SOM management in the tropics: Why feeding the soil macrofauna?

Patrick Lavelle*, Eleusa Barros, Eric Blanchart, George Brown, Thierry Desjardins,
Lucero Mariani & Jean-Pierre Rossi
*IRD, 32 rue H. Varagnat, 93143 Bondy Cedex, France; *Author for correspondence*
(e-mail: patrick.lavelle@bondy.ird.fr)

Abstract

This paper synthesises information on the food requirements of soil macroinvertebrates and some of their effects on soil organic matter dynamics. Some clues to techniques that would optimise their activities through organic matter management are suggested. Soil macroinvertebrates can consume almost any kind of organic residues in mutualistic association with soil microflora. Significant amounts estimated at several T per ha of predominantly easily assimilable C are used yearly in natural ecosystems as energy to sustain these activities. Sources of C used are highly variable depending on the feeding regime. The largest part of the energy assimilated (e.g., 50% by the tropical earthworm *Millsonia anomala*) is actually spent in burrowing and soil transport and mixing. Bioturbation often affects several thousand tons of soil per hectare per year and several tenth of m^3 of voids are created in soil. A great diversity of biogenic structures accumulate and their nature and persistance over time largely controls hydraulic soil properties. The OM integrated into the compact biogenic structures (termite mounds, earthworm globular casts) is often protected from further decomposition. Most management practices have negative effects on the diversity and abundance of macroinvertebrate communities. Structures inherited from faunal activities may persist for some weeks to years and the relationship between their disappearance and soil degradation is rarely acknowledged. When SOM supply is maintained but diversity is not, the accumulation in excess of structures of one single category may have destructive effects on soil. It is therefore essential to design practices that provide the adequate organic sources to sustain the activity and diversity of invertebrates. Special attention should also be paid to the spatial array of plots and rotations in time.

Introduction

Soil macroinvertebrates, particularly the 'ecosystem engineers' that effect bioturbation are major determinants of processes in tropical soils (Lavelle et al., 1997; Brussaard, 1998; Folgarait, 1998). Climatic conditions rarely limit their activities. They use significant amount of soil organic matter (SOM) for feeding and produce huge amounts of biogenic structures. They determine the activities of microorganisms and other smaller invertebrates included in their 'functional domains' defined as the sum of biogenic structures that they have created in soil and the organisms that inhabit them (Lavelle, 1997; Beare and Lavelle, 1998). They regulate soil hydraulic properties and affect SOM dynamics in different ways depending on the time scales considered, from hours and days to months, years and decades (Martin, 1991; Parmelee et al., 1998). They considerably accelerate mineralisation during gut transit and often stimulate plant production through the release of assimilable nutrients and through a number of other interactions (Spain and Okello-Oloya, 1985, Brown et al., 1999; Brussaard, 1998). At larger scales of months to years, they regulate SOM dynamics via the biogenic structures that they create and the resulting physical organisation of the soil. SOM may be significantly protected from further decomposition (Lavelle et al., 1997). Protection occurs in the compact structures of their casts, fabrics or mounds produced by the so-called 'compacting spe-

cies' whereas drainage and aeration enhanced by the 'decompacting' species may further stimulate microbial activities (Blanchart et al., 1999). The resulting effect largely depends on the overall composition of the community and spatial distribution of populations of different functional groups (Rossi, 1998).

Most land use practices reduce the abundance and/or diversity of soil macroinvertebrate communities by disturbing their physical environment and reducing the diversity and abundance of organic inputs that they normally use for feeding (Curry, 1987; Decaëns et al., 1994; Eggleton et al., 1997). This results in a significant reduction of production of new biogenic structures with likely effects on SOM dynamics and physical structure. We hypothesise that maintaining active communities of 'ecosytem engineers' in soils would considerably improve the sustainability of cropping systems through regulations of soil processes at several scales of time and space. This could result from practices that would maintain plant cover with a diverse plant community in cultivated plots and diverse types of vegetation in the farming system. Such practices already exist, but their interaction with soil invertebrates have not been studied. For example, the cost in organic inputs in having active invertebrate communities and their benefits to plant production and soil quality are not known. Similarly, organic inputs required to maintain a balance between invertebrate functional groups, especially the compacting and decompacting species, has not been worked out.

This paper presents the existing knowledge on the amount and nature of organic matter used by soil macrofauna, and relates these energy inputs to the amount of structures created in soils and to changes in plant production. The impact of different agricultural practices on these activities are reviewed, and modifications to the existing cropping systems to increase the abundance and diversity of communities are discussed.

Organic sources used by soil fauna

Soil invertebrates are able to use almost all the organic resources available in the soil system, especially termites and earthworms have developed sophisticated digestive mutualisms with soil microflora (Barois and Lavelle, 1986; Bignell, 1994; Lavelle, 1997). These invertebrates often have highly efficient digestive systems that allow them to feed on wood, leaf litter, dead or live root tissues, or different fractions of soil organic matter (Butler and Buckerfield, 1979; Cockson, 1987; Scheu, 1993). Termites are classified according to their feeding regime into wood, grass or humus feeders. They have developed mutualistic associations with specialised micro-organisms to compensate for the unfavourable C:N ratios of their ingested food materials by increasing their N intake or by selectively eliminating C from their food source to decrease the C:N ratio (Higashi et al., 1992). Earthworms have not developed the ability to directly feed on wood although some species may digest lignin (Scheu, 1993). Species from the 'oligohumic endogeic' functional group have developed the ability to live on savanna soil from the 30 to 60 cm depth strata where OM content is less than 0.5% (Lavelle, 1978). Most endogeic geophagous earthworms feed on relatively 'young' material. In a maize crop on a former forest soil site in France, Martin et al. (1992) found that earthworms mainly use C derived from the current crop. In soils of the humid tropics, the same authors (Martin et al., 1991) found that the endogeic earthworm *Millsonia anomala* may feed on all particle size fractions of OM with no significant differences in their rates of incorporation into body. Thus in warm conditions of the humid tropics, the digestive mutualism between the earthworm and the ingested microflora is extremely efficient, and allows them to use C from the slow and possibly passive organic pools that are said to comprise a large proportion of the smaller particle size fractions. The experimental design used by Martin et al. (1991), however, does not refute the hypothesis that earthworms suppress physical protection of SOM during gut passage and actually digest the part of every particle size fraction that is easily accessible to microbial degradation.

Field and laboratory data suggest that endogeic earthworms grow best on the large particle size OM (>50 μm) that contains freshly deposited organic residues (Martin and Lavelle, 1992; Barois et al., 1999). Other experiments using natural ^{13}C labelling techniques have demonstrated that the earthworm *Pontoscolex corethrurus* is able to feed on root material, presumably exudates and recently deposited root litter in sugarcane plantations (Spain et al., 1990). In a similar experiment conducted for 6 months with maize plants grown in pots in the presence of earthworms, Brown (2000) calculated that 8% of C incorporated into biomass of *P. corethrurus* came from the maize plants.

A wide range of digestive enzymes may be found in guts of earthworms and termites like e.g. cellulase,

laccase or phenolase that allow them to use complex substrates (Lattaud et al., 1998). Nitrogen fixation may also occur in termite or earthworm guts which allows them to use extremely poor N sources (M'ba, 1987; Tayasu et al., 1994). Part of these enzymes are produced by microorganisms in mutualistic associations that may be internal to body ('inhabitational' sensu Lewis, 1985) or external ('exhabitational') when invertebrates reingest their faeces or special food structures ('fungus combs' of termites and leaf cutting ants) produced after they have been partly digested by microorganisms. As a result, they may overcome the main limitations to decomposition of organic materials of high C:Nutrient ratios well above the threshold of 20 beyond which N is immobilised, N combination in polyphenolic complexes or breakdown of polysaccharides with long and complex chains (Swift et al., 1979; Toutain, 1987; Higashi et al., 1992; Pashanasi et al., 1992; Lavelle et al., 1993).

Termites and earthworms have the most efficient digestive abilities since they develop both inhabitational and exhabitational mutualisms with microflora in a variety of such external structures as fungus gardens, earthworm casts and 'middens' (accumulations of dead leaves around the opening of galleries with specific microbial and micro- and mesoinvertebrate communities) or burrow linings.

The cost of having active soil engineers

Energy budget of soil invertebrates

Energy budgets have been established for a few termite and earthworm species. Termites have extremely high assimilation rates that range between 54 and 93% of the food eaten (Wood, 1978). Most of the energy ingested is therefore used for biomass production burrowing and bioturbation.

Earthworms have much lower assimilation rates, especially tropical endogeics that usually assimilate only a few percent of the energy contained in the ingested food. In humid savannas of Lamto (Côte d'Ivoire), populations of the endogeic *Millsonia anomala* ingest yearly $800 - 1100$ t dry soil ha^{-1}. Of the 14–15 t organic matter thus ingested, less than 10%, i.e. ca. 1.2 t are assimilated (Lavelle, 1978), which is the cost of having an active population of *M. anomala* in this savanna. Of the energy thus derived, only a small proportion (4%) is used for tissue production and the rest is divided between the production of
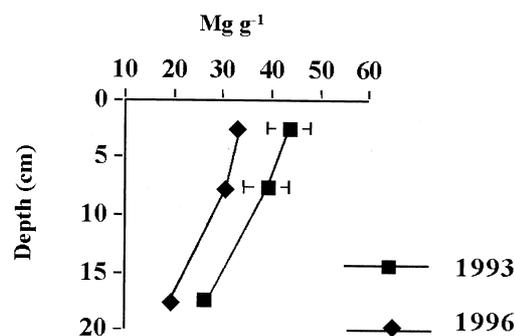
Figure 1. Changes in carbon contents at different depths of a pasture soil after invasion of the endogeic earthworm *Pontoscolex corethrurus* (Glossoscolecidae)(Manaus, Brasil)(Barros, 1999).

cutaneous mucus and respiration. Although no measurement of mucus production exists, it is generally assumed that it may account for half of the respiration cost. The energy cost of mechanical activities that accounts for the largest part of respiration may therefore be evaluated at ca. 0.5–0.6 Mg ha^{-1} soil organic matter. With this energy, *M. anomala* populations annually built 800 t of macroaggregates of >0.5 mm size, deposit some 3–7 Mg ha^{-1} large casts at the soil surface and left an equivalent volume of voids in soil (3–7 m^3 ha^{-1}) assuming bulk density close to 1.

Carbon balances and faunal activities

The results presented above emphasise the relationship between soil organic matter dynamics and the production of biogenic structures. In an abandoned pasture at Manaus, invasion by the exotic earthworm *Pontoscolex corethrurus* resulted in the formation of a 5 cm thick continuous surface crust which impeded water infiltration and caused anoxic conditions below the crust (Barros, 1999; Chauvel et al., 1999). This crust was formed in 3 y. During that time, C content decreased significantly in the upper 30 cm of soil (Figure 1) resulting in the overall loss of 18 Mg ha^{-1} C in the upper 20 cm of soil. We can speculate that half of these losses may have corresponded to earthworm assimilation and the cost of mechanical acitivities, the other half corresponding to increased microbial activities, possibly in the form of methanogenesis promoted by anoxic conditions in soil.

Other examples emphasise the need for carbon resources to sustain macro-invertebrate activities in man-made ecosystems. Termite feeding on litter deposited as mulch at the surface of a crusted sahelian soil increased the proportion of macropores larger than 3 mm from 0% of the area of fine sections in control

to 16.1% in mulched treatment, and porosity larger than 0.1 mm from 5.5 to 24.4% respectively (Mando and Miedema, 1997). In rubber plantations of different ages, Gilot et al. (1995) observed significant changes in the composition and abundance of macroinvertebrate communities with age; they concluded that tree trunks left after deforestation fed invertebrate communities for almost 30 y with a dominance of wood eating termites directly feeding on wood during the first 5 y, followed by a peak of humivorous termites presumably feeding on structures and feces accumulated by wood feeding termites, and then endogeic earthworms assumed to feed on biogenic structures rich in organic matter produced by humivorous termites. This study, and a few others show that soil ecosystem engineers may use organic resources accumulated in the ecosystem and release nutrients that may play a role in regeneration phases of natural successions (Bernier, 1998), or participate in the maintenance of soil structural properties via the production of biogenic structures, aggregates, pores and fabrics.

An other important role of soil organic matter is the stabilisation of biogenic structures produced by invertebrate engineers. In a 7-y experiment at Yurimaguas, a continuous maize crop was maintained with fertilisers in a site that had been previously occupied by a 20-year-old secondary forest thus allowing a precise study of SOM dynamics through natural ^{13}C labelling (Charpentier, 1996). Soil was cleared from native earthworms by an application of carbofuradan and half of the experimental enclosures were reinoculated with 35 g m^{-2} of endogeic earthworms *(Pontoscolex corethrurus)*. In all treatments, plants were surrounded by a circular nylon net 60 cm in diameter and down to 60 cm depth to avoid undesired movements of earthworms. Earthworm inoculation significantly increased plant production, with different effects on different plant parts. After 6 crops, grain production had increased by 2.1 t ha^{-1} (i.e. +46% of uninoculated controls) stover, by 2.9 t ha^{-1} (+ 34%) and roots 0.3 t (+23%). Grains being exported and stover deposited at the soil surface, a limited proportion of this supplementary production was actually incorporated to the soil. After 6 y, SOM content of the soil had decreased more in the earthworm inoculated plots than outside. ^{13}C labelling of soil associated to particle size fractionation showed a significant depletion of large-sized particles due to assimilation and comminution, and increase in the amount of C in small-sized particles (<2 μm) (Charpentier, 1996).
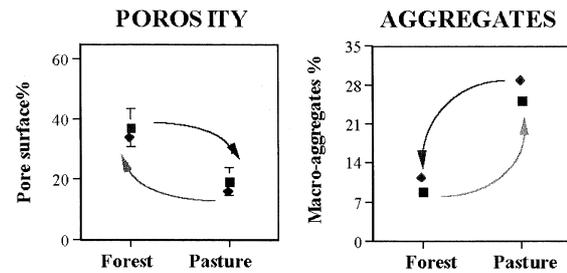
Figure 2. Changes in the proportions of soil porosity and dense areas measured on thin sections of soil in monoliths (25×25×30 cm) one year after their transplantation from a forest with a diverse soil macrofauna to a pasture invaded by the endogeic earthworm *Pontoscolex corethrurus* (Glossoscolecidae) and vice versa (Barros, 1999).

The importance of biodiversity

In natural ecosystems, a given proportion of energy captured through photosynthesis is used by soil invertebrate engineers for bioturbation and burrowing activities. This energy flows through a large number of populations that produce different sorts of biogenic structures. In the Colombian llanos at Carimagua, for example, Decaëns (1999) identified 14 different types of biogenic structures deposited at the soil surface by termites, ants and earthworms. Termite biogenic structures generally had relatively high contents of Al, organic matter and nutrients (K, Mg and P) and were comprised of a large proportion of macroaggregates. Ant structures had small-size aggregates which were low in organic matter, nutrients and Al saturation of the cation exchange capacity. Earthworm casts differed from termite structures by their low Al content and Al saturation, high pH and elevated bulk density. Biogenic structures comprise a wide range of pores and aggregates of highly diverse shapes, sizes and stability. Invertebrates may either fragment soil into aggregates of the size of their mandibulae (ants, some termites) or ingest them and disperse them in their gut (Barois et al., 1993). Digested soil is egested as faecal pellets that may be either compacted into large paste like units or deposited as relatively dry and loose granules. This difference depend on the anatomy of the anterior and distal part of the gut (Lapied and Rossi, 2000) and separates species which are 'compacting' from those ones 'decompacting' soils. Recent studies have shown that the coexistence of several such functional groups is necessary to maintain physical properties of the soil (Chauvel et al., 1999). Infiltration of water in soil, for example, may be influenced by the balance of activities of 'decompacting' spe-

cies that produce loose structures and decrease bulk density, and compacting species that increase bulk density by producing compact structures (Blanchart et al., 1997). These functional groups may regulate soil physical properties separately when they have opposite spatial distribution in the field, or jointly when their populations are mixed (Rossi, 1998). When a single species, or a single functional group, becomes excessively predominant, severe problems may arise, e.g., the building of 2000 earth mounds 1 m high and 1 m in diameter per hectare by the ant *Camponotus punctulatus* in abandoned paddy rice fields in North Eastern Argentina (Folgarait et al., unpubl. data) or the formation already mentioned of a surface crust by the endogeic earthworm *Pontoscolex corethrurus* in amazonian pastures. In the late case, soil monoliths 25×25×30 cm were taken from the degraded pasture with a low diversity of invertebrates and inserted in holes of the same size dug in soil of the original forest. When exposed to the diversity of forest invertebrate community, this soil almost recovered the level of porosity and aggregation of the forest within one year; in a similar experiment where forest blocks were exposed to the less diverse community of the degraded pasture, the formation of the surface crust occurred in one year (Barros, 1999; Chauvel et al., 1999) (Figure 2).

Impact of land use practices

Land use practices have strong impacts on soil macroinvertebrate communities and their activities. Annual crops generally severely deplete their communities whereas pastures enhance earthworm populations, often represented by single populations of exotic species, and tree plantations allow a better conservation of communities in terms of species richness and abundance. The loss of termite species diversity during the conversion of tropical forest to temporary or permanent arable use has been well documented (Collins, 1980; De Souza and Brown, 1994; Martius, 1994; Eggleton et al., 1996). During moderate soil disturbances, modifications of species composition is a more obvious consequence than change in abundance or biomass, but heavy disturbance sharply reduces species diversity and abundance. The effects of invertebrates, however, are not suppressed immediately after the disappearance of their populations. Biogenic structures may persist a long time after the death of the invertebrates that have produced them
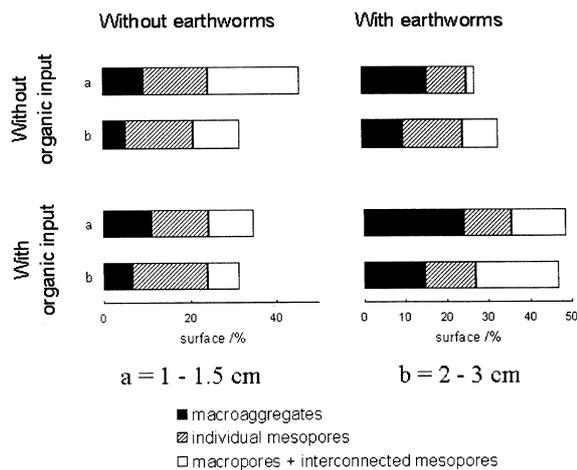
Figure 3. Changes in porosity and aggregation of an ultisol from Peruvian Amazonia after six cropping cycles with different organic inputs and earthworm (*Pontoscolex corethrurus*) inoculation or exclusion (Hallaire et al., 2000).

and their effects on soil physical properties are conserved. Decaëns (1999) observed that surface casts of the large anecic earthworm species *Martiodrilus carimaguensis* may persist for more than one year in a natural savanna from Eastern Colombia. In field experiments at Lamto, earthworm inoculation of annual cropping systems caused protection of soil organic matter only in Yam crops (Villenave et al., 1999). In this system soil had lost its structure when preparing the earth mounds in which yam is sown. We hypothesised that protection of organic matter observed in this system was due to re-aggregation of soil by inoculated earthworms following mechanisms described by Martin (1991). In maize cultures in which no tillage had been effected, no difference was observed between treatments with and without earthworms because soil aggregation inherited from past earthworm activities continued to play a role in the physical protection of SOM (Villenave et al., 1999).

Interactions between organic inputs and the stability of biogenic structures

The stability of aggregates produced by a given species may depend on the organic matter content of the egested soil. In a field experiment conducted at Yurimaguas (Peru), a crop rotation was maintained for three years with six different treatments, i.e. three levels of organic inputs (no inputs, application of crop residues produced in the plots, and crop residues

plus legume green manure, and with and without the inoculation of earthworms (30 g m^{-2} *Pontoscolex corethrurus*) (Pashanasi et al., 1996). Earthworms significantly affected soil aggregation and porosity as compared with no earthworm treatments. They produced a huge amount of casts close to the surface. These casts were unstable in the treatments with no organic inputs and they soon formed a compact layer of a few cm of soil with low porosity and massive structure. In treatments with application of crop residues and addition of legume green manure, casts were far more stable and earthworms increased significantly the proportion of macroaggregates and macropores in the upper few centimetres of soil (Figure 3).

In the latosols at Manaus with a pasture cover, the relatively high organic content of soil did not prevent large populations of *P. corethrurus* from building a 5 cm thick compact layer. In that case, the constantly humid conditions of soil at the surface may not have allowed drying of surface casts, a necessary step towards the stabilisation of fresh casts that are naturally unstable (Blanchart et al, 1993). As a result, casts disintegrated into a uniform muddy paste that soon formed an impermeable crust creating anoxious conditions in the soil (Barros, 1999; Chauvel et al., 1999).

Similarly, the influence of termites on soil structural stability in the vicinity of their mounds seems to be independent on the ecological strategies and nesting locations of the species involved. Garnier-Sillam (1988) reported the contrasting effects of two species in a humid African forest environment. The soil-feeding species *Thoracotermes macrothorax* increased the structural stability of the soil in its area of influence while the fungus-cultivating species *Macrotermes muelleri* reduced it.

Discussion

This brief review shows the importance of organic matter as an energy source to maintain soil fauna communities and as a physical component to allow the stabilisation of the biogenic structures that they produce. The direct effect of soil invertebrates on nutrient cycling seems to be rather limited (Andrén et al., 1999). Earthworm populations may mineralise yearly ca. 10 – 100 kg of N ha^{-1} as ammonium and a few kg of P. The effect of this input has little effects on plant growth except in extremely nutrient poor soils where this contribution may represent a sizeable fraction of

the nutrient flux, (Barois et al., 1999; Brown et al., 1999). Major effects of invertebrates seem to result from their 'engineering' activities. Soil bioturbation has considerable effects on the regulation of microbial activities and the accumulation of biogenic structures is responsible for the macroaggregate structure of most tropical soils in the surface 10 – 20 cm. The macroporosity created by burrowing and digging activities of soil engineers affects soil hydraulic properties in sometimes spectacular ways . Similar effects have been indicated for termites (Elkins et al., 1986; Mando and Miedema, 1997). Diversity of invertebrate populations is essential to allow the formation of pores and aggregates of different sizes and compositions, and a rapid turnover of these structures.

Recent research has demonstrated that soil structure is related to the composition of soil invertebrate 'engineers' communities, and that changes in their communities may modify soil physical properties in surprisingly short periods (months to a few years), and affect the soil to the B horizon (Mando and Miedema, 1997; Barros, 1999). Once produced and stabilised by e.g., drying followed by remoistening, these structures seem to persist for long periods of time, much longer in most cases than the life duration of the invertebrates that produced them (Decaëns et al., 1999; Le Bayon and Binet, 1999). This seems to be especially true for endogeic structures that persist after the elimination of the organisms that produced them (Alegre et al., 1996; Blanchart et al., 1999) since they are protected from the intense weathering processes of the soil surface. The most likely mechanism for rejuvenation of these structures is their ingestion or breaking by another invertebrate. As a consequence, most soils retain the legacy of invertebrate activities long after unfavourable management options have eliminated their populations. This is probably one reason why the disappearance of soil invertebrate engineers is rarely acknowledged as a cause for soil physical degradation that occurs years or even decades afterwards. Research to support these ideas is needed.

Environment friendly management practices should consider soil invertebrate engineers as a resource and properly manage it (Lavelle et al., 1999). The first requirement is to properly feed them to allow a significant amount of activity. There is evidence that all the practices that allow a significant return of plant residues to the soil maintain high levels of invertebrate activities. This is the case, e.g., for minimum tillage techniques that favour root production and the incorporation of dead root material to the soil; mulch-

ing, application of cow dung and other organic manures and wastes have similar effects. In most cases, however, little is known of the feeding requirements of these invertebrates. A better knowledge of organic matter cycling and budgets in cultivated systems would allow to properly design techniques that sustain invertebrate activities at a minimal cost. This poses questions such as: What amount of organic residues is necessary, what does each group of 'useful' invertebrates actually eat: fresh litter at the soil surface? Organic residues in the 'particulate organic fraction' organic matter as microbial biomass or watersoluble extracts? When should they be applied and where in the soil (at the surface or incorporated to the soil) to feed the pools that will be used by the invertebrates? What are the best qualities of residues to sustain given levels and qualities of invertebrate activities? Can the maintenance of a minimum diversity of invertebrate species be managed through the diversity and/or quantity of organic inputs?

The conceptual model of Figure 4 indicates ways in which faunal activities might be managed as part of a farming system. In some cases, part of the rotation will be occupied by crops that cannot maintain faunal populations; this is the case for most annual crops (e.g., maize, rice, wheat). Assuming that soil physical properties inherited from previous invertebrate activities are maintained for some months to years, these crops will be maintained for some time until signals of degradation appear. Then crops that restore biological activities, like pastures or legume intercrops, will be installed. The build up of invertebrate communities will come from local relictual populations or from migration from adjacent favourable areas. Another option to maintain invertebrate activities may be to favour the colonisation of unfavourable areas by active populations from an active site through an adequate management of the spatial arrangement of cultivated plots. These management options raise the important question of colonisation ability of soil invertebrate engineers and the effect on genetic diversity of landscape fragmentation and selection of individuals in the adverse conditions of intensive cropping systems.

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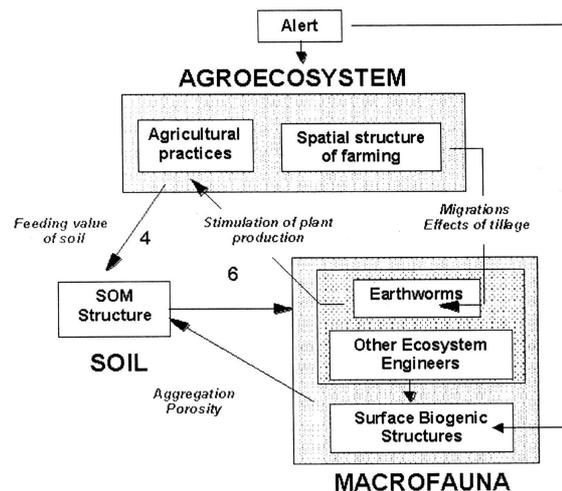
Figure 4. A conceptual model for management of macroinvertebrates in agroecosystems (Mariani, unp. data). Three interactive compartments are considered. (1) Agroecosystem where practices and the spatial and temporal allocation of soil to different types of land use are considered; (2) soil parameters (organic matter contents and physical structure) and (3) soil macrofauna defined by the abundance and composition of communities and the physical structures that they create. Agricultural practices determine activities of macrofauna indirectly via the feeding quality of soil and possibilities for colonisation of unfavourable habitats from a favourable one, or directly through negative effects of tillage and application of harmful pesticides. Macrofauna affects plant production directly through their activities and indirectly through the accumulation of biogenic structures that influence hydraulic and other soil properties. The late effect may persist some time after macrofauna has been eliminated by any detrimental practice. An indicator of the current physical state of biogenic structures may alert on the necessity to restore faunal activities when physical structure is degraded; shift of management practices to another type may allow restoration of soil quality.

References

Alegre JC, Pashanasi B & Lavelle P (1996) Dynamics of soil physical properties in a low input agricultural system inoculated with the earthworm *Pontoscolex corethrurus* in the amazon region of Peru. SSSA Journal 60: 1522–1529

Andrén O, Brussaard L & Clarholm M (1999) Soil organism influence on ecosystem-level processes – by passing the ecological hierarchy? Appl Soil Ecol 11(2–3): 177–188

Barois I., Lavelle P, Brossard M, Tondoh J, Martinez M, Rossi JP, Senapati BK, Angeles A, Fragoso C, Jimenez JJ, Decaëns T, Lattaud C, Kanyonyo J, Blanchart E, Chapuis L, Brown GG & Moreno A. (1999) Ecology of earthworm species with large environmental tolerance and/or extended distribution. In: Lavelle P, Brussaard L & Hendrix P (eds) Earthworm Management in Tropical Agroecosystems, pp 57–86. Wallingford, UK: CAB International Press

Barois I & Lavelle P (1986) Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidæ, Oligochæta). Soil Biol Biochem 18(5): 539–541

Barois I, Villemin G, Lavelle P & Toutain F (1993) Transformation of the soil structure through *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. Geoderma 56: 57–66

Barros ME (1999) Effet de la macrofaune sur la structure et les processus physiques du sol de paturages dégradés d'Amazonie, Doctorate thesis, University Paris VI

Beare M & Lavelle P. 1998 Regulation of Microbial Activity and Organic Matter Dynamics by Macroorganisms: Integrating Biological Function in Soil. ISSS Congress, Symposium n° 9 (CD-Rom), Montpellier, France

Bernier N (1998) Earthworm feeding activity and development of the humus profile. Biol Fertil Soil 26: 215–223

Bignell, DE (1994) Soil-feeding and gut morphology in higher termites. In: Hunt JH & Nalepa CA (eds) Nourishment and Evolution in Insect Societies, pp 131–158 Boulder, Colorado: Westview Point

Blanchart E, Albrecht A, Alegre J, Duboisset A, Villenave C, Pashanasi B, Lavelle P & Brussaard L (1999) Effects of earthworms on soil structure and physical properties. In: Earthworm Management in Tropical Agroecosystems, pp 149–172. Lavelle P, Brussaard L & Hendrix P (eds). Wallingford, UK: CAB International Press

Blanchart E, Lavelle P, Braudeau E, Le Bissonais Y & Valentin C (1997) Regulation of soil structure by geophagous earthworm activities in humid savannas of Cote d'Ivoire. Soil Biol Biochem 29(3/4): 431–439

Brown GG, Pashanasi B, Villenave C, Patron JC, Senapati BK, Giri S, Barois I, Lavelle P, Blanchart E, Blakemore RJ, Spain AV & Boyer J (1999) Effects of earthworms on plant production in the tropics In: Lavelle P, Brussaard L & Hendrix P (eds). Earthworm Management in Tropical Agroecosystems, pp 87–148. Wallingford, UK: CAB International Press

Brown GG (2000) Comment les vers de terre influencent la croissance des plantes: études en serre sur les interactions avec le systèmes racinaire. Doctorate thesis, University Paris VI.

Brussaard L (1998) Soil fauna, guilds, functional groups and ecosystem processes. Appl Soil Ecol 9: 123–135

Butler JHA & Buckerfield JC (1979) Digestion of lignin by termites. Soil Biol Biochem 11: 507–513

Charpentier F (1996) Effets de l'inoculation d'un ver de terre endogé sur la dynamique de la matière organique d'un sol ferrallitique cultivé de l'Amazonie Péruvienne. Doctorate thesis, University Paris VI

Chauvel A, Grimaldi M, Barros E, Blanchart E, Desjardins Th, Sarrazin M & Lavelle P (1999) Pasture degradation by an Amazonian earthworm. Nature 389: 32–33

Cockson LJ (1987) [14]C- lignin degradation by three Australian termites. World Sci Technol 21: 11–25

Collins NM (1980) The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. Oecologia 44: 263–275

Curry JP (1987) The invertebrate fauna of grassland and its influence on productivity. 1. The composition of the fauna. Grass For Sci 42: 103–120

Decaëns T (1999). Rôle fonctionnel et réponses aux pratiques agricoles des vers de terre et autres ingénieurs écologiques dans les savanes Colombiennes. Doctorate thesis, University Paris VI

Decaëns T, Lavelle P, Jimenez Jaen JJ, Escobar G & Ripstein G (1994) Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. Eur J Soil Biol 30(4): 157–168

De Souza OFF & Brown VK (1994) Effects of habitat fragmentation on Amazonia termite communities. J Trop Ecol 10: 197–206

Eggleton P, Bignell DE, Wood TG, Sands WA, Mawdsley N, Lawton JH & Bignell NC (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. Phil Trans Roy Soc London B 351: 51–68

Eggleton P, Homathevi R, Jeeva D, Jones D, Davis RG & Maryati M (1997) The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. Ecotropica 3: 119–128

Elkins NZ, Sabol GZ, Ward TJ & GW Whitford (1986) The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. Oecologia 68: 521–528

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7: 1221–1244

Garnier-Sillam E, Toutain F. & Renoux J. (1988) Comparaison de l'influence de deux termitières (Humivore et champignoniste) sur la stabilité structurale de sols forestiers tropicaux. Pedobiologia 32: 89–97

Gilot C, Lavelle P, Blanchart E, Keli J, Kouassi P & Guillaume G (1995) Biological activity of soils in Hevea stands of different ages in Côte d'Ivoire. Act Zool Fennic 196: 186–190

Hallaire V, Curmi P, Duboisset A, Lavelle P & Pashanasi B (2000) Soil structure changes induced by the tropical earthworm *Pontoscolex corethrurus* and organic inputs in a Peruvian ultisol. Eur J Soil Biol 36: 35–44

Higashi M, Abe T & Burns TP (1992) Carbon-nitrogen balance and termite Ecology. Proc Roy Soc London B 249: 303–308

Lapied E & Rossi JP (2000) relating internal morphology of three tropical earthworms to their effects on soil aggregation. XII International Colloquium of Soil Zoology. Abstracts, p 43

Lattaud C, Locati S, Mora P, Rouland C & Lavelle P (1998) The diversity of digestive systems in the tropical geophagous earthworms. Appl Soil Ecol 9: 189–195

Lavelle P (1978) Les Vers de Terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème, Doctorate thesis, University Paris VI

Lavelle P, Blanchart E, Martin A, Martin S, spain A, Toutain F, Barois I & Schaefer R (1993) A hierarchical model for decomposition in terrestrial ecosystems. Application to soils in the humid tropics. Biotropica 25(2): 130–150

Lavelle P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. Adv Ecol Res 27: 93–132

Lavelle P, Bignell D, Lepage M et al. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J Soil Biol 33(4): 159–193

Lavelle P, Pashanasi B, Charpentier FR, Gilot C, Rossi P, Derouard L, André J, Ponge JF & Bernier N (1998) Large-scale effects of earthworms on soil organic matter and nutrient dynamics. In: Edwards CA (ed) Earthworm Ecology, pp 103–122. Columbus, Ohio: St. Lucie Press.

Lavelle P, Brussaard L & Hendrix P (eds) (1999) Earthworm Management in Tropical Agroecosystems. Wallingford, UK: CAB International Press

Le Bayon RC & Binet F. (1999) Rainfall effects on erosion of earthworm casts and phosphorus transfers by water runoff. Biol Fertil Soils 30: 7–13

Lewis DH (1985) Symbiosis and mutualism: crisp concepts and soggy semantics. In: Boucher DH (ed) Biology of Mutualism, pp 29–43. Beckenham: Croom Helm

Mando A & Miedema R (1997) Termite-induced change in soil structure after mulching degraded (crusted) soil in the Sahel. Appl Soil Ecol 6(3): 241–249

Martin A (1991) Short- and long-term effects of the endogeic earhworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. Biol Fertil Soil 11: 234–238

Martin A, Mariotti A, Balesdent J & Lavelle P (1991) Soil organic matter assimilaion by a geophagous tropical earthworm based on ^{13}C measurements. Ecology 73(1): 118–128

Martin A & Lavelle P (1992) Effect of soil organic matter quality on its assimilation by *Millsonia anomala*, a tropical geophagous earthworm. Soil Biol Biochem 24: 1535–1538

Martin A, Balesdent J & Mariotti A (1992) Earthworm diet related to soil organic matter dynamics through ^{13}C measurements. Oecologia 91: 23–29

Martius C (1994) Diversity and ecology of termites in Amazonian forests. Pedobiologia 38: 407–428

M'ba C (1987) Vermicomposting and biological N-fixation. In: Szegi J (ed) Symposium on Soil Biology and Conservation of the Biosphere, pp 547–552. Budapest: Akademiai Kiado

Parmelee RW, Bohlen PJ & Blair J (1998) Earthworms and nutrient cycling processes: Integrating across the ecological hierarchy. In: Edwards CS (ed) Earthworm Ecology, pp 123–143. Boca Raton: St. Lucie Press

Pashanasi B, Lavelle P & Alegre J (1996) Effect of inoculation with the endogeic earthworm *Pontocolex corethrurus* on soil chemical characteristics and plant growth in a low-input agricultural system of Peruvian Amazonia. Soil Biol Biochem 28(6): 801–810

Pashanasi B, Melendez G, Szott L & Lavelle P (1992) Effect of Inoculation with the Endogeic Earthworm Pontoscolex Corethrurus (Glossoscolecidae) on N Availability, Soil Microbial Biomass and the Growth of Three Tropical Fruit Tree Seedlings in a Pot Experiment. Soil Biol Biochem 24(12): 1655–1659

Rossi JP (1998) Rôle fonctionnel de la distribution spatiale des vers de terre dans une savane humide de Côte d'Ivoire. Doctorate thesis, University Paris VI

Scheu S (1993) Litter microflora soil macrofauna interactions in lignin decomposition – a laboratory experiment with C-14-labelled lignin. Soil Biol Biochem 25(12): 1703–1711

Spain AV, Safigna PG & Wood AW (1990) Tissue carbon sources for *Pontoscolex corethrurus* (Oligochaeta, Glossoscolecidae) in a sugarcane ecosystem. Soil Biol Biochem 22: 703–706

Spain AV and Reddell P 1996 Δ^{13}C values of selected termites (Isoptera) and termite-modified materials. Soil Biol Biochem 28: 1585–1593

Spain V & Okello-Oloya T (1985) Variation in the growth of two pasture plants on soils associated with the termitaria of *Amitermes laurensis* (Isoptera: Termitinae). 4th Australian Conference on Grassland Invertebrates Ecology, Lincoln College, Canterbury, 13–17 May 1985, Caxton Press

Swift MJ, Heal OW & Anderson JM (1979) Decomposition in Terrestrial Ecosystems. Oxford: Blackwell Scientific

Tayasu I, Subimoto A, Wada E & Abe T (1994). Xylophagous termites depending on atmospheric nitrogen. Naturwissenschaften 81: 229–231

Toutain F (1987) Activité biologique des sols, modalités et lithodépendance. Biol Fertil Soils 3: 31–38

Villenave C, Charpentier F, Lavelle P, Feller C, Brossard M, Brussaar L, Pashanasi B, Barois I & Albrecht A (1999) Effects of earthworms on soil organic matter and nutrient dynamics. In: Lavelle P, Brussaard L and Hendrix P (eds) Earthworm Management in Tropical Agroecosystems, pp 173–197. Wallingford, UK: CAB International Press

Wood TG (1978) Food and feeding habits of termites. In: Brian MV (ed) Production Ecology of Ants and Termites, pp 55–80. Cambridge: Cambridge University Press