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Ecosystem engineers, functional domains and processes in soil. Looking for integrative concepts

Organismes ingénieurs, domaines fonctionnels et processus du sol. A la recherche de concepts intégrateurs

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Soils organisms have extremely diverse sizes and functions and they comprise a huge number of species: ca. 4000 bacterial species per gram of soil and 1000 invertebrates species in a single m² of a beech forest. The aim of this symposium is to review and discuss the concepts that have been proposed to comprehensively describe their role in soil function.

Soil processes are regulated by a suite of hierarchically organised factors (Lavelle et al., 1993; Beare et al., 1995) operating at nested scales of space and time in the order: climate, soil (clay and nutrient status) properties, organic matter quality and organisms. Factors that operate at large scales of time and space (climate, soil) usually constrain the ones that fluctuate at smaller scales (i.e., organic matter quality, macro- and microorganisms). However, the hierarchy, may be locally modified when higher level constraints are reduced (e.g., climate in wet and hot climates) allowing factors at lower levels to predominate (e.g., plants producing especially low - or high-quality litter or intense activity of termites and earthworms in tropical soils). Feed back (bottom up) mechanisms modulate these effects in most cases.

Soil organisms therefore act as proximate regulators of most transformations since they are responsible for 80 to 99% of chemical transformations occurring in soil; micro-organisms in turn are responsible for ca. 90% of soil respiratory activity, roots excluded. Larger soil organisms (including roots) can influence soil physical properties through the breakdown and deposition of organic residues, the formation and occlusion of pores, and the formation and stabilization of aggregates.

This symposium discusses the two major approaches proposed to integrate the roles of these organisms in soil function:

- the foodweb approach with attention to the specificity or generality of specific trophic interactions and their temporal and spatial variability,
- the biological systems of regulation approach, with attention to the role that ecosystem engineers play in regulating the structure and function of soil ecosystems.

Keywords: ecosystem engineers, functional domains, biological systems of regulation

Mots Clés: organismes ingénieurs, domaines fonctionnels, systèmes biologiques de régulation

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Soil function mainly involves recycling of organic inputs and maintenance of physical structure. These processes are regulated by a suite of hierarchically organised factors (Lavelle et al., 1993; Beare et al., 1995) operating at nested scales of space and time in the order: climate, soil (clay and nutrient status) properties, organic matter quality and organisms. Factors that operate at large scales of time and space (climate, soil) usually constrain the ones that fluctuate at smaller scales (i.e., organic matter quality, macro- and microorganisms). However, the hierarchy, may be locally modified when higher level constraints are reduced (e.g., climate in wet and hot climates) allowing factors at lower levels to predominate (e.g., plants producing especially low - or high-quality litter or intense activity of termites and earthworms in tropical soils). Feed back (bottom up) mechanisms modulate these effects in most cases.

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Soil organisms have extremely diverse sizes and functions and they comprise a huge number of species: There may be as many as 4000 bacterial species per gram of soil (Torsvik et al., 1990) and 1000 invertebrates species in a single m² of a beech forest (Schaefer and Schauerman, 1980).

Two major approaches have been proposed to integrate the roles of all these organisms in soil function:

- 1) the foodweb approach with attention to the specificity or generality of specific trophic interactions and their temporal and spatial variability (e.g., Hunt et al., 1987; Moore and de Ruiter, 1991),

- 2) the biological systems of regulation approach, with attention to the role that ecosystem engineers play in regulating the structure and function of soil ecosystems.

Foodwebs: Conceptual and simulation models of foodwebs in soil have been developed in a limited number of cases including those representing grassland, desert and arable land ecosystems. They are « organism-oriented » models (Paustian, 1994) that focus principally on the interactions among microbes, microfauna and mesofauna. In most cases, organisms are grouped into broadly defined functional units (e.g., bacteria, saprophytic fungi, fungivorous nematodes or predaceous mites). Predation is the only interaction that is actually taken into consideration. Satisfactory simulations of patterns of nutrient fluxes in soils have been provided in a number of cases. However, they do not usually consider the role of larger invertebrates or plant roots (ecosystem engineers) nor the consequences of mutualistic interactions for soil function (Beare et al., 1995).

Biological systems of regulation: this approach was first approached by Hiltner (1904) for the rhizosphere of roots, followed by Bouche (1975) who coined the term drilosphere to describe the thin layer of soil (2mm thick) surrounding an earthworm burrow and the microflora that inhabit. This concept was further extended to the whole set of structures created by earthworms and generalised to include other biologically relevant spheres of influence like the rhizosphere of roots, termitosphere of termites and litter system (or detritosphere) of litter invertebrates (Lavelle, 1984; Beare *et al.*, 1995). These “ecosystem engineers” (sensu. Jones et al., 1994) have a dominant role in regulating the activities of many others. The composition and diversity of their communities may be critical to developing and maintaining the diverse mosaic of resource patches, and microhabitats in soils (earthworm casts, termite galleries etc...)(Beare et al, 1995) that have been termed biogenic structures (Lavelle, 1997). The physical and (bio)chemical characteristics of these biogenic structures as well as their spatial and temporal distribution (as mediated by the ecosystem engineers) define their suitability as microhabitats for other organisms. In this way, a limited number of organisms may have an overriding influence on the composition of other soil organism communities (nested biodiversity hypothesis)(Lavelle, 1996). Several authors have since helped to better define and refine these concepts (Anderson, 1993; Brussaard and Juma, 1996; Coleman and Crossley, 1995). Comprehensive reviews of these functional domains have also been presented. Despite these advances, the functional domain approach faces challenges in defining clear spatial and temporal boundaries, making the concept difficult to integrate into simulation models.

On the other hand, alternative paradigms that consider microenvironments irrespective of their origine have been proposed. They are the porosphere (sum of pores , Vannier, 1973) and the aggregatusphere (Beare et al., 1995). While they may originate from a combination of physical and biological processes, they are clearly modified by biological forces that influence the structure and function of soil biological communities.

This symposium paper will present a detailed, up-to-date examination of these approaches with the objective of achieving a more comprehensive integration of the contributions of organisms to soil function. It is our goal in this symposium to propose commonly agreed definitions for all domains and to develop some new approaches to conceptualizing and modelling the arrangement of these domains in space and time.

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