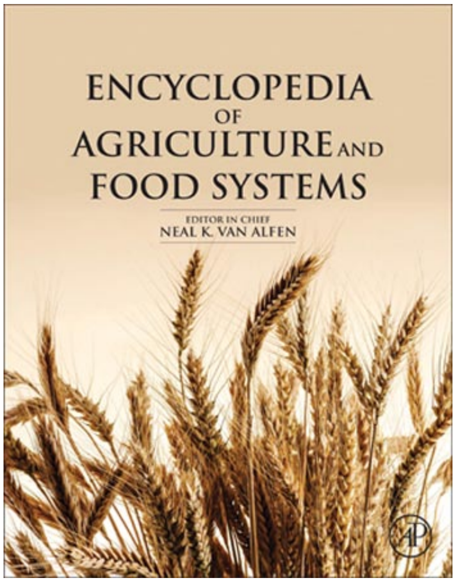

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Biodiversity: Conserving Biodiversity in Agroecosystems

P Lavelle, Institute of Ecology and Environmental Sciences, Paris, France
F Moreira, Universidade Federal de Lavras (UFLA), Minas Gerais, Brazil
A Spain, The University of Western Australia, Perth, Australia

Glossary

Biochory Passive, unintentional transport of spores, eggs, microbial cells, or small animals by organisms that move in the litter and soil, thereby promoting the dispersal of almost immobile organisms.

Bioturbation Soil mixing carried out by organisms in soils, mainly earthworms, termites, and ants, plus a few Coleoptera, nymphal Cicadidae, Isopoda, or Grylotalpidae ('mole crickets'). Bioturbation may be effected by ingesting the soil and passing it through the animal gut (earthworms and humivorous termites), or by constructing mounds, digging galleries and chambers to accommodate colonies and food reserves (ants and foraging and fungus-growing termites). Roots also affect some degree of bioturbation through creating holes that are further used by other organisms as habitats and passageways for movement once the root has died and disappeared.

Catena of soils A succession of soils arrayed down a slope, with profiles changing according to their topographic position. The low-lying parts of the catena generally have a higher moisture status and receive elements eluviated, detached, and transported from the higher parts. The upper parts of the catena may become depleted in clay and nutrients by these processes.

Chemolithotrophy The ability to use energy obtained by the oxidation of inorganic compounds.

Comminution The physical transformation of leaf and root litter with limited chemical (digestive) decomposition. This is an essential process in litter recycling whereby large plant-derived structures, such as leaves, are progressively fragmented into increasingly smaller pieces, thereby increasing the surface area exposed to microbial attack.

Drilosphere A word coined by Bouché (1972) that describes the 'functional domain' created within soil by earthworms ('drilos' in Greek) and is analogous to the well-recognized 'rhizosphere,' the sphere of influence of roots. The drilosphere is thus the sum of earthworms and the structures that they create in soil as casts, galleries, and pores of different sizes and shapes, together with the communities of smaller organisms, invertebrates, and microorganisms that inhabit the habitats thus constructed. The earthworm gut is the critical component of the drilosphere in which earthworm digestion in conjunction with microorganism activity provides the energy necessary to maintain this structure.

Geophagous An organism that ingests soil. Endogeic earthworms and humivorous termites are the main groups using this feeding regime. They actually digest the organic part of the soil, in a mutualistic association with the ingested microflora. The activity of the microflora is greatly enhanced during gut transit and makes part (usually some 10%) of the ingested organic matter available to the earthworm as a product of microbial digestions. A further fraction, as yet unevaluated, is converted into microbial biomass.

Inoculation (with microorganisms, invertebrates, or plants) Addition to the soil of an organism that is absent or present in such low quantities that its effect on, for example, soil structural formation or plant protection is no longer observed. Inoculations are possible only if suitable conditions are present. Re-inoculating an organism that has disappeared from the environment due to impairment of its natural living conditions requires restoration of these conditions. Inoculation of exotic species of microorganisms or invertebrates is often rendered impossible through competition or other effects of local species, an important point to consider when trying to improve plant growth by using microbial supplements and inoculates.

Mineralization/immobilization When microorganisms use a substrate to meet their maintenance and growth needs, they secrete enzymes that degrade the substrate and absorb the metabolites thus made assimilable. Nutrients are absorbed according to the needs of the organism in proportions that can be fixed or variable. When nutrients are assimilated in excess, they are secreted into the external medium in mineral forms as, for example, NH_4 or NO'_3 for nitrogen. When the element is deficient in the substrate used, microorganisms use whatever source of the element that occurs in the soil in mineral form. The result is a decrease in concentration of this mineral element and is referred to as immobilization within the microbial biomass.

Protocooperation An association between microbial and other communities that allows the degradation of a substrate which they would not be capable of degrading alone.

Stoichiometric imbalances Occur when the composition of assimilable nutrients in a food source is so different from their relative tissue concentrations that growth of organisms using this resource becomes dependent on the concentration of the most limiting nutrient.

Theca The external skeleton of some Protoctists of the thecamaebian group and formed from silica. This often sub-spherical envelope protects the organism from predators and drought.

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Introduction

The Green Revolution boosted agricultural production approximately 2.5 times and was associated with an approximately 40% price reduction in the cost of food (MA, 2005). Following on the euphoria of this success there has been increasing pressure to diversify production and to improve the planet's environment (Hubert *et al.*, 2010). Successful realization of this pressure will require better soil management. However, current conditions are very different from what they were 50 years ago. The success of the Green Revolution came at the expense of the natural capital, such that 18 of the 24 currently acknowledged ecosystem services have been impaired. Although soils have aided climate regulation by sequestering an estimated 2 Gt carbon (C) per annum from fossil fuel burning, they have lost part of their capacity to regulate hydrological fluxes and nutrient cycles and therefore to support plant production.

The soils of the earth are now being asked to produce 70% more food over the next 35 years, while also producing biofuels, regulating climate through further C sequestration, and helping to conserve biodiversity. However, the other side of this coin is the declining amount of land remaining available for conversion to agroecosystems and the increased cost of energy, which has led to a substantial increase in the price of fertilizers. Further, world sources of phosphorus (P) are being rapidly depleted and the toxic effects of pesticides are now forcing the replacement of these former pillars of intensive agriculture with new technical options.

Agriculture now needs to sustain high levels of production while preserving or restoring the natural capital of the soil. Maintenance of an appropriate level of soil biodiversity is critical to achieving this goal, but in order to protect the soil resource and optimize its long-term use, new land use practices are needed to be developed, based on much greater understanding of the factors controlling its functioning.

This article summarizes the current knowledge of the composition and taxonomic richness of the soil biota. It then examines the participation of the soil biota in the major soil functions and discusses ways to reconcile the conservation and/or improvement of this natural capital with the production of critical ecosystem goods and services.

Components of Soil Biodiversity

Soils were the first terrestrial biotope to be colonized from the marine environment. Hence, they have retained a large component of aquatic organisms in their water-filled pore spaces while evolution has progressively added aerial organisms adapted to living within the soil air spaces. Several hundred millions of years of continuous evolution in this confined environment has conserved some of the most primitive forms of life. It has also created novel associations among organisms with no equivalents in less-constraining parts of the ecosystem.

General Constraints to Life in the Soil Habitat

Life in soil is constrained by three major soil features (Lavelle and Spain, 2001; Lavelle, 2012):

1. A compact soil matrix that possesses few open pores as habitat and limited systems of connected pores, thereby constraining internal flows of air and water;
2. Low-quality food, composed of dead leaves and roots rich in decomposition-resistant polyphenolic compounds, humified and stabilized organic matter, living roots, and other organisms; and
3. Variable moisture conditions that result in the alternation of flooding and drought at the scale of a soil pore, with increasing incidence of saturated anaerobic conditions as pore size decreases.

No single group of soil organisms has been able to adapt optimally to living with all these constraints. Although the smallest microorganisms find relatively constant conditions in the water-filled pores, they have a very limited ability to remain active in aerial conditions. Consequently, once they have exhausted their existing substrate they enter a resting stage – most commonly as a spore or a small dormant bacterial colony. Thus, soil-based microorganisms frequently exist in dormant stages; however, fungi are more active and may be more readily transported by biotic or abiotic agents than bacteria (Lavelle and Spain, 2001). Fungal hyphae, able to cross between pores without water, are generally better adapted to higher water potentials than bacteria, which makes them more tolerant of water deficit. They often rely on invertebrates for the dispersion of their spores (Lavelle and Spain, 2001).

Dormant microorganisms can resume activity when such physical or biological agents as water flows and disturbance caused by mixing, bioturbation, or biochory by roots and invertebrates move microorganisms toward a new source of food. For example, spores of mycorrhizal fungi may be activated when they come into contact with root exudates, leading to the initiation of a mutualistic symbiosis with the host plant. Through this association, a continuous supply of plant-derived carbon substrates is supplied to the fungus, which provides the energy for it to actively colonize the soil and so provide its host plant with soil-derived nutrients (Smith and Read, 2008).

In contrast to microorganisms, large soil invertebrates of the 'soil ecosystem engineer' group, which are principally termites, earthworms, ants, and some Coleoptera and Isopoda, have developed the ability to move and work the soil (bioturbation). This is achieved either by digging with strong legs or mandibles or, as in the case of earthworms, by ingesting the soil and compacting it with their hydrostatic skeleton. These invertebrates, however, have very limited abilities to digest litter and soil resources on their own and consequently interact with microorganisms to take advantage of their outstanding capacities for digestion.

Adaptive Strategies of Soil Fauna

The primary indicator of general adaptive strategy is size (**Figure 1**: Decaëns, 2010 after Swift *et al.*, 1979).

The smallest animals – micro-fauna – are invertebrates smaller than 0.2 mm. They are the predators of the microorganisms and principally comprise proctoctists, nematodes, and a number of groups of lesser importance, such as tardigrades and rotifers. Most of the micro-fauna consume fungi or bacteria and are, therefore, referred to as 'microbial grazers.'

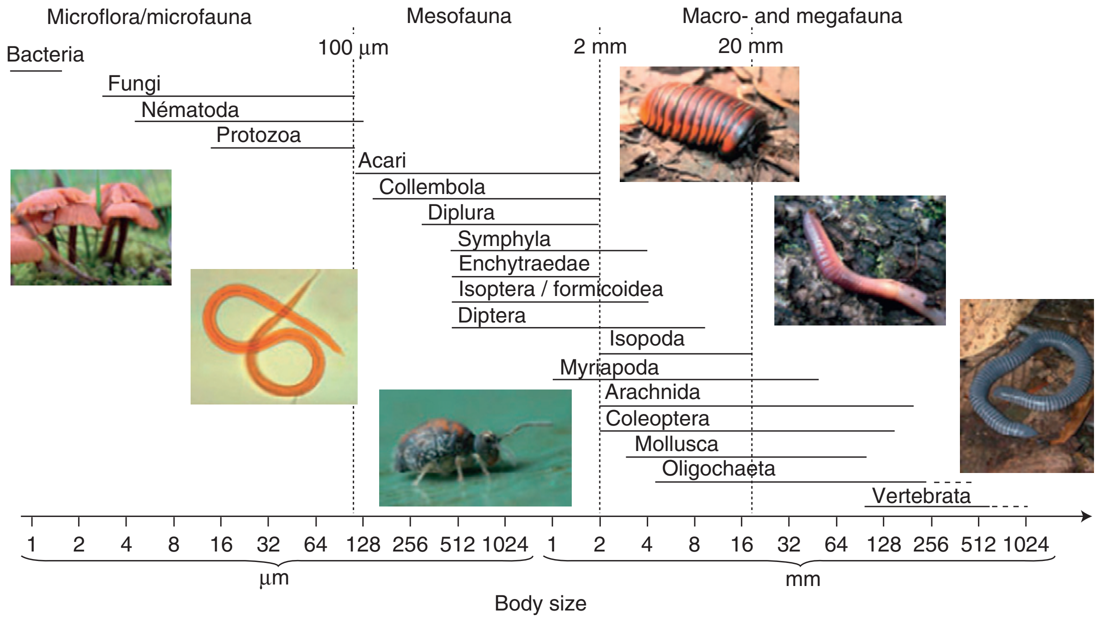

Figure 1 Representation of the main taxonomic groups of soil organisms on a body size basis. Reproduced from Decaëns, T., 2010. Macroecological patterns in soil communities. Global Ecology and Biogeography 19, 287–302 after Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Oxford: Blackwell Scientific.

They exert the primary control of microbial populations and communities. As a result of stoichiometric imbalances, they excrete available forms of mineral nitrogen (N) and other nutrients into the soil solution. Consequently, the complex foodwebs that they form are of great importance to the biological control of microbes and to soil organic matter (SOM) dynamics and the cycling of nutrients (Moore *et al.*, 2004). This is especially true in ecosystems where arid conditions, deep disturbance, or agrichemical stress restrains the activities of larger invertebrates. Such foodwebs based on microbial grazing are of lesser relative importance in natural ecosystems where ecosystem engineers have large populations (Wardle and Lavelle, 1997; Lavelle *et al.*, 2006).

The next group, the meso-fauna, and some large litter-dwelling invertebrates feed on above- and below-ground dead plant material. The comminution and limited digestive processes that they carry out allow some degree of composting. They have been called 'litter transformers' and they accelerate nutrient release on short time scales. Commonly, their fecal pellets are subjected to microbial incubation, thereby releasing assimilable compounds, which will then be consumed by themselves or other invertebrates. This is known as 'external rumen digestion' (Swift *et al.*, 1979; Hassall and Rushton, 1985). Alternatively, the released nutrients may be utilized by microorganisms, thus increasing the microbial biomass.

The largest invertebrates are the 'soil ecosystem engineers.' Members of this group have developed the most efficient interaction with microorganisms and have a sophisticated mutualistic digestion system contained within their own gut (Lavelle *et al.*, 1995). Efficient digestion allows the capture of the large amounts of energy required to ingest several times their own weight of soil daily or to dig dense gallery networks (Lavelle *et al.*, 1997). Where ecosystem engineers are active, the entire upper 10–15 cm of soil may be ingested over the course of a couple of years. This creates a macro-aggregated structure that has highly favorable physical properties, providing resistance to erosion and the promotion of water infiltration and storage. Many ants are, however, predators and are clearly an exception to the above. The 'leaf cutter ants' in particular, and some termites, enter into 'external rumen' relationships with microorganisms; some termites also produce an efficient suite of enzymes in their mid guts.

The correspondence between invertebrate size and function tends to spread their activities across a number of well-separated and discrete scales. The proximate control of microbial communities and their activities by micro-foodwebs occurs mainly within pores and aggregates 50–100 µm in size (Hattori and Hattori, 1976). Litter transformers, however, vary in size from mm to cm and operate at larger scales in the leaf or root litter. The ecosystem engineers operate at even larger scales (from cm to >m), creating structures such as ant or termite colonies, or patches where earthworm populations dominate (Ettema and Wardle, 2002; Rossi, 2003; **Table 1**).

Different Groups and Their Respective Species Richnesses at Local and Global Scales

Although soil biodiversity comprises a large part of global diversity, no precise data are available (**Figure 2**). Recent estimates of total diversity suggest that both bacteria and fungi may each comprise as many as 1.5 million species.

Generally, many of the larger organisms represented in the soil biodiversity have been described, but estimates suggest that only 0.1% of species in the micro-fauna and microorganisms have been described so far (Decaëns, 2010; Wurst *et al.*, 2012).

Another interesting feature of soil organisms is the relative rate of endemism – measured by the local α, to regional β, or

Table 1 Main parameters of the adaptive strategies of organisms in soils

Functional group	*Microorganisms*	*Micro-fauna*	*Meso-fauna*	*Macrofauna*
Body width	0.3–20 mm	< 0.2 mm	0.2–10 mm	> 10 mm
Taxa	Bacteria and fungi	Proctoctists nematodes	Microarthropods Enchytraeidae	Termites earthworms myriapoda, ants, etc.
Water relationships	Hydrobiont	Hydrobiont	Hygrobiont	Hygrobiont
Interactions with microorganisms	Antibiosis mutualism competition	Predation	Predation	Mutualism (external rumen and facultative/obligate internal mutualism)
Ability to change the physical environment	Very limited	None	Limited (fecal pellets)	High (galleries, burrows, and macro-aggregates)
Resistance to environmental stresses	High (cysts, spores, etc.)	High (cysts, spores, etc.)	Intermediate	Low but possible behavioral compensation
Intrinsic digestive capabilities	High	Intermediate	Low	Low

Source: Reproduced from Lavelle, P., Spain, A.V., 2001. Soil Ecology. Amsterdam: Kluwer Scientific Publications.

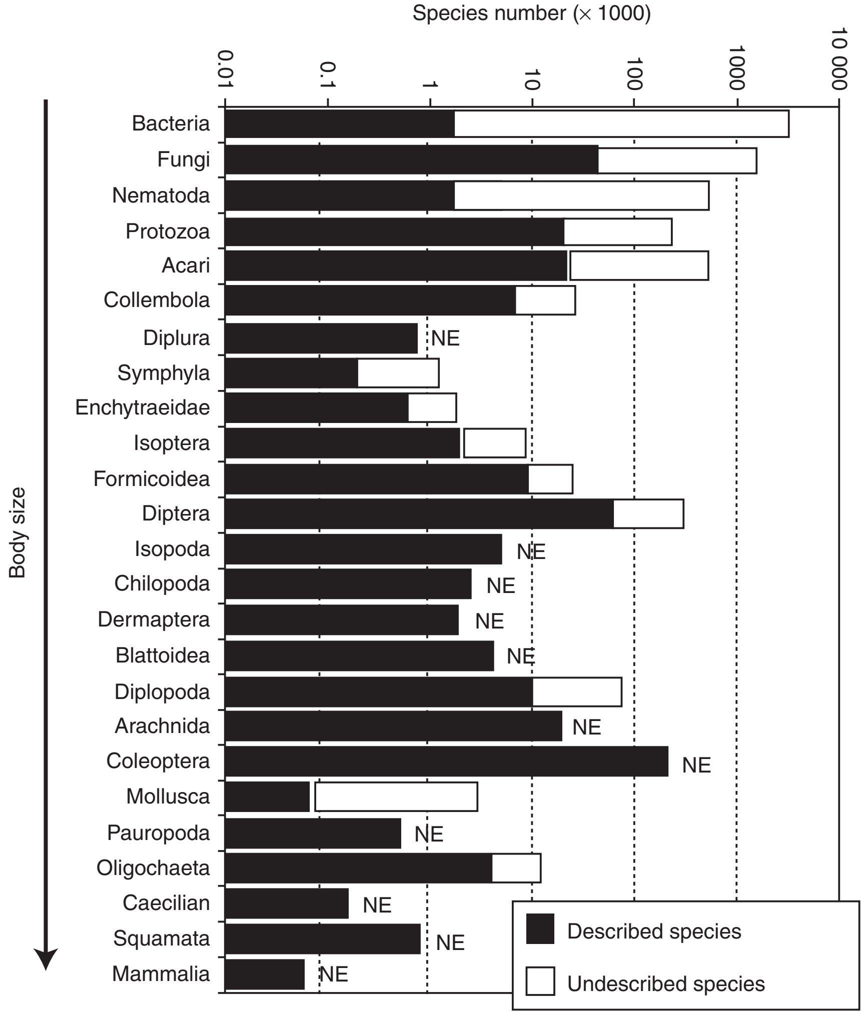

Figure 2 Biodiversity range in dominant soil-dwelling organisms. NE, not estimated. Reproduced from Decaëns, T., 2010. Macroecological patterns in soil communities. Global Ecology and Biogeography 19, 287–302.

global γ diversity. Generally the smallest microorganisms/microflora have the largest worldwide distributions. The arbuscular mycorrhizal fungi, for example, are relatively ubiquitous, and a significant proportion of the known species may be found at a single site (e.g., 33% in Amazonia) (Stürmer and Siqueira, 2011). Earthworms, however, have very high rates of endemism and two points separated by 500–1000 km have little chance of sharing common species; nonetheless, a small set of populous species may be found almost everywhere (Lavelle and Lapied, 2003).

Organization of Soil Biodiversity

Species of the same taxonomical group (families or orders) can adapt to soil conditions in different ways and so belong to different functional groups; the number and relative importance of which represent their functional diversity. To avoid competition, communities typically adapt during the course of evolution with limited niche overlap among species.

However, adaptation to soil conditions has led organisms to develop interactions with other organisms of different taxonomic groups at the same site. For example, earthworms depend on interactions with microflora for their digestion, whereas microorganisms are dependent on bioturbation and the habitats created by earthworms to resume activity after periods of dormancy in microsites where organic substrates were exhausted or out of reach. Similarly, small invertebrates, microorganisms, and the roots of plants occupy these nutrient-rich habitats created by earthworms and other ecosystem engineers. Roots usually follow earthworm galleries and fine roots tend to concentrate in fresh casts, which sometimes have high concentrations of easily absorbed nutrients and even growth hormones

As a result, the presence and abundance of populations of a given species may be as dependent on its relationships with species of the same functional group within a community of species of the same family or order ('horizontal biodiversity'), as with soil organisms of other functional groups (the 'vertical biodiversity').

Within-group diversity: Functional groups

Communities of a given functional group of soil-dwelling organisms are comprised of populations with well-developed functional differences. In each group, functional classifications have been produced to describe niche partitioning among different species and the diversity of functions that they fulfill (Table 2).

Microorganisms, such as fungi, bacteria, and archaea, are responsible for more than 90% of the chemical transformations associated with organic matter decomposition and nutrient cycling. They can be classified according to the range of their abilities to digest and degrade specific chemical substrates ranging from easily assimilated glucids and proteins to complex humic and phenolic molecules that require very specific metabolic abilities. Simple molecules, like glucose, may be metabolized by most microorganisms, whereas the most complex ones, including cellulose and starch, are used by fewer species, usually fungi and actinobacteria. Finally, the phenol–protein complexes that comprise 85% of dead leaf and root nitrogen may only be decomposed by a few basidiomycetes of the 'white-rot' fungal group (Lavelle and Spain, 2001; Kadimaliev *et al.*, 2010). Methanotrophs and methylobacteria use substrates with only one molecule of carbon, whereas cellulolytic bacteria are able to decompose cellulose polymers that have thousands of carbon molecules. Only a few soil arthropods and earthworms have efficient cellulolytic enzymes and are able to digest cellulose because of symbiotic interactions with microorganisms in their guts. Complex substrates are usually degraded by consortiums of diverse microorganisms (Zanaroli *et al.*, 2010) in protocooperative interactions. The nutrient composition of organic matter, specifically expressed by the C:N, C:P, and C:S ratios, also plays an important role in the processes of mineralization or immobilization in organic molecules of nutrients within the soil. Mineralization requires high relative concentrations of nutrients (e.g., C:N ratio < 20) and is inhibited when nutrient deficiencies limit the growth and activities of the decomposers.

Another functional classification of microorganisms is based on their mode of respiration: aerobic, anaerobic, or microaerophilic. This reflects their capacities to be active in different oxygen environments.

Finally, the decomposition of organic matter is associated with numerous biochemical reactions linked to the nutrient cycles mediated by microorganisms, principally bacteria. For example, chemolithotrophy is the ability to use the energy obtained by the oxidation of inorganic compounds; thus chemolithotrophs mediate reactions that are important steps in nutrient cycles, such as nitrification, denitrification, methanogenesis, and the use of reduced sulfur, copper, iron, and other

Table 2 Major functional groups in some groups of soil-dwelling organisms

Taxa	*Functional groups*					*References*
Bacteria	Bacteria	Carbon cycle: e.g., photosynthetic, methanogenic, methylotrophs, and celulolitic	N cycle: e.g., N2 fixers, nitrifiers, amonifiers, and denitrifiers	P, K, Ca, and Mg: Solubilizers	S: Oxidation of sulfur, thiosulphate, tetrathionate or sulphides Reduction of sulfate ions to hydrogen sulfide	Moreira and Cassia (2013)
Fungi	Antagonists	Saprophytes	Symbiotic	Pathogenic		Wainwright (1988)
Nematodes	Bacterivores	Fungivores	Root feeders	Carnivores	Mixed feeders	Banage (1966)
Collembola	Epiedaphic	Hemiedaphic	Euedaphic			Gisin (1943)
Acari	12 groups based on: Occurrence of phoresy, feeding habits, demography, and type of reproduction					Siepel (1994)
Earthworms	Epigeic	Anecic	Endogeic			Bouché (1977)
Termites	Wood feeders	Fungus growers	Humivores	Litter feeders		Waller and LaFage (1987)
Ants	Omnivorous	Predators	Fungus growers	Homoptera breeders		Korasaki *et al.* (2013)

minerals. As an example, biological nitrogen fixation and the reduction of N_2 to NH_3 is mediated by some specialist bacteria.

Invertebrate functional classifications reflect their responses to the three main constraints they face in the soil.

Micro-fauna (protoctists, nematodes, and a few other groups generally of a size $<200\ \mu m$) are mainly predators of microbes and other smaller invertebrates or herbivores. They are aquatic organisms that have no ability to create habitats in soil by digging, or bioturbation. They survive dry periods with a large variety of extraordinarily efficient mechanisms involving dormancy in different forms (spores, cysts, and desiccated individuals) (Lavelle and Spain, 2001).

Protoctists comprise three main taxonomic groups: ciliates, amoebae, and flagellates. Each group is characterized by different capacities to resist drought: amoebae, for example, can be more active than other proctoctists, because they can enter very small pores and shelter in theca that they secrete.

Nematodes are classified according to their feeding regimes (trophic groups): plant parasites, bacterivores (bacterial feeders), fungivores (fungal feeders), predators, and omnivores (Bongers, 1990). The relative proportion of 'persisters,' with relatively slow population turnover (k strategists), to 'colonizers,' with highly active turnover (r strategists), has been used to calculate the 'maturity index' of soils. It is considered a reliable indicator of the state of a soil and includes all soil nematodes except the plant parasites. A high maturity value indicates a low level of soil general stress due to drought, or nutrient deficiency, whereas a low value denotes high soil disturbance and difficult conditions for life, such as those generally found in soils subject to intensive agriculture (Bongers, 1990).

Ecosystem Engineers

Earthworms have been classified into three groups (epigeics, endogeics, and anecics) according to their main feeding habits and habitats. A suite of biological traits (morphology, anatomy, feeding regime, and demographic profile) is associated with these basic adaptive strategies. Epigeics are very active, small, and thoroughly pigmented earthworms that feed on fresh leaf litter and live within the surface litter itself. Their small size and use of a relatively rich food allow fast growth and active reproduction, a necessary demographic strategy in the face of high mortality from predators and the unstable moisture conditions that occur within their habitat. In contrast, Endogeics live in the soil and feed on it, having a purely geophagous regime based on the consumption of soils of high (polyhumic), medium (mesohumics), or low (oligohumics) organic matter contents (Lavelle, 1983). Anecics are very large earthworms ($>$ 20 cm in length) with an antero-dorsal pigmentation. They live in vertical galleries that open at the soil surface and feed on a mixture of partly decomposed leaves and soil. The conditions of the humid tropics favor communities of large dominant mesohumic and oligohumic endogeic populations, whereas with the declining temperature the proportion of epigeics and polyhumics increases. The decrease in the efficiency at lower temperatures of the mutualistic digestion based on interactions with ingested soil bacteria (Barois and Lavelle, 1986; Lavelle, 1983) forces earthworms to rely on higher quality resources, thus favoring litter feeders rather than geophagous organisms.

In cropped agroecosystems, earthworm populations often decline as survival, growth, and reproduction are severely affected by the general decrease in organic resources or the unfavorable temperature and moisture conditions during the frequent periods when tilled soil is bare or treated with pesticides. Thus, in intensive European cropping systems, endogeics may become dominant, as long as the intensification does not exceed a still to be identified degree. Permanent pastures are often the habitat of large communities of anecics (Lavelle and Spain, 2001).

Ants have been classified according to several criteria: feeding regime (herbivores feeding on grains or cultivated fungi, aphid growers, and carnivores (Korasaki *et al.*, 2013); behavior (dominant or submissive); habitat (soil 'cryptic' or tree dwelling); or whether they are specialists or generalists (Andersen, 1995). For practical field work, ants can be classified into six main categories: subterranean carnivores (specialists or generalists); litter-based carnivores (specialists or generalists); arboreal/epigeic carnivores (specialists or generalists); subterranean herbivores; litter-based herbivores; or arboreal/epigeic herbivores (Bignell *et al.*, 2008).

Termites have been classified according to their feeding behaviors with additional subdivisions based on the nature and location of the nest.

Self-organization between groups across five-size scales

Self-organization that creates interactions among organisms of different types, with complementary functions, results in the concentration of biological activities at different scales, nested into one another (Lavelle *et al.*, 2006). Five relevant scales of physical structure have thus been identified with regard to soil physical organization (**Figure 3**). At each scale, interactions among organisms of one or more groups develop within the boundaries of structures, such as biofilms, meso-aggregates, or the accumulations of biogenic structures of invertebrate ecosystem engineers (Lavelle *et al.*, 2006). Structures at Scale 1 are generally embedded into larger scale structures made or inhabited by larger organisms that organize space on larger scales. For example, the rhizosphere, at Scale 3, hosts structures of Scale 1 (the bacterial colonies that develop at the surface of the root) and Scale 2 with communities of micropredators and the microenvironment in which they live.

Although these scales are implicitly acknowledged, based on empirical observations, such a discrete organization of the soil environment is still not proven. Although discrete patterns of physical organization have been observed in both porosity and aggregate size distribution across a limited range of scales (Menendez *et al.*, 2005; Globus, 2006; Fedotov *et al.*, 2007), data are still rather scarce and fragmentary.

Scale 1: Microbial biofilms and colonies. The smallest habitat in soils is represented by assemblages of mineral and organic particles approximately 20 μm in size, called micro-aggregates (**Figure 3**, Scale 1). Microorganisms in these microsites are involved in most chemical transformations that result in organic matter cycling and improved soil nutrient fertility. Guts of invertebrate ecosystem engineers or fecal

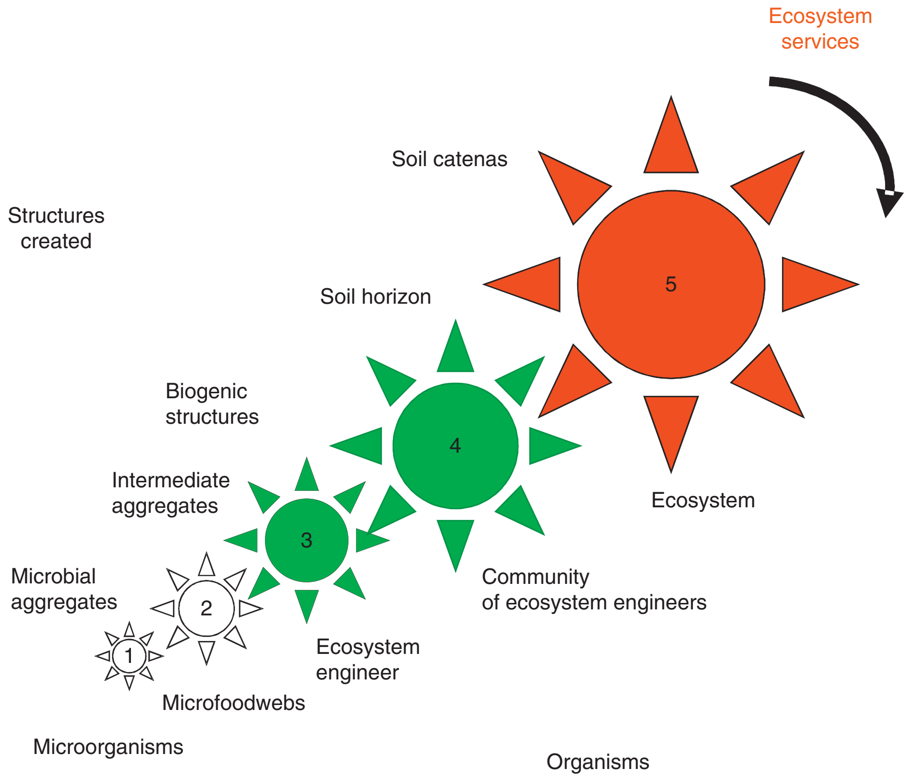

Figure 3 Self-organizing systems in soils at different scales from microbial biofilms and aggregates (1) to intermediate aggregates, (2) individual ecosystem engineer functional domains, (3) mosaics of functional domains in an ecosystem, (4) landscape, (5) and the biosphere (6, not represented), where ecosystem services are delivered along soil catenas. A community of interacting organisms, a set of physical structures that they inhabit and, in some cases, have created themselves, and the processes that operate at this scale of time and space define each scale. Modified from Lavelle, P., Decaens, T., Aubert, M., *et al*., 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology 42, S3–S15.

pellets of litter transformers (Scale 3) are typical microsites where these Scale 1 structures are to be found.

Scale 2: Micropredator foodwebs in meso-aggregates. At a scale of approximately 100–500 µm, micro-aggregates form assemblages that leave spaces among them where micropredators, such as nematodes and protoctists, can feed on microbial biomass, thus controlling their populations and activities. Specific assemblages of microorganisms in the rhizosphere, such as mycorrhizal fungi, also operate within pores of this size scale representing an autotrophic option for meso-aggregate interactions (Högberg and Read, 2006; Grayston *et al.*, 1998).

Scale 3: At the scale of decimeters to decameters, ecosystem engineers and abiotic factors determine the architecture of soils through the accumulation of aggregates and pores of different sizes: micro-aggregates of Scale 1; meso-aggregates of Scale 2; and the macro-aggregates that they produce (Lavelle, 2002). These spheres of influence (or functional domains) extend horizontally over areas ranging from decimeters (e.g., the rhizosphere of a grass tussock) to 20–30 m (drilosphere of a given earthworm population) or more and from a few centimetres up to a few meters in depth, depending on the organism (Decaëns and Rossi, 2001; Jimenez *et al.*, 2006).

Scale 4: Functional domains are distributed in patches that may have discrete or nested distributions and form a mosaic of patches (Scale 4). Such a mosaic has been described, for example, by Rossi (2003), who observed the distribution of two groups of earthworms with opposing effects on soil aggregation. One group, called 'compacting' earthworms, stimulates soil macro-aggregation through the accumulation of large (~1 cm) compact casts, which reduce soil macroporosity (Blanchart *et al.*, 1997). 'Decompacting' earthworms, however, have the opposite effect by breaking large aggregates into smaller pieces. This reduces the bulk density of the soil and allows an increased density of rootlets in this more favorable environment. More complex spatial domains of ecosystem engineer communities probably mix the structures of termites, ants, earthworms, and plant roots, although their structure and the relationships between their different constituents have very seldom been described or understood (**Figure 4**).

Scale 5: Ecosystem and landscape. At the landscape level, different ecosystems coexist in mosaics with often clearly visible patterns. The occurrence and distribution of land cover types in landscapes may result from natural variations in the environment or human land management. Soil formation processes, for example, are very sensitive to topography, which is reflected in the formation of catenas of related soils from upper to lower lying areas. Significant differences in soil type at this scale often determine different vegetation types and hence the ecosystem (Sabatier *et al.*, 1997). Conversely, there is growing evidence that the composition and structure of artificial mosaics created through different land management

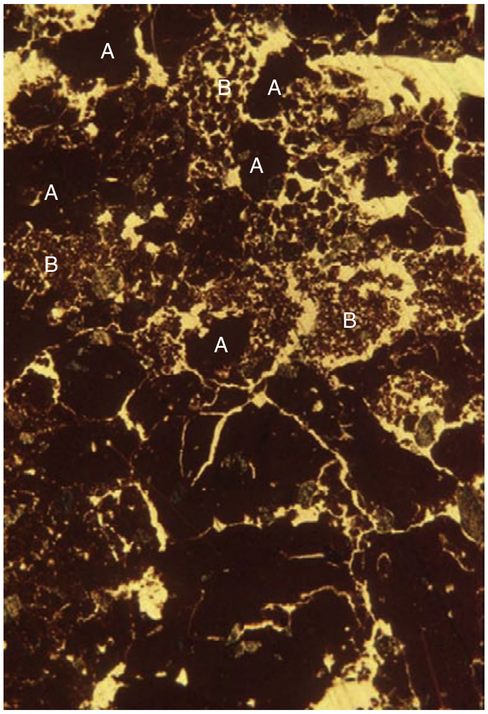

Figure 4 Thin section of a forested oxisol from Central Amazonia (X 0.5) showing accumulation of biogenic structures made by different ecosystem engineers. (a) compact earthworm casts and (b) dispersed pellets of soil deposited in a soil cavity by ants or termites.

practices have effects on biodiversity and the distribution of soil habitats.

Above these five scales there is, of course, the biosphere where all ecosystem services merge. At this global scale, atmospheric composition, temperature conditions, and the dynamics of the ozone layer are determined.

Examples of vertical organizations in soils

Climatic conditions determine the production of biomass by different ecosystems and so may significantly influence the amount and quality of organic matter produced. This, in turn, affects the populations of ecosystem engineers (Figure 5).

For example, dry or cold desert soils have no earthworms and the common ecosystem engineers are mainly ants (which have little influence on SOM dynamics) and termites. In such conditions, microbial communities tend to be dominated by fungal components and a discontinuous and relatively modest contribution of soil ecosystem engineers to soil processes (Scales 3 and 4). This gives foodweb control (Scale 2) a predominant role in these systems (Moore *et al.*, 2004).

Following soil and climate natural variations, the set of embedded processes that represent soil function may have different importance and composition. In the same region, different soils – or different types of natural or managed vegetation on a similar soil type – may have rather different species communities. Plant communities typically have a strong effect on the community of soil organisms (De Deyn and Van der Putten, 2005). Forest ecosystems tend to produce litter of a rather low quality and decomposition processes generally rely on communities dominated by fungi and arthropods that decompose the litter *in situ*. Earthworms that bury leaves in soil to stimulate decomposition by bacteria and open the soil structure to allow deeper rooting are often in very low densities in such environments. In contrast, grasslands and pastures are generally more favorable for earthworms, so the overall system shifts from fungi/micro-foodweb/arthropod to earthworm/bacteria-dominated litter decomposition systems. In agriculture, data from many different environments indicate a general depletion of macro-faunal communities when natural vegetation is replaced by managed systems (Lavelle and Spain, 2001).

Communities of ecosystem engineers (plants and invertebrates) organize their functional domains in ecosystem mosaics, which create a diversity of habitats for smaller organism communities in the rhizospheres of different plants (Marschner *et al.*, 1986). The continuous release of readily available substrates into the rhizosphere stimulates a high diversity and abundance of soil biota, especially heterotrophic microorganisms. However, Blackwood and Paul (2003) suggested that this activation selects only fast-growing microorganisms which take advantage of the release of easily decomposed C sources for growth, extract nutrients from the surrounding soil, and release them when they are preyed upon by small predators (Clarholm, 1985). Once completed, this flush of activity diminishes as root tips move away and fine roots die, allowing a different microflora to form in the root litter. Plants are also associated with specific communities of mycorrhizal fungi, which substantially enhance the ability of plants to forage for nutrients and water and protect them from diseases (van der Heijden *et al.*, 1998; Hedlund and Harris, 2012).

Similarly, collembola and acari may have rather different communities inside or outside of patches dominated by a given earthworm population (Loranger *et al.*, 1998). They thereby exert different effects on fungal communities by selectively feeding on their hyphae, or by dispersing their spores.

There is also abundant evidence in the literature that invertebrate ecosystem engineers (earthworms and termites) have similar specific effects within their respective functional domains. For example, intestinal mucus of earthworms, or the saliva of termites, has analogous effects as root exudates in stimulating a specific microflora that digests the ingested organic matter. They then continue their activities for a while in the excreta of these animals and thus become part of the macro-aggregated fraction of soils (Barois and Lavelle, 1986).

Response of Soil Communities to Agricultural Practices and Other Disturbances

Agricultural soil management strongly affects the whole ecosystem as it can change the dominant type of vegetation (forest to grassland or annual crops), the quality and amount of organic inputs (often reduced when plant cover is not continuous and chemical fertilizers are used), and affect some basic soil characteristics, such as pH.

In contrast, it has been shown that changing from tillage to 'no till' agriculture can increase the microbial biomass as well as the ratio of fungal to bacterial biomass (Beare *et al.*, 1997). In this way, it is clear that there can be a significant decrease in

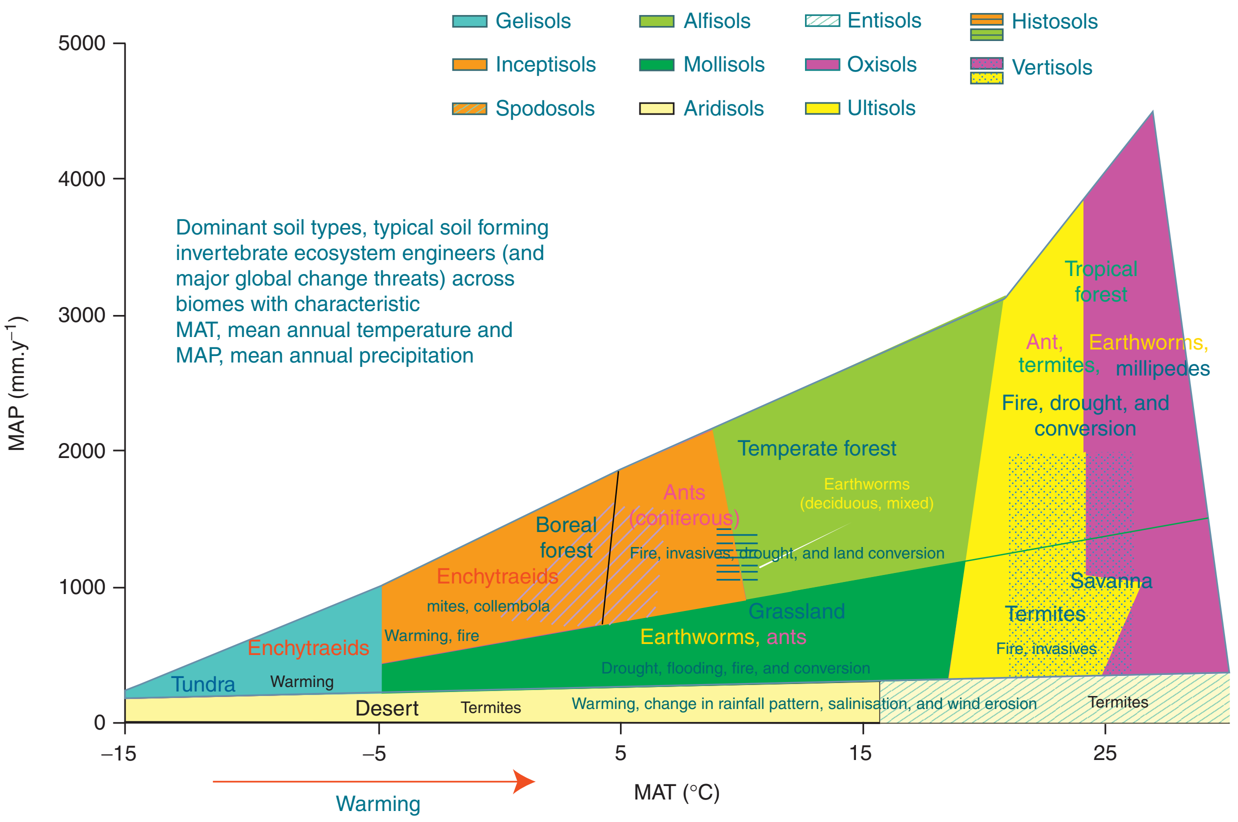

Figure 5 Dominant groups in soil faunal communities across a climate gradient. Reproduced from Brussaard, L., 2012. Ecosystem services provided by the soil biota. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., *et al.* (Eds.), Soil Ecology and Ecosystem Services. Oxford, UK: OUP, pp. 45–58.

functional diversity of microbial communities along a gradient of increasing agricultural intensification (Degens *et al.*, 2000) (**Figure 6**).

T-RFLP and cloning data obtained in representative land use systems in Western Amazonia have shown that diversities of total bacteria, symbiotic nitrogen-fixing bacteria, and arbuscular mycorrhizal fungi are not affected by land use systems (Jesus *et al.*, 2009; Lima *et al.*, 2009; Stürmer and Siqueira, 2011; Leal *et al.*, 2013). However, the relative abundance of these functional groups is affected, probably due to the different rhizosphere characteristics of the various plant communities. However, diversity and density of macro-fauna, like beetles, decrease with land use intensification from forest to pasture (Korasaki *et al.*, 2013). A significant relationship between ecological functions (seed dispersion, dung removal, soil excavation, and abundance of fly larvae/biological control) and the density and diversity of dung beetles was also found, in which the highest diversity of dung beetles was related to an increase in all these functions *in situ* (Braga *et al.*, 2013). Traditional management by local human communities, i.e., shifting cultivation, can even restore diversity to levels larger than those characteristic of the nearby natural vegetation.

Invertebrate communities are all significantly affected by agricultural practices, although to different degrees and in different directions. Some practices, like the establishment of improved pastures with better-performing African grasses, legumes, and liming, enhance their communities, whereas others, like traditional annual crops, severely deplete their density and diversity (Lavelle and Pashanasi, 1989; Decaens *et al.*, 1994; **Figure 7**).

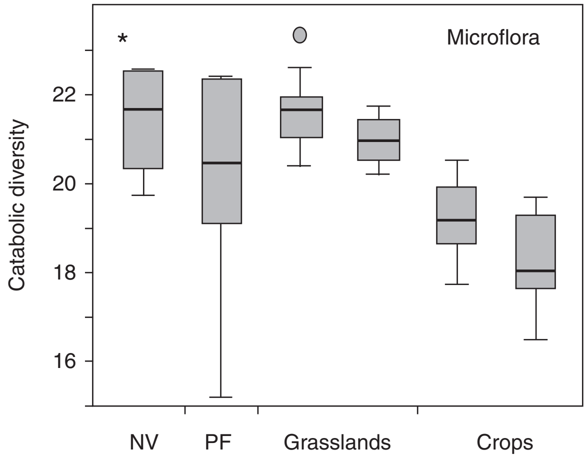

Figure 6 Effects of land use on the functional diversity of soil microflora in New Zealand. NV, native vegetation and PF, pine forest; in the box plot representation, horizontal line = median, limits of the gray rectangle = confidence interval, error bars = interquartile range, and isolated points = outliers. Reproduced from Degens, B.P., Schipper, L.A., Sparling, G.P., Vojvodic Vukovic, M., 2000. Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. Soil Biology and Biochemistry 32 (2), 189–196.

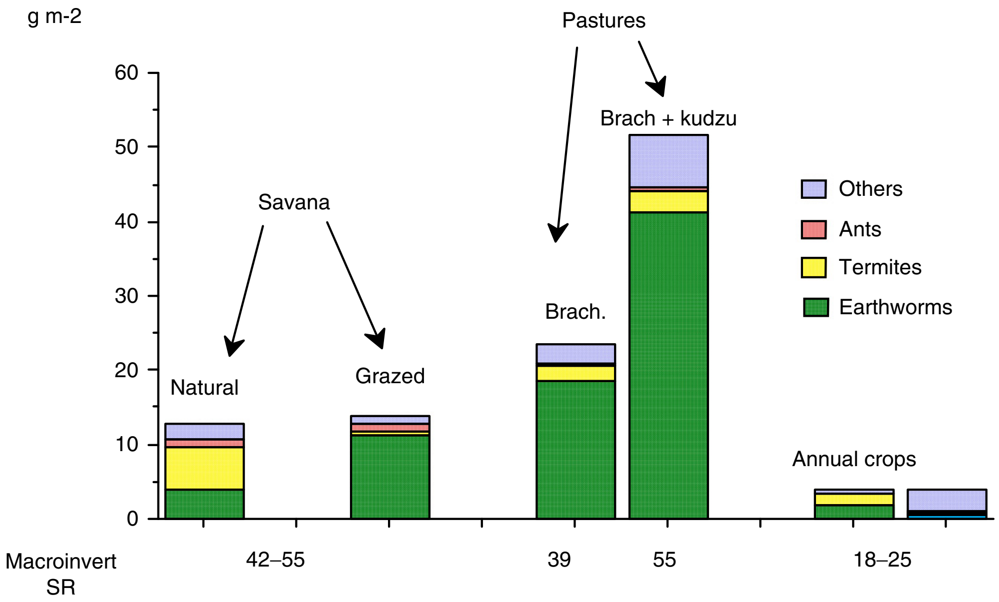

Figure 7 Density per m² of soil ecosystem engineers and other components of the macrofauna in soils from the Llanos Orientales de Colombia under six different plant covers. Reproduced from Decaens, T., Lavelle, P., Jaen, J.J.J., Escobar, G., Rippstein, G., 1994. Impact of land management on soil macrofauna in the oriental Llanos of Colombia. European Journal of Soil Biology 30 (4), 157–168.

Biodiversity and Soil Function: Why Maintaining Abundant and Diverse Communities Is Beneficial?

Ecosystem services provided by soils directly depend on the diversity and intensity of biological activities. Although microorganisms mediate more than 90% of all chemical transformations involved in nutrient cycling and the chemical protection of organic matter, the large ecosystem engineers create habitats for the smaller organisms and thus determine soil hydraulic properties. All organisms play important and sometimes very specific roles in sustaining plant production and protecting them from pests and diseases.

Ecosystem Engineers: Soil Structure and Hydraulic Properties

When water infiltrates into the soil, it is either stored for later use by plants or released to recharge aquifers. Soil water status and the balance among these important functions are made possible by soil porosity and the effect of gravity. Porosity is a very complex and dynamic soil attribute that has both a textural and a structural component. Textural porosity is a function of mineral particle size, whereas structural porosity is formed by either physical (e.g., creation of cracks in drying soil) or biological processes, such as bioturbation and burrowing. The latter is what allows vertical and horizontal water flows and plant provisioning.

The literature provides ample illustration of the importance of soil invertebrates and plant roots for the formation of macro- and meso-porosities (Lavelle and Spain, 2001). Subtle balances among soil-dwelling invertebrates that compact and aggregate soil particles and those that decompact and disaggregate these structures determines the size, shape, and organization of the pore space. This balance, which is strongly influenced by plant roots, seems to optimize the permeation of water into the soil by infiltration (in pores > 100 μm), plant provisioning from pores of a size between 0.02 and 6 μm, whereas the transfer of water to deep aquifers and rivers occurs through the largest macropores (Figure 8).

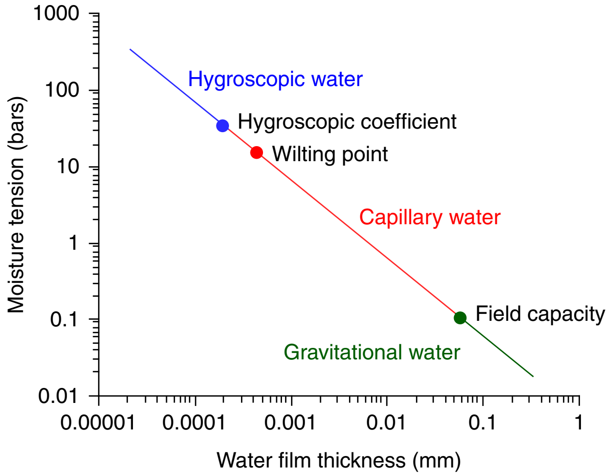

Figure 8 Different kinds of water according to the size of pores within which it is retained.

Soil aeration and water dynamics, therefore, largely depend on the activities of ecosystem engineers, which themselves are dependent on a biodiverse ecosystem. Losses of biodiversity may lead to imbalances in the dynamics of pore formation, including, for example, by invasive compacting earthworms (*Pontoscolex corethrurus*) causing severe soil compaction (Chauvel *et al.*, 1999) or the uncontrolled multiplication of surface structures by ants *Camponotus punctulatus*, as in abandoned rice fields in Northeast Argentina (Folgarait, 1998;

Figure 9 Uncontrolled multiplication of mounds created by *Camponotus punctulatus* in Northeast Argentina.

Figure 9). It is evident, therefore, that the diverse activities of soil invertebrate ecosystem engineers are of the utmost importance in agricultural ecosystems, especially those that do not use mechanical tillage.

Decomposition and SOM Dynamics

Decomposition of SOM is the result of two contrasting processes: mineralization and humification. Mineralization allows the release of nutrients contained in dead organic matter into inorganic forms and is important in their uptake by growing organisms, especially plants. Humification is the opposite process and leads to the conservation of organic matter in the ecosystem in protected forms. Protection may occur through chemical processes (by condensation of large-weight molecules or accumulation of undigested compounds) or through physical processes, in which organic elements are protected from microbial attacks within compact aggregates. An important attribute of mineralization is the synchrony in time and space between nutrient release and its uptake by plants and microbial biomass. Synchrony is best achieved in natural ecosystems, within which the combined diversity of decomposing material and decomposer communities allows a fine tuning of the process (Swift and Anderson, 1994; Myers *et al.*, 1994). Agroecosystems most often lose large amounts of nutrients to aquifers and the atmosphere because synchrony is no longer achieved, as in systems that receive excessive chemical fertilizer inputs (Lavelle *et al.*, 2005). Regarding humification, it has recently been argued that the addition of small amounts of easily assimilated organic compounds, like glucose, can allow microorganisms to further assimilate more complex substrates, like cellulose or lignin, and that this can relatively easily release chemical protection (Martin *et al.*, 1992; Fontaine and Barot, 2009). Thus, it would appear that the putative chemical resistance is nothing other than a physical separation of decomposers from their feeding resources. If this assumption is proven it would actually reduce the cases of chemical protection to a very few specific components.

Plant Growth Stimulation and Plant Protection

Sustaining plant production is the third major ecosystem service provided by soils through biological activities. During the course of million of years of coevolution, plants have developed mutualistic relationships with microbes and invertebrates that allow sustained growth and protection from pests and diseases.

Mutualisms with microorganisms

Nitrogen-fixing prokaryotes

Nitrogen is the element required in the largest quantities by plants. The sources of N in soil are: organic matter, usually very low, especially in tropical ecosystems; artificial nitrogen fertilizers, quite expensive and potential pollutants; and biological nitrogen fixation. Biological nitrogen fixation, the conversion of gaseous N_2 into ammonium, is one of the most important functions for the sustainability of life on the planet. Only some groups of bacteria and archaea are able to fix N_2 symbiotically. These prokaryotes can live freely in soil and water or in mutualistic relationships with fungi, lichens, and certain plants. The most important among these relationships are those of rhizobial bacteria with some legumes (Leguminosae). This is due to the economic relevance of many nitrogen-fixing legumes as crops, as well as their widespread occurrence in natural ecosystems. Development of molecular techniques in the last three decades has allowed a significant increase in the knowledge of rhizobial diversity: from the 6 species in a single genus known in 1984 to approximately two hundred species in 12 genera today. The mutualistic relationships between legumes and rhizobial species range from very specific to rather promiscuous. This diversity must be considered in the selection of specific bacterial strains to produce effective inoculum for a given plant species.

Mycorrhizal fungi

Although not required in such large quantities as nitrogen, phosphorus is usually the nutrient element mostly limiting plant growth in tropical ecosystems. The low availability of phosphorus is due to its immobilization through strong chemical fixation on components of weathered soils to form insoluble inorganic calcium, aluminum, and iron phosphates. Phosphorus also has a very low mobility in soil, which further limits its availability.

Mycorrizal fungi can establish mutualistic relationships with the majority of plant species (Read, 1991). Hyphae infect the roots of plants and spread through the soil exploring a soil volume much larger than that which could be explored by the roots alone. They thereby scavenge nutrients such as phosphorus and zinc from sources very distant from the root system. There are seven types of mycorrhizal fungi, but the most important ones are arbuscular or endomycorrhizas and ectomycorrhizas. They also enhance plant resistance to various stresses, such as heavy metal contamination and drought, as well as provide some protection against pathogens.

The use of rhizobial nitrogen fixation by legumes to replace artificial nitrogen fertilizers is an outstanding example of the contribution of biological processes within sustainable agriculture (Sileshi *et al.*, 2008). For example, the inoculation of soybeans in Brazil with selected *Bradyrhizobium* strains completely replaces nitrogen fertilizers, saving billions of US dollars annually. Unfortunately, this practice is virtually restricted to soybean (99%) and only 1% is applied to the bean *Phaseolus vulgaris*.

Plant interactions with invertebrates

Soil invertebrates have well-identified and measured effects on plant growth, some directly through physical conditioning of the soil and others indirectly through protection against pests and diseases or the selection and activation of mutualistic microbial populations. Pot experiments, with or without almost any type of non-pest micro- to macro-fauna, have typically found significant increases in growth/biomass (Setälä and Huhta, 1991; Brown *et al.*, 1999; Scheu, 2003), especially above ground. In addition, below-ground biomass can sometimes be reduced, even under conditions of high nutrient fertility (Lavelle and Spain, 2001).

In the case of earthworms, five mechanisms have been identified that promote a better growth and protection of plants (Brown *et al.*, 2000). They are:

- Enhanced nutrient release in fresh casts that are then subsequently colonized by plant fine roots (Lavelle *et al.*, 1992; Chapuis-Lardy *et al.*, 1998; Decaëns *et al.*, 1999);
- Improved soil physical conditions, which enhance plant water supply;
- Enhanced root mycorrhizal colonization;
- Direct control of plant parasites;
- Production of hormone-like compounds (Blouin *et al.*, 2005).

Conserving Soil Biodiversity in Agroecosystems through Management Options at Different Scales

Soil biodiversity is highly sensitive to human intervention at five scales (**Figure 3**), so good soil and vegetation management is important for its conservation. Large organisms are more sensitive to disturbance than smaller ones, and changes in communities of large organisms can have cascading effects on the communities of smaller organisms.

The organization of the agricultural landscapes (Scale 5) influences the regional pool of biodiversity (β diversity) and possible recolonization of degraded farm land. At the plot/farm scale (Scale 4), soil tillage, irrigation, the use of chemical fertilizers and pesticides, and the configuration of the plant communities all have strong effects on above- and below-ground biodiversities. At the scale of individual plants (Scale 3) and their associated ecosystem engineers, introduction of plants with specific ecological or environmental properties (such as, e.g., those with high N contents in N fixing plants, allelopathic properties for other plants and microbes, strongly anchoring or fine and dense root systems) may be used to manipulate the biodiversity of the meso- and micro-fauna, and the microflora. For example, plant parasitic nematodes can be controlled/regulated by earthworms that create assemblages of soil aggregates and soil pores that are favorable/unfavorable habitats for nematodes (Scale 2). Likewise, microbial supplements can be inoculated into soils to directly modify and enrich microsites with favorable microorganisms (Scale 1).

Scale 5: Landscape

The organization of eco-efficient landscapes that combine satisfactory economic performance with equitable and adequate social development and the conservation or improvement of their natural capital is slowly becoming a priority in rural development (Jackson *et al.*, 2012; Leakey, 2012). This awareness comes from the understanding that most ecosystem services are delivered at the landscape scale rather than at smaller scales. Pollination is a clear example that shows that if natural areas are not conserved close to intensively managed plots, dramatic deficits in pollination will occur (MA, 2005). Conversely, when landscape intensification is associated with a decrease in biodiversity, soil ecosystem services, such as hydrological functions, carbon storage, and nutrient cycling (Lavelle *et al.*, 2014), may be impaired or lost.

Ways to manage landscape composition and structure are still poorly studied and understood (Nelson *et al.*, 2009). However, the total number of patches of different types of land use (e.g., natural forest vs. annual crops) seems to be a determining feature affecting biodiversity and ecosystem services. In a study of deforested areas in Amazonia, the crucial tipping point in the relationship between landscape intensification and biodiversity maintenance corresponded to landscapes with at least 50% of tree cover, 20% of which was natural forest. This ratio may serve as an indicator for restoration projects in degraded landscapes. Landscape structure, however, is also important as exemplified by the creation of biodiversity corridors (Rantalainen *et al.*, 2006). However, such relationships may not be immediate and simple as it now seems that the biodiversity of plants is not necessarily linked with biodiversity of other groups. However, delay may occur between the reconstitution of a desired plant community and the expected levels of soil ecosystem services during the early steps of an adaptive cycle *sensu* (Holling, 2001).

Scale 4: Manipulation at Ecosystem Level in a Crop Plot: Tillage, Rotations

Processes of ecosystem reconstruction at the plot scale are much better understood as this is the scale that has frequently been considered, often almost exclusively, by farmers and agronomists.

At this scale the following four major technical elements should be considered to allow an appropriate management of biodiversity (Cavigelli *et al.*, 2012).

- The nature and diversity of plant cover;
- The need for tillage and soil mechanical preparation;
- Fertilization and protection of plants from pests and diseases;
- Application of organic materials as a way of promoting biological activities.

Plant cover: Structure, composition, and diversity

Although plant diversity in cropped land has considerably decreased since the advent of the Green Revolution (Cavigelli *et al.*, 2012), a large number of studies suggest that appropriate levels of plant diversity may be a prerequisite to conserving the diversity of other organisms and the provision of ecosystem services (ES), even within areas of primary production being the first one to respond to this increased diversity. Relationships among plant diversity, the diversity of other organisms, and the provision of ES, however, are not always clear and the impacts may not be visible for many years (Hector *et al.*, 1999; Hector, 2002).

In general, agroecosystems that mimic the original system – for example, agroforestry systems in a forest area or an improved pasture in a savanna area – are better at conserving biodiversity than those based on monocultures of annual crops. For example, in the savannas of the Colombian Orinoco, macro-invertebrate communities are greatly enhanced, both in total density and species richness in improved pastures with African grasses (Decaens *et al.*, 1994; **Figure 6**). Under such conditions, annual crops have highly deleterious effects, whereas perennial tree crops do not differ significantly from the original savanna. Similar patterns are observed in rainforest areas where agroforestry systems generally have larger communities of invertebrates than annual crops (Barros *et al.*, 2002).

Some plants directly stimulate organisms (e.g., legumes for biological N fixation), whereas others have more systemic effects at keeping soil covered with their stolons and litter production, upper tree canopy shade, or by sustaining generalist predators that will control pests and make applications of toxic agrochemicals unnecessary (Velasquez *et al.*, 2012; Settle *et al.*, 1996; Leakey, 2014).

Plants affect soil biodiversity through the amount and quality of organic material they contribute to the soil as dead leaves and roots (Vohland and Schroth, 1999; Lavelle *et al.*, 2001). They also have a direct effect on soils through the deposition of root exudates, exfoliation of tip cells, and death of fine roots. In some cases, the addition of particular plant species may greatly enhance, or decrease, specific elements of the soil community. This is the case in the approximately 20 000 species within the family Leguminosae, which produce grains, wood, gums, and green manure and which establish symbioses with N-fixing rhizobial bacteria. These legumes have high N contents ($>3\%$) that can be released during organic matter decomposition, or be transferred to other species by the hyphae of mycorrhizal fungi that form root connections and supply N to other plants. Legumes also enhance earthworm activities, with subsequent effects on soil aggregation and physical properties. For example, in Amazonian pastures that contain *Brachiaria brizantha*, the partial or total substitution by the legume fodder plant *Arachis pintoi* allows earthworm density to significantly increase from 217 to 365 individuals per square meter (68%), with a subsequent 87% increase in the fraction of biogenic aggregates to 25.3% and a 15% decrease in non-macro-aggregated soil. Plant-available water in these soils increased 20%, from 79 to 95 $\mathrm{g\,kg^{-1}}$ (Velasquez *et al.*, 2012).

In contrast, some plants may have intrinsic detrimental effects on soil biota. Particular attention has recently been brought to new cultivars of soybean that no longer favor rhizobial associations and to rice cultivars that do not respond favorably to earthworm or organic matter additions (McCouch, 2004; Noguera *et al.*, 2011).

Polycultures (e.g., agroforestry) with diverse plant community composition have greater rhizosphere diversity than monocultures, as significantly greater amounts of carbon substrates are released by roots. This stimulates greater biodiversity among the invertebrate litter decomposers (Vohland and Schroth, 1999) and primary consumers living close to the root systems. They attract predators and other organisms vital to foodweb functioning. In Africa, the ratio of organism densities in agroforestry systems to conventional farming systems varied from 1 (parasitic nematodes) to 2–3 (nonparasitic nematodes, acari, collembola, ants, and coleoptera), and other ratios were as follows: earthworms (3.1), chilopoda (5.6), and diplopoda (6.1) (Barrios *et al.*, 2012).

Tillage

Tillage and other soil mechanical preparations are a further critical element of agroecosystems that may profoundly influence soil-living communities. The recurrent destruction of soil structure by plowing maintains soils at an early successional stage, according to Holling's (2002) adaptive cycle paradigm. Under such conditions, species that require stable environmental conditions and mutualistic relationships with other organisms for their development are progressively eliminated as negative interactions (competition and predation) prevail. Tillage affects soil biota both directly by killing them and indirectly by decreasing the food resource base and destroying their habitat. This is illustrated by the mortality of large invertebrates and the destruction of fungal networks (Cavigelli *et al.*, 2012) and the significant reduction of earthworm numbers and diversity with its consequent negative impacts on soil physical properties (Wardle, 1995; **Figure 10**).

Similar results have been reported for a variety of soil invertebrates (Marchao *et al.*, 2009) in cropping systems derived from the Cerrado vegetation of Brazil, where, with the exception of termites and ants, most groups benefit from a shift from tillage to 'no-till' systems. Nevertheless, Dominguez *et al.* (2009) reported that no-till systems had a lower population density than the natural grassland (70 individuals per square meter as compared to 297 in the original ecosystem).

Systems with reduced tillage can have higher microbial biomass and higher fungi:bacteria (F:B) ratios (Beare *et al.*, 1997), but recent studies suggest that this is not the general situation. In Laos, for example, in no-till and cover crops systems in tropical grasslands, Lienhard *et al.* (2012) did not find a change in the F:B ratio, although a clear relationship was observed between the density and the quantity of microbial groups and diversity of crop residues (**Figure 11**). Overall genetic diversity of the microbial community showed a different pattern linked to soil chemical parameters, such as soil acidity (exchangeable Al, pH, and CEC) and C:N ratio. Similarly, Strickland and Rousk (2009) had indicated that these results were far from general. However, Helgason *et al.* (2009) did not find that effect of tillage in intensive tilled versus untilled soils of the Great North plains (Beare *et al.*, 2009).

Fertilizers and plant protection

Agrochemicals are yet another element of agroecosystems that impact strongly on soil biodiversity. Some chemicals usually have positive (e.g., liming) or neutral effects (chemical fertilizers), whereas others (most pesticides) are detrimental (**Figure 12**).

Liming reduces soil acidity and generally increases overall biological activity, and there is a trend for the F:B ratio to decline (Rousk *et al.*, 2010). Earthworms respond to this by significantly increasing their biomass (Edwards and Bohlen, 1996; Davidson *et al.*, 2004; Potthoff *et al.*, 2008). In the

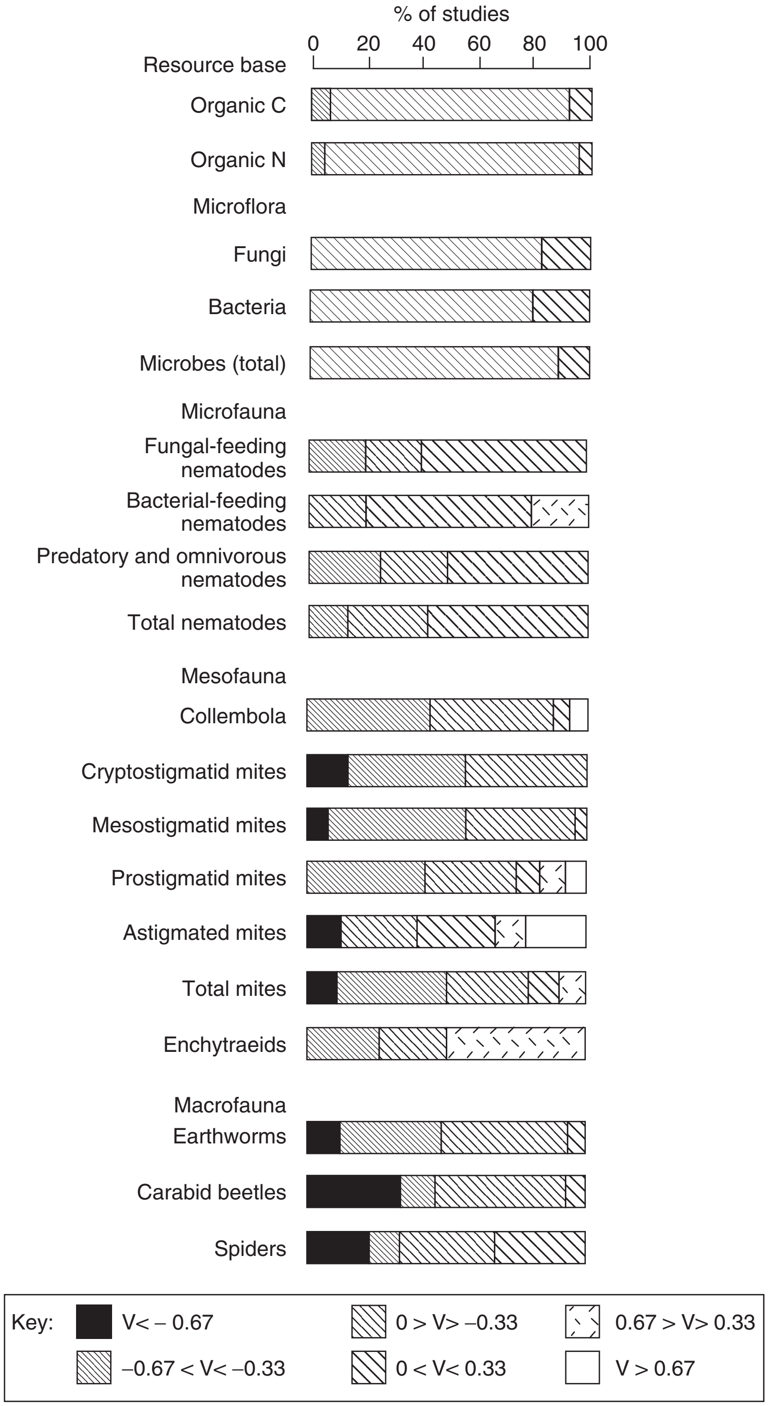

Figure 10 Effect of tillage on abundance or biomass of soil organism populations. V is the ratio of no-till to control tilled systems. Reproduced from Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil and Tillage Research 61, 61–76.

Colombian savannas, the positive effect of exotic pastures (Figure 7) is also a system response to liming and changes in the vegetation cover. However, liming aimed at counteracting the effects of atmospheric acid deposition in forests in Europe did not affect species richness but did significantly decrease macro-invertebrate densities, with contrasting effects on different groups. Although some coleoptera were favoured, the majority of Araneae families (Lithobiidae) and Coleoptera (Staphylinidae) had larger densities in nontreated plots (Auclerc *et al.*, 2012). Part of the observed detrimental effect was related to the increased aluminum toxicity that occurs in some soils when pH is increased (Larssen *et al.*, 1999).

Industrial chemical fertilizers usually do not directly affect soil organisms (Beauregard *et al.*, 2010) but increase plant production. However, the production of certain soil enzymes that are involved in nutrient cycles (e.g., amidase in the

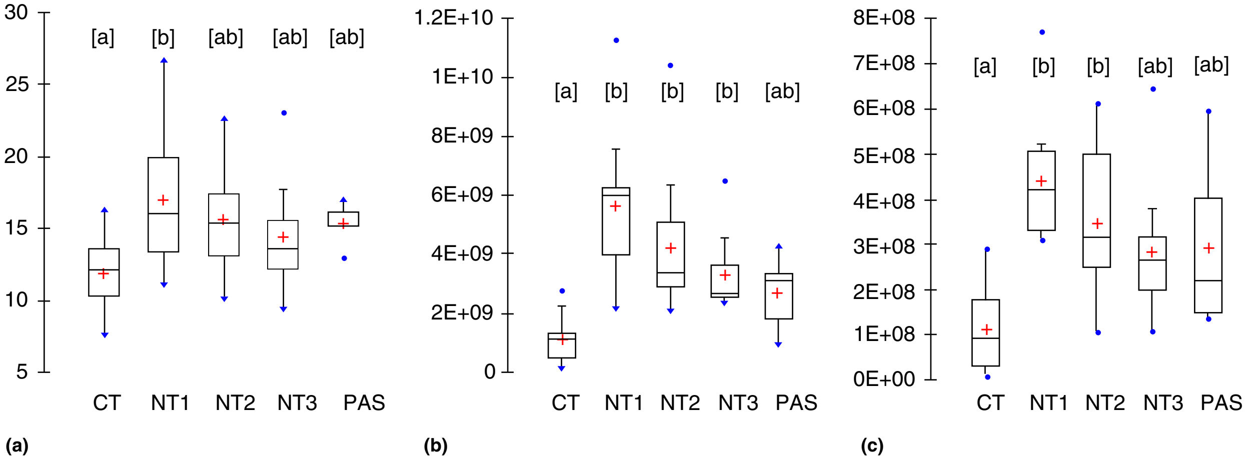

Figure 11 Effect of tillage on microbial diversity in crops from Laos (Lienhardt *et al.*, 2010). Box and whisker representation of (a) molecular biomass (micrograms and per gram of soil), (b) bacterial density (copy of 16S rDNA per gram of soil), and (c) fungal density (copy of 18S rDNA per gram of soil) recorded in natural pasture land (PAS), conventional tillage (CT), and no-till systems (NT (1, 2, and 3)). Letters in brackets indicate significant differences (Kruskal–Wallis test ($P < 0.05$, Bonferroni corrections).

Figure 12 Adult cicada from a gallery forest killed by aerial applications of *Beauveria* in nearby industrial crop fields in the Llanos Orientales region of Colombia (Photo Patrick Lavelle).

nitrogen cycle), which normally releases mineral nutrients, may be significantly depleted (Dick, 1992). Loss of such functions may explain, at least in part, the decrease in production generally observed when shifting from conventional to organic agriculture.

Pesticides are by far the most detrimental agrochemicals with regard to biological activity and biodiversity. However, their wide chemical diversity, the large variation in frequency and quantity of applications, and the resulting soil reactions make generalizations difficult. This is exacerbated by poor assessment methodologies. The literature is also limited and generally focused on one type of pesticide, although it suggests that one-time applications have only small effects in the medium term, because the product is biodegraded, allowing microbial or invertebrate communities to return to pre-application levels within a few weeks (Cavigelli *et al.*, 2012). Repeated applications, however, may lead to more serious and durable changes in soil biology (Stromberger *et al.*, 2005; Larink, 1997; Edwards and Bohlen, 1996). Studies with the herbicide glyphosate indicate few long-term effects on microbial communities and their activities (Kremer and Means, 2009). However, increased susceptibility to fungal diseases (*Fusarium*, *Phytophthora*, and *Pythium* spp.) has been detected. Selection of the most aggressive parasitic nematodes in the presence of pesticides has been also observed (Lavelle *et al.*, 2004). This may perhaps explain why the need for pesticide applications is growing in highly intensive crop systems, especially in the tropics. A special mention should finally be made here of biological insect-control agents (such as the fungus *Beauveria* or *Bacillus thurigiensis*) that have less contaminating effects but still have undesired nontarget effects on non-pest insect populations.

Organic amendments

As a generalization, organic inputs increase the species richness and abundance of soil organisms as compared with conventional cropping systems (Bengtsson *et al.*, 2005; Hole *et al.*, 2005), although in some cases no response has been observed (Cavigelli *et al.*, 2012). This may result from the absence of species that would have benefited from the improved conditions.

A large part of the detrimental effects of intensive agriculture on soil organisms is due to starvation. Although residue inputs are severely decreased by weeding and the exportation of large part of the above-ground plant biomass, the use of chemical fertilizers reduces food sources even more (Lavelle *et al.*, 2004). In contrast, organic agriculture based on diverse materials, such as animal and green manures, biosolids, biochar, compost, decomposing plant lixiviates, small branches, and other wood residues, provides organisms with beneficial substrates while it increases biomass and plant species diversity, with a wide range of organic inputs (Cavigelli *et al.*, 2012). All this diversity leads to great variation in decomposition, mineralization, and humification, which is further varied by the effects of climate and soil differences at large scales and by invertebrate and microbial communities at smaller scales (Lavelle *et al.*, 1993).

An early consequence of depositing organic matter on the soil surface is the enhancement of communities associated with litter, such as micro-arthropoda, myriapoda, isopoda, and a large number of insects (Ruiz-Camacho *et al.*, 2011). This community participates in the composting of organic residues and their further mineralization by soil microorganisms in the casts of endogeic or anecic earthworms. A common situation following organic inputs is an increase in aggregation and aeration leading to improved soil physical structure through the enhanced activities of ecosystem engineers (Lavelle *et al.*, 1997).

Another interesting function of organic inputs is the maintenance of dense invertebrate populations that provide food for generalist predators which can switch to any invertebrate pests emerging on crops, thereby providing an element of biological control (Settle *et al.*, 1996). However, there are significantly different effects of different types of organic materials on soil macro-fauna. In a study involving 13 cereal crops, 4 pastures, and 5 forests conducted on similar soils of the Bassin Parisien region of France, Ruiz *et al.* (2011) found significant differences in the biodiversity, abundance, and species composition of macro-invertebrate communities depending on the quality of the organic inputs. A mixed compost of sewage sludge, green manure, and urban solid waste compost did not greatly increase either the total density or biodiversity over that of conventional cropping plots. However, a mixture of farm yard manure, liquid compost of green waste, and the organic fraction of municipal solid waste compost increased the total abundance of macro-invertebrates up to fourfold. However, total species richness per sample did not vary much except in one direct-drilled system with a winter cover crop in which species richness more than doubled and reached similar values to those of nearby forest sites.

Scale 3: Manipulation of Populations of Ecosystem Engineers: Plants and Invertebrates

Increases in the density of beneficial organisms are often sought through the direct inoculation of plants, invertebrates, or microorganisms. The aim is to enhance ecosystem engineering in its physical, chemical, and biological dimensions.

However, these inoculated organisms will survive only if suitable conditions for their activities occur. These include adequate moisture and temperature, appropriate soil pH and nutrient status, and sufficient organic matter quality and quantity (Lavelle *et al.*, 1993).

As is the case in agroecosystems managed by tillage or the use of agrochemicals, plant communities are relatively easy to manipulate, so long as natural competing communities are suppressed or eliminated. The use of other plants integrated into farming systems as companion crops to provide ecological/environmental goods and services is also widely implemented to enhance production. Some introduced species have physical roles, forming erosion-control barriers or windbreaks, whereas others may be N-fixing legumes included for soil fertility management. Such plants may be so effective that N fixed in these artificial systems is equal to 1.5 times N fixed in natural ecosystems (Lavelle *et al.*, 2005; MA, 2005). Other plants may be used as traps for pests, especially phytoparasitic nematodes, parasitic weeds like *Striga*, and cereal stem borers (Khan *et al.*, 2007; Cook *et al.*, 2007).

Inoculation of earthworms has been widely practiced to improve exotic grass pastures in New Zealand (Edwards and Bohlen, 1996). Likewise, earthworm inoculation has been used as part of the FBO (Fertilization Bio Organique) patented technology (Senapati *et al.*, 1999) in which earthworms are inoculated into trenches where the highly organic conditions create small islands of favorable soil functionality (Brown *et al.*, 1999). Interestingly, in addition to occasional spectacular increases in production, this technology also improved the organoleptic quality of tea from plantations in India and China by 15–30%.

Scale 1: Manipulation of Microbial Communities

Microorganisms, such as N-fixing bacteria, plant growth promoters that release growth phytohormones in soil, bacteria that protect plants from fungal (*Fusarium* and *Phytophthora*) diseases (*Pseudomonas* spp. and *Trichoderma*), and fungi that feed on phytoparasitic nematodes, are by far the most frequently used organisms for agroecological manipulations. Soil microbial communities, however, occupy specific microsites in soil, built by ecosystem engineers (macro-invertebrates and roots). They are, furthermore, subject to predation from micropredators and to competition with other microbial colonies (Lavelle and Spain, 2001). This particular ecological circumstance is a substantial obstacle to microorganism inoculation in soils because before they reach the expected target (e.g., a root) they may be preyed upon by any element of the predator micro-fauna, be lost in a micropore where no root will penetrate for months, or be eliminated by more competitive microorganisms even if they arrive at the right site.

Because these conditions are not taken into consideration or, as often so, not really understood, inoculation may only be effective when careful inoculation techniques are implemented.

In a survey of 62 preparations available in SSA Africa, Jefwa *et al.* (2013) found no effect at all in 95% of cases. Of the 31 products tested, only 42% of those claimed to contain Rhizobia actually contained the expected strain, with no contaminant, whereas 34% only had contaminants. In total, for the 62 preparations, 54 strains of bacterial nonrhizobial products of the 147 announced and 26 of 73 mycorrhizal products had the expected strain. Of 13 preparations referred to as mycorrhizal inoculants, only three had a substantial effect under laboratory conditions, although seven had smaller than expected; the remaining three preparations produced no colonization at all. Of 37 bacterial strains not supposed to be present in these preparations, eight had potentially severely harmful effects for human health and one for plants. Out of 18 nonbacterial preparations, only 33% increased maize growth, whereas in soybean only 22% of tested products were effective (Jefwa *et al.*, 2013).

However, many countries have developed legislative frameworks to control the quality and efficiency of inoculants and a large proportion of the products are delivered with detailed instructions for an efficient use.

Future Research in Soil Biodiversity

A large number of studies have shown the importance of conserving and managing biological activities within agriculture and at the same time have indicated that the soil biota is a vulnerable resource. To better use and protect this essential resource, research efforts must continue, with special emphasis on (1) the determination of effective indicators and (2) development of techniques for conserving and using soil biodiversity.

Indicators

The need for indicators: Synthesis of existing approaches and a proposal for establishing a unique set of tools with ISO labeling

A large and diverse number of biological, chemical, physical, and synthetic indicators of soil quality and ecosystem services have been proposed in the literature (Turbé *et al.*, 2010). However, a comparative analysis of the respective advantages and disadvantages of these indicators is needed before testing.

Conservation of biodiversity and manipulation of communities to improve the provision of soil ecosystem services must be considered across all scales simultaneously

This article has shown the vulnerability of soil biological components and the difficulty of managing them properly. This follows directly from the inherent complexity of biological interactions in soils and the imperfect understanding. To improve this understanding and enhance the potential for ecological manipulations at different scales, research should focus on the following:

Scale 1: Microbial inoculants

In situ field tests of survival and development of the inoculated populations are necessary to determine the range of conditions for the use of these microbial inoculants and to provide quantitative estimates of the benefits obtained in the short and longer term.

Scale 2: Control of plant-parasitic nematodes

Determine how to enhance the biodiversity of parasite communities for ecosystem level control through earthworm activities. Of particular importance is assessment of the density and distribution of microsites in which micro-foodweb processes occur and analysis of their impacts on microbial communities.

Scale 3: Earthworm inoculation, service plants, and ants and termites

There is a need to better understand the internal mechanisms affecting the specific interactions that operate between plants and invertebrate ecosystem engineers. This is especially so of the interactions among the different functional domains derived from the activities of different groups of ecosystem engineers, their precise geography in soil, and their successional processes. In addition, the potential to modify the expression of resistance genes in plants should be further explored.

Together, the outputs of such research could lead to better disease control and an enhanced delivery of ecological services from soil biodiversity.

Scale 4: OM applications and biological control

With regard to the determination of appropriate sources of OM for nutrient release, plant protection, C sequestration, biodiversity enhancement, and on-farm production of OM inputs, there is a need to investigate the effects of soil OM quality on nutrient availability, water retention, and carbon sequestration, especially with regard to the activity of soil engineers.

Scale 5: Ecoefficient landscapes

There is now growing evidence that biodiversity conservation and critical ecosystem services, such as pollination, pest and disease control, decontamination, water infiltration, and supply to plants, need to be delivered at landscape scale. There is consequently a need to improve the design of landscapes for enhanced function through such means as biodiversity corridors and the creation of more natural ecosystems within which natural resource capital, such as trees and conserved water bodies, meets the needs of humanity and the environment. Further natural principles to be included are recycling and composting of organic waste using vermiculture and related techniques.

Conclusion

The conservation and management of soil biodiversity is central to the attainment of agriculture that is productive and sustainable over long periods. From this, it follows that greater effort is now needed to maximize the benefits flowing from a wise and conservative use of natural capital. This particularly applies to the soil taht has become seriously degraded both in fertility and agroecological function and is responsible for the declining productivity that is the main cause of the nutritional insecurity and poverty prevalent in many developing countries (Leakey, 2012). Urgent tasks are, therefore, to prevent further resource degradation by maintaining diverse soil covers and adding organic inputs to the soils. Ultimately, a better understanding of ecological processes is required, including the improved, naturally based management of pests and diseases. This, together with a reduction in pollution, is necessary to reverse declining fertility and improve crop yields in ways that have much improved environmental and social consequences for local people, as well as the global community. Once understood, these mechanisms should be urgently integrated and enhanced in the next generation of agricultural systems to promote greater agricultural productivity and ecosystem conservation.

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