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Effects of Earthworms on Phosphorus Dynamics – A Review

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ABSTRACT

Belowground biotic interactions are known to influence soil fertility and plant growth by changing the physical environment and the soil nutrient cycles. Among the great diversity of soil biota, earthworms are keystone soil organisms in regulating nutrient cycling through: (i) their own metabolism that leads to high availability of carbon (C) and nitrogen (N) from metabolic wastes such as urine, mucus and tissue, (ii) the dispersal and the stimulation of soil microorganism activity associated with passage through the intestinal tract and (iii) the distribution and the mixing of organic matter and soil mineral particles. While many studies have examined impacts of earthworm on C and N fluxes in soils, less attention has been paid to the impact of earthworms on soil phosphorus (P). This paper reviews the current state of knowledge of the global earthworm's impact on soil P dynamics in order to evaluate further involvements: i) on plant production and ii) on P transfer by runoff waters at the plot scale. This mini-review aims at considering research issues at several ecological levels, from individual earthworms (P distribution during food assimilation and excretion; gut microbial activities) to earthworm populations and communities (ecological categories and their influence on P dynamics) and, to the full extent, to the ecosystem scale (storage and/or loss of P). Interacting effects with other organisms (plants, microorganisms) are taken into account as well as the role of earthworms on physicochemical parameters (casting and burrowing activities, soil stability). Such a synthesis highlights the necessity to conduct interdisciplinary studies on biological, chemical and physical processes to better understand the effects of earthworms on P cycling at the ecosystem and landscape levels.

Keywords: drilosphere, ecological level, erosion, microorganism, plant

CONTENTS

INTRODUCTION

Belowground biotic interactions in terrestrial ecosystems are known to influence soil fertility and plant growth by changing soil nutrient cycling and the physical environment (Wardle 2002). Belowground communities include a large variety of organisms showing highly complex interactions across trophic or non-trophic groups (Coleman 2008). Among the great diversity of soil biota, earthworms are key components to regulate nutrient cycling processes in many ecosystems (Edwards and Bohlen 1996; Bohlen *et al.* 2004). Already in 1881, Darwin was one of the first scientists who noted that the topsoil consisted mostly of earthworm castings thus highlighting the importance of earthworms in pedogenesis processes. Darwin's observations pointed out the importance of earthworm activities in the decomposition of organic matter and its intimate mixing with mineral particles leading to the formation of the so called "vegetable mould". Indeed, earthworms function as ecosystem engineers, i.e. they modify directly or indirectly the chemical, physical and biochemical properties of the soil thus affecting the availability of resources to other organisms (Stork and Eggleton 1992; Jones *et al.* 1994, 1997; Lavelle *et al.* 1997). At the heart of the engineering concept is the great ability to move through the soil and to create organo-mineral structures as faeces (casts) and burrows, activities commonly referred to as "bioturbation". As pointed out by Lavelle (1997), the soil biogenic structures created by earthworms, commonly termed drilosphere (Beare *et al.* 1995; Brown *et al.* 2000), may have several functions in the soil system: i) they serve as a food resource, or even habitat (Tiunov and Scheu 2000), for smaller organisms, mainly microorganisms, because of their high energetic status and especially the high contents of organic matter (Jégou *et al.* 1998; Buck *et al.* 1999; Jégou *et al.* 2000; Le Bayon and Binet 2006) and, ii) they are directly involved in the formation and/or stabilization of soil structure (porosity, aggregation) and thus contribute to the soil maintenance and fertility. The abundance and variety of biogenic structures are also known to modulate the turnover of soil organic matter which is entrapped in earthworm dejections (McInerney *et al.* 2001; Marhan and Scheu 2006; Don *et al.* 2008). While many studies have examined impacts of earthworm on carbon (C) and nitrogen (N) fluxes in soils (Bohlen *et al.* 1997; Bouché *et al.* 1997; Lavelle *et al.* 1997; Whalen and Janzen 2002), less attention has been paid to how and to the extent to which earthworms influence the dynamics of soil phosphorus (P).

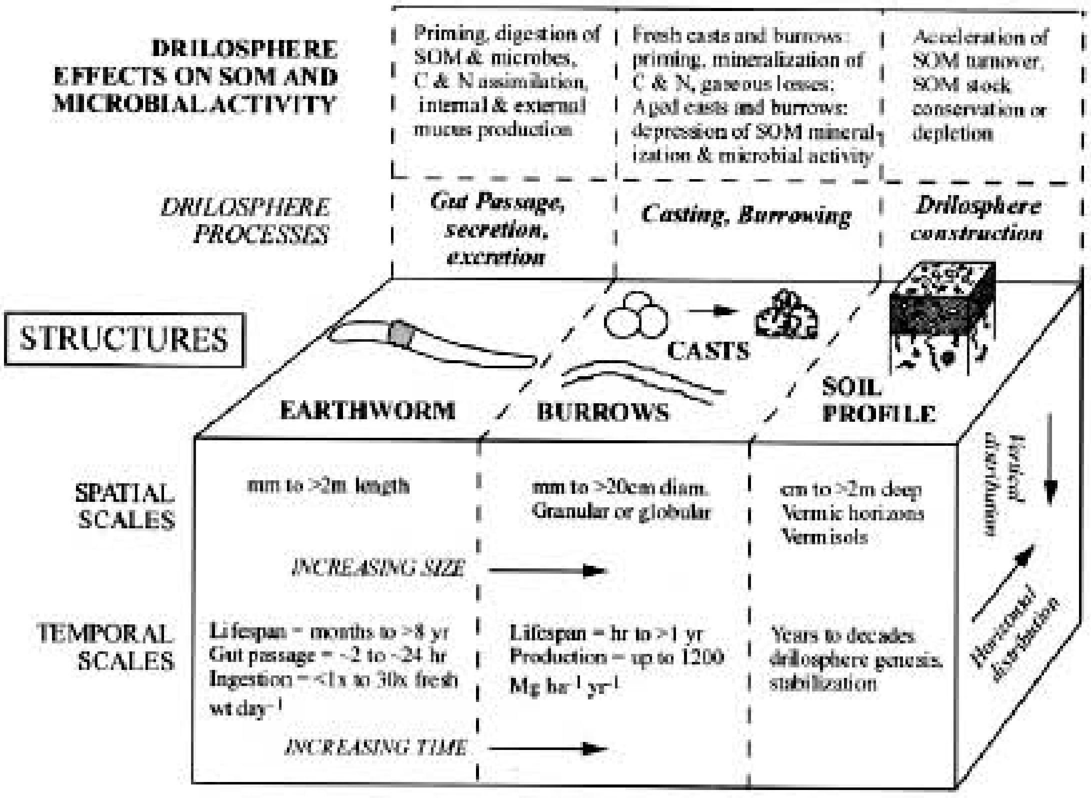

Fig. 1 The effect of drilosphere structures and processes (internal and external) on soil organic matter dynamics and microbial activity at different scales of space and time, from the earthworm gut up to the soil profile and from a few hours up to decades. Adapted from Brown GG, Barois I, Lavelle P (2000) Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains. *European Journal of Soil Biology* 36, 177-198, ©2000, with kind permission of the authors and Elsevier.

Growing interest in the dynamics of P is mainly due to two aspects. On the one hand, after N, P is the second most limiting element for plant growth (Vance *et al.* 2000; Hinsinger 2001; Vance 2001). In addition, P is by far less soluble in water and consequently less mobile and available to plants in comparison with the other major nutrients in soils, especially N. Indeed, P ions (mainly $H_2PO_4^-$ and HPO_4^{2-}, which are the effective P forms absorbed by plant roots) tend to strongly react with numerous soil constituents on which they adsorb, thus inducing a low proportion of P ions in the soil solution. The weak availability of P in soils is related to several factors as (i) the pH, (ii) the concentrations of anions that compete with P ions for ligand exchange reactions and, (iii) the concentrations of metals (Ca, Fe and Al) that can co-precipitate with P ions (Hinsinger 2001). As commonly observed in the vicinity of plant roots in the so-called rhizosphere soil (Li *et al.* 2008a, 2008b; Guppy and McLaughlin 2009), the physicochemical conditions of the drilosphere may considerably differ from those of the bulk soil, as a consequence of a range of processes that are induced either directly by the activity of earthworms themselves or by those of the specific microflora living in earthworm biogenic structures (faeces, burrow-linings) (Devliegher and Verstraete 1997; Brown *et al.* 2000). On the other hand, at a larger scale, the second reason that leads us to focus on P is that runoff and potential transfer of this element from soils is a primary factor in the eutrophication of continental waters (rivers, lakes, etc.). In particular, available forms of P, comprising P in dissolved and particulate forms, are mostly involved in surface water eutrophication (Sharpley 1993). Several studies have focused on particulate soil detachment; however, less attention has be directed towards the contribution of earthworm surface casts to soil erosion despite their enrichment in P compared to the surrounding soil (Sharpley and Syers 1976, 1977; Sharpley *et al.* 1979; Le Bayon and Binet 1999; Le Bayon *et al.* 2002; Le Bayon and Binet 2006).

This paper aims to review the current state of knowledge of the global earthworm's impact on soil P dynamics in order to evaluate further involvements: i) on plant production and, ii) on P transfer by runoff waters at the plot scale. Research issues at several levels of the ecological hierarchy are considered, from individual earthworms (P distribution during food assimilation and excretion; gut microbial activities) to earthworm populations and communities (ecological categories and their influence on P dynamics) and, to the full extent, to the ecosystem scale (storage and/or loss of P).

EARTHWORMS AND PHOSPHORUS CYCLING: A HIERARCHICAL APPROACH

By studying the effect of earthworms on nutrient cycling, and especially on P, many investigations have focused on small-scale processes and functions, i.e. in casts and burrows. The extrapolation of the results obtained to the ecosystem scale is therefore quite difficult. In addition to this spatial dimension, taking into account the temporal variation is also a challenge for future modelling approaches in order to better understand the whole role of earthworms. The schematic diagram proposed by Brown *et al.* (2000) outlines the combination of all of these aspects by illustrating the drilosphere effects on soil organic matter (C, N) and microbial activity (**Fig. 1**). These authors highlight the drilosphere as a "dynamic sphere" of earthworm influence on soil which is constantly changing in space and in time depending for instance on the periods of activity of earthworms, the duration of the different structures they have created, the horizontal and vertical distribution of earthworms according to biotic and abiotic factors, etc. This concept may be applied to P and the following section gathers together several ecological levels to better understand how earthworms influence the P cycle.

The earthworm individual level

Earthworms are known to preferentially ingest a mixture of organic matter and sand grains (Schulmann and Tiunov 1999; Lavelle and Spain 2001) with the latter facilitating the mechanical fragmentation of organic residues during gut transition, thus enhancing microbial accessibility to organic matter (Marhan and Scheu 2005; Curry and Schmidt 2007). The diet of earthworms mainly consists of organic material in various stages of decay and of the microorganisms that colonize it (Lee 1985; Curry and Schmidt 2007). Earthworm guts actually act as bioreactors where the microbial activity is enhanced due to favourable conditions with readily available C of mucus and water (Lattaud *et al.* 1997; Tiunov and Scheu 2000). Microorganisms have been reported to proliferate in the gut and dejections of earthworms (Parle 1963a, 1963b; Edwards and Bohlen 1996; Brown *et al.* 2000). Microclimatic conditions in surface-casts and burrows are favourable for a high microbial activity and several studies have described the taxonomic composition of the microbial community in earthworms' biogenic structures (Tiunov and Scheu 2000; Tiunov *et al.* 2001; Orazova *et al.* 2003; Prakash *et al.* 2008). Evidence of a mutualistic digestion involving earthworms and their microflora was brought by Lavelle and Spain (2001), Brown *et al.* (2000) and Trigo *et al.* (1999), where it was demonstrated that the favourable conditions of the earthworm's gut enhance the digestion of organic matter by microorganisms. During the gut transit, the ingested soil is completely rearranged and restructured (Barois and Lavelle 1986; Barois *et al.* 1993) leading to the mobilization of clay particles (Marinissen *et al.* 1996) and the disruption of the existing cation bridges in the aggregates, but also conversely to the formation of new bonds (Shipitalo and Protz 1988, 1989). The global reorganization of mineral and organic particles generally occurs in the posterior intestine of earthworms (Barois *et al.* 1993).

In this context, the fine processes closely related to P dynamics in the earthworm's gut remain already partially unknown. According to several authors and reviewed by Kuczak *et al.* (2006), the increase of P in soil that passes through the intestinal tract of earthworms is probably due to several factors: (i) a significantly greater pH of the gut contents along the earthworm intestinal tract (6.8 and 6.0 for the anterior and posterior parts and 5.0-5.4 for the soil, respectively) (Barois and Lavelle 1986); (ii) large amounts of mucus secreted in the earthworm gut, which release carboxyl groups from carbohydrate compounds that can block and compete for P sorbing places, and in turn, increase soluble P (López-Hernández *et al.* 1993); and (iii) an increase in the microbial activity during digestion processes (López-Hernández *et al.* 1993). In addition, the ingestion and thorough mixing of soil in the intestinal tract of *Lumbricus rubellus* and *Aporrectodea caliginosa* favors the dissolution of phosphate rock and thus the availability of the derived-P in the soil (Mackay *et al.* 1982). Moreover, Kuczak *et al.* (2006) have conducted a fractionation of the different chemical forms of P recovered in casts and they have found that the earthworm gut passage and/or the selective ingestion could influence both available P (extracted through a resin or with bicarbonate) and moderate available P (linked to oxides or extracted with diluted HCl 1 M). Thus, not only the concentrations but also the chemical forms of P may be modified by the ingestion and the thorough mixing of soil in the intestinal tract of earthworms. However, the activities within the gut of an earthworm are not yet entirely understood and future research is still needed for a better understanding of the physicochemical processes that occur all along the digestive system of the earthworm.

Following digestion, the egested casts upon the soil (e.g. surface-casts) or within the soil usually depend on the species of earthworm, on soil density and on location of the food resource (Lee 1985; Edwards and Bohlen 1996; Binet and Le Bayon 1999). Nevertheless, and because several works were conducted on the earthworm biogenic structures, it was demonstrated that concentrations of organic matter and available nutrients are higher in earthworm casts than in non-ingested soil (Lee 1985; Zhang and Schrader 1993; Oyedele *et al.* 2006). The available forms of P follow this general rule as demonstrated by a large panel of researchers. Thus, Sharpley and Syers (1976, 1977) showed three times more available P in freshly-deposited casts of *A. caliginosa* under a permanent pasture in New-Zealand. The geophageous tropical earthworm *Pontoscolex corethrurus* from Venezuela was also found to concentrate exchangeable-P in casts due to a change in the P-sorption complex during the gut transit (López-Hernández *et al.* 1993). These results were confirmed by Chapuis-Lardy *et al.* from an 18-year-old secondary forest in the Peruvian Amazonia (1998) and from cropping systems in Malagasy Highlands in Madagascar (2009). Brossard *et al.* (1996) also compared fresh surface casts of *Polypheretima elongata* and non ingested soil from Vertisols in the South East Martinique (French West Indies) and found an increased P availability in earthworm dejections through ingestion of P-rich particles thus modifying the relative proportions of different P forms. Recently, Kuczak *et al.* (2006) showed in central Amazonia that earthworms from the Glossoscolecidae family increased labile P pools (extracted with resin strips, $NaHCO_3$ 0.5 M, NaOH 0.1 M, HCl 1 M) in casts through gut passage and/or selection of ingested materials in several ecosystems (agroforestry, secondary forest, pasture). Looking at earthworm burrows that are usually lined by a layer of flattened casts and mucus, they seem to follow the opposite trend in terms of P dynamics. The few researches that have been conducted thus showed a lower Olsen-P content in burrow linings than in surface casts and surrounding soil (Le Bayon and Binet 2006). Moreover, Jensen *et al.* (2002) observed that lining material desorbed quite large amounts of labile P at solution concentrations below approximately 1 mg PO_4-P L^{-1} and at short contact times ranging from 5 minutes to 2 hours.

Concomitantly to the P behavior in earthworm biogenic structures, an increased basic acid phosphatase activity was found in *Lumbricus terrestris* burrow-linings and casts from a temperate agroecosystem in France (Le Bayon and Binet 2006). In the United Kingdom's, Satchell and Martin (1984) also previously recorded a high phosphatase activity (both acid and alkaline forms) in wormcasts from cultures of paper waste sludge inoculated with *Eisenia fetida*, *Dendrobaena veneta*, *L. rubellus* and *A. caliginosa*. Similar results were obtained in Germany by Buck *et al.* (1999) with *L. terrestris* and *Octolasium cyaneum* varying mulch types, as well as by Flegel and Schrader (2000) working with *D. octaedra*. As a consequence, the enzymatic activities may be influenced by the food quality provided that could affect the specific nutrient state of the casts. Indeed, Flegel and Schrader (2000) showed an interesting correlation between acid and alkaline phosphatase activities and the organic C and total N contents in casts. Not only the food nutrient status but also the enhanced mineralization of nutrients, the high substrate concentrations and the high moisture favor enzymes activities in fresh casts (Parthasarathi and Ranganathan 1999) that tend to decline with cast ageing (Parthasarathi and Ranganathan 1999; Le Bayon and Binet 2006). However, finding a better phosphatase activity in earthworm faeces was not systematically verified as pointed out by Zhang *et al.* (2000) in China for the earthworms *Metaphire guillelmi* and *E. fetida*.

More interestingly, the recent finding of an alkaline phosphatase in burrow-linings; this enzyme activity was strictly allocated to the earthworm proper gut microflora (Satchell and Martin 1984; Le Bayon and Binet 2006). This latter result raised the question about the origin of the earthworm's gut microflora: while it is now commonly accepted that the earthworm's gut microflora comes from both the ingestion of soil and from the earthworm itself (Brown *et al.* 2000), the proportions are still unknown. Moreover, the gut microflora and the digestive abilities have been shown to differ from an earthworm species to another (Lattaud *et al.* 1997) suggesting a huge variety of the subsequent effects on nutrient cycles and especially for P.

The earthworm population and community levels

As described above, earthworms affect soil physical and chemical properties and contribute to the transfer of organic matter and soil into organo-mineral and mineral soil layers. It becomes obvious that at the plot scale, parameters as the earthworm population and community size, growth, reproduction rate, survival and mortality have clear consequences on casting and burrowing activities. Moreover, the ecological and functional group of earthworms is quite obviously crucial regarding bioturbation processes that depend mostly on the location and availability of food resources. As reviewed by Bouché (1977), Lee (1985) and Curry and Schmidt (2007), earthworms are divided into detritivores (epigeic and anecic species) which usually feed at or near the soil surface mainly on plant litter, and geophages (endogeic species) feeding deeper in the soil profile and ingesting large quantities of soil. As a consequence, the spatial distribution of field earthworm populations and communities varies a lot and is usually closely linked to soil properties. The aggregate distribution of earthworms leads to hot spots of activity and a recent review of Feller *et al.* (2003) pointed out that the amount of soil brought up to the surface by worms in various temperate ecosystems ranged from 2.2 to 91.6 t ha^{-1} yr^{-1}. In tropical conditions, this cast production even reached 115 tonnes ha^{-1} year^{-1} in North Vietnam (Jouquet *et al.* 2008a). Such large amounts of fine soil materials surfaced at the top soil layers may increase P stocks in the first 12 cm, especially with exotic earthworms and deep-burrowing species (Suarez *et al.* 2003). A positive association between earthworms and soil P content was also previously observed by Nuutinen *et al.* (1998) and thus reinforces the importance of earthworm activities on P cycling.

However, the great majority of the studies (or even the totality) has focused on earthworm surface-casts, which may constitute only a small proportion of the total cast production, i.e. aboveground and belowground dejections, as pointed out by Bohlen *et al.* (2004). As a consequence, the quantification of casting activities into the soil profile is needed in relation to earthworm populations and communities (ecological category, diversity, and biomass). Such studies should be conducted both in laboratory experiments and at the field scale to give an overview of the global impact of earthworm on P cycling. Phosphorus balance, i.e. for instance the amount of P that returns into the soil by the way of earthworm activities and the total P fluxes through earthworm biomass, is unfortunately still poorly known whatever the spatiotemporal scale.

Earthworm populations and communities are also acknowledged to influence plant growth, either physically by changing the structure of the soil and thus offering preferential pathways for plant roots via the burrow network system or by modifying the soil P availability as revealed by Guerra (1982; in Kuczak *et al.* 2006) who found that plant P uptake was up to three times higher in the presence of *P. corethrurus*. The high concentration of P found in earthworm casts, especially in available forms (essentially $H_2PO_4^-$ and HPO_4^{2-}), are usually beneficial for plants growth (Mackay *et al.* 1983). However, opposite results have been highlighted by Milleret *et al.* (2009) who investigated the single and combined effects of three important actors which were earthworms (the endogeic *Allolobophora chlorotica*), arbuscular mycorrhizal fungi (AMF; *Glomus intraradices*) and leek plants (*Allium porrum*) on soil structure, nutrient concentration and plant growth by using an original compartmental experimental design without P addition. Contrarily to previous studies that aimed at determining mycorrhizae–earthworm interactions (Tuffen *et al.* 2002; Wurst *et al.* 2004), Milleret *et al.* (2009) observed no main significant effect of earthworms on P availability and plant biomass. However, AMF improved P transfer from the soil to the plant and significantly increased plant biomass. By measuring the N:P ratio in the leek shoots, Milleret *et al.* (2009) pointed out a clear P limitation in their experimental conditions, especially for plants grown without AMF. The authors therefore suggested that the effects of earthworms and AMF on plant production may depend on the limiting factors in the soil, mainly N and P. They concluded that in P limited conditions, AMF had dominant effects by improving plant P uptake, whereas in N limited conditions, earthworms can play a major role by enhancing N mineralization (Scheu 1994). As a consequence of this limiting effect of P in the soil-plant system, the quality of the organic matter returning as litter (shoots, roots) may decrease over time. These changes in substrate quality were associated with the reduction of the decomposer microbes and subsequently with reduced rates of litter decomposition (Bardgett 2005). A P limitation may consequently have severe implications for the global nutrient cycling and may modify drastically the structure of earthworm communities and, in a larger extend, the associated plant communities (Bardgett 2005).

The ecosystem and landscape levels

How earthworms affect the balance between P storage and conservation versus P losses from the system is one of the main topical questions that would help to satisfy requirements of the necessity to fertilize cultivated lands and to preserve concomitantly waters quality. At the ecosystem level, Kuczak *et al.* (2006) estimated that earthworm casts could constitute 41.0, 38.2, and 26.0 kg ha^{-1} of total available P stocks in an agroforestry system, pasture and secondary forest, respectively. The stability of P forms may also be modified in biogenic structures (Brossard *et al.* 1996) and once egested, fresh earthworm casts are initially subject to soil destabilization (Schrader and Zhang 1997) and then prone to stabilization processes through thixotropic or age gardening (Shipitalo and Protz 1988, 1989; Marinissen *et al.* 1996) that may be reversible. Regarding lifetimes of surface-casts, Decaëns (2000) observed in Colombia that the half-life of casts may range between 2 and 11 months in the pastures, 5 months in the savannah and may remain more than one year at the soil surface after being excreted. Thus, earthworms directly initiate the formation of organic matter rich microaggregates (Pulleman *et al.* 2005a, 2005b) that may stabilize the soil through several mechanisms due to the presence of recalcitrant organic matter, amorphous oxides of Fe and Al, calcium humate secreted in the worm's gut, fungal hyphae and/or polysaccharides from microbial mucilage (Marinissen and Dexter 1990; Six *et al.* 2004; Shipitalo and Le Bayon 2004; Oyedele *et al.* 2006). These stabilization processes implied as evidence a potential sequestration of organic P contained in soil organic matter due to enclosure in stable aggregates (physical protection) that reduced accessibility and oxygen for microorganisms. Such mechanisms have hence consequences on the turnover of organic matter at several space-temporal scales (Lavelle 1997; Brown *et al.* 2000) and potentially organic P, the most important P pool in soils that may represent 30 to 80% of the total P. The enclosure of organic matter in stable earthworm casts of *L. terrestris* and *L. rubellus* has already been demonstrated, especially for dried aged casts that were less dispersible than moist fresh ones, the effects of ageing and drying increasing as cast organic C content increased (Shipitalo and Protz 1988). On a long-term scale, McInerney *et al.* (2001) assumed that organic matter occluded in casts of anecic and endogeic earthworms could remain as it is and could maintain its stabilization status more than two years before changes may occur. One of the most important factors that govern stabilization/destabilization processes is clearly the soil texture. Indeed, an increased sand content generally increases carbon mineralization of enclosed organic matter in earthworm casts (Marhan and Scheu 2006) while clay minerals that are more intimately mixed with organic matter in the presence of earthworms (Scullion and Malik 2000) may contribute to the stabilisation of organic matter and its protection against microbial degradation (Feller and Beare 1997; Six *et al.* 2004; Lehmann *et al.* 2007).

In contrast to these phenomena of stabilization, earthworm casts and burrows may also contribute to nutrient losses through soil erosion and/or lixiviation. Nevertheless, how earthworms affect soil erosion is not clear: on the one hand, the general idea from the literature is that the presence of earthworms decreases runoff up to 2-15 times by increasing soil water infiltration. Using dye and tracer techniques, several studies have shown that burrows from endogeic and anecic worms may conduct water (Joschko *et al.* 1992; Shipitalo *et al.* 2000). Edwards *et al.* (1990) estimated that monitored burrows of *L. terrestris* over 12 season storms collected until 10% of the rainfall and an average of 13 times more water than predicted based solely on the diameter of the burrows at the soil surface. Burrows from anecic species are usually the most efficient on water infiltration (Bouché and Al-Addan 1997), in particular *L. terrestris* in no-till systems (Willoughby *et al.* 1997). Using artificial burrows, Joschko *et al.* (1989) and Roth and Joschko (1991) showed that earthworms enhance macroporosity by the burrows network or continuous channels they created, and the persistence of open burrow holes at the soil surface led to decreased runoff from crusted soils. Moreover, by their surface casting activities i.e. egesting soil and burying organic matter, earthworm casts enhance the soil surface roughness and then reduce soil crusting, which in turn improves water flow into the soil (Kladivko *et al.* 1986).

On the other hand, earthworm casts that are deposited on soil surface are subject to splash erosion (Vanhooff 1983) and the fine soil materials as well as plant nutrients they contain are exposed to an easy detachment and transport during rainfall events. Sharpley and Syers (1976, 1977) and Sharpley *et al.* (1979) reported the potential role of earthworm casts for the P enrichment of runoff waters under permanent pasture in New Zealand. These results partly contradict those of Le Bayon and Binet (2001) who used a simulated rainfall and demonstrated that earthworm activities act as a physical brake for soil erosion by (i) creating a surface roughness with the deposition of surface casts and (ii) reducing water runoff by associated enhanced water percolation. Only once the breaking-down point of the physical resistance of casts was reached, all surface casts were then quickly disintegrated and finally completely washed away. Transfers of nutrients (C, N and P) occurred then subsequently over a short-distance through successive deposition/suspension of soil particles in the water runoff. Cast erosion was also significantly and positively correlated to initial mass when casts were young but not when they were old (Le Bayon and Binet 2001). The erodibility of casts at different stages of their ageing process was also studied in Colombia by Mariani *et al.* (2007) who showed that under simulated rainfall, dry casts were slowly eroded into large aggregates, showing thus a progressive detachment of soil particles. These authors suggested that nutrients as C, N and P might have deposited around the cast during the rainfall events in the rainy season. At the opposite of all these results, a recent study in North Vietnam using a water runoff simulation showed that, despite the study was conducted under a tropical climate leading to strong rainfall intensities, earthworm casting activity significantly decreased water runoff velocity (Jouquet *et al.* 2008b). The authors assumed that the high stability of casts from the anecic *Amynthas khami* and particularly the rapid drying of the faeces might explain the low contribution of earthworms to soil loss even under intense rainfalls. Therefore, with regards to these three main studies, it appears that further work is needed on earthworm casts erosion to better predict their effects on soil and nutrient losses, especially P.

CONCLUSION

As illustrated in **Fig. 2**, several questions remain unsolved about the global earthworm's impact on soil P dynamics. At the finest scale, i.e. in the digestive tract of the earthworm itself, the biochemical processes during the gut transit are still not clearly understood, especially regarding the microflora specialized in the organic P mineralization and the re-

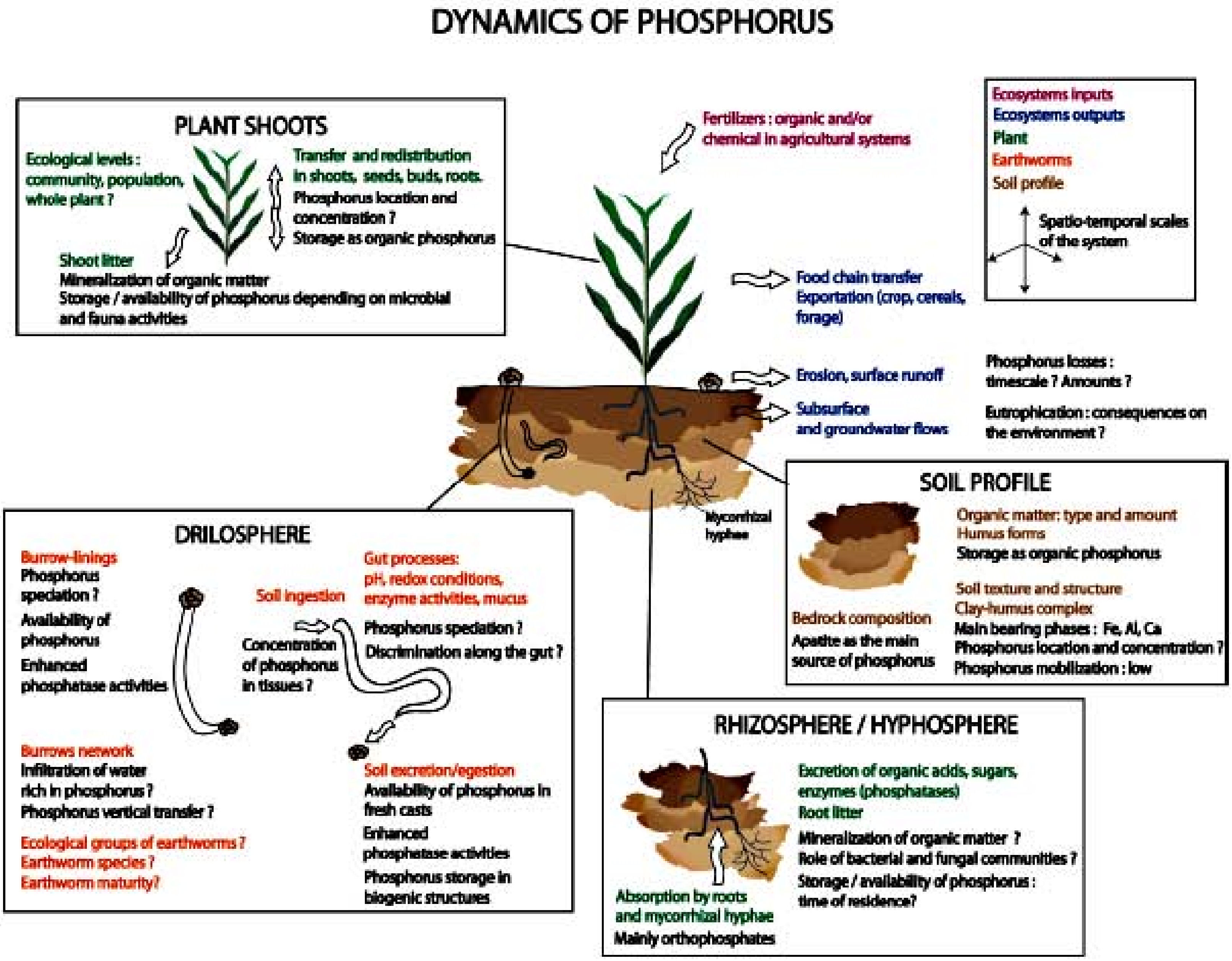

Fig. 2 Dynamics of phosphorus at the ecosystem level. Four compartments are represented: the soil profile as a whole, plant shoots, the rhizosphere and the drilosphere. Questions still unsolved are raised and ecosystem outputs are underlined.

lease of available P ions. At the community level, the ecological category of earthworms appears to be predominant in the P transformation and storage. Thus, mainly due to their food preference and their behaviour, anecics, endogeics and epigeics move through a variety of soil layers and ingest different proportion of organic matter and mineral particles. As a consequence, depending on the location into the soil profile (near or far away the drilosphere for instance) and relative to the type of biogenic structures created by earthworms (architecture of the burrow network, size of the aggregates, proportion of aboveground and belowground dejections, composition of casts and burrow-linings, aggregate stability, etc.), earthworms will directly and/or indirectly influence P dynamics. This includes the chemical aspects (proportions of total, organic and inorganic P), the kinetics (mobility, sorption processes) and indeed the availability of P for plants and microorganisms (bacteria and fungi). At the ecosystem scale, the contribution of earthworm surface-casts and burrows to the transfer of P is not yet clear and intimately linked to biotic factors (earthworm species, ecological group, abundance, biomass, vegetation cover, etc.) and abiotic parameters (gentle or steep slope, type of climate, intensity and frequency of the rainfall events, aggregate stability, etc.). Having a holistic view of the complexity of the P dynamics highlights the necessity to conduct interdisciplinary studies at multiple hierarchical levels. Such challenge involving biological, chemical and physical factors would help to better understand the effects of the soil biota, and especially earthworms, on P cycling and would bring information useful to model and predict P cycle at the ecosystem and landscape levels.

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