

Chapter 2

Soils Supporting Biodiversity

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Abstract Soils are complex systems. Soil organisms and mineral components interact to generate high diversity and complexity, feeding back to biodiversity through habitat provision. Vascular plants link the aboveground and belowground components of ecosystems by litter inputs, root exudates, and influence soil chemistry and structure. Soil mineral composition and soil organisms together determine soil characteristics and fertility. Soils organisms differing in size and function create soil structure and aggregates, which are hotspots of microbiological diversity and activity. Soil structure is thus both a product and a cause of soil biodiversity.

Soil structure degradation leads to compaction, which decreases transfers of fluids and nutrients. An adequate input of organic matter is necessary to maintain soil fertility by enhancing aggregate stability and organic matter input is therefore an easy measure to improve soil fertility.

Soil use affects above and belowground biodiversity through cascading effects across all spatial scales. However soil biodiversity is generally not considered in land-use planning and the vast majority of soil organisms are unknown.

Long-term ecological studies and recent advances in molecular methods provide huge potential for assessing the relationship between soil taxonomic and functional diversity and ecosystem function and the consequences of biodiversity loss and changes in community structure.

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Given its functional importance, soil biodiversity clearly deserves more attention in education programs, improved knowledge transfer and more resources for fundamental and applied research.

Unsustainable use of soil is partly psychosocial in nature, stemming from diverse representations of the environment. Sociological approaches should be given more attention to improve the successful implementation of knowledge into sustainable soil management.

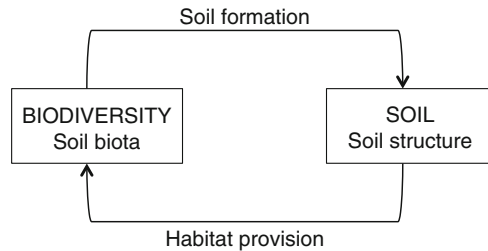
2.1 Introduction

Ecosystems are truly complex systems. This is especially true for the soil compartment of terrestrial ecosystems and this complexity is the key to their role in supporting biodiversity. In this chapter we will address some of the main aspects of soil complexity with special reference to the way it influences biodiversity and ecosystem function. We will particularly focus on soil structure as it is at the same time the product of biological activity and, through feedback effects, the main driver of soil biodiversity.

Biodiversity, which has been a very popular concept for over two decades amongst both scientist and the larger public, is mainly used as a tool to measure the state or the quality of a given ecosystem. This is intuitively based on the assumption that ecosystems are more valuable if their species count is higher. This view however fails to acknowledge the value of naturally species-poor ecosystems such as Northern *Sphagnum*-dominated peatlands, which are of global significance for C cycling and regionally of high value for biodiversity conservation (e.g. in Switzerland where they do not naturally account for a high proportion of the landscape). The basic concept of biodiversity does not either account for functional biodiversity, i.e. the diversity of ecosystem functions or how species contribute to them. For instance, species diversity can be very high in urban ecosystems, often substantially higher than in adjacent agricultural landscapes (e.g. Savard et al. 2000; Alvey 2006; McKinney 2008). However this high diversity is primarily due to the presence of exotic species (Faeth et al. 2011), which do not necessarily play important ecological roles in the communities. Furthermore many of these species would not be able to maintain viable populations naturally while others behave invasively and constitute a threat to biodiversity and/or to human health. Research is therefore increasingly focusing on how biodiversity relates to ecosystem function.

Biodiversity loss is of increasing concern at both scientific and policy levels (Mace et al. 2005). However the link between biodiversity and ecosystem function – and hence the degree to which its loss should be a matter of broader concern – although now relatively well studied for the above-ground compartment of terrestrial ecosystems (Hooper et al. 2005) remains less well understood in soils (Decaëns 2010). For instance, a forest in the narrow sense of the term should be described as a community of living organisms, plants, animals and microorganisms that can – theoretically – be quantified (e.g. species number) and qualified (e.g. interactions among species

Fig. 2.1 The soil functional loop



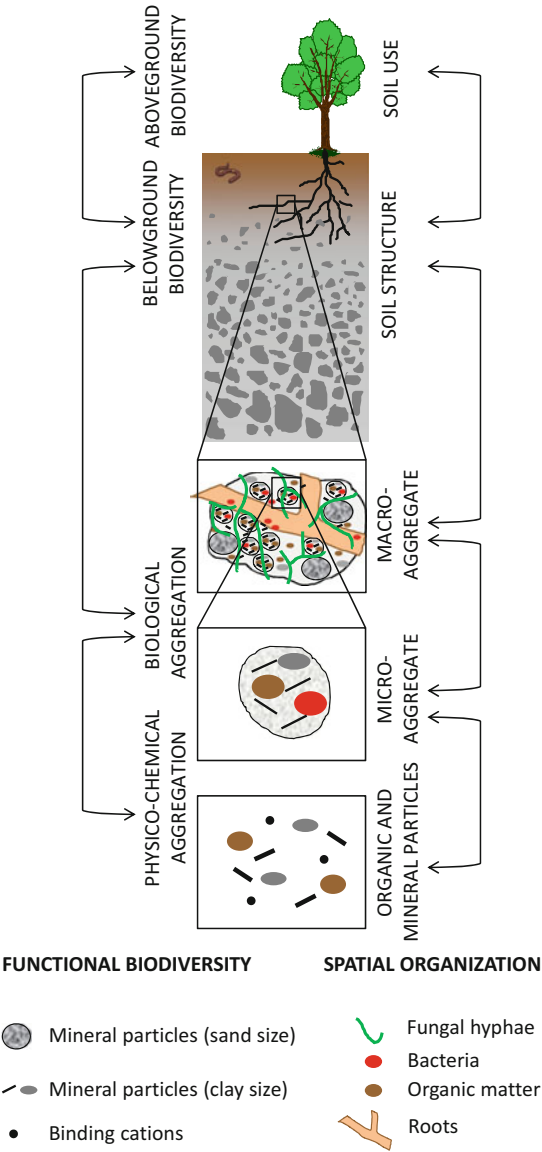
and between species and their environment). The presence and interactions of forest organisms depend on external environmental factors such as climate, geology or topography. In contrast to the forest example, soils represent more than only a spatial portion of an ecosystem harbouring adapted species; they are ecological systems in which the living organisms are inextricably and functionally intertwined with inorganic components (Fig. 2.1). This tight connection enhances their diversity (both taxonomic diversity and diversity of soil types) and structural and functional complexity. Soil biodiversity also stems from the tiny size of organisms relative to the spatial scale of the aboveground part of terrestrial ecosystems and the arrays of functions involved in decomposition mechanisms, which are almost uniquely performed in soils and that further contribute to increasing soil complexity (Adl 2003).

A key functional role of soil biodiversity is its direct contribution to creating soil spatial structure. Moreover, as soil is a decisive factor shaping all terrestrial ecosystems we acknowledge, in accordance with Lavelle (2012), that soil variables, and especially the biogenic soil structure, are key factors regulating both aboveground and belowground biodiversity (Fig. 2.2). It follows that soil use and soil management are critical aspects of ecosystems management and largely determine the degree to which terrestrial ecosystems can support biodiversity, with cascading effects from local to global scales.

2.2 Soils as Complex Systems

Being complex systems, soils are obstructive to an analytic approach, which usually seeks to reduce a system to its elementary components and to comprehend direct interactions among these elements. The analytical approach is adequate for the study of simple systems mediated by linear interactions and ruled by general laws, such as gravity. For instance, knowing the mass of a falling object, its height and the gravitational constant allows predicting its speed and impact point. The elementary properties of simple systems are additive and relations between their elements mostly linear. On the contrary, complex systems are defined by a large diversity of components linked together by strong *feedback* interactions which in turn modify the initial state of the (eco)system. They are notably characterized by a *hierarchical*

Fig. 2.2 Cross-scale linkages between macroscopic surface characteristics and microscopic soil characteristics through spatial organization and functional biodiversity, *left*: from aboveground biodiversity to physic-chemical processes at the microbial scale, illustrating the role of soil functional biodiversity, and *right*: from soil use to the organisation of organic and mineral soil constituents at the microbial scale, illustrating the spatial organisation across spatial scales



organization, each level of the system being embedded within another. This approach is therefore also well adapted to soils where spatial structures vary from the molecular to the landscape scale, each level being formed by the elements of the lower level. Micro-aggregates coalesce to form macro-aggregates, which in turn are integrated in larger clods; further, specific structures define different types of horizons, themselves characterizing different types of soil (Fig. 2.3).

Each successive level is distinguished by newly acquired *emergent properties* and not by simple addition of lower level properties, and is defined by specific *temporal*

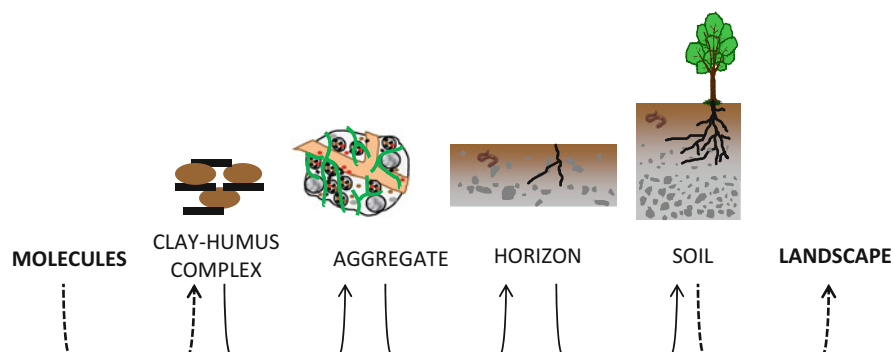


Fig. 2.3 Multi-scalar organization of soils (Modified from Gobat et al. 2004)

and spatial limits. Within soils, processes leading to development of aggregates are mediated by relatively small organisms (bacteria, fungi and micro-arthropods), acting at seasonal pace, but the effects appear also at larger time and landscape scales, for example when flood events are prevented by enhanced drainage due to increased soil porosity resulting from a greater abundance of soil aggregates. Other fundamental features of complex systems also characterize ecosystems' organization (Frontier et al. 2008) and can be successfully applied to the soil subsystem. The *homeostasis* concept, i.e. the property that tends to maintain a system or each defined level of the system in dynamic equilibrium conditions, has often been applied to ecosystems. Homeostasis results mainly from *negative feedback* effects, such as prey-predator relationships that regulate the soil communities.

Finally, soils are the main drivers in *self-organization* of ecosystems as they also shape the aboveground communities. Co-evolution of soils with the vegetation they support is mediated through changes in the quality and quantity of organic matter supplied by the vegetation, leading to acquired structure and self-organization which, theoretically, reaches its climax at the end of ecosystem succession. Young ecosystems, such as floodplains at the early stage of ecological succession, are characterized by a predominantly mineral abiotic environment with poorly developed biotic communities and weakly developed soil; their *resistance* (capacity to withstand disturbance) is therefore low. When the flood events become scarce/or the fluvial dynamic no longer exert a disturbing effect due to the construction of flood protection structures, alluvial ecosystems evolve towards the climax and acquire stronger aggregation due to earthworm activity, allowing increased resistance to further disturbance (*positive feedback*) (Bullinger-Weber et al. 2007). Inversely, mature ecosystems, such as temperate deciduous forests displaying well-established biotic communities and food-webs, particularly in the soil, show better resistance. However, when soil properties and functions are altered, as is the case of European forest affected by atmospheric nitrogen deposition resulting from the burning of fossil fuels and from agriculture, the capacity to resist perturbation is impaired. Enhanced N-deposition leads to both acidification and eutrophication that affect mycorrhization and fine root biomass. The storm "Lothar" in December 1999 caused unprecedented forest damage in Switzerland and the magnitude of the effect was partly attributed to reduced rooting due to the

altered soil status (Braun et al. 2003). Nevertheless, *resilience* (capacity to recover after major disturbance) may be preserved, due to the ability of soil communities to maintain basic functions of nutrient cycling even if the aboveground component of the ecosystem is subjected to major perturbation and temporarily destroyed (for example by fire, logging or storm) (Bret-Harte et al. 2013). Hence, there is a need to take into account all levels of the hierarchy, particularly soil organisms, as the emergent ecological properties and ecosystem functions and services at the scale of landscape ultimately link back to soil dwellers including microbes at the microphysical scale (e.g. Decaëns et al. 2006). The systemic approach, which considers a system in its totality and dynamic functioning, is therefore suitable for understanding ecosystems and thus, their most complex component: the soil (Ritz 2008).

Production and decomposition are the two main functions of soils related to plant growth (Brussaard et al. 2007). Both are defined by *biomass and energy fluxes* through the ecosystem, namely the food web. The aboveground part of a food web, involving mainly production and consumption, is often represented as pyramid-shaped with relatively simple interactions between primary producers, herbivores and carnivores of diverse levels. Such a vision is impossible to implement below-ground, as the relations between organisms responsible for decomposition are highly intertwined: here the notion of “web” is particularly appropriate to describe the complexity of interactions among the organisms responsible for organic matter transformations. This complexity mirrors the species diversity and the heterogeneity of the soil environment, as described in two aspects for bacteria diversity by Horner-Devine et al. (2004), and should be extended to whole soil habitat: on the one hand as structural heterogeneity, i.e. discontinuities in space and time and on the other hand as complexity in resources, conditions and/or interacting populations. The overwhelming complexity of (bio)physical, (bio)chemical and biological interactions in soils between environment and organisms or between organisms themselves prevents us from applying a solely analytic approach which concentrates on the elements and emphasizes the details.

Global perception, even if imperfect and partial, is an efficient approach and necessary condition when dealing with nonlinear and complex soil systems, including aboveground effects such as plant growth. However, due to the complexity of possible interactions among all biotic components and environmental factors one must acknowledge that exploring all these combinations is an impossible task (van der Putten 2009). Hence we must adopt a somewhat reductionist approach. As quoted by Andrén and Balandreau (1999), while looking inside the soil “black box” we have opened a “can of worms”; in order to reveal critical variables for plant growth we are now compelled to consider the system as a whole and accept its partly unfathomable features.

2.3 Soils as a Product of Species Diversity

Soils are alive. This somehow provocative statement underlines the fact that, unlike water or air, which are also considered as basic components of ecosystems, the very existence of soils is primarily defined by the presence of living organisms. They do

not just inhabit soils; they create them, almost entirely, at least for the upper part we mostly depend upon for growing food or fibre.

The prominence and functional significance of life in soils was acknowledged since the beginnings and the formalisation of soil science. Biota was indeed designed as one of the five factors of soil formation (Jenny 1941). Soils form as rocks break up and dissolve due to physical and chemical factors, but also with consistent contribution of soil organisms, including plants and fungi (Jongmans et al. 1997), releasing organic compounds, creating particles that bind with organic matter to form aggregates. Given the central roles played by soil dwellers in soil formation and functioning, soils can be considered as an emerging property of life. Soils are the product of a large array of biological processes and, contrary to air or water they depend for their structure and functioning on living organisms.

More than any other components of terrestrial and aquatic ecosystems, soils are subjected to the process of metabiosis as most soil organisms depend indirectly on others for their existence through modifications of their environment (Waid 1999). This form of ecological dependency has been well described in the case of earthworms (e.g. Tiunov 2007; Eisenhauer 2010), the ultimate ecosystem engineers. But a closer insight into soils reveals that most soil organisms or soil functional groups are metabionts and modify the environment or supply resources, allowing dependent organisms to thrive. Examples include bacterial consortia and rhizosphere microbial feedbacks.

Despite substantial research efforts devoted in recent decades to the functional role of soil organisms in soil formation processes, progress remains limited by poor taxonomic expertise and methodological barriers, particularly for small-bodied taxa, such as bacteria or protists (Decaëns 2010; André et al. 2002; Pawlowski et al. 2012; Foissner 2008).

2.3.1 Functional Roles of Soil Dwellers

Underground organisms, including plant roots, participate in many ways in the formation and evolution of soils and also affect, directly or indirectly all above-ground ecosystem functions. For instance, agricultural productivity depends directly on soil borne organisms, which regulate nutrient availability and uptake, and indirectly on maintenance of soil structure and regulation of hydrological processes. Many other mechanisms underpin and support primary production and enhance nutrient release in the rhizosphere, particularly biochemical processes related to mutualistic interactions among microorganisms, mycorrhizae and plants, N-fixation through symbiotic bacteria, volatile-mediated plant growth promotion (e.g. Bailly and Weiskopf 2012), or abiotic stress tolerance through plant-growth-promoting rhizobacteria (e.g. Yang et al. 2009). On the other hand, plants themselves developed a sophisticated system of biochemical products allowing them to modulate in an antagonistic or synergistic manner various soil-borne pathogens (e.g. Pieterse et al. 2009). Clearly, all size categories of soil organisms contribute to some essential function (Table 2.1).

Table 2.1 Examples of diverse soil organisms within functional groups, related to their ecological functions and their main impact on soil properties and to their principal sphere of influence

Soil organisms	Functional group	Ecological function	Soil properties	Sphere of influence
Bacteria Archaea	Decomposers, nitrogen fixers, trace-gas producers	Nutrient cycling (e.g. N-fixation, nitrification, P-solubilisation, etc.) Decomposition Binding, weathering (release of organic compounds)	Mineral fertility Exchange capacity Structure, texture	Detritusphere, agregatosphere, rhizosphere, drilosphere
Fungi	Decomposers, symbionts	Iron oxidising/reducing Nutrient cycling Decomposition Release of binding compounds, enmeshing	Redox potential Mineral fertility Exchange capacity Structure	Detritusphere, agregatosphere, rhizosphere
Plant roots, lichens, bryophytes	Primary producers	SOM cycling, weathering	Texture, porosity, hydric regime, pH Structure	Rhizosphere, porosphere
Algae, diatoms, cyanobacteria	Primary producers	SOM cycling, weathering	Structure	Porosphere
Protista	Predators (bacterivores) Decomposers	Biological population regulation Decomposition		Detritusphere, agregatosphere, rhizosphere, drilosphere
Nematoda	Plant feeders, predators (bacterivores, fungivores, etc.)	Biological population regulation	Exchange capacity	Detritusphere, rhizosphere
Collembola	Saprovores, predators	Decomposition, biological population regulation	(Micro-)structure (faecal pellets)	Detritusphere
Acari	Saprovores, predators	Decomposition, biological population regulation	(Micro-)structure (faecal pellets)	Detritusphere
Enchytraeids	Saprovores, bacterivores	Decomposition, biological population regulation, transportation	Structure (Micro-)porosity	Detritusphere, agregatosphere
Arthropoda	Predators, decomposers	Decomposition, biological population regulation, transportation	Structure, porosity, hydric regime, clay-humus complex	Detritosphere
Earthworms	<i>Ecosystem engineers</i> ; burrowers, saprovores, geophages	Decomposition, formation of aggregates, transportation		Drilosphere

Compiled from: Lavelle (1996), Adl (2003), Gobat et al. (2004), Wall (2004), Brussaard et al. (2007), and Brussaard (2012)

The more recently developed ecosystem services concept (e.g. Wall 2004; Wall et al. 2010) also applied to soils aims to understand globally the interactions between soil biota and soil functions or functioning. This approach is mainly based on the distinction of taxa according to their effective body width. Even if this basically corresponds to a measure of the ability of different organisms to move through different soil pore size categories, it also reflects their impact on different soil processes. At the smaller spatial and temporal scales, the smallest sized organisms (microflora) are responsible for the digestion and transformation of complex organic molecules into simpler molecules and mineral elements available for plants uptake. Bacteria or fungi are responsible for most chemical processes controlling nutrient cycling (e.g. N-fixation, nitrification, P-solubilisation, iron-oxidation or reduction). Protozoa are also involved in many of these processes but this role is poorly studied and it is currently unclear how relevant they are in soil biogeochemical cycling (Finlay and Fenchel 1991; Ali et al. 2004; Hongoh et al. 2008; Risgaard-Petersen et al. 2006; Wilkinson and Mitchell 2010). On the other hand, the comminution (i.e. size reduction by fractionation) of fresh litter and the development of soil structural stability require longer time and are rather controlled by larger species, such as earthworms or arthropods which belong to the meso- or macrofauna. However, it is impossible to link the size of organisms to specific temporal and spatial scales; for example, the process of mineral weathering of parent material which occurs over a long period of time partly depends on organic acid production by many bacteria and fungi (Lavelle et al. 2006).

The degree of functional redundancy among soil organisms is an intensively studied and debated question and represents a challenge for the understanding of biodiversity-ecosystem function relationships. Some studies have shown there is no clear relationship between soil microbial diversity and microbe-driven functions (Griffiths et al. 2001; Nannipieri et al. 2003). A possible explanation is that diversity-function relationships exists only at the poor end of the diversity gradient while at higher diversities functional redundancy increases (Setälä and McLean 2004). Furthermore the degree to which diversity influences function may relate to resource levels (Philippot et al. 2013). For example, the degree to which microbial community structure controls C cycling in soil may differ between the rhizosphere or litter and the mineral soil because the rate limiting processes depend on resource availability (Schimel and Schaeffer 2012).

Effects of community composition may however be stronger than diversity changes *per se* if functionally important species are lost (Nielsen et al. 2011). The same could be true about overall biomass or abundance. Long-term data sets are highly valuable to address such questions but are unfortunately quite rare. Good examples include the DOK experiment in Switzerland (Maeder et al. 2002; Birkhofer et al. 2008) and the Rothamsted long-term research site in the UK (Glendining et al. 1996). The vast majority of existing data are derived from experiments in controlled conditions over short time periods. A challenge with long-term observational or experimental studies is however to guarantee that results will be comparable over decades, especially for rapidly evolving methods such as molecular analysis of microbial diversity. Another challenge is that only a small fraction of biodiversity is usually studied in such programs (e.g. Maeder et al. 2002).

The current shortcoming of taxonomic knowledge about soil organisms and thus the lack of information on the precise functional roles of individual species prevents a detailed mechanistic understanding of functional consequences of biological interactions among soil organisms (Fitter 2005). One way to overcome these limitations is to use the functional diversity approach to study the multiple biological or biochemical interactions in soils. This can be achieved either by grouping species fulfilling similar functions in ecosystems, the so called functional groups (Brussaard et al. 2007), or by looking at specific communities of organisms acting at similar spatial and temporal scale, such as major regulator (e.g. earthworms or roots) (Lavelle 2000, 2002) (Table 2.1). While this approach clearly neither accounts for the full complexity of *soil functioning* nor for the diversity of soil organisms it nevertheless allows assessing the relationships between soil biota and functioning. This approach is especially useful to study ecological gradients and effects of natural or experimental perturbation of the soil environment.

2.3.2 *Plants Considered as Soil Dwellers*

Obviously, higher plants, at least their underground part, should also be included in the category of soil dwellers as they root in soils, influence physically and biochemically and play a major role in pedogenesis through their roots, their exudates and their aboveground and belowground litter quality and quantity. Thus, higher plants, as primary producers, are not just a part of the food chain; they also influence soil physico-chemical characteristics. They are active at all spatial scales but they interact most closely with other soil organisms in the direct vicinity of fine roots – the rhizosphere (Gobat et al. 2004). For instance, vascular plants are the main source of oxygen for the soil biota living in the proximity of small roots (Waid 1999) while old root channels allow preferential flow of water and air (Gobat et al. 2004; van Noordwijk et al. 2004). Rhizodeposition (lysates, exudates, mucilages, etc.) affect soil chemistry and especially nutrients concentrations in the vicinity of roots. Root biomass production can be higher than aboveground biomass, particularly in grasslands. For instance, the belowground biomass of a swamp meadow in Switzerland represented between 79 and 94 % of the total biomass (Buttler 1987). Chevallier et al. (2001) found that in pasture converted from sugarcane in Martinique root inputs were entirely responsible for an increase in organic carbon in the upper part of a vertisol. Some trees such as the cohune palm in Central America develop massive underground structures, roots and storage organs. Once dead, the decomposition of these organs creates large hotspots of organic matter and patches of moister soil as a result of the slow collapse of the surface (Kricher and Plotkin 1999).

Vascular plants are the main drivers of ecological linkages between aboveground and belowground subsystems (Wardle et al. 2004). At a global scale in non-disturbed environment, vegetation and soils have undergone a long ecological

co-evolution resulting in dynamically stable ecosystems (at the biogeocenosis level) characterised by complex interactions between abiotic factors (climate, parental mineral material, etc.) and biotic components. Plants have a lasting effect on the soil environment and evolutionary processes (e.g. how plants life history characteristics vary along succession stages) strongly influence pedogenesis and soil communities (van der Putten 2009). Thus, vegetation and soil as a biotic/abiotic subsystem are deemed to be in long-term equilibrium, mediated by feedback interactions; soils providing water and nutrient for plant growth; plants supporting the soil biota by organic matter inputs. However, the theory of hierarchical structure of ecosystems, with one particular level being embedded in another one of larger scale, leads to expectation that processes taking place at higher level will have significant effects on the lower one. Thus, as vegetation is also controlled by herbivores consumption, changes in plant community composition will affect the root-associated biota (Wardle et al. 2004). For example, Veen et al. (2010) reported that exclusion of cattle and rabbits from grassland changed the structure of nematodes communities more by altering vegetation composition than by altering soil abiotic characteristics. They hypothesised that these changes may result from effects related directly to living plant roots and indirectly to root exudates and inputs of organic matter. Plant-soil interactions are therefore a complex issue involving numerous and diverse feedbacks that occur between primary producers, consumers and decomposers (Bardgett 2005).

2.3.3 *Soil Properties and Soil Organisms*

Soils are usually described in terms of components, properties and processes, which are generally well known to soil scientists. These characteristics provide a decision-making framework for soil use. As soils are extremely heterogeneous, and cannot all fulfil the diverse societal needs, land management is sometimes – or at least should be – based on their suitability for specific uses (e.g. food and timber production, flood or landslide prevention). Land-use suitability planning refers primarily to basic soil properties (e.g. texture), to specific characteristics (e.g. depth) or to aggregated features (e.g. suitability for growing winter cereals). Soil biodiversity is approached through biological survey networks (e.g. Rutgers et al. 2009; Ranjard et al. 2010), but is generally not considered in land-use planning. Indeed, the functional link between soil properties and soil biodiversity is still not considered by policymakers and land-use planners and is only partly understood by scientists, although soil organisms, as pedogenic factor, are responsible for the major part of soil characteristics (Table 2.1).

There is no consensus on a standard list of physical and chemical soil properties (Baize 1993). Here we discuss those mostly related to plant growth, such as texture, structure, porosity, hydric regime, mineral fertility, etc. (Fig. 2.4). Soil temperature is not explicitly mentioned because it underlies most or all other properties and

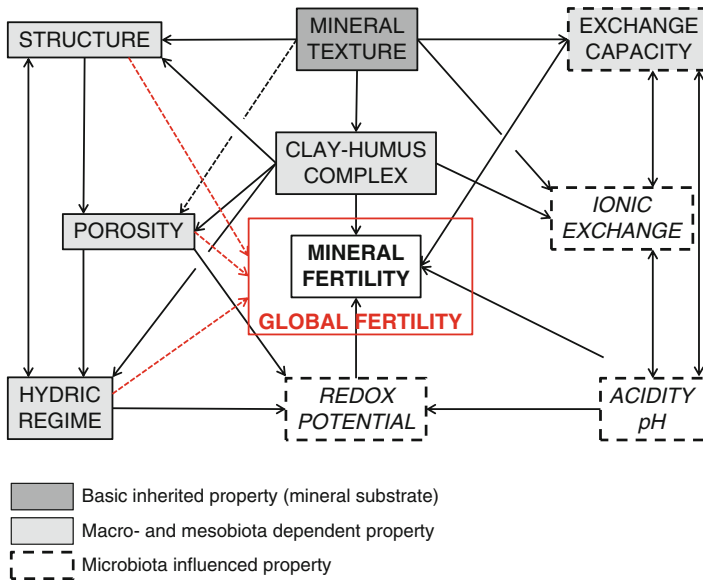


Fig. 2.4 The major soil properties depend mainly on biological activity and are therefore tied back to soil biodiversity. Some properties are prone to change in short-term (*in italics*) while others are more stable. Rapidly changing properties are mainly mediated by microbiota (Modified from Gobat et al. 2004)

influences them indirectly (Gobat et al. 2004). Some properties are purely physical (e.g. texture) while others reflect rather physicochemical and functional aspects (e.g. cation exchange capacity).

Soil textural composition refers to the respective proportion of mineral particles of different size (e.g. clay, silt and sand). It is inherited from mineral parent material and is the only soil property that is originally not influenced by living beings and by any other property. Soil texture is considered as a stable characteristic, although it is subject to long-term changes resulting from soil processes including biological weathering. All further considered soil characteristics depend directly or indirectly on texture (Ellis and Mellor 1995; Gobat et al. 2004), are connected by a system of complex interrelations and are more or less strongly dependent on biological activity (Fig. 2.4). Soil organisms are directly responsible for some properties including the granular structure of topsoil, which in turn determines porosity and hydric regime, and, the formation of clay-humus complex. Other properties are a product of the physicochemical inherited nature of soil modified by biological activity (e.g. pH or redox potential). The mineral fertility, on which plant growth relies heavily, could thus be considered as an emerging property of the soil system but even then, plant ion uptake depends on complex feedback mechanisms between rhizodeposition and the presence of microorganisms (ionic exchange). However, soil fertility is determined not only by mineral fertility but also on other soil properties (Fig. 2.4).

2.4 Aggregates as Functional Units

2.4.1 *Structure, a Key Property of Soils*

Structure is an obvious feature of soils. However, it is also probably the most difficult to measure objectively. Soil structure refers to the rearrangement of solid particles, both mineral and organic, into secondary particles called aggregates. These are primarily described in terms of size as macroaggregates ($>250\ \mu\text{m}$) and microaggregates ($<250\ \mu\text{m}$) and of shape. Depending on authors, macroscopic aggregates can be subdivided into five or more categories, usually including rounded granular structure, angular structure (prismatic, platy, blocky) and structure characterized by absence of aggregates (massive, single-grain) often inherited from parental material (Brady and Weil 2008; Ellis and Mellor 1995; Gerrard 2000; Gobat et al. 2004). Moreover, the degree of aggregation expresses the structure stability where the forces of cohesion between and within aggregates should be weak, moderate or strong. The size and the shape of aggregates are qualitatively appreciated by direct observation or with microscopy of thin sections (Dexter 1988; Oades 1993) while their stability can be quantified by measurement techniques (Le Bissonais 1996; Six et al. 2000; North 2006). Structure is a pivotal property in soil functioning. Structure degradation was identified in the European Strategy for Soil Protection as one of the eight major risks (Thot et al. 2008). Porosity, which refers to the size and patterns of structural voids (volume and connectivity between pores), influences the infiltration of water and air, the transfer of fluids such as leaching or water drainage which lead to soil differentiation. It also affects plant growth and roots penetration and more globally determines the suitability of life conditions for soil organisms. Unlike texture, structure changes over time; it is modified by changes in water and organic matter content, the degradation of stabilizing agents (e.g. breakup of macroaggregates, decay of hyphae or decomposition of bacterial poly-saccharides). Its persistence over time therefore depends on the balance between processes of formation and degradation.

2.4.1.1 Good Structure Versus Bad Structure

How can we define a good soil structure, and inversely a poor one? Implicitly, the beneficial aspects of soil structure are considered in relation to agricultural management practices and generally a “good” soil structure is associated with the organic matter content while “poor” soil structure is defined as absence or poor aggregation, for example in sodic environments (Nelson and Oades 1998). According to Dexter (1988) “good” structure is described by its stability and by the presence of all hierarchical orders of aggregates. However, in environments where the activity of earthworms is impeded by natural factors (e.g. arid climate), the soil organic matter content is naturally low. Likewise, soils characterized by the presence of dispersive cations (e.g. natural salinity or sodicity) and low aggregation rates cannot

be considered as “poor”. There is indeed a natural balance between soil properties, including structure and the soil biota and plants. “Loss” or “degradation” of the structure ultimately leads to the destruction of aggregates, leading to a single-grain structure (Brady and Weil 2008). On the other hand, as soil structure influences directly or indirectly all other soil properties, its loss or degradation is of crucial concern for human activities. Decreasing soil organic matter levels, compaction, salinization or reduction of soil faunal activity leading to structural degradation will ultimately result in economic losses and related social consequences (Nawaz 2013). The term “degradation” usually refers to detrimental changes in soil structure due to human activities and resulting in impaired aeration, water movement or root growth (Oades 1993).

2.4.2 Formation of Aggregates

The mechanisms involved in aggregates formation differ between the upper and the lower part of the soil. The rounded structure, more frequent in the topsoil is mostly a product of biological activity, while the characteristic angular structure of lower soil horizons stems from physical processes. Macroaggregates are one of the keys to plant establishment and growth (Wagner et al. 2007) since well-developed porosity associated with macroaggregates facilitates rooting and air supply as well as the biological activity of organisms responsible for organic matter degradation and thus nutrient supply. Macroaggregates also represent hotspots of microbiological activity and associated biochemical transformations (e.g. mineralization), as well as biological regulation by micro- and mesofauna.

2.4.2.1 Physical Mechanisms in Subsoil

Macroaggregates in the mineral, deeper soil horizons (B horizons) are typically angular. If the organic matter content is low, as is usually the case in the lower part of soils, wetting-and-drying cycles promote or enhance aggregation and give rise to a stable structure. This is mostly due to physical process of clay shrinking and swelling driven by hydrological changes. The main factors controlling this process are therefore clay content and quality (Baize and Jabiol 1995; Baize and Girard 2009; Girard et al. 1998; Ellis and Mellor 1995; Gerrard 2000; Wagner et al. 2007). The shrink-swell capacity is highest in smectite-rich clays (Oades 1993), and lower in kaolinite-clays (Murray 1999). Thus, the cohesive behaviour of clays is the dominant factor leading to the development of aggregates and cracks. The stability of such aggregates depends primary upon the strength and the persistence of drying/rewetting cycles (Oades 1993). Nevertheless, biological processes also influence this predominantly physical mechanism by enhancing the drying processes through root colonization of the soil and plant evapotranspiration.

Even if the origin of angular macroaggregates remains incompletely understood (Gerrard 2000), we can assume that the lower soil horizons mostly lack biologically-formed structure (Baize and Girard 2009; Girard et al. 1998). Physical forces involved in aggregates formation also include freeze/thaw cycles that lead mainly to platy structure (Brady and Weil 2008; Ellis and Mellor 1995). This structure can, however also be associated to direct or indirect biological causes (animal trampling, agricultural machinery). However, the effects of freeze-thaw cycles on structure or structural stability are ambiguous or nonlinear as they depend on numerous variables such as clay or organic matter content, moisture level, number of freeze-thaw cycles, and their complex interactions (see review in Six et al. 2004). Henry (2007) argues that many studies suffer from methodological weaknesses (e.g. using unrealistic temperature fluctuations) and thus that further investigations are necessary.

2.4.2.2 Biological Mechanisms in Topsoil

Biota mediated processes shape mostly, but not only, the structure in the upper part of soils. Numerous species, ranging from bacteria to macrofauna (namely soil engineers such earthworms, ants and termites) and plant roots, create various structures, which differ in size, stability and quality. Several factors (texture, clay mineralogy, cation content, crystalline and amorphous oxides and hydroxides) influence the effectiveness of aggregation but soil organic matter plays a crucial role particularly in structure stability (Bronick and Lal 2005; Abiven et al. 2009). Organic compounds increase the stability of aggregates by up to one order of magnitude but this depends on the quality of the organic constituents (Abiven et al. 2009). Labile compounds (e.g. released by bacteria) exhibit strong but transient effect on aggregate stability while more recalcitrant compounds (e.g. decomposed manure) have smaller initial, but longer-lasting effect. As aggregate stability is a critical factor of soil fertility, and soil organic carbon content is a manageable property, an adequate input of organic matter is the easiest way to maintain, enhance or restore the fertility of agricultural soils.

Several mechanisms lead to the formation of microaggregates, constituted primarily from organic molecules bound to clay particles by polyvalent cations. The release of extracellular polymeric compounds by bacteria binds these primary organo-mineral particles to form bacterial microaggregates. Similar processes were described involving fungus-derived polysaccharides (Chenu 1989) and glomalin, a glycoprotein released from arbuscular mycorrhizal fungi, which is thought to act as a “glue” due to its hydrophobic properties and thus to reduce aggregate breakdown during wetting and drying cycles (Miller and Jastrow 2000; Rillig and Mummey 2006).

The hierarchical arrangement of soil aggregates is the most common model to describe the process of aggregation with microaggregates being bound by organic polymers, that stick particles together, or are enmeshed by hyphae or plant roots to form macroaggregates (Dexter 1988; Tisdall and Oades 1982; Tisdall 1996; Miller and Jastrow 2000). In some soil types, however (Oxisol) stabilizing agents are

oxides rather than organic compounds (Oades and Waters 1991). Oades (1984) further hypothesised that microaggregates should also form within macroaggregate: as the particulate organic matter around which macroaggregates concentrically coalesce is decomposed, microbial exudates are released and microaggregates form inside (Bronick and Lal 2005).

At a larger scale, earthworms modify the soil structure by producing casts and forming large biopores. Other representatives of the soil macrofauna (termites, ants, spiders, larvae of insects, etc.) also contribute to the creation of soil porosity. Earthworms ingest mineral and decaying organic material and excrete stable macroaggregates, deposited on the burrow walls or on the soil surface (Brown et al. 2000). The stabilization of macroaggregates within casts, but also the formation and disruption of microaggregates within the intestine of earthworms, result from numerous physical, chemical and biochemical processes, involving also bacteria living in the digestive tract of earthworms (reviewed in Shipitalo and Le Bayon 2004). Where earthworms are scarce or absent (e.g. owing to unfavourable climatic conditions, acidity, etc.), the faecal pellets produced by microarthropods or enchytraeids influence the structure of upper organic horizons and can even make up the major part of forest litter layers, typically in moders (Rusek 1985; Lee and Foster 1991; Ponge 2003). Due to their small size (and weakness), microarthropods are usually unable to reach the deeper mineral or organo-mineral horizons and they are rather confined to pre-existing porosity (Lee and Foster 1991). The layers of accumulated faeces of epigeic fauna condition the development of specific communities and they become densely colonized by fungi (Oades 1993). The fungal community is dominated by ectomycorrhizal basidiomycetes, which allow the vegetation to take up nutrients sequestered in decaying litter and faecal pellets and released by detrital fungi and animals (Ponge 1990). Moreover, Lee and Foster (1991) observed in thin sections of faecal pellets a dense accumulation of bacterial cells. Lavelle (1996) suggests that these holorganic structures are incubators for microbial activities; when enchytraeids and arthropods re-ingest their droppings they also assimilate metabolites that have been released by the bacteria.

The above-mentioned interactions among soil organisms illustrate the complexity of interactions involved in the formation, stabilisation and disintegration of aggregates, which take place at different spatial and temporal scales (Six et al. 2004). The heterogeneity of the belowground habitat and functioning created by these multiple mechanisms can be compared to the complexity of the aboveground component of terrestrial ecosystems. This also shows that soil biodiversity is both a cause and a consequence of soil complexity. The belowground habitat should thus indeed be approached using a holistic view and a systemic approach.

2.5 Biodiversity as a Product of Soils

After the Rio Conference in 1992 and the popularization of the biodiversity concept, research on soil biodiversity gained momentum, especially with respect to its contribution to provisioning key ecosystem services (see Wall 2004). However, an

accurate estimation of specific soil biodiversity remains challenging because its assessment should include both organisms that spend their whole life in the soil as well as species that live only temporarily in the soil.

Gobat et al. (2004) propose a classification of soil animals based on the permanence or not in soils and their state of activity. Thus, temporal inactive geophiles, such as the caterpillars of many butterfly species, only bury in the ground for nymphosis; even so they constitute an important food source for other edaphic species. Temporal active geophiles, such as dipterans with edaphic larvae (e.g. Tipulidae), spend the first (and often longest) stage of life in soils, from egg to mature larva. Other species (e.g. scarabids) belong to periodic geophiles; although they spend their entire life in soil, if the ecological conditions become adverse they are able to change location through aerial dispersion. Finally, strict geobionts live permanently in soils and thus have low dispersal ability. Moreover, numerous species living in “soil annexes” i.e. aboveground structures such as dead wood, carrions or epiphytic soils, should also be considered as part of soil biota as they partake in organic matter “degradative successions” which eventually lead to soil organic matter cycling (Gobat et al. 2004). According to Decaëns et al. (2006), at least one quarter of all living species belongs to strict soil or litter dwellers, but bacteria and fungi are not covered by these estimations.

2.5.1 Heterogeneity of Habitats and Functions

The broad diversity of soil biota is closely related to the diversity as well as the spatial and temporal variability of soil types. Obtaining a reliable overview of soil heterogeneous habitats is therefore the first step and also a major challenge for global biodiversity assessment and assessment of its ecosystem functions.

Soils are spatially and temporally highly heterogeneous three-dimensional bodies, from landscape to micro-meter scale, and lower. They offer an overwhelming diversity of habitats for organisms, whose size varies from micrometre to decimetre. Soils could be compared to an underground jungle with a huge diversity of ecological conditions and niches. Mutual influences among soil organisms can be found across all scales (Ettema and Wardle 2002). As soils are spatially as well as functionally heterogeneous it is not surprising that soil organisms are studied in relation to their body size as well as to their functional roles. These two approaches are detailed hereafter.

2.5.1.1 Approach According to Body Size

Body size is related to the concept of ecological niche as many characteristics (e.g. feeding, locomotion and life modes) depend on the size and to the spatial domain of organisms (Gobat et al. 2004; Wolters 2000). The extreme variety of spatial dimensions and related ecological conditions create numerous and contrasted belowground “sub-ecosystems” which are as distinct as are forests or ponds in aboveground ecosystems.

For the microorganisms (size less than 0.2 mm), the soil is considered to be a semi-aquatic environment. The microbiota thrives within the water film around mineral particles or the interstitial soil water, which remains in micropores below the permanent wilting point. Prokaryotes, protists, small nematodes, rotifers and tardigrades are typical inhabitants of these micropores. Until now, the major part of taxonomic and functional studies focussed on microflora, i.e. bacteria (and archaea) owing to their central role in nutrient cycling. The prokaryotes are by far the most numerous group of organisms in soils (Torsvik and Ovreas 2002). In terrestrial systems, sediments and soil, they largely exceed their aquatic counterpart both in terms of biomass and density (Torsvik et al. 2002). This difference is most likely due to the structural heterogeneity and the complexity of soil resources (Torsvik et al. 2002; Horner-Devine et al. 2004).

The diversity, biogeography and specific functional roles of soil protists remain comparatively poorly studied despite significant advances in the understanding of the soil microbial loop and rhizosphere interactions (Bonkowski 2004; Clarholm 1981, 2005). Evidence for cryptic diversity (Heger et al. 2011; Kosakyan et al. 2012), restricted geographical distributions (Heger et al. 2013), strong impact on bacterial communities which can be contrasted even for closely related protists (Gluecksmann 2010) and likely unknown or under-evaluated role in biogeochemical cycles (Wilkinson 2008; Wilkinson and Mitchell 2010) suggest that a strong potential exists for significant discoveries on protists.

To what size category do fungi belong? This apparently simple question is actually not straightforward. Fungi are usually included in the microflora category but the hyphae influence soil properties and processes at a very large scale. One square metre of soil may contain up to 10,000 km of total length of mycelial filaments (Gobat et al. 2004) and Ritz and Young (2004) cite several studies stating that hyphal length is of the order $10^2 - 10^4 \text{ m g}^{-1}$ in arable, pasture and forest topsoils. Mycelial network, particularly in mycorrhizal symbiotic associations, plays a pivotal role in plant nutrition by translocation of water and mineral substances by exploring large soil volume and thus increasing the surface area for absorption. The role of fungi is also well recognized in the salient ecosystem process of soil aggregation (e.g. Rillig and Mummey 2006) as mycelia increase physically and biochemically the cohesion of particles. Their ramified structure and their products such as glomalin contribute largely to aggregates formation. Moreover, due to their ability to also grow through nutrient-impovertished zones and even through air (Ritz and Young 2004), the foraging strategy of fungi enables them to link remote places and to bridge different layers of soil such as the litter horizons and the rhizosphere. Hence, fungi are a perfect illustration of a paradoxically “minute” organism whose effects extend well beyond their size at higher functional ecosystem scales.

When compared with bacteria and fungi on one hand and macrofauna on the other, the mesofauna (length ranging from 0.2 to 4 mm) seem to suffer from the “middle-position child” syndrome and even if their diversity and ecological importance are recognized, comprehensive knowledge of these neither big nor small soil dwellers remains comparatively scarce. The role of mesofauna which usually

colonize the air filled pore system of soils (Lavelle et al. 2006) is rather examined in relationship to microorganisms on which they feed (e.g. Wolters 2000; Cole et al. 2004) as the decomposition rates are predator controlled (Vreeken-Buijs and Brussaard 1996) or in relationship to microstructure as the nematodes, collembolans, acari or enchytraeids, the main representatives of mesofauna, are typical producers and consumers of faecal pellets (Wolters 2000; Deschaseaux and Ponge 2001; Lavelle et al. 2006). In some cases, in a broad range of climatically different ecosystems, a whole organic upper layer may be made up by faecal pellets conferring this material its micro-granular peculiar feature (e.g. Loranger et al. 2003; Sadaka and Ponge 2003; Bernier and Ponge 1994). By producing these biogenic structures, microarthropods promote the activity of microbes, which would otherwise have very limited ability to move towards adequate substrates to decompose, and thus indirectly affect the global nutrient cycling (Lavelle et al. 2005).

Among macrofaunal organisms (length ranging from 4 to about 80 mm), earthworms, ants and termites, are known to enhance habitat heterogeneity mainly at the macrostructure scale. They are commonly designated as ecosystem engineers for they change the physical, as well as the biochemical soil conditions and therefore regulate the availability of biotic and abiotic resources (habitat, food, etc.), also to the benefit of other species (Jones et al. 1994; Lawton 1994; Jones et al. 1997; Eisenhauer 2010). Earthworms, probably one of the most studied group of edaphic invertebrates play a dominant role in pedogenesis by burrowing, ingesting soil and dead organic matter, excreting modified biogenic structures. In particular, soil structure is chemically and structurally reorganized during gut transit (e.g. Shipitalo and Le Bayon 2004). They are thought as being the most effective bioturbators, followed by ants and, to a lesser extent, termites (Paton et al. 1995). However, it is still not clear whether some soils have an extended burrow system because they provide appropriate conditions for earthworm development or if the earthworm activity improves the soil conditions (Kretzschmar 2004). Furthermore, following the reflections of Jones et al. (1994, 1997), Jouquet et al. (2006) discuss the differences between ants and termites being “extended phenotype engineers” (creating biogenic structures that directly influence their own needs) while earthworms mostly belong to “accidental engineers” (creating biogenic structures as a by-product of their movements through the soil in order to be as close as possible to their optimal environment). Nevertheless, both categories of soil engineers contribute to structural and functional heterogeneity of soils and influence to a large extent the global functioning. Besides the feedback loop effect and the creation of suitable conditions for other species (micro-, meso- and macroorganisms), vegetation is also dependent on these modifications in soil physical and biochemical properties. For instance, ants influence the composition of plant communities and increase overall species richness as some species tolerate better than others the repeated disturbance or seed predation and thus prosper on ant mounds (Carlson and Whitford 1991; Sebastia and Puig 2008). More generally, it is widely admitted that earthworm activities promote plant performance by a large array of processes including among others enhancement of oxygen and nutrient availability or physical accessibility to the roots (e.g. Brown et al. 2000). Other representatives of macrofauna include arthropods

with permanent or temporal edaphic stage, or gastropods and larger species of enchytraeids, which get involved in the first stages of the decomposition food chain, particularly in fragmentation (Gobat et al. 2004).

2.5.1.2 Approach According to the Function of Organisms

While the body size of some organisms is easy to define (e.g. a bacterium), this is not the case for many soil organisms. For example higher plants act simultaneously at different spatial and temporal scales (e.g. small rootlets, litter deposition or macroscopic aerial parties such as decaying trunks). The functional approach represents an alternative to the classification of organisms according to body size. This approach refers to the volume under the influence of soil organisms, which is determined by their ability to move through or occupy space (e.g. mobility of microbial or invertebrate species, extent of mycorrhizal hyphae or soil volume influenced by bacterial activity). This approach is useful to overcome the complexity of interactions between the aboveground and belowground parts of the ecosystems. It allows a better understanding of the global soil system and of ecosystem functions and services. The functional approach indeed represents a useful framework for the understanding and management of ecosystems.

Functional domains are characterized as “biologically relevant spheres of influence” (Beare et al. 1995). Although they occupy only ca. 10 % of the soil volume, they concentrate up to 90 % of the biological activities. This approach divides the soil functional complexity “black box” into smaller entities. The categories of functional domains broadly refer to soil biota communities sharing the same spatial and temporal environment and sharing similar adaptations.

The functional approach is analogous to the synusia approach based on the spatio-temporal organization levels to study vegetation (Gillet et al. 1990). A synusia is defined as a plant species assemblage characterized by uniformity of life form or height, having similar ecological requirements and occurring in similar habitat. Species belonging to one particular synusia thus occupy a similar spatial and temporal space. Several major functional domains or biological systems of regulation have been described (Beare et al. 1995; Brown et al. 2000; Lavelle and Spain 2001). Their characteristics (extension, origin, and role) vary over time and space. They are referred to as “hotspots of activity”. This approach is useful to study the complexity of the soil subsystem by considering smaller subsystems (Table 2.2).

Two of these functional domains (*detritusphere* and *rhizosphere*) are closely related to the plants, especially as organic matter sources. Plant debris is quantitatively the main aboveground input of organic matter although animal dejections and remains also represent a locally significant source. As plant productivity strongly depend on climate, the quantity of litter (*sensu stricto*) broadly varies among latitudinal gradients. Agricultural use of soils is the main factor modifying litter inputs qualitatively and quantitatively, with cascading impact on decomposer communities. For example, the replacement of temperate deciduous forest by cultivated land diminish annual litter fall from ca. 11 t ha⁻¹ to 0.3–2.0 t ha⁻¹ (Gobat et al. 2004, various sources).

Table 2.2 Functional domains in soil: main sphere of influence according to their origin and major soil functions and processes

Functional domain	Characterization	Role
Porosphere	Soil voids (macropores, mesopores, micropores)	Structural condition of soil, habitat for most of the larger invertebrate species, root penetration, air and water circulation
Aggregatosphere	Aggregated particles of different sizes and their immediate vicinity	Structural condition of soil, related to porosity; habitat for microorganisms and mesofauna
Drilosphere	Soil volume under earthworm influence (internal features in contact with the ingested soil and external structure created by earthworm activities)	Depends on the species and ecological categories of earthworms
Termitosphere	Termite nest and mounds	Changes in soil structure and chemical characteristics
Myrmecosphere	Ant nest and mounds	Changes in soil structure and chemical characteristics
Rhizosphere	Zone under the influence of the roots, immediate vicinity of rootlets	Biologically active interface; external boundaries indistinct, linked to the mycorrhizosphere and the hyphosphere
Detritusphere	Plant litter accumulation (upper organic horizons)	Corresponds to litter system (Lavelle and Spain 2006), habitat for epigeal communities

Compiled and adapted from: Linderman (1988), Andrade et al. (1998), Beare et al. (1995), Brown et al. (2000), Gobat et al. (2004), and Lavelle and Spain (2001)

Lal (2004) estimates, that conversion to agricultural ecosystems during both preindustrial and industrial eras led to depletion of the soil organic carbon by about 60 % in temperate regions and 75 % or more in the tropics. The losses of the original carbon pool are mostly due to i) the imbalance between outputs (yield) and inputs (manure), ii) accelerated mineralization provoked by tillage practices or iii) to the dominant form of soil degradation, i.e. erosion derived from the loss of soil structural stability (e.g. Morgan 2005; Pimentel 2006). The rhizosphere is often underestimated as a source of soil carbon and quantitative data are still scarce. The contribution of roots and mycorrhizae has been estimated to account for 63–70 % of total net primary production in coniferous forests where 4–5 times more material is returned to the soil by roots than by leaf and branch litter (Fogel 1983). The role of root decomposition in soil carbon sequestration and nutrient cycling is increasingly recognised (Silver and Miya 2001). But we still do not know much about the rates of root decay and how microbial communities and other soil organisms influence it. The rhizosphere is clearly the main interface between plant and soil. In this narrow zone directly influenced by root secretion (rhizodeposition) bacterial and fungal activities are especially high. The rhizosphere partly overlaps with the latter expanded concepts of *mycorrhizosphere* (distinguished from the rhizosphere soil around nonmycorrhizal roots) and

hyphosphere (affected only by the mycelium of mycorrhizal fungi), which induce presumably quantitative if not qualitative changes in microbial associated communities (Linderman 1988; Andrade et al. 1998).

Beside the rhizosphere, three other functional domains (*drilosphere*, *termitosphere*, *myrmecosphere*) are directly controlled by ecosystem engineers, which have evolved specific strategies to overcome the poor soil quality feeding resource and to evade abiotic adverse conditions such as density that can make foraging activities difficult (Lavelle and Spain 2001). These extended phenotype engineers (Jones et al. 1994, 1997) create patches of biogenic structures, more (nests of ants and termites) or less (earthworms' galleries) permanent and thus optimise their own living conditions while creating beneficial effects for other organisms (e.g. Jouquet et al. 2007).

The different functional domains, as described above and including the *aggregatosphere* and *porosphere*, are spatially and functionally superposed. For example earthworm activity contributes to creating porosity, which can be subsequently colonized by plant roots. Such synergistic or particular effects induce enhanced biological activity and they globally contribute to the awe-inspiring soil biodiversity.

2.5.2 Why Is Soil Biodiversity So High?

The quantification of biodiversity, notably at species level among soil organisms is far from being completed and both theoretical and practical aspects have still to be addressed. For example, species concepts, particularly those applied to micro-organisms are an issue not yet resolved, although recently developed molecular methods have a vast potential to overcome technical difficulties in sampling and quantifying the microbial functional diversity (Pankhurst et al. 1996; Pawlowski et al. 2012). Moreover, the functional role of soil biota has received considerable attention, as ecological processes seem driven more by the degree of functional dissimilarities among species than by the species number (Heemsberger et al. 2004). We suggest that understanding the reasons of the generally accepted overwhelming soil biodiversity and not only its state or its consequences, will be an important step towards sustainable soil and ecosystem management.

2.5.2.1 Spatial Heterogeneity

The theory of ecology postulates that species richness depends on the availability of niches; following the principle of competitive exclusion, the coexistence of species is only possible if their niches do not overlap. They must differ in at least one essential ecological factor such as their period of activity, their spatial repartition or their food source (Gobat et al. 2004). Thus, niche differentiation and resource partitioning in a given part of an ecosystem support strongly the diversity of species and the stabilization of communities' dynamics (Levine and HilleRisLambers 2009). The diversity of niches in the aboveground part of ecosystems is mainly determined by exogenous

physical and endogenous biotic factors; soil characteristics as an abiotic factor also contribute to aboveground diversity. However, at a smaller spatial level, soil regarded as a subset of the ecosystem supplies itself numerous spatial niches. Beside the general factors determining species diversity including among others inter- and intraspecific competition and ecosystem development stage, the soil specific spatial heterogeneity related to gradients in physical and chemical factors (pore dimension, water content and relative humidity, pH, soil atmosphere, texture, etc.) in both horizontal and vertical dimensions provides a major explanation for high soil biodiversity (Giller 1996). As discussed above, soil structure is the key property of soils, influencing and influenced by soil organisms. Thus, maintenance of agricultural productivity ultimately means maintaining soil structure and its role in key ecosystem processes such as decomposition, nutrient cycling and global soil fertility, all of which are mediated by soil organisms.

2.5.2.2 Food Resources

Based on the fundamental principle that energy flows through ecosystems, while elements cycle within the system, an ecosystem should be considered in terms of matter and energy coupled in the biomass. The primary source of energy in ecosystems is supplied through photosynthetic process and plants and algae are by far the main organisms able to convert solar energy into a chemical form of energy utilisable by heterotrophs. Solar energy can be considered as an unlimited resource but plant productivity is regulated by the availability of nutrients and water, and constrained by climate. All heterotrophic organisms are dependent on matter and energy transfer through trophic levels, from herbivores to higher predators, and energy contained in food is the principal limiting factor. The amount of matter – and thus energy – decreases from one level to the next by about a factor 10 as most of it is used for the metabolism or lost otherwise (dejections, necromass, etc.) (Lindeman 1942). However, the very end of the trophic chain is not achieved with the highest predators; the organic wastes (carcasses and dejections) enter the final stage of decomposition, humification and mineralization essentially performed by numerous and diversified soil biota. The reduction of energy at each successive trophic level, therefore the theoretical diminution of biomass along the food chain, is compensated in decomposition webs by increased quantity supply and partly trophic specialization. Although it has been reported that most of the soil organisms are trophically non-specialists, this view seems to be based on a limited number of studies (Giller 1996) and may also simply reflect our current ignorance of soil biota diversity (including cryptic species). All stages of food chain, i.e. primary production, herbivory, predation, parasitism and decomposition are also represented in soils, enabling unprecedented species diversification. Clearly, the trophic structure of edaphic communities does not correspond to a simple chain, but rather to an incredibly complex food web.

Gobat et al. (2010) propose a theoretical and simplified approach of the detritus web by describing three functional compartments corresponding to the size of organisms (Fig. 2.5). The two first compartments include macrofauna and mesofauna and are

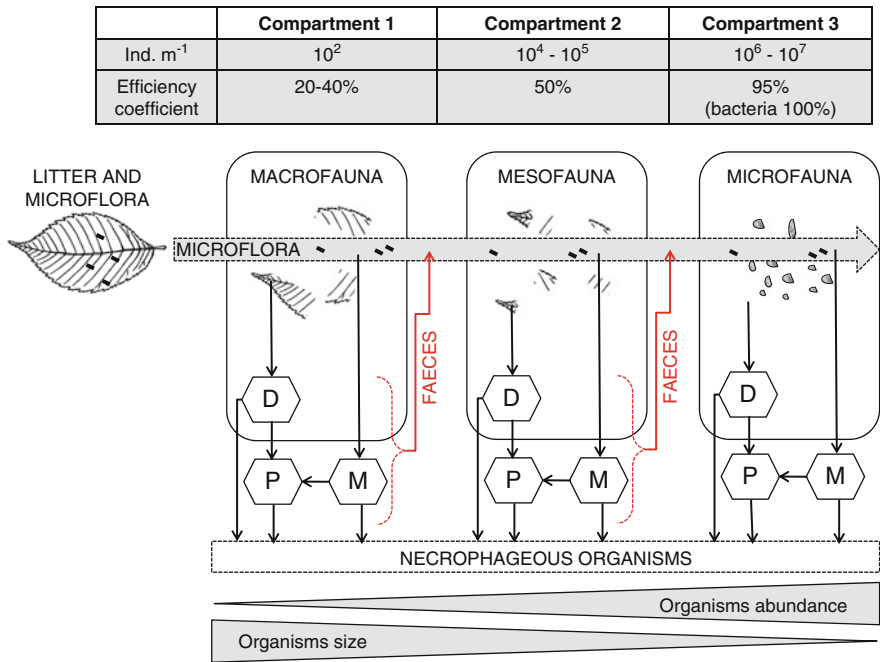


Fig. 2.5 Schematic and simplified soil detritus web through 3 functional compartments. **D** decomposers, **P** predators, **M** microphages (Modified from Gobat et al. 2010)

essentially characterized by fragmentation and burrowing processes, also by dispersion and selection of microflora present in the digestive tubes of the invertebrates. Biochemical processes mediated by microflora occur in the third compartment, which comprises mainly protozoa and micro-metazoa (nematodes, rotifers, etc.), acting as biological regulators of bacterial and fungal populations. In each compartment, organic matter is transformed, rejected as faeces and several times re-ingested. Predators and parasites are present at each stage; microphageous and necrophageous organisms enhance also diversity in the whole decomposition food web. Several features should be noted: (i) the permanent presence of microflora through the three compartments, (ii) the size of invertebrates and of plant particles diminish regularly, (iii) inversely, the abundance of organisms increases. Contrary to the aboveground food chain where the loss of energy is about 90 % between each trophic level, Gobat et al. (2010) ascribe to each compartment an “efficiency coefficient” which explains the species richness of decomposition food web. This coefficient with a value between 20 and 40 % in the first compartment rises up to 50 and 95 % respectively in the two successive modules and also explains why so many species can live in soils.

Actually, each food chain or web must start with a producer and, even if photo-synthetically active algae can be abundant on the soil surface or in large cracks of soils (Metting 1981), the major part of organic input in soils is based on plant production (aerial and roots inputs) on which both the grazer and decomposer food

chains depend. Lavelle (2012) states that on average 90 % of aboveground and belowground primary production ends up in the decomposition system, which is also enriched by the addition of dead soil organisms themselves. Furthermore, different qualities of soil organic material (fresh litter, organic residues, humic compounds) allow multiple feeding strategies and contribute to the diversity of soil food niches.

Soil communities' diversity and crucial soil functions necessary to humans depend therefore primarily on organic matter management regardless of the use of soil as organic matter is the major driver of soil biodiversity, and thus of soil ecosystem services.

2.6 Conclusion: Beyond Soil Science

Within the meaning of the theory of complex systems, soils may be considered as the ultimate emergent property of the Earth. They are the unique environmental medium where solid and fluid mineral and organic components merge to form original structures displaying specific and unpredictable characteristics such as the cation exchange capacity. We demonstrate that most of these characteristics are dependent on the aggregates, which in turn are closely linked to biological activity; aggregates are mostly formed by soil organisms and, in turn, determine habitat suitability for these organisms. Ecosystems functioning can be described in terms of fluxes of matter and energy, both being coupled in the biomass and transferred through the trophic chains. While the aboveground part of terrestrial ecosystems supports the primary productivity function almost all recycling processes, necessary to achieve the turnover of the matter, are provided by soils.

It is commonly admitted that soils contain a large proportion of the terrestrial biodiversity, higher than that of aboveground habitats. Spatial heterogeneity, defined by the structural state of soils, can explain, in part, the variety and quantity of suitable ecological niches leading to numerous adaptive strategies in terms of dwelling, moving, respiring and feeding of soil organisms. High resource availability and energy use efficiency in the decomposition food webs further explain the abundance and diversity of the soil biota. Actually, the highly fractal pattern of soils due to aggregation enhances the potential of exchange surfaces, necessary for transfers of matter and energy and thus for sustaining life. Due to this complexity, holistic reasoning constitutes an effective approach in soil science.

However, if complex thinking is essential to improving knowledge on soil functioning, two concomitant steps are to be simultaneously undertaken. On one side, ahead of the global understanding of the whole soil system, its components should continue to be identified and their place and contribution to the functioning clarified. In this respect progress is uneven. New molecular methods now allow major progress to be done on the inventory of soil biodiversity on a genetic level but the morphological, ecological and physiological characterisation of this diversity lags behind. Classical physical and chemical analyses of soils have a longer history but

a current challenge is now to link the newly discovered diversity of soil organisms to soil functions, structure, and chemical properties. This may imply the need to develop new approaches for the study of classical soil characteristics, or to adapt existing ones. On the other side, even if the complexity of soil is (largely) appreciated and (partly) understood, implementing this knowledge into sustainable management e.g. conservative agricultural practices implies facing challenges that cannot solely be overcome by soil scientists.

Some of the problems bound to the unsustainable use of soil are of a psychosocial nature and stem from diverse representations of the environment. In his book “The fear of the nature”, Terrason (1991) highlights the irrational fear of occidental civilizations for “nature” and especially for gloomy and humid places such as fens and marshes. By analogy, we consider that soils are an integral part of the “dark side” of the environment. Thus, although science should be addressed objectively soils and especially soil organisms are thus unconsciously ignored while defining priority research domains. Poor perception of visible soil invertebrates and of invisible microbes makes them appear repulsive, diverts attention from their study and slows down knowledge acquisition. A similar bias exists against botany according to Hallé (1999) who stresses the role of the emotional link (“zoocentrism”) between humans and the organisms they study, mainly vertebrates, who feed, breed, move and behave in “similar” ways as human do. Such irrational perceptions in turn lead to biased perceptions of the diversity of living organisms, their functional roles and complexity of life cycles or physiology. Although such an analysis appears seemingly inappropriate in the context of soil science, it underlines the latent perception shortcoming between soil scientists and the general public. Likewise, while exploring the reasons why French farmers do not integrate environmental measures into their practices, Weiss et al. (2006) brought to light the fact that the representation of the farmers’ own professional activity and the low level of credibility they give to scientific advice even if they are presented with figures are explicative of their behaviours.

These quite varied considerations imply that the involvement of social scientists in an interdisciplinary research (e.g. Bouwen and Taillieu 2004; Young et al. 2005) but also policymakers and stakeholders is proving to be the next challenge if we want to effectively promote awareness, propose operative solutions (Havlicek 2012) and strengthen the implementation of scientific results for a truly sustainable management of soils.

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