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Soil fauna and soil function in the fabric of the food web

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Summary

Over the last four decades, spanning David Coleman's career, and in no small measure thanks to him, soil ecologists have made tremendous progress in describing and understanding the overwhelming complexity of biological, biophysical and biochemical interactions in soil. These interactions shape the soil as a habitat for the soil food web and the vegetation and, thereby, regulate the two main life-supporting processes on Planet Earth: production and decomposition. Changes in decomposition and production processes are governed by (human-induced) changes in vegetation composition/cover, the amounts and quality of organic residues and (in)organic fertilizers entering the soil. Such modifications alter the physical environment and the soil biota. Hence, decomposition and production processes cannot be understood and/or manipulated without explicitly addressing the composition and activity of the soil food web. Using a conceptual model, we argue that quantitative understanding of biophysical interactions, in particular those between soil fauna and soil structure, are paramount to understanding biological and biochemical processes in soil and the availability of water and nutrients to plants. The need to increase the efficiency of crop production worldwide, to reverse soil degradation and to increase soil resilience will set the agenda for soil ecologists in the near future.

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Introduction: plants versus soil biota as ecosystem engineers

In the Academic Press Dictionary of Science and Technology (Morris, 1992), two out of four definitions given for "fabric" are relevant for this article. In one of these, fabric is defined as "the physical properties of a soil that depend on the spatial arrangement of its particles." In the other one fabric is defined as "the arrangement and physical relationship of components or constituents of something." We are most familiar with the first definition in soil research. However, soil organisms are constrained in their functioning not only by the spatial arrangements of primary particles, but also by that of roots, plant litter and soil organic matter (SOM). Hence, the second definition is more fitting. Indeed, higher plants, especially long-lived plants such as trees, may be seen as the main fabric of the environment for other plants such as epiphytes and the aboveground fauna. Therefore, higher plants are not just part of the terrestrial food web, they are also, together with the bedrock and minerals in soil, the fabric of the food web.

Plants play a key role in the two major life-supporting processes in ecosystems: production and its mirror image, decomposition. In terrestrial ecosystems higher plants are quantitatively the most important primary producers. We tend to think of primary production as mainly an aboveground process, but, depending on growth conditions, most of the production may occur as roots and root-derived materials belowground (Manlay et al., 2002a–c; Martin and Merckx, 1993). We also tend to think of decomposition as mainly a belowground process, but the canopies of trees are home to a plethora of relatively small habitats, such as the hearts of bromeliad epiphytes in tropical forests. Epiphytes are a case in point, because they create a suitable microclimate for mosses and together they promote the accumulation of dead organic matter on the branches where they sit. These accumulations have the characteristics of an organic soil to the extent that tree branches even colonize them with roots, creating a habitat that not only looks like soil, but, indeed, functions like soil (Nadkarni et al., 2002). If trees (and possibly other long-lived plants) engineer, and benefit from the decomposition of substrate aboveground, do they also do this belowground? Different plant species may create an environment belowground that considerably modifies the composition of the rhizosphere biota. Also, the quality of litter varies considerably between trees and between plant species in general, which affects the decomposer food web and nutrient cycling (Tian et al., 1993, 1997a; Wardle et al., 2004). Plants connect the two subsystems, not only by photosynthesis and by creating habitats where decomposition can take place, but also by "accommodating" other organisms, which spend parts of their life cycles aboveground and in soil. Tree canopies also act as sources for organisms that can colonize the soil because they can inhabit both. For example, following removal of the organic horizons, some species of nematodes recolonized the soil from the tree canopy (de Goede, 1996).

The engineering properties of higher plants also affect the abiotic environment. Plant cover mitigates fluctuations in soil temperature by intercepting solar radiation. Rainfall is intercepted by the canopy and partitioned among evaporation, throughfall and stem flow, while throughfall and stem flow are partitioned among surface flow and infiltrated water in soil. Surface water flows and sub-surface vertical and lateral flows of water are intercepted by roots, as are the particles and solutes carried in the water (Bardgett et al., 2001). Old root channels result in bypass flow (van Noordwijk et al., 2004) and they are preferential growth avenues for new roots (Cadisch et al., 2004). The roots intercepting water affect evapotranspiration and the magnitude and direction of the remaining water flow in soil. Roots take up nutrients and exude a qualitatively diverse array of substances, some of which promote weathering of the bedrock and the formation of secondary minerals (Landeweert et al., 2001).

With (higher) plants as such important ecosystem engineers (sensu Jones et al., 1994), what role is left for the soil fauna in engineering the soil? The objective of this paper is to explore how the soil fauna is influenced by, and in turn, affects the fabric of the food web and what this may mean for the functioning of the soil in terms of water and nutrient fluxes and, ultimately, plant growth.

The issue of scale

Ever since Jenny (1941), soil scientists and ecologists are aware of the five soil-forming factors: time, climate, relief, parent material and biota. In the current "anthropocene" (Crutzen, 2002) biota clearly includes humans. These factors operate in a hierarchical fashion. On a geological *time* scale the movements of tectonic plates determine the macro*relief* of the earth surface. The (bio-)geographic positions of continents and the nature of the *parent material* influence the effects of *climate* on the relative importance of abiotic factors (such as freeze-thaw and dry-wet alternations) versus *biota* in soil formation. Biota here means community structure and species assemblages, which are the outcome of evolutionary processes at a geological time scale, defining the "playground" for ecological and evolutionary processes in contemporary time.

The spatial dimension in soil spans at least ten orders of magnitude, considering that soils are three-dimensional entities, which vary from the landscape to the micrometer scale (Hooper et al., 2000; Tisdall and Oades, 1982) to the molecular scale (Waters and Oades, 1991). There is evidence that even at the landscape scale, spatial patterns of soil biota are not static and not just controlled by environmental heterogeneity, but are dynamic and also influenced by intrinsic population processes such as dispersal, reproduction and competition, and further modified by all kinds of disturbances (Ettema and Wardle, 2002; Fig. 1). At the other end of the size spectrum, roughly below 30 μm, the size of (organo-) clay particles is closely associated with the size of pores and organisms (Waters and Oades, 1991). In this size range, differences in habitable pore space between organisms in different size classes (such as bacteria, protozoa, nematodes and mites/springtails/enchytraeids) define the protective pore space for the smaller size class organisms against predation (Elliott and Coleman, 1988; Elliott et al., 1980; Postma and van Veen, 1990). So far we have thought of these interactions in a too static way, because even bacteria appear to modify the microstructure they live in upon arrival of a food source (Young and Crawford, 2004). It is also well known that bacteria produce polysaccharides which lead to clear orientations of clay particles (Tisdall and Oades, 1982). Arbuscular mycorrhizal fungal hyphae produce glomalin, which has hydrophobic properties affecting water flow (Rillig et al., 2002) and fungi entangle soil aggregates (Degens, 1997). Moreover, all mesofauna comminute organic food sources and excrete faecal pellets, while enchytraeids also ingest mineral soil particles and excrete organo-mineral faecal pellets (Didden, 1990). Termites, earthworms and various other macrofauna invertebrates create channels, redistribute soil and excrete organo-mineral faeces which are, or may turn into aggregates (Lavelle et al., 1997). Megafauna, such as moles, gophers, aardvark, etc. burrow more locally but more intensively. So the picture emerges that at each spatial scale there are "engineers" altering the (micro)habitat for themselves and other organisms. Whether or not we call them "ecosystem engi-

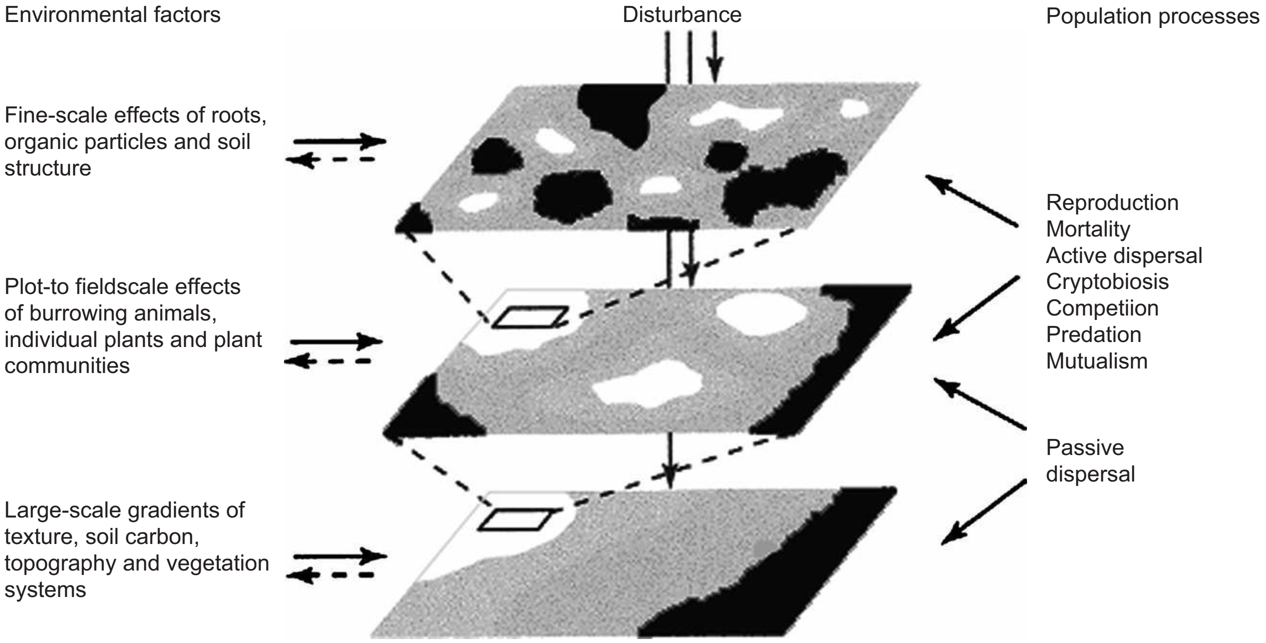

Figure 1. Determinants of spatial heterogeneity of soil organisms. Spatial heterogeneity in soil organism distributions occurs on nested scales, and is shaped by a spatial hierarchy of environmental factors, intrinsic population processes and disturbance. Disturbance operates at all spatial scales and can be a key driver of spatial heterogeneity, for example through biomass reduction of dominant organisms or alteration of the physical structure of the soil substrate. Feedbacks between spatial patterns of soil biotic activity and heterogeneity of environmental factors add further complexity (dotted arrows). The scales at which population processes operate are dependent on soil organism body size, dispersal mechanisms and life-history characteristics. (From: Ettema and Wardle, 2002).

Table 1. Grouping of soil-related processes and components based on time.

Highly dynamic	Dynamic	More static, slow
Soluble nutrients	Adsorbed nutrients	Nutrient reserves in minerals
Active or soluble organic matter	Labile organic matter adsorbed to clay	Chemically stabilized organic matter
Solution and movement of soluble components	Weathering of carbonate minerals	Weathering of silicates and clay minerals
Microorganisms	Micro- and mesofauna Plants	Vegetation (forest)

(Modified after Coleman et al., 1992).

neers" seems to depend on our ability to connect them with ecosystem properties and processes at plant to plot to landscape scales and this appears to be the case more for trees (roots) and the mega- and macrofauna, than for the smaller, invisible, organisms.

Contrary to events in space, events in time are less easily expressed in orders of magnitude, but soil-related processes can be expressed on a relative scale from "static/slow" to "highly dynamic" at spatial scales from microbial size to rhizosphere to landscape (Coleman et al., 1983, 1992, Table 1).

Considering spatial and temporal scales, the issue of interest here is not just one of "where" and "how" and "how much" the engineering soil fauna contribute to ecological processes "now". The issue rather is the feedbacks to the ecosystem and its functioning both "now" and "later". In other words, is the soil macrofauna just engineered by the fabric-determining, microclimate-mediating and organic substrate-providing role of higher plants or does it feed back as ecosystem engineers to plants as well?

Linking species and ecosystem functioning

In view of the bewildering diversity of soil organisms and our appalling lack of knowledge about which organisms are there and what they do, system ecologists usually express ecological processes in terms of carbon and nutrients as a currency, because they are related to the global solar energy input transformations to which all biota contribute. The spatial scale is often chosen as a watershed (Coleman et al., 1992), because we can rather easily measure water and nutrient inputs and outputs at that scale. The temporal scale is usually chosen as years at most, which is, more than anything else, dictated by the time for which research funds are awarded. These choices do not necessarily imply explicit consideration of (soil) organisms. Energy, water and nutrient budgets can be made on a watershed scale with only an implicit account of organism effects on rate parameters. The same holds for modeling SOM. So, why bother about the composition of the (soil) biota and the different modes and rates with which (assemblages of) species populations contribute to ecological processes?

Some answers to this question have been suggested in the literature. Andrén et al. (1999) started from the null hypothesis that an ecosystem functions as an "averaging engine" with process rates controlled by external abiotic influences. Under conditions of change the system may or may not enter into a different state. Change may pertain to temperature, land use, greenhouse gases, species invasions, etc. If the change has effects within the limits within which the system was defined, the change in a process rate may be predictable (Smith et al., 1998; Fig. 2) and effects on organisms need not be considered. If, however, the change affects the soil biota or biotic interactions in such a way that the process rate is altered, the system does not respond in a predictable way (Fig. 2). Andrén et al. (1999) summarized the biota and interactions at risk under change, with subsequent effects on ecosystem process rates, as follows:

(1) keystone species, i.e., species which affect process rates disproportionately to their biomass/numbers,
(2) functional groups with low dispersal rates,
(3) species-poor functional groups, i.e., groups of only few species which affect process rates similarly,
(4) narrow-physiology microorganisms, which exert crucial biochemical transformations such as nitrogen fixation, nitrification and ligninolysis,
(5) interactions such as predation, mutualism (mycorrhizas, rhizobia-plant symbioses, nest-building social insects with fungal growth chambers) or rhizovory, to the extent that they exert controls on ecosystem process rates.

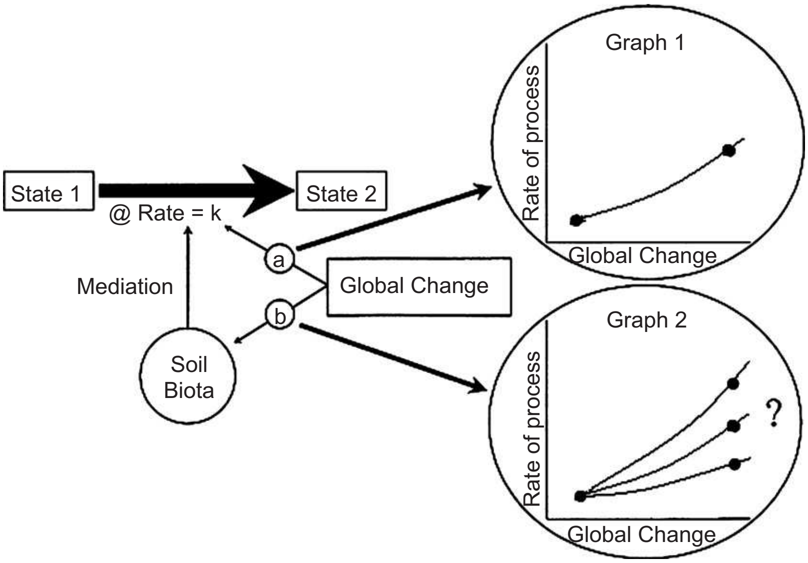

Figure 2. Schematic diagram of a soil process converting a component from state 1 to state 2 at rate k. It is assumed that the process rate is mediated by the soil biota present. It is postulated that change may affect the process directly (route 'a') or through an effect on soil community function (route 'b'). If change acts only through route 'a', the future process rate should be predictable as long as the change is within limits of model calibration. If change also acts through route 'b' and the mediating effect of the soil biota on the process rate is altered, the future process rate may not be predictable. The diagram was developed in the framework of a global change discussion, but appears to be applicable to any kind of change. (From: Smith et al., 1998).

Some widespread soil ecosystem engineers belong to these categories, such as earthworms (categories 1, 2 and 3), termites (1, 2 and 5) and ants (1, 2 and 5).

The quantitative importance of the soil fauna (from protozoa to nematodes, arthropods and earthworms) for ecosystem processes, such as decomposition, nutrient cycling, humification and plant production, often goes beyond expectations from biomass estimations alone (reviewed in Brown et al., 2004; Brussaard, 1998; Brussaard and Juma, 1996; Coleman et al., 1983; Verhoef and Brussaard, 1990; modelled in de Ruiter et al., 1993, 1995; Marinissen and de Ruiter, 1993; Neutel et al., 2002). These groups exert their effects at spatial scales related to their sizes and activity ranges. Early work of Elliott et al. (1980), Heijnen and van Veen (1991) and Postma and Van Veen (1990) showed the quantitative importance of differences in soil architecture (texture/structure) for the dynamics of bacteria, protozoa and nematodes, with positive effects of increasing grazing and predation on nitrogen mineralization under nutrient-limited conditions (Hassink et al., 1993; Verhoef and Brussaard, 1990). In structured soils, the effects of grazing and predation on populations and C and N dynamics will be controlled by soil pore/aggregate formation and degradation (Elliott and Coleman, 1988). However, the linkage between soil biological activity, C and N mineralization and stabilization and soil structure dynamics is not straightforward. Five major factors influence this link: soil fauna, microorganisms, roots, inorganics and physical processes (Six et al., 2004). While freeze-thaw and dry-wet alternations and plant roots contribute to soil porosity/aggregation and pore/aggregate size distribution and stability, the soil macrofauna also play an important role, depending on the mineralogy and texture of the soil (Six et al., 2004). For example, going from a conventional arable to an organic arable to a grassland system on a Calcaric Fluvisol in The Netherlands, the impact of earthworms on soil structure formation increased from 10 to 23 and 54% in the 0–10 cm layer and from 5 to 33 and 49% in the 10–20 cm layer, respectively (Pulleman et al., 2003). Earthworm excrements form macroaggregates (>250 μm) that are often enriched in carbon compared with the surrounding soil and contain large amounts of stable microaggregates (50–250 μm). This indicates the existence of an earthworm-induced pathway of microaggregate formation within macroaggregates and associated C stabilization (Bossuyt et al., 2004, 2005; Pulleman et al., 2005a, b). Such worm casts contribute to the physical protection of SOM in the medium-to-long term (Blanchart et al., 1999; Bossuyt et al., 2004, 2005; Pulleman et al., 2005a, b). However, the relation between earthworm activity and the presence of macroaggregates that are highly enriched in organic matter and stable microaggregates is not linear, but depends strongly on soil management or land use (Pulleman et al., 2005a, b), indicating the importance of interactions between earthworm activity and the availability and quality of organic resources (Shipitalo and Protz, 1989).

Earthworms also affect the hydraulic properties of soil, e.g. by causing bypass flow (Edwards et al., 1990). Termites likewise form microaggregates as faecal or oral pellets, which improve the microstructure of the soil (Bignell and Holt, 2002; Jungerius et al., 1999; Lobry de Bruyn and Conacher, 1990), which may make up as much as 20% of the topsoil matrix in an oxisol in Kenya (Kooyman and Onck, 1987). Their burrowing activity breaks up crusted surfaces, accounting for over 60% of topsoil total porosity (Mando and Miedema, 1997) and leading to enhanced infiltration and water storage (Mando et al., 1996).

The "importance" of the ecosystem engineering soil flora and fauna for soil processes

The relative importance of roots and aboveground litter in the formation of (biogenic) soil structure has been little investigated. In a field study using ^{15}N-labeling of roots versus aboveground plant parts in tree-base systems in Kenya, almost equal percentages of ^{15}N were recovered in the clay+silt size fraction (22% and 20%, respectively), while roots and foliage differed in their contributions to water-stable aggregates $>20\,\mu$m (39% and 31%, respectively) and free organic matter $>20\,\mu$m (39% and 49%, respectively). It was concluded that roots play a larger role in soil structure formation than foliage (Albrecht et al., 2004). Using ^{14}C labelling to monitor changes in the concentration of new surface residue- and root-derived C in aggregates of different sizes and stabilities during a 1 year incubation under simulated no-till conditions, Gale et al. (2000) found that new-root derived C is more important than surface residue-derived C in the stabilization of 250–2000 μm macroaggregates against slaking. Unfortunately, the soil macrofauna was not considered as agents of aggregate formation in these studies.

The relative contribution of roots and soil macrofauna to the formation of biogenic structures and pores has rarely been studied, either. In a study in a young pasture of *Digitaria decumbens* on a Vertisol in Martinique, Chevallier et al. (2001) manipulated plant-derived and earthworm biomass in soil. They found that after 4 years a substantial increase in soil organic carbon in the top 10 cm was entirely due to root inputs. However, at increasing depths to 40 cm, the contribution of earthworms to enhanced soil carbon and the observed higher percentage of water-stable aggregates increased (Fig. 3; Albrecht et al., 2004). Unfortunately, no treatment without roots but with earthworms was included which could give us a better insight into the importance of the interaction between organic resource availability and earthworm activity on soil carbon and aggregate stability (Pulleman et al., 2005a).

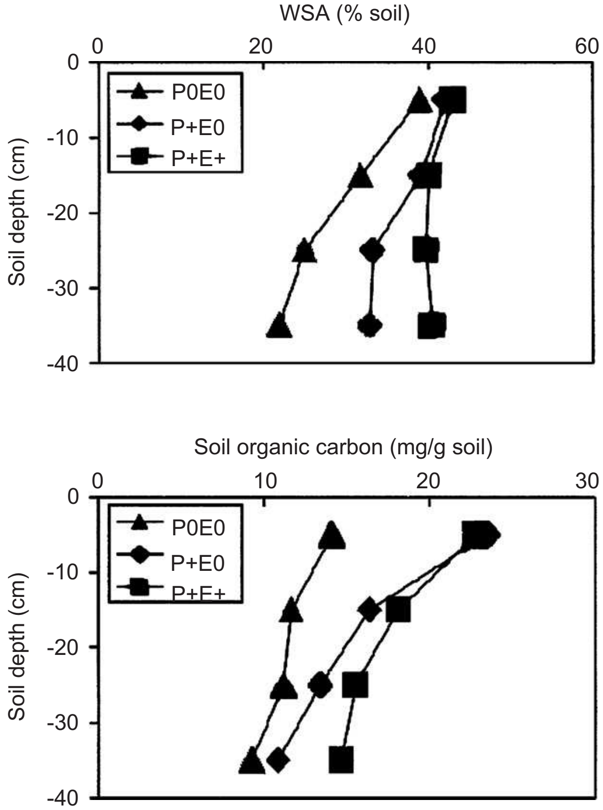

Figure 3. Impact of root inputs and earthworm activity on water-stable aggregates (WSA) in soil and on soil organic carbon, evaluated using herbicides and nematicides. P0E0: exclusion of roots and earthworms. P+E0: root effect only. P+E+: root and earthworm impact. (From: Albrecht et al., 2004).

So far, very few studies have quantitatively assessed the contribution of the soil macrofauna to soil structure formation and the dynamics of these structures relative to other soil structure forming agents, such as roots, microorganisms and physicogenic factors. Micromorphological analysis of soil structure in thin sections provides an excellent tool to quantify the contribution of different soil structure forming processes under different land use or management systems, as has been shown by Jongmans et al. (2003) and Pulleman et al. (2005a). This technique, and CT-scanning techniques (Young and Crawford, 2004) can be used for future studies and can also be applied to compare different climates or soil types.

The effects of the engineering soil fauna on carbon and nutrient cycling are rarely quantitatively integrated with their effects on soil physical properties and transport processes, although plant growth and productivity are mediated by the latter. For example, in an otherwise excellent review, Wardle et al. (2004) mention earthworms as being promoted by plants in fertile, productive (but not unfertile, unproductive) ecosystems, but, conversely, soil ecosystem engineers are not mentioned when dealing with effects of the soil community on aboveground communities. In the same issue of Science, featuring a section on Soils – The Final Frontier, Young and Crawford (2004) make a convincing plea for an integrated approach to studying soil with emphasis on the interactions between physical and biological processes, but this plea is entirely based on such interactions at the scale of microbes, without considering soil fauna as ecosystem engineers.

So, although more than 10 years have passed, the observation of Juma (1994) is still correct: "In order to bridge C and N cycling and soil structure formation, it is now necessary to

(1) develop a model which describes soil porosity in three dimensions and incorporates food web dynamics within this matrix or
(2) expand current SOM models with explicit definition for microbial and faunal activity for specific microsites in soil."

A rare example of the latter is reported by Lavelle et al. (2004), who used the CENTURY model of SOM dynamics (Parton et al., 1987) and experimental data on the decomposition of organic matter in undisturbed and 2 mm-sieved earthworm casts from a tropical savanna to evaluate the effects of earthworm removal on SOM decomposition. They estimated that, with earthworm removal, 10% of the carbon would disappear in 30 years, largely from the "slow" pool, which is the organic matter binding microaggregates to macroaggregates.

Biogenic structure as a unifying concept

Because of the myriad of species and ecological interactions in soil, it will be very difficult to gain a quantitative understanding of soil fauna for soil functioning following a reductionist approach and scaling up (Andrén et al., 1999). This problem has been addressed to some extent by Beare et al. (1995), who view soils as being composed of a number of biologically relevant spheres of influence (detritusphere, drilosphere, porosphere, aggregatusphere, rhizosphere) that define much of the soil's spatial and temporal heterogeneity regulating interactions between organisms and biogeochemical processes. Such spheres of influence can be considered microsites where food web dynamics operate sensu model no. 1 of Juma (1994, see above). The spheres of influence of Beare et al. (1995) are similar to the domains (= habitat space influenced by an organism) of Anderson (2000) for larger organisms, which create patches that have a cascade of effects on smaller organisms. They are also similar to the "functional domains" of Lavelle (2002), which are defined by a regulator (a physical agent of soil perturbation or a soil ecosystem engineer), the structures they create (characterized by aggregates and pores of various shapes and sizes) and the biota for which these structures constitute a habitat (Fig. 4; Lavelle, 2002).

Although different species of soil ecosystem engineers may create different structures in terms of aggregation (aggregate size, stability and quality and content of organic matter), porosity (pore volume and pore size distribution) and soil biota inhabiting these structures, differences between structures produced by broad taxonomic groups (earthworms, ants and termites) appear to be larger than differences within such structures (Lavelle, 2002). It may be inferred that a functional classification of structures is possible. If so, a quantitative elaboration of Juma's (1994, see above) model no. 1, which seems to be lacking so far, comes within reach. A case in point is a simple spatial model that captures the role of biogenic, mainly termite-mediated macropores in water infiltration and runoff (Léonard and Rajot, 2001; Léonard et al., 2004). This simple model could be further improved and linked to existing crop-soil models.

While recognizing that structures may also come about by abiotic factors, this model may conceptually take the shape of Fig. 5 for biotic ecosystem engineers (roots and soil fauna). In this model, biogenic soil structure is the unifying concept, with SOM (including microbes), the mineral soil, soil fauna and roots all contributing to its dynamics (formation and breakdown), with subsequent effects on ecological processes such as water, carbon and nutrient fluxes. For example, stable soil aggregates not only reduce runoff and erosion

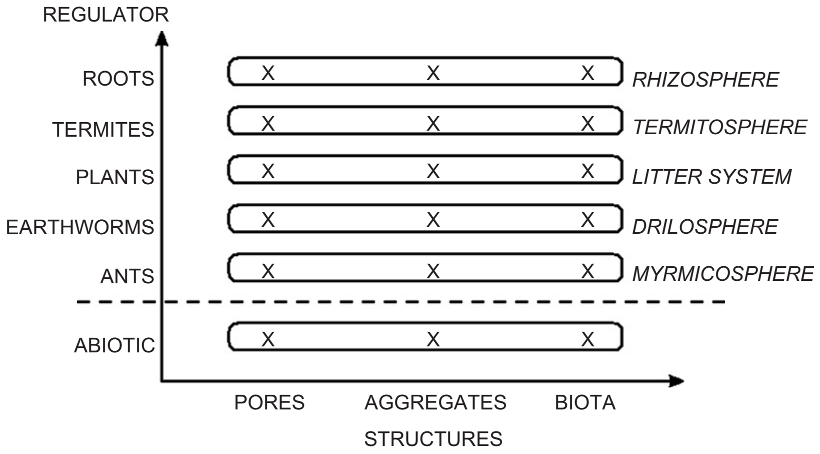

Figure 4. Functional domains in soils are defined by a regulator (ecosystem engineer or any physical agent of soil perturbation), the structures created (aggregates and pores) and the biota that are hosted in the environment created. (From: Lavelle, 2002).

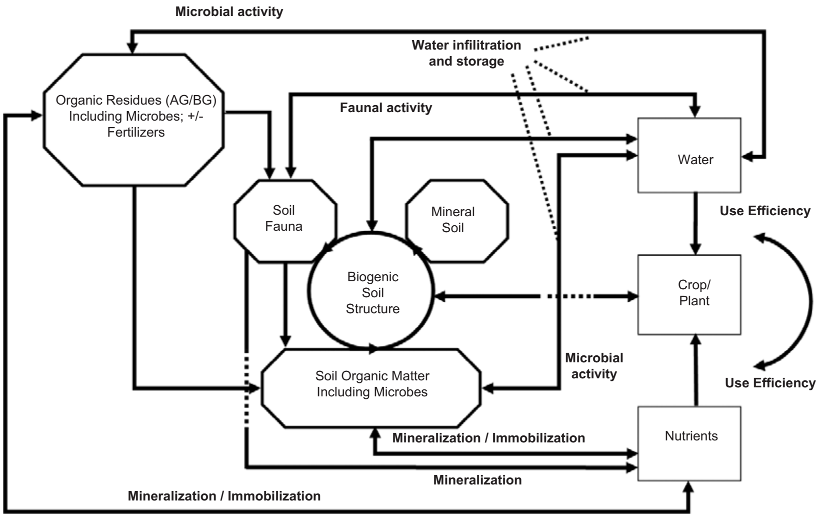

Figure 5. Biogenic soil structures as a unifying concept for regulation of water, carbon and nutrient fluxes, affecting water and nutrient use efficiencies of the vegetation. The biogenic structures are formed by interacting soil fauna, mineral particles and SOM. (Modified from original drawing by M.M. Pulleman).

(Barthes and Roose, 2002), but also physically protect SOM (Tisdall and Oades, 1982). Until now, aggregates have mostly been studied as static entities, whereas recent studies indicate that the turnover of aggregates is at least as important in determining C and N dynamics as aggregate size and stability (Six et al., 1999; Denef et al., 2001). The turnover of macroaggregates ($>250\,\mu$m) has to be sufficiently slow to allow the formation of microaggregates (53–250$\,\mu$m) within macroaggregates. These microaggregates are formed around decomposing organic residues that gradually become encrusted with clay and microbial cells and exudates (Six et al., 2000) or their formation is directly induced by earthworms (Bossuyt et al., 2004, 2005; Pulleman et al., 2005a, b). Microaggregates account for most of the medium to long-term C sequestration (Jastrow et al., 1996; Six et al., 2002). In addition, aggregates form temporary N pools that release N upon breakdown (Elliott, 1986), acting like a slow-release fertilizer.

However, scaling up from microsites would still require a quantitative understanding of the abiotic buffering of fluxes at higher scales. To avoid this problem, scaling down from higher scales may identify the spatial/temporal level(s) at which ecosystem properties and processes can be understood as emerging from structures produced by, and activities of the underlying species (Anderson, 2000). Lavelle et al. (2004) give a number of examples of the aggregated distribution of earthworm populations, which, in some places, was independent of basic soil parameters. Furthermore, different earthworm populations showed spatial patchiness, while the dynamics in such patches were not synchronous with that in other patches. The patch dynamics of populations will have cascading effects on populations of other species and bio-physical and bio-chemical processes. These effects may be simultaneous, if the other species respond immediately, but, given the structural complexity of soil, effects are more likely postponed until these other species have colonized. Indeed, a succession of patches may occur for large species that produce large casts and tend to compact the soil and smaller species that produce fine granular casts after ingesting the larger casts of the first type of species. The two different actions by differently sized species coincide with the protection and decomposition of carbon, respectively (Blanchart et al., 1999; Decaëns and Rossi, 2001). By focusing on short-term, small-scale effects of these earthworms and then scaling up, their effects on ecosystem functioning would have been entirely misinterpreted.

Identifying scales at which soil ecosystem engineers make a difference to ecological processes appears to be achieved best under conditions of change (Andrén et al., 1999; Smith et al., 1998) or stress (Tian et al., 1997b). For example, earthworm-associated soil porosity rapidly declined after the demise of indigenous earthworms due to deforestation, followed by rapid colonization of one compacting species in the Amazon (Lavelle, 2000). Conversely, water infiltration, plant re-establishment and crop productivity on crusted soils of the sub-Sahel rapidly followed the recolonization of these soils by termites making burrows and galleries after mulching (Mando et al., 1996, 1997a, 1999). Just as in spatial scales, a caution is in order as well when considering time scales. Because biogenic structures, such as earthworm excrements and termite oral and faecal pellets may persist for months or even years (Kooyman and Onck, 1987; Blanchart et al., 1999), their effects on ecosystem processes will not always be readily detected in experiments with versus without soil ecosystem engineers, as long as the soil still contains those legacies (Villenave et al., 1999).

Bioassays of ecosystem-level effects of biogenic structures

From a utilitarian point of view, the scaling-down exercise to identify engineering effects of the soil fauna on ecosystem functioning should focus on the spatial and temporal levels at which human-induced changes in biogenic structure dynamics become noticeable in terms of agricultural productivity or biodiversity or any other human goal. In the case of agriculture, management of (formerly) forest or savanna may be directed at maintaining or restoring sufficient plant biomass and plant cover to maintain/restore the SOM input and microclimate that is conducive to the original soil macrofauna to maintain/restore their engineering effects. More realistically, however, management may be directed at attaining a new assemblage of soil ecosystem engineers under agricultural conditions that do not allow the persistence of the entire original fauna. Recent studies revealing the intimate relation between aggregate turnover and SOM dynamics indicate the need for agricultural management that balances macro- and microaggregate turnover in order to optimize their protective (soil and SOM stabilization, associated increase in CEC and nutrient conservation) versus productive (nutrient release) functions. Particularly tillage and organic residue quality govern the rate of aggregate turnover (Six et al., 2001) and, therefore, aggregate size distribution and the content of carbon and nitrogen in each aggregate size class (Mando et al., 2005a, b), but their quantitative and integrative effects on aggregate and SOM dynamics are poorly understood (Vanlauwe et al., 2001). In addition, the capacity of the soil for C sequestration is affected by physicochemical soil properties like soil texture and mineralogy (Six et al., 2002).

Climate, soil texture and management also determine the activity of soil macrofauna such as termites and earthworms, producing biogenic structures. Given that the dynamics of biogenic structures affect water (Anderson, 1988; Mando, 1997b) and carbon and nutrient fluxes (Bossuyt et al., 2004, 2005, Pulleman et al., 2003, 2005a) with quantitatively important feedbacks on plant production (Brown et al., 2004), we propose the water and C and nutrient use efficiencies of crops/cropping systems as bioassays of the success of management of the soil macrofauna in agriculture aimed at an optimal balance between the protective and productive functions of soil aggregates (Fig. 6). Organic matter quality, crop rotation and (reduced) soil tillage will be important management factors, supplemented by fertilization, which determine the (beneficial) role of the soil fauna in (sustainable) agroecosystems.

There is evidence that this is a useful approach. For example, ecosystem nutrient use efficiency is not just an outcome of the characteristics of the plant species that comprise the system, but also of factors that affect soil nutrient supply (Hiremath and Ewel, 2001). Moreover, Tian et al. (1997a) suggested that the manipulation of earthworm activity with high- and low quality mulches improves the synchronization of soil nutrient supply and crop demand. Mulching-induced termite recolonization of bare crusted soils in the sub-Sahelian region of Burkina Faso led to a rapid increase in water infiltration, number of plant species, plant biomass production and water use efficiency during three consecutive growing seasons (Mando, 1998; Mando et al., 1999). In a termite-dominated agricultural soil in mid-Burkina Faso (Ouédraogo et al., 2006; Fig. 7), the soil fauna enhanced the water use efficiency and apparent nitrogen use efficiency in plots with high-quality organic additions, but reduction in nitrogen use efficiency was observed in plots with low-quality organic additions, which was probably due to initial nitrogen immobilization. This finding underlines the importance of integrating and synchronizing low-quality organic and (in)organic fertilization to attain the highest nutrient use efficiency. An increase in water use efficiency was not observed in the case of cattle dung which has a low mulching effect. This finding underlines the importance of balancing the nutrient-supplying and soil microclimate-enhancing effects of mulching. Future research will have to quantitatively relate these results to the dynamics of biogenic structures in soil.

By definition, the dynamics of biogenic structures is influenced by the presence and abundance of the structure-forming biota. What do we need to know about such biota in order to understand and, finally, predict the effects of management on the dynamics of biogenic structures? Climate and soil type as ultimate factors and soil management (application of organic residue quantity and quality, tillage, etc.) as a set of proximate factors select for or against components of the soil biota. This implies that after a shift in soil management (re-)colonization will depend on the newly created habitat conditions and on presence and distance of source areas as related to the intrinsic dispersal abilities of soil structure-forming species concerned (cf. Fig. 1). Hence, their occurrence, i.e. colonization and settlement, will be related to the habitat-selecting factors under which the species concerned evolved on an evolutionary time scale. Although in this respect all species will show differences, it has been observed that species fulfilling similar roles in ecosystems and having similar life-history-strategies can be grouped into so-called functional groups, based on microhabitat, food choice, feeding behavior and ecophysiology (Hunt et al., 1987). Regarding the soil structure-forming fauna, we hypothesize that biogenic structures can be traced back to certain functional groups. For earthworms, different functional groups have been described as epigeics (superficially living plant litter transformers), anecics (transporting organic residues from the surface into vertical burrows and actively mixing them with soil) and endogeics (foraging on organic matter in the soil

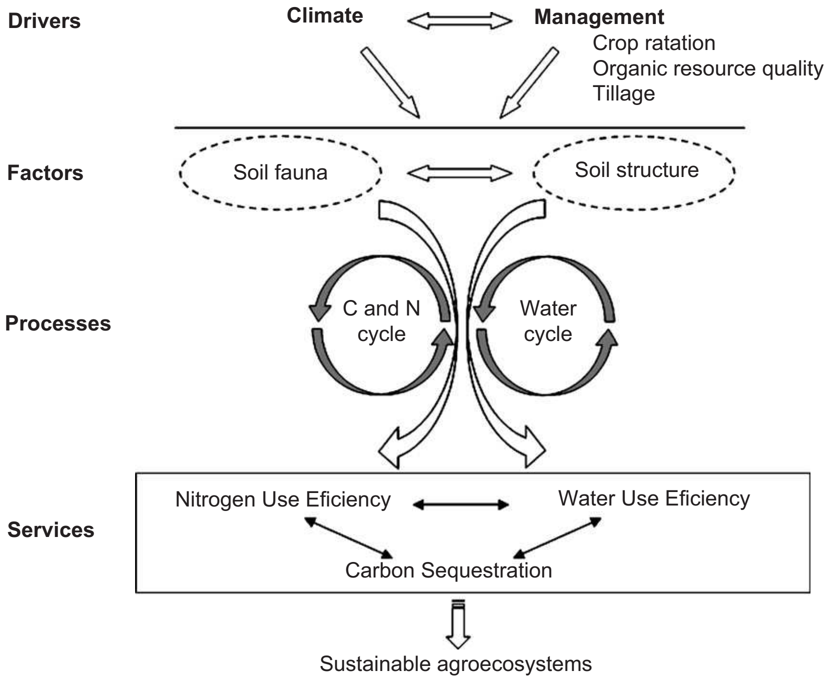

Figure 6. Conceptual diagram of drivers, factors, processes and environmental services in determining agroecosystem sustainability. (Modified from original drawing by J. Six).

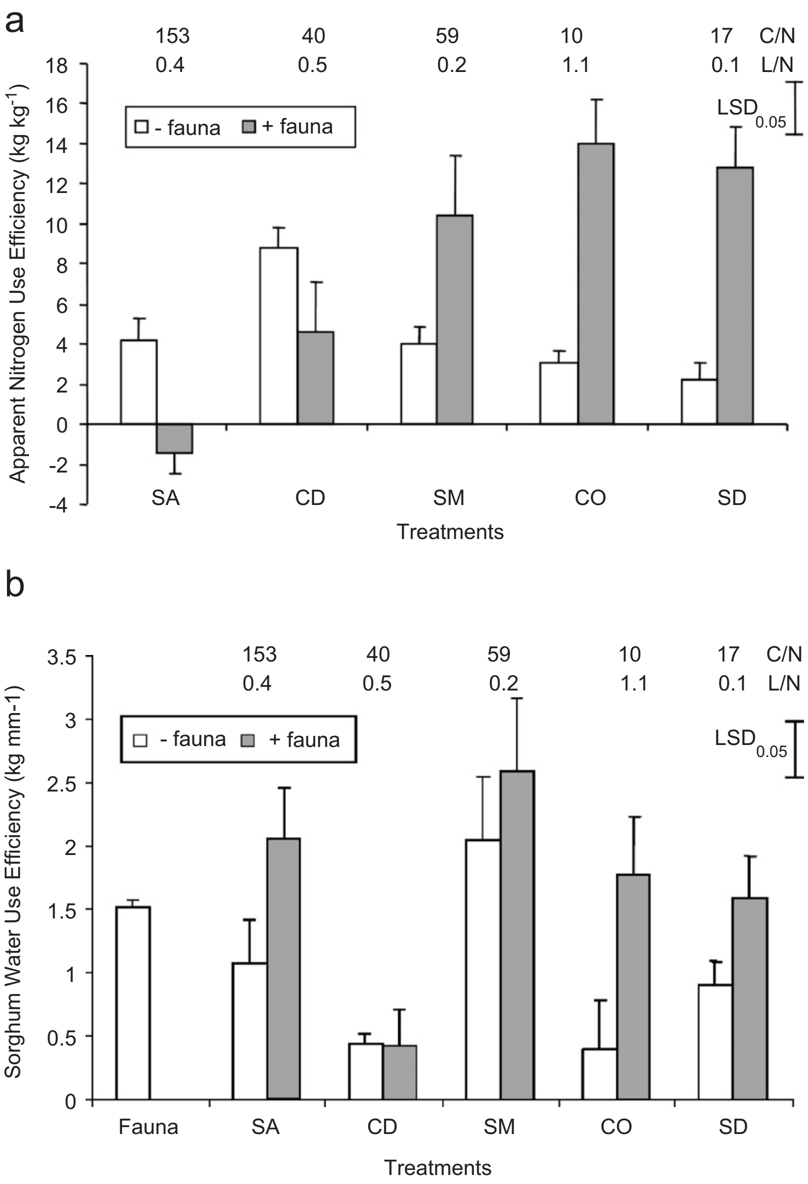

Figure 7. (a) Sorghum apparent nitrogen use efficiency (ANUE) in fauna and no-fauna plots at Kaibo, Burkina Faso, after application of organic resources of different qualities. SA = *Andropogon* straw, CD = cattle dung, SM = maize straw, CO = compost, SD = sheep dung. Bars represent standard deviations. LSD = Least Significant Difference at $P = 0.05$. C/N = Carbon : Nitrogen ratio, L/N = Lignin: Nitrogen ratio; (b) Sorghum water use efficiency (WUE) in fauna and no-fauna plots at Kaibo, Burkina Faso, after application of organic resources of different qualities. Legend as in Fig. 7(a). (From: Ouédraogo et al., 2006).

proper, largely forming horizontally orientated burrows), which can be further subdivided in three subgroups (Lavelle et al., 1998). Termite functional groups are soil feeders, wood feeders, soil/wood interface feeders and litter feeders (Jones and Eggleton, 2000). They can be further subdivided into 17 'functional taxonomic groups' (Davies et al., 2003). Differential land management effects on these groups will translate into differential effects on the structures they produce, affecting soil organic matter, soil aggregation, porosity and water and nutrient availability to plants. A case in point are the soil-feeding termites. Ecological and energetic constraints have kept their distribution limited to equatorial rainforest with stable food supply and microclimate (Davies et al., 2003). Among the termites they appear to be the most affected in agricultural land cleared from tropical forest, which may have negative effects on agricultural productivity (Eggleton et al., 2002). As they have the lowest dispersal abilities among the termites (Davies et al., 2003), the chance of spontaneous re-colonization following a change in agricultural management, which would restore their habitat, will be relatively very low. Because in large parts of the world little is known about the spatial distribution of different functional groups of soil fauna in agricultural soils across climate regions and soil types and of the management practices that promote or impair their activity, this is clearly an important area of research in any context where increasing the efficiency of plant production is at stake.

Increasing water and nutrient use efficiencies is pertinent both in high and low input agriculture, now that water is becoming a (seasonally) scarce commodity almost all over the globe, fertilizer mines are rapidly depleted, and fossil fuels and artificial fertilizers are not affordable or available to many smallholder farmers.

The resulting agro-ecosystems may not always show maximum water and nutrient use efficiencies with reference to a natural ecosystem or an agroecosystem managed with more external inputs than locally available or affordable. This is obviously a consequence of the choice of farmers for crops and cropping systems which have to sustain the livelihoods of their families under given circumstances. However, such choices are not inflexible, if scientifically sound options for improved management link up with farmers' practices (Mando et al., 2006) and broader livelihood interests (Brown et al., 2004).

Conclusions

Plants producing structural materials can be considered both as components of the ecosystem-level food web and as ecosystem engineers in that stems, branches and roots create habitats for other organisms both aboveground and in the soil. Soil macrofauna such as earthworms and termites likewise can be considered both as components of the food web and as ecosystem engineers, in that they modify the inorganic and organic fabric of the soil. The resulting biogenic structures, such as aggregates and pores of various shapes and sizes are habitats for other organisms and modulate biophysical and biochemical processes observed as water, carbon and nutrient fluxes, with feedbacks on plant production and the environment. There is evidence that faunal-produced macroaggregates are important microsites for the formation of microaggregates and, thereby, for the stabilization of SOM and the storage of nutrients, which are slowly released upon their degradation. So far, however, very few studies have quantitatively assessed the contribution of the soil macrofauna to the dynamics of these structures relative to other causal agents, such as roots, microorganisms and abiotic factors. Micromorphological analysis of soil thin sections and CT scanning techniques provide excellent tools to quantify the contribution of different aggregate formation processes to soil structure and how the balance is affected by biophysical conditions, land use and soil management.

For a quantitative understanding of water and nutrient fluxes, as influenced by the soil macrofauna, the spatial and time scales of activity of macrofauna populations, the spatial distributions of the structures they produce, and the persistence of those structures through time have to be addressed. To manipulate such fluxes with the goal of sustainable management of agricultural systems, the soil fauna and the structures they produce, need to be manipulated by altering the soil microclimate and organic matter inputs and quality, i.e. by changing crop rotations/cropping systems, tillage intensity, and residue retention. We propose that the water and nutrient use efficiencies of crops/cropping systems are useful bioassays of the success of such management systems. There is ample circumstantial evidence that this is a useful approach, but quantitative research is needed. Tracing back the biogenic structures to certain functional groups of soil fauna will be an important component of such research.

Increasing water and nutrient use efficiencies is pertinent almost all over the globe. Agricultural management to achieve this should link up with locally derived knowledge and broader livelihood interests of farmers. In this context will it be meaningful to further investigate soil fauna and soil function in the fabric of the food web.

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