5

Soils are Biosystems, Habitats and Reserves of Biodiversity

5.1. Introduction

About 3.8 billion years ago, life that had settled in bacterial (prokaryotic) form in the oceans began to colonize continents, when the atmosphere became oxidative during the Proterozoic era (2.3 billion years ago). It developed with eukaryotic (algal, fungal, amoebic) forms about 1.2 billion years ago. With the diversification of plants (about 400 million years ago) and the first small animals, the first pedoclimatic environments and the precursors of the continental ecosystems appeared. This life has generated a variety of energy sources and nutritional strategies driving and regulating the biogeochemical cycles (carbon, nitrogen, sulfur, iron, etc.), and has intervened in the water cycle associated with plants. Microorganisms are significantly involved at all stages of the carbon and the nitrogen cycle, from the most oxidized states (CO_2, NO_3) to the most reduced states (CH_4 and NH_4) and vice versa, contributing to the biodegradation, transformation, mineralization, biosynthesis and production of all major types of organic compounds during these processes [BER 07]. Their ability to act in all environments, even those that are extreme, especially for bacteria and archaea, is fantastic [MAD 09, BER 11].

A quarter of the species currently described are soil organisms which make the soil a rich and diverse environment [VAN 06, DEO 10, GOB 10, JEF 10]. We only know, especially for the smallest organisms, a few species. In fertile soils, the total average biomass of microorganisms (bacteria, archaea, fungi, algae, protozoa) reaches 5 t/ha for the first 20 cm.

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Soil fauna is abundant (1 to 5 t/ha) and diverse, with up to 1,000 species of invertebrates per m^2. It includes, by diversifying them by their size, the microfauna (e.g. nematodes), the mesofauna (e.g. mites, springtails and enchytraeids), the macrofauna (e.g. Coleoptera, molluscs and Oligochaeta), and the megafauna (e.g. vertebrates). Plants (with an average root biomass of 6 t/ha), for growth, draw nutrients and water from the soil and reintroduce organic matter and nutrients as well as provide soils with chemical energy in the form of reduced organic carbon compounds [GOB 10].

Our knowledge of soil biodiversity is increasing as many species are regularly discovered, especially for small organisms (microorganisms, nematodes, mites). By their properties and organization favorable to life, soils must be considered as complex biogeochemical reactors, as reservoirs of living organisms [TOT 10, BER 11]. Soils, or the pedosphere (see Chapter 1 of this volume), form a major compartment of continental ecosystems, and they are the key component of the Critical Zone of human activities. They are open, interactive, four-dimensional (space-time) biosystems with five types of constituents; namely organic matter, mineral matter, water (solutions), gas (soil atmosphere) and living organisms (microorganisms, animals, plants) [GOB 10, BER 11]. Soils are biosystems [MUN 17] whose functions and services are determined by the dynamics and activity of living organisms and environmental parameters, whether they are natural or of anthropic origins. The richness of energy substrates and the structures in porous systems and aggregates guarantee the diversity and activity of organisms [BRU 17, MUN 17]. In addition, the organisms shape habitats in soils, which are favorable to their activity and their survival [DOM 70, HAT 73, STO 86, LAV 01, GOB 10, MAR 10, DEC 10, COL 15, MUN 17].

This chapter is not exhaustive, but it emphasizes the richness of the communities of soil living organisms and their functional diversity. It underlines:

– the potential of this biological wealth;

– the need to maintain and protect these soil properties and qualities;

– the need to know and understand the organisms better, as well as their ecology, the conditions of their activities and the interactions between “organisms and environments” to better define, model and manage the soil–plant systems, and also in view of using it intensively for improving plant production.

5.2. Emergence and development of microbial ecology and soil biology

5.2.1. *Discovery of the microbial world, a turning point in the knowledge of the functioning of soil–plant systems*

In the 1870s, chemists thought that they could solve the questions of plant nutrition like the origin of nitrates in soils, while Pasteur had already suggested a bacterial explanation (cited by Berthelin *et al*. [BER 06]). It was the work of Schloesing and Muntz between 1877 and 1879 that proved the role of microorganisms, and then that of Winogradsky, who, in 1890, isolated nitrifying bacteria [WIN 49].

It was Winogradsky, on the one hand, and Beijerinck, on the other hand, who, by discovering the richness of the microbial world, initiated soil microbiology at the end of the 19th Century [BER 06]. First, it was developed for agronomic purposes before becoming microbial soil ecology. This discipline had (and still has) a major role in the emergence and development of biogeochemistry, geomicrobiology, phytopathology, biotechnologies and environmental engineering (water treatment, mineral and organic raw materials, waste) and in the definition of parameters to control the quality of water, air, etc. [BER 06, BER 07].

5.2.2. *Discovery of the role of fauna and development of soil biology*

Interest in soil fauna began in the antiquity. Aristotle described the easily visible organisms and said that earthworms are like the Earth’s entrails, whereas Cleopatra declared earthworms as sacred because of their impact on soil fertility on the banks of the Nile [FEL 03, BER 06]. It was only with Charles Darwin at the end of the 19th Century that earthworms were recognized for their beneficial role. At the same time, P.E. Müller related the existence of certain humus forms to the presence of earthworms. Concerning termites, it was the first works of H. Drummond that connected them to the fertility of tropical soils.

The works of the early 20th Century concentrated more on taxonomy, the way of life or the biology of the species. In-depth ecological studies of ecosystems and agrosystems of fauna did not develop until the years 1960–1970.

5.3. Soil microbial communities

5.3.1. *Richness and diversity of microbial communities*

Currently, humans have not finished discovering soil microorganisms [VAN 06, LEM 17, MUN 17]. Soils are home to all major groups of microorganisms, as well as viruses and enzymes of plant and microbial origin, which significantly contribute to soil functioning [BUR 02, CAL 05]. Bacteria and archaebacteria are the most numerous and the most diverse. Their number can reach from 10 million to 10 billion per g of dry soil, and their biomass can reach 1,500 kg/ha for the first 20 cm of soil. Fungi develop mycelial filaments (fungal hyphae), which can reach from

100 to 1,000 m per g of soil (Figure 5.1). Their dynamics and activity depend on pedoclimatic conditions and land use patterns (Figure 5.1) [KUR 07]. Average biomasses of fungi, algae and protozoa were evaluated, respectively, for the first 20 cm of soil, at 3,500, 10 to 1,000 and 250 kg/ha.

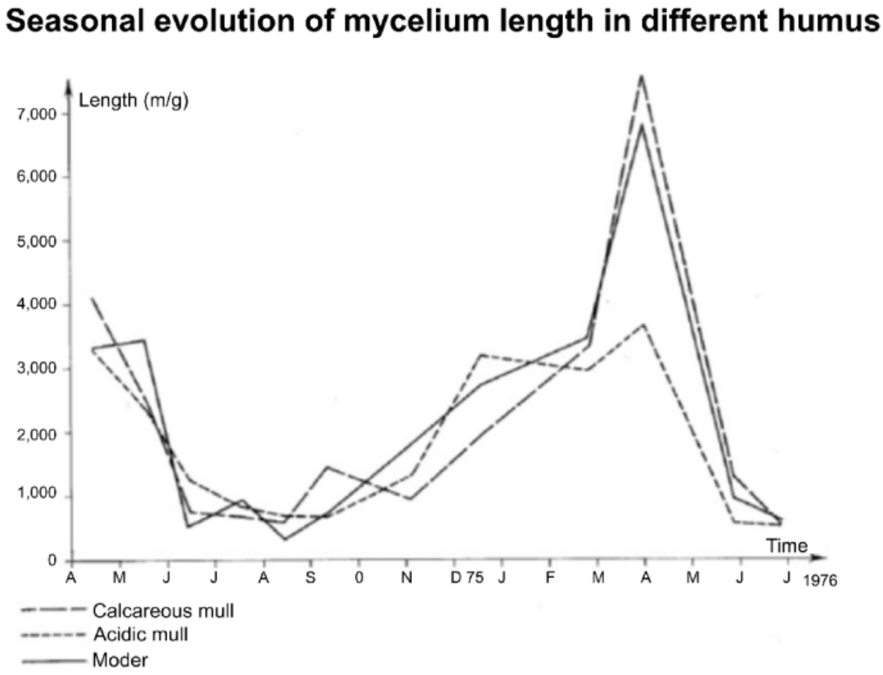

Figure 5.1. *Seasonal variation over one year of the length of mycelial filaments in three types of beech forest humus in eastern France (in m per g of dry matter litter) (source: J. Berthelin and F. Toutain). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

Bacteria are often observed in the form of rods or coccobacilli, separated or in groups of different forms, for example, "clusters", on or in soil aggregates [MUN 17], and also in biofilms like on minerals and roots (Figure 5.2). Fungi are most often observed in the form of mycelia or mycelial webs, more or less dense (Figure 5.3) and they form fructifications (white carpospores in the figure).

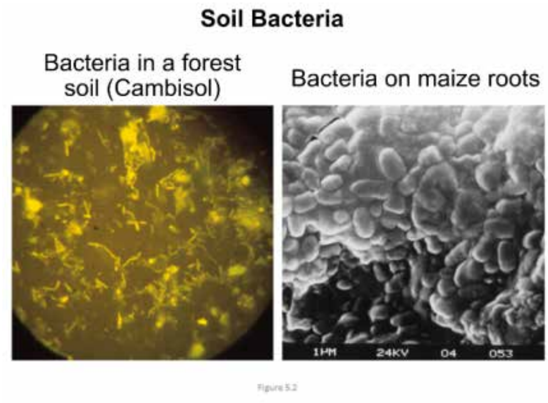

Figure 5.2. *Bacteria in the shape of rods and coccobacilli (about 0.5 to 1.0 µm in diameter – 1 to 2 µm long) on a glass slide buried in the surface horizon of a forest Cambisol and observed after fluorescent staining (FITC) in light microscopy. Bacteria forming a biofilm on maize roots observed in scanning electron microscopy (SEM) (source: J. Berthelin). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

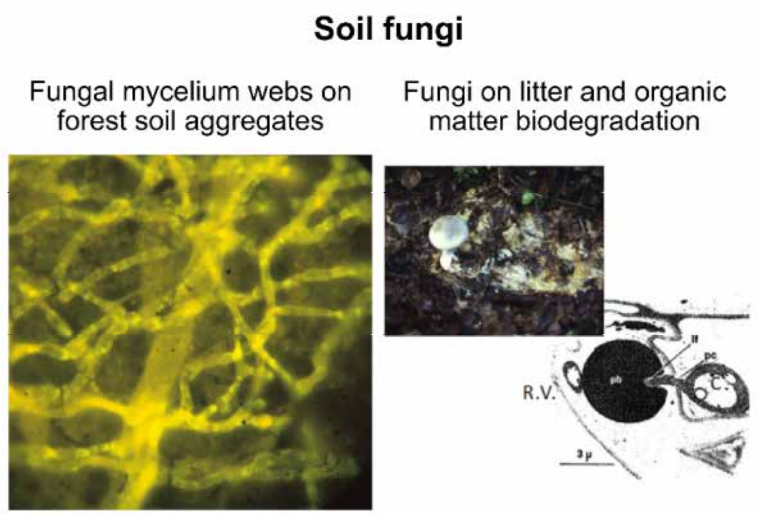

Figure 5.3. *Fungal mycelium web on organo-mineral aggregates, after fluorescent staining (FITC) in yellow (diameter of hyphae 1 to 3 µm, photon microscopy). Fungal mycelium with fruiting of the so-called white rot fungi on litter and hyphae (H) degrading organic matter (R.V., beech leaf plant residues, with black pigments, transmission electron microscope observation (source: J. Berthelin and F. Toutain)). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

Bacteria and fungi can be in the form called “free”. Some fungi form more or less specific associations with the roots of plants. The roots of most plants are associated with fungi to form mycorrhizal symbiosis beneficial to both organisms; here we speak of mutualism. About 80% of vascular plants are “endomycorrhizal” (arbuscular mycorrhizae, AM): some fungi (e.g. glomeromycetes) develop an intracellular mycelium with arbuscules and vesicles in root tissue. An extracellular mycelium (Figure 5.4) also develops around the roots. About 10% of plants (mainly woody plants) form another type of symbiotic association, and they have ectomycorrhizal roots with mycelium and extracellular infections in the root and abundant extraracinar mycelium (Figure 5.5).

Mycorrhizae are beneficial associations for plants and fungi. The plant, through photosynthesis, provides organic nutrients and energy to fungi that in turn contribute to water supply and mineral nutrients for the plant by expanding the volume of soil that roots can extract [LEY 91], and by implementing mechanisms of nutrient mobilization for the plant. These mycorrhizal symbioses are already used as an aid for plant production [DUP 17]. Considerable progress has been made [SMI 08], but knowledge of plant–fungi interactions [BÉC 17] needs to be advanced in order to improve crop production on the basis of this inherent soil potential.

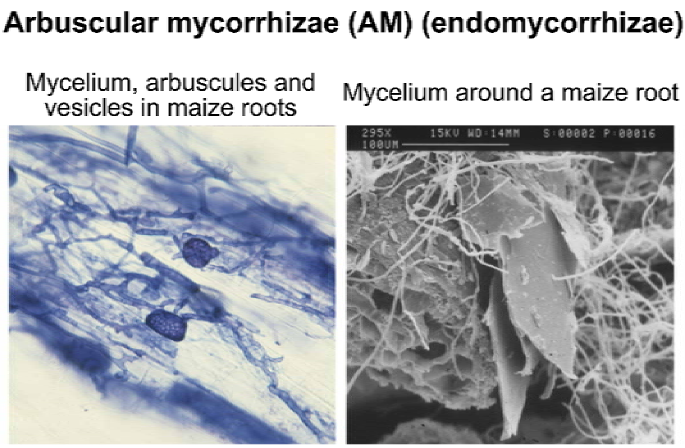

Figure 5.4. *Endomycorrhizal symbiosis, arbuscular mycorrhiza between a fungus (Glomus) and maize roots. Trypan blue staining of mycelium and arbuscular vesicles in the root (photonic microscopy) and mycelium around a maize root, embedding mineral particles (mica) observed under a scanning electron microscope (source: F. Laheurte and J. Berthelin). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

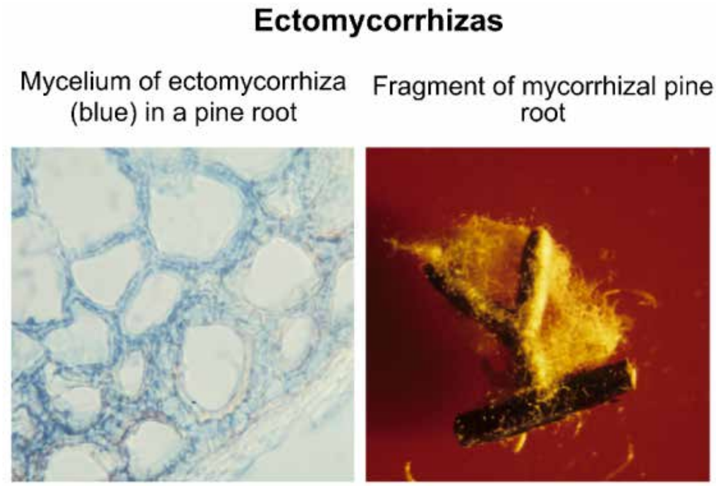

Figure 5.5. *Ectomycorrhizal pine root and mycorrhizal pine root fragment. Cut of a root showing an ectomycorrhizal infection. The fungus (colored in blue) develops in a web, between the cells of the root, in the “mantle” around the roots, and with a mycelium that extends in a large volume of soil (source: J. Berthelin, M. Chakly and D. Bauzon). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

Another type of symbiosis with considerable progress in knowledge involves the infection of a few families of plants by only a few genus of bacteria. It concerns the fixation of molecular nitrogen and essentially involves: 1) associations between leguminous and gram-negative bacteria, for example, rhizobia (*rhizobia*) resulting in nitrogen-fixing nodules in roots [ALU 17]; and 2) associations between plants of several non-leguminous families (e.g. Alder) and gram-positive bacteria of the Frankia genus [SAN 13].

5.3.2. *Evolution of methodologies in soil microbial ecology*

Until recently, methodologies used in environmental microbiology were not able to analyze the multitude of species present, since only the cultivable microorganisms, on more or less selective media, were known and described. Large processes controlling the stages of biogeochemical cycles (carbon, nitrogen, sulfur, phosphorus, iron, etc.) were known, and some for more than a century. In contrast, microbial communities remained in the dark until the development of molecular methods.

Molecular, genomic (DNA), transcriptomic (RNA), proteomic (protein) and metabolomic (substrates, fluxes, products) methods have led to major advances. To progress in the knowledge and management of soil–plant systems, these approaches must be associated with the definition of environmental parameters that drive the growth of organisms and populations, the expression of genes and the activity of enzymes [BAV 16].

5.4. Diversity of energy and nutritional pathways of microorganisms, key players in biogeochemical cycles

5.4.1. *Heterotrophy, autotrophy and extreme environments*

Soil microorganisms consist of the following four major groups of energy and nutritional activities involved in the functioning of biogeochemical cycles (Figure 3.6) [BER 07]:

– Chemo-organotrophic (heterotrophic) microorganisms use organic mattter as sources of carbon and energy. They are the most numerous and the most diverse. They include all fungi and most of the bacteria and archaea. They not only carry out functions of biodegradation, mineralization of organic matter and nutrient release, but also biosynthesis of humic substances, metabolites of environmental, pharmaceutical, agronomic or food interest. They are involved in the dissolution-alteration, absorption-accumulation or neoformation processes of minerals and organo-mineral compounds.

– A second, smaller group consists of chemolithotrophic (autotrophic) bacteria and archaea, which uses reduced mineral compounds (ammonium, ferrous iron, sulfur reduced from sulfide, etc.) as a source of energy and inorganic carbon (CO_2) as a carbon source. Their role is fundamental to the functioning of many biogeochemical cycles (Fe, N, S, etc.) (nitrifying bacteria, sulfo-oxidizing, ferro-oxidizing, etc.).

Two other groups, which use light energy and carry out photosynthesis, are present in particular habitats (zones and horizons of soil surface, lacustrine and littoral zones, etc.):

– Photolithotrophic, eukaryotic (algae) and prokaryotic (cyanobacteria) organisms use inorganic carbon as a carbon source. Their role is essential in various environments (nitrogen fixation by cyanobacteria, colonization of extreme environments, desert, mountain-alpine environments and pioneer associations of soil colonization (e.g. lichens).

– Photo-organotrophic organisms, a group that is even more modest in number (e.g. the so-called non-sulfurous purple bacteria) whose impact on soil function is very limited.

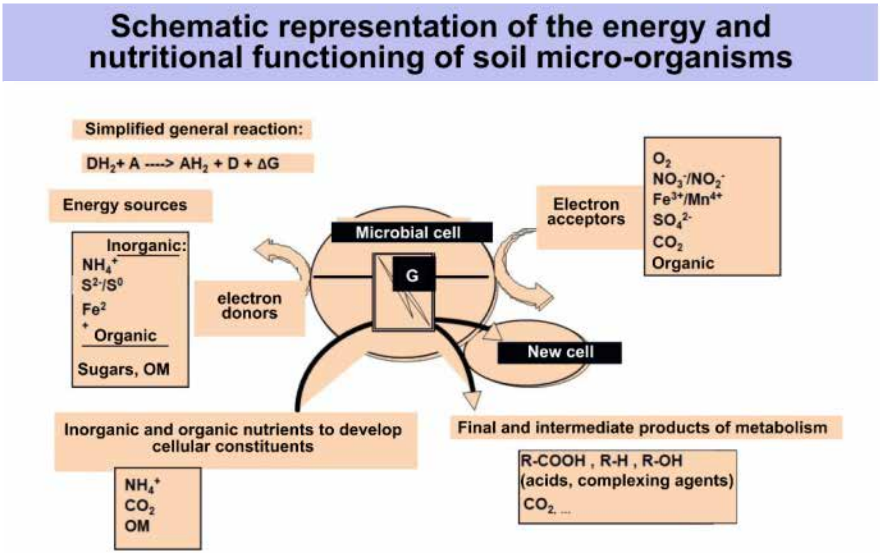

Figure 5.6. *Schematic representation of the energy and nutritional functioning of soil microorganisms (source: J. Berthelin). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

5.4.2. *Soils, environments where life is active with or without oxygen*

Soil microorganisms can live in the presence or in the absence of oxygen. Many of them have aerobic respiration systems (oxygen is the electron acceptor). This is the case for virtually all fungi and a large number of bacteria. Others live in the absence and in the presence of oxygen: they are aero-anaerobic organisms. Finally, many bacterial communities live in the total absence of oxygen and they are strict anaerobes. Some of them use mineral electron acceptors other than oxygen (nitrate, ferric iron, manganous manganese, sulfate and carbon dioxide); some bacteria, and also yeasts (fermentative), use organic electron acceptors (fumarate) and produce acids or alcohols.

5.5. Richness and diversity of soil fauna

5.5.1. *Diversity of soil fauna*

Soil fauna includes all invertebrates and vertebrates that live there permanently, such as earthworms, or transiently, like many insect larvae whose adults leave this environment. Animals living on the soil surface, in decomposing organic matter, are also part of the soil fauna. Soil invertebrates belong to many taxa; Table 5.1 shows average density and biomass values of these organisms:

– Nematodes, round worms without segmentation from 200 μm to a few mm of which 30,000 species, or only 5% of the total existing, have been described. They are parasites of plants or invertebrates, or live in free forms feeding on microorganism communities;

– Tardigrades (or water bears), close to arthropods, are poorly studied in soils. About 1,000 species have been described;

– Rotifers, in the form of trumpets, of 50 μm to 1 mm, live in the water films or in the micropores. A total of 2,000 species have been described;

– Springtails, close to insects, are small (2–3 mm) and are involved in the decomposition of litter (scavenger activity);

– Mites (subclass arachnids), a few mm long, without apparent segmentation, have four pairs of legs. It is a very diverse group with nearly 50,000 species described for a total estimated at one million;

– Myriapods (subphylum of arthropods), including centipedes, remain to be better discovered (10,000 species enumerated);

– Isopods are crustaceans, commonly called woodlice, 0.5 to 2 cm long. The number of species described is close to 4,000;

– Insects are another class of subphylum hexapods (*hexapoda*) characterized by three pairs of legs, a chitin exoskeleton, a pair of antennae and tracheal respiration. This group consists of the most species described on Earth (1.3 million). They include many taxa mainly represented by blattodea (termites, 2,600 species and cockroaches, 4,600 species), Hymenoptera (ants, 12,500 species), beetles (400,000 species), Diptera (150,000 species), the Dermaptera (earwigs, 1,900 species), etc.;

– Oligochaetes (subclass of the Annelida branch) have a long body, which is divided into segments each carrying four pairs of setae. They include enchytraeids (suborder Tubificina, 700 species described), very small, translucent or white, and earthworms (suborder Lumbricina, 3,800 species described);

– Other groups, such as gastropods, snails and slugs, or spiders, Diplura, Thysanura (hexapods), Pauropoda and Symphyla (myriapods) are also present, though mainly on the soil surface.

	Average density (ind/m^2)	Average biomass (kg/ha)
Protists	10^9–10^{11}	150–700
Nematodes	10^2–10^7	10–300
Mites	10,000–200,000	2–40
Springtails	100–45,000	1–20
Insect larvae	0–500	0–50
Myriapods	20–700	10–250
Isopods	0–1,800	0–40
Earthworms	50–400	200–4,000

Table 5.1. *Average densities and biomasses of the main taxa of soil organisms (source: E. Blanchart)*

5.5.2. *Classification by size*

This widely used classification distinguishes three categories, namely microfauna, mesofauna and macrofauna. Microfauna includes organisms of size between 10 and 200 µm; these are mainly nematodes. Mesofauna includes microarthropods and enchytraeids whose size is between 200 µm and 2 mm. Finally, macrofauna includes invertebrates larger than 2 mm, such as earthworms, insects (adults and larvae), centipedes and woodlice. Class size limits are arbitrary and vary from one classification to another. Extraction and observation methods generally define these categories.

5.5.3. *Functional classification* sensu lato

This classification is based, on the one hand, on the trophic regimes of the organisms in six large groups and, on the other hand, on the modes and zones of activities in the soil profiles. Decomposers are the microorganisms that provide the transformation and mineralization of organic matter. Microbivorous (or microregulators) are organisms that, like springtails or nematodes, consume microorganisms. Litter engineers are saprophagous macrofauna organisms (insect larvae, diplopods, isopods, etc.) or mesofauna (mites, enchytraeids) living in the litter. Soil engineers include macrofauna organisms such as earthworms, termites and some insect larvae. Pests are mostly plant feeders or root feeders. Finally, predators (e.g. ground beetles) are actors of ecological balances. Some groups retain specific classifications such as epigeic, anecic, endogeic worms, and epedaphic, hemiedaphic, euedaphic springtails [PET 82, CHA 05], depending on the domain and mode of activity in the soil profile.

5.5.4. *Characterization of the fauna*

The study methods depend mainly on the size of the organisms; however, new molecular techniques are developing:

– macrofauna is usually sampled according to the standard physical method known as TSBF (*Tropical Soil Biology and Fertility*, [AND 93]). Harvests are made by a soil monolith, distinguishing soil horizons and possibly using expellants [PEL 09];

– mesofauna is generally extracted by the Berlese–Tullgren apparatus;

– extraction of nematodes (microfauna) can be achieved using different techniques;

– identification of species usually requires a great deal of expertise. Recently, molecular techniques have been developed that are close to those used for microorganisms, and in particular that of “barcoding”. New species of earthworms, springtails, mites and ants have been discovered [DEC 16], and trophic networks identified via DNA analysis of the gut content of predators, but the crossover of methods is necessary for an integrated and precise approach. Near-infrared spectroscopy (NIRS) has also been used to successfully identify termite species [JOU 14].

5.6. Soils, environments with energy and nutritional conditions favorable to microbial life and fauna

Soils provide mineral energy sources derived from their mineral constituents, used by chemolithotrophic organisms, and especially organic energy sources and photosynthates essentially originating from plants. Inputs into the soil, by fallout from the above-ground vegetation, are estimated at 1 to 15 tons per hectare per year, ranging from boreal ecosystems to tropical ecosystems, corresponding to considerable inputs of energy and nutrients, and made available for microorganisms and fauna. Soil microorganisms provide most of the organic matter mineralization that the continental surfaces gain. They essentially contribute to the flow with about 60 gigatons (Gt) of carbon (CO_2) per year from the continental surface to the atmosphere, 10 times more than the fluxes from human activities.

5.7. Determinants and remarkable sites of diversity and soil biological activities

Soil biodiversity is determined by heterogeneous environments on various scales, from microsites to large climatic zones, and due to the influence of various factors, namely climates, mineral substrates, topography, vegetation and land uses (see Chapter 1 of this volume). Communities of active organisms differ according to soil types and uses. They exhibit temporal, spatial and functional variability, which is related to environmental conditions [DEC 10, RAN 13, BAV 16, MUN 17]. The ubiquity of microorganisms is well recognized in soils via observations of functional type [DOM 70], but their detection presents difficulties because of the protective structures and the organization of these environments [DEL 11]. Several sites of the soil–plant systems, as well as the digestive tubes and excreta of invertebrates, are privileged sites for the dynamics and activity of soil organisms.

5.7.1. *Parameters and major activity sites*

The climatic and pedoclimatic parameters (see Chapter 1 of this volume) react on continental, regional and local scales to drive the dynamics of organisms. For example, termites, mites and ants have specific richness, stronger in tropical than Mediterranean or temperate conditions [LAV 01], and the composition of nematode families is related to temperature and annual rainfall [NIE 14].

Some soil compartments support remarkable activity, such as the rhizosphere (soil volume under root influence), the spermosphere (environment of seeds and their rootlets), litter, fecal pellets, or excretions (casts) of earthworms and enchytraeids, the digestive tract of soil fauna and the poral space. They constitute exchange sites and intense biochemical activities for the organisms. Some soil areas are “dormant” and confined because they do not exchange water, gas, and/or nutrients. Microorganisms are in a dormancy state, but they are potentially active inocula if the conditions become favorable to express their activity. The organization and geometry of soils, whose characteristics are now easier to determine, are major parameters that control microbial activities [BAV 16, BRU 17, CHE 17].

The original constituents of soils, clays, oxides, oxyhydroxides, hydroxides, organic matter, bacteria and fungi have large specific surface areas, and permanent and variable surface charges (dissociable as a function of the pH of the medium). They thus possess great chemical and physicochemical reactivities, at the origin of strong particle interactions and associations, which also contribute to the protection and survival of microorganisms [DOM 70, HAT 73, STO 86, BER 11] (Figure 5.7).

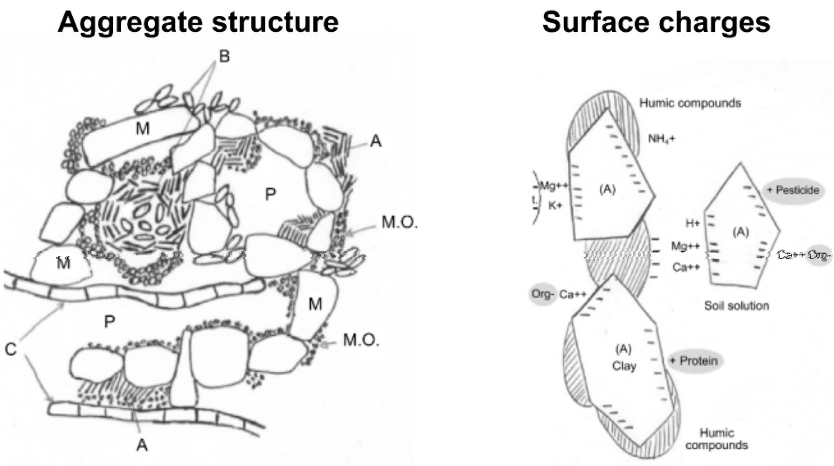

Figure 5.7. *Schematic representations of a soil aggregate and interactions between constituents. Bacteria (B), fungus mycelium (C), clays (A), mineral (M), organic matter (OM), pores (P) and interactions between clay particles, clay-humic particles, mineral ions (Mg ++, etc.) and organic (Org-). Moreover, bacteria have colloidal-type properties with variable charges and intervene in the "surface–bacteria" interactions (source: J. Berthelin). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

5.7.2. *Impact of land use*

Land use is an important determinant of distributions of species richness or abundance of organisms. This has been shown for all groups of organisms. For example, in the Brittany region (France), earthworms have mean densities of 260 ind.m^2 with higher values for meadows (350 ind.m^2) than for forests (50 ind.m^2) [CLU 09]. By comparing various types of agricultural practices, recent results on the La Cage site (Versailles) showed that soil organisms had higher densities and biomasses in agroecological systems (organic system and conservation agriculture system) than in the so-called conventional systems [HEN 15] (see Chapter 6).

5.7.3. *Humus, integrators and developers of specific biological activities*

Forest humus is an excellent integrator of biological activity, depending on the conditions of the environment [PON 02]. Three major types of temperate humus, namely mulls, moders and mors have distinct biological activities and distinct biological communities.

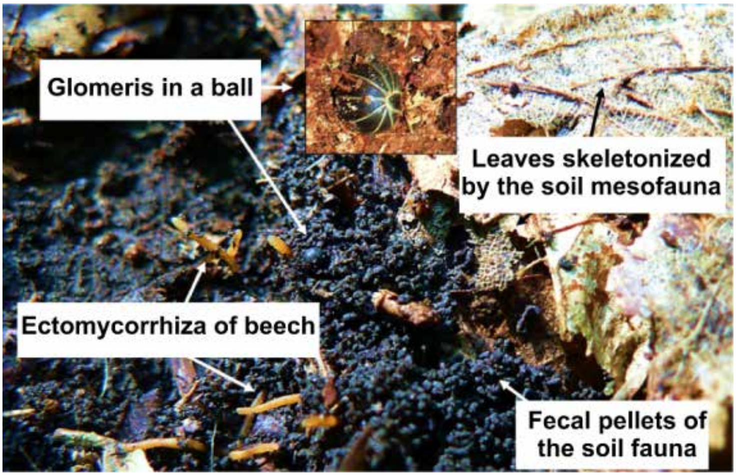

Figure 5.8. *Fecal pellets of the soil fauna, arthropod of the Glomeridae family (Glomeris) under beech litter in Haute-Normandie (France) with a moder humus (source: J. Trap). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

Mulls, mostly present on the most productive soils (the most fertile), are characterized by a greater diversity of organisms with a high density of earthworms and bacteria. The moders, associated with less productive ecosystems, exhibit less intense biodegradation, with fragmentation and fecal pellet accumulation of fauna (see Figure 5.8). Finally, mor-type humus, mostly under forest stands, even less productive due to mineral properties, is characterized by the presence of a thick litter and a fauna which consists mainly of mites and springtails (e.g. soils of the Podzol type).

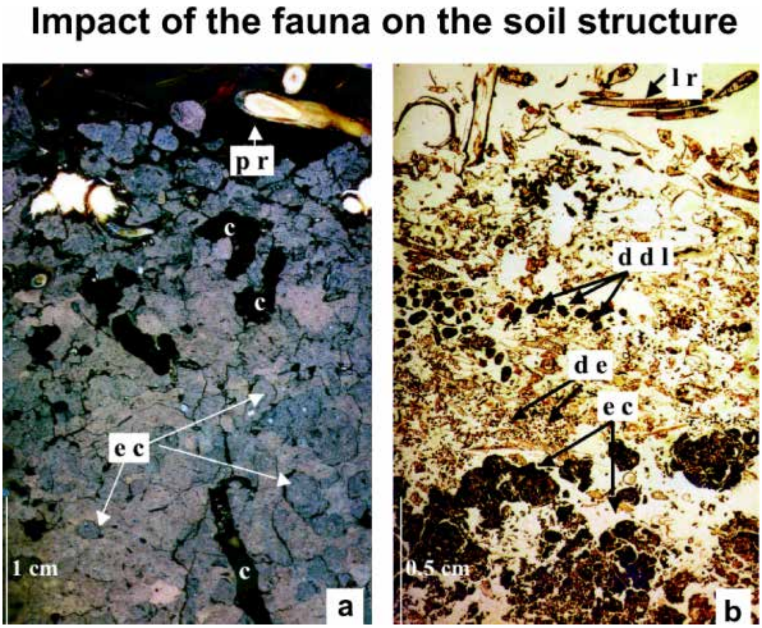

Figure 5.9. *Vertical sections of undisturbed soils: (a) role of earthworms in the development of canals (c) in a prairie (meadow) soil (ec are earthworm droppings); (b) droppings of Diptera larvae (ddl), enchytraeids (de) and earthworms (ec) in a Tangel-type humus (Germany) (source: U. Babel). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

5.7.4. *The rhizosphere, a site of major interactions of soil–plant systems*

The rhizosphere, defined by Hiltner in 1904 as the volume of the soil under the influence of root systems, is in fact the key site of interactions between plant roots, microorganisms, fauna, mineral and organic constituents of soils. Roots modify the mechanical, chemical and physicochemical properties of soils [HIN 09], take up nutrients, but produce root exudates and root litter, and thus provide very favorable energy and nutritional conditions for microorganisms and microfauna. Soils provide water and nutrients, and they build a strong support for plants. Rhizosphere interactions depend: 1) on the dynamics and activities of microbial communities (i.e. symbiosis, antibiosis, nitrogen fixation, plant growth stimulation, soil stabilization, water uptake, nutrients, enzyme release, allelopathy, microbial and plant competitions, phytotoxicity, plant pathology); and 2) on microfauna (i.e. predation and regulation of microbial populations). The rhizosphere is an excellent area for studies of soil structure and aeration, humification, and the dynamics of water, nutrients, mineral alteration, plant growth and plant quality [ROO 16].

Protozoa and nematodes are abundant in the rhizosphere, where they feed on microbes. Fauna can promote nutrient availability through the biodegradation and mineralization of organic matter and microbial lysates [TRA 15, TRA 16]. Root–microorganism–microfauna interactions modify the plant's hormonal system [BON 09] and colonization by organisms (e.g. nematodes) [TRA 15].

5.8. Tools for understanding the habitats of soil organisms

Similar to the tools of molecular biology and biochemistry, chemical and physical methods of analyzing soil constituents and their organization, and methods of data processing and modeling have also made considerable progress [TOT 10, ROO 16, BRU 17, CHE 17] (see Chapter 1 of this volume). Methods such as magnetic resonance imaging (MRI) or computer-assisted X-ray tomography allow for very accurate observations of root development in soils, definition of soil interactions, and establishment of relationships with chemistry, biochemistry and rhizosphere biology to better understand processes and establish robust models [ROO 16].

5.9. Specificities of the soil fauna

Soil fauna is involved in four major ecological functions that are at the basis of the ecosystem services provided by soils:

– dynamics of organic matter;

– nutrient recycling;

– development and maintenance of the soil structure;

– regulation of pests and diseases.

Two types of communities can be distinguished, namely microregulators (nematodes and protozoa) and the so-called litter and soil engineers (enchytraeids, earthworms and termites).

5.9.1. *Microregulators*

Protozoa, through the consumption of bacteria and fungi, contribute to the regulation of nitrogen and phosphorus flows and to the control of pests like the fungus ameba *vampyrellids*. Nematodes are:

– plant feeders (or herbivorous);

– bacteria feeders;

– fungal feeders;

– predators of other invertebrates;

– omnivorous;

– entomopathogens.

They intervene to regulate microbial biomass, the availability of nutrients and the increase in primary production [TRA 16]. Plant feeders can cause great damage to crops. Some species that react quickly to changes in their environment or other species with long life cycles [FER 09] could be good indicators of the state of the environment.

5.9.2. *The communities of organisms called "engineers"*

5.9.2.1. *The litter "engineers": springtails, Isopoda and Diplopoda*

Springtails contribute to the degradation and decomposition of organic matter by either consuming the litter or regulating the mineralizing activity of the microorganisms. Fungal-feeding springtails can play an important role on organic matter decomposition by modifying the composition of fungal communities, mycorrhizal or not [CRO 12]. Isopods and diplopods are involved in litter fragmentation and the production of fecal pellets, favorable to the mineralization of organic matter [DEO 10], which is a source of nutrients for roots and mycorrhizae.

5.9.2.2. *The soil "engineers"*

These are mainly earthworms, termites, ants and some Coleoptera larvae that consume soil, move and change its organization, structure and physical properties [LAV 06]. The quantities of soil consumed and then rejected annually by earthworms are very large, ranging from 300 to 1,300 tons/ha. Higher values are found in tropical areas. Anecical earthworms dig vertical to subvertical burrows or networks, semi-permanent and up to one-meter deep galleries. Endogeic earthworms deposit most of their dejections in the soil and contribute to the development of macro-aggregated structures [BLA 99]. These earthworm activities promote hydric regimes, erosion resistance, increase aggregate stability, improve infiltration and limit soil loss [BOU 97, BLA 99, BLA 04]. Earthworms promote, in the short term, the decomposition of organic matter by modifying the microbial activities and the release of nutrients [BER 12]. In the long term, this "earthworm" effect tends to decrease because of the physical protection of organic matter in old Casts. These earthworm activities can improve plant production in agrosystems and intervene in plant community dynamics [VAN 14, COU 14]. Termites, particularly abundant in tropical areas, build very large termite mounds by transporting large quantities of soil, and modify the texture and the chemical properties of soils (nutrient recycling, water content and availability, microbial activities) [LEE 71, JOU 11]. Some effects are observed over long periods of time, well beyond the life of termite mounds, which are sometimes used as fertilizers. Figure 5.8 shows the role of various organisms in the "construction and the functioning" of the soils (porosity, formation of aggregates and organo-mineral constructs).

5.10. Soil organisms: ecosystem service actors

Ecosystem services, defined as the benefits that humanity derives from ecosystems [MIL 05], have been classified into four categories:

– provisioning services that enable the production of goods such as food, wood, fiber, genetic and pharmaceutical resources and water;

– regulating services of climate, air quality, erosion, diseases, etc.;

– cultural services that can be recreational, religious and aesthetic;

– supporting services at the origin of other services, allowing the development of life on Earth: soil formation, oxygen production, biogeochemical cycles, etc.

The MEA report has clearly placed biodiversity at the center of the implementation of these services, as it is responsible for all the ecological processes and functions on which services depend. In the soil, ecological processes are those that link organisms and their environment. They are organized into four interrelated ecological functions, namely organic matter dynamics, nutrient cycling, soil structure maintenance and pathogen regulation [KIB 08] (see Figure 5.9).

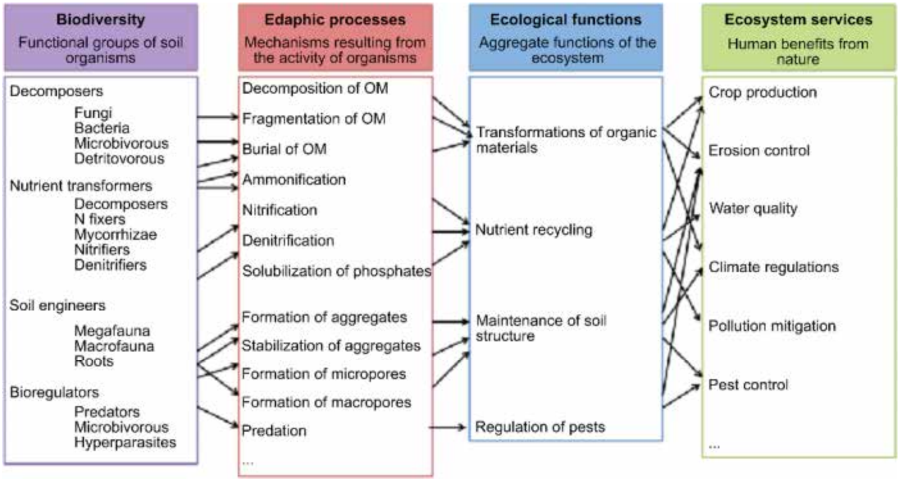

Figure 5.10. *Links between functional biodiversity, ecological processes and functions, and ecosystem services. Ecological processes carried out by soil organisms can be grouped into aggregated ecological functions, which are at the root of the establishment of ecosystem services (source: table drawn by E. Blanchart, according to M.G. Kibblewhite). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

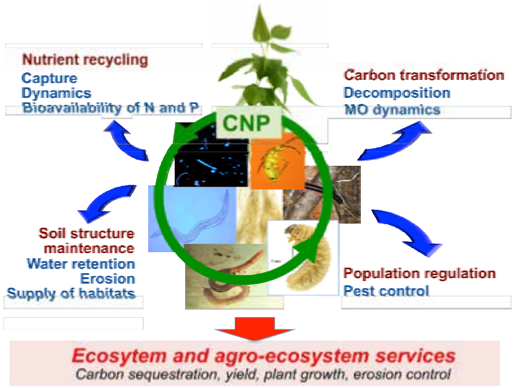

Figure 5.11. *Conceptual diagram of soil functioning describing the importance of interactions between soil functional groups (decomposers, microregulators, soil and litter engineers, predators, pests), for the realization of the four main ecological functions necessary for the supply of soil ecosystem and agroecosystem services. The flow of carbon and nutrients (green arrow) passes through these actors in interactions with each other and with their environment (source: diagram redrawn by E. Blanchart after M.G. Kibblewhite and photos by E. Blanchart, R. Randriamanantsoa, C. Villenave and L. Bernard). For a color version of this figure, see www.iste.co.uk/berthelin/soils1.zip*

5.11. Soil quality indicators

Although the term “soil quality” was used as early as 1977 [WAR 77] for agricultural soils, it was not until the 1990s that definitions appeared, and scientific work focused on this topic [DOR 94]. Gradually, the definition evolved from an agricultural framework related to productivity towards a much more “multifunctional” vision of soils. The definition of “soil quality”, given by Karlen *et al*. [KAR 97] as the “capacity of a soil to function”, implies that soil management must sustainably support animal and plant production, maintain, or enhance the quality of water and air, and support human health. The quality of a soil could now be defined by its “ability to provide goods and ecosystem services”.

What indicators can be used to evaluate it? In the same way, can we consider, in an integrated way, in one indicator, all the ecosystem services, that is, the “multiservices” of soils? Should we admit that soils should provide all services, only one service or only a few of the services? It is difficult to apply this aspect to agricultural soils, as society requires these soils to provide a large number of services: producing food by avoiding erosion, limiting the pollution of water and the environment, conserving biodiversity, supporting carbon sequestration, ensuring the quality and diversity of landscapes, etc. The quality of an agricultural soil is, without doubt, incredibly difficult to evaluate.

Indicators are measurable properties of the soil or harbored and supported organisms, and help understand how it functions. They are usually based on physical, chemical, or biological properties or processes. Physical and chemical parameters are well or better defined than biological parameters and indicators (bioindicators) considered here.

5.11.1. *Soil organisms as indicators*

Land uses and agronomic and forestry practices have relatively well-known impacts on soil organisms (bacteria, fungi, nematodes, springtails, earthworms, etc.) and on some of their activities [PÉR 11, CLU 12, HEN 15].

Bacteria and fungi, and some of their activities (soil respiration, mineralization of organic matter, microbial biomass, bacterial, fungal, ratio of these biomasses) [BIS 17, STA 14], are often named indicators of the functioning of soil–plant systems. Protozoa, on the other hand, are rarely used, taking into account their difficult taxonomic determination and their ability to rapidly encystize in a passive form.

The interest in nematodes as indicators of the state of soils [FER 09] is developing, as they constitute a group fulfilling highly contrasting specific functions within the trophic networks (microbivorous, plant feeders, predators of other animals and omnivores). In addition, they respond quickly to a change in the environment, have morphological characters facilitating identification and are present in most soils.

Some earthworm species (such as *Aporrectodea caliginosa* or *Allolobophora chlorotica*) are sensitive to metal pollution, while others (such as *Lumbricus castaneus* or *Dendrobaena rubida*) persist in polluted environments [NAH 03]. Earthworms and some Coleoptera appear as good indicators of pollution.

Work on various organisms and parameters associated with their dynamics aim to provide species reference systems for a given environment together with a series of situations [COL 11, CLU 12].

5.11.2. *Ecological functions as indicators*

When considering ecological functions (Figures 5.9 and 5.10), more integrative approaches to soil functioning adopt *in situ* methods of biodegradation of organic matter or mineral weathering (methods of porous bags buried with organic matter or minerals) [BER 90, KUR 07]. These methods, such as those known as *Bait lamina* or *Tea Bag Index*, are intended, for example, to collect uniform data for the decomposition of organic matter [KEU 13].

5.12. Conclusion and perspectives

Soils are complex biosystems that undoubtedly harbor the greatest terrestrial biodiversity. The modes of formation and functioning of soils are determined by the interactions between organisms and the constituents and structures of the compartments. These interactions, on various scales of space and time, determine the functions of soils and their capacity to provide ecosystem services. However, soil organisms and these interactions remain, for the most part, to be better defined or discovered. A better knowledge of the organisms and the conditions of their activities will make it possible to better determine and prioritize the biotic and abiotic factors that control the biochemical activities, and the functions and services of the soil–plant systems. These parameters must be established and validated for the pedoclimatic conditions of the considered, studied and managed soils.

Sustainable agriculture based on ecological intensification and/or various robust and relevant agroecological approaches must integrate the "driving forces" of the environment, which are defined by physical, physicochemical, chemical, biochemical as well as socio-economic parameters. This aggregation is necessary for a harmonious development.

From this perspective, priority could be given to those functions that support soil conservation and plant growth with reduced or at least adjusted and controlled requirements for mineral fertilizers and plant health products. These approaches must be integrated with land uses and soil management. Functions to be taken into account in agricultural soils as well as in forestry concern: availability and mobilization of nutrients for plants; the prerequisites for efficient expression of fungal (mycorrhizal) or bacterial (nitrogen fixing) symbioses; the activation and expression of rhizopheric microorganisms gene coding for beneficial effects on plants (PGPR, *Plant Growth Promoting Rhizobacteria*) (root growth, mineral nutrition, defense against pathogens, etc.); the metabolic pathways of formation of humic substances that initiate and stabilize the soil structure; the degradation of pollutants due to constant diffuse or accidental inputs and phytosanitary products or products with allelopathic effects.

A thorough knowledge of the role of organisms in the coupling of biogeochemical cycles [BER 07, REC 17] and the conditions of mineralization of C, N, S and P would lead to a better regulation of greenhouse gas emissions, plant nutrition and water quality. Inter- and multi-disciplinary approaches are needed as they should allow defining relevant and robust models and indicators for soil quality and soil management.

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