# Functional domains in soils

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Soil processes are significantly regulated by biological activities. Soil ecosystem engineers (predominantly termites, earthworms and ants) and roots produce biogenic structures, aggregates or pores that determine the structure and architecture of soil. The sum of structures produced by a population or community of invertebrate engineers creates a specific environment defined here as a functional domain. Functional domains are characterized by (i) the nature and spatial array of the biogenic structures, solid aggregates, mounds or constructs and pores of different shapes or sizes; (ii) the specific communities of smaller organisms from the meso- and microfauna and microorganisms that they host; and (iii) the spatial and temporal scales at which soil processes operate. The regulation of organic resources have been described and quantified in several studies. In soil, the relative importance of regulation imposed by ecosystem engineering is likely to be greater than regulation by trophic relationships because of the specific ecological constraints observed in this environment when compared to above-ground conditions.

Key words: biogenic structures; ecosystem engineers; food webs; soil fauna; soil processes.

# INTRODUCTION

At the confluence of soil science and ecology, soil ecology is progressively making its way and becoming a truly interdisciplinary field of scientific innovation, with proper concepts and theories (Swift *et al.* 1979; Coleman & Crossley 1996; Lavelle & Spain 2001). The greatest challenge is to integrate physical, chemical and biological processes that occur within soils into true interdisciplinary approaches. These processes are very different in nature and develop across multiple scales of time and space, which makes their integration even more difficult.

A first step has been to recognize that soils have a hierarchical organization and that their function is determined by a suite of hierarchically organized determinants (Lavelle *et al.* 1993; Beare *et al.* 1995). These conceptual clarifications have allowed for a greater understanding of the role that different organisms play in overall soil function and to identify the different scales at which they influence soil processes. This paper defines and develops the concept, first coined by Anderson (1993), of functional domains in soils; that is, parts of the soil that organisms influence by bioturbation and thus regulate soil processes. Other processes that affect soil turbation (e.g. freezingthawing or drying-moistening alternations) may also create their own functional domains. While these are taken into consideration in the general conceptual model, the main part of the discussion considers domains created by living organisms. The value of functional domains in providing a comprehensive understanding of soil function is discussed and compared with a food web approach that only considers trophic relationships.

# HIERARCHICAL NATURE OF SOIL FUNCTION

Soil processes are submitted to a hierarchy of determinants operating in nested scales of time

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and space (Lavelle et al. 1993). Determinants that operate at the largest scales (climate followed by soil properties) constrain determinants that operate at smaller scales: plant communities (which determine the quality and quantity of organic inputs to the soil), 'macro-organisms' (= macroinvertebrates + roots) and microorganisms. Feed back (or 'bottom-up') retroactions exist, however, whereby determinants at lower levels of the hierarchy may influence upper levels. Furthermore, this hierarchy may not be fully operational locally. When the climate is not constraining (e.g. in the humid tropics), when soils have no active clay minerals, such as smectites, that strongly influence microbial activities through several mechanisms, and when the organic matter produced is homogeneous and easy to decompose, the main regulation for microbial activity may be exerted by macro-invertebrates (earthworms and termites) via passage though their gut and the biogenic structures that they create.

The value of this concept may be illustrated by two examples from contrasting environments. In Swedish pine forests, the combined effect of seasonal variations in temperature and moisture may explain 95–99% of the rate of decomposition of litter (Jansson & Berg 1985). In contrast, many publications have emphasized the importance of the chemical quality of litter on decomposition rates in tropical environments (Spain & Le Feuvre 1987; Nussbaumer *et al.* 1997; Lavelle & Spain 2001; Loranger *et al.* in press).

# ORGANIZATION OF SOIL BIOTA COMMUNITIES

Micro-organisms are the main decomposers responsible for over 90% of the mineralization occurring in soils (Lavelle & Spain 2001); they may decompose any kind of natural substrate and individuals that can be cultivated in the laboratory multiply and tremendously increase their biomass in short periods of time (in the order of days). The turnover time of microbial biomass in field conditions, however, generally varies between 6 and 18 months, which indicates that they are inactive most of the time. A likely interpretation of this inactivity is starvation that results from the inability of micro-organisms to move towards new substrates once their immediate surroundings are exhausted. The apparent contradiction between laboratory and field observations has been named the 'Sleeping Beauty paradox' (Lavelle & Spain 2001). The 'Prince Charming' of the story is a macro-organism or any physical process that may bring micro-organisms in contact with new substrates to decompose. In turn, macro-organisms are known to have limited digestive abilities and they largely rely on the ability of micro-organisms to digest a wide range of substrates for them (see Barois & Lavelle 1986; Trigo et al. 1992; Abe 1995). In the gut content of several temperate and tropical earthworms, Lattaud et al. (1999) have found enzymes that were not produced by sterile earthworm gut tissue cultures. Gut tissues of the tropical earthworms Pontoscolex corethrurus and Millsonia anomala did not produce cellulase and mannanase (an enzyme that degrades mannan, which is an essential component of root material). However, another tropical earthworm, Polypheretima elongata, was able to produce these enzymes showing that general pattern-specific situations may occur.

Macro-organisms have been classified into three categories depending on the type of trophic relationships that they have with micro-organisms, and on the biogenic structures that they may produce through their mechanical activities in the soil (Lavelle et al. 1997). The smallest macroorganisms, the Protozoa, Nematoda and other microfauna that live in water-filled soil pores are micro-predators of micro-organisms and do not create any structures. The larger macro-organisms, the non-social arthropods and small oligochaetes (e.g. Enchytraeidae) are litter-transformers that produce organic biogenic structures in the form of fecal pellets. These structures serve as incubators for microbial digestion and do not usually last for long. They may alter the timing and spatial patterns of decomposition, but they generally have limited impact on soil physical properties. In a 40 day microcosm experiment, Hanlon and Anderson (1980) have observed a three phase response of microbial activity to the inoculation of isopods: a sharp decrease in the 2 days following inoculation, a phase of strong stimulation with a maximum respiration 40-100% greater than in the control after 9 days, and a progressive decrease to values 30% lower than the control after 40 days (in treatments that had the greatest number of individuals). This experiment shows that some regulation may occur that limits microbial activity after an initial phase of significant activation. In general, these structures do not last very long because they are often ingested by the same organism or other coprophages.

Soil ecosystem engineers are predominantly termites, ants and earthworms, although many other invertebrates may occasionally create structures. These species are type 4 ecosystem engineers as defined by Jones et al. (1994); they transform soil, an abiotic material, into other structured materials that influence the fluxes of resources used by other organisms. Soil ecosystem engineers produce large amounts of solid organo-mineral biogenic structures that may persist much longer than the organisms that have produced them (see Goss 1991 for roots and Le Bayon & Binet 1999 and Decaëns 2000 for earthworms). They have significant effects on the dynamics of soil organic matter (SOM) and soil physical processes at different scales of time and space (Martin 1991; Mando et al. 1996; Decaëns et al. 1999). Regulation of SOM decomposition involves short-term activation resulting from digestion and further microbial incubation in fresh casts and pellets. After a few days, conditions in casts and pellets become unfavorable for microbial activity and mineralization is greatly decreased. This phase of inhibited microbial activity may last as long as the structures exist, that is, weeks to months to years depending on the size and resistance of the structure. For example, Decaëns (2000) showed that surface casts of the large anecic earthworm, Martiodrilus carimaguensis, from Colombian Eastern llanos have a half life of 5 months in a native savanna and 11 months in an ungrazed pasture. Casts deposited in the soil of large termite nests may last for much longer periods depending on the conditions. Through the modifications of the environment and through the changes in resource availability that they promote, soil ecosystem engineers largely influence the composition and activity of organisms of a smaller size (or 'lower' functional importance) that inhabit their structures or compete with them (e.g. for surface leaf litter) (Marinissen & Bok 1988; Loranger et al. 1998; Decaëns et al. 1999). Many examples show significant differences between communities of micro-organisms, micro, meso and macro-fauna inside and outside a particular functional domain. In pastures of Martinique (French West Indies), populations of the earthworm *Polypheretima elongata* are distributed in discrete patches 20–30 m in diameter (Rossi *et al.* 1997). Loranger *et al.* (1998) observed significant increases in the overall density (8900–13300 m<sup>-2</sup>), species richness (23–28 sp.) and diversity Shannon index (2.74–3.53) of Collembola communities inside these patches when compared to areas outside (Fig. 1). Decaëns *et al.* (1999) also showed a concentration of small soil invertebrates in ageing casts of *Martiodrilus carimaguensis* and an increased root biomass in the upper centimeters of soil below the cast.

#### FUNCTIONAL DOMAINS IN SOILS

Organisms accumulate structures that give soils specific architectures. Networks of galleries, the accumulation and spatial array of biogenic aggregates, and surface deposits are among the conspicuous features that can be observed in the field or via micromorphological studies (Binet & Curmi 1992; Bernier & Ponge 1994; Barros *et al.* 2001). The nature and array of these structures depends



Fig. 1. Comparison of Collembola communities inside and outside patches of the earthworm *Polypheretima elongata* in a pasture of Martinique (French West Indies) Loranger *et al.* (1998). The bars indicate the total density of the community and the composition among different size classes [size increases from bottom (black) to top (white)]. (N sp.), species richness; (H), Shannon index.

on the organisms that have produced them and the diversity and structure of their communities. The physical and chemical parameters of the soil that was used to make the biostructures are also important as they determine the resistance and persistence of these structures (Chauvel *et al.* 1999). The concept of functional domains is based on the assumption that structures created by a species or a group of ecologically related species may be identified and separated from the soil volume; the sum of structures deposited over time by these organisms have specific textural, structural and architectural properties that influence physico-chemical properties of soil and the smaller fauna and microflora that live in this environment.

### DEFINITION

Functional domains are parts of the soil that are influenced by a major biotic or abiotic regulator. They are recognizable in a set of structures (pores, aggregates, fabrics etc.) generated by the regulator that can be physically separated from the soil matrix (Fig. 2). They are colonized by rather specific communities of micro-organisms, other invertebrates and possibly roots. They are places where basic processes of soil function operate at specific spatial and temporal scales.

Every structure existing in soils is part of a functional domain. Some functional domains, however, may be closely related and their frontiers may be are difficult to identify with precision.

#### REGULATORS

Regulators may be biotic or abiotic. Ecosystem engineers such as earthworms, termites or ants create their own functional domains (i.e. the drilosphere, termitosphere and myrmecosphere, respectively). Plants create two different spheres of influence in soils, the rhizosphere of roots and the litter system formed by the accumulation of dead leaves and shoots at the soil surface. Biotic functional domains are synonymous to the 'biological systems of regulation' described by Lavelle (1984). Abiotic regulators may also create sets of recognizable structures; this is the case for freezing– thawing alternations that create mosaic patterns in REGULATOR



Fig. 2. Functional domains in soils. Functional domains are defined by a regulator (a soil ecosystem engineer or any physical agent of soil turbation), the set of structures that they create (aggregates and pores) and the biota that are hosted in the environment created.

soils, or drying-wetting cycles that produce considerable bioturbation and the formation of cracks in soils with high contents of swelling clay minerals.

#### STRUCTURES

Functional domains comprise a set of pores, aggregates and fabrics that have been accumulated by the regulators. The association of pores and aggregates of definite shapes and sizes characterizes every functional domain. Biogenic structures can be considered as extended phenotypes of species (sensu Dawkins 1982), and have been regarded as intermediates between 'taxonomic' and 'functional' diversity (Lavelle et al. 1997). A new research avenue aims at classifying them into homogenous groups and relating their properties to measurable effects on specific soil properties and processes (Mando et al. 1996; Blanchart et al. 1999). For example, in the savannas and pastures of the Eastern Plains of Colombia, 14 species of ecosystem engineers produce biogenic structures at the soil surface; physical and chemical analyses of these structures show differences among all the species. However, an ordination of structures using a multivariate analysis separates three main



Fig. 3. Ordination of biogenic structures collected from a Colombian savanna in the space defined by the first two axes of a principle components analysis (PCA). (a) Eigenvalues and (b) correlation circle between variables and axes; (c) Localization of biogenic structures in the plane defined by axes 1 and 2. This analysis shows that variability is lower inside a large taxonomic group than between groups. (Al), Aluminium concentration; (Al%:%), aluminium saturation of absorbing complex; (K, Mg, Ca, N), potassium, magnesium, calcium and nitrogen contents; (Ptotal and P Bray II), total phosphorus content and the amount of phosphorus that can be assimilated, and extracted by the Bray technique; (MWD), mean weight diameter of water stable aggregates; (BD), bulk density. V, T and F are barycenters of points representing individual species of earthworms (V), termites (T) and ants (F), respectively.

groups, mostly based on a broad taxonomic classification. (Decaëns *et al.* 2001) (Fig. 3). At the scale of the soil profile, micromorphology coupled with image analysis or 3-D tomography have proved to be efficient tools to identify and quantify structures created in the soil (Binet & Curmi 1992; Bernier & Ponge 1994).

#### **COMMUNITIES**

Soil ecosystem engineers and abiotic regulators create specific conditions of environment and resource availability in their domain. For example, the availability of carbon, mineral nitrogen and phosphorus that can be assimilated may be significantly enhanced in fresh earthworm casts or fresh termite pellets when compared to the ingested soil (Lavelle & Spain 2001). As a result, specific communities of organisms from subordinate groups (litter transformers, micropredators and microorganisms) and fine roots may become established in these domains. The food webs that are formed have their composition and energy inputs determined by the activities of the primary regulator. If functional domains are physically isolated one from another, trophic regulations are expected to operate separately inside each domain. In this case, the discrete distribution of food webs in space would make them secondary regulators of processes dominated by the activities of ecosystem engineers. The regulation of populations or activities of soil ecosystem engineers through predation may have specific, and as yet unstudied, effects on soil function.

# PROCESSES

Most processes that operate in functional domains are non-specific. This is the case for all transformations linked to carbon and nutrient cycles that follow the same pathways and are performed by the same micro-organisms everywhere in the soil. Conversely, other processes may be considered as highly specific. This is the case for fluxes of energy and matter across food webs inside functional domains and priming effects on microbial activities resulting from the production of specific resources such as exudates or mucus (Jenkinson 1966; Lavelle & Gilot 1994).

### SCALES

Functional domains affect the dynamics of various processes at different scales of space and time, sometimes with contrasting effects between scales.

In general, mineralization of organic matter is greatly enhanced in microsites (e.g. gut contents of termites or earthworms or root tips where exudates are produced), whereas undecomposed organic matter, further included in aggregates (rhizosphere aggregates, earthworm casts or termite mound walls), may be efficiently protected from mineralization for periods extending from months to years or decades depending on the lifespan of the structure. This regulation of processes that extends over several time scales (from hours to weeks to months to years) and the diverse micro-environments characterize functional domains.

# FOOD WEBS, PHYSICAL SPHERES AND FUNCTIONAL DOMAINS

In previous attempts to identify specific entities or scales at which to study soil processes, a number of related concepts have been proposed or adapted.

In particular, the food web approach has been developed as a way of generating simulation models of nutrient cycling and fluxes through the soil system (Hunt et al. 1987; Ingham et al. 1989; De Ruiter et al. 1993; Zheng et al. 1999). The main drawback of this approach is that, until recently, only trophic relationships were taken into consideration. To date, the models have poorly integrated environmental changes in resources produced by the engineering of large macro-invertebrates and roots (Wardle & Lavelle 1997). This limitation theoretically restricts their predictions to soils in which no engineers operate: this is largely the case for desert and arable soils where reasonably good simulations of nutrient fluxes have been provided by these models. A comparison of this approach to that of functional domains suggests that food webs are actually the sum of organisms classified on the basis of their trophic relationships, irrespective of their inclusion into structures built by a specific regulator (Fig. 4). Inclusion into different domains may impede or favor specific interactions depending on the preference of a given species or group of species for a specific domain.

Ecosystem engineers, however, have their own predators and the indirect effect of these predators on soil function would be an interesting topic to address.



Fig. 4. Alternative functional classifications based on pores, aggregates or communities. The sum of pores (porosphere), aggregates (aggregatusphere) or biota (food web) in the soil may be considered separately. Knowledge of their origin is essential to understanding their dynamics and general properties.

The concepts of the 'porosphere' (Vannier 1987; Beare et al. 1995) and the aggregatusphere that define the sum of pores and aggregates, respectively, with no reference to their origin can also be interpreted as 'vertical' readings of the conceptual model described in Fig. 1. They are well-defined functional entities assessed by a number of efficient methodologies. However, the functional domain approach emphasizes the need to characterize the origin of their components (e.g. meso- or macropores or galleries built by rootlets or termites) to better understand their individual structure, array and time dynamics. For example, a cast from the African geophagous earthworm, Millsonia anomala, is surrounded by a 15  $\mu$ m thick pellicle of hydrophobic organic and mineral colloids that limits remoistening after they have been dried (Blanchart et al. 1993). This cast may be attractive to other geophagous species, such as smaller earthworms, because of the quality of organic matter that it contains, or it may be repulsive to other soil organisms, such as the worm that produced it, because of its compact structure and relatively low moisture content. Such an ageing cast, classified by the physicist as a round macroaggregate of a

diameter larger than 5 mm, may have a very different life expectancy and different hydraulic properties than an aggregate of a similar size that would have been formed in the rhizosphere by a combination of root and microbial effects.

### NEW HYPOTHESES AND APPROACHES TO ANSWER OLD QUESTIONS

The concept of functional domains identifies specific parameters to assess and specific spatial and temporal scales at which to study the interactions among biotic and abiotic soil components. By doing so it provides new approaches to the resolution of research questions in soil ecology.

The relationships between SOM dynamics and soil physical properties may, in part, be explained by considering the scale of individual biogenic structures and their spatial and temporal arrangements in soils. Blanchart et al. (1993) and Martin (1991) have shown how the structure of compact earthworm casts covered with an external, finely textured cortex may favor sequestration of the carbon included in this structure. Blanchart et al. (1999) have shown that the balance between soil compacting and decompacting species may have effects on the bulk density and water infiltration in soil. Part of the mechanisms that underlie the expected relationships operate at the scale of the biogenic structures created by soil engineers, through the composition and architecture of their biostructures, their effects on subordinate communities and, finally, the scales and rates at which the processes operate inside the micro-environments created by the accumulation of their structures. There is a rapidly growing set of data describing and comparing these biostructures and relating their abundance, on the one hand, to the spatial patterns of distribution of engineer organisms that created them and, on the other hand, to the measurable physical or chemical soil properties (Poier & Richter 1992; Jimenez & Rossi 2001).

The relationship between the biodiversity of organisms and soil function may be better understood if raised in the context of functional domains (Hooper *et al.* 2000). Soil physical structure is dependent to a large extent on the nature and diversity of biotic and abiotic turbators. Largescale compaction of soil observed in an Amazonian pasture because of an imbalance between compacting and decompacting species is an example of this relationship. The relative distribution in the soil profile of biogenic and abiotic structures has rarely been studied, and even fewer studies have examined their changes over time (Bernier & Ponge 1994; Blanchart *et al.* 1999).

Beyond their effect on soil physical organization, functional domains are likely to affect decomposition processes through their specific influence on the diversity and trophic organization of other organisms. The direct and indirect effects of soil ecosystem engineers on top soil predators have never been considered in soil function models; the same applies to the evaluation of predation on the activities of influent soil engineers and its consequences for soil function (Cuendet 1979).

Finally, the issue of control treatment or sample for soil ecological studies is clearly questioned by the concept of functional domains. At the small scale of a biogenic structure, for example, earthworm casts or a termite mound wall, control soil is usually taken some distance away from the structure. This soil, however, is itself a set of structures that have been created by different organisms or abiotic processes at different times. Depending on the parameter investigated, a comparison between the fresh structure created by an organism and this soil may not be the best way to characterize the effect of the organism on soil properties. A rigorous way to proceed in that case would be to compare freshly produced structures of different origins among themselves, and with ageing structures of defined ages and origins.

At the larger scale of a soil, the effect of inoculations or exclusions of invertebrates or plants with specific root systems may also be hidden by the effect of inherited structures that persist much longer than the organisms themselves. For example, the effect of inherited structures was seen in a set of experiments comparing the effects of the presence and absence of earthworms on soil organic matter changes in tropical annual cropping systems (Villenave et al. 1999). In systems that had not been tilled, no difference was observed between inoculated and non-inoculated systems. By contrast, in a yam culture made on mounds, organic matter content was significantly greater in the inoculated treatment than in the noearthworm system after 3 years. In this system, soil

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macro-aggregate structure had been dispersed to build the mounds and re-aggregation by active earthworm populations had favored protection of organic matter. In the other experiments, it appears that the conservation of the macro-aggregate structure inherited from past earthworm and other engineer activities had hidden the present effect of inoculated earthworms.

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