Chapter 8
Role of Soil Macrofauna in Phosphorus Cycling

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8.1 Introduction

Soils play a major role in the providing of goods and services by ecosystems to humans. They are involved in the main biogeochemical cycles (H_2O, C, N, P). They support agriculture, forestry, and pasture systems, and participate in climate regulation and detoxification. The importance of soils for ecosystem goods and services is based on their biological functioning, i.e., the whole biological functions carried out by soil biota in interactions with physical and chemical components of soil. These functions ensure, e.g., soil organic matter dynamics, nutrient recycling, soil structure and water retention. They are carried out by organisms of different sizes (from bacteria to macrofauna) and functional roles (decomposers, microbial regulators, soil engineers, and predators) (Lavelle et al. 2006).

Invertebrates of the macrofauna are key species for soil functioning. They participate in litter decomposition, mix organic and mineral matter, create and maintain soil structure by digging burrows and modifying aggregation, regulate microbial diversity and activity, and protect plants against pests and diseases (Lavelle et al. 2006). Following Jones et al. (1994), ecosystem engineers are

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organisms able to modify the physical environment and availability of nutrients for other organisms. Lavelle (1997) defined the organisms fulfilling these functions in soil as soil engineers. They develop very complex interactions with other soil biota. For instance, the gut and biogenic structures (burrows, casts, nests) of earthworms and termites are specific habitats in which soil microbial activities are either stimulated or attenuated. Freshly egested earthworm casts are generally characterized by an intense mineralization of organic matter and the release of nutrients for plants. Conversely, the mineralization in old casts is reduced, which allows for long-term carbon and nutrient storage in soil (Martin 1991).

It is now recognized that soil engineers can improve soil fertility due to their role in nutrient dynamics at different spatial and temporal scales (review in Brown et al. 1999). They have been shown to affect the availability of nitrogen (N) and phosphorus (P), the main growth-limiting nutrients (e.g., Lee and Wood 1971; Bignell and Eggleton 2000; Brown et al. 2000; Brossard et al. 2007; Le Bayon and Milleret 2009). Numerous studies showed an increase in plant growth in the presence of earthworms, although the mechanisms are not fully understood; one of them being an increase in nutrient availability (Brown et al. 1999).

The objective of this chapter is to highlight, in a non-exhaustive view of published data, the role of soil macrofauna on P cycling. We will focus on the main soil engineers, i.e., earthworms and termites, whose roles in soil functioning have been frequently studied.

8.2 Earthworms

8.2.1 Phosphorus Contents and Forms in Earthworm Biogenic Structures

The first scientific studies on earthworm ecology, in the 1940s, related earthworm activity and soil fertility. Earthworms may affect soil structure and processes in different ways, according to their feeding and burrowing behaviors (synthesis in Brown et al. 2000). Three broad functional groups of earthworms have been described by Bouché (1977): epigeic, endogeic, and anecic. Epigeic earthworms live in the litter layer, consume plant litter and rarely ingest soil. Endogeics are mostly soil organic matter feeders and burrow extensively both horizontally and vertically within the soil. Anecics feed on particulate organic matter mixed with soil particles and often form deep, primarily vertical, burrows in which they bury surface litter. Numerous studies report results on chemical or physicochemical properties of earthworm casts, i.e., the by-products of gut passage, in comparison with surrounding soil. Most of these studies show that casts are characterized by higher P content, especially water-soluble or available (Bray- or Truog-P) P content (e.g., Nijhawan and Kanwar 1952; Bates 1960; Gupta and Sakal 1967; Graff 1970; Sharpley and Syers 1976; review in Edwards 1981; de Vleeschauwer and Lal 1981, review in Lal 1987; Mulongoy and Bedoret 1989; López-Hernández et al. 1993). More recently, Kuczak et al. (2006) studied different P fractions (available P, moderately available P, and resistant P) in earthworm casts and soil in Amazonia. They observed that casts were characterized by higher total P and percentage of labile P pools (available and moderately available P). Guggenberger et al. (1996) found higher levels of alkali-extractable organic P in earthworm casts than in the surrounding oxisol. At this same site, Jiménez et al. (2003) worked in the field and analyzed inorganic and organic P fractions, including microbial P, in casts and surrounding soil. Under field conditions where earthworms ingest soil plus organic residues, total P concentrations were higher in casts than in surrounding soil. This increase was distributed over all inorganic and organic P fractions, including increased microbial P.

Because castings and earthworm-processed soils have the potential for higher P availabilities than uningested soils, the role of earthworm activities over the long term in soil P dynamics and the transfer of P into growing plants still needs consideration, especially in low-P status soils (e.g., Brown et al. 1999; Patrón et al. 1999; Chapuis-Lardy et al. 2009).

8.2.2 Phosphorus Dynamics and Availability in Earthworm Casts

Earthworm activity creates a series of geochemical and biological effects that are especially important for the cycling of P in soils (Brossard et al. 1996; Chapuis-Lardy et al. 1998, 2009; Nziguheba and Bünemann 2005; Le Bayon and Milleret 2009).

The availability of P is strongly influenced by the physical adsorption or fixation of P in soil (Frossard et al. 1995 and references therein). The phosphate ion (hereafter abbreviated as PO_4) concentration in the soil solution (C_P) may also decrease as a direct consequence of P removal by root uptake. This depletion gives rise to a replenishment of P from the solid phase, which is time- and C_P-dependent. This PO_4 exchange reflects the buffer power of the soil for PO_4 and varies with the composition and the physicochemical conditions of the soil. Isotopic exchange kinetics (IEK) utilizing ^{32}P as a tracer has been extensively used to specifically assess inorganic P availability in a variety of soils (e.g., Morel et al. 1994; Fardeau 1996; Sinaj et al. 2001). Such approaches (see details in Frossard et al. 2011) have been used to evaluate P availability in earthworm casts or in soil in the presence or absence of earthworms.

We briefly focus here on the case of *Pontoscolex corethrurus* (Glossoscolecidae, Oligocheta), a widespread tropical endogeic earthworm. López-Hernández et al. (1993) reported higher P availability in fresh casts derived from two tropical soils with contrasting P sorption capacity. Chapuis and Brossard (1995) found higher C_P and $E_{(1\ \mathrm{min})}$ (the amount of PO_4 that is isotopically exchanged within 1 min) values in casts egested by *P. corethrurus* fed with a Peruvian Ultisol. These changes in P availability were ascribed to (1) the higher pH of the gut content

(Barois and Lavelle 1986), (2) changes in sorption complexes induced by competition for sorbing sites between PO_4 and carboxyl groups of a mucus glycoprotein produced by the earthworm in its gut (López-Hernández et al. 1993), and (3) an increase in microbial activity during digestion (López-Hernández et al. 1993). More recently, IEK experiments were carried out to measure, describe, and compare the PO_4 exchange between liquid and solid phases of soil suspensions as a function of C_P and time, for two Malagasy soils and the associated casts egested by *P. corethrurus* (Chapuis-Lardy et al. 2009). The question arises whether the earthworm-induced modifications can change the ability of the soil solid phase to buffer C_P. The endogeic worm *P. corethrurus* increased the ability of PO_4 bound to the soil solid phase to exchange with PO_4 in soil solution (Fig. 8.1), because soil ingestion induced transformation of inorganic P to a more rapidly exchangeable form.

Tuffen et al. (2002) studied the transfer of ^{32}P in soil and between plants inoculated with arbuscular mycorrhizal fungi (AMF) in the presence of a temperate endogeic earthworm (*Aporrectodea caliginosa*). These authors reported enhanced ^{32}P transfer in soil and also between AMF-inoculated donor and receiver plants in the presence of earthworms.

Casts of earthworms usually contained larger amounts of organic P (e.g., for *P. corethrurus*, Chapuis-Lardy et al. 1998; Patrón et al. 1999), probably derived from a selective ingestion of soil particles (Chapuis-Lardy et al. 1998). Several

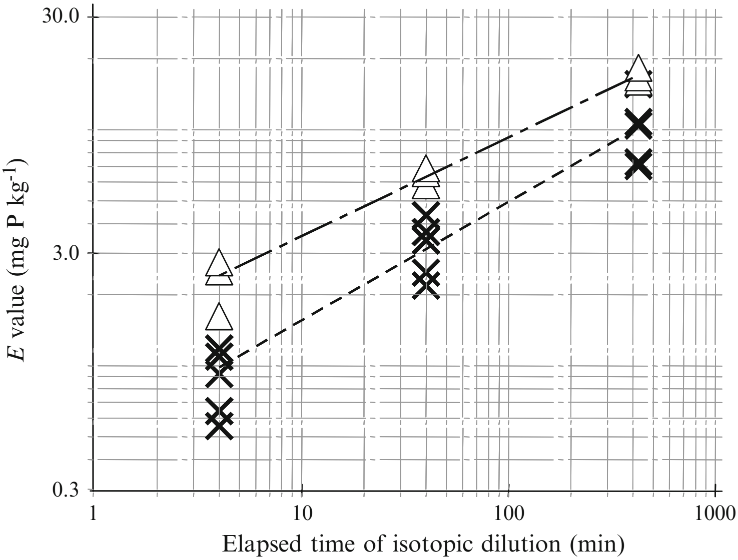

Fig. 8.1 Kinetics of isotopically exchangeable P ions (*E*, mg kg^{-1} soil) transferred between solid and liquid phases and the associated regression lines (*E* vs. time *t*) in control soil (from Andranomanelatra site) (*crosses*, *dashed line*) and casts of *Pontoscolex corethrurus* (*triangles*, *semi-dashed line*). The *x*- and *y*-axes are represented in log–log scales. Modified from Chapuis-Lardy et al. (2009)

studies reported increased enzymatic activity in earthworm casts and the stimulation of microbial activity (Sharpley and Syers 1976; James 1991; López-Hernández et al. 1993; Chapuis and Brossard 1995; Brossard et al. 1996; Le Bayon and Binet 2006). However, Zhang et al. (2000) observed an increase of inorganic P in soils in the presence of earthworms, despite a decrease of acid and alkaline phosphatase activities in earthworm casts, suggesting that P-containing organic matter is digested in the gut rather than in the casts. This confirms the results of Devliegher and Verstraete (1996), who showed that the increase of inorganic P in soils in the presence of earthworms was due to the production of alkaline phosphatases by earthworms (Satchell and Martin 1984; Park et al. 1990) and a stimulation of microbial (acid) phosphatase production by earthworm activity (Satchell and Martin 1984). Devliegher and Verstraete (1996) concluded for the anecic earthworm *Lumbricus terrestris* that the increase of organic P mineralization and inorganic P availability in the presence of earthworms is more of a gut-associated process than a cast-associated process. Overall, the higher P availability observed in soils in the presence of earthworms may be linked to a rapid turnover of an increased organic P content. However, depending of the dominant species, earthworm activity could also result in the protection of organic P in stable macroaggregates and the increased fixation of inorganic P in Fe and Al hydroxides (Scheu and Parkinson 1994a, b; Suarez et al. 2004). It is concluded that earthworms markedly change the biogeochemical status of P (availability, organic P pool, enzymatic activities) in their guts and in the soil where they are active (drilosphere, sensu Lavelle et al. 1997), including casts and burrow linings. However, their impact on P dynamics and availability in the soil depends on the particular properties of soil, the organic P source, and the specific burrowing behavior and food preferences of worms.

The assumptions on earthworm-mediated transformations of organic P and related effects on P cycling in soils could be efficiently verified using soil labeling with radioactive P, especially if performed before chemical extraction (see methodological aspects in Frossard et al. 2011).

8.2.3 Surface-Cast Erosion and Phosphorus Transfer

The earthworm ecological category, and especially the feeding behavior, determines the type of surface-casts egested (Lee 1985; Curry and Schmidt 2007) as well as the architecture of the earthworm-induced macropores (Jégou et al. 2000; Bastardie et al. 2003). Such biogenic structures are involved in the regulation of soil physicochemical processes. However, how earthworms affect soil erosion is poorly understood (Blanchart et al. 2004). Surface-casts may be impacted by raindrops, and the fine soil particles they contain easily detached and transported during rainfall events (Le Bayon et al. 2002; Mariani et al. 2007). Structural stability of the biogenic structures is, together with rainfall intensity and field slope, an important determinant of soil erosion. Hence, earthworms can be proposed as important moderators of soil erosion. Where stability is low and rainfall intense, material from the biogenic structures could be transported downstream by water runoff, thus leading to a significant loss of soil particles and associated P. Several studies have been performed to better understand the processes involved in surface-cast erosion and P transfer. Nevertheless, comparison between these investigations are difficult because of very variable experimental conditions (in situ annual monitoring or simulated rainfall events), different chemical analyses of P (colorimetric methods, anion exchange resins, sequential extractions, loss by ignition), and different expression of the results (actual measurements or estimations).

Sharpley and Syers (1976, 1977) and Sharpley et al. (1979) were the first to report a contribution of earthworm casts to P enrichment in runoff waters. They estimated under a temperate permanent pasture in New Zealand that surface-casts of the endogeic *A. caliginosa* may account for 45% of the annual transfer of P (0.25 kg of particulate P ha^{-1}, and 75% of the annual soil losses, i.e., 800 kg of soil ha^{-1}). In a tropical forest in Ivory Coast, the contribution of surface-casts to soil losses reached 1,200 kg ha^{-1} year^{-1}, which corresponded to a maximum release of 0.23 kg of total P ha^{-1} year^{-1} (Nooren et al. 1995). Focusing on the impact of raindrops that cause the disintegration of fresh and dry old casts of *Martiodrilus carimaguensis* in Colombia, Mariani et al. (2007) used simulated rainfall events and demonstrated a significant effect of soil drying on cast dispersion. They estimated that the mass of fresh casts dispersed could range between 4 and 32 tons ha^{-1} year^{-1}, which might be equivalent to 0.025 and 0.354 kg of available P ha^{-1} year^{-1} in savannah and pasture, respectively. However, opposite results were reported in a temperate agro-ecosystem in France by Le Bayon and Binet (2001). Rainstorm events were simulated on a maize plot with a gentle slope of 4.5% populated by two dominant species of earthworms, the endogeic *A. caliginosa* and the anecic *L. terrestris* (Binet and Le Bayon 1999). Despite a high cast abundance on the soil surface (25% of the area), amounts of P recovered in runoff waters were twice as high without surface-casts (0.35 and 0.86 kg of particulate P ha^{-1} rainfall^{-1} with and without casts, respectively). Earthworm casts were thus proposed to act as a physical brake on soil erosion by creating a surface roughness, and this was recently confirmed by Jouquet et al. (2008) in steep-slope ecosystems of North Vietnam. Nevertheless, Le Bayon and Binet (2001) observed that once the breaking-down point of the physical resistance of casts is reached, all surface-casts may then be quickly disintegrated and washed away. Hence, transfer of P can occur over a short distance through successive suspension/deposition of soil particles in the water runoff.

Simultaneous investigations were conducted on annual variations of earthworm surface-casting and P transfer (Le Bayon et al. 2002), including a 2-month period in spring when earthworm activities are enhanced (Le Bayon and Binet 1999). Working at such different temporal scales highlighted the possibility that the contribution of earthworm surface-casts to soil and P transfers could be over-estimated. For instance, a total of 0.05–0.20 kg of particulate P ha^{-1} year^{-1} were actually measured in runoff waters during one year, whereas 0.25–0.49 kg of particulate P ha^{-1} year^{-1} were estimated to be lost during the 2-month study of intensive earthworm activity in spring. Moreover, belowground egestions, which may represent large amounts of casting activities (Decaëns et al. 1999; Bohlen et al. 2004), and earthworm burrows need to be taken into account for a better understanding of P fluxes (Jensen et al. 2000).

In conclusion, despite the high variability of the data presented in different studies, a contribution of earthworm casts and burrows to the transfer of P has been demonstrated. This is intimately linked both to biotic factors (earthworm species, ecological group, abundance, biomass, vegetation cover, etc.) and also abiotic parameters (slope, climate, intensity and frequency of the rainfall events, aggregate stability, etc.).

8.3 Termites

8.3.1 Phosphorus Contents in Termite Mounds

Termites play an important role in the transformation processes of organic compounds in savannahs and tropical forest ecosystems (e.g., Lee and Wood 1971; Bignell and Eggleton 2000; Holt and Lepage 2000; López-Hernández 2001). Data on the P content of termite mounds in relation to adjacent soils are sometimes contradictory. Extensive studies of mounds and other structures of various Australian and African termites showed little difference in P concentration between termite structures and the soil from which they were built (Lee and Wood 1971; Leprun and Roy-Noël 1977). However, Okello-Oloya et al. (1985) for Australian *Amitermes* mounds, and Nutting et al. (1987) for subterranean North American desert termites, found that extractable P was significantly greater in mounds than in associated soils. López-Hernández et al. (2006) reported, for neo-tropical termites, significantly higher levels of both total and available P in termite mounds of *Nasutitermes ephratae*, a common plant-debris-feeding termite, compared with the adjacent soil. Moreover, in a comprehensive P-fractionation study of *Nasutitermes*, López-Hernández (2001) showed that all P levels were significantly higher in the mounds than in the adjacent soils. Similar results were found when comparing $E_{(t)}$ (the amount of PO_4 that is isotopically exchanged within t minutes) values of isotopically exchangeable P (López-Hernández et al. 1989a). Rückamp et al. (2010) also reported P enrichment in various termite mounds collected from seven dominant Brazilian ecosystems.

The relative P enrichment of the mound may have two main sources: (1) a biological origin from salivary, fecal, and plant debris used in the mound building, and (2) a mineral origin from an accumulation of clay within the mound. As a result of different feeding habits, termites collect different materials to build their nest structures (López-Hernández et al. 2006). Wood et al. (1983) differentiate plant-debris-feeding termites, which employ the selection of certain particle sizes (e.g., clays with high P-fixing capacity from the subsoil) to cement soil particles with saliva alone or with saliva and feces (Lee and Wood 1971; Wood et al. 1983), from soil-feeding termites that mainly employ ingestion of organic-rich fractions mixed with soil particles (mostly from the topsoil). Then, they reported that available P appears to be proportionally more abundant in mounds of soil-feeding termites than in the mounds of plant-debris-feeding termites when compared to adjacent soils.

8.3.2 Phosphorus Dynamics and Availability in Termite Mounds

Fardeau and Frossard (1992) showed that P isotopically exchangeable in 1 min [$E_{(1\ \mathrm{min})}$] increased from 2.2 mg kg^{-1} in the bulk soil to 87.0 mg kg^{-1} in the centre of a *Trinervitermes geminatus* nest. The P sorption processes are strongly reduced in organic-matter-enriched mounds compared with adjacent soils for both grass-feeders *T. geminatus* and *N. ephratae* (Table 8.1). On the other hand, *Macrotermes* species forage mostly from the organic carbon-deficient subsoil and preferably selected finer soil particles for the nest construction (Leprun and Roy-Noël 1976; Pomeroy 1983; López-Hernández and Febres 1984; López-Hernández et al. 2006). Their mounds built with clay-enriched materials have very high P-sorbing capacities and consequently a lower P availability than the adjacent topsoil (Table 8.1). For the subterranean species (*Ancistrotermes cavithorax* and *Microtermes toumodiensis*), there was more P sorption in nest structures than in associated soils (Table 8.1). The low concentration of water-soluble P (C_P) found in the subsoil reflects strong P sorption in this soil layer, probably due to the presence of the materials enriched with high P-sorbing clay.

The higher levels of water-soluble inorganic P (C_P) in the termite nests presented in Table 8.1 may also result from the transformation of organic P through enzymatic activity in the fresh biostructures, as observed for earthworm casts (Sharpley and Syers 1976; Le Bayon and Binet 2006). Comparisons of phosphatase activities between termite nests and adjacent soils have already been made for several termite species (López-Hernández et al. 1989b; Roose-Amsaleg et al. 2005). Phosphatase activities in the soil and mounds for the South American *N. ephratae* ranged from 0.56 to 2.32 μmol *p*-nitrophenol g^{-1} h^{-1}. Comparison of phosphatase activities for both mound and associated soils showed no statistical difference (López-Hernández

Table 8.1 Isotopically exchangeable P [$E_{(1\ \mathrm{min})}$, mg kg^{-1} soil] and water-soluble P (C_P, mg L^{-1}) in termite nests and adjacent soils

Termite species	Nest		Soil	
	$E_{(1\ \mathrm{min})}$	C_P	$E_{(1\ \mathrm{min})}$	C_P
Macrotermes bellicosus	0.29	0.002	0.34	0.021
Trinervitermes geminatus	3.11	0.221	0.19	0.010
Cubitermes severus	0.33	0.016	0.13	0.006
Nasutitermes ephratae	1.88	0.124	0.46	0.006
Ancistrotermes cavithorax	0.33	0.006	0.20	0.008
Microtermes toumodiensis	0.45	0.009	0.24	0.009

Adapted from López-Hernández et al. (2006)

et al. 1989a, b). Increases in enzyme activities and microbial biomass are expected to occur in mounds as a result of the increase in their organic matter content. Therefore, enzyme activity in the *N. ephratae* mounds might be inhibited as a consequence of the relatively high available P found in those structures. In contrast to the results of López-Hernández et al. (1989a), Roose-Amsaleg et al. (2005) found that soil-feeding termites affect soil phosphatase activity, with lower activities in mature nests than in surrounding soils. Comminution and mixing by termite activity allows for a greater surface area of substrate to come into contact with appropriate microorganisms and enzymes (Garnier-Sillam et al. 1987). Roose-Amsaleg et al. (2005) found that phosphatase activities tend to decrease with ageing from fresh to old and mature nests, and concluded that the released inorganic P could have a retroactive effect, inhibiting phosphatase activities as previously reported by López-Hernández et al. (1989a).

So far, it seems that termite feeding and nest-building habits have a strong influence on P availability parameters in mound, nest, and gallery structures. Humivorous and plant-feeding species cause a substantial increase of PO_4 bioavailability in nests, associated with a reduction of P sorption, whereas *Macrotermes* sp. (which in many cases build very large mounds) reduce PO_4 availability, with an associated increase of P sorption, by transporting finer soil materials from deeper soil layers.

8.3.3 Termite Mounds and Phosphorus Transfer

Phosphorus transport from the mound into the soil can happen in several ways. Termites might directly relocate nest materials into the soil. Furthermore, relocation can happen when termite mounds with dying colonies decay and erode. Although intact, inhabited termite mounds often have a dense surface that is particularly impermeable to water (e.g., Lal 1988; Contour-Ansel et al. 2000; Jouquet et al. 2004), the partial erosion and leaching from inhabited termite mounds may add P to the adjacent soil. However, erosion rates can be variable for a given species: Roose (1981) reported for *T. geminatus* that erosion of mounds can vary from 810 to 2,670 kg ha^{-1} $year^{-1}$, representing 10–33% of the mound's mass (Brossard et al. 2007).

Coventry et al. (1988) measured the nutrient content of a range of termite mounds and used a lower estimated rate of erosion of the mounds to calculate the amounts of nutrients returned to soil each year. Given annual erosion losses from the mounds of 3.5% (Bonell et al. 1986), they estimated that mound-building termites are responsible for the return of at least 15 g ha^{-1} of weak acid-extractable P per year. These estimates did not take into account the return of P as a result of erosion of structures other than mounds, such as feeding galleries. The amounts of soil contained in such structures may be of a similar magnitude to the amounts of soil incorporated in mounds (Lee and Wood 1971) and, if taken into account, might double the above estimates.

Finally, considering water infiltration as a major process, in particular in semi-arid and savannah areas, the influence of large macropores derived from soil macrofauna activity has been studied for about two decades (e.g., Elkins et al. 1986; Léonard et al. 2004). However, the results vary depending on measurement methods, and the processes involved deserve further consideration. Janeau and Valentin (1987) showed for *Trinervitermes* spp. that termite activity reduced the rate of water infiltration as a consequence of declines in soil surface porosity. However, Roose (1981), in a study on the sealing crusts in *T. geminatus*-affected soils, reported an increase in soil infiltration induced by termite activity. Léonard and Rajot (2001) showed that the influence of the large macropores made by termites was better described as a runoff interception process than as ponded infiltration. The P transfers through these processes (infiltration, runoff) are all related to P associated with soil particles. For soils with low-P status, the PO_4 pool in soil solution involved in these transfers is not well defined and very difficult to measure.

8.4 Conclusion

Macrofauna affects soil P cycling in a way that differs according to functional groups (i.e., feeding and construction behavior). However, P contents are usually larger in biogenic structures than in the surrounding soil, ultimately leading to higher P availability through a rapid turnover of organic P and/or enhanced PO_4 exchange. Further research efforts should be directed at investigating macrofauna-mediated processes in agricultural systems because these are potentially important for enhancing soil P availability to cultivated plants. Isotopic labeling techniques have the potential to elucidate soil P dynamics and should be extensively used to identify such processes. Controlled laboratory studies must be conducted to better understand the impact of gut passage, the microbial populations associated with guts, and the egested materials on P forms and availability in the biogenic structures. Experiments with a wide gamut of species and ecological strategies comprising a community will permit upscaling from the individual to community and population levels. Companion field studies should aim to better understand the volume of soil impacted and the dynamics of the biogenic structures produced, on a landscape scale. Coupled modeling approaches can also be useful to fully understand the complex interplay of biogeochemical interactions and to upscale from cast levels to soil profile and the entire ecosystem (Standing et al. 2007; Blanchart et al. 2009).

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