

## Soil function in a changing world: the role of invertebrate ecosystem engineers<sup>1</sup>

Patrick Lavelle<sup>(1)\*</sup>, David Bignell<sup>(2)</sup>, Michel Lepage<sup>(3)</sup>,  
with Volkmar Wolters<sup>(4)</sup>, Pierre Roger<sup>(5)</sup>, Philip Ineson<sup>(6)</sup>, O.W. Heal<sup>(7)</sup> and Shivcharn Dhillon<sup>(8)</sup>

<sup>(1)</sup> Orstom, Laboratoire d'écologie des sols tropicaux, 32, avenue Varagnat, 93143, Bondy cedex, France.

<sup>(2)</sup> School of Biological Sciences, Queen Mary & Westfield College, University of London, London, E1 4NS, UK.

<sup>(3)</sup> CNRS Laboratoire d'écologie, École normale supérieure, 46 rue d'Ulm, 75230 Paris cedex 5, France.

<sup>(4)</sup> Dept of Animal Ecology, University of Giessen, Stephanstrasse 24, 35390 Giessen, Germany.

<sup>(5)</sup> Orstom, Laboratoire de microbiologie des anaérobies, Université de Provence, 163 avenue de Luminy, 13288 Marseille cedex 9, France.

<sup>(6)</sup> Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria, LA11 6JU, UK.

<sup>(7)</sup> Institute of Ecology and Resource Management, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JG, UK.

<sup>(8)</sup> Dept of Biology and Nature Conservation, Agricultural University of Norway, Postboks 5014, AS, Norway.

\* Corresponding author

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### Abstract

In this review, the interactions between plant, animal and microbial components of the soil biota are represented by a model which allocates a pivotal functional role to the large, abundant invertebrates which ingest or manipulate both organic and mineral material, forming long-lasting microstructures. These invertebrates are designated **soil ecosystem engineers** and it is argued using data on numerical and biomass densities, geographical distribution and known functional roles, that earthworms and termites are the most important engineers in terrestrial ecosystems. Evidence is presented that they may exert influence on the diversity and activity of biota in subordinate trophic levels, for example litter transformers, micropredators and microfloras mediating fundamental nutrient transformations. Links between the activity and diversity of engineers and the physical properties of soils, including structural heterogeneity, stability, distribution of organic matter and infiltration and retention of water are also described.

In considering the probable effects of global change on engineers, it is hypothesized that living plants affect both the abundance and diversity of engineers, through the quantity and quality of litter and other effects. Changes in their communities will therefore affect engineers. Expected changes in temperature will expand the latitudinal distribution of termites and favour humivorous termites and endogeic earthworm species that feed in the soil. In some regions, however, these changes will not occur since local fauna may not include representatives of these groups. Although elevated CO<sub>2</sub> may impact engineers through effects on plant growth (notably an increase in C/N ratio), land use intensification, particularly physical disturbance of forests, is of more immediate concern as changes in the functional group balance within engineers communities can be demonstrated. In addition, exotic species of earthworms may colonize disturbed land, with adverse effects on soil structure. Disturbance affects termites by reducing diversity (especially of soil-feeding forms) and some species may reach crop pest status, owing to changes in the availability of organic matter.

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In general, a decrease in abundance of engineers will decrease C stocks in soils; imbalance among functional groups ('compacting' vs. 'decompacting') may also result in physical degradation of soil. Remediation of degraded land by earthworm inoculation is briefly discussed as both an ecological and an economic policy. © Elsevier, Paris

**Keywords:** Termites, earthworms, ecosystem engineers, fertility, climate change, land use, intensification, restoration, soil zoology, soil ecology.

## Résumé

Cette revue place au centre des interactions entre les plantes, les animaux et les microorganismes du sol, les invertébrés abondants et de grande taille qui ingèrent des particules organiques et minérales produisant ainsi des structures durables. Ces invertébrés sont appelés organismes ingénieurs du sol et les données disponibles sur leur abondance, leur distribution géographique et leurs rôles fonctionnels montrent que les vers de terre et les termites en sont les principaux représentants. Ils influencent la diversité et l'activité des organismes appartenant à des groupes fonctionnels subordonnés, les transformateurs de litière, les microprédateurs et les microorganismes régulant ainsi les transformations de nutriments. Les liens entre l'activité et la diversité des ingénieurs et les propriétés physiques du sol sont détaillés ; une mention particulière est faite de leurs effets sur l'hétérogénéité du sol, sa stabilité structurale, la distribution de la matière organique dans le profil, l'infiltration et la rétention de l'eau.

Il est probable que les changements globaux attendus affecteront l'abondance et la diversité des organismes ingénieurs par le biais de la quantité et de la qualité de la litière et d'autres effets liés aux modifications des plantes et de leurs peuplements. Les changements de température attendus pourraient élargir la distribution latitudinale des termites et favoriser les termites humivores et les vers de terre endogés à régime géophage. Dans certaines régions, cependant, ces changements ne pourront s'observer car la faune locale ne comprend pas de représentants de ces groupes. Dans l'immédiat, c'est surtout l'intensification de l'usage des terres et, en particulier, la perturbation des milieux forestiers qui est préoccupante car des modifications de l'équilibre des groupes fonctionnels d'organismes ingénieurs s'observent déjà. De plus, l'invasion des écosystèmes perturbés par des vers de terre exotiques colonisateurs agressifs peut avoir des effets adverses sur la structure du sol. La perturbation affecte les termites en réduisant leur diversité, particulièrement celle des humivores et quelques espèces peuvent devenir des parasites des cultures pour pallier le déficit des apports organiques.

En général, une diminution de l'abondance des organismes ingénieurs aura tendance à diminuer les stocks de carbone du sol; un déséquilibre entre les groupes fonctionnels (par exemple des « compactants » aux dépens des « décompactants ») peut aussi entraîner une dégradation physique du sol. La restauration des sols dégradés par l'inoculation de vers de terre est brièvement discutée dans ses implications écologiques et économiques. © Elsevier, Paris

**Mots-clés :** Termites, vers de terre, organismes ingénieurs, fertilité, changement de climat, utilisation des sols, intensification, restauration, zoologie des sols, écologie des sols.

## CONTENTS:

<b>1. INTRODUCTION .....</b>	<b>161</b>	<b>3.3. Patterns of horizontal distribution</b>	
<b>2. CONCEPTUAL FRAMEWORK .....</b>	<b>162</b>	<b>4. ROLE OF ENGINEERS</b>	
2.1. Soil ecosystem engineers: definition of terms and statement of hypotheses		<b>IN SOIL PROCESSES .....</b>	<b>170</b>
2.2. Direct interactions of engineers with micro-organisms		4.1. Soil physical properties	
2.3. Engineers as keystone species		4.2. Decomposition and dynamics of soil organic matter	
<b>3. ENGINEER BIODIVERSITY AND COMMUNITY ORGANIZATION .....</b>	<b>166</b>	4.3. Other invertebrate groups as soil engineers	
3.1. Biogeographical distribution and diversity		<b>5. EFFECTS OF GLOBAL CHANGE ON ENGINEERS .....</b>	<b>178</b>
3.2. Abundance and biomass		5.1. Elevated CO <sub>2</sub> and climate change	
		5.2. Land uses and agricultural intensification	
		<b>6. CONSEQUENCES FOR ECOSYSTEMS AND ECONOMIC IMPLICATIONS .....</b>	<b>184</b>

6.1. Diversity of communities and soil structure	
6.2. Management of engineers to sustain fertility and assist in land restoration	
6.3. Economic implications	
7. CONCLUSIONS .....	186
8. REFERENCES .....	187

## 1. INTRODUCTION

Ecosystem engineers are organisms that directly or indirectly affect the availability of resources to other organisms through modifications of the physical environment (Jones *et al.*, 1994). Soil ecosystem engineers are the physically large elements of the biota (usually invertebrates, but the broadest definitions could include some vertebrate animals and living plant roots) which have sufficient numerical and biomass densities to exert a predominant influence in the formation and maintenance of soil structure and to regulate processes to an extent that overrides organisms in other functional categories (Stork & Eggleton, 1992; Lavelle, 1997). At the heart of the engineer concept is the ability to move through soil and to build organo-mineral structures; for these reasons, earthworms and termites are the organisms most often identified as the principal engineers of the terrestrial ecosystem, although ants may also play important roles especially regarding soil physical properties (Folgarait, in press). In this paper, we will attempt to draw together and compare the information available on both groups, including biogeography, biodiversity, biomass, abundance, community structure and relationships with other organisms. Knowledge of their impact on soil processes is then summarized, with specific attention to their responses to, and influence on, ecological successions, both of a natural and anthropogenic nature.

The likely effects of anthropogenic global changes on earthworm and termite communities and activities are then discussed and hypotheses regarding consequences for soil function are formulated. Some instances in which other invertebrates take on the engineer role are also described, though it is argued that the ecosystems concerned are unusual.

One of the themes of this paper will be to emphasize the wide range of scales, both temporal and spatial, on which soil functions and the influence of engineers need to be assessed. In essence, soils are changing environments. Pedogenic processes integrating orogenic movements, long-term climate changes and the consequent responses of vegetation are slow but continuous, while within these are nested medium-term events such as ecological succession, short-term cycles such as seasonal weather patterns, day-to-day sequences such as rainfall and drainage, and even hour-to-hour regimes of heating and cooling (*fig. 1*).

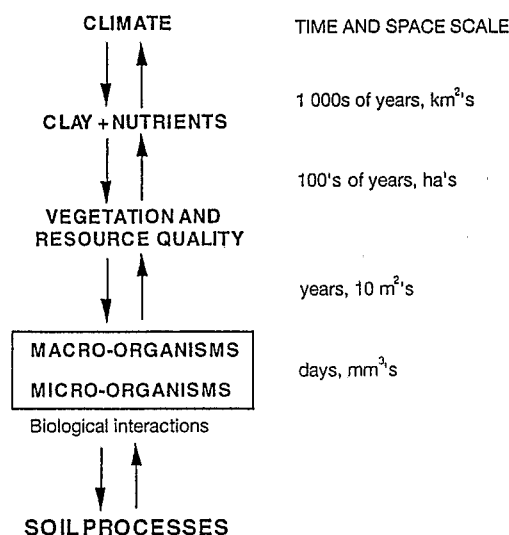


Figure 1. – A hierarchical model of determinants of soil processes (Lavelle *et al.*, 1993).

The most fundamental transformations of both inorganic and organic materials are carried out by micro-organisms within microhabitats measured in micrometres. These, however, generally have limited abilities to move and are dependent on much larger invertebrates and living roots to activate and transport them to new substrates after periods of inactivity, as well as providing them with readily assimilable substrates, such as earthworm intestinal mucus or root exudates (Lavelle *et al.*, 1994a).

Between these extreme groups are a variety of small to medium-sized animal groups (protozoans, nematodes, mites, collembolans, and larger litter arthropods such as arachnids, diplopods, isopods, etc.) which influence microbial activity, directly by predation, or indirectly through the physical and chemical modification of organic detritus. These animals are in turn dependent on engineers to generate and maintain a soil structure in which pore spaces of an appropriate size, together with usable organic resources, are available. Human activities also impose trends at differing scales, for example forest exploitation and mining are large scale perturbations, while agricultural intensification has both local effects, changing the quality and quantity of plant material returned to the soil, and global impact through the displacement of native species by exotics (Ljungstrom, 1972; Lee, 1985). Pollution is also scaled; for instance, heavy metals and pesticides incorporated into soils may have cumulative effects such as nitrogen deposition that progressively affects the growth and metabolism of organisms on all scales, from that of the individual microbe to whole stands of higher plants.

Similarly, while soil organisms may exhibit some degree of resistance or resilience to perturbations at individual or population levels, at the community level

species diversity and functional structure (= distribution of species amongst functional groups) are likely to change. Such changes are superimposed on long-term or very long-term progressions, for example, features of community structure inherited from past climatic events and even continental drift (Bouché, 1983a; Eggleton *et al.*, 1994).

In this paper, we attempt to describe the general patterns of the structure and abundance of engineer communities and to identify their climatic and biogeographic determinants. This will assist prediction of the impact of expected changes. We clearly distinguish changes in land use, that already have had, and continue to exert, considerable impact on soil fauna communities, from other global changes (elevation of concentrations of greenhouse gases and climate changes). The latter have not yet been studied and we provide here fundamental background for their study and the formulation of preliminary guesses and hypotheses.

## 2. CONCEPTUAL FRAMEWORK

### 2.1. Soil ecosystem engineers: definition of terms and statement of hypotheses.

#### 2.1.1. Major functional groups

The smallest soil invertebrates (protozoans, nematodes and many of the mites) constitute a microfauna (< 0.2 mm), which simply ingest micro-organisms or microbial metabolites, or participate in micropredator foodwebs by feeding on other animals within the same general size category (Hunt *et al.*, 1987; De Ruiter *et al.*, 1993; Wardle, 1994; Ingham & Thies, 1996). Medium sized invertebrates (the mesofauna, approx. 0.2-10.0 mm) are a taxonomically diverse assemblage (including many annelids, insects, crustaceans, myriapods, arachnids and other minor arthropod groups) which function as litter transformers that ingest a mixture of organic matter and microbial biomass. They may digest some of this material directly, but they also generate large amounts of rather fragile faecal material in which further microbial growth is enhanced by favourable conditions of moisture and the intense mixing which has occurred in the gut. At a later time (days to weeks), the same invertebrate or another one quite different in nature may re-ingest these pellets (coprophagy) and assimilate a further set of substrates made available by the most recent burst of microbial activity (Hassal & Rushton, 1985; Szilávecz & Pobožsny, 1992). Alternatively, faecal pellets may accumulate to form the H horizon of specific humus types (Delecour, 1980).

The largest invertebrates (> 1 cm) make up the macrofauna (usually dominated by lumbricid annelids, molluscs, myriapods and a variety of insect groups

including termites). Some of them, mostly non-social arthropods and litter dwelling (epigeic) earthworms, produce holorganic faecal pellets and function as litter transformers. Others, mainly termites, burrowing (anecic) and soil feeding (endogeic) earthworms, ingest a mixture of organic and mineral debris, thus forming faeces which are organo-mineral complexes. Unlike holorganic pellets, the complexes are stable over periods ranging from months (for example, earthworm casts: Kretzschmar, 1982; Blanchart *et al.*, 1993; Marinissen, 1995) to decades (for example, the larger termite mounds: Wood, 1996), and consequently a biogenic structure is superimposed on longer-term pedogenic processes. Where earthworms and/or termites are abundant, additional contributions to the mixing of organic and mineral materials may be made by salivary secretions to bind particles in mound and gallery construction (see Wood & Sands, 1978; Wood, 1988, 1996) or the addition of water and intestinal mucus (Barois & Lavelle, 1986). The impact of the larger and more abundant structure-forming invertebrates is therefore profound, in the sense of generating permanent or semi-permanent stability and processing a major part of the organic detritus available, and critical in the sense of determining specific pathways for decomposition and functional domains (drilosphere for earthworms, termitosphere for termites) in which litter transformers and micropredators can be active.

#### 2.1.2. Diversity of ecosystem engineer and soil function

The link between diversity of macrofauna and soil function is still poorly researched and too little discussed. Figure 2 illustrates both what is generally agreed about this link (in central triangle) and what might also be true if four crucial hypotheses are accepted or proven experimentally (model outside the triangle). It is not disputed that the activity of invertebrate engineers creates structures in soil which then promote and constrain soil processes on a range of temporal and spatial scales: nutrient mineralization (microsites available to micro-organisms), physical stabilization (hydrological properties and resistance to erosion), stabilization (retention and humification) of organic matter, nutrient conservation and, ultimately, pedogenesis.

The more crucial question is whether the abundance and diversity of engineers are themselves constrained and whether, as a consequence, the soil functions which are dependent on them can vary in intensity or be shifted along spatial and temporal gradients. Hypothesis 1 (H1) holds that the size of engineer populations (numerical and/or biomass densities) can be affected by shortages and surpluses of organic materials and by their quality (as C/N ratio). In a soil with depleted organic resources, foodwebs tend to have a reduced number of trophic levels and fewer components at each level (a simple application of the productivity hypothesis to explain species richness; Giller,

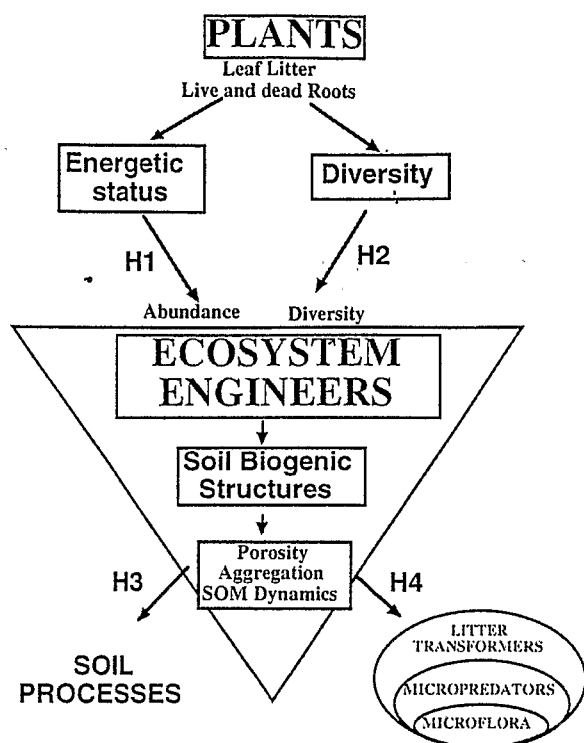


Figure 2. – Relationships between biodiversity of soil invertebrates and soil function, incorporating four hypotheses. H1: that the size of engineer populations can be affected by shortages and surpluses of organic materials, as well as by its quality (C/N ratio); H2: that engineer diversity tracks the diversity of live plants; H3: that engineer diversity and soil structural heterogeneity are causally linked; H4: that engineers are keystone species, generating associated communities of litter transformers, microfauna and microflora. The biodiversities of these groups are nested such that engineer diversity also promotes diversity at other trophic levels (Lavelle, 1996).

1984). Thus, for example, the casts of earthworms or the epigeal mounds of termites that serve as a food resource for smaller animals and micro-organisms would have a lower energetic value in an impoverished soil, or be fewer and the dependent soil functions would be diminished in intensity, and structural stability would also be reduced (Blanchart *et al.*, 1993). At the ecosystem scale, it might be possible to determine the threshold of organic resources (of a given quality) which are critical for the activity of macrofaunas. In the savanna of Lamto (Ivory Coast), the earthworm community consumes  $1.2 \text{ t ha}^{-1} \text{ y}^{-1}$  of organic matter from relatively young pools (Lavelle, 1978; Martin *et al.*, 1991); impoverishment of soil by the reduction of organic inputs below this level would presumably constrain earthworms and therefore, all dependent processes.

Similarly, it can be argued that the diversity of engineers tracks that of the living plant community (hypothesis 2, H2). Considerable evidence exists that the composition, biomass, distribution and activity levels of engineers are influenced by plant community

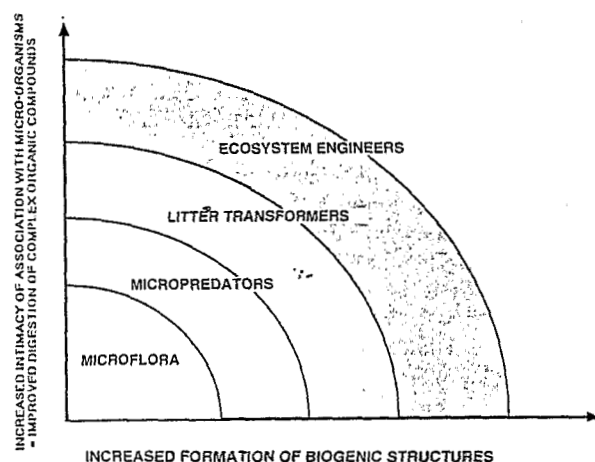
composition, which may itself be determined by the pattern of agricultural (especially grazing) practices and by soil nutrient status (*e.g.* Miles, 1985; Fragoso & Lavelle, 1992; Charpentier unpubl. data in Wardle & Lavelle, 1997; Gilot *et al.*, 1995). This is further supported by patterns of earthworm communities in temperate forests planted with different tree species (Lavelle, 1983). Although different plant communities influence termite and earthworm assemblage composition (especially plant successional stages), it is not yet clear if there is a specific link between particular plants and specific engineers as a few authors suggest (Boettcher & Kalisz, 1991; Grandval, 1993).

Hypothesis 3 (H3) holds that engineer diversity and soil structural heterogeneity are linked, *i.e.* that diversity in soil invertebrates results in the production of structures whose abundance and variety promote the conservation and modulate the turnover of organic matter. This diversity provides sustained nutrient release and the maintenance of physical properties that are essential for a sustained primary production. The evidence supporting this hypothesis is dealt with in sections 4.1 and 4.2. Special emphasis is placed on the character of soil structures: shape, location, abundance and composition. Ultimately, structures delimit the microsites available for the activities of micro-organisms and hence, are determinants of nutrient dynamics.

In hypothesis 4 (H4), soil engineers are assessed as keystone species. This concept holds that the location and processing sequences of organic resources in the soil are primarily determined by the activity and composition of the engineer assemblage, on which the lower-level communities of litter transformers, micropredators and micro-organisms are dependent. Therefore, the diversity of engineers should correlate with the diversities of litter transformers, microfauna and microflora. Further, the diversities of organisms in these descending categories are nested, in the sense that each variety of engineer will spawn a more or less specific set of litter transformers within the domain of structure it creates, and litter transformers will similarly influence communities of microfauna, and microfauna will in turn determine the composition of assemblages of the micro-organisms which mediate fundamental transformations. This hypothesis is expanded in section 2.3.

## 2.2. Direct interactions of engineers with micro-organisms

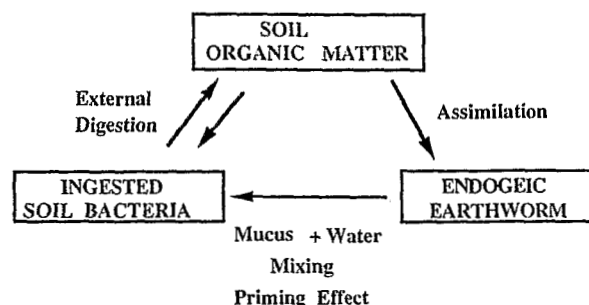
It is apparent that a gradient of interaction with micro-organisms can be seen in the digestive processes of soil animals as they increase in size (and assume different functional roles, contributing progressively more to the formation and maintenance of structure) from micropredators to ecosystem engineers (*fig. 3*). Thus, we assume that in micropredators, the basic process is one of cellular lysis, the contents of microbial



**Figure 3.** – Interactions among micro- and macro-organisms in soils. As the size of organisms increases, their relationships with microflora gradually shift from predation to external and internal mutualism, and they produce biogenic structures of increasing strength. When present, larger organisms tend to be more competitive than smaller ones, but their activity is more frequently limited by low temperature and moisture conditions (Lavelle, 1997).

tissues being directly digested and assimilated. In litter transformers however, there is the additional capacity to assimilate the more labile products temporarily accumulated in the matrix of organic matter by successive waves of microbial colonization. However, the requirement for prior conditioning by fungi, actinomycetes and bacteria is a critical constraint and the most abundant resources, the fibrous components of plant cell walls including cellulose, hemicellulose, lignin and their derivatives, are not accessible without the previous intervention of biochemically more versatile micro-organisms. Micro-organisms are especially active in fresh faecal pellets that function as external rumens before they are re-ingested and products of microbial digestion are assimilated. In engineers, by contrast, micro-organisms are directly harnessed by the intestinal machinery as mutualists and degrade recalcitrant materials, either within the gut or in an external rumen arrangement, at a rate which is consistent with the metabolic demands of the host and which can be optimized by adjustment of the physiological conditions under which the growth and metabolism of the microbes take place (Barois & Lavelle, 1986; Bignell, 1984, 1994). With these arrangements, engineers can therefore successfully utilize organic material in its most recalcitrant state.

Mutualistic digestive systems have been described in several endogeic earthworm species from both temperate and tropical biomes (Barois & Lavelle, 1986; Trigo & Lavelle, 1993; Zhang *et al.*, 1993; Lattaud *et al.*, 1997; see fig. 4). Free-living soil micro-organisms find suitable conditions for growth in the anterior part of the gut: neutral pH, a high water content (100-150% of the dry wt of soil) and most importantly,



**Figure 4.** – Mutualist digestion system in endogeic earthworms (Barois & Lavelle, 1986).

large quantities of secreted intestinal mucus (5-40% of the dry wt of soil) which can be readily utilized as substrate. In the middle intestine, mucus secretion is discontinued and mucus that had not been degraded is reabsorbed; the micro-organisms therefore apparently revert to the degradation of soil organic matter at a much greater rate (up to 30-fold higher) than under undisturbed field conditions at the same temperature. The products of this digestion seem to be reabsorbed with water in the posterior part of the gut. As a result, an estimated 3-19% of the ingested soil organic matter is assimilated during a single transit of the gut in as little as 30 min to 4 h (Lavelle, 1978; Barois *et al.*, 1987; Martin & Lavelle, 1992; summarized in fig. 4). Precise information on changes in microbial communities that occur during the gut transit, and their participation in degradation of soil organic matter, is still needed to generalize or extend this model. Literature data indicate that the fate of the ingested microflora varies largely depending on species: some may be digested by worms, especially Protozoa, algae and some fungi or bacteria whereas a large proportion remains unharmed (*e.g.* see Brusewitz, 1959; Cooke & Luxton, 1980; Pearce & Phillips, 1980; Cooke, 1983; Rouelle, 1983). Marked differences seem to exist among species since bacterial densities increase during gut transit in *L. terrestris* and *L. rubellus*, but decrease in the gut of *Apporectodea caliginosa* (Kristufek *et al.*, 1992; Parle, 1963). Finally, some astomatous ciliates and filamentous bacteria seem to be permanent residents of the gut of anecic earthworms (de Puytorac, 1954; Pearce & Phillips, 1980; Rouelle, 1983; Daniel & Anderson, 1992).

After more than 70 years of investigation, confident statements concerning the supposed roles of intestinal flagellates and bacteria in digesting cellulose in termite guts appear in many textbooks. However, while a mutualistic relation undoubtedly exists, the precise role of gut microbes (and those present in fungus gardens) remains unclear (Bignell, 1994; Bignell *et al.*, 1994; Slaytor *et al.*, 1997). Figure 5 summarizes current understanding. All grass-eating and xylophagous species so far investigated have been shown to produce their own cellulase enzyme complex, independently of



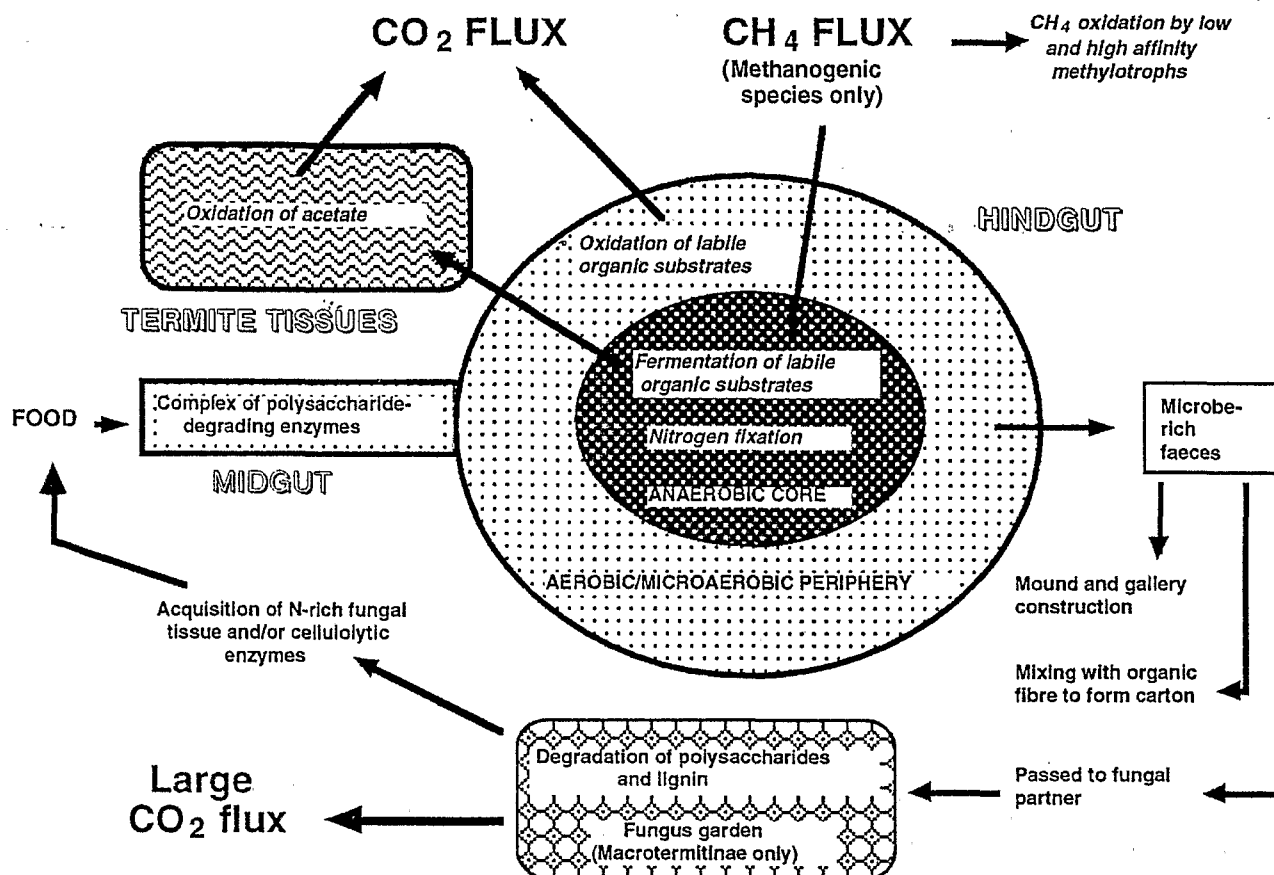


Figure 5. – Digestion system in termites (Bignell, 1994).

any associated microbiota, which is sufficiently competent against natural forms of cellulose to match metabolic needs (e.g. Veivers *et al.*, 1991; reviews by Slaytor, 1992 and Slaytor *et al.*, 1997). There is also growing evidence for the digestion of hemicelluloses (xylans) within the gut (e.g. Rouland *et al.*, 1988, 1991; Breznak & Brune, 1994), although it is presently unclear how much of this is attributable to enzymes of termite origin. Possible roles for the gut microbiota include the metabolism of pyruvate (Slaytor *et al.*, 1997), nitrogen fixation (Breznak *et al.*, 1973; Congdon *et al.*, 1993) and the (partial) degradation of polyaromatic compounds (Kuhnigk *et al.*, 1994; Brune *et al.*, 1995). At least part of the hindgut is anaerobic, and the accumulation of acetate and other short chain fatty acids, together with the efflux of methane from many species can be taken as evidence that fermentation is occurring, but the substrates degraded have not been identified (Breznak, 1984; Breznak & Brune, 1994; Slaytor *et al.*, 1997).

The evolution of soil-feeding is a major trend in higher termites (Noirot, 1992; Bignell 1994), with the intestinal microbiota showing a number of characteristic features, including a predominance of filamentous prokaryotes, possibly related to actinomycetes (Bignell

*et al.*, 1979; Bignell *et al.*, 1991). However, little firm information exists concerning the nature of the substrates degraded. Despite the expectation that polyaromatic compounds would be degraded, physiological data suggest that carbohydrate dissimilation is the basis of respiration (Nunes *et al.*, 1997). This is supported by gut content analyses showing that ingested lignin passes through the gut undegraded (Donovan, Bignell & Eggleton, unpubl.).

In higher termites of the subfamily Macrotermitinae, there is an obligate association with cultivated fungus gardens of the genus *Termitomyces* (Sands, 1969; Abo-Khatwa, 1978; Rohrmann & Rossman, 1980; Rouland *et al.*, 1988; Wood & Thomas, 1989; Darlington, 1994). The fungus is housed either in the central part of elaborately constructed epigeal mounds or in subterranean chambers and supplied with partially digested forage which has passed once through the gut of host worker termites (Sands, 1960; Badertscher *et al.*, 1983). This material is extensively colonized and degraded by the fungus, after which both the mature mycelium and the conidia it produces are consumed by termites. The precise contribution of the fungal processing is unclear (there is evidence that functioning cellulases are acquired by the termites when fungal tissues are con-

sumed, but the same tissues are also much richer in nitrogen than the original forage), but the principle involved is clearly that of the external rumen. Available evidence suggests that the microbiology and physiology of the alimentary canal of Macrotermitinae is similar to that of other termites (Veivers *et al.*, 1991; Anklin-Mühlemann *et al.*, 1995). The net effect is a very efficient degradation of the plant residues foraged, with most of the organic carbon mineralized directly to CO<sub>2</sub> (by the fungus garden), without passing through to other trophic levels (Wood & Sands, 1978)

### 2.3. Engineers as keystone species

Diversity in plant communities determines below-ground diversity in the following order: plant diversity → ecosystem engineers → litter transformers → microfauna → microflora (Lavelle, 1996) (fig. 2). This hypothesis can be seen as an analogue of hypothesis B1 developed by Solbrig *et al.* (1991) stating that 'key-stone' species are essential for maintaining species richness in communities (Terborgh, 1989; Gautier-Hion, 1989). Such species modify the habitat and trophic resource base of organisms that are smaller and less mobile.

Diversity of smaller invertebrates, from the micro-foodweb and litter transformer categories, is thus likely to be at least partly determined by that of ecosystem engineers and plants (Lavelle, 1996). Recent studies have shown strong effects of plants on invertebrate communities. In the rainforest of French Guiana, Charpentier *et al.*, (unpubl. data in Wardle & Lavelle, 1997) showed that trees that produce litters of contrasted qualities may have significantly different soil invertebrate communities. This effect referred to as 'single tree effect' has been repeatedly observed in a large number of ecosystems (Garay, 1980; Boettcher & Kalisz, 1991). Ecosystem engineers may also influence communities of smaller invertebrates in their functional domain. For example, this is the case for Collembola of a pasture from Martinique (French West Indies) that have larger individual sizes, and increased diversity and abundance in patches where earthworms (*Polypheretima elongata*) concentrate than in patches with low earthworm abundance (Loranger, 1995). In patches with high earthworm abundance ( $133 \pm 8 \text{ m}^{-2}$ ), microarthropod density ( $80\,000 \pm 30\,000 \text{ m}^{-2}$ ) was significantly higher than in patches with depleted populations where  $31 \pm 14$  worms and  $49\,000 \pm 18\,000$  microarthropods, respectively, were collected. Diversity of microarthropod communities followed a similar pattern and the Shannon index of diversity of Collembola was, 3.53 and 2.74 inside and outside earthworm patches, respectively, while the average size of individuals was larger inside than outside the patches (fig. 6).

In addition, specific plant communities are often associated with termite mounds or their immediate environment, and may appear in a successional sequence from grasses to shrubs and trees as mounds age and

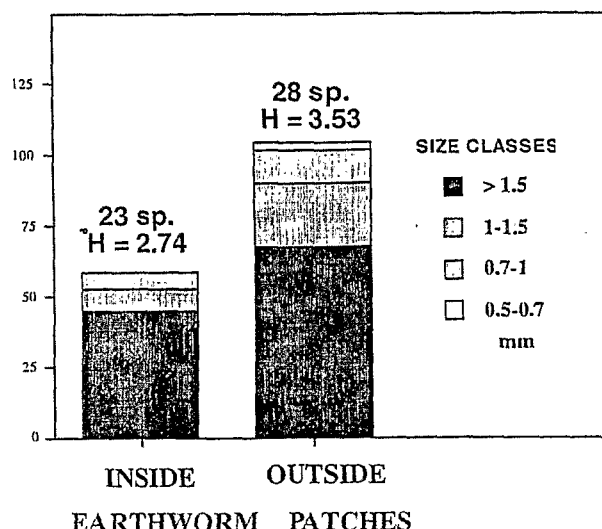


Figure 6. – Density and size-class structure of Collembola communities inside and outside patches of concentrated populations of the endogeic earthworm *Polypheretima elongata* in a pasture of Martinique (French West Indies) (Loranger, 1995).

grow (Harris, 1971; Wood & Sands, 1978; Wood, 1996). Plant diversity has also been shown to be influenced by grazing and both these variables are related (differently) to termite mound size and density in semi-arid Eastern Mali (Dhillon & Traoré, unpubl.) (table 1). The size of termite mounds was highly correlated with woody plant density and grazing intensity, and was also correlated with organic matter and fungal biomass in non-mound soils. Termite mound density was positively correlated with microbial biomass carbon, permitting the general conclusion that plant diversity (mediated by grazing) was affecting the accumulation of organic matter in soil via the activities of termites.

## 3. ENGINEER BIODIVERSITY AND COMMUNITY ORGANIZATION

### 3.1. Biogeographical distribution and diversity

The assemblage character, biomass, distribution and activities of ecosystem engineers are influenced by a suite of factors that operate at different scales of time and space, *i.e.* climate along latitudinal and altitudinal gradients, soil types and plant community composition, in natural and managed environments (Miles, 1985; Frago & Lavelle, 1992; Gilot *et al.*, 1995; Charpentier *et al.*, unpubl. data in Wardle & Lavelle, 1997).

Termites are most active in the tropics although they occur between the approximate latitude of 30° N and 40° S (Wood, 1978). Within this range, species diversity declines regularly with distance from the Equator



**Table 1.** – Relationships of selected community variables with three levels of grazing intensity based on number of goats (approx. 0, 40 and 130 heads allowed access to each site) and density and size of termite mounds in Toro (semi arid eastern Mali). two areas per grazing intensity each of approximate 20 ha were studied with nested sampling design (Dhillon & Traoré, unpubl. data).

Variable	Grazing intensity				Termite mounds	
	scares lands		common property lands		density	size
	0	40	130	$r^2$	$r^2$	$r^2$
Density of termite mounds	med	high	low	0.28*		
Size of mounds	high	med	low	0.79**		
Plant cover	high	med	low	0.72**	0.07	0.67**
Diversity of plants						
all	med	high	low	0.36*	0.82**	0.11*
herbaceous	med	high	low	0.21*	0.87**	0.09
woody	high	med	low	0.82*	0.13*	0.69**
Organic matter	high	med	low	0.75**	0.11	0.65**
Microbial -C	med	high	low	0.17*	0.76**	0.19*
Fungal biomass	high	med	low	0.65**	0.17**	0.72**

\*  $P < 0.05$ ; \*\*  $P < 0.01$

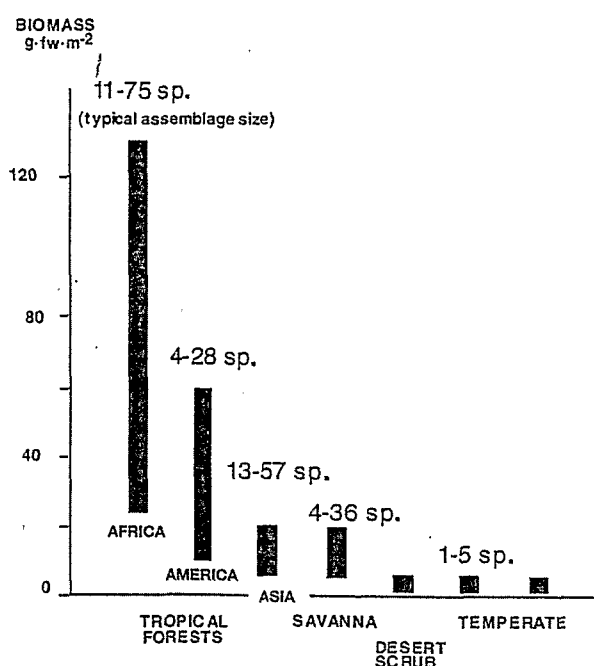
(Coaton & Sheasby, 1972; Eggleton & Bignell, 1995) (fig. 7).

Most termite communities are a mosaic of different functional groups and species with a variety of physical styles of feeding: soil feeding humivorous, wood feeding xylophagous, fungus-growers or harvesters, with diverse foraging strategies inside each group. The balance between these types and, therefore, the character of assemblages varies consistently between ecosystems, although biogeographical, historical, climatological, pedological and vegetational factors can all be

perceived as causal agents (Eggleton & Bignell, 1995; Sleaford *et al.*, 1996; Bignell *et al.*, 1997).

Dry areas with steppe or grass savanna have dominant grass and litter foraging populations, and fewer than 10 termite species. Fungus growers tend to partly replace these groups as rainfall increases and woody vegetation develops. Humivorous termites follow a similar trend and they significantly contribute to the increase in diversity and abundance of termite communities in tropical rainforest of Africa (Lepage, in Menaut *et al.*, 1985; Kouassi, 1987) (fig. 8). The lower termites are best represented at higher latitudes. An inventory of termite generic richness shows that the Ethiopian biogeographical region is most genus-rich, while the neotropical and Indo-Malayan regions are less rich and the former lacks fungus-growers altogether (Eggleton *et al.*, 1994). In tropical forests where disturbance is light, both species richness and biomass appear to be higher than in adjacent savannas, and soil-feeding forms (chiefly associated with the subfamilies Apicotermittinae and Termitinae) are particularly abundant (Wood & Johnson, 1986; Martius, 1994; Eggleton & Bignell, 1995; Eggleton *et al.*, 1995). When annual rainfall exceeds 1 500 mm, species richness reaches maximum values of > 50 sp. in Africa, and 10-60 sp. in America.

The relative abundance of earthworm functional groups varies along a thermo-latitudinal gradient, (Lavelle, 1983) (fig. 9). Earthworms occur from coniferous forests of the cold temperate areas down to the Equator. They are excluded from dry areas; in tropical Africa, for example, they are restricted to areas with at least 800 mm average annual rainfall. As mean temperature increases, they progressively become able to digest resources of lower quality (*i.e.* with less organic matter and more mineral soil) and their communities integrate anecics (that feed on a mixture of soil and leaf litter) and endogeics feeding on medium quality soil organic matter (mesohumic) and low quality soil organic matter of the deep horizons (oligohumics).



**Figure 7.** – Geographical variations in biomass and species richness in termite communities (Eggleton & Bignell, 1995).

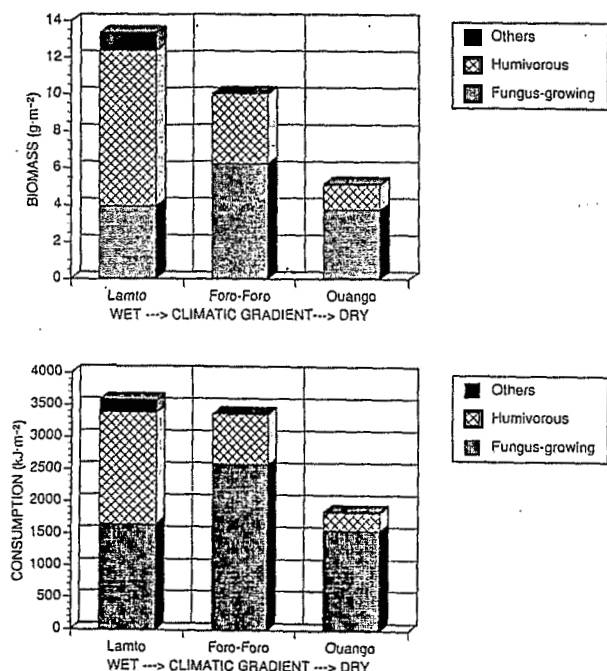


Figure 8. – Changes in termite biomass and the relative proportion of trophic groups across a rainfall gradient in Ivory Coast (Lepage, 1983).

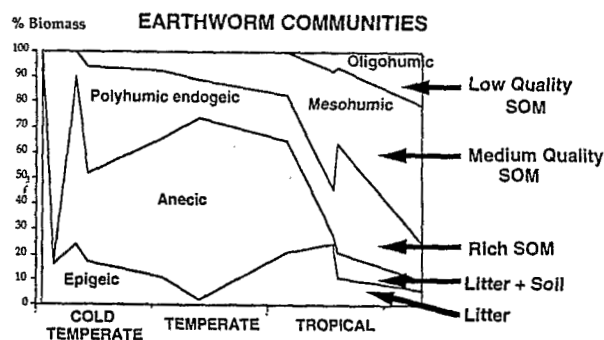


Figure 9. – Changes in the relative abundance of earthworm trophic groups along a thermo-latitudinal gradient (Lavelle, 1983).

Interestingly, the number of species found does not change much along this gradient and fluctuates between 6 and 15 species. Functional diversity, however, increases via the progressive incorporation of new functional groups.

### 3.2. Abundance and biomass

Macro-invertebrate communities often comprise several thousands of individuals·m<sup>-2</sup> with a fresh biomass in the range of 5 to 100 g fresh mass (fm; equivalent to 0.5 to 10 g dry weight). Earthworms and

termites are dominant components of these communities.

Earthworms comprise the major animal biomass in a number of ecosystems that experience less than a few consecutive months of drought or frost in an average year. Density is often in the range of 100 to 500 individuals·m<sup>-2</sup> and may be as high as the 2 000 ind·m<sup>-2</sup> reported from such environments as temperate pastures in New Zealand or irrigated orchards in temperate Australia (Lee, 1985). Live biomass commonly ranges from 30 to 100 g fm·m<sup>-2</sup>. Maximum biomasses of 200 to 400 g have been recorded in fertilized pastures in temperate regions (e.g. see Cotton & Curry, 1980) and tropical pastures (Barois *et al.*, 1988). In most cases, forests have lower biomasses than grasslands, in the range of 10–70 g·m<sup>-2</sup> depending on vegetation type and climatic conditions (Lee, 1985).

Markedly different patterns of abundance occur at different spatial scales (see reviews in Lavelle, 1983; Lee, 1985; Edwards & Bohlen, 1996):

(i) – at a global scale, there is a clear thermolatitudinal gradient, as mean population density in natural environments tends to increase from a few tens on average in cold temperate areas to maximum values of several hundreds in tropical areas. In contrast, biomass increases from 30 to 100 g fm·m<sup>-2</sup> from cold to mild temperate environments and then decreases again towards tropical latitudes (Lavelle, 1983);

(ii) – at a regional scale, the type of soil and vegetation greatly influences earthworm abundance. Grasslands tend to have much larger populations than forests; this is the case, for example, of temperate or tropical pastures colonized either by exotic peregrine species, or by local adapted species that may have biomasses of 1 t fm·ha<sup>-1</sup> or more when an adjacent forest will have *ca.* half as much (Lavelle & Pashanasi, 1989). Large biomasses may also be associated with nutrient richness as observed for communities in tropical rainforests (Fragoso & Lavelle, 1992).

(iii) – at a local scale, variation in soils, vegetation patterns, land use and cultivation techniques greatly affect earthworm populations (see section 5.2).

Estimates of termite abundance for savannas (50–4 400 m<sup>-2</sup>) overlap with that of forests (1 000–7 130 m<sup>-2</sup>), with that of secondary forests/plantations (120–10 470 m<sup>-2</sup>) and that of agricultural systems (1 500–6 825 m<sup>-2</sup>) (Eggleton & Bignell, 1995). The reliability of individual estimates depends on the rigour of the sampling protocols, but it does seem possible to conclude that the highest termite numerical densities are associated with tropical forests. Overall, it is considered that termites constitute about 10% of all animal biomass in the tropics (Wilson, 1993), and as much as 95% of soil insect biomass (Watt *et al.*, 1997).

A comparison of estimated termite biomass in different biomes based on subjective extrapolation from existing point data, calibrated (*i.e.* the scaling of total populations relative to nest populations) by reference

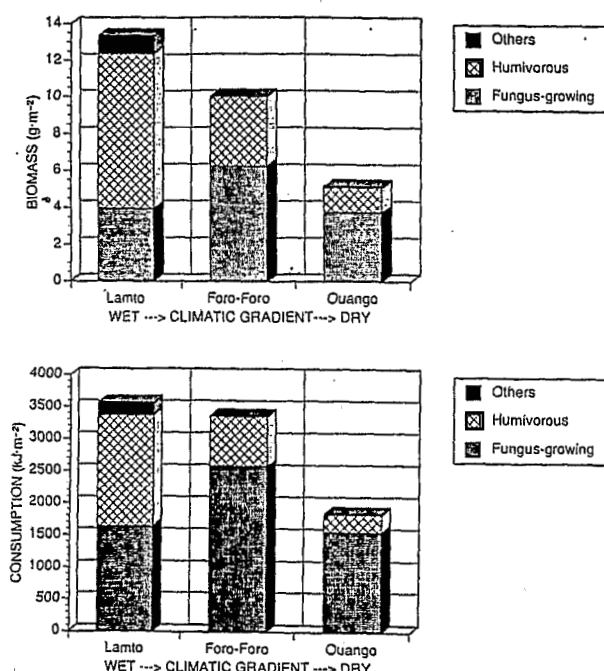


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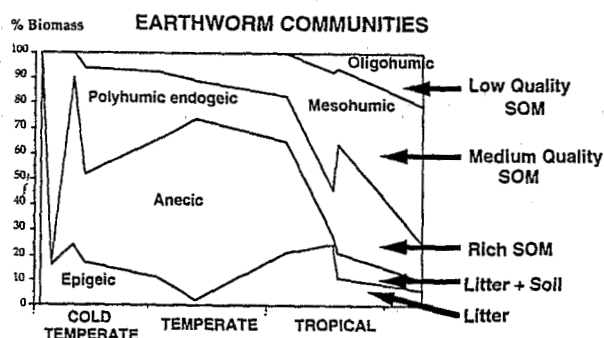


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A comparison of estimated termite biomass in different biomes based on subjective extrapolation from existing point data, calibrated (*i.e.* the scaling of total populations relative to nest populations) by reference

to the well-documented assemblage of southern Cameroon, was presented by Bignell *et al.* (1997) and summarized in *fig. 7*. Biomass estimates vary from a few  $\text{g fm}^{-2}$  to a maximum value of 130  $\text{g fm}^{-2}$  in a forest of Central Africa. Most values are close to 10  $\text{g fm}^{-2}$  and forest populations have the highest records. The major factors, other than latitude, influencing termite abundance, biomass and diversity are rainfall (see *fig. 8*), altitude (termites are restricted to lower altitudes), type of vegetation (termites are more abundant in forests than savannas) and disturbance (agriculture reduces most species but may promote others to local pest status; see section 5.2).

### 3.3. Patterns of horizontal distribution

Most soil invertebrates have aggregative patterns of distribution. Measurement of aggregation for populations of 7 tropical earthworm species from the Lamto savanna (Ivory Coast) using Taylor's Power Law parameters showed an inverse relationship of this index with the size of species, life expectancy at birth and growth period, and a positive relationship with fecundity (Rossi & Lavelle, 1998). This aggregation may be an intrinsic property of populations that results from such processes as the concentration of juveniles hatched from large batches of eggs, pseudosocial or social behaviours. In other cases, a slight lack of synchrony between environmental driving variables and population dynamics creates a patchy structure of discrete units with different age structures (Martin, 1990; Rossi *et al.*, 1997). In a pasture of Martinique, *e.g.* populations of the endogeic exotic species *Polychaeta elongata* are distributed in patches 20–40 m in diameter, with different age structures, in a location pattern that is independent from an obvious gradient of clay and organic matter concentration.

In other cases, earthworm distribution may be determined by the occurrence of a specific type of litter, like in the tropical rainforest of Guiana (Charpentier *et al.*, unpubl. data in Wardle & Lavelle, 1997), or a set of more or less well-defined soil and litter parameters (Phillipson *et al.*, 1976; Poier & Richter, 1992). There is some evidence that patchy distributions may also correspond to minisuccessional processes that occur at spatial scales of patches a few tenth metres in diameter. Blanchart *et al.* (1997) suggest that soil aggregation is regulated by 'compacting' and 'decompacting' species that may occur together, or follow each other in time. Successional processes of vegetation dynamics such as those observed in natural forests may precede, or follow, significant changes in the organic status of soils. Several examples indicate that earthworm activities during these successions vary significantly (Miles, 1985) and may be limited to periods when organic matter that they can digest is available. This hypothesis is supported by observations of Bernier & Ponge (1994) in an alpine forest of France located at a 1550 m elevation. In a succession of forest patches

from 10 to 190 years old, significant changes in earthworm communities were observed. In the early stages, earthworm density was high with a clear dominance of endogeic populations. Density decreased steadily during the following twenty years and, after 60 years, when the forest was mature, earthworm populations started to increase again, although their density was low. These population changes coincided with clear changes in the amounts and quality of organic matter stored in the humus layers. The proportion of organic matter bounded to minerals, *i.e.* organic matter that has been mixed into the soil by earthworm activities, was greatest at ten years and then decreased steadily, being almost absent after 60 years. In the late stages of succession, bound organic matter resumed accumulation. This is evidence that during the cycle of growth, maturation and senescence of the forest, humus type changed with a maximum development of a moder at 60 years and mull at 10 years. It is hypothesized that a forest accumulates organic matter as litter and raw humus during the early phases of growth, when primary production is high. Then, earthworm populations start to develop at the expense of these organic accumulations and they progressively incorporate the non-digested part of this raw organic matter into organo-mineral complexes. This process results in the release of large amounts of nutrients and the creation of physical structures (macro-aggregates, macropores and galleries) typical of a mull type humus. This medium is believed to be favourable for the establishment and growth of seedlings.

In forests, the quality of litter produced affects the structure of communities; for example, in temperate countries, deciduous forests have a larger proportion of endogeic earthworms than coniferous forests. Within deciduous forests, stands planted with species that produce litter with high polyphenol contents (*e.g.* *Fagus* sp., or *Quercus* sp.) have earthworm communities that are more similar to those of coniferous forests than communities under tree species with low polyphenols and high water soluble carbohydrate contents (Lavelle, 1983). Earthworm communities are also sensitive to nutrient concentrations in soils. In tropical rainforests, for example, community structure was correlated with the soil nutrient status (Fragoso & Lavelle, 1992).

In tropical areas, different functional groups of termites and earthworms may participate in similar successional processes. Observations in a diachronic series of rubber plantations in Ivory Coast provide an example of such processes (Gilot *et al.*, 1995) (*fig. 10*). During the early stages of the plantation, soil faunal communities were dominated by termites, especially xylophagous species. After a few years, the abundance of this group of termites declined and other groups dominated the termite communities. After 20 years, earthworms became dominant: mesohumic and endogeic categories prevailed. Finally, in a 30-year plantation, soil faunal abundance decreased steadily, as did the production of rubber.

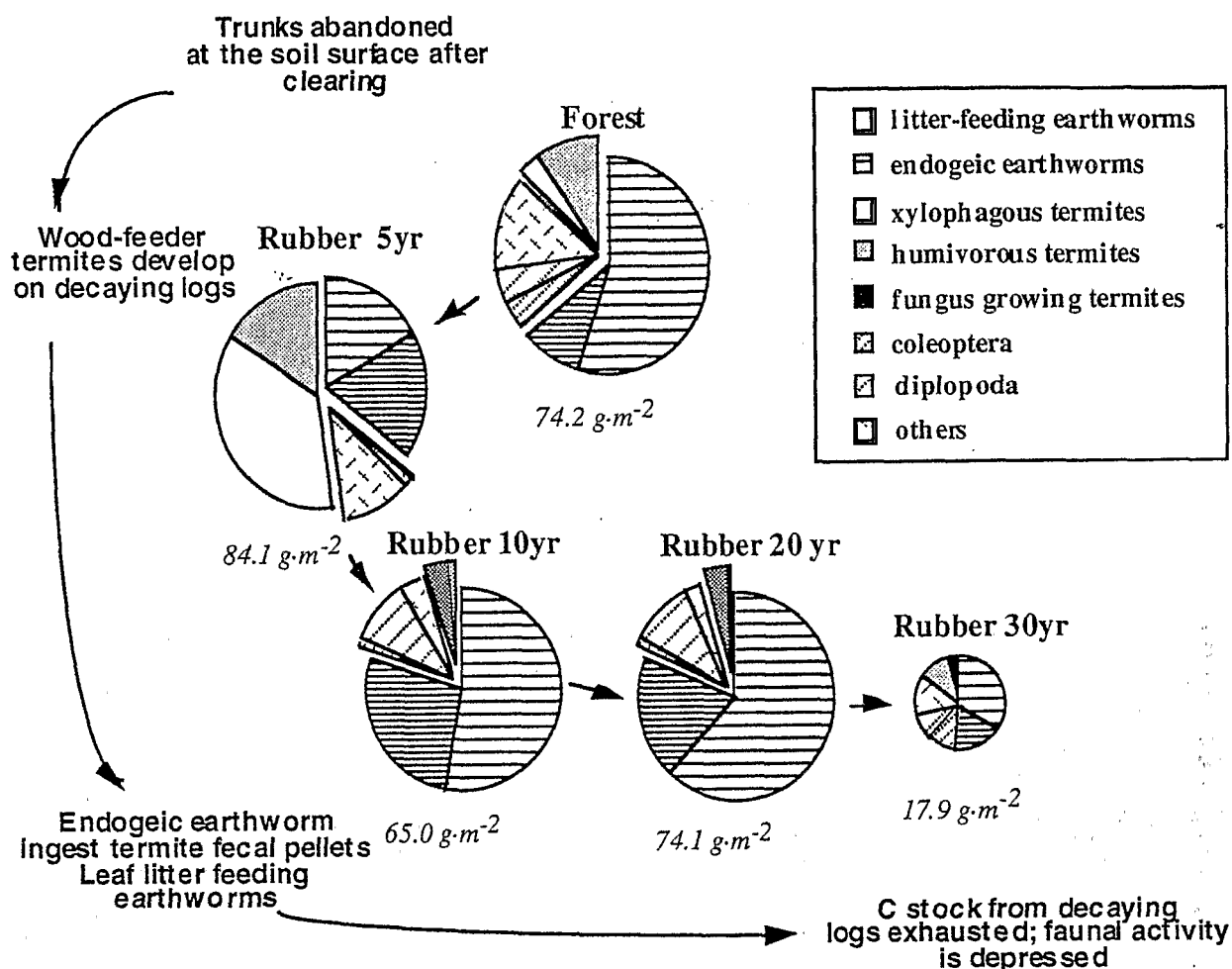


Figure 10. – Changes in soil macrofauna communities in a primary forest and a succession of ageing rubber plantations (Gilot *et al.*, 1995).

It has been suggested that these changes could reflect successions in soil fauna communities following changes in the quality and quantity of organic matter. When the plantations were created, woody material from the primary forest was left at the soil surface. Xylophagous termites were the first invertebrate group to use this resource. They transformed decaying wood into faecal pellets that may have been used by other groups of termites and surface-living earthworms. Eventually, faecal pellets of humivorous termites may have been incorporated into the soil and used as food by endogeic mesohumic and oligohumic species of earthworms. Once organic matter from the wood had passed through this food chain and lost most of the energy stored as carbon compounds, the food resource base for soil faunal communities was reduced to the plant residues currently available in the rubber plantation and their populations decreased drastically. Interestingly, this sharp decrease in numbers coincided with a decrease in rates of mineralization of C and N by soil

microflora and eventually a reduced production of rubber. These observations suggest that soil fauna, especially termites and earthworms, may at some stage use carbon sources that have been previously stored in the ecosystem at different stages of natural or artificial successional processes. In the case of the rubber plantation, it is hypothesized that soil faunal activities are sustained, at least partly, by the energy progressively released from the decaying logs with positive effects on rubber production.

#### 4. ROLE OF ENGINEERS IN SOIL PROCESSES

Ecosystem engineers directly affect soil physical properties and decomposition, by their digestion and transfer of organic matter and soil. Indirectly, they profoundly affect the soil and litter environment by accumulating their biogenic structures (casts, pellets, galleries, chambers and mounds) and determining spe-



cific pathways for decomposition at scales of time and space larger than their life-span.

#### 4.1. Soil physical properties

Earthworm and termite activities affect soil structure through: i) the selective ingestion of mineral and organic particles; ii) their egestion as faecal pellets and organomineral aggregates at some distance from the ingestion; iii) digestion processes that may modify the colloidal properties of organic matter; and iv) building of long lasting galleries, chambers and mounds.

Each species or functional group produces structures that have specific properties regarding their size, texture, stability and life duration. In most soils, surface horizons are mainly composed of an accumulation of these structures. The overall dry mass of soil ingested by earthworms often reaches 500 to 1 000 t·ha<sup>-1</sup>·yr<sup>-1</sup> (Lavelle, 1978). In moist savannas of Ivory Coast, humivorous termites ingest 45 t dry soil·ha<sup>-1</sup>·yr<sup>-1</sup>, and significant amounts of soil are also incorporated in mounds and surface sheetings produced by termites of other functional groups. Gallery networks made by earthworms may be extremely dense: in temperate pastures in France, Kretschmar (1982) found 4 000 to 29 800 galleries·m<sup>-2</sup> with a total length of 142 to 890 m·m<sup>-2</sup> depending on the season. Sixteen percent of these galleries were found deeper than 60 cm deep and the overall surface of gallery walls was 1.6–12 m<sup>2</sup>·m<sup>-2</sup>. In a large survey in several regions of France, Lopes-Assad (1987) examined 24 different soil profiles and found 60–290 active (*i.e.* opened to the surface) galleries·m<sup>-2</sup>; their total length ranged from 6.2 to 66.6 m·m<sup>-2</sup> and they comprised *ca.* 0.6% of the total volume of soil. Termites and ants also contribute large volumes, depending on the site and nature of communities. In east African savannas, termites built *ca.* 15 km galleries and 90 000 storage chambers·ha<sup>-1</sup> which occupy approximately 0.4% of the soil volume down to 20 cm deep (Darlington, 1982; Wood, 1988). At Lamto (Ivory Coast), Lepage (unpubl. data) estimated the volume of galleries and chambers created by fungus growing termites to be 0.37–0.59 m<sup>3</sup>·ha<sup>-1</sup>, and the volume of modified soil that surrounds these structures was 4.32 m<sup>3</sup>.

Termite structures, composed largely of soil, contain more organic C and N and have higher C/N ratios than adjacent soil. This may reflect an absence of nitrogen fixation in trophic groups utilizing highly decayed wood or soil organic matter. In grass- and wood-feeding forms where nest materials are composed of carton (a mixture of faeces and macerated wood fibre) and nitrogen fixation is more intensive, C/N ratios are typically in the range 20:1 to 100:1, but this may be less than the ratio in ingested food or unprocessed forage (Wood, 1988). In Macrotermitinae, faeces are used to construct fungus combs and are not incorporated into mound materials, which consequently contain less carbon and show C/N ratios more typical of their parent soils (Matsumoto, 1976; Wood & Sands, 1978; Lobry de Bruyn & Conacher, 1990; Wood, 1996).

The extensive subterranean networks of galleries and nest spaces produced by termites should have significant long-term effects on soil porosity, aeration, water-holding capacity and drainage, but there are few direct studies of these phenomena. Some investigations, notably those of Spears *et al.* (1975) and Whitford (1991), have compared the overall hydrological characteristics of soils in which natural termite populations are active with those of enclosures from which the insects were excluded by the liberal application of pesticide. The results showed significant (though not necessarily completely consistent) effects on rainfall runoff, rates of infiltration, total porosity, suspended sediment and total bedload. Remarkably, striking changes in the floristic character of termite-free plots were seen with time. In similar experiments where termites were excluded by physical rather than chemical means, Veeresh & Belavadi (1986) and Kalides & Veeresh (1990) showed that termite-free plots achieved higher soil organic carbon, nitrogen and plant biomass. More studies of this kind, perhaps using microcosm and mesocosm study systems, are urgently required.

The resulting effect of faunal activity depends on the total amount of structures thus created, their characteristics and persistence over time (*fig. 11*). Most studies have demonstrated that faunal activities tend to increase soil porosity and surface structures, such as earthworm casts, termite sheetings or ant excavation pellets (Lobry de Bruyn & Conacher, 1990; Elkins *et al.*, 1986).

These beneficial effects, however, often represent the result of two contrasting effects, *i.e.* compaction by invertebrates that accumulate large and compact aggregates, and decompaction by animals that break down these aggregates into smaller ones, by eating them and releasing small faecal pellets, or simply digging their way through these structures (Blanchart *et al.*, 1997). In soils with intense faunal activities, soil structures seem to have rather short life-spans since they are constantly built and destroyed by successions of invertebrates that ingest the soil. These structures, however, may be rather stable and persist for long periods if invertebrates are eliminated. In a sandy alfisol of a humid African savanna, Blanchart *et al.* (1989) showed that the solid macro-aggregate structure made by accumulated earthworm casts could persist months to years after earthworms had been eliminated. Persistence of aggregates seemed to be correlated with soil organic content. When small filiform earthworms (Eudrilidae) were added, they would break down these large aggregates into smaller ones in a few months. Similar processes have been described by Marinissen (1995) in polder soils of The Netherlands, although the lifetime of aggregates formed by Lumbricidae earthworms in this soil seemed to be limited to a few months.

Termites have attracted attention for their ability to move soil particles from one horizon to another during the construction of nests and galleries (either subterranean, epigeal or arboreal) and their subsequent erosion.








	FEEDING REGIME	STRUCTURES	EFFECTS ON BIODIVERSITY	EFFECTS ON FUNCTION
MICRO- PREDATORS	Microbial predators	none	- selection of microflora?	- enhanced mineralization
LITTER TRANSFORMERS	Saprophagous	 holorganic structures (Organic faecal pellets)	- selection of microflora  - microhabitats for smaller invertebrates  - food for other invertebrates	-Enhanced mineralization + -sequestration of organic matter (depending on time scale)
ECOSYSTEM ENGINEERS	Saprophagous + Geophagous  Macropredators	 Large compact structures (large compact casts, mounds)   smaller aggregates (small casts, surface deposits)   macropores (galleries, burrows, chambers)	-selection on litter transformers  - associated microfauna  - selection on microflora  - effects on root development	- Bioturbation  - Dissemination of spores (mycorrhizae, fungi)  - Regulation of structural porosity  - Water storage capacity  - Infiltration rates  - Aeration  - SOM dynamics at different scales of time  - Nutrient cycling (synchrony)  - Surface structures (runoff, infiltration etc.)  - Aggregation (compaction or decompaction)
ROOTS	Absorption of nutrients	  Rhizosphere structures	- production of polysaccharides  - selection on microflora  - associated food- webs  - root + root litter feeders	- Aggregation  - Plant production  - Overall biodiversity (through energy supply and diversity of primary food resources)

Figure 11. – Relationship among structures created by major functional groups of invertebrates and roots, the structures they produce in soil, biodiversity of smaller organisms affected by these structures and major soil processes (Lavelle, 1996).

Data summarized by Lee & Wood (1971), Wood & Sands (1978) and Lobry de Bruyn & Conacher (1990) suggest that between  $2 \times 10^3$  and  $2 \times 10^6$  kg of soil in each tropical hectare has been recently manipulated by termites (recently in the sense of within the life-span of colonies currently living). The manipulation is selective in that smaller particles, especially clay-sized subsoils, are often preferred for construction, and accompanied by the addition of organic material in the form of saliva and faeces, which are formed into an admixture with the mineral soil. Termite structures may persist for long periods, probably centuries, leaving deep micro-aggregated horizons in oxisols (Wielemaker, 1984; Eschenbrenner, 1988, 1994) and circular mounds of a few m in diameter and 20-50 cm high where large termitaria have disappeared.

These results lead to two important conclusions: i) invertebrates can make structures that may persist for variable time periods in the absence of the animals that have created them; and ii) when biodiversity is decreased, there is a risk that either 'compacting' or 'decompacting' species become overdominant with disastrous effects on soil physical properties. Examples of such processes are given in section 6.

#### 4.2. Decomposition and dynamics of soil organic matter

Decomposition is a cascade process whereby primary dead organic material experiences a succession of physical and chemical transformations in the soil leading to mineralization of part of the resource, and storage of resistant compounds as 'humus' (Swift *et al.*, 1979). Decomposition pathways and rates are determined by a hierarchical suite of factors that operate at nested scales of time and space (Lavelle *et al.*, 1993) in the following order: climate, soil characteristics (mainly the abundance and mineralogy of clay and nutrient status), quality of decomposing resources

(linked to plant communities and their production), currently living macro-organisms (including roots and invertebrates) and micro-organisms. Micro-organism enzymes catalyse most of the chemical transformations at rates that are primarily determined by temperature and moisture conditions. Their activity is also restrained by chemical and physical blockages. Excessive C/nutrient ratios, immobilization of nitrogen in phenol-protein complexes and physical protection of organic matter in aggregates of different sizes are major limitations.

Invertebrates affect decomposition directly through comminution and digestion and indirectly, by their effects on microbial activities. These effects may occur at different scales of time and space from the few mm<sup>3</sup> and hours of a gut transit, to m<sup>3</sup> and decades in soil profiles. Ecosystem engineers introduce dead plant material into their functional domain (*sensu* Anderson, 1993), the drilosphere of earthworms and the termitosphere of termites where decomposition will follow specific pathways, with generic effects of large functional groups (*e.g.* accumulation of litter as middens around the opening of anecic earthworm burrows and further ingestion and mixing to the soil and release in casts; transformation of litter into fungus combs in termitaria of fungus growing Macrotermiteinae). Comminution also occurs at the level of particle size fractions in soil organic matter. In a 7-year continuous maize crop at Yurimaguas (Peruvian Amazonia), for example, earthworm activities resulted in a significant decrease of the proportion of organic matter in coarse fractions, and an increase in fine fractions resulting from comminution and digestion (Charpentier, 1996). Similar effects had been observed by Martin (1991) when comparing soil before and after ingestion by the endogeic earthworm *Millsonia anomala*.

Effects of engineers on soil organic matter dynamics can therefore be considered at four different scales of time and space (*fig. 12*), encompassing: i) the transit of the intestine itself (hours); ii) the enhancement of

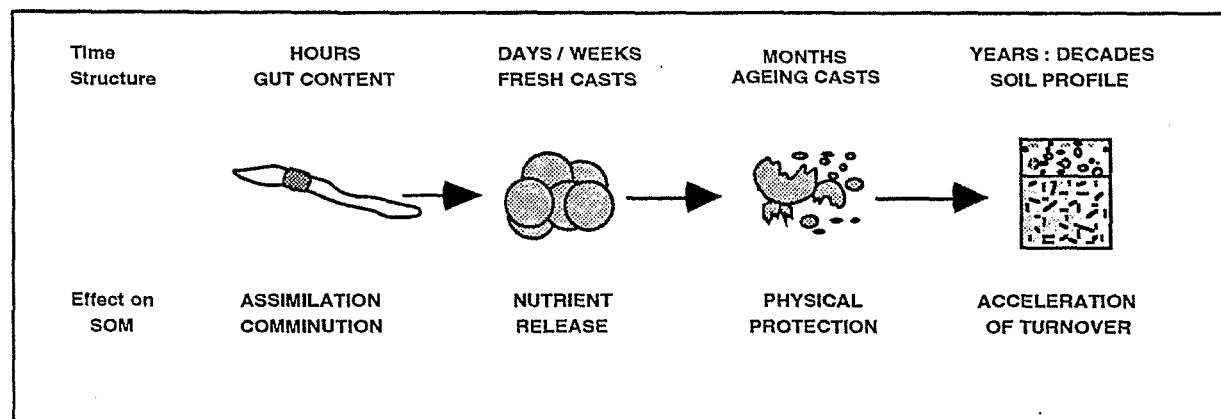


Figure 12. – Effects of earthworms on SOM (soil organic matter) dynamics at different scales of time and space (Lavelle, 1997).

microbial activity in, and the release of labile nutrients from, fresh faecal material (days); iii) the sequestration and protection of undegraded organic matter in ageing casts and constructions (weeks); and iv) the redistribution and turnover of soil organic matter in whole profiles (years to decades). The last three processes occur inside biogenic structures created by engineers; as a result, they largely depend on the size, composition and persistence of these structures.

#### 4.2.1. Ingestion rates and mineralization of C

Where abundant, anecic earthworms may incorporate the total annual litter production into the soil in as little as 2-3 months (Lee, 1985) and their activity seems to be limited by food availability rather than by the environmental determinants of their activity. In a microcosm experiment conducted at 12°C with a population of *Lumbricus terrestris* equivalent to ca. 800 kg fm-ha<sup>-1</sup>, 85% of litter deposited at the soil surface had disappeared in 3 months (Binet, 1993). In southern France, Bouché (1983b) estimated that earthworms had assimilated 30% of the carbon available in litter in 17 weeks. Such a figure is only acceptable if earthworms re-ingest the litter contained in their casts several times.

In the humid savannas of Ivory Coast, anecic earthworms annually incorporate the equivalent of 180 to 510 kg of dry litter to the soil in regularly burnt savannas. This represents ca. 30% of the weight of litter annually decomposed (*i.e.* mineralized or incorporated into the soil instead of being destroyed by fire), but less than 10% of the annual production. In unburnt savannas, ingestion increases up to 980 kg-ha<sup>-1</sup>, which represents 9% of the annual litter biomass decomposed (Lavelle, 1978).

Endogeic earthworms may annually ingest from several hundreds of Mg to more than 1 000 Mg dry soil-ha<sup>-1</sup> (Lavelle, 1978; Boström, 1988). In four arable soils with unfertilized and fertilized barley, grass and lucerne crops, respectively, annual cast production by *Aporrectodea caliginosa* was estimated to be between 36 and 108 Mg-ha<sup>-1</sup>, 20 to 50% of which was deposited at the soil surface. In humid tropical grasslands, endogeic earthworms may ingest daily 5-6 (*Pontoscolex corethrurus*) and up to 25-30 (*Millsonia anomala*) times their own weight of soil (Lavelle, 1975; Lavelle *et al.*, 1987). As a result, the overall annual cast production may commonly be as high as several hundreds, and up to a maximum of 1 250 Mg-ha<sup>-1</sup>. As indicated before, only a small proportion of these casts (5 to 20% depending on species) are deposited at the soil surface and subterranean casts form the component units of stable macro-aggregate structures.

Studies in a variety of savanna sites indicate that termites are directly responsible for up to 20% of total C mineralization. By comparison, the equivalent value for forests, where available, is 1-2% (Bignell *et al.*,

1997), despite the tendency for forest populations to have greater numerical and biomass densities, and reports that as much as 30% of leaf litter is consumed (Matsumoto & Abe, 1979; Collins, 1983). The latter estimate is, however, based on a semi-deciduous humid forest system in southern Cameroon where species of *Macrotermes* are very rare or absent. This is an important caveat, as Macrotermitinae consume 5-6 times more food than termites not associated with fungi, presumably to support the high metabolic rate of the fungus garden (Wood & Sands, 1978; Collins, 1981). In a Guinean savanna of Ivory Coast, with an overall termite biomass of 133.8 kg fm (46.4 dry weight), fungus growing Macrotermitinae yearly transform 1 300 to 1 500 kg dry litter-ha<sup>-1</sup> into fungus combs that are consumed after fungi have grown and transformed the material; xylophagous termites ingest 20-30 kg dry wood, foragers 50-100 kg grasses and humivorous, 45 t dry soil-ha<sup>-1</sup> (fig. 13) (Lepage, unpubl. data).

#### 4.2.2. Direct effect of digestion

As the gut environment stimulates the growth of micro-organisms and leads to the degradation of at least a portion of ingested organic matter in both earthworms and termites, there is an immediate and striking enhancement of mineralization associated with passage through the intestine resulting in the release of substantial amounts of CO<sub>2</sub> and CH<sub>4</sub>. While the efficiency of cellulose and hemicellulose digestion in termite guts is very high, approaching 90%, the extent of lignin breakdown is uncertain (Breznak & Brune, 1994). Butler & Buckerfield (1979) and Cookson (1988) have shown that <sup>14</sup>C labels incorporated into natural lignin or synthetic analogues can be recovered as <sup>14</sup>CO<sub>2</sub> after passage through the guts of wood-feeding termites (*Nasutitermes* spp.), but the rates of degradation do not seem very impressive when compared with the breakdown of cellulose (Slaytor *et al.*, 1997; Nunes *et al.*, 1997).

Rates of assimilation of organic matter by earthworms largely depends on the quality of the ingested material. Estimates vary, therefore, from 2.9, 3.3, and 10.5% for fine (0-20 µm) and coarse (> 250 µm) fractions of SOM (soil organic matter) and green leaves of the legume *Eriosema* sp., respectively, ingested by a geophagous tropical earthworm (*Millsonia anomala*, Martin & Lavelle, 1992), to 11.6-28.5% for a number of litter feeding Lumbricidae (Crossley *et al.*, 1971), and 30-75% for *Lumbricus rubellus* fed litter of different qualities (Dickschen & Topp, 1987; Daniel, 1991). Additional organic material is redistributed and chemically modified, largely as a consequence of gut transit and the subsequent incorporation of faeces into nest/mound materials and gallery linings (Wood, 1988, 1996; Lee & Foster, 1991).

The elevation of mineral-N (to as much as 900 mg·kg<sup>-1</sup>) and of extractable-P (to as much as

48 mg·kg<sup>-1</sup>) has been noted in fresh earthworm casts (Sharpley & Syers, 1977; Barois *et al.*, 1987; Lavelle *et al.*, 1992; Blair *et al.*, 1994), while similar effects (and of equal magnitude in soil-feeding species) have been observed in freshly constructed termite mound materials and walls of fungus garden chambers (Lee & Wood, 1971; Anderson & Wood, 1984; Wood, 1988; Abbadie & Lepage, 1989; Lobry de Bruyn & Conacher, 1990). Ca and K also seem to be generally elevated in termite mounds, as are exchangeable cations, but Wood (1988) cautions that some effects are due to particle selection during the ingestion of soil, which favours silt and clay fractions. In Macrotermitinae, the organic components of mound materials are derived from saliva, not faeces, and in consequence, there tends to be fewer differences from soil (Boyer 1973; Pomeroy, 1983; Wood, 1988). However, all termite constructions have a higher organic carbon content than their parent soils.

#### 4.2.3. Nutrient release and reorganization in faecal pellets

A decline of microbial activity in earthworm casts begins within days of deposition and seems to be correlated (under laboratory conditions) with the disappearance of labile nutrients (Lavelle *et al.*, 1989; Scheu & Wolters, 1991). Comparable studies in termites are lacking, but investigations of the faeces produced by the soil-feeding *Cubitermes fungifaber* using molecular probes specific to eubacterial rRNA have shown that both freshly repaired mound walls and soil immediately under active mounds are sites of more intensive bacterial metabolism and growth (Boulaud, Brauman & Bignell, unpubl.). Litter transformers (mainly large arthropods like Diplopoda, Isopoda or insects) may also greatly enhance mineralization at short scales of time and space, during gut passage and in the first few days following deposition of faecal pellets that serve as incubators for microbial activities (Anderson *et al.*, 1983; Hassal & Rushton, 1985). At larger time scales, there is some evidence that microbial activities decline in pellets and therefore, some protection of soil organic matter may occur (Hanlon & Anderson, 1980; Toutain *et al.*, 1982; Scheu & Wolters, 1991). Nonetheless, these structures being purely organic and prone to further ingestion by other invertebrates, it is unlikely that significant effects of these invertebrates operate at the larger scales of years to decades, as is the case for engineers.

#### 4.2.4. Protection in organo-mineral structures

Following the decline of labile nutrients, the more recalcitrant organic matter becomes integrated into the compact structures created by the engineer as organo-mineral micro-aggregates, where it is largely protected from decomposition as long as the structures are main-

tained (Garnier-Sillam, 1987; Garnier-Zarli & Harry, 1995).

The faeces of wood-feeding termites are characteristically enriched in lignin (Bracewell, Griffiths & Bignell, unpubl.), which presumably enhances the stability of faecal material incorporated into mounds or distributed throughout the soil. Glycoproteins secreted with the saliva of termites cement particles together (Wood, 1988). In compact earthworm casts, C mineralization is significantly lower than in the same soil sieved on a 2-mm size mesh (Martin, 1990).

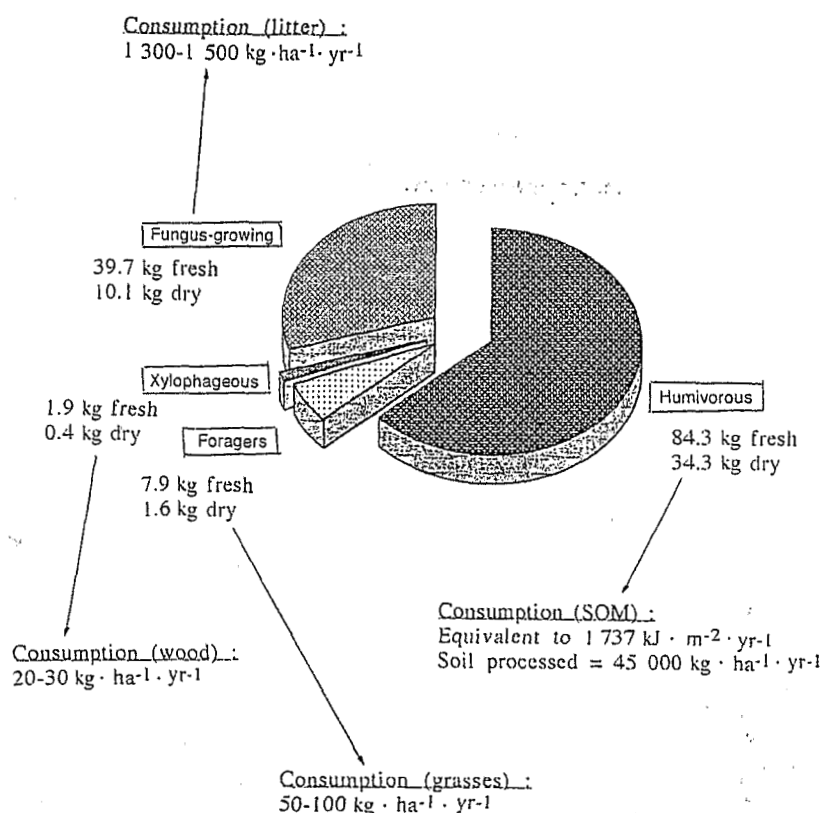
The life-span of engineer-generated structures, generally measured in months to years, depends on the care that organisms may dedicate to their maintenance (e.g. termite mounds, galleries), their initial stability (i.e. their texture and organic matter content), the extent to which further chemical humification of organic matter can occur and the occurrence of decomposing species that break down casts, galleries and mounds by re-ingesting the soil or digging holes through them (Garnier-Sillam, 1987; Marinissen, 1995; Blanchart *et al.*, 1997).

#### 4.2.5. Long-term effects on turnover and distribution

At the broadest scale, the long-term effects are measured over decades and centuries, and concern the turnovers of both mineral materials and organic matter in whole soil profiles. The constructions made by termites are quite variable (see Wood, 1996), but those incorporating significant amounts of faeces derived from ingested plant material will accentuate humification, as the lignin content will be high. In the longer term, it is clear that pedoturbation by termites has a significant effect in removing fine-grained material from deeper horizons. Soil worked by termites (and especially mound soil) generally has greater bulk density and aggregate stability than undisturbed soils, though the effects are temporary as mounds and surface galleries are eventually eroded (Lobry de Bruyn & Conacher, 1990).

Depending on soil type and other invertebrate communities, it would probably take several years before inherited structures broke down and protection of soil organic matter induced by the activities of engineers ceased. A simulation made by Martin & Parton (unpubl. data in Lavelle *et al.*, 1997) using the CENTURY model showed that removal of earthworms from tropical sandy alfisols, reducing subsequent aggregate formation, would result in a significant decrease of soil organic matter content after 3 decades, especially in the slow pool with an average turnover time of about 25 years. In another simulation, in which the short scale (digestion) effect of earthworms on decomposition was taken into account in a low input culture of Peruvian Amazonia, C stock first decreased more rapidly in the presence of earthworms (Lierman & Woormer, unpubl. data). The effect was reversed

Figure 13. – Distribution of termites among trophic groups and estimates of litter, wood, grass and soil organic matter consumption in a humid savanna (Lamto, Ivory Coast) (Lepage, unpubl. data).



after 12 years and C stock was 28% greater after 30 years in systems with earthworms. These simulations clearly point at the importance of endogeic earthworms in the chemical and physical protection of organic matter.

Field experiments have been conducted for periods of 3 to 7 years to assess the effect of introduced earthworm activities in tropical ecosystems (Charpentier, 1996; Gilot-Villeneuve *et al.*, 1996; Pashanasi *et al.*, 1996). Inoculation seems to produce an overall acceleration of the turnover of soil organic matter and a relative decrease of the overall stock present in soil. Protection of soil organic matter at this scale was only observed where soil macro-aggregates had been previously broken down by sieving. Charpentier (1996) has estimated that the carbon cost of introducing earthworm populations into a maize cropping system in Peruvian Amazonia was 0.5 t C · ha<sup>-1</sup> · yr<sup>-1</sup>, mainly taken from coarse fractions, although a compensating increase in crop production of about 50% was observed. Different effects are, therefore, observed over increasing scales of time and the overall effects of earthworms and termites over the longest periods of time are not clear. The possibility that engineers reduce soil organic matter in the short term, while retaining it in the long term, implies a subtlety of interactions which require further investigation.

#### 4.2.6. Effects on soil fertility and plant growth

Termites can enhance plant growth as well as impede it. Apart from species associated with mounds, Lee & Wood (1971) listed a number of generalized beneficial effects of termite activity, such as improvements in soil drainage, the accumulation of greater soil depth in very stony profiles, enhanced water retention due to the addition of clay brought from deeper horizons and increase in organo-mineral complexes and base status. However, investigations of the biomass of micro-organisms in a range of soil types in Australian semi-arid savannas showed a strong negative relationship with termite mound density, while particle-size distribution and available P were unaffected (Holt, 1996). One interpretation put forward by Holt is that in these ecosystems, seasonal drought is a more crucial factor than the activities of engineers in determining microbial biomass and processing capacity. Where inhibition is marked, termites can expand into the niche normally occupied by soil micro-organisms as more organic matter becomes available for foraging. If correct, this interaction would be of the opposite character to that generally expected between engineers and micro-organisms in soil.

Interestingly, mound soil itself contains an active microbial population (possibly stimulated by higher water availability or the enrichment of organic material

with nitrogen fixed by termite symbionts) responsible for as much as one-third of the total  $\text{CO}_2$  flux from the mounds (Holt, 1987; Holt, unpubl.).

Returns from mounds may have considerable local significance for soil fertility, most notably, the estimated 16% of soil inorganic nitrogen derived by leaching from mounds of *Amitermes laurensis* (Congdon *et al.*, 1993), although earlier estimates are lower (2% of all plant growth nutrients in topsoil: Wood & Sands, 1978). Generally, termite modified soils also have higher Ca, K, Mg and available P than adjacent soil and a higher total cation exchange capacity due to the addition of clay and organic matter (as faeces and saliva). Increases are usually modest, but soil-feeding termites with a high intestinal pH produce mound material in which available P is elevated four times over the parent soil (Anderson & Wood, 1984). The incorporation of faeces into soil generally lowers its pH. Estimates of the return of C and N to the soil from the decay of termite corpses and through predation are discussed at length by Wood & Sands (1978). Their conclusions were that inputs from these sources might exceed those from faeces in some ecosystems (for example Sahel and Southern Guinea savannas), but not in derived savannas.

Earthworm activities also influence plant growth. Over the last century, many researchers, mostly in the temperate zone, have described the effects of a few widespread Lumbricidae earthworm species on plant production (primarily in agricultural settings). They showed that earthworms generally exert beneficial effects on plant growth, although in a few cases, negative or null effects may be induced under particular situations (Edwards & Lofty, 1980; Lee, 1985; Edwards & Bohlen, 1996). Spectacular results have been observed when European Lumbricidae were introduced at the large scale of fields and pastures in New Zealand (Stockdill, 1982) and in Dutch polders (Hoogerkamp *et al.*, 1983).

Recently, experiments were undertaken in 6 tropical countries, involving 14 plant species, 6 great groups of soils, and at least 11 species of earthworms (Brown *et al.*, in press). Additional data were taken from the literature (Blakemore, 1995; Senapati *et al.*, in press) totalling over 240 data points on the percent increase in plant growth in the presence of over 30 earthworm species. The overall average increase obtained was  $\geq 63 \pm 11\%$  (SE), significant at  $P < 0.07$ , and the greatest increases were observed in soils with high sand content, poor in organic matter and with a moderately acid pH (fig. 14). Under the conditions of these experiments, effect on plant growth was proportional to the earthworm biomass (fig. 15); significant effects started to appear at biomass values  $> 30 \text{ g fm}$ . Grain production increased more than stover and root production. Not all earthworm species had the same impact, and not all plant species responded positively (fig. 16) (Brown *et al.*, in press).

### 4.3. Other invertebrate groups as soil engineers

Although we have stressed the overwhelming importance of earthworms and termites as the principal engineers in terrestrial soil ecosystems, other invertebrate groups in which individuals have comparable size and where populations can reach high biomass in special circumstances (e.g. where high acidity or waterlogging are incompatible with the viability of earthworms and termites) may assume equivalent although more lim-

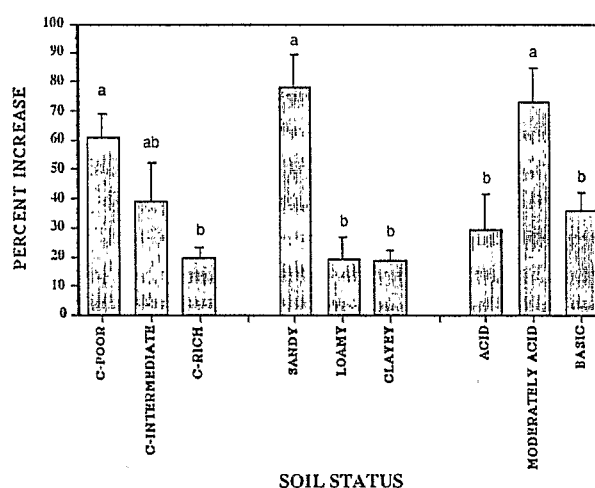


Figure 14. – Overall average % increase of tropical plant production due to earthworm activities in relation to soil texture, richness (% C content), and pH. Poor soils had  $< 1.5\%$  C; rich soils,  $> 3\%$  C; and intermediate soils,  $1.5 < \% \text{ C} < 3$ ; sandy soils had  $> 65\%$  sand and  $< 10\%$  clay; clayey soils had  $> 30\%$  clay; and intermediate soils include all other textures represented; acid soils had  $\text{pH} < 5.6$ ; basic soils,  $\text{pH} > 7.0$ ; moderately acid soils,  $5.6 < \text{pH} < 7.0$ . Different letters on bars within the figure indicate significant differences ( $P < 0.005$ ) (Brown *et al.*, in press).

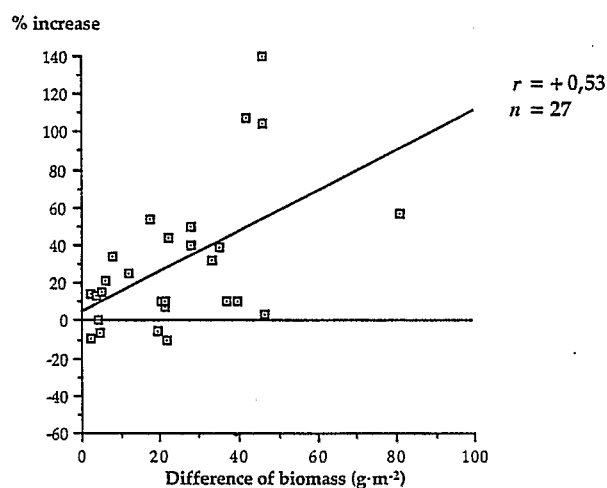


Figure 15. – Effect of biomass (difference between inoculated treatments and controls) of earthworms and % increase in grain yield in humid tropical low input cropping systems (Pashanasi *et al.*, 1996).



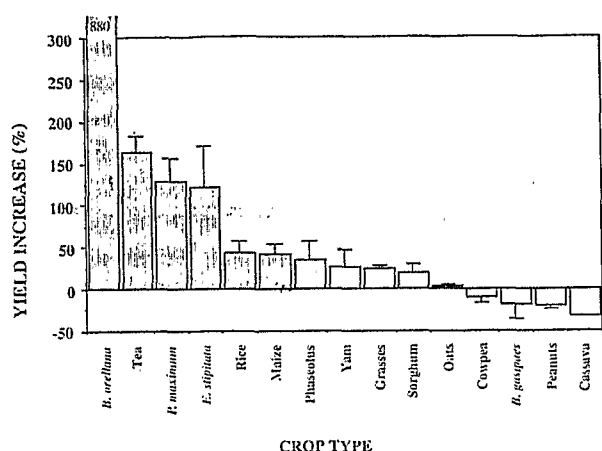


Figure 16. – Response of different plants to earthworm inoculation in the humid tropics (Brown *et al.*, in press).

ited roles (Wolters & Ekschmitt, 1997). This is the case for isopods or Coleoptera (Tenebrionidae) that achieve considerable pedoturbation in some desert ecosystems, gastropods that contribute to the formation of aggregates through production of mucoproteins in their slime and faeces, arthropods that break down organic acids produced in the litter thus impeding the destruction of clay by acid leachates, and various groups such as diplopods, centipedes, dipterous larvae and Enchytraeidae that alter soil physical properties by burrowing through the soil. Another example is represented by Tubificidae in wetland ricefields.

#### 4.3.1. Role and importance of Tubificidae in wetland ricefields

Tubificidae (Oligochaetes) are a key component of the soil fauna in wetland ricefields (about 130 million ha of land). Their ecology and roles in ricefields were reviewed by Roger (1996). Populations are contagiously distributed and positively correlated with total soil organic C; they increase after organic matter or N fertilizer application. These relationships are probably mediated through increased populations of bacterial decomposers and primary production in floodwater, which provide food for oligochaetes. Estimates of biomasses range from 0 to 630 kg fm<sup>-1</sup>·ha<sup>-1</sup>. Tubificidae are adapted to low O<sub>2</sub> concentrations and move back and forth between the reduced soil and the floodwater while displacing soil and water by their burrowing and passage through their gut.

This activity causes a vertical redistribution of soil particles, larger particles and plant residues being gradually concentrated in the lower soil layer and finer particles in the upper layer. This redistribution also explains the weeding effect of tubificids, which move seeds 3–5 cm under the soil surface into a zone where O<sub>2</sub> concentration is too low for their germination. The effects of oligochaetes in ricefields as summarized by

Roger (1996) include: i) stimulation of OM mineralization, ii) biostratification of the soil, iii) reduction of weed abundance, iv) destruction of the oxidized soil surface layer, v) enhancement of nutrient transfer across the soil-floodwater interface, vi) increased soil pH, vii) decreased soil oxidoreduction potential, viii) changes to soil microbial populations, ix) increased biotic and abiotic oxygen demand, x) provision of a food source for aquaculture species, and xi) enhancement of denitrification and nitrification in the soil. The major role of Tubificidae with regard to soil fertility is the translocation from the surface to the deeper soil layer of components of the photosynthetic aquatic biomass (cyano-bacteria, micro-algae and aquatic macrophytes) and its breakdown products accumulating in the detritus layer at the soil-water interface. This significantly contributes to the replenishment of the soil microbial biomass and the provision of nutrients to the rice plant.

A decrease of populations of aquatic oligochaetes by pesticide application will affect nutrient translocation and the biological activity in floodwater thus reducing soil fertility. Currently, only indirect evidence is available – showing that the nitrogen input from the photosynthetic aquatic biomass contributes about 20% to the replenishment of soil microbial biomass (Roger, 1996).

## 5. EFFECTS OF GLOBAL CHANGE ON ENGINEERS

Global change constitutes a series of linked anthropogenic perturbations to the biosphere of sufficient magnitude to impact natural biotic communities and ecological processes. Climate change (greenhouse forcing) and agricultural intensification (deforestation, soil erosion and nutrient depletion) are the most widely discussed of these trends, but pollution (especially increased nitrogen deposition from the atmosphere and the use of fertilizers and pesticides in arable farming) should also be considered with the same seriousness. Having outlined the status and roles of engineers in natural and semi-natural ecosystems, the remaining two sections of this article are devoted to a discussion of the likely effects of global change on earthworms and termites, and a prediction of the costs and benefits to the human economy which may result from modifications to the processes mediated by engineers. The main outcomes of global change in terrestrial ecosystems (integrating the effects of the main perturbations) are expected to be: i) a general decrease in the organic resources available for soil invertebrates, including soil organic matter; ii) the fragmentation of habitats with a consequent enhancement of short-scale successional events; iii) the modification of assemblage structure, with changes in the balance of functional groups and the replacement of some native species by exotics; iv)

the decrease of community biodiversity; and v) the reduction of the genetic diversity of populations.

### 5.1. Elevated CO<sub>2</sub> and climate change

In general, the soil fauna are adapted to life under high CO<sub>2</sub> conditions, with soil atmospheres frequently ranging between 0.3 to 3%, and reaching values as high as 5-10%. Insects living in warm, moist soil are adapted to concentrations of CO<sub>2</sub> up to 3-5% and some can even tolerate CO<sub>2</sub> levels above 35% (Vannier & Kilbertus, 1983). Within this context, it is clear that elevated CO<sub>2</sub> is unlikely to exert any direct effects on soil biological activity and that only effects mediated via changes in plants are likely to be of importance.

Elevated concentrations of CO<sub>2</sub> may affect soil faunal activity indirectly through changes in both litter amount and quality. Increased plant productivity under elevated CO<sub>2</sub> concentrations has been observed for a wide range of plant species and growth conditions. In a major synthesis of over 60 controlled CO<sub>2</sub>-exposure studies, Wullschlegel *et al.* (1995) reported a mean increase of 32% in growth response of a large number of species exposed to elevated CO<sub>2</sub> equally allocated to all plant organs. Thus, the amount of C and energy available to the soil faunal community will be greater under elevated CO<sub>2</sub>.

Plant material generated under elevated CO<sub>2</sub> has been shown to have decreased litter N concentrations with a resulting increase in C/N and lignin/N ratios, leading to a slow down in field litter decomposition rates and modifications in the distribution pattern of N within the plant, with greater proportions of N being translocated into metabolically active tissues (Norby *et al.*, 1986; O'Neill *et al.*, 1987; Barnes & Pfirrmann, 1992; Cotrufo & Ineson, 1996). CO<sub>2</sub> treatment does not appear to exert any effect on litter decay rates when there are no measurable changes in leaf chemical composition.

Increased concentrations of lignin and phenolics have been reported in plants exposed to high levels of atmospheric CO<sub>2</sub> (Melillo, 1983; Cipollini *et al.*, 1993; Cotrufo *et al.*, 1994) possibly due to a limitation of nutrient supply, rather than a direct effect of CO<sub>2</sub> enrichment (Lambers, 1993). Concentration of tannins also increases in plant tissue, with the extent of response being species-specific (Norby *et al.*, 1986; Lindroth *et al.*, 1993). Enriched CO<sub>2</sub> has also been associated with an increase in leaf thickness, due to an increased number of palisade cells (Vu *et al.*, 1989).

The few data available on changes in N concentration of leaf litters show contrasting results, with no effects being reported for oak (Norby *et al.*, 1986) and estuarine marsh plant (Curtis *et al.*, 1989) litters, whereas a significant decrease in N concentrations of leaf litter tissues exposed to enriched CO<sub>2</sub> atmosphere has been observed for other tree species (Couteaux *et al.*, 1991; Cotrufo *et al.*, 1994).

The effects of elevated CO<sub>2</sub> on nutrients other than N are somewhat more confused. There is evidence that P concentrations (unlike N) in plant tissue do not decline under elevated CO<sub>2</sub> levels (Oberbauer *et al.*, 1986; Owensby *et al.*, 1993), but decreases in P concentrations in plants grown under enriched CO<sub>2</sub> have been observed (Barnes & Pfirrmann, 1992; Woodin *et al.*, 1992). Tissue concentrations of K, Mg and Ca were found to be unaffected in seedlings of the tree *Maranthos corymbosa* grown in fertile soil and exposed to 700 ppm CO<sub>2</sub> when compared to control (350 ppm CO<sub>2</sub>) trees (Berryman *et al.*, 1993). In contrast, reduced K, Mg and Ca concentrations were observed for *Calluna vulgaris* (L.) plants raised in nutrient poor peat soil under elevated atmospheric CO<sub>2</sub> levels (Woodin *et al.*, 1992), but no significant changes in P, K, Ca or Mg concentrations were reported for tree leaf litters generated under elevated CO<sub>2</sub> atmosphere when compared to control litters (Cotrufo *et al.*, 1994).

From the observations reported above, there is ample evidence that enhanced CO<sub>2</sub> levels may induce changes in chemical composition and quality of plant tissues, but the direction and magnitude of the effects are highly species-specific and dependent on other environmental factors, such as soil nutrient status, and plant growth conditions. Since resource quality can have a major effect on the palatability of litter to the soil macrofauna, these reported reductions in leaf quality found under elevated CO<sub>2</sub> are likely to increase litter consumption rates by earthworms (see Martin & Lavelle, 1992), although opposite results have been proposed by Bocock (1963) for Glomeridae. The effects on consumption by termites are less easy to predict, as many species have the capacity to fix nitrogen, but the energy cost of this process together with a shortage of other nutrients might be expected to reduce production, while consumption remains unchanged. Cotrufo (unpubl.) has compared the palatability of ash and sycamore leaves grown under ambient and elevated CO<sub>2</sub>, with the conclusion that significantly less (-16%) litter material was consumed when derived from elevated CO<sub>2</sub>.

Elevated CO<sub>2</sub> can exert effects, via the plant, on soil physical properties yet the impacts are extremely difficult to quantify and predict. Increases in plant productivity may potentially result in lower soil temperature and moisture through interception by a larger canopy, but stomatal responses tend to raise soil moisture contents. However, soils cropped with cotton under ambient and elevated (550 ppm) CO<sub>2</sub> concentrations did not differ in these properties, with no significant differences in soil water content, pH and bulk density, being observed between CO<sub>2</sub> treatments (Rogers *et al.*, 1992).

#### 5.1.1. Temperature and moisture regimes

Increases in temperature are likely to accelerate microbial activities and, therefore, enhance digestion

processes developed by microflora in engineer's guts. When temperature is reduced from 27 to 15°C, the stimulation of microbial respiratory activity in the gut contents of the endogeic earthworm *Pontoscolex corethrurus* was reduced to only twice the control value and earthworms failed to grow (Barois, 1987). This may explain why earthworms from temperate or cold soils more commonly ingest organic materials of higher quality, and the proportion of endogeic species found in assemblages is lower (Lavelle, 1983; Lavelle *et al.*, 1994b) (fig. 9). Evidence that more mucus is secreted into the intestine (relative to the dry weight of soil ingested) in temperate and tropical peregrine species (exotic invaders following anthropogenic disturbance) than in African native soil-feeding species, is presented by Lavelle *et al.* (1994b). Therefore, increases in temperature are likely to modify the functional structure of earthworm communities, with a relative increase of endogeic populations and activity developed deeper into the soil profile.

In termites, the question of the effects of temperature on the mutualistic digestive system has to be approached indirectly since termites are naturally restricted to tropical and subtropical biomes where anthropogenic greenhouse effects may be less marked and also since their social organization, combined with complex nest and gallery architecture, gives them the ability to regulate the core temperatures of colonies (Grassé, 1984). The temperature dependences of key physiological processes in termites are largely uninvestigated, but some evidence exists that physiological processes such as fluid secretion and CO<sub>2</sub> production are optimal in the range 28–30°C (Littlewood & Bignell, unpubl. observations; Lo, unpubl. observations). The termite hindgut is in essence a continuous culture chemostat supplying key intermediary metabolites (Bignell, 1994), which may not function efficiently enough below 26°C to meet host requirements. Such a dependence on symbiont support may explain the remarkable latitudinal restrictions of termites.

The supply of water and ambient humidity appear to be more important determinants of abundance and biomass, and these are ultimately determined by overall climatic patterns, including temperature regimes. This is particularly important for soil-feeding forms (in fact the majority of genera), in which resistance to desiccation is relatively poor and where many colonies appear to have a relatively ephemeral existence and lack behavioural mechanisms for the conservation or sequestration of water.

## 5.2. Land uses and agricultural intensification

Disturbances linked to land use practices seem to severely affect species richness and abundance of soil invertebrate communities world-wide. This effect may however be less marked in northern temperate areas that have been recolonized by aggressive colonists

adapted to disturbances after the recession of continental glaciers (table 2).

### 5.2.1. Effects on species richness

The nature of the original ecosystem greatly influences the effect of land use practices. Conversion of savannas into pastures generally maintains a large part of the original earthworm community, with some changes induced by grazing. At Carimagua (eastern plains of Colombia), for example, conversion of the savanna into an improved pasture with African grasses and herbaceous legumes increased the abundance and biomass of native earthworm communities and maintained a large proportion of native species of macro-invertebrates (49 'morphotypes' out of 57) (Decaëns *et al.*, 1994). Of the 8 earthworm species recorded in the original savanna, 7 were maintained in improved pastures and the overall earthworm biomass was increased 5-fold. Exotic species present in the area did not invade the pastures.

In contrast, in a pasture derived from the forest at Manaus, species richness of macro-invertebrate communities had decreased from 151 to 48 sp., and only 22 species of the original communities had resisted the change. Native earthworm communities have disappeared and the exotic species *Pontoscolex corethrurus* had occupied the empty niche building large populations. The dominance of this species and depletion of invertebrates with a decompacting effect on soil resulted in a significant degradation of the soil physical structure (Barros *et al.*, 1996).

Exotic and native earthworm species have rather different adaptive strategies. Exotics often have higher demographic performances than natives, although size is always the most important determinant irrespective of the origin of species (Barois *et al.*, in press). Most exotics have a small to medium size and their populations turn over faster than populations of large species that always have restricted geographical distributions. They have much broader ranges of tolerance for the most important parameters of the edaphic environment, and a large number of them are parthenogenetic which facilitates the settlement of populations. These species with some exceptions, do not invade natural ecosystems where native species tend to be more competitive. However, they are often better adapted to the strong disturbances that go along with human activities and tend to replace native species following the spread of anthropic transformations.

### 5.2.2. Abundance and structure of communities

Seventy three macro-invertebrate communities from 29 different sites have been subjected to a principal component analysis to identify the major trends of composition and the relative effect of vegetation type, biogeography and land use practices (Lavelle *et al.*,

Table 2. – Effect of expected changes in climate and soil conditions on ecosystem engineer communities, and associated costs.

	ELEVATED CO <sub>2</sub>	LAND USE (INTENSIFICATION)	CLIMATE (temp. increase + rain uncertainty)	POLLUTION (increased N deposition)	MONETARY VALUE	COMMENTS
POPULATIONS						
EARTHWORMS	Resource Q change	<ul style="list-style-type: none"> <li>– Loss of diversity</li> <li>– Invasion of exotics</li> <li>– Loss of litter feeders</li> <li>– Modification of termite/earthworm ratio</li> </ul>	<ul style="list-style-type: none"> <li>– Promotes soil feeders</li> <li>– Invasion of exotics</li> </ul>	<ul style="list-style-type: none"> <li>– Resource quality change promotes acid tolerant spp.</li> </ul>	<ul style="list-style-type: none"> <li>– cost of re-inoculation</li> </ul>	<ul style="list-style-type: none"> <li>– sandy, medium acid soils most vulnerable</li> <li>– accidental introductions with parasites and/or predators will increase</li> </ul>
TERMITES		<ul style="list-style-type: none"> <li>– Loss of diversity</li> <li>– Loss of soilfeeders</li> <li>– Concentration of biomass in few spp.</li> </ul>	<ul style="list-style-type: none"> <li>– reduce soil feeders</li> <li>– Extend latitudinal altitudinal ranges</li> <li>– Increase fungus-growers in Africa (deep nesting)</li> </ul>	<ul style="list-style-type: none"> <li>– Resource quality change</li> </ul>	<ul style="list-style-type: none"> <li>– uncertain</li> </ul>	<ul style="list-style-type: none"> <li>– subsistence agriculture most affected by termite changes</li> </ul>
FUNCTIONS						
STRUCTURES	Increased stratification	<ul style="list-style-type: none"> <li>– Risk of compaction</li> <li>– Adverse hydrology</li> </ul>	<ul style="list-style-type: none"> <li>– disturbance of aggregation</li> <li>– increase of heterogeneity</li> </ul>	<ul style="list-style-type: none"> <li>– increased stratification</li> </ul>	<ul style="list-style-type: none"> <li>– cost of restoration</li> </ul>	<ul style="list-style-type: none"> <li>– small scale technologies based on management of earthworm activities available for tropics</li> <li>– intensive plantation systems, e.g. tea have highest benefit from restoration</li> </ul>
ORGANIC CARBON	More C accumulated	<ul style="list-style-type: none"> <li>– More C lost</li> </ul>	<ul style="list-style-type: none"> <li>– more C lost or uncertain</li> </ul>	<ul style="list-style-type: none"> <li>– more C accumulated</li> </ul>	<ul style="list-style-type: none"> <li>– cost of carbon trading</li> </ul>	<ul style="list-style-type: none"> <li>– sandy soils most sensitive to engineers</li> <li>– wetlands most critical globally</li> </ul>
LIMITING NUTRIENTS FOR PRODUCTION	Increased N stress	<ul style="list-style-type: none"> <li>– decreased reliance on engineers</li> </ul>	<ul style="list-style-type: none"> <li>– sequestration and storage in pockets</li> </ul>	<ul style="list-style-type: none"> <li>– decreased reliance on engineers</li> </ul>	<ul style="list-style-type: none"> <li>– cost of fertilization</li> </ul>	<ul style="list-style-type: none"> <li>– Tree crops more responsive than herbs and shrubs.</li> <li>– legumes least responsive</li> </ul>
PLANT PRODUCTION	Long term nutrient stress	<ul style="list-style-type: none"> <li>– decreased resilience (short-term increase in prod.)</li> </ul>	<ul style="list-style-type: none"> <li>– latitude dependent</li> </ul>	<ul style="list-style-type: none"> <li>– nutrient imbalances</li> </ul>	<ul style="list-style-type: none"> <li>– cost of intensification</li> </ul>	<ul style="list-style-type: none"> <li>– tropical systems most vulnerable</li> <li>– mid-latitude systems may benefit</li> </ul>

1994b) (fig. 17). A major outcome of this analysis has been the identification of three major groups, *i.e.* termites, earthworms and litter arthropods, that tend to react separately within ecosystem types and land use practices. Termites and/or earthworms are dominant in most cases. Termites are important components of many African and Australian soils, possibly less so in Central/South America, due in part to limitations of their functional diversity. In South America for example, the fungus growing termites do not occur. Another important characteristic of termites is that they have adapted to a wide range of semi-arid systems where earthworms are not found. Earthworms are best represented in grasslands situated in humid areas; their abundance decreases towards both forested and dry areas. At a finer scale of resolution, they are sensitive to the nutrient status and organic contents of soil (Fragoso & Lavelle, 1992). Litter arthropods seem to be predominant in ecosystems where sufficient litter is available as a consequence of low termite and earthworm activities. They are mainly represented by milli-

pedes or coleopterans which, in some areas may account for the dominant proportion of the biomass as in the case of millipedes in the miombo woodlands, of Zimbabwe (Dangerfield, 1990) and coleopteran larvae in Mexican tropical pastures (Villalobos & Lavelle, 1990). In such ecosystems, mesofaunal communities may also have higher densities than in those systems dominated by earthworms and termites where their abundance is very low (Adis, 1988). Ants are not characteristic of any particular system since they may be abundant in most soils.

Annual crops on land recently cleared of natural vegetation always have highly depleted macro-invertebrate communities. They have the lowest biomass (5.1 g fm<sup>-2</sup> on average) and a highly depleted diversity. Earthworms and litter arthropod populations soon disappear as native species seldom withstand major disturbances, and they are not replaced by adaptable exotic species. Some groups of termites (mainly humivorous) tend to resist better and they comprise a

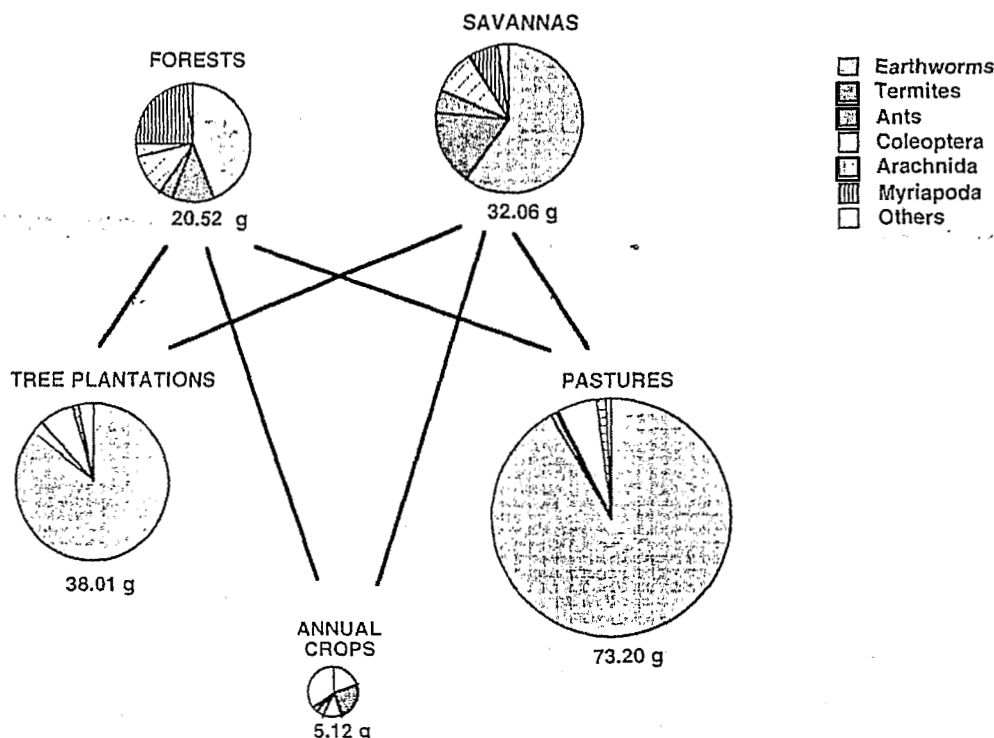


Figure 17. – Effect of different types of land use on the abundance and composition of soil macro-invertebrate communities (Lavelle *et al.*, 1994b).

significant proportion of the overall biomass. Cultivation of soils often results in a significant decrease of organic matter contents. This is especially true in annual cropping systems, and less so in tree plantations, agroforestry and pasture systems that may even enhance organic contents in some occasions. In humid tropical soils, decrease in organic stocks, especially of the coarse organic fraction ( $>50$  mm) has been directly linked to the depletion of earthworm communities in annual crops (rice and maize) (Gilot, 1994). Plant communities that do not produce enough residues at the soil surface (leaf litter) and in the soil (root litter) cannot sustain communities at sufficient levels of abundance to enhance their production. In a natural humid savanna at Lamto (Ivory Coast), an earthworm community with a mean biomass of  $40 \text{ g fm}^{-2}$  mineralizes each year  $1.4 \text{ t}$  organic matter. On average, the cost of having active earthworm populations may be of the order of  $1 \text{ t C}$  in assimilable forms, mainly as coarse fractions. Since one early sign of degradation of organic stocks is the decrease of SOM in coarse fraction, this explains the general depletion of earthworm communities in annual cropping systems.

Pastures are functionally similar to savannas. They are highly favourable to earthworm development when they have been established in forest areas with high annual rainfall, provided adaptable species are present. This is actually the case in many sites where peregrine species with a pantropical distribution (mainly *Pon-*

*toscolex corethrurus* and *Polypheretima elongata*) establish a biomass of several hundreds to  $4\,000 \text{ kg fm}^{-2}$  (e.g. see Barois *et al.*, 1988; Lavelle & Pashanasi, 1989). Interestingly, sugar cane plantations show similar patterns with earthworm biomasses of respectively  $33$  and  $53 \text{ g m}^{-2}$  in two sites in tropical Mexico and Guadeloupe, respectively (Barois *et al.*, 1988; Fragoso *et al.*, unpubl.). This indicates that these plantations have characteristics similar to those of humid grasslands.

Tree plantations such as palm-trees with herbaceous legume cover, or cocoa with a litter layer at the soil surface and a stratum of high trees, usually have numerous and diverse communities. They retain components of the original fauna because part of the original species are still present as the overall structure is close to that of a degraded forest. Nonetheless, the disturbance and/or the establishment of an herbaceous stratum provide niches that allow some exotic species to colonize it. This is particularly the case for earthworms which may build up sizeable populations. As a result, tree plantations have an average biomass of  $38 \text{ g fm}^{-2}$  which is higher than that found in both natural forests ( $20.5 \text{ g m}^{-2}$ ) and savannas ( $32.1 \text{ g m}^{-2}$ ).

The maala system investigated in Congo is an interesting exception to the general patterns observed elsewhere in the tropics (MBoukou, 1997). It is actually the only annual cropping system that enhances earthworm communities. Annual crops are grown on

mounds in which grass had been previously buried and slowly burnt up inside the mound. This practice keeps ashes and a significant proportion of carbon in the soil, with positive effects on earthworm abundance. As observed in *table 3*, earthworm density decreased from 79 to 18 m<sup>-2</sup> in the slash-and-burn system. In the maalas, earthworm density increased more than 5-fold and biomass reached 160 g·m<sup>-2</sup> during the first year. Endogeics and anecics were more stimulated than epigeics. Earthworm abundance decreased during the second and third year, but still remained higher than in the savanna. Termite abundance was highly decreased in all systems, although the maala system seemed to be less detrimental than slash-and-burn.

Termite abundance, biomass and species richness are generally greatly reduced when a forest is cleared (Collins, 1980; Wood *et al.*, 1982; Eggleton *et al.*, 1995, 1996), although in some cases the evidence is equivocal, possibly the consequence of edge effects, biogeographical factors and the tendency of many investigations to be made in areas where forest and savanna are contiguous (see Eggleton & Bignell, 1995). Less extreme disturbances such as foraging, hunting, selective logging, conversion to tree plantation and even small-scale subsistence agriculture and agroforestry produce much smaller effects on abundance and biomass (and in some cases no effects), but there is a turnover of species, with a tendency for wood-feeding forms to replace soil-feeders, reflecting the greater availability of lying dead wood for colonization and consumption (Eggleton *et al.*, 1995, 1996). Shifts in functional groups are also seen in savanna assemblages as the climate becomes more arid. In Africa and Asia, this often takes the form of the deletion of humivorous forms and their replacement by fungus-growers, mostly grass-foragers and litter-feeding species adapted to periods of drought (Lepage, unpubl. data).

Cultivation and the application of nematicides and fungicides generally have highly negative effects on earthworm abundances. On the other hand, most herbi-

cides have no significantly harmful effects and cattle grazing in pastures has positive effects (Edwards & Lofty, 1982; House & Parmelee, 1985; Lee, 1985; Mac Kay & Kladivko, 1985; Lavelle & Pashanasi, 1989; Haines & Uren, 1990; Parmelee *et al.*, 1990; Yule *et al.*, 1991).

### 5.2.3. Modification of termite-earthworm relationships

In tropical soils where termites and earthworms co-exist, there seems to exist an inverse relationship between abundances of both groups (Fragoso & Lavelle, 1992). Such an inverse relationship has been observed in such diverse situations as tea plantations in India (Senapati *et al.*, 1994), natural savannas and pastures submitted to fire and different grazing intensities in the oriental Llanos of Colombia (Decaëns *et al.*, 1994), and savannas and soils submitted to different cultivation practices in Congo (Mboukou, 1997). In Guinean savannas at Lamto (Ivory Coast), Kouassi (1987) observed opposite peaks of seasonal abundance of earthworms and termites, with a dominance of termites during the dry season, and earthworms during the wet season. The relative abundance of termites is also said to increase when grazing is absent or where trampling and erosion are severe, leading to the conclusion that termites contribute to problems of denudation. However, such changes may be more apparent than real, as termites which forage on the surface of the ground can become more abundant without any change in overall consumption rates (Wood, 1996). The removal of organic residues and natural mulches which follows cultivation and conversion to permanent arable-use selects residual species which can resist desiccation by deep nesting and feed directly on crop plants (Wood & Cowie, 1988; Wood, 1996). Hence, termite activity may become highly apparent although overall biomass and abundance decline. The difference

**Table 3.** – Earthworm and termite abundance in different land use systems of the Niari region (Congo) (nos are in m<sup>-2</sup> and SE in brackets) (Mboukou, 1997).

	Savanna	Slash and burn	Maalas 1st year	Maalas 2nd year	Maalas 3rd year
Epigeic earthworms	18 (6)	5 (0.42)	31 (9)	37 (17)	16 (5.3)
Anecic earthworms	0	0	33 (12)	11 (4.3)	0
Endogeic earthworms	61 (19)	13 (2)	363 (139)	146 (30)	138 (4)
Total m <sup>-2</sup>	79 (25)	18 (2.42)	427 (160)	194 (51.3)	154 (9.3)
Termites	2 026 (*)	282	690	243 (*)	400

\* not available.



between termites and mammals is that the latter can migrate if organic resources become scarce; termites lack this option and manage, at least for some time, by extending their feeding to include all plant residues and even living roots, as well as making use of food stores, a common adaptation of savanna forms (Lepage, 1981). The existence of large epigeal mounds and deep subterranean nests also assists the resilience of termites under drought stress or food depletion.

#### 5.2.4. Invasion by exotics

Some five centuries ago, the world-wide development of transfers of cultivated plants and other resources began, and a progressive extension of cultivated area followed the demographic revolution. These events have widened the distribution of invertebrate species that used to be highly limited in natural conditions. Changes in ecosystems linked to human activities are by far the prevailing change that occurs at present. Climatic changes, especially of temperature regimes, will also affect decomposition processes and ecosystem engineer communities, but direct effects may not be conspicuous for a long time. The composition and diversity of communities is fundamentally modified by human practices. Furthermore, the detailed spatial and temporal dynamics of invertebrate populations that goes along with successional processes in ecosystems may be profoundly affected.

Peregrine species of earthworms have been introduced in many countries several centuries ago. These earthworms clearly have adaptive strategies of aggressive colonists that have allowed them to invade most temperate areas of other continents. Spectacular cases of invasions include such examples as the ongoing progression of *Dendrobaena octaedra* in forest areas of southern Alberta in Canada (Scheu & Mc Lean, 1993), the progressive invasion of Possession Island by *Dendrobaena rubida tenuis* (Frenot, 1985), or the displacement of giant native species of Australia and South Africa by introduced Lumbricidae species (Ljungström, 1972; Abbott, 1985).

Peregrine termite species with wide geographical distribution do not exist. There is a consistent order in the observed distribution patterns of most termite genera (Pearce & Waite, 1994), which enables centres of endemism to be identified with little uncertainty. This general pattern seems to result from the uniformity of feeding habits within taxa, the weakness of the flight of reproductives that ensures dispersal and the requirement for subsequent pairing before the foundation of new colonies and general bradytelic evolution.

Unlike earthworms that are always considered beneficial, sometimes in exaggerated fashion, termites may cause severe problems as pests in cropping systems. Wood (1996) has noted that termites do not fit into the classic pest category of 'introduced species'. Forms that become harmful to crops (arable or timber) are

invariably already present in the environment and elevation to pest status normally results from reductions in the availability of food as long as the species concerned is able to withstand physical stresses (e.g. greater diurnal temperature fluctuations and periodic drought) associated with the conversion of land to arable use. The biology and population dynamics of termites attacking crops is now well documented, especially in Africa (Sen-Sarma, 1986; Black & Wood, 1989; Cowie & Wood, 1989; Wood & Pearce, 1991; Mill, 1992). A very wide range of crops are at risk, including cereals (especially maize), groundnuts, dryland rice, cotton, yam, cassava, tea, cocoa, coconut, sugarcane, coffee, rubber and fruit. Seedlings of fast-growing exotic tree species, including softwoods, are also highly vulnerable and termites may, therefore, impact timber plantations or agroforestry schemes adversely. Impacts of termites on rangelands have been reported (e.g. Watson & Cay, 1970; Roonwal, 1979; Collins, 1982) but it is unclear whether there is a direct competition with grazing livestock, even where stocking levels are beyond carrying capacity.

The common features of such termite attacks are that damage is more likely in dry periods rather than in periods of regular rainfall, in plants under stress rather than in vigorous stands, to exotic rather than indigenous varieties and species, in monocultures rather than mixed cropping systems, and where termite assemblage composition is simplified by the reduction of mulching or litter inputs.

## 6. CONSEQUENCES FOR ECOSYSTEMS AND ECONOMIC IMPLICATIONS

Communities of ecosystem engineers generally have relatively low species richness. The more diverse termite communities have 20 to 60 species (occasionally more) and earthworm communities 5 to 18 species. As a result, loss of species may have dramatic effects on the overall function of these invertebrates. Since invertebrates make structures that may persist over time, when biodiversity is decreased, there is a risk that either 'compacting' or 'decompacting' species become overdominant with adverse effects on soil physical properties.

### 6.1. Diversity of communities and soil structure

This point has been illustrated in a traditional rotation in Peruvian Amazonia in which all invertebrates had been eliminated: the introduction of *Pontoscolex corethrurus* resulted in significant soil compaction. Bulk density was increased and water infiltration rate decreased (Alegre *et al.*, 1996). Earthworms created a strongly aggregated structure made of casts that are round shaped dense aggregates. They highly influenced the abundance and composition of porosity by

creating a compact layer in the upper 4 cm of soil due to a significant decrease of micropores and disaggregation and coalescing of casts with low structural stability that worms egest at the soil surface (Duboisset, 1995). Overall porosity decreased from 30-50% in the upper 2 cm of soil to 10-20% in inoculated treatments, mainly due to a drastic reduction of macropore (surface  $> 18 \mu\text{m}^2$ ) abundance. In treatments with organic inputs (crop residues + legume green manure), casts were more stable and they resisted disaggregation. The overall porosity was maintained in the upper 2 cm of soil and slightly increased at 3 cm depth (Duboisset, 1995).

A similar process has been observed in pastures close to Manaus with even more severe consequences for soil physical structure, water dynamics and, ultimately, for plant growth (Chauvel *et al.*, unpubl. data). In this case, the dramatic decrease of biodiversity and virtual disappearance of decomposing species (ants, some termites and arthropods) was a primary factor of the degradation of pastures. Conversion of the primary forest into pastures destroyed a large proportion of native soil invertebrates (table 4). This was especially the case for groups like ants and Coleoptera that break down large aggregates in soil and deposit small soil granules at the surface and thus, have a decomposing effect. The niches thus left vacant were massively filled by a population of the robust exotic earthworm *Pontoscolex corethrurus* that built up populations of up to 600 ind. $\text{m}^{-2}$ . This species compacted the soil by accumulating casts with low intermediate porosity (pores  $10^2$  to  $10^4$  nm in diameter) in the upper 20 cm of the soil (Fontaine, 1994). In the latosol that is naturally prone to compaction, macroporosity was reduced to retraction fissures and cracks, and structure was continuous and massive. This situation probably resulted from the coalescing of numerous casts of *P. corethrurus*: during the rainy season, a large amount of casts with a high water content and a muddy structure mixed together form a continuous layer 2-5 cm thick at the soil surface. When dry, this layer forms a compact

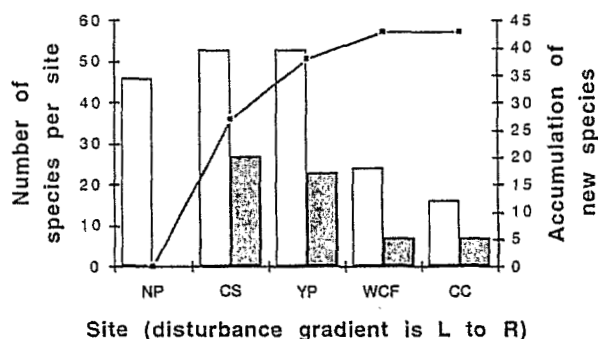
crust with virtually no porosity  $> 0.1 \mu\text{m}$ , low water retention and retraction. Below this crust, soil is saturated and an-aerobic conditions discourage growth of roots and stolons. This state, however, is reversible if climatic conditions allow a slow remoistening of the crust and growth of stolons that break down the crust (Chauvel, Grimaldi & Sarrazin, unpubl. data).

The losses of termite species diversity during the disturbance of tropical forest and its conversion to temporary or permanent arable use have recently been documented (e.g. Collins, 1980; Wood *et al.*, 1982; De Souza & Brown, 1994; Eggleton *et al.*, 1995, 1996). At light to moderate levels of disturbance, species turnover is a more obvious consequence than changes to abundance or biomass, but heavy disturbance reduces species diversity and abundance sharply (fig. 18). Therefore, termites are not critically limited by tree species number or type. Rather, given a suitable microclimate, adequate food and a more or less closed canopy, termites are resilient to quite severe perturbation, for example so-called 'low impact' logging or the conversion of primary or old growth secondary forest to timber plantation or agroforestry schemes. However, it is clear that this resilience is not simply due to the maintenance of the original forest assemblage, but is accompanied by large changes in the relative abundances of trophic groups, as wood-feeding species take advantage of the greater quantities of litter made available by disturbance. Soil-feeders are particularly strongly affected by the perturbation of forests, so the mixing of mineral and organic material which is characteristic of their activities is presumably reduced. Preliminary data show that abundances of soil-feeding species (which do not appear to fix atmospheric  $\text{N}_2$ ) are correlated with available N, but this requires confirmation. De Souza & Brown (1994) showed that fragments of forest in Amazonia surrounded by cleared

**Table 4.** – Effect of conversion of a primary forest to pasture at Manaus (Central Amazonia) and Carimagua (Eastern Llanos of Colombia) on community structure and species richness of macrofauna communities (Decaëns *et al.*, 1994; Barros *et al.*, 1996).

Biome	Manaus (Amazonia)		Carimagua (Llanos)	
Land use	Forest	Pasture	Natural savanna	Improved pastures
Total density ( $\text{m}^{-2}$ )			2 830	1 540-2 270
Total biomass ( $\text{g fm}^{-2}$ )	53.3	51.9	15.3	28.8-62.5
Earthworm biomass	44.5	44	4.8	23-51
Total sp n°	151	48	31-57	42-55
% sp in common		15		54

\* this category includes grazed natural savannas



**Figure 18.** – Species richness and turnover (from qualitative 100 m transects) along a forest disturbance gradient in the Mbalmayo Forest Reserve, southern Cameroon. White bars show the total number of species sampled at each site; black bars, the number of species sampled not found in the next least disturbed site (i.e. the site one place to the left). The superimposed line shows the total accumulation of new species (not already sampled in less disturbed sites) along the gradient. NP, near primary forest; OS, old growth secondary forest (40 years); YP, young forest plantation (5 years); WCF, weeded manually cleared forest; CC, complete clearance by bulldozer.

areas have termite assemblages that appear to be dependent on the spatial patchiness of the original forest, *i.e.* the fragmentation process has an inherent stochastic component which is superimposed on more general relationships with soil chemistry and the availability of woody substrates. Where savanna species are available locally, cleared forest plots are rapidly colonized by these forms and an apparently higher biodiversity of termites results than from the clearance of deep-forest sites (Wood *et al.*, 1982; Eggleton *et al.*, 1996). However, the generalization that the new assemblages are dominated by wood-feeding species still holds, with the additional feature that these species may show greater tolerance to physical stresses.

## 6.2. Management of engineers to sustain fertility and assist in land restoration

Earthworm communities may be manipulated to improve soil fertility or allow restoration of degraded soils. Peregrine species that have a high potential to adapt to disturbances are most likely to be used. A catalogue of species with potential for manipulation in tropical soils has been proposed (Fragoso *et al.*, in press). Techniques that use low-quality organic wastes (sawdust, tea prunings, coffee husks, etc.) and these worms are proposed to enhance tree growth and improve soil conditions in old plantations (tea), to stimulate mycorrhizal infection and growth of tree seedlings in nurseries, as are new techniques for peri-urban horticultural production that associate earthworms and organic wastes of different qualities (sawdust, chicken slurry, coffee husks, etc.) (Senapati *et al.*, in press). In India, for example, significant increases in production and profitability have been obtained with a technique that associates the use of low (tea prunings) and high (cowdung) quality organic inputs, in a specific spatiotemporal array, and inoculation of an active endogeic peregrine earthworm species (Senapati *et al.*, in press). Direct manipulation of termite activities has never been proposed, except for their elimination when they become pests in cropping systems.

Indirect manipulations may also develop through the management of landscape in time and space, so as to maintain refuges for useful macro-invertebrate species and/or have fields that provide suitable conditions for invertebrates and serve as reservoirs for colonization of adjacent plots.

Such technologies will probably develop rapidly and become a current option in soil management once the idea that engineers are a resource that needs to be used is widely accepted.

Part of these species, however, may become aggressive colonists and cause problems of compaction. Management options will, therefore, include some controls on the abundance of these species, and maintenance of other invertebrates with opposite effects on soil structure.

## 6.3. Economic implications

Earthworms, and soil fauna in general, may be considered a resource that should be better managed, especially in low input agricultural systems. Techniques that associate the use of soil fauna and low quality organic wastes are being developed (Senapati *et al.*, in press). This resource has a cost that has been evaluated in a few cases: massive production of endogeic earthworms *Pontoscolex corethrurus* for inoculation costs ca. 4 US\$·kg<sup>-1</sup> whereas collection from adjacent fields raises the cost to 6-18 US\$·kg<sup>-1</sup> depending on local conditions. On the basis of these evaluations, the cost of an earthworm community of 400 kg fm·ha<sup>-1</sup> may be estimated at a minimum value of 1 600 US\$. This estimate does not take into account the value of diversity and the difficulty in rearing native species instead of robust easy-to-handle exotics. Restoration of earthworm communities costs more than simply inoculating worms; they need suitable trophic and microclimatic conditions to survive and grow.

## 7. CONCLUSIONS

1. **Large engineers** have a key role in structuring the soil and modifying the soil environment, thereby influencing microbial and other soil processes.

2. **Earthworms and termites** are the major taxonomic groups which function as macro-engineers across a wide range of tropical and temperate biomes. Earthworms particularly influence crumb structure, particle aggregation and porosity within the **soil profile**, resulting in horizontal (vertical) mixing (homogenization), mainly in the upper 20 cm. In contrast, termites tend to increase lateral **patch scale heterogeneity** with long-term consequences for vegetation and pedogenesis, as well as promoting stabilization of organic matter. **Absence of macro-engineers** (in cold, acid, waterlogged environments) results in strong profile differentiation, except where cryoturbation replaces the role of engineers.

3. **Other large engineers** (isopods, diplopods, and diptera larvae) function mainly in organic matter comminution and smaller scale aggregate (faecal) formation. In wetlands, **tubificids** play a significant role by redistributing vertically soil particle and translocating OM and increasing nutrient transfer between soil and water. **Burrowing vertebrates** have a similar role to macro-engineers in both vertical and horizontal pattern development in many biomes.

4. The influence of earthworms and termites on **microbial processes** is through intimate mutualistic/symbiotic relationships within the gut, or within termittaria (fungus garden) and through less intimate but microscale substrate concentration or environmental modification in the 'drilosphere' and 'termittosphere'. The consequence is micro/mesoscale enhancement of CH<sub>4</sub> and N<sub>2</sub>O fluxes, and general enhancement of CO<sub>2</sub>

emission. The consequence of earthworm and termite activity on **physical properties**, mainly particle aggregation, are increased water-holding capacity and nutrient storage.

5. **Diversity of engineer communities** is important to the function of the ecosystem since different functional groups may have different impact on soil processes. Differences in the nature of **biogenic structures** produced may actually differently affect processes such as the dynamics and location of organic matter, water infiltration and retention.

6. **Intensification of land management**, particularly physical disturbances, reduces anecic earthworms and mound-forming termites, but has less effect on endogeic earthworms and subterranean termites. Return following reduction in management intensity (e.g. abandonment/fallow) is a medium-term/decadal process, but can be more rapid when patch size is a hectare or less.

7. **Effect of climate change** will be less than those of land use change and will mainly be indirect through change in vegetation productivity and litter quality. Migration of both earthworms (except peregrine species) and termites is of the order of metres per year and is an order of magnitude slower than the expected redistribution of plant species and assemblages. Physical barriers and soil discontinuities will significantly retard migrations of large engineers. Thus without human action/intervention, soil development-profile formation, crumb structure and fertility will be slower than expected on purely climatic criteria.

8. The **loss of earthworms** through intensive land management or other factors will result in increased costs of re-inoculation (as in New Zealand), land restoration, carbon trading, fertilization and management intensification. **Termite loss** will particularly affect subsistence agriculture in the tropics.

## REFERENCES

- Abbadie L. & Lepage M. (1989). – The role of subterranean fungus comb chambers (Isoptera, Macrotermitinae) in soil nitrogen cycling in a preforest savanna (Ivory Coast). *Soil Biol. Biochem.*, **21**, 1067-1071.
- Abbott I. (1985). – Distribution of introduced earthworms in the northern Jarrah forest in western Australia. *Aust. J. Soil Res.*, **23**, 263-270.
- Abo-Khatwa N. (1978). – Cellulase of fungus-growing termites: a new hypotheses on its origin. *Experimentia*, **34**, 559-560.
- Adis J. (1988). – On the abundance and density of terrestrial arthropods in Central Amazonian dryland forests. *J. Trop. Ecol.*, **4**, 19-24.
- Alegre J., Pashanasi B. & Lavelle P. (1996). – Dynamics of soil physical properties in a low input agricultural system inoculated with the earthworm *Pontoscolex corethrurus* in Peruvian Amazonia. *Soil Sci. Soc. Am. J.*, **60**, 1522-1529.
- Anderson J.M. (1993). – Soil organisms as engineers: micro-site modulation of macroscale processes. In: Jones C.G. & Lawton J.H. (Eds.). *Linking Species and Ecosystems*. New York: Chapman & Hall, pp. 94-106.
- Anderson J.M. & Wood T.G. (1984). – Mound composition and soil modification by two soil-feeding termites (Termitinae, Termitidae) in a riparian Nigerian forest. *Pedobiologia*, **26**, 77-82.
- Anderson J.M., Ineson P. & Huish S.A. (1983). – The effects of animal feeding activities on element release from deciduous forest litter and soil organic matter. In: Lebrun H.M.A.Ph., De Medts A., Grégoire-Wibo C. & Wauthy G. (Eds.). *New Trends in Soil Biology*. Louvain-la-Neuve: Dieu-Brichart, pp. 87-100.
- Anklin-Mühlemann R., Bignell D.E., Veivers P.C., Leuthold R.H. & Slaytor M. (1995). – Morphological, microbiological and biochemical studies of the gut flora in the fungus-growing termites *Macrotermes subhyalinus*. *J. Insect Physiol.*, **41**, 929-940.
- Badertscher S., Gerber C. & Leuthold R.H. (1983). – Polyethism in food supply and processing in termite colonies of *Macrotermes subhyalinus* (Isoptera). *Behav. Ecol. Sociobiol.*, **12**, 115-119.
- Barnes I. & Pfirrmann T. (1992). – The influence of CO<sub>2</sub> and O<sub>3</sub>, singly and in combination, on gas exchange, growth and nutrient status of radish (*Raphanus sativus*). *New Phytol.*, **121**, 403-412.
- Barois I. (1987). – Interactions entre les vers de terre (oligochaeta) tropicaux géophages et la microflore pour l'exploitation de la matière organique du sol. Thèse. Université Paris VI, France.
- Barois I. & Lavelle P. (1986). – Changes in respiration rate and some physicochemical properties of tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.*, **18**, 539-541.
- Barois I., Verdier B., Kaiser P., Mariotti A., Rangel P. & Lavelle P. (1987). – Influence of the tropical earthworm *Pontoscolex corethrurus* (Glossoscolecidae) on the fixation and mineralization of nitrogen. In: Bonvicini A.M. & Omodeo P. (Eds.). *On Earthworms*. Bologna, Italy: Mucchi, pp. 151-158.
- Barois I., Cadet P., Albrecht A. & Lavelle P. (1988). – Systèmes de culture et faune des sols. Quelques données. In: Feller C. (Ed.). *Fertilité des sols dans les agricultures paysannes caribéennes. Effets des restitutions organiques*. Orstom-Martinique, pp. 85-96.
- Barois I., Lavelle P., Brossard M., Tondoh J.E., Martinez M.A., Rossi J.P., Senapati B.K., Angeles A., Fragoso C., Jimenez J.J., Decaëns T., Lattaud C., Kanyonyo K., Kajondo J., Blanchart E., Chapuis L., Brown G. & Moreno A. (in press). – Ecology of species with large environmental tolerance and/or extended distributions. In: Lavelle P., Brussaard L. & Hendrix P. (Eds.). *The potential for management of earthworm activities in tropical agrosystems*. Wallingford, UK: CAB-I, pp. 38-60.
- Barros M.E., Blanchart E., Neves A., Desjardins T., Chauvel A. & Lavelle P. (1996). – Relação entre a Macrofauna e a agregação do solo em tres sistemas na Amazonia central. In: *Solo/Suelo, XII Congresso Latino Americano de ciencia do solo*. Aguas de Lindoia, S P, Brazil, 4-8 August 1996.
- Bernier N. & Ponge J.F. (1994). – Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. *Soil Biol. Biochem.*, **26**, 183-220.
- Berryman C.A., Eamus D. & Duff G.A. (1993). – Influence of CO<sub>2</sub> enrichment on growth, nutrient content and bio-



- mass allocation of *Maranthes corymbosa*. *Aust. J. Bot.*, **41**, 195-209.
- Bignell D.E. (1984). – Direct potentiometric determination of redox potentials of the gut contents in the termites *Zootermopsis nevadensis* and *Cubitermes severus* and in three other arthropods. *J. Insect Physiol.*, **30**, 169-174.
- Bignell D.E. (1994). – Soil-feeding and gut morphology in higher termites. In: Hunt J.H. & Nalepa C. (Eds.). *Nourishment and Evolution in Insect Societies*. Boulder: Westview Press, pp 131-158.
- Bignell D.E., Oskarsson H. & Anderson J.M. (1979). – Association of actinomycete-like bacteria with soil feeding termites (Termitidae: Termitinae). *Appl. Environ. Microbiol.*, **37**, 339-342.
- Bignell D.E., Anderson J.M. & Croose R. (1991). – Isolation of facultatively aerobic actinomycetes from the gut, parent soil and mound materials of the termites *Proculitermes aburiensis* and *Cubitermes severus*. *Microbiol. Ecol.*, **85**, 151-160.
- Bignell D.E., Slaytor M., Veivers P.C., Muhlemann R. & Leuthold R.H. (1994). – Functions of symbiotic fungus gardens in higher termites of the genus *Macrotermes*: evidence against the acquired enzyme hypothesis. *Acta Microbiol. Immunol. Hung.*, **41**, 391-401.
- Bignell D.E., Eggleton P., Nunes L. & Thomas K.L. (1997). – Termites as mediators of carbon fluxes in tropical forests: budgets for carbon dioxide and methane emissions. In: Watt A.D., Stork N.E. & Hunter M. (Eds.). *Forests and Insects*. London: Chapman and Hall.
- Binet F. (1993). – Dynamique des peuplements et fonctions des lombriciens en sols cultivés tempérés. Doctorat. Université de Rennes I, France.
- Black H.I.J. & Wood T.G. (1989). – The effects of cultivation on the vertical distribution of *Microtermes* spp. (Isoptera: Termitidae, Macrotermitinae) in soil at Mokwa, Nigeria. *Sociobiology*, **15**, 133-138.
- Blair J.M., Parmelee R.W. & Lavelle P. (1994). – Influences of earthworms on biogeochemistry in North American ecosystems. In: Hendrix P.H. (Ed.). *Earthworm Ecology in forest, rangeland and crop ecosystems in North America*. Chelsea, MI: Lewis Pub., pp.127-158.
- Blakemore J. (1995). – Improving productivity of brigalow soils through the introduction of earthworms. PhD thesis. Brisbane, Queensland, Australia.
- Blanchart E., Lavelle P. & Spain A.V. (1989). – Effects of two species of tropical earthworms (Oligochaeta: Eudrilidae) on the size distribution of aggregates in an African Soil. *Rev. Écol. Biol. Sol*, **26**, 417-425.
- Blanchart E., Bruand A. & Lavelle P. (1993). – The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savanna soils (Ivory Coast). *Geoderma*, **56**, 119-132.
- Blanchart E., Lavelle P., Braudeau E., Le Bissonais Y. & Valentin C. (1997). – Regulation of soil structure by geophagous earthworm activities in humid savannas of Ivory Coast. *Soil Biol. Biochem.*, **29**, 431-439.
- Bocock K.L. (1963). – The digestion and assimilation of food by Glomeris. In: Doeksen J. & Van der Drift J. (Eds.). *Soil Organisms*. Amsterdam: North Holland, pp. 86-91.
- Boettcher S.E. & Kalisz P.J. (1991). – Single-tree influence on earthworms in forest soils in eastern Kentucky. *Soil Sci. Soc. Am. J.*, **55**, 862-865.
- Boström U. (1988). – Ecology of earthworms in arable land. Population dynamics and activity in four cropping systems. Doctorate thesis. Uppsala.
- Bouché M.B. (1983a). – The establishment of earthworm communities. In: Satchell J.E. (Ed.). *Earthworm Ecology: from Darwin to Vermiculture*. London: Chapman and Hall, chap. 38, pp. 431-448.
- Bouché M.B. (1983b). – Ecophysiologie des lombriciens : acquis récents et perspectives. In: Lebrun H.M.A.Ph., De Medts A., Grégoire-Wibo C. & Wauthy G. (Eds.). *New Trends in Soil Biology*. Louvain-la-Neuve: Dieu-Brichart, pp. 321-333.
- Boyer P. (1973). – Quelques aspects de l'action des termites sur les argiles. *Clay Mineral.*, **17**, 453-462.
- Breznak J.A. (1984). – Biochemical aspects of symbiosis between termites and their intestinal microbiota. In: Anderson J.M. et al. (Eds.). *Invertebrate-microbial interactions*. Cambridge: Cambridge University Press, pp. 173-204.
- Breznak J.A. & Brune A. (1994). – Role of microorganisms in the digestion of lignocellulose by termites. *Annu. Rev. Entomol.*, **39**, 453-487.
- Breznak J.A., Brill W.J., Martins J.W. & Cattel H.C. (1973). – Nitrogen fixation in termites. *Nature*, **244**, 577-580.
- Brown G.G., Pashanasi B., Gilot-Villenave C., Patron J.C., Senapati B.K., Giri S., Barois I. & Blakemore R.J. (in press). – Effects of earthworms on plant growth. In: Lavelle P., Brussaard L. & Hendrix P. (Eds.). *The potential for management of earthworm activities in tropical agroecosystems*. Wallingford, UK: CAB-I.
- Brune A., Miambi E. & Breznak J.A. (1995). – Roles of oxygen and the intestinal microflora in the metabolism of lignin-derived phenylpropanoids and other monoaromatic compounds by termites. *Appl. Environ. Microbiol.*, **61**, 2688-2695.
- Brusewitz G. (1959). – Untersuchungen über den Einfluss des Regenwurms auf Zahl, Art und Leistungen von Mikroorganismen in Boden. *Arch. Mikrobiol.*, **33**, 52-82.
- Butler J.H.A. & Buckerfield J.C. (1979). – Digestion of lignin by termites. *Soil Biol. Biochem.*, **11**, 507-513.
- Charpentier F. (1996). – Effets de l'inoculation d'un ver de terre endogée sur la dynamique de la matière organique d'un sol ferrallitique cultivé de l'Amazonie Péruvienne. Thèse Doctorat. Université Pierre et Marie Curie, Paris VI, France.
- Cipollini M.L., Drake B.G. & Whigham D. (1993). – Effects of elevated CO<sub>2</sub> on growth and carbon/nutrient balance in the deciduous woody shrub *Lindera benzoin* (L.) Blume (Lauraceae). *Oecologia*, **96**, 339-346.
- Coaton W.G.H. & Sheasby J.L. (1972). – Preliminary report on a survey of the termites (Isoptera) of south west Africa. *Cimbebasia*, **2**, 1-130.
- Collins N.M. (1980). – The effect of logging on termite (Isoptera) diversity and decomposition processes in lowland Dipterocarp forests. In: Furtado J.I. (Ed.). *Tropical Ecology and Development*. Kuala Lumpur, Malaysia, pp. 113-121.
- Collins N.M. (1981). – The role of termites in the decomposition of wood and leaf litter in southern Guinea savanna of Nigeria. *Oecologia*, **51**, 389-399.
- Collins N.M. (1982). The interaction and impact of domestic stock and termites in a Kenya Rangeland. In: Breed M.D.,

- Michener C.D. & Evans H.E. (Eds.). *Biology of Social Insects*. Boulder, Colorado: Westview Press, pp. 80-84.
- Collins N.M. (1983). – Termite populations and their role in litter removal in Malaysian rainforests. In: Sutton S.L. et al. (Eds.). *Tropical Rainforests: Ecology and Management*. Oxford: Blackwell.
- Congdon R.A., Holt J.A. & Hicks W.S. (1993). – The role of mound-building termites in the nitrogen economy of semi-arid ecosystems. *Proceedings of the 6th Australian Grassland Invertebrates Conference*, Hamilton, New Zealand.
- Cooke A. (1983). – The effect of fungi on food selection by *Lumbricus terrestris* L. In: Satchell J.E. (Ed.). *Earthworm Ecology*. London: Chapman and Hall, pp. 365-373.
- Cooke A. & Luxton M. (1980). – Effect of microbes on food selection by *Lumbricus terrestris*. *Rev. Écol. Biol. Sol*, **17**, 365-370.
- Cookson L.J. (1988). – The site and mechanism of  $^{14}\text{C}$ -lignin degradation by *Nasutitermes exitiosus*. *J. Insect Physiol.*, **34**, 409-414.
- Cotrufo M.F. & Ineson P. (1996). – Elevated  $\text{CO}_2$  reduces field decomposition rates of *Betula pendula* Roth. leaf litter. *Oecologia*, **106**, 525-530.
- Cotrufo M.F., Ineson P. & Rowland A.P. (1994). – Decomposition of tree leaf litters grown under elevated  $\text{CO}_2$ : Effect of litter quality. *Plant Soil*, **163**, 121-130.
- Cotton D.C.F. & Curry J.P. (1980). – The effects of cattle and pig slurry fertilizers on earthworms (Oligochaeta, Lumbricidae) in grassland managed for silage production. *Pedobiologia*, **20**, 189-196.
- Coûteaux M.M., Mousseau M., Célérier M.L. & Bottner P. (1991). – Increased atmospheric  $\text{CO}_2$  and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos*, **61**, 54-64.
- Cowie R.H. & Wood T.G. (1989). – Damage to crops, forestry and rangeland by fungus-growing termites (Termitidae: Macrotermitidae) in Ethiopia. *Sociobiology*, **15**, 139-153.
- Crossley D.A.J., Reichle D.E. & Edwards C.A. (1971). – Intake and turnover of radioactive cesium by earthworms (Lumbricidae). *Pedobiologia*, **11**, 71-76.
- Curtis P.S., Drake B.G., Leadley P.W., Arp W.J. & Whigham D.F. (1989). – Growth and senescence in plant communities exposed to elevated  $\text{CO}_2$  concentrations on an estuarine marsh. *Oecologia*, **78**, 20-26.
- Dangerfield J.M. (1990). – Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats. *Pedobiologia*, **34**, 141-150.
- Daniel O. (1991). – Leaf-litter consumption and assimilation by juveniles of *Lumbricus terrestris* L. (Oligochaeta, Lumbricidae) under different environmental conditions. *Biol. Fert. Soils*, **12**, 202-208.
- Daniel O. & Anderson J.M. (1992). – Microbial biomass and activity in contrasting soil materials after passage through the gut of the earthworm *Lumbricus rubellus* Hoffmeister. *Soil Biol. Biochem.*, **24**, 465-470.
- Darlington J.P.E.C. (1982). – The underground passages and storage pits used in Kajiado, Kenya. *J. Zool. (London)*, **198**, 237-247.
- Darlington J.P.E.C. (1994). – Nutrition and evolution in fungus-growing termites. In: Hunt J.H. & Nalepa C.A. (Eds.). *Nourishment and Evolution in Insect Societies*. Boulder, Colorado: Westview Press, pp. 105-130.
- Decaëns T., Lavelle P., Jimenez Jaen J.J., Escobar G. & Rippstein G. (1994). – Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. *Eur. J. Soil Biol.*, **30**, 157-168.
- Delecour F. (1980). – Essai de classification pratique des humus. *Pedologie*, **30**, 225-241.
- De Ruiter P.C., Van Veen J.A., Moore J.C., Brussaard L. & Hunt H.W. (1993). – Calculation of nitrogen mineralization in soil food webs. *Plant Soil*, **157**, 263-273.
- De Souza Ô.F.F. & Brown V.K. (1994). – Effets of habitat fragmentation on Amazonia termite communities. *J. Trop. Ecol.*, **10**, 197-206.
- Dickschen F. & Topp W. (1987). – Feeding activities and assimilation efficiencies of *Lumbricus rubellus* (Lumbricidae) on a plant-only diet. *Pedobiologia*, **30**, 31-37.
- Dubois A. (1995). – Caractérisation et quantification par analyse d'image des modifications structurales engendrées par *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta) sur un sol ferrallitique cultivé (Pérou). DEA Pédologie. Université Nancy I.
- Edwards C.A. & Bohlen P.J. (1996). – *Biology and Ecology of Earthworms*. 3rd ed. London: Chapman and Hall.
- Edwards C.A. & Lofty J.R. (1980). – Effects of earthworm inoculation upon the root growth of direct drilled cereals. *J. Appl. Ecol.*, **17**, 533-543.
- Edwards C.A. & Lofty J.R. (1982). – Nitrogenous fertilizers and earthworm populations in agricultural soils. *Soil Biol. Biochem.*, **14**, 515-521.
- Eggleton P. & Bignell D.E. (1995). – Monitoring the response of tropical insects to changes in the environment: troubles with termites. In: Harrington R. & Stork N.E. (Eds.). *Insects in a Changing Environment*. London: Academic press, pp. 434-497.
- Eggleton P., Williams P.H. & Gaston K.J. (1994). – Explaining global termite diversity. Productivity or history? *Biodivers. Conserv.*, **3**, 318-330.
- Eggleton P., Bignell D.E., Sands W.A., Waite B., Wood T.G. & Lawton J.H. (1995). – The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. *J. Trop. Ecol.*, **11**, 85-98.
- Eggleton P., Bignell D.E., Wood T.G., Sands W.A., Mawdsley N., Lawton J.H. & Bignell N.C. (1996). – The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, Southern Cameroon. *Philos. Trans. R. Soc. B*, **351**, 51-68.
- Elkins N.Z., Sabol G.Z., Ward T.J. & Whitford W.G. (1986). – The influence of subterranean termites on the hydrological characteristics of a Chihuahuan desert ecosystem. *Oecologia*, **68**, 521-528.
- Eschenbrenner V. (1988). – Les glébules des sols de Côte d'Ivoire. Nature et origine en milieu ferrallitique modalités de leur concentration. Rôle des termites. Tomes 1 et 2. Thèse. Paris: Orstom.
- Eschenbrenner V. (1994). – The influence of fungus-cultivating ants (Hymenoptera, Formicidae, Attini) on the morphology of Andosols in Martinique. In: Ringrose-Voase A.J. & Humphreys G.S. (Eds.). *Soil Micromorphology: Studies in Management and Genesis*. Amsterdam: Elsevier, pp. 405-410.
- Folgarait P. (in press). – Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.*



- Fontaine V. (1994). – Rôle des macroinvertébrés dans la structuration de sols dégradés d'Amazonie. Mem. DEA. Paris XII.
- Fragoso C. & Lavelle P. (1992). – Earthworm communities of tropical rainforests. *Soil Biol. Biochem.*, **24**, 1397-1408.
- Fragoso C., Moreno A., Kanyonyo ka Kajondo J. & Rodriguez C. (in press). – A survey of tropical earthworms: Taxonomy, biogeography and environmental plasticity. In: Lavelle P., Brussaard L. & Hendrix P. (Eds.). *The potential for management of earthworm activities in tropical agroecosystems*. Wallingford, UK: CAB-I, pp. 4-18.
- Frenot Y. (1985). – Étude de l'introduction accidentelle de *Dendrobaena rubida tenuis* (oligochaeta, lumbricidae) à l'île de la Possession. *Bull. Écol.*, **16**, 47-53.
- Garay I. (1980). – Relations entre la dynamique des humus forestiers et la structure des peuplements de Microarthropodes. Thèse 3<sup>e</sup> cycle. Paris VI.
- Garnier-Sillam E. (1987). – Biologie et rôle des termites dans les processus d'humification des sols forestiers tropicaux du Congo. Thèse Doctorat. Université Paris XII.
- Garnier-Zarli E. & Harry M. (1995). – Distribution of humic compounds in mounds of some soil-feeding termite species of tropical rainforests: Its influence on soil structure stability. *Insectes Soc.*, **42**, 167-185.
- Gautier-Hion A. (1989). – Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, **70**, 1826-1833.
- Giller P.S. (1984). – *Community Structure and the Niche*. London: Chapman and Hall.
- Gilot C. (1994). – Effets de l'introduction du ver géophage tropical *Millsonia anomala* Omodeo en systèmes cultivés sur les caractéristiques des sols et la production végétale en moyenne Côte d'Ivoire. Thèse INAPG.
- Gilot C., Lavelle P., Blanchart E., Keli J., Kouassi Ph. & Guillaume G. (1995). – Biological activity of soils in Hevea stands of different ages in Ivory Coast. *Acta Zool. Fennica*, **196**, 186-190.
- Gilot-Villenave C., Lavelle P. & Ganry F. (1996). – Effects of a tropical geophagous earthworm, *Millsonia anomala*, on some soil characteristics, on maize-residue decomposition and on maize production in Ivory Coast. *Appl. Soil Ecol.*, **4**, 201-211.
- Grandval A. (1993). – Mise en évidence d'une structure spatiale du système de décomposition en relation avec la qualité de la litière en forêt Guyanaise. Mémoire DEA d'écologie. Paris VI.
- Grassé P.P. (1984). – *Termitologia*. tome II: Fondation des Sociétés - Construction. Paris: Masson.
- Haines P.J. & Uren N.C. (1990). – Effects of conservation tillage farming on soil microbial biomass, organic matter and earthworm populations, in North-Eastern Victoria. *Aust. J. Exp. Agr.*, **30**, 365-371.
- Hanlon R.D.G. & Anderson J.M. (1980). – Influence of Macroarthropod feeding activities on microflora in decomposing oak leaves. *Soil Biol. Biochem.*, **12**, 255-261.
- Harris W.W.V. (1971). – Termites nest recognition and control. 2nd ed. London: Longman.
- Hassall M. & Rushton S.P. (1985). – The adaptive significance of coprophagous behaviour in the terrestrial isopod *Porcellio scaber*. *Pedobiologia*, **28**, 169-175.
- Holt J.A. (1987). – Carbon mineralization in semi-arid Northeastern Australia: the role of termites. *J. Trop. Ecol.*, **3**, 255-263.
- Holt J.A. (1996). – Mound-building termites and soil microbial biomass. An interaction influencing termite abundance. *Insectes Soc.*, **43**, 427-434.
- Hoogerkamp M., Rogaar H. & Eijssackers H.J.P. (1983). – Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. In: Satchell J.E. (Ed.). *Earthworm Ecology: from Darwin to Vermiculture*. London, New York: Chapman and Hall, pp. 85-105.
- House G.J. & Parmelee R.W. (1985). – Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. *Soil Till. Res.*, **5**, 351-360.
- Hunt H.W., Coleman D.C., Ingham E.R., Ingham R.E., Elliott E.T., Moore J.C., Rose S.L., Reid C.P.P. & Morley C.R. (1987). – The detrital foodweb in a shortgrass prairie. *Biol. Fertil. Soil*, **3**, 57.
- Ingham E.R. & Thies W.G. (1996). – Responses of soil food-web organisms in the first year following clearcutting and application of chloropicrin to control laminated root rot. *Appl. Soil Ecol.*, **3**, 35-47.
- Jones C.G., Lawton J.H. & Shachak M. (1994). – Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.
- Kalides P. & Veeresh G.K. (1990). – Effect of termite foraging on soil fertility. In: Veeresh G.K., Mallik B. & Viraktamath C.A. (Eds.). *Social Insects and the Environment*. New Delhi: Oxford and IBH, pp. 608-609.
- Kouassi P.K. (1987). – Étude comparative de la macrofaune endogée d'écosystèmes guinéens naturels et transformés de Côte d'Ivoire. Doctorat de 3<sup>e</sup> cycle (écologie). Université d'Abidjan.
- Kretzschmar A. (1982). – Description des galeries de vers de terre et variations saisonnières des réseaux (observations en conditions naturelles). *Rev. Écol. Biol. Sol*, **19**, 579-591.
- Kristufek V., Ravasz K. & Pizl V. (1992). – Changes in densities of bacteria and microfungi during gut transit in *Lumbricus terrestris* and *Aporrectodea caliginosa* (Oligochaeta: Lumbricidae). *Soil Biol. Biochem.*, **24**, 1499-1500.
- Kuhnigk T., Borst E.M., Ritter A., Kampfer P., Graf A., Hertel H. & König H. (1994). – Degradation of lignin monomers by the hindgut flora of xylophagous termites. *Syst. Appl. Microbiol.*, **17**, 76-85.
- Lambers H. (1993). – Rising CO<sub>2</sub>, secondary plant metabolism, plant-herbivore interactions and litter decomposition. *Vegetation*, **104/105**, 263-271.
- Lattaud C., Zhang B.G., Locati S., Rouland C. & Lavelle P. (1997). – Activities of the digestive enzymes in the gut and in tissue culture of a tropical geophagous earthworm, *Polypheretima elongata* (Megascolecidae). *Soil Biol. Biochem.*, **29**, 335-339.
- Lavelle P. (1975). – Consommation annuelle de terre par une population naturelle de vers de terre (*Millsonia anomala* Omodeo, *Acanthodrilidae*, Oligochaeta) dans la savane de Lamto (Ivory Coast). *Rev. Écol. Biol. Sol*, **12**, 11-24.
- Lavelle P. (1978). – Les vers de terre de la savane de Lamto (Ivory Coast) : peuplements, populations et fonctions dans l'écosystème. Thèse de Doctorat. Université Paris VI.
- Lavelle P. (1983). – The structure of earthworm communities. In: Satchell J.E. (Ed.). *Earthworm Ecology: from Darwin to Vermiculture*, London: Chapman & Hall, pp. 449-466.
- Lavelle P. (1996). – Diversity of soil fauna and ecosystem function. *Biol. Int.*, **33**, 3-16.

- Lavelle P. (1997). – Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Adv. Ecol. Res.*, **27**, 93-132.
- Lavelle P. & Pashansi B. (1989). – Soil fauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia*, **33**, 283-291.
- Lavelle P., Barois I., Fragoso C., Cruz C., Hernandez A., Pineda A. & Rangel P. (1987). – Adaptive strategies of *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta), a peregrine geophagous earthworm of the humid tropics. *Biol. Fert. Soils*, **5**, 188-194.
- Lavelle P., Schaefer R. & Zaidi Z. (1989). – Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. *Pedobiologia*, **33**, 379-388.
- Lavelle P., Blanchart E., Martin A., Spain A.V. & Martin S. (1992). – Impact of soil fauna on the properties of soil in the humid tropics. In: *Myths and Science of Soils of the Tropics*. SSSA Special Publication, **29**, 157-185.
- Lavelle P., Blanchart E., Martin A., Martin S., Barois I., Toutain F., Spain A. & Schaefer R. (1993). – A hierarchical model for decomposition in terrestrial ecosystems. Application to soils in the humid tropics. *Biotropica*, **25**, 130-150.
- Lavelle P., Lattaud C., Trigo D. & Barois I. (1994a). – Mutualism and biodiversity in soils. *Plant Soil*, **170**, 23-33.
- Lavelle P., Dangerfield M., Fragoso C., Eschenbrenner V., Lopez-Hernandez D., Pashanasi B. & Brussaard L. (1994b). – The relationship between soil Macrofauna and tropical soil fertility. In: Swift M.J. & Woomer P. (Eds.). *Tropical Soil Biology and Fertility*. New York: John Wiley-Sayce, pp. 137-169.
- Lavelle P., Pashanasi B., Charpentier F., Gilot C., Rossi J.P., Derouard L., André J., Ponge J.F. & Bernier N. (1997). – Large-scale effects of earthworms on soil organic matter and nutrient dynamics. In: Edwards C.A. (Ed.). *Earthworm Ecology*. St Lucie Press, Chap. 20.
- Lee K.E. (1985). – *Earthworms: their ecology and relationships with soils and land use*. New-York: Academic Press.
- Lee K.E. & Foster R.C. (1991). – Soil fauna and soil structure. *Aust. J. Soil Res.*, **29**, 745-775.
- Lee K.E. & Wood T.G. (1971). – *Termites and Soils*. London: Academic Press.
- Lepage M. (1981). – The impact of foraging populations of *Macrotermes michaelseni* (Sjostedt) (Isoptera, Macrotermitinae) in a semi-arid ecosystem (Kajaiido-Kenya). II. Food offtake comparison with large herbivores. *Insectes Soc.*, **28**, 309-320.
- Lindroth R.L., Kinney K.K. & Platz C.L. (1993). – Responses of deciduous trees to elevated atmospheric CO<sub>2</sub>: productivity and insect performance. *Ecology*, **74**, 763-777.
- Ljungström P.O. (1972). – Introduced earthworms of South Africa. On their taxonomy, distribution, history of introduction and on the extermination of endemic earthworms. *Zool. Jb. Syst.*, **99**, 1-81.
- Lobry de Bruyn L.A.L. & Conacher A.J. (1990). – The role of termites and ants in soil modification: a review. *Aust. J. Soil Res.*, **28**, 55-93.
- Lopes-Assad M.L. (1987). – Contribution à l'étude de la macroporosité lombricienne de différents types de sols de France. Université, USTL, Montpellier.
- Loranger G. (1995). – Distribution spatiale de la mésafaune dans des vertisols Martiniquais. Influence du mode d'exploitation du sol et des vers de terre. Mémoire DEA Pédologie. Nancy I.
- Mackay A.D. & Kladvko E.J. (1985). – Earthworms and rate of breakdown of soybean and maize residues in soil. *Soil Biol. Biochem.*, **17**, 851-857.
- Marinissen J.C.Y. (1995). – Earthworms, soil-aggregates and organic matter decomposition in agro-ecosystems in the Netherlands. Thesis. Wageningen University.
- Martin A. (1991). – Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biol. Fert. Soils*, **11**, 234-238.
- 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., Mariotti A., Balesdent J. & Lavelle P. (1991). – Soil organic matter assimilation of a geophagous tropical earthworm based on d<sup>13</sup>C measurements. *Ecology*, **73**, 118-128.
- Martin S. (1990). – Modelisation de la dynamique et du rôle d'une population de ver de terre *Millsonia anomala* dans les savanes humides de Côte d'Ivoire. Thèse. Université Paris VI.
- Martius C. (1994). – Diversity and ecology of termites in Amazonia forests. *Pedobiologia*, **38**, 407-428.
- Matsumoto T. (1976). – The role of termites in an equatorial forest ecosystem of West Malaysia. I. Population density, biomass, carbon, nitrogen and calorific content and respiration rate. *Oecologia*, **22**, 153-178.
- Matsumoto T. & Abe T. (1979). – The role of termites in an equatorial rain forest ecosystem of West Malaysia. II. Leaf litter consumption on the forest-floor. *Oecologia*, **38**, 261-274.
- Mboukou I. (1997). – Les Macroinvertébrés du sol dans différents systèmes d'agriculture au Congo : cas particulier de deux systèmes traditionnels (écobuage et brûlis) dans la vallée du Niari. Thèse. Université Paris VI, France.
- Melillo J.M. (1983). – Will increases in atmospheric CO<sub>2</sub> concentrations affect decay process? In: *The Ecosystem Center*. Massachusetts, USA: Annual Report. Marine Biological Laboratory, Woods Hole, pp. 10-11.
- Menaut J.C., Barbault R., Lavelle P. & Lepage M. (1985). – African savannas: Biological systems of humification and mineralization. In: Tothill J.C. & Mott J.J. (Eds.). *Ecology and management of the world's savannas*. Canberra: Australian Academic Sciences, pp. 14-33.
- Miles J. (1985). – Soil in the ecosystem. In: Atkinson D., Fitter A.H., Read D.J. & Usher M.B. (Eds.). *Ecological Interactions in Soil: Plants, Microbes and Animals*. Oxford, Great Britain: Blackwell Scientific Publications, pp. 407-427.
- Mill A.E. (1992). – Termites as agricultural pests in Amazonia, Brazil. *Outlook Agr.*, **21**, 41-46.
- Noirot C. (1992). – From wood- to humus-feeding: an important evolutionary trend in termite evolution. In: Billen J. (Ed.). *Biology and Evolution of Social Insects*. Leuven: Leuven University Press, pp. 107-119.
- Norby R.J., Pastor J. & Melillo J.M. (1986). – Carbon-nitrogen interactions in CO<sub>2</sub>-enriched white oak: physiological and long-term perspectives. *Tree Physiol.*, **2**, 233-241.

- Nunes L., Bignell D.E., Lo N. & Eggleton P. (1997). – On the respiratory quotient (RQ) of termites (Isoptera). *J. Insect Physiol.*, **43**, 749-758.
- Oberbauer S.F., Sionit N., Hastings S.J. & Oechel W.C. (1986). – Effects of CO<sub>2</sub> enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan Tundra plant species. *Can. J. Bot.*, **64**, 2993-2998.
- O'Neill E.G., Luxmoore R.J. & Norby R.J. (1987). – Elevated atmospheric CO<sub>2</sub> effects on seedling growth, nutrient uptake, and rhizosphere bacterial population of *Liriodendron tulipifera* L. *Plant Soil*, **104**, 3-11.
- Owensby C.E., Coyne P.I. & Aven L.M. (1993). – Nitrogen and phosphorus dynamics of a tallgrass prairie ecosystem exposed to elevated carbon dioxide. *Plant Cell Environ.*, **16**, 843-850.
- Parle J.N. (1963). – Micro-organisms in the intestines of earthworms. *J. Gen. Microbiol.*, **31**, 1-11.
- Parmelee R.W., Beare M.H., Cheng W., Hendrix P.F., Rider S.J., Crossley D.A. & Coleman D.C. (1990). – Earthworms and enchytraeids in conventional and no-tillage agroecosystems: a biocide approach to assess their role in organic matter breakdown. *Biol. Fert. Soils*, **10**, 1-10.
- 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**, 801-810.
- Pearce M.J. & Waite B. (1994). – A list of termite genera with comments on taxonomic changes and regional distribution. *Sociobiology*, **23**, 247-263.
- Phillipson J., Abel R., Steel J. & Woodell S.R. (1976). – Earthworms and the factors governing their distribution in a beech woodland - Wytham Woods, Oxford. *Oecologia (Berl.)*, **33**, 291-309.
- Pearce T.G. & Phillips M.J. (1980). – The fate of ciliates in the earthworm gut: an *in vitro* study. *Microbial Ecol.*, **5**, 313-319.
- Poier K.R. & Richter J. (1992). – Spatial distribution of earthworms and soil properties in an arable loess soil. *Soil Biol. Biochem.*, **24**, 1601-1608.
- Pomeroy D.E. (1983). – Some effects of mound-building termites on the soils of a semi-arid area of Kenya. *J. Soil Sci.*, **34**, 555-570.
- Puytorac de P. (1954). – Contribution à l'étude cytologique et taxonomique des Infusoires. *Ann. Sci. Nat. Zool.*, **11**, 82-270.
- Roger P.A. (1996). – *Floodwater Ecosystem in Ricefields*. Orstom/IRRI. Los Banos: Philippines.
- Rogers H.H., Prior S.A. & O'Neill E.G. (1992). – Cotton root and rhizosphere responses to free-air CO<sub>2</sub> enrichment. *Crit. Rev. Plant Sci.*, **11**, 251-263.
- Rohrmann G.F. & Rossman A.Y. (1980). – Nutrient strategies of *Macrotermes ukuzii* (Isoptera: Termitidae). *Pedobiologia*, **20**, 61-73.
- Roonwal M.L. (1979). – Termites of the Oriental region. In: Krishnan K. & Weesner F.M. (Eds.). *Biology of Termites*. Vol. 2. New York: Academic Press, pp. 315-391.
- Rossi J.P. & Lavelle P. (1998). – Earthworm aggregation in the savannas of Lamto (Ivory Coast). *Appl. Soil Ecol.*, **7**, 195-200.
- Rossi J.P., Lavelle P. & Albrecht A. (1997). – Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity. *Soil Biol. Biochem.*, **29**, 485-488.
- Rouelle J. (1983). – Introduction of amoebae and *Rhizobium japonicum* into the gut of *Eisenia foetida* (Sav.) and *Lumbricus terrestris* L. In: Satchell J.E. (Ed.). *Earthworm Ecology*. London: Chapman and Hall, pp. 375-381.
- Rouland C., Civas A., Renoux J. & Petek F. (1988). – Synergistic activities of the enzymes involved in cellulose degradation, purified from *Macrotermes mülleri* and from its symbiotic fungus *Termitomyces* sp. *Comp. Biochem. Physiol.*, **91B**, 459-465.
- Rouland C., Lenoir F. & Lepage M. (1991). – The role of symbiotic fungus in the digestive metabolism of several species of fungus-growing termites. *Comp. Biochem. Physiol.*, **99A**, 657-663.
- Sands W.A. (1960). – Initiation of fungus comb construction in laboratory colonies of *Ancistrotermes guineensis* (Silvestri). *Insectes soc.*, **7**, 251-263.
- Sands W.A. (1969). – The association of termites and fungi. In: Krishna K. & Weesner F.M. (Eds.). *Biology of Termites*. Vol. 1. New York and London: Academic Press, pp. 495-524.
- Scheu S. & McLean M.A. (1993). – The earthworm (*Lumbricidae*) distribution in Alberta (Canada). *Megadrilogica*, **4**, 175-185.
- Scheu S. & Wolters V. (1991). – Influence of fragmentation and bioturbation on the decomposition of <sup>14</sup>C-labelled beech leaf litter. *Soil Biol. Biochem.*, **23**, 1029-1034.
- Senapati B.K., Panigrahi P.K. & Lavelle P. (1994). – Macrofaunal status and restoration strategy in degraded soil under intensive tea cultivation in India. In: *15th World Congress of Soil Science*. Acapulco: ISSS 4a, pp. 65-75.
- Senapati B.K., Pashanasi B., Decaëns T., Jimenez J.J., Albrecht A., Blanchart E., Mahieux M., Rousseaux L., Thomas R. & Panigrahi P. (in press). – Earthworm technologies. In: Lavelle P., Brussaard L. & Hendrix P. (Eds.). *The potential for management of earthworm activities in tropical agrosystems*. Wallingford, UK: CAB-I.
- Sen-Sarma P.K. (1986). – Economically important termites and their management in the Oriental region. In: Vinson S. B. (Ed.). *Economic Impact and Control of Social Insects*. New York: Praeger, pp. 69-102.
- Sharpley A.N. & Syers J.K. (1977). – Seasonal variation in casting activity and in the amounts and release to solution of phosphorus forms in earthworms casts. *Soil Biol. Biochem.*, **9**, 227-231.
- Slaytor M. (1992). – Cellulose digestion in termites and cockroaches: what role do symbionts play? *Comp. Biochem. Physiol.*, **103B**, 775-784.
- Slaytor M., Veivers P.C. & Lo N. (1997). – Aerobic and anaerobic metabolism in the higher termite *Nasutitermes walkeri* (Hill). *Insect Biochem. Molec. Biol.*, **27**, 291-303.
- Sleaforth F., Bignell D.E. & Eggleton P. (1996). – A pilot analysis of gut contents in termites from the Mbalmayo Forest Reserve, Cameroon. *Ecol. Entomol.*, **21**, 271-288.
- Solbrig O.T. (Ed.) (1991). – *From genes to ecosystems: a research agenda for biodiversity*. Paris: IUBS Scope Unesco.
- Spears B.M., Ueckert D.N. & Whigham T.L. (1975). – Desert termite control in a short-grass prairie. Effect on soil physical properties. *Environ. Entomol.*, **4**, 899-904.

- Stockdill S.M.J. (1982). – Effects of introduced earthworms on the productivity of New Zealand pastures. *Pedobiologia*, **24**, 29-35.
- Stork N.E. & Eggleton P. (1992). – Invertebrates as determinants and indicators of soil quality. *Am. J. Alt. Agr.*, **7**, 38-47.
- Swift M.J., Heal O.W. & Anderson J.M. (1979). – *Decomposition in terrestrial ecosystems*. Oxford: Blackwell Scientific.
- Szlavec K. & Pobożny M. (1992). – Coprophagy in isopods and diplopods: a case for indirect interaction. *Anim. Zool.*, **196**, 1-11.
- Terborgh J. (1989). – *Where have all the birds gone?: Essays on the biology and conservation of birds that migrate to the American tropics*. Princeton: Princeton University Press.
- Toutain F., Villemin G., Albrecht A. & Reisinger O. (1982). – Étude ultra structurale des processus de biodégradation II. Modèle Enchytraeides-litière de feuillus. *Pedobiologia*, **23**, 145-156.
- Trigo D. & Lavelle P. (1993). – Changes in respiration rate and some physicochemical properties of soil during gut transit through *Allolobophora molleri* (Lumbricidae, Oligochaeta). *Biol. Fert. Soil*, **15**, 185-188.
- Vannier G. & Kilbertus G. (1983). – Participation des insectes collembolés et des microorganismes telluriques aux processus de migration des substances organo-minérales. In: *Colloques Internationaux du CNRS*. Vol. 303, pp. 133-144.
- Veeresh G.K. & Belavadi V.V. (1986). – Influence of termite foraging on the fertility status of the soil. *J. Soil Biol. Ecol.*, **6**, 53-66.
- Veivers P.C., Muhlemann R., Slaytor M., Leuthold R.H. & Bignell D.E. (1991). – Digestion, diet and polyethism in two fungus-growing termites: *Macrotermes subhyalinus* and *Macrotermes michaelseni*. Sjøstedt. *J. Insect Physiol.*, **38**, 675-682.
- Villalobos F.J. & Lavelle P. (1990). – The soil coleoptera community of a tropical grassland from Laguna Verde, Veracruz (Mexico). *Rev. Écol. Biol. Sol*, **27**, 73-93.
- Vu J.C.V., Allen L.H. & Bowes J.R.G. (1989). – Leaf ultra-structure, carbohydrates and protein of soybeans grown under CO<sub>2</sub> enrichment. *Environ. Exp. Bot.*, **29**, 141-147.
- Wardle D.A. (1994). – Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. *Adv. Ecol. Res.*, **26**, 105-185.
- Wardle D. & Lavelle P. (1997). – Linkages between Soil Biota, plant litter quality and decomposition. In: Cadisch G. & Giller K.E. (Eds.). *Driven by Nature*. Wallingford, UK: CAB-International, pp. 107-125.
- Watson J.A.L. & Cay F.J. (1970). – The role of grass-eating termites in the degradation of a mulga ecosystem. *Search*, **1**, 43.
- Watt A.D., Stork N.E., Eggleton P., Srivastava D. & Bignell D.E. (1997). – Impact of forest loss and regeneration on insect abundance and diversity. In: Watt A.D., Stork N.E. & Hunter M. (Eds.). *Forests and Insects*. London: Chapman and Hall.
- Whitford W.G. (1991). – Subterranean termites and long-term productivity of Desert Rangelands. *Sociobiology*, **19**, 235-243.
- Wielemaker W.G. (1984). – Soil formation by termites, a study in the Kisii area, Kenya. Doctor in de Landbouwwetenschappen. Wageningen University.
- Wilson E.O. (1993). – *The diversity of life*. Harvard: Harvard University Press.
- Wolters V., Ekschmitt K.N.Y. (1997). – Gastropods, Isopods, Diplopods and Chilopods - Neglected Groups of the Decomposer Food Web. In: Benckiser G. (Ed.). *Fauna in Soil Ecosystems*. New York: Marcel Dekker Inc., pp. 265-306.
- Wood T.G. (1978). – Food and feeding habits of termites. In: Brian M.V. (Ed.). *Production ecology of ants and termites*. Cambridge: Cambridge University Press, pp. 55-80.
- Wood T.G. (1988). – Termites and the soil environment. *Biol. Fert. Soils*, **6**, 228-236.
- Wood T.G. (1996). – The agricultural importance of termites in the tropics. *Agr. Zool. Rev.*, **7**, 117-155.
- Wood T.G. & Cowie R.H. (1988). – Assessment of on-farm losses in cereals in Africa due to soil insects. *Insect Sci. Appl.*, **9**, 709-716.
- Wood T.G. & Johnson R.A. (1986). – The biology, physiology and ecology of termites. In: Vinson S.B. (Ed.). *Economic Impact and Control of Social Insects*. New York: Praeger, pp. 1-68.
- Wood T.G. & Pearce M.J. (1991). – Termites in Africa: The environmental impact of control measures and damage to crops, trees, rangeland and rural buildings. *Sociobiology*, **19**, 221-234.
- Wood T.G. & Sands W.A. (1978). – The role of termites in ecosystems. In: Brian M.V. (Ed.). *Production Ecology of Ants and Termites*. Cambridge: Cambridge University Press, pp. 245-292.
- Wood T.G. & Thomas R.J. (1989). – The mutualistic association between Macrotermitinae and *Termitomyces*. In: Wilding N., Collins N.M., Hammond P.M. & Webber J.F. (Eds.). *Insect-fungus interactions*. London, England: Academic Press, pp. 69-92.
- Wood T.G., Johnson R.A., Baccus S., Shittu M.O. & Anderson J.M. (1982). – Abundance and distribution of termites in a Riparian forest in the Southern Guinea Savanna vegetation zone of Nigeria. *Biotropica*, **14**, 25-39.
- Woodin S., Graham B., Killick A., Skiba U. & Cresser M. (1992). – Nutrient limitation of the long term response of heather (*Calluna vulgaris* (L.) Mull.) to CO<sub>2</sub> enrichment. *New Phytol.*, **122**, 635-642.
- Wullschlegel S.D., Post W.M. & King A.W. (1995). – On the potential for a CO<sub>2</sub> fertilization effect in forest trees. Estimates of a biotic growth factor based on 58 controlled-exposure studies. In: Woodwell G.M., Mackenzie F. & Mackenzie T. (Eds.). *Biospheric feedbacks in the global climatic system: Will warming feed the warming?* New York: Oxford University Press, pp. 85-107.
- Yule D.F., Reddy M.V., Reddy V.R., George P.J. & Cogle A.L. (1991). – Effects of soil management on population abundance and biomass of earthworm in a semi-arid tropical alfisol. In: *Soil tillage and agricultural sustainability: proceedings of the 12th international soil tillage and resource organization*. Ibadan, Nigeria, pp. 63-71.
- Zhang B.G., Rouland C., Lattaud C. & Lavelle P. (1993). – Activity and origin of digestive enzymes in gut of the tropical earthworm *Pontoscolex corethrurus*. *Eur. J. Soil Biol.*, **29**, 7-11.