Diversity of Soil Fauna and Ecosystem Function

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Introduction

Soils are natural resources of utmost importance for a number of ecosystem and biosphere processes such as plant production, cycling of organic matter and nutrients, storage of C and water, and release of nitrous oxides, CO^2 and methane. Soil degradation, through various processes, is a matter of great concern, since their integrity is absolutely critical to increasing food production (FAO, 1995), and regulating atmospheric fluxes of greenhouse gases (Jenkinson, 1991; Wallace, 1994).

In this context, the present concern for the loss of biodiversity in soils is more closely linked to the possible role of species in the protection of the productive potential rather than to ethical, aesthetic, or economic considerations (Solbrig, 1991; Freckman, 1994).

Except for a few spectacular species like the 3m-long giant "gippsland" earthworm *Megascolides australis* of Southern Australia, soil fauna species do not appear on lists of endangered species that require protection. The limited knowledge (among the local farmers) of this fauna is mainly due to (Ortiz *et al.*, 1994) the small size and the difficulty in extracting and observing most species. (André *et al.*, 1994) easily explain this situation. For several decades, research mainly concentrated on a few pests, looking at efficient chemical treatments that would eliminate them. More recently however, there has been considerable development in research on the role of the whole invertebrate community in soil function. These studies consider soil fauna as a resource with potential for soil biodiversity management (Lavelle and Barois, 1988; Swift and Woomer, 1994). Attempts are being made to either biological control some of the more serious pests, or use their communities as indicators of the quality of the soil system, as most are highly sensitive to perturbations and disturbances (Bongers, 1990 for nematodes; Lavelle, 1988 and Decaens *et al*, 1995 for macroinvertebrates).

In a single square meter of soil of a European beech forest, as many as 1000 species of invertebrates may be collected (Schaefer and Schauermann, 1990). Richness differs greatly between taxa. Microarthropod communities may comprise hundreds of species with a diversity of up to 400 to 500 species of Acari and 60 to 80 species of Collembola . Under comparable conditions, nematodes may comprise up to 90 species, Protozoa, 60; Enchytraeidae, 22 ; earthworms, 15-17 ; Diplopoda, 15. In African savannas, termite communities may comprise up to 60 species. Villalobos and Lavelle (1990) collected 113 species of soil Coleoptera. Similar richness occurs in a large range of ecosystems, and a large proportion of these species have not yet been described. It is assumed for example, that the 3000 earthworm species already described only represent half of the total number of existing species. In smaller groups with high specific richness, the situation is much more critical (Hawksworth and Mound, 1991). André *et al.* (1994) explain that the selectivity of extraction methods and sampling sites, and the lack of interest for some groups of small species, has probably led to an

underestimation of microarthropod species richness of 1-2 orders of magnitude. In general, much less species have been identified in tropical than in temperate areas.

During the last 10 years, great efforts have been made to understand the role of invertebrates in soil processes, and their interactions with the abiotic factors of soil function (Lavelle *et al.*, 1993, 1994; Beare *et al.*, 1995; Wardle and Lavelle, in press). Dramatic effects have been observed in the regulation of microbial activity, soil aggregation and hydraulic properties, dynamics of decomposition and soil organic matter, plant growth and pedogenesis. Although effects have often been quantified in experiments performed at the organisms scale, and less often at those which are relevant to agronomic or pedologic issues, there is clear evidence that these processes may actually operate at the ecosystem level. In addition, it was found that the functional importance of invertebrate activities is often disproportionate to their actual abundance (Anderson, 1988).

Soil invertebrate communities are deeply affected by human activities; in most agroecosystems, they tend to disappear. Little if any mention is made of possible links between the elimination of such important regulators of soil processes and the lack of sustainability of most agricultural systems (Lavelle *et al.*, 1994). On the other hand, cases exist where the replacement of a diverse native fauna by a few opportunist exotic species adapted to highly disturbed areas result in the disappearance of key functional groups. Severe degradation of the soil (by endogeic earthworms, Rose and Wood, 1980) or damages to plant crops (by termites, rhizophagous Coleoptera larvae, or parasitic nematodes) may also occur. For example, there is evidence that at least part of the degradation process that affects pastures in Central Amazonia is due to a pullulation of the earthworm species *Pontoscolex corethrurus*, at the expense of the loss of all earthworm species and the majority of arthropods from the native forest. P. corethrurus produces high amounts of compact casts at the soil surface and severe soil compaction and subsequent depressed water infiltration rapidly occur, as those species that would have normally decompacted the soil have been largely eliminated (Chauvel, Grimaldi, Desjardins, Matos, Blanchart, De Oliveira Barros and Lavelle, unpublished data).

It is therefore urgent to describe the diversity of soil invertebrate communities and evaluate their functions in order to identify management options that eventually optimise their activities. Diversity should be addressed at the population level (genetic diversity in key species), community (specific richness) and ecosystem (functional groups) levels. The need to incorporate management of soil faunal communities as part of farming systems, land remediation and other types of landuse clearly set priority on the ecosystem level. According to Elliott and Lynch (1994), a goal for soil biodiversity management should not only mean maximizing the number of species in an ecosystem. More likely it means the ability to retain the current macro-(fauna) and microflora and to emphasize certain species and processes to accomplish specific objectives. Obviously, the broad main objective is to manage biodiversity for maximum soil resilience.

This paper attempts to synthesise the existing knowledge on the perception and function of biodiversity of invertebrates in soils. New research areas and hypotheses are proposed to improve our understanding and promote the idea that fauna is a resource that needs careful management, in the same right as currently accepted physical, chemical and microbiological components of soil fertility. Part of the ideas and hypotheses presented below have been discussed at a recent TSBF/UNEP workshop held at Hyderabad (India)(Giller *et al.*, in press and Swift, in press).

First described are the functions of invertebrates in soils, followed by the current perception of soil biodiversity, and some hypotheses on the role of this diversity. Challenges that lay behind these scientific questions are also presented.

Invertebrates and the Soil System

Soil function is the result of complex interactions among physical, chemical and biological factors. A general hierarchical model has been proposed to describe the potential importance of these factors as determinants of soil processes. Inside this model, soil organisms are separated into four broad functional groups, again presented in a hierarchical order, depending on their function and on the nature of the interaction they develop with other organisms.
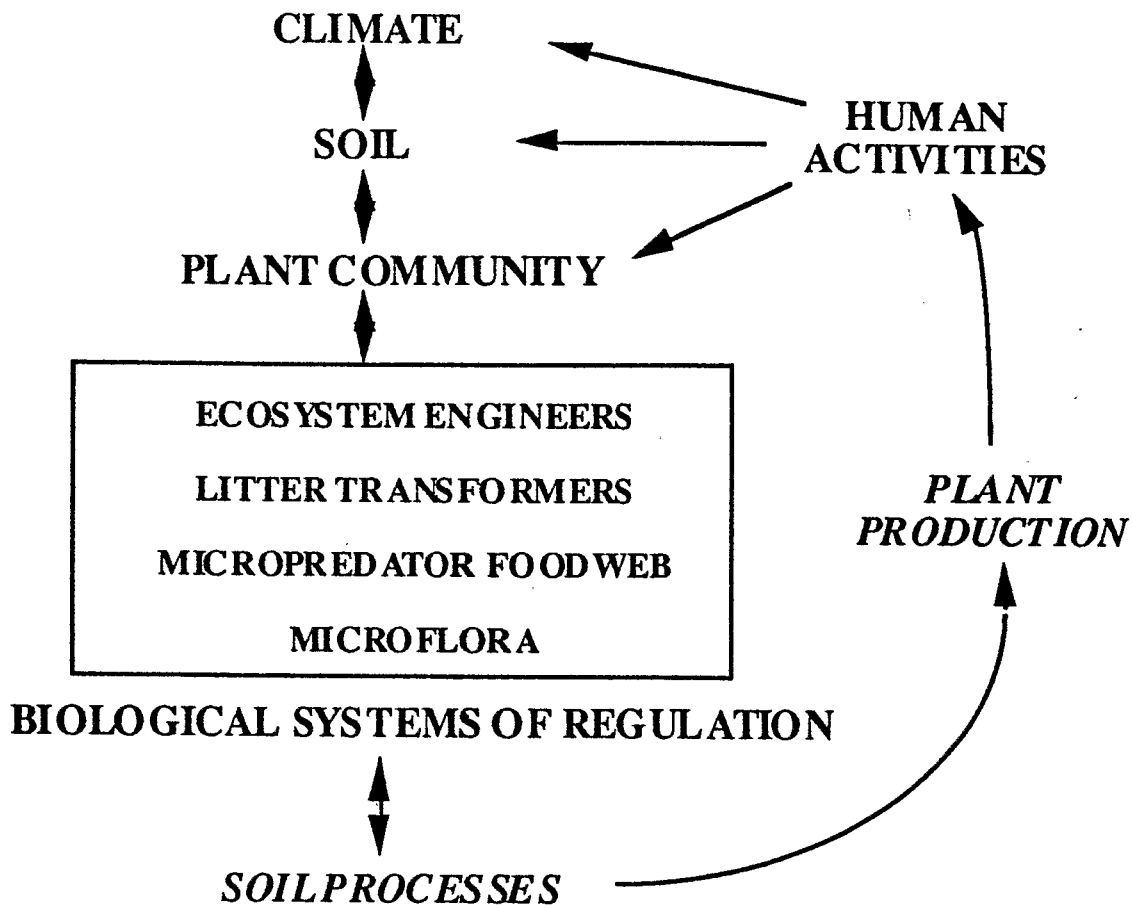
1. The hierarchical model

A hierarchical model has been proposed in which soil processes are determined by a suite of factors whose potential effect is determined by the scales of time and space at which they operate (Lavelle *et al.*, 1993). This hierarchy is a "control hierarchy" as defined by Solbrig (1991), in which factors that operate at large scales of time and space may constrain factors that operate at smaller scales. It is not, however, a rigid hierarchy since factors may affect a wide range of processes that are operating at different scales (Solbrig, 1991). The intensity of the constraint may be low, whereby factors operating at lower levels of the hierarchy then become predominant.

At the lowest level of determination, this suite of factors includes 'Biological Regulatory Systems' which comprise all soil organisms, divided into micro- and macroorganisms. According to this model, any soil process is likely to be firstly influenced by climate, then by edaphic factors (mainly clay abundance and nutrient status), followed by the quality of material produced by the plant community and brought as energy and nutrient sources, and finally biological systems of regulation, i.e., a broad mutualist association of macroorganisms (roots and invertebrates) with microorganisms (Fig.1). Evidently, human activities deeply influence the system and can be potentially one of the strongest determinants. This is, however, a potential hierarchy in which all levels interact, and in some situations when higher level factors are not particularly constraining, such as the quality of organic inputs, or the presence and activity of key invertebrate groups may be major determinants of processes. For example, this is the case for the role of termites and earthworms in tropical cropping systems, where neither the climate (in its macro- and microscales) nor soil (with little active clay minerals) or litter quality (almost homogeneous throughout the system) may significantly regulate such processes as decomposition of litter or soil physical structure.

A natural corollary to the rules which is also implicit in this model is that, depending on the intensity and relative importance of constraints operating at the upper levels of the hierarchy, the role of soil invertebrates as measured by their effect on rates of a specific ecosystem process may, or may not, be significant. In the former case, discussing their function is a relevant issue; in the latter, invertebrates may simply be used as indicators of ecosystem function since their impact is not significant to soil functioning.

Figure 1: An hierarchical model of soil function (after Lavelle *et al.*, 1993)

CLIMATE

SOIL ← HUMAN ACTIVITIES

PLANT COMMUNITY

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┌─────────────────────────────────┐
│  ECOSYSTEM ENGINEERS            │
│                                 │
│  LITTER TRANSFORMERS            │
│                                 │
│  MICROPREDATOR FOODWEB          │
│                                 │
│  MICROFLORA                     │
└─────────────────────────────────┘
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PLANT PRODUCTION

BIOLOGICAL SYSTEMS OF REGULATION

SOILPROCESSES

2. Major Functional Groups in Soils

All invertebrates in soils (and also roots) have developed interactions with microorganisms. The kind of relationship (predation or mutualism) and the nature of the microsites where developed (i.e., gut content or external structures like faecal pellets) allow the outline for a broad functional classification of soil organisms.

Microorganisms : The Sleeping Beauty Paradox

Unlike most invertebrates, microorganisms as a whole have the capacity to digest any substrate in the soil. However, their relative inability to move (which is more critical in bacteria than fungi) and the discontinuous distribution of organic resources at the scale at which they operate, cause them to be *inactive for most of the time*, i.e., in resting stages that can last from months to years. Microbial communities appear as a *huge largely dormant population, with an enormous richness of species and an ability to survive hard times* (Jenkinson and Ladd, 1981). Turnover times of microbial biomass are in the range of 6-18 months in nature, that is 1,000 to 10,000 times more than in optimal laboratory conditions. Activation of resting microbiota and redistribution of microorganisms and organic substrates is performed by invertebrates and roots that mix the soil, add water and readily assimilable substrates to the soil. This function of invertebrates and roots in the activation of dormant microflora has been referred to as

the "Sleeping Beauty Paradox" (Lavelle *et al.*, 1995). The nature of the association between micro- and macroorganisms, however, varies greatly and mainly depends on the size of the invertebrates involved. The presence and nature of structures produced by the invertebrates that serve as incubators for microbial activities provide the division of invertebrates into three major functional groups: micropredators, litter transformers and ecosystem engineers.

Micropredators

The smallest invertebrates, Protozoa and Nematodes of the microfauna (average size <0.2mm) do not build any structure. Predation is the only means they have to take advantage of microbial activity. They participate in microfood webs that may include several levels, with microbial grazers and one or two levels of predators (Hendrix *et al.*, 1986; Hunt *et al.*, 1987); Moore and De Ruiter, 1991. The impact of such systems is an overall stimulation of mineralisation of organic matter (Darbyshire, 1972; Ingham *et al.*, 1985). In microcosm studies, there is evidence that increased complexity of this foodweb accelerates mineralisation (Setälä *et al.*, 1991; Couteaux *et al.*, 1991).

Litter Transformers

At the next level, litter transformers include the small Oligochaeta Enchytraeidae and arthropods of the mesofauna (<2mm) and macrofauna (>2mm). These invertebrates build holorganic structures (their faecal pellets) that serve as incubators for microbial activities; some time after deposition, they reingest these pellets to assimilate metabolites that have been released by the microflora. Cases of reingestion of pellets of a given individual or population by other individuals or populations are most likely frequent (Vannier, 1985; Lussenhop, 1992). In these pellets, mineralisation may be enhanced in short periods, but in the longer term, a relatively compact structure that limits aeration and water storage as well as the accumulation of resistant humidified molecules may result in a significant decrease of mineralisation, lasting as long as the structure's integrity is maintained (Hanlon and Anderson, 1980; Toutain *et al.*, 1982). In types of humus where H horizons are made of accumulated pellets of Enchytraeidae and Microarthropods, these structures may last for several decades and significantly affect the soil's function through the organisation of humus types (Jabiol *et al.*, 1992). At an even larger scale of time and space, leaching of organic acids released in these structures is known to alter clay minerals and thus participate in the formation of highly weathered soils (Berthelin *et al.*, 1979).

Ecosystem Engineers

A few large invertebrates (mainly earthworms) and social insects (ants and termites) are able to efficiently dig the soil and produce organo-mineral structures (casts and organo-mineral pellets that are resistant macroaggregates, mounds and nests) and a large variety of pores (galleries, chambers and voids resulting from an uncomplete backfilling of galleries). The size of these organisms allows the development of anisosymbiotic relationships with microflora in their proper gut, which is likely to be much more efficient than the external relationships in faecal pellets. Mineralisation linked to the digestive process may be high, especially in grass eating termites that may assimilate up to 93% of the ingested material (Wood, 1978). Endogeic earthworms may assimilate between 5 to 19% of the ingested organic matter depending on species and soil types, in the course of a gut transit that may last no more than 20' to 4 hours (Lavelle, 1988).

This represents a several hundred-fold increase when compared to standard *in-situ* field measurements.

The role of structures created by these organisms may be highly significant in the ecosystem function since they often are privileged sites for all basic soil processes (i.e., C and N mineralisation, denitrification or N-fixation, water and air infiltration), and one single structure, or group of structures, may affect processes that operate at very different scales of time and space. Some processes may be finely regulated within the functional domain of ecosystem's engineers when complementary, or opposite effects are observed at different scales of time and space. A simple example is represented by termites that accelerate tremendously the mineralisation of litter through their internal and external (fungus gardens) digestive processes, but then accumulate the remaining carbon and nutrients by aggregating their pellets into the highly compact structure of the termitaria where virtually no mineralisation occurs until the colony dies.

3. The Main Biological Systems of Regulation (BSR)

The functioning of biological systems of regulation largely depends on the nature and biological characteristics of all three major components i.e., characteristics of the energy source, microbial communities and invertebrates . It is therefore possible to separately consider (i) the litter systems, which comprise leaf litter as a food supply, surface lateral roots, epigeic invertebrates (mainly arthropods) and microbial communities dominated by fungi; (ii) the drilospheres, which include earthworms, soil organic matter as a food source, and free-living soil microflora dominated by bacteria; and (iii) the termitospheres, i.e., the whole volume of soil and organic resources that termites affect through their activities, in association with obligate or optional mutualist microorganisms. The rhizospheres, i.e., living subterranean roots and the soil and microflora that they influence are another important biological system of regulation that has an analogous functioning to that of the above mentioned systems.

4. Processes Affected by Invertebrate Activities

Invertebrate activities have significant effects on soil organic matter dynamics, the organisation and structure of soil, and plant growth . One common characteristic is that a single process like ingesting and digesting a mixture of soil and litter may have effects on a large range of processes, at different scales of time and space, i.e., short-term enhancement of mineralisation during gut transit, and delayed effects in fresh and ageing structures produced by these organisms (Fig. 2). The selective ingestion of organic and mineral particles, mixing of soil and organic matter, and excavation of galleries and chambers accumulated over time may have dramatic impact on the morphology and function of soil (Fig.3). An important attribute of soils such as aggregation, i.e., the organisation of particles in micro- to centimetre aggregates is largely dependent on the activities of invertebrates that produce aggregates (as organomineral faecal pellets), or other species that split them into smaller units when they excavate , or feed on these large structures. This is the consequence of huge ingestion rates by earthworms and termites that range from several hundred to more than one thousand t ha-1 dry soil in soils with intense macrofauna activities.
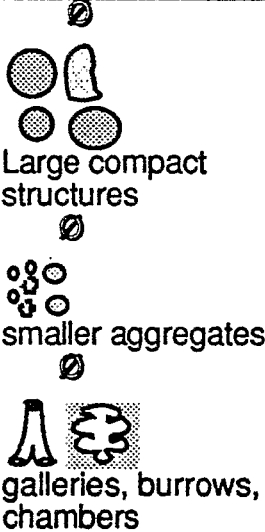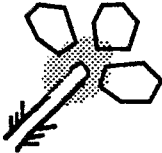
Figure 2: Consequences of the activities of an Ecosystem Engineer (an earthworm in that example) on soil processes operating at different scales (Lavelle *et al.*, in press)

PEDOGENESIS
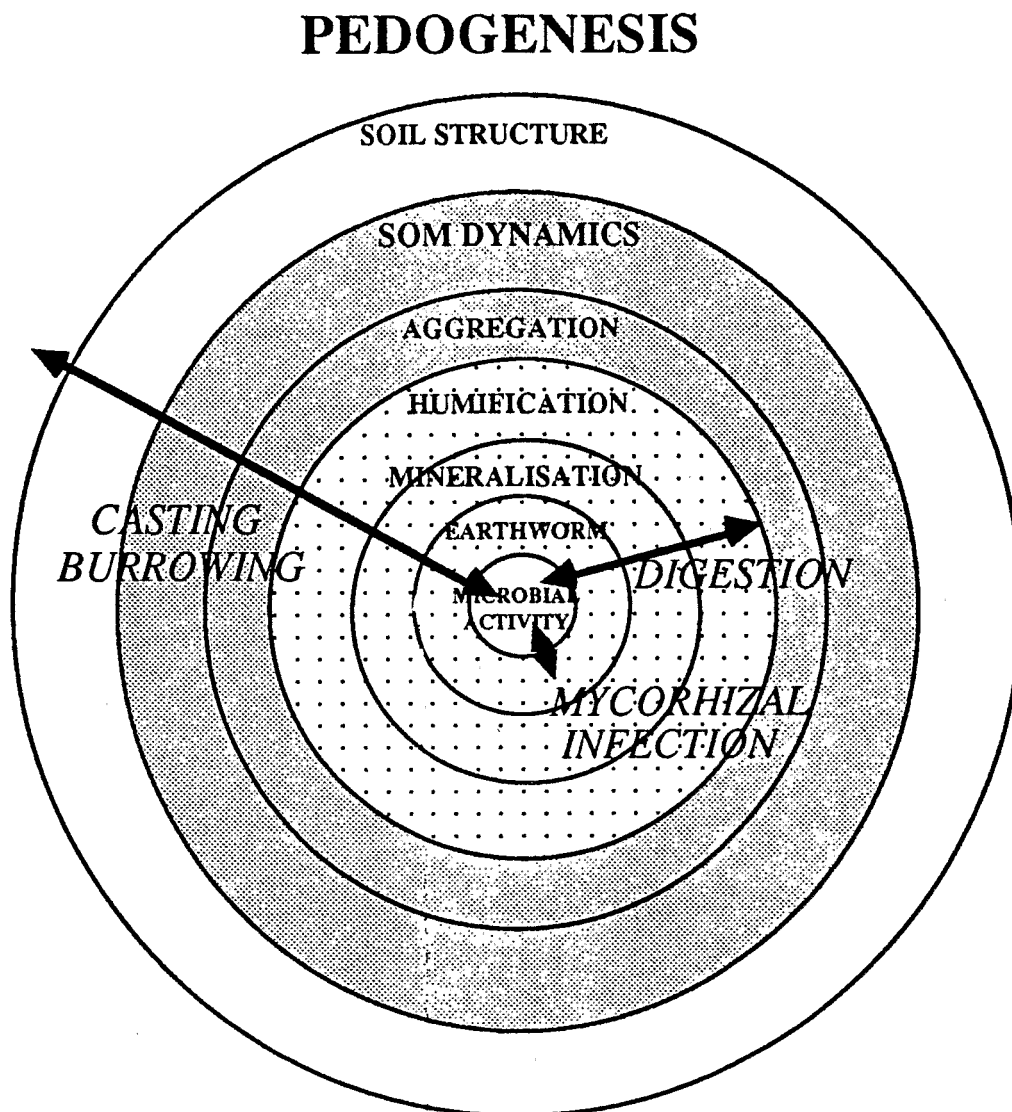
The Function of Biodiversity in Soils

Soil zoologists have long asked themselves why so many species inhabited soils (Ghilarov, 1977; Anderson, 1977; Vannier, 1985). A currently admitted reason is the large diversity of resources and microhabitats that soils offer, a mixture of highly microdivided aerial and aquatic phases. It has also been argued that the extended occurence of mutualistic relationships between macro- and microorganisms increase the niche space and hence the possibility of having increased numbers of species (Lavelle, 1986; Lavelle *et al.*, 1995).

Figure 3: 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

	STRUCTURES	EFFECTS ON BIODIVERSITY	EFFECTS ON FUNCTION
MICRO-PREDATORS	none	- selection of microflora?	- enhanced mineralisation
LITTER TRANSFORMERS	Organic fecal pellets	- selection of microflora - microhabitats for smaller invertebrates - food for other invertebrates	-Enhanced mineralisation + -sequestration of organic matter (depending on time scale)
ECOSYSTEM ENGINEERS	Large compact structures smaller aggregates galleries, burrows, chambers	-selection on litter transformers -associated microfauna - selection on microflora - effects on root development	- Bioturbation - Dissemination of spores (mycorhizae, 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..)
ROOTS	Rhizosphere structures	- production of polysaccharides - selection on microflora - associated food-webs - root + root litter feeders	- Aggregation - Plant production - Overall biodiversity (through energy supply and diersity of primary food resources)

Classifications of soil invertebrates based on the consequences that their activities have on soil processes (also referred to as their "function") are required. Such classifications also imply a better knowledge of the interactions existing among organisms to focus on species, or groups of species, that determine the diversity of other ones, and establish the bases of a classification based on the functions that are actually performed.

1- Species Redundancy and Functional Groups

The idea that many species are redundant (di Castri and Younès, 1990) in soil has been long implicitly accepted by those scientists who proposed diverse functional classifications for most zoological groups (Gisin, 1943 for Collembola; Grassé, 1984 for termites; Lee, 1958 and Bouché, 1977 for earthworms). However, there is almost immediate feedback between the effect an organism has on its environment and the consequences for its future conditions of life. Therefore, if we can admit in a first instance Andren's (1995) remark that *organisms have evolved through selection to maximize their contribution to future generations ....not to serve functions in the ecosystem*, we have to add that the effect of a dominant species on soil processes is likely to affect their resource base in the future. Selection may have operated on the long term consequences of function of a species on its life condition.

On the other hand, the idea that a few keystone species (Paine, 1966) or functional groups, that possibly comprise related taxa or mixed phyla, may determine the abundance and diversity of smaller species, is receiving growing acceptance (Wardle and Lavelle, 1996). The model presented in Fig.1 clearly points out the importance of ecosystem engineers as possible regulators and determinants of communities of smaller invertebrates. As a result, there is a need for functional classifications that 1) group redundant species; 2) are based on well identified functions in soils, 3) give prominent status to species or groups with key functions, but 4) recognise that some groups that do not significantly affect the rates of any ecosystem process may serve as indicators of on-going processes.

2- The Present Status of Functional Classifications

Zoologists have attempted to reduce the huge species richness of many soil invertebrate groups into a smaller number of functional groups; these would implicitly group redundant species regarding their function in soils, be easy to recognise on the basis of morphological features, and have homogeneous impacts on soil processes. Several classifications have been proposed since, sometimes more than one for a same taxonomic group. Classifications grouping several large taxonomic groups with similar ecological niches have rarely been proposed (Table 1).

These classifications are clearly centered on biological and ecological features that describe some aspects of adaptive strategies. They have proved to be useful to describe foodwebs comprised of microorganisms, micro- and mesofauna (Hunt *et al.*, 1987; Ingham *et al.*, 1986; De Ruiter *et al.*, 1993). They are certainly insufficient in the case of larger invertebrates whose function exceeds simple trophic processes by far. Improvements are still required, and should radicate in a clear view of the roles that invertebrates play in soils, at the scale of the whole soil system, and in their respective functional domains also called biological systems of regulation. Research is needed to provide a clear framework for the definition of such groups.

3-The Structure and Functional Significance of Biodiversity in Soils: Research Hypotheses

Biological systems of regulation characterise large functional domains that have general features in common that differenciate them from other large domains. An example is the drilosphere, *viz.* earthworms, the sum of structures (macropores, galleries, aggregates) that they have built and the smaller organisms (microflora, fauna) that inhabit these

structures. Inside these entities, different species will have differing impacts and therefore different functions in the soil. To properly assess the role of biodiversity in soils, and the conditions for its maintenance, it is essential to 1) clearly identify the links existing among species, especially in the functional domain of a given BSR, to test to which extent the presence of a given organism may influence the occurence of other ones, as the hierarchical structure proposed in Fig 1 would suggest; 2) try to group key species (ecosystem engineers, or litter transformers) that may have similar impacts in the environment, on the basis of their real effect irrespective of their taxonomic affinities, and morphology, when these criteria will prove to be irrelevant ; and 3) consider biodiversity in the context of energy fluxes, a very important issue in managed systems in which the drastic reduction in carbon fluxes may indirectly affect biodiversity. Research hypotheses that address these topics may be formulated as follows:

Table 1 : Functional classifications proposed for a few major groups of soil invertebrates

Taxonomic Group	Author	Main criteria	Categories Proposed
Nematodes		Feeding regime	Saprophages Bacterial feeders Fungivorous Omnivorous
Collembola	Gisin, 1943	Size & morphology as related to location in the soil profile	Hyperedaphic Epiedaphic Hemiedaphic Euryedaphic
Earthworms	Lee, 1958 Bouché, 1977 Lavelle, 1981	Feeding regime, Habitat, Characters of burrows, Size, Morphology, pigmentation, Demographic profil, anatomy, diapause	Epigeic Anecic Oligo-, meso-, or poly-humic endogeic
Termites	Grassé, 1984	Feeding regime, associated micro-organisms	Xylophagous Fungus growers Harvesters Humivorous

Hypothesis 1. Nested biodiversities

Diversity in plant communities determines below-ground diversity in the following order : plant diversity --> ecosystems engineers --> litter transformers --> microfauna --> microflora.

This hypothesis is a soil analogous of Hypothesis B1 developped by Solbrig (Ed., 1991) stating that 'keystone' species are essential for maintaining species richness in communities...(Terborgh, 1989; Gautier-Hion and Michaloud, 1989). This hypothesis first considers the existing links between diversity of plant and below-ground invertebrate communities, and the effect of "ecosystem engineers" (sensu Stork and Eggleton, 1992; Lavelle, 1994) on community structure of smaller invertebrates and microorganisms. It is hypothesised that structures created by these organisms considerably modify the habitat and trophic resource base of organisms that are smaller and less mobile. To test this hypothesis, communities of macro- and microarthropods,

enchytraeidae, nematodes, and microorganisms will be sampled at three different spatial scales:

- by comparing diversity and abundance of small organisms in sites with contrasting abundances and diversities of ecosystem engineers;
- at a smaller intra-site scale, communities may also be compared in patches with high densities of the key species considered, and patches where they are not found (when populations of plants and ecosystem engineers have aggregated distributions);
- at a microsite level, investigations will compare communities found in structures produced (e.g., termite or ant mounds and nests, earthworm casts) to 'bulk soil' that was not recently modeled by faunal activities.

Hypothesis 2. The role of structures as intermediates between diversity and function

Diversity of soil invertebrates results in the production of structures whose abundance and diversity are critical to the conservation and dynamics of soil organic matter, nutrient release and maintenance of physical properties that are essential for a sustained primary production (Fig. 2).

This hypothesis, rather specific to the soil environment, points at the importance of metabiotic processes in soils: structures created by keystone species influence the location and evolution of organic resources that are commonly used by large part of the soil community. Special emphasis is set on the role of the characters of structures, their composition, shape, location, abundance etc., as specific microsites for the activities of microorganisms, and hence determinants of soil organic matter and nutrient dynamics; as specific components of the overall soil structure (macropores, aggregates, mounds, ant cemeteries) biological structures also influence hydraulic properties of soils and their resistance to erosion. Testing this hypothesis is another way of identifying invertebrate functions in terms of their impact on soil properties, and the activity of smaller organisms, irrespective of the taxonomic unit they belong to.

Hypothesis 3. The energetic bottle neck

In a soil with depleted organic resources, foodwebs tend to have a reduced number of trophic levels, and less components at each level. This hypothesis is a simple application of the well known productivity hypothesis to explain species richness (Giller, 1984) concerning soils. It can be casts of a given species of earthworm or organo-ineral faecal pellets of large Diplopoda that could serve as a food resource to a diverse microflora and fauna of populations of micro- and mesofauna. When the invertebrates feed on an impoverished soil, the energetic value of casts is lower and they will not sustain invertebrate and microbial populations that would normally have developped in these structures. These structures with lower organic contents are also likely to have a lower structural stability (Blanchart *et al.*, 1993).

At the scale of an ecosystem, it may be important to determine thresholds of organic resources of a given quality beyond which critical levels of key faunal activities are observed. In the African savannas of Lamto (Côte d'Ivoire) for example, the annual cost of having an active earthworm community has been evaluated at 1.2t ha-1yr-1 organic matter from relatively young pools, irrespective of particle-size (Lavelle, 1978; Martin *et al.*, 1991). Similar data for other groups and situations are stll very scarce. If maintenance of soil invertebrate communities at a significant level were to be

considered as part of sustainable management practices, this kind of information would be extremely useful.

Perspectives for the Management of Soil Biodiversity

At present, there is a critical need to: (1) clearly understand the roles that invertebrates play in soils, especially representatives of key functional groups; and (2) assess the value of diversity to design management practices that optimize the conservation of species, in accordance with well identified objectives. In some cases, the objective may be conservation, in other situations, a sustainable use of soils. In the first case, the objective will probably be to maintain a minimum diversity of plants that provide the diversity and abundance of resources necessary to sustain a complex community. In the case of agroecosystems and soils submitted to rehabilitation techniques, the objective is to maintain key functional groups. It is essential to know if key species really exist and what they are, and how many are necessary to sustain soil processes and plant production at given rates. Other species that do not have the status of 'key species' may be useful indicators of the state of the system to monitor changes occuring in the function. They may be species that reflect specific structural or trophic characteristics of the soil.

References

Anderson, J.M. (1977) The organization of soil animal communities. In: U.L. &. T. Persson (Eds), *Soil Organisms as Components of Ecosystem*. Ecological Bulletins, Stockholm, Sweden. 15-23.

Anderson, J.M. (1988) Spatio-temporal effects of invertebrates on soil processes. *Biology and Fertility of Soils*. 6.

André, H.M., Noti, M.I., & Lebrun, P. (1994) The soil fauna - the other last biotic frontier. *Biodiversity and Conservation,*. 3(1):45-56.

Andren, O., Bengtsson, J. & Clarholm, M. (1995) Biodiversity and species redundancy among litter decomposers. In: H.P. Collins, G. P. Roberston, & M.J. Klug (Eds) *The Significance and Regulation of Soil Biodiversity*. Kluwer Academic Publishers, Amsterdam. 141-151.

Beare, M.H., Crossley Jr., D.A., Coleman, D.C., Hendrix, P.F. & Odum, E.P. (1994) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and Soil*. 31:1-18.

Berthelin, J., Souchier, B. & Toutain, F. (1979) Intervention des phinomhnes biologiques dans l'altiration. *Sciences du Sol*, Bulletin de l'AFES. 2(3):175-187.

Blanchart, E., Bruand, A. & Lavelle, P. (1993) The physical structure of casts of *Millsonia anomala* (Oligochaeta:Megascolecidae) in shrub savanna soils (Côte d'Ivoire). *Geoderma*. 56:119-132.

Bouché, M.B. (1977) Stratégies lombriciennes. In: Soil Organism as Components of Ecosystems. *Ecology Bulletin* . Stockolm. 122-132.

Bongers, T. (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia*. 83:14-19.

Couteaux, M.M., Mousseau, M., Cilirier, M.L. & Bottner, P. (1991) Increased atmospheric CO_2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos*. 61:54-64.

Di Castri, F. (1991) Ecosystem Evolution and Global Change. In: O. Solbrig & G. Nicolis (Eds), *Perspectives on Biological Complexity*. IUBS, Paris. 189-213.

Di Castri, F. & Younès, T. (1990) Fonction de la diversité biologique au sein de l'écosystème. *Acta Oecologica*, 11(3):429-444.

De Ruiter, P.C., Vanveen, J.A., Moore, J.C., Brussaard, L. & Hunt, H.W. (1993) Calculation of nitrogen mineralization in soil food webs. *Plant and Soil*. 157(2):263-273.

Elliott, L.F. & Lynch, J.M. (1994) Biodiversity and soil resilience. In: D.J. Greenland & I. Szabolcs (Eds) *Soil Resilience and Sustainable Land Use*. CAB International, Wallingford, U.K. 353-364.

Gautier-Hion, A. (1989) Are figs always keystone resources for tropical frugivorous vertebrates? *A Test in Gabon.* 70(6):1826-1833.

Ghilarov, M.S. (1977) Why so many species and so many individuals can coexist in the soil. In: U. Lohm & T. Persson (Eds), *Soil Organisms as Components of Ecosystems.* Stockholm. 593-598.

Giller, P.S. (1984) *Community Structure and the Niche.* Chapman and Hall, London.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M. & Swift, M.J. (1995). Agricultural Intensification, Soil Biodiversity and Ecosystem Function. *Journal of Applied Soil Ecology.* In press.

Gisin, H. (1943) Ökologie und Lebensgemeinschaften der Collembolen im Schweizerischen Exkursionsgebiet Basels. *Revue Suisse de Zoologie,* 50 (4):183-189.

Grassé, P.P. (1984) *Termitologia.* Masson,Paris.

Hanlon, R.D.G. & Anderson, J.M. (1980) Influence of Macroarthropod feeding activities on microflora in decomposing oak leaves. *Soil Biology and Biochemistry.* 12:255-261.

Hawksworth, D.L. & Mound, L.A. (1991) Biodiversity Databases: The Crucial Significance of Collections. In: D.L. Hawksworth (Ed),*The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture.* CAB International, Wallingford. 17-31.

Hendrix, P.F., Parmelee, R.W., Crossley Jr., D.A., Coleman, D.C., Odum, E.P., & Groffman, P.M. (1986) Detritus food webs in conventional and non-tillage agroecosystems. *BioScience.* 36(6):374-380.

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. *Biology and Fertility of Soil.* 3(57):57.

Inghan, R.E., Anderson, R.V., Gould, W.D. & Coleman, D.C. (1985) Vertical distribution of nematodes in a shortgrass prairie. *Pedobiologia.* 28:155-160.

Ingham, E.R., Trofymow, J.A., Ames, R.N., Hunt, H.W., Morley, C.R., Moore, J.C. & Coleman, D.C. (1986) Trophic interactions and nitrogen cycling in a semi-arid grassland soil. I. Seasonal dynamics of the natural populations, their interactions and effects on nitrogen cycling. *Journal of Applied Ecology.* 23:597-614.

Jabiol, B., Brjthes, A., Brun, J.J., Ponge, J.F. & Toutain, F. (1992) Une classification morphologique et fonctionnelle des formes d'humus. Propositions du réferentiel pédologique 1992. *Rev. For. Fr.* 46(2):152-166.

Jenkinson, D.S. & Ladd, J.N. (1981) Microbial biomass in soil: measurement and turnover. In: J.N. Ladd & E.A. Paul (Eds), *Soil Biochemistry.* Dekker, New York. 415-471.

Jenkinson, D.S., Adams, D.E. & Wild, A. (1991) Model estimates of CO^2 emission from soil in response to global warming. *Nature.* 351:304-306.

Lavelle, P. (1978) Les vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème. Thèse d'Etat, Paris VI. Publication du Laboratoire de Zoologie de l'ENS.

Lavelle, P. (1986) Associations mutualistes avec la microflore du sol et richesse spécifique sous les tropiques: l'hypothèse du premier maillon. *Compte-Rendu de l'Académie des Sciences de Paris.* 302 III(1):11-14.

Lavelle, P. (1988) Earthworm activities and the soil system. *Biology and Fertility of Soil.* 6:237-251.

Lavelle, P. (1994) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In: *XVth ISSS Congress, 1,* Acapulco, Mexico. 189-220.

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(2):130-150.

Lavelle, P., Lattaud, C., Trigo, D. & Barois, I. (1994) Mutualism and biodiversity in soils. *Plant and Soil.* 170(1):23-33.

Lee, K.E. (1958) Biological studies of some tussock-grassland soils. 10. Earthworms. *New Zealand Journal of Agricultural Research.* 1(6):998-1002.

Lussenhop, J. (1992) Mechanisms of Microarthropod - Microbial Interactions in Soil. *Advances in Ecological Research.* 23:1-33.

Martin, A. (1991) Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. *Biology and Fertility of Soils,* 11:234-238.

Moore, J.C., & de Ruiter, P.C. (1991) Temporal and spatial heterogeneity of trophic interactions within below-ground foodwebs. *Agriculture, Ecosystems and Environment.* 34:371-397.

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist.* 100:65-75.

Rose, C. J. & Wood, A.W. (1980) Some environmental factors affecting earthworm populations and sweet potato production in the Tari Basin, Papua New Guinea highlands. *Papua New Guinea Agricultural Journal*. 31(1-4):1-13.

Schaefer, M. & Schauermann, J. (1990) The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia*. 34(5):299-314.

Setälä, H., Tyynismaa, M., Martikainen, E. & V, H. (1991) Mineralization of C, N and P in relation to decomposer community structure in coniferous forest soil. *Pedobiologia*. 35(5):285-296.

Solbrig, O.T. (1991) Ecosystem Complexity in Time and Space. In: O. Solbrig & G. Nicolis (Eds), *Perspectives on Biological Complexity*. IUBS, Paris. 163-188.

Stork, N.E. & Eggleton, P. (1992) Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture*. 7 (1-2):38-47.

Swift, M.J. & Woomer, P. (1994) *The Biological Management of Tropical Soil Fertility*. Wiley, New York.

Terborgh, J. (1989) *Where Have All the Birds Gone: Essays on the Biology and Conservation of Birds that Migrate to the American Tropics.*. Princeton University Press, Princeton.

Toutain, F., Villemin, G., Albrecht, A., & Reisinger, O. (1982) Etude ultrastructurale des processus de biodegradation II. Modèle Enchytraeides-litière de feuillus. *Pedobiologia*. 23:145-156.

Vannier, G. (1985) Modes d'exploitation et partage des ressources alimentaires dans le système saprophage par les microarthropodes du sol. *Bulletin d'Ecologie*. 16(1):19-34.

Van Praagh, B. (1992) The biology and conservation of the giant Gippsland earthworm *Megascolides australis* Mccoy, 1878. *Soil Biology and Biochemistry*. 24(12).

Villalobos, F.J. & Lavelle, P. (1990) The soil coleoptera community of a tropical grassland from Laguna Verde, Veracruz (Mexico). *Revue d'Ecologie et Biologie du Sol*. 27(1):73-93.

Wallace, A. (1994) Strategies to avoid global greenhouse warming - stashing carbon away in soil is one of the best. *Communications in Soil Science and Plant Analysis*. 25(1-2):37-44.

Wardle, D.A. & Lavelle, P. (1996) Linkages between soil biota, plant litter quality and decomposition. In: G. Cadisch & K.E. Giller (Eds), *Driven by Nature*. Wye College.

Wood, T.G. (1978) Food and feeding habits of termites. In: M.V. Brian (Ed), *Production Ecology of Ants and Termites*. Cambridge University Press, Cambridge. 55-80.