthworm gut up to the soil profile and from a few hours up to decades of time (modified from Lavelle [96]).

erties can cause earthworm effects to persist for a longer time or over a wider area than that delimited strictly by the earthworm community's temporal and spatial distribution. For example, the physically stabilized soil in compact casts or burrows may outlive the earthworms that produced them and lead to long-term conservation of SOM by physical protection from decomposition. Earthworm activity is thus a key regulator in this process (*figure 4*) through their feeding, physical activities (casting and burrowing) and interactions with microflora.

Earthworm feeding on soil and organic (particulate and stabilized) materials and gut passage dramatically modify OM structure and integrity [10], accelerating microbial decomposition (see section 3). Once egested, active (labile) C in the form of micro-organisms, plant litter and particulate organic fragments are placed within compact burrow walls or castings, where physical protection after a drying and stabilization process can lead to reduced microbial decomposition. Because passage of soil through earthworm guts results in some of the most important changes in the drilosphere environment (both internal and external to the earthworm; *figure 2*) the following discussion on this topic has been included as a separate section in this paper, before addressing the interactions of the drilosphere with the other soil functional domains.

3. EARTHWORM DIGESTION

Earthworm digestion is portrayed in *figure 3* as being the shortest in time scale. However, due to assimilation and impact on microbial activity, this process can be very important in the regulation of SOM dynamics, depending on the overall ingestion rates of the different species in a community. In gut passage, the ingested materials (minerals and OM) are rapidly (from 2 to 16 h depending on the species [10, 24, 65]) and completely de-structured and re-structured in physical, chemical and biological ways [10]. In epigeic earthworms and/or litter feeders, changes in the ingested substrate are obvious; the casts are completely different from the original substrate (manure, coffee pulp, litter), being generally black, porous and mull humus-like in appearance [4]. In endogeic earthworms, the egested material seems only to change in its physical structure (e.g. high water instability, clay disorientation) at first glance, although more subtle but profound changes also occur, particularly with ageing (see section 7.2).

3.1. Earthworm enzymes

The major enzymes found in the gut of different earthworm species are: chitinase, protease, phos-

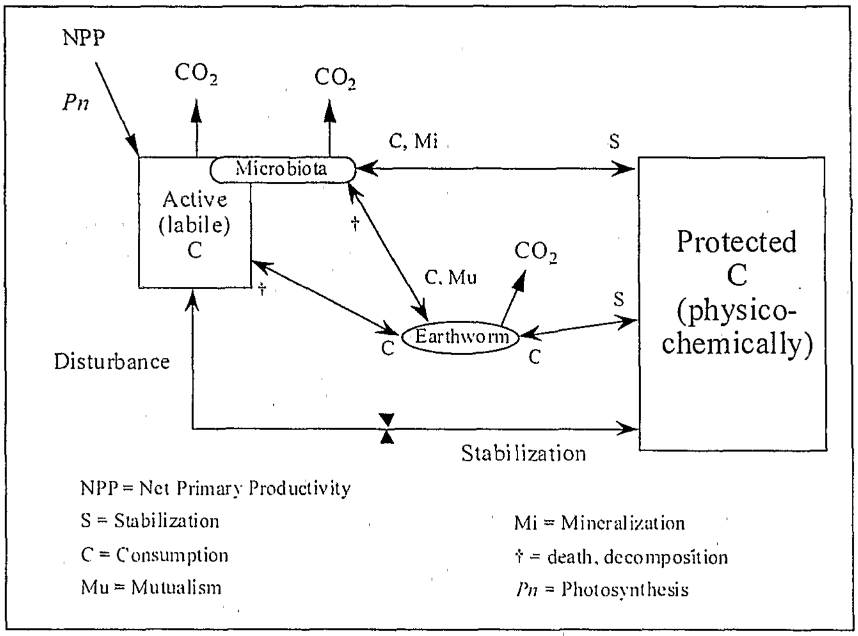

Figure 4. The effect of earthworms and microbes on active and protected soil C pools. Circle and box sizes represent the approximate contribution of each pool to the total soil C. Earthworms are considered separately from the active C pool for graphical purposes and because they act as a controlling mechanism (knot on the lower line) in the processes of C protection (stabilization) and priming (disturbance).

phatase, cellulase and many other glucosidic enzymes [70, 89–91, 106, 110, 141, 165, 174]. These enzymes allow them to digest bacteria, protozoa, fungi and partly decomposed plant debris; no enzymes capable of digesting lignin or other polyphenolic and humified substances have been found so far [107]. Nevertheless, some earthworm species may participate in the decomposition of lignin and the process of humification [145] since peroxidases, which destroy the aromatic links of lignin, have been observed in earthworm guts (e.g. *Eisenia fetida*) [66, 124].

Only a few detailed studies on earthworm gut glucosidic enzyme systems has been performed. The origin of these enzymes (earthworm or microbial) has been determined in five tropical and two temperate species: *Polypheretima elongata*, *Pontoscolex corethrurus*, *Millsonia anomala*, *Dichogaster terrae-nigrae*, *Hyperiodrilus africanus*, *Hormogaster elisae* [89–91, 174] and *Eisenia fetida andrei* [169]. Each species had a distinct enzyme complex and activity, and its origin could be from the gut wall, and thus presumably proper to the earthworm, or from the microbiota living in the gut. For example, *P. corethrurus*, *H. elisae* and *M. anomala* required microbial activity to synthesize mannanase and cellulase while *P. elongata*, *D. terrae-nigrae*, *H. africanus* and *E. andrei* appeared to have a rather complete and intrinsic enzyme production. All species, nevertheless, had enzymes capable of digesting fungi and dead roots [90, 91].

3.2. The 'Sleeping Beauty paradox'

The assimilation efficiency of endogeic earthworms (in terms of C) feeding in natural environments is in the range of 8–19 % [44, 97, 102], which is low compared with that of litter-feeding earthworms (> 30 %) [35, 38] or other soil-inhabiting organisms (e.g. nematodes, protozoa). Despite many reports of earthworms feeding on the microbial biomass and the fact that part of the earthworm's diet probably comprises of fungi, protozoa and other microbes (e.g. algae, nematodes; see reviews in [24, 39]), these organisms rarely comprise more than 5 % of the total soil C [39, 68] and thus are probably not a sufficient source of energy (C and N) for earthworm metabolism. Therefore, endogeic earthworms consume predominantly dead SOM, although certain micro-organisms and rhizo-deposition may form an important complement to their diets. To help digest this SOM, these earthworms have developed a mutualistic relationship with the soil microbiota [9, 102, 168], based on the 'Sleeping Beauty paradox'. The basis of this paradox is that soil microbial communities (the 'Sleeping Beauties') have the ability to digest almost any organic substrate yet are dormant most of the time, because they need assimilable carbon (food resources) but have a limited ability to move throughout the soil in order to reach these resources. Earthworms (the 'Prince Charming') secrete mucus ('the Kiss' = resources), move within the soil and provide the suitable temperature, moisture and organic resources within their guts for microbes to be activated (*figure 5*). This activation by an extra contribution of assimilable C is what Jenkinson [76] called a 'priming effect'. Several results presented in the following discussion provide evidence for the 'priming effect' and the 'Sleeping Beauty paradox', through measurements performed on several earthworm species and ecological categories from both temperate and tropical regions.

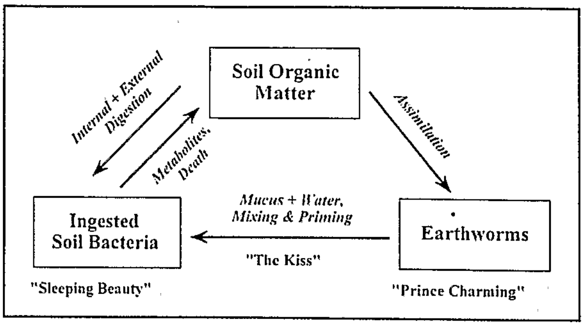

Figure 5. Mutualistic digestion of soil organic matter in earthworm guts (modified from Lavelle et al. [102]); the 'Sleeping Beauty paradox'.

3.3. Intestinal mucus, 'the Kiss'

The feeding habits of different earthworm species promote a selection of substrates, particularly in endogeics, often resulting in a concentration of specific soil aggregates rich in OM and clays [11], increasing the relative C and N contents of ingested materials (compared with the bulk soil). In the crop and gizzard, the ingested materials are submitted to a mixing and grinding (de-structuration of the soil) process. Then, in the anterior part of the gut, a high amount of water is provided (60–150 % of the weight of gut materials), the pH is neutralized and a high concentration of water soluble-C (intestinal mucus) is secreted, increasing microbial activity in the middle and posterior gut. In these latter gut parts, most of the water and mucus are re-absorbed, but the fresh casts (< 24 h old) always have a higher content of water and water soluble-C than the surrounding substrates; furthermore, the pH returns to values close to the ingested soil [9, 129, 166, 167].

Martin et al. [117] showed that this intestinal mucus is a mixture of low-molecular weight (about 200 Da) amino acids with sugars and glycoproteins of high molecular weight (40 000–60 000 Da). The total C and N content of the intestinal mucus of six earthworm species from Mexico (two epigeic and four endogeic) ranged from 39–44 % C and 7–7.3 % N (Barois et al., unpubl. data). Therefore, the intestinal mucus seems to be similar across different species and ecological categories. Lavelle and Gilot [97] compared the microbial activity (oxygen absorption) of an in vitro incubation of an African Alfisol supplemented with 7 % glucose and 7 % intestinal mucus of *M. anomala.* Oxygen absorption was initially very high and then gradually decreased with mucus, while with glucose the increase in O_2 absorption was slower but more constant (linear). These data clearly show the particularity of earthworm intestinal mucus in provoking a rapid priming effect, triggering microbial activity.

Trigo et al. [168] provide more data to confirm the mutualistic OM digestion hypothesis. Intestinal mucus production was quantified in earthworm species from different ecological categories, temperate and tropical regions, and of native or exotic (introduced) origin. Mucus of different species from the same soil or a species found in three soil types with different SOM content was also studied. When combining previously published data [8, 9, 97, 99, 102, 117, 166, 167] with those of Trigo et al. [168], the observed pattern of intestinal mucus (hydro-soluble fractions) production was similar for the seventeen species studied. Highest concentration was found in the anterior gut contents (50–800 mg mucus·g^{-1} dry gut contents; *figure 6*). In the middle and posterior gut, the mucus concentration was reduced to < 50 % of that found in the anterior gut. In fresh casts, the concentration of water-soluble fractions is generally > 50 % higher than in the non-ingested substrates. In soil the water-soluble fraction is very low (2–7 mg·g^{-1} sdw – substrate dry weight), while in the organic substrates it can reach values of 70 mg·g^{-1} sdw. There was a tendency for a slight decrease in C and N content of mucus in the posterior gut (Barois, unpubl. data) and, in the casts of the endogeic species *P. elongata* and *Glossoscolecidae* sp., C and N contents of the water-soluble fraction were at least half that of the respective contents in intestinal mucus.

In the same soil (Alfisol) from a pasture in Mexico, exotic species (*P. elongata*, *P. corethrurus*) had higher mucus contents than native species (*Balanteodrilus* sp., *Glossoscolecidae* sp.; *figure 6*). However, to adequately compare the intestinal mucus production from earthworms feeding on different quality substrates, the ratio of the water-soluble fractions in the anterior gut portion to that in the respective substrate (gut contents) (HAs/HS) was calculated for nine species [168]. The results (*figure 7*), showing the relative intestinal mucus production, reveal that endogeic earthworms produce more mucus than epigeics; anecics seem to have an intermediate production, although more data on this ecological category are needed to confirm the present trend. Highest relative mucus production was observed in temperate species, which is probably the result of a greater need to stimulate the microbiota because of the lower mean annual temperatures in the earthworms' (soil) environment. Since microbial activity and efficiency increase with higher temperatures [7], less intestinal mucus is produced in the tropical regions, probably due to higher mean annual temperatures that increase the efficiency of water-soluble OM additions in stimulating microflora. An inverse relationship of soil C content with relative mucus production was found for two species; the epigeic *E. andrei* and the endogeic *H. elisae* (*figure 7*). In the rich substrates (coffee pulp and oak forest soil, respectively), *E. andrei* and *H. elisae* produced relatively less mucus than in the poor substrates (cow manure and pasture soil) [168].

The intensity of the 'Sleeping Beauty paradox', or interaction between microbiota and earthworms for the digestion of the SOM, is thus conditioned by several parameters: the ability of earthworms to produce

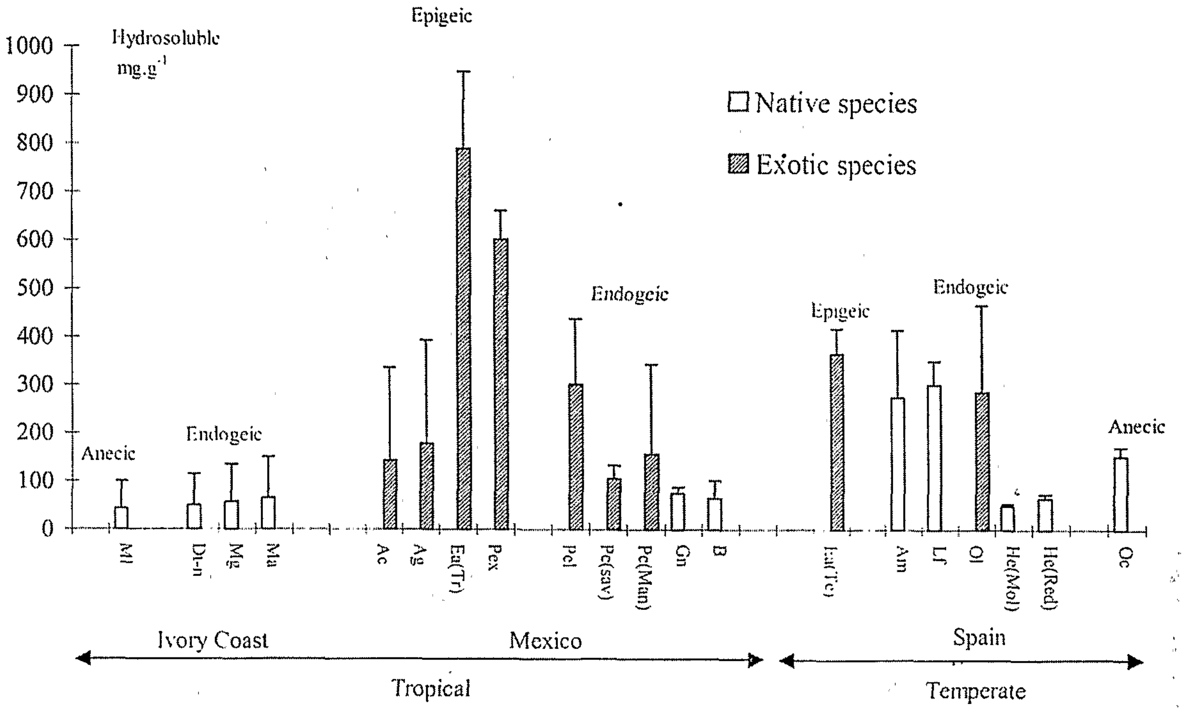

Figure 6. Anterior intestinal mucus content (mg hydro-soluble fraction·g^{-1} gut content dry weight) of earthworm species from tropical and temperate regions and of different ecological categories (epigeic, anecic and endogeic). In Ivory Coast, *Millsonia lamtoiana* (Ml) [99], *Dichogaster terrae-nigrae* (Dt-n), *M. ghanensis* (Mg) and *M. anomala* (Ma) from savannahs at Lamto (Ivory Coast) [117]. In Mexico, *Amynthas corticis* (Ac), *A. gracilis* (Ag) [8], *Perionyx excavatus* (Pex) and *Eisenia andrei* in coffee pulp (Ea(Tr)); *Polypheretima elongata* (Pe), *Glossoscolecidae* sp. (Gn) and *Balanteodrilus* sp. (B) in a savannah-pasture Alfisol and *Pontoscolex corethrurus* under pastures in an Alfisol (Pc(sav)) and Entisol (Pc(Man)) [168]. In Spain, *E. andrei* in cow manure (Ea(Te)), *Hormogaster elisae* from pasture soil at El Molar (He(Mol)) and woodland soil at Redueña (He(Red)); *Lumbricus friendi* (Lf), *Octodrilus complanatus* (Oc) [168], *Allolobophora molleri* (Am) [166] and *Octolasion lacteum* (Ol) [167].

proper digestive enzymes, SOM quantity and quality and temperature. The result is a conditional mutualism between earthworms and soil micro-organisms where both perform 'mutual exploitation for mutual gain' [23], permitting a better utilization of the ingested soil organic resources.

4. DRILOSPHERE × LITTER SYSTEM (DETRITUSPHERE) INTERACTIONS

The litter system, or detritusphere, consisting of the L, F and H horizons (A_o) used in soil classification, includes all plant and animal remains deposited on the soil surface, and in various stages of decomposition. The earthworms that are most important in modifying this domain are the epigeic and the anecic ecological categories (*figure 2*).

4.1. Epigeics

Epigeic species are small earthworms that live in and consume, comminute and digest (partly) surface litter, ingesting little soil. They are thus 'litter transformers', sensu Lavelle [96]. Under particular conditions, such as drought or lack of food, some epigeics such as *Eudrilus eugeniae* (often used in vermicomposting systems) or *Lumbricus rubellus* may enter the top few cm of the soil [26], and thus have an impact on topsoil properties. Several studies have shown effects of epigeics on litter decomposition rates using either litter bags of different mesh sizes to exclude or include earthworms [45, 134, 151] (some of these experiments also included anecic species), or other methods such as the simulation of forest floors [2, 72] and the application of biocides [131]. These and other studies [128, 146] have shown that epigeic earthworm activities can result in decreases in litter and coarse OM standing stocks, increased microbial activity due to greater surface area for decomposition, greater nutrient leaching into the soil, reduced immobilization by surface-litter dwelling fungi and changes in the litter microfauna and flora communities. In addition, further processing of epigeic faeces by other organisms or earthworm species may release nutrients still tied up in the cast's undigested organic fractions.

Epigeic species, in comparison with endogeics and anecics, have received much less attention, and little research has been undertaken to address their role in litter-soil interface processes in natural ecosystems or

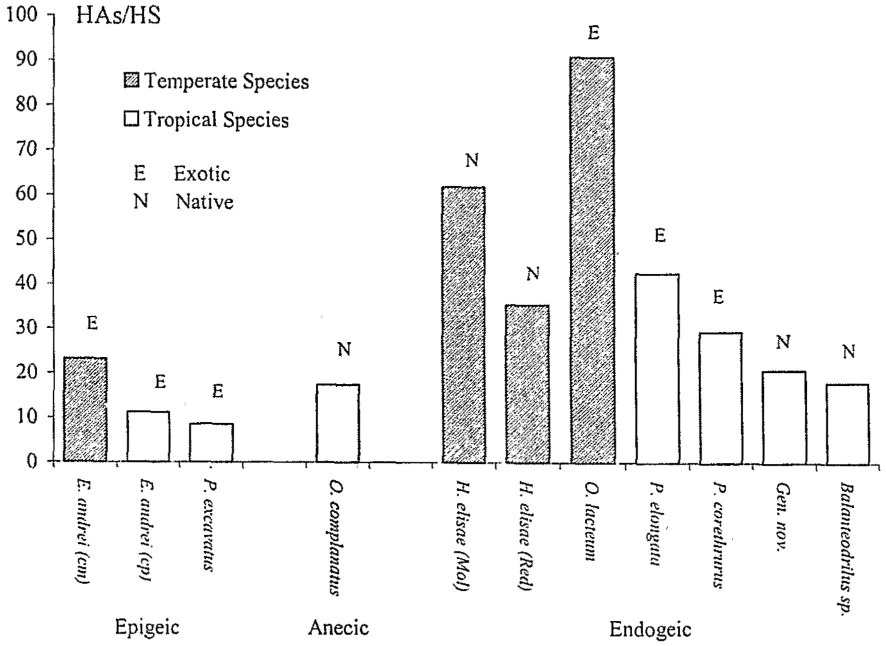

Figure 7. Relative anterior intestinal mucus production of earthworm species. HAs/HS is the ratio of the hydro-soluble fractions in the anterior gut (HAs) over that in the non-ingested substrate (HS). *E. andrei* were in cow manure (cm) in Spain and coffee pulp (cp) in Mexico. *H. elisae* (Spain) were in soil under pasture at El Molar (Mol) and under oak (*Quercus faginea*) woodland at Redueña (Red) (modified from Trigo et al. [168]).

even agroecosystems. In the latter case, under tree plantations or no-tillage fields, the accumulation of OM at the soil surface often permits the re-establishment or enhancement of epigeic populations that are generally absent under conventional tillage [71]. Most of the attention devoted to epigeics has been concentrated on the role of species such as *E. eugeniae*, *E. fetida* or *E. andrei* and others in vermiculture [47]. When fed pure OM sources such as animal manures, sewage sludge, coffee or paper mill pulp, sugarcane bagasse or other organic residues, these are rapidly transformed into stable faecal pellets covered with a peritrophic membrane. These pellets (castings) are then gathered and used as organic fertilizer with dramatic effects on horticultural crops and ornamental plants in nurseries throughout the world [4, 43].

4.2. Anecics

Anecic earthworms are of a large size (when adults) and produce primarily vertical burrows and often the characteristic soil-surface features called 'middens' (*figure* 2). The main function of these organisms is to remove litter from the litter system and place it within the soil or in middens. These structures seem to act as 'external rumens' [161], in which microbes multiply and to which other fauna are attracted, creating an activity 'hot-spot' [19, 24, 112]. This activity enhances the microbial degradation of the uningested litter and the organic fragments in and around the casts, increasing their palatability, after which point they are re-ingested by the earthworms or other fauna present in the middens. When anecics are abundant, the soil may undergo dramatic transformations typical of the ecosystem engineer earthworm guild [96, 103]. For example, in apple orchards of Holland and deciduous forests in Minnesota and Wisconsin more than 90 % of the annual leaf fall can end up in middens of the temperate species *Lumbricus terrestris* [84, 125, 137]. Furthermore, the long-term activity of this species, or its invasion into new sites, can reduce litter stocks and accelerate humification, transforming soils from the mor or moder types to mull [88], create coprogenous horizons (such as A_1 horizons in forest soils) [125], and accelerate SOM turnover [159].

Much less is known of the effects of anecic species in tropical environments. In Lamto (Ivory Coast) savannahs, *Millsonia lamtoiana* may incorporate 30 % of the annually decomposed grass litter into the soil [92]. In tropical forests of Central and South America, large anecics of the Glossoscolecidae family are present [57, 123], yet virtually nothing is known of their effects on the litter system.

The amount of litter ingested by anecics is greatly influenced by the quality, i.e. C/N ratio, amounts of lignin, tannins, polyphenolics or other chemical substances, and its microbial colonization status. Litters high in N, low in hard-to-digest and decompose substances or colonized by particular fungi species [32, 67, 120] seem to be preferred. The preferential consumption of low C/N maize litter by *L. terrestris* and sorghum residues by *L. rubellus* (an epigeic species that sometimes behaves as an anecic, producing small middens) increases the C/N of the remaining litter in no-till agroecosystems [19, 26]. These behaviours may therefore lead to marked changes in both the quantity and quality of the litter system as well as the micro-organisms colonizing it [24, 120]. Furthermore, microbe and insect litter colonizers may be buried and their populations reduced, while other populations may find suitable conditions in middens [3, 24, 112]. For example, over twenty species of fungi (several of them plant pathogenic) and five species of insects (some of them pests) were buried by *L. terrestris* in apple orchards [24].

5. DRILOSPHERE × RHIZOSPHERE INTERACTIONS

The rhizosphere, or the zone < 0.5 mm surrounding plant roots, can be deeply influenced by earthworms, both directly and indirectly. Thus, there can be important consequences to root growth and plant production. The direct effects are related to how much earthworms feed on and are active in the rhizosphere, a matter of much present contention and speculation, which few experiments have addressed. Results in the literature and our experience in this area have revealed contrasting results depending on the approach used and the earthworm and plant species and soil type in question. The indirect effects have to do with changes in soil physicochemical and biological properties and processes that affect root growth; much more is known about these phenomena.

Earthworm activities in the rhizosphere can be assessed through direct visual observation (e.g. in rhizotrons), although they are generally measured indirectly, e.g. by estimating the amount of root, mycorrhizal or other rhizosphere matter in earthworm guts or the assimilation of root-derived nutrients in earthworm tissues.

5.1. Indirect measures of earthworm activity in the rhizosphere

Four experiments addressing this issue were performed under greenhouse conditions employing the stable isotopes ^{13}C and ^{15}N, two common tropical geophagous (soil-feeding) endogeic earthworm species (*P. corethrurus* and *P. elongata*) and three plant types (common bean, *Phaseolus vulgaris*; maize, *Zea mays*; and *Brachiaria decumbens*, a perennial grass pasture) grown in three soils, two of them sandy loams from managed agroecosystems and the other a clayey forest soil [25].

(1) In the first experiment, when *P. corethrurus* collected from a tropical rainforest (C_3 vegetation) was placed in the clayey soil from the same site ($\delta^{13}C = -27.3$ ‰) and maize (C_4 plant, $\delta^{13}C = -13.5$ ‰) was grown for 6 months, their body ^{13}C contents shifted from the low $\delta^{13}C$ values of forest earthworms toward higher (less negative) $\delta^{13}C$ values indicating that they were assimilating the newer forms of C (C_4-C) derived from the maize plant roots. This new C was assimilated by up to 8 % after 6 months, although the proportion of root-derived C assimilated by the earthworms was similar to the amount of new C (C_4, maize-C) entering the soil through rhizodeposition (7 %). Thus it appeared that *P. corethrurus* was not 'preferentially' feeding on or assimilating root derived C.

On the other hand, when ^{15}N-labelled maize residues were placed on the soil surface, the N-derived from maize residues (Ndfr) found in *P. corethrurus* tissues was up to > 20 times higher when the earthworms were in the presence of growing maize plants (Ndfr = 1 %) than in their absence (Ndfr = 0.04 %). Little is known of the N assimilation efficiencies of this species, while C assimilation efficiencies seem relatively high (compared with other tropical species), perhaps up to 19 % [101]. Thus, based on the amount of maize-derived C and N assimilated, shown by the shift in $\delta^{13}C$ and $\delta^{15}N$ values of their body tissues (*figure 8*), *P. corethrurus* was assumed to be active in this plant's rhizosphere. These results agree with those of Spain et al. [150] and Spain and Le Feuvre [149] who found that *P. corethrurus* concentrated and fed in the rhizosphere of sugar cane, another C_4 crop.

(2) Conversely, in the second experiment, when *P. corethrurus* and *P. elongata* were placed for 3 months in a sandy loam soil derived from a shrub savannah (intermediate C_3-C_4, $\delta^{13}C = -19.1$ ‰), sown with common beans (C_3 plant, $\delta^{13}C = -27.7$ ‰), no significant change in the $\delta^{13}C$ signature of their body tissues was observed due to the presence of bean plants. Therefore, it was not possible to show that earthworms were active in this plant's rhizosphere, since no changes in the $\delta^{13}C$ signature of earthworm tissues were detected due to the presence of bean plants.

(3) In the third experiment, when *P. elongata* was placed in a sandy loam soil sown with maize for 3 months, and 10.5 atom% ^{15}N-labelled KNO_3 was

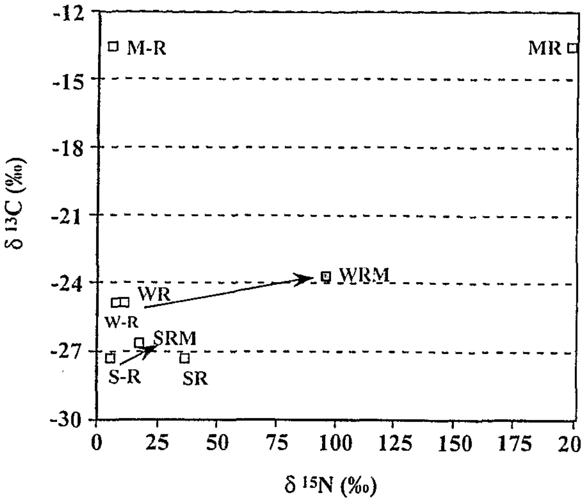

Figure 8. Earthworm (*P. corethrurus*) tissue, maize, and soil $\delta^{15}N$ and $\delta^{13}C$ changes after 6 months of maize (C_4 plant) culture in a tropical rainforest (C_3 vegetation) soil from Los Tuxtlas, Veracruz. M, maize plants; -R, no residues; R, + residues; W, earthworms; S, soil. Arrows show the effect of residues and maize presence on ^{15}N and ^{13}C increase in soil and earthworms [25].

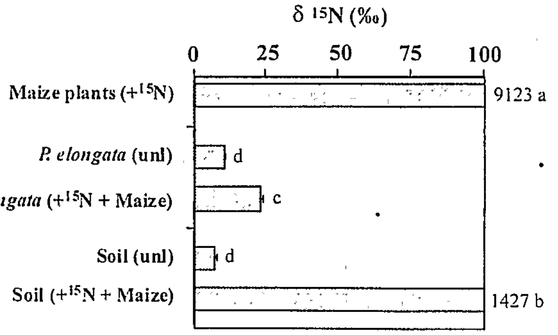

Figure 9. Effect of maize cultured for 90 d with 150 kg·ha^{-1} application of 10.5 atom% ^{15}N-labelled KNO_3 on ^{15}N uptake (expressed as ‰) by the maize plants, and labelling of earthworm (*Polypheretima elongata*) tissue and soil (Entisol) from La Mancha, Veracruz [25]. unl, Unlabelled (natural abundance ^{15}N values).

added at the rate of 150 kg·ha^{-1}, the soil became labelled at 0.88 atom% ($\delta^{15}N > 1\,400$ ‰) and the plants were labelled at 3.36 atom% ($\delta^{15}N > 9\,000$ ‰), yet the earthworm tissues were only slightly more labelled ($\delta^{15}N = 24$ ‰) than those that had not been in the ^{15}N-fertilized soil ($\delta^{15}N = 9$ ‰) (*figure 9*).

Several reasons may account for the aforementioned phenomena: a) the time lapse with the beans could have been insufficient to detect changes; b) the beans produced less roots (observed) and possibly exuded less C (not measured) than maize; c) *P. corethrurus* may prefer feeding in and around the maize rhizosphere than the bean root zone; d) *P. elongata* may not be a preferential bean or maize rhizosphere or rhizobiota feeder, and is probably obtaining its food mostly from non-rhizosphere SOM. This is in agreement with the results of Lattaud et al. [89] on in vitro gut tissue cultures of this species which show that it is able to digest much of its own food without such an intimate mutualistic relationship with the microflora as is found for *P. corethrurus*.

(4) In the fourth experiment, Brown et al. [28] used arbuscular mycorrhizae (AM)-free and AM-inoculated soil in the presence and absence of *P. corethrurus* to separate the effects of AM from those of the earthworms, and study their interaction (see results displayed in *table I*). No significant effects of earthworms or AM individually were observed on root production, although these authors found that several treatments with earthworms had a lower percentage of root fragments infected by AM, while others had higher infection, depending on the depth of the sample and the fertilizer treatment.

With NK, plant shoot production was enhanced by both earthworms and AM individually due to enhanced P availabilities and plant uptake from the P-limiting soil used. However, no further benefit of combining AM and earthworms was observed on shoot biomass; similarly, this treatment presented lower root colonization by AM in the presence of earthworms. Conversely, in the unfertilized treatment, the highest of all shoot yield increases (+84 % over AM-Worm control) was observed when both AM and earthworms were introduced; higher root colonization

Table I. Effects of presence or absence of fertilization (NK or NPK) and earthworm (*P. corethrurus*) and/or mycorrhizae inoculation on *B. decumbens* pasture shoot and root production, AM infection of roots at two depths, total plant fertilizer ^{15}N uptake, earthworm biomass and ^{15}N values (‰) of plant, soil and earthworm tissues after 70 d of growth under greenhouse conditions [28]. Original earthworm biomass inoculated was approximately 3 g. Different letters within the same row indicate significant ($P < 0.05$) differences between treatments (n.d., not determined). Unf, no fertilizers; N, P, K, 200, 100, 200 kg·ha^{-1} of each element in fertilizer mixed into the soil; AM, vesicular arbuscular mycorrhizae. ^{15}N-Labelled fertilizer was 0.76 atom% $^{15}NH_4{}^{15}NO_3$.

	Plus mycorrhizae (+AM)						Minus mycorrhizae (-AM)					
Measured	Unf		NK		NPK		Unf		NK		NPK	
parameter	Worm +	Worm –	Worm +	Worm –	Worm +	Worm –	Worm +	Worm –	Worm +	Worm –	Worm +	Worm –
Yield (t·ha^{-1})												
Shoot	1.26c	1.06d	0.72ef	0.71ef	6.31a	6.48a	0.81e	0.67ef	0.63f	0.47g	6.21a	4.14b
Root	0.12c	0.13c	0.14c	0.09c	1.17a	0.63b	0.13c	0.14c	0.12c	0.08c	0.72ab	0.38bc
AM infected root fragments (%)												
0–10 cm	36ab	37ab	39a	43a	21b	32ab						
10–20 cm	66b	54c	55c	78a	63bc	79a						
Mean	51bc	49c	48c	61a	45c	60a						
Fertilizer ^{15}N uptake (%)			6.2c	6.7c	45.2a	40.4a			5.8c	5.0c	34.8ab	26.1b
Earthworm biomass (g)	3.4a		1.3ab		1.7ab		1.2ab		1.2ab		0.2b	
^{15}N (‰)												
Roots	6.8b		217a		213a				202a		229a	
Earthworms	9.1d		80c		168a				100bc		129ab	
Plants	8.4b		551a		533a				535a		496a	
Soil	4.7c		79a		46b				74a		55b	

by AM in the 10–20 cm horizon of this treatment was also observed with earthworms (*table I*). When NPK was applied, the plants grew more vigorously and assimilated more ^{15}N; significantly greater quantities of the applied ^{15}N-labelled fertilizer were recovered (up to 45 %) by the pasture plants when either AM, worms or both were included (no additional effect of combining both was observed).

Many factors control both earthworm abundance and AM colonization of roots, including P and N fertilization and soil disturbance [44, 58, 73, 74, 107]. In the present case, earthworm burrowing and casting activity in the rhizosphere may have disturbed the AM hyphal network, decreasing root colonization [133], or they may have been ingesting AM components directly (hyphae, spores), although this was not measured. Earthworm survival was affected positively by AM presence; combining all the treatments, on average twice the biomass was recovered after 70 d when AM were present compared with treatments without AM (*table I*). Only a small proportion of the ^{15}N initially applied was recovered in earthworm tissues (0.2–0.3 %) and, despite slightly higher δ^{15}N signatures of *P. corethrurus* tissues in the presence of AM, these values were not significantly greater than in absence of AM. Thus, no preferential assimilation of ^{15}N from the myco-rhizosphere was detected, despite the observed lower AM colonization of roots in the presence of earthworms in treatments with ^{15}N (*table I*).

5.2. Roots as a food source of earthworms

Several authors have found root fragments in earthworm guts and this has often been associated with rhizophagous behaviour [27]. However food choice can be quite variable between individuals of the same community and both absence and presence has been found for the same species depending on the site (e.g. the common temperate earthworms *Aporrectodea caliginosa* and *A. rosea*) [22, 53, 81, 135]. In addition, roots generally represent a very small fraction of the total weight of ingested materials; soil generally being the most predominant fraction ingested, even for litter-feeding anecics, reaching up to more than 95 % depending on the species [98]. Furthermore, root tissue varies tremendously in quality and is often not very palatable or even useful for earthworms; several studies have shown that when worms are fed root tissues they lose weight or grow poorly compared with a soil-only diet [6, 100]. For example, Lavelle et al. [100] and Martin and Lavelle [116] showed the poor role of roots in maintaining growth of *M. anomala*; when fed fresh native-savannah grass roots, or roots that had decomposed for 2 and 10 weeks, the resulting growth rates were similar to the controls (savannah soil) for the first two treatments and reduced to a half in the latter treatment. Still, absence or low levels of root tissues in the guts or low growth rates when fed root tissues does not imply that earthworms are not feeding in the rhizosphere, or near it, since they may be ingesting rhizosphere products such as mucilages and root exudates or rhizobiota such as mycorrhizae and other fungi, nematodes or protozoa [20, 39]. In fact, the above results [25, 149, 150] suggest that feeding in the root zone of plants may be a common practice of many endogeic earthworms (especially polyhumics) and that an important proportion of their nutrient (C and N) requirements may come from rhizo-deposited (and other fresh OM) resources, and less from more stabilized (older) SOM.

5.3. Indirect effects of earthworms on the rhizosphere

Finally, other interactions between the drilosphere and the rhizosphere include the dispersal of beneficial symbionts such as inoculated *Rhizobia* [158], which have led to greater *Rhizobium*-induced root nodule formation by up to 100 times in clover [162] and the doubling of clover production compared with worm-free soils [40] in laboratory and greenhouse experiments (particularly in Australia and England) using temperate earthworm species. The actinomycete *Frankia* was shown to be dispersed by *P. corethrurus* and propagules were viable to infect susceptible host plants [138]. Further research in this area, particularly in the field, must determine the extent of stimulation of nodule formation using various earthworm and crop combinations in both temperate and tropical regions.

The importance of certain species of lumbricid earthworms for the dispersal of biocontrol agents and reduction of fungal and bacterial root diseases was elegantly illustrated for both take all (*Gauemannomyces tritici*) and bare patch (*Rhizoctonia solanii*) pathogens of wheat in the region of Adelaide, South Australia [41, 154–157]. These authors found that *G. tritici* root lesions were reduced by earthworm presence alone and by dispersal of the biocontrol agent (*Pseudomonas corrugata*), while for *R. solanii*, earthworm presence alone was effective at reducing root lesions.

Other indirect effects of earthworms on the rhizosphere are due primarily to physicochemical modifications of soil properties, particularly its nutrient status. Root proliferation into castings (*figure 2*) and expansion into burrows were reported by Darwin [36], and has been observed by many other authors [37, 46, 50, 51, 83, 109, 170]. Roots follow burrows as preferentially easy pathways of elongation (*figure 2*) and benefit not only from improved aeration and gaseous exchange but also their nutrient-rich wall coatings [62, 63]. Casts also provide hot-spots of nutrient availability to roots, particularly if placed deeper in the soil, where the difference between fertility of castings and soil is more polarized [37, 121]. Finally, decomposing earthworm tissue may also be an important local source of nutrients to plant roots growing near the place where the earthworm has died [171].

5.4. Earthworms and root production

Given all these interactions between the earthworms and roots, we must conclude that rhizosphere health, microbial composition, and its extent, as measured by root biomass, volume and density can all be significantly affected by earthworm activity. However, drilosphere effects on root biomass tend to be less dramatic than for shoots since, when given the chance, plants will usually invest more energy into shoot rather than root production [56, 114]. Thus, the drilosphere effects on plant growth are primarily focused on plant aboveground yields, which are the most commonly harvested portions in managed ecosystems. This preferentially greater effect on shoots may be because the plant derives a better nutrition in the presence of earthworms and does not have to divert as much energy into below-ground production, thus resulting in higher shoot:root ratios. These phenomena, documented in many cases in the literature, are summarized in Brown et al. [27] for the tropical regions. In some cases, however, negative or null effects on plant roots have also been observed [25, 27], although these do not always reflect negatively on plant shoot production. Furthermore, although total root biomass may be lower in the presence of earthworms, root density may be higher, indicating more smaller roots which are the ones mainly responsible for nutrient uptake [25].

6. DRILOSPHERE × POROSPHERE INTERACTIONS

Pores in the soil are surrounded by the soil fabric, but earthworm-derived pores differ from other cracks, pores and voids within the soil in that they are often coated with or surrounded by either mucus from the earthworm's body tissue or earthworm castings. Thus, earthworm-produced macropores (burrows, aestivation chambers) and micropores (in casts and burrow walls) can be surrounded by soil rich in nutrients and polysaccharides, which give the burrow walls and castings their consistency by binding soil particles together. The importance of these structures to microbial activity and SOM dynamics is discussed below.

Earthworm burrows generally occupy only a small proportion of the total pore volume of the soil [86, 87] (*figure 1*). Nevertheless, an important part of the macropores in soil (> 2 mm in diameter) can be of earthworm origin [48, 107]. Root-derived macropores have a similar function in the soil as earthworm macropores, and there can be important interactions between them [85, 87, 152]. These large pores are especially important in water infiltration and gaseous exchange [48]. Their significance in terms of microbial activity and SOM dynamics are mostly indirect, via modifications in the soil's physical environment (see section 7.1). Leaching of nitrates, soluble organic-C and other chemicals through the soil profile and into the groundwater (if water tables are high) can also be influenced by earthworm burrows [48, 49, 153].

Blanchart et al. [18] showed how different earthworm species can have contrasting effects on soil porosity, and how the soil type in which the earthworm is found also plays an important role [17]. The ultimate effects of the community on soil porosity seem to be intimately related with the soil type and the earthworm species composition which determine the type of structures produced and their interactions. For example, a community dominated by the earthworm *P. corethrurus* was shown to develop the macroporosity of a tropical forest soil under low-input cropping in Peru, at the expense of microporosity [17, 42]. On the other hand, in communities comprising both compacting and decompacting species, the results of the first group may be arrested by the latter, and vice versa. The ultimate balance of the activity of the two groups will determine the overall effect of the earthworm community on soil porosity.

7. DRILOSPHERE × AGGREGATUSPHERE INTERACTIONS

There are two main ways in which earthworm activities produce aggregates: (1) burrowing and (2) casting.

7.1. Burrowing

Burrowing produces aggregates on the burrow walls through axial and radial pressures and the deposition of external mucus. It appears that much C can be lost from earthworms in mucus production, perhaps even more than in respiration. For example, using ^{14}C, Scheu [144] estimated that 6 % of the body weight of the endogeic earthworm species *Octalasium lacteum* was lost in 1 month due to mucus production, amounting to 63 % of the total C losses, the other 37 % being due to respiration. It is not known whether this phenomenon occurs at a similar magnitude in other earthworm species. If this is the case, huge amounts of C and N, probably in the order of several $t \cdot ha^{-1}$, may be deposited yearly by earthworms in the soil. To certify this, further estimates of mucus production rates (and their nutrient content) by different earthworm species must be performed. The low C:N ratio of cutaneous mucus [33, 144] (for example mucus C:N = 3.8 for the temperate species *O. lacteum* [144]) can stimulate microbial activity, increasing respiration and mineralization rates in the burrow system. This is particularly the case with the burrows of the anecic earthworms, such as those of *L. terrestris* which are coated with mucus and organic materials incorporated, fragmented and made to adhere to the burrow walls by the earthworm. These burrows can thus be significantly enriched with oxidized Fe [75], plant available-P and N, Exch. Ca and K [62, 63].

In addition to mucus secretions, N excretion from the earthworm bodies (mostly urea and ammonia) is also added to the burrow walls and/or to castings depending on whether the earthworms have external and/or internally discharging nephridia (*figure* 2). As with mucus C, few proper characterizations of N excretion rates have been performed for different earthworm species; most data were collected decades ago for a few lumbricids [54, 122, 163] and a couple of metaphires [5, 82]. Future efforts should concentrate on obtaining accurate excretion rates (e.g. using evenly ^{15}N-labelled worms) for a wide range of species, since earthworm excretion can represent an important although much ignored component of the N cycle within the soil. Ferrière and Bouché [55] showed how ^{15}N from labelled earthworms was rapidly transferred into growing plant tissues in a pasture, presumably due to mucus secretion and N excretions. Other work of this type is necessary, with evenly labelled earthworms of different ecological categories and species to ascertain the generality of this rapid-transfer phenomenon.

Because of the relative richness of the burrows compared with bulk soil, a concentration effect of micro-organisms has been observed, with higher numbers of aerobic asymbiotic N_2-fixing bacteria, and denitrifying bacteria in the 2-mm zone along the walls [15] (*figure 2*). Microbes, such as bacteria transported with H_2O [111] and other organisms (e.g. collembolans, mites) may use burrows as pathways for movement or even for temporary or permanent dwelling, particularly once they are abandoned.

7.2. Casting

Egested earthworm casts can take on various forms, from a paste-like slurry to granular and globular shapes in a range of sizes. These can be deposited on the burrow walls, within the burrow itself, or on the soil surface (*figure 2*). The amount of cast production by earthworms in the tropical zones can reach huge proportions, in the order of a few t·ha^{-1} up to many hundreds of t·ha^{-1}, such as in savannahs at Lamto, Ivory Coast or in pastures of Veracruz, Mexico [95]. These may account for a significant proportion of the total soil volume (*figure 1*). In fact, in some regions, the whole of the topsoil profile (A horizon) may be comprised of relatively fresh (months or years old) earthworm castings, and it is likely that most of the top 10–30 cm of the soil in many regions has been ingested by earthworms at some time or another in the past. This is because geophagous endogeic earthworms (especially in the tropics) can consume from 5 to 30 times their own body weight every day [95]. Given that these earthworms are generally selecting soil particles (particularly of clay sizes) and regions richer in SOM, the different types of casts produced (globular and granular, compacting and decompacting) and the different feeding strategies of earthworms (from epigeic to geophagous oligohumic-endogeic) will determine the effects on OM dynamics and microbial activity. These can be very different depending on the time scale, the earthworm community and the ecosystem in question (e.g. tropical agroecosystem vs. mountain forest). The proportion of casts deposited on the soil surface as opposed to subterranean casts may vary tremendously depending on the species and soil type. In the Lamto savannahs for example, the proportion of surface deposition varies from 0 % (*Millsonia ghanensis*) to 1 % (*M. anomala*), 7 % (*M. lamtoiana*), 16 % (*Chuniodrilus zielae*) to almost 100 % (*H. africanus*) [92, 164].

7.2.1. *Short- to medium-term effects*

In earthworm casts, at the scale of a few hours or perhaps days, microbial activity, nutrient and C mineralization are increased, but after drying out and remaining stable, if not destroyed for several weeks up to months, these same casts can be sites of reduced microbial activity and lower mineralization rates (*figure 3*). Regarding the shorter time-scale (fresh to a few-d-old casts) there are many data showing how earthworms stimulate microbial activity and populations [24, 39, 44] and nutrient availability [11, 107]. At the medium time-scales, much less information is available. In a few experiments, casts have been incubated for several weeks or months, demonstrating how the stabilization process and the ultimate cast characteristics are largely influenced by the interactions with the microflora, and the parent material characteristics [113, 115–116, 130, 142, 143, 148].

7.2.2. *Long-term effects*

At the scale of months to years, the few experiments undertaken have revealed an important role of earthworms in determining soil aggregation and stability status [18], microbial activity and C mineralization rates [159] (*table II*). For example in Yurimaguas, Peru, the activity of a population of *P. corethrurus* over 7 years under continuous maize decreased C stocks in the soil by 3.2 t·ha^{-1} (*table II*), despite increases in plant production in most years [31]. However, when these activities were entered into the Century model and slow and passive stocks simulated over 30 years, after about 15 years mineralization rates of both stocks were reduced in the plots with worms [61, 173] (*figure 10*). Hence, at the end of 30 years, plots with earthworms would have 28 % more total organic C, most of which would be in the slow pool. This is presumably due to the protective nature of *P. corethrurus* casts and the long-term regulatory force of the drilosphere on soil C stocks and mineralization dynamics.

At Lamto, Ivory Coast, Gilot [60] (*table II*) observed a 5 % decrease in C mineralization rates with only 3 years of yam culture in the presence of *M. anomala* versus its absence. With the same period of maize cropping, only a slight (and not significant) effect was found [59]. The difference between these two results may be related to the original destructuration of the soil performed with the yam crop but not with the maize [59]. If the same simulation over a longer period as that performed at Yurimaguas were applied to the maize at Lamto, the result would likely show reduced C mineralization because the compact

Table II. Soil C budgets in three long-term experiments with earthworm (*P. corethrurus* or *M. anomala*) additions to annual cropping systems compared with non-inoculated treatments [31, 59–61] and the result of two simulations [104, 108, 173].

Site, Country	Species added	Land use	Duration	Effect on C dynamics
Yurimaguas, Peru	*P. corethrurus*	Multiple crop rotation	3 years	No sign. diff.
		Continuous maize	7 years	3.2 t·ha^{-1} loss
			100-year simulation	Decrease in C mineralization after 40 years
Lamto, Ivory Coast	*M. anomala*	Yam	3 years	5 % decrease in C mineralization
		Maize	3 years	No sign. diff.
		Grass savannah	100-year simulation	Conservation of slow C pool

casts of *M. anomala* are known to physically protect C from microbial attack [115].

Other experiments undertaken in a maize-based agroecosystem in Ohio, USA, comparing earthworm addition, reduction (electro-shocking) and ambient earthworm populations treatments seem to agree with the initial trends (short-term) found at Yurimaguas. McCartney et al. [119] observed increased pools of intermediate and coarse OM fractions after 3 years of earthworm reduction, implying that earthworm activity was the cause of lower OM stocks. Similarly, Blair et al. [16] found significantly greater microbial biomass-N in the same earthworm reduction treatments. Increased earthworm population treatments on the other hand, led to higher soil respiration rates on several occasions [147], and greater nitrate levels in soils with inorganic fertilizer applications [16], and to higher leachate volumes with greater amounts of dissolved organic N [160]. Reasons for these phenomena may be due to liberation of N tied up in microbial biomass, or due to higher metabolic rates (activity quotients) of the microflora community [69, 172], in the enhanced or ambient earthworm population sites (responsible for increasing C and N mineralization). Using data on the fate and durability of C and N in lumbricid spp. castings and the proper earthworm ecological and demographic data, the long-term consequences of these treatments on soil C and N stocks could be modelled to ascertain whether in fact earthworms were reducing these stocks or just causing a more rapid turnover but at a lower total level. Hence, the possible transience of the observed decreases could be detected (as at Yurimaguas).

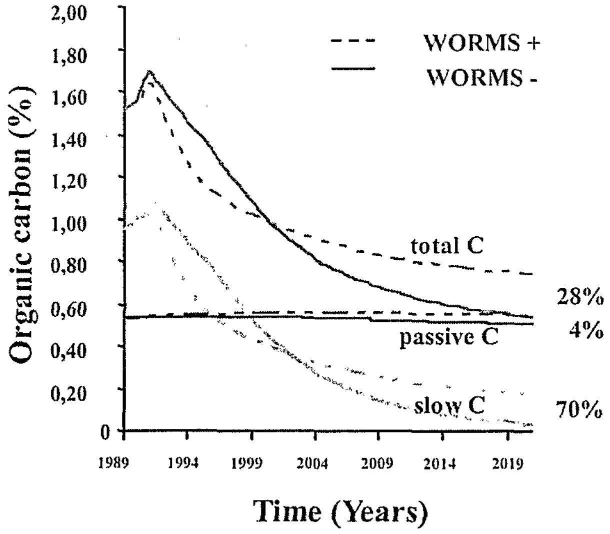

Figure 10. Simulation of C dynamics over 30 years, in a 7-year continuous maize experiment with addition of *P. corethrurus* to small (0.28 m^{-2}) plots at Yurimaguas, Peru, using the Century model [173].

Newly invaded sites and earthworm invasion fronts also provide the opportunity to study these processes without the confounding effects of long-term previous earthworm presence. For example, *Amynthas hawayanus* invasion patches in a NY, USA, deciduous forest had higher pH, microbial biomass C and N, soil NO_3, C mineralization rates and denitrification activity and lower %C in the O and A horizon [30]. When lumbricid earthworms invaded a deciduous forest in north Minnesota, USA, Alban and Berry [1] observed an average decrease of 0.6 Mg C·ha^{-1}·year^{-1} over 14 years to a 50-cm depth, and in New Zealand pastures, O'Brien and Stout [127] found increased C turnover of 0.3–1.0 Mg C·ha^{-1}·year^{-1}, probably due to degradation of accumulated OM. At a pasture N of Manaus, Brazil, 18 t C·ha^{-1} disappeared in 3 years in the upper 20 cm of soil following pullulating of a *P. corethrurus* population [12]. Although these results point to rapid and large C losses induced by earthworm invasion or rapid population increase, it is unlikely that these losses continue indefinitely. More likely, a new equilibrium is reached once the earthworm invasion process has ended and stabilized, although these soils will likely maintain higher turnover rates and lower C-stocks than the formerly uncolonized soils. Furthermore, the distribution of C in the different particle size fractions will probably also change [31, 61].

In summary, the evidence thus far suggests that earthworm activities lead to increased microbial activity and mineralization processes in fresh and few-d-old casts and in the soil profile over a few years scale, but as casts age and with longer time-scales (years to decades) of earthworm colonization of new sites, the stimulatory effects are reduced and static effects begin to predominate, promoting C and N conservation and a regulation of microbial activity.

Table III. Estimate of annual inputs and requirements for maintenance and production of an earthworm population under a winter cereal field [34]. Average earthworm biomass = 0.6 Mg·ha^{-2}, abundance = 3.5–4.7 million individuals·ha^{-1}.

Inputs/Requirements	Mg dry matter·ha^{-1}	Mg N·ha^{-1}
Litter OM inputs (stubble, cattle slurry)	0.48	0.06
Roots and rhizo-deposition	0.30	0.05
Total inputs	0.78	0.11
Population requirements (excretion losses, production)	0.3–1.0	0.05–0.07

8. CONCLUSION: REACHING GENERALIZATIONS

The drilosphere can exert an important regulatory role in soil function, including its physical structure (aggregation, porosity), chemical properties and processes, biological interactions and plant production. There is considerable overlap between the drilosphere and other soil functional domains. In fact, one may question whether the drilosphere can even be separated from these other spheres (or vice versa), or even the value of considering separate spheres. This review highlights the importance of the drilosphere as a separate entity, focusing on its properties and some soil processes affected and the role of its interaction with other functional domains.

Several attempts have been made over the last few years to address and estimate the functional consequences of drilosphere interactions with microorganisms on soil properties and processes at the field scale [39, 104, 105, 131, 132]. These have generally taken the form of annual estimations of earthworm community roles in C and N cycling. However these attempts have always been limited by lack of accurate field data due to the overriding and confounding effects of spatial and temporal variability in earthworm populations, controlled by environmental or other difficult-to-manage factors. Furthermore, the poor knowledge of several basic biological and physiological processes of different earthworm species, such as mucus secretion and nephridial excretion rates, makes many field estimates less reliable. Throughout the present review, we have pointed to several areas for which there is scarce available data. These could be complemented with further research in the following three priority areas.

8.1. Earthworm biology and ecology

There is a great need of more information for many earthworm species (particularly non-lumbricids and tropical earthworm species) on issues such as: taxonomic identification; estimates of cutaneous and intestinal mucus secretion and N excretion, ingestion rates (soil, OM and detritusphere materials) and C and N assimilation efficiencies; food preference; gut microbial communities and the effect of gut passage; enzymes produced in the gut and their source (earthworm vs. microbial); amounts of casts deposited on the surface vs. below ground; burrowing patterns and field population demographics.

These basic data on biological/physiological earthworm characteristics open the way for making more accurate estimations at the field level of processes such as the type and amount of food (organic materials, C and N) of a particular quality necessary to support an earthworm community (an example of annual inputs and requirements to maintain an earthworm population under a winter cereal field in Ireland [34] is shown in *table III*), as well as the potential contributions of earthworm biomass, gut, burrow and cast processes to C and N cycling and nutrient availability to plants.

8.2. Long-term studies

Most studies are limited to a few months or at most a few years, which is often too short to reach adequate conclusions as to the long-term effect of earthworms on the processes studied. An effort should be made to promote and find funding for long-term investigation sites, within representative ecosystems (agricultural and natural) and climate regions (from tropics to temperate), that could be used to produce models of the effects of earthworms on ecosystem function. At these sites, emphasis should be taken to properly assess annual earthworm population biomass turnover rates – separately for each species –, the life-span of casts and burrows, and the nutrient and microbial (activity, species changes) dynamics in these structures as they age. To aid in the detection of changes in mineralization rates (and nutrient status in soils) due to earthworms, stable isotopes such as ^{13}C and ^{15}N could be used to properly trace the different C and N pools.

8.3. Spatially-sensitive studies

Since Satchell [140] described patchiness of earthworm populations, only in the last few years has the highly patchy nature of many earthworm populations been well characterized using spatial (geo)statistics. Further efforts should be made to identify the factors governing this patchiness in order to understand how soil management can be changed to enhance earthworm communities and their activity. Rossi et al. [139] have developed a relatively rapid and simple means of characterizing horizontal earthworm distribution in the field, consisting of manual sorting of up to 100 samples of about 25 × 25 cm square and > 20 cm deep. There is much potential for utilizing this methodology in long-term experiments, and with repeated samples on the same area, if earthworms are returned to the soil. Simplified methods of using traditional ecological techniques such as mark-recapture (e.g. using dyes [52, 118]) also need to be developed for widespread use. Dyes can also be applied to trace earthworm structures (casts and burrows), their production in time and their durability. These techniques allow an assessment of the vertical dynamics of the population and the production patterns of different burrow systems. These data are also essential to estimate potential effects on nutrient and microorganism movement through the soil profile and the effects of any potential agricultural practice (e.g. tillage) on their populations. Further confirmation of earthworm attraction to particular plant rhizospheres [25] or regions of high microbial activity is also necessary.

A more adequate assessment of the drilosphere's biological, physiological, morphological, physical, chemical and temporal features using these research initiatives on a wide gamut of species and ecological strategies comprising a community will permit upscaling from the earthworm as an individual, to community and population levels at the ecosystem scale, thus properly estimating the functional roles of earthworms in the soil ecosystem.

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