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Life in the Soil: From Taxonomy to Ecological Integration

1.1. Importance of soil organisms

If it is possible to speak of soil as an ecosystem in its own right [PON 15], then soil is among the most diverse ecosystems in the world: unlike the ecosystems described on the basis of dominant vegetation, soil covers all submerged lands and has diverse climates and considerable bedrock [ORG 16]. Even locally, when considered as a compartment of an ecosystem described in terms of vegetation, soil is usually the most diversified compartment. It hosts representatives of the three domains (*Eukaryota, Bacteria and Archaea*) and a great diversity of clades of eukaryotes, including *Animalia, Fungi, Plantae, Chromista and Protozoa*. Each group contains a large number of species, that is, between 10^4 and 10^7 of bacteria in one gram of soil, representing a biomass corresponding to 1–4% of soil carbon [ORG 16]. Much more work needs to be carried out to characterize this diversity, especially for the smallest species, whose estimated taxonomic deficit is the greatest [DEC 10].

The biomass of the different taxa can be very high and represents, for one hectare of temperate grassland, a total of about 5 tons, that is, 20 times more than the mass of sheep usually present on this grassland. Plant roots, meanwhile, can be approximately 10 tons.

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The ancestors of these organisms have not always lived in terrestrial environments. Following the appearance of multicellular eukaryotes about 700 million years ago, plants and then metazoa colonized land approximately 430 million years ago. Soil was formed as a result of the colonization of living organisms, through their activities that resulted in the aggregation of organic matter and minerals weathered from the bedrock, as we can still see today in areas with receding glaciers, recent lava flows, polders or constructed Technosols [DEE 16, VER 17]. In particular, bioturbation by soil invertebrates has played a major role in pedogenetic processes (see also *Soils as a Key Component of the Critical Zone: Functions and Services*), in a way that has deeply influenced the evolution of metazoa at the end of the Precambrian era [MEY 06]. Organisms continue to adapt to the activities of their congeners or organisms of different species and are the subject of many surprising discoveries.

Microorganisms possess an enzymatic arsenal that macroorganisms such as plants or soil macrofauna orchestrate. These interactions are at the origin of flows of matter (water cycle, elements such as N, P, K or carbon), energy (organic matter) and information (signal molecules) (see Chapter 2), various modifications in soil structure (aggregation), sometimes even soil texture, and affect the functioning of the above-ground compartment of the ecosystem. For example, a meta-analysis reports that plant growth increases by 23% on average in the presence of earthworms [VAN 14].

These multiple ecological functions support the delivery of many ecosystem services, such as soil's resistance to erosion and regulation of its water-related properties, the decomposition of organic matter responsible for recycling plant essential nutrients on the basis of crop production, climate regulation, notably through carbon storage, pollution remediation, regulation of plant pathogens or parasites, as well as recreational and educational services [BLO 13, LAV 06] (see in the same collection, *Soils as a Key Component of the Critical Zone: Functions and Services*). These ecosystem services are essential to the well-being of human beings [MIL 05] (see in the same collection, *Soils as a Key component of the Critical Zone: Societal Issues*). However, because of the increase in human population and its activities, the soil biodiversity and its ecosystem services are under threat (see in the same collection, *Soils as a Key component of the Critical Zone: Degradation and Rehabilitation*). The cost of inaction against this degradation would amount to 50 billion euros per year and could reach 14 trillion euros in 2050 [BRA 08].

A better understanding of soil biodiversity, its functions and the services provided consists of integrating naturalistic approaches that have been independently developed on distinct taxonomic groups such as fauna, vegetation and microorganisms. The difficulty lies in the fact that these different taxa have very different properties (organism size, living space, population size, speed of evolution, etc.) and that their study requires specific observation methodologies. It also means a better understanding of the links between living organisms and their biotic and abiotic environment. A historical perspective of this research on fauna, vegetation and soil microorganisms provides a better understanding of current trends that lead towards an increasingly integrated soil ecology.

1.2. Historical perspective

1.2.1. *Fauna: convergence between soil science and ecology*

The formation and ecological functioning of soils is the result of interactions over time between the climate, the geological substratum and living organisms. After Dokuchaev [DOK 89] revealed this founding principle in 1889, the conceptual framework has remained fairly unchanged for nearly a century. Soil ecology has most often applied theoretical models and research hypotheses stemming mainly from the general ecology of the above-ground populations of ecosystems, that is, mostly plants, vertebrates and insects.

The International Biological Program (1964–1974) hosted in France by Maxime Lamotte, François Bourlière and Claude Delamare Debouteville enabled the first quantitative inventory of soil organisms and the analysis of their energy balances. The French contribution passed through metropolitan and African sites in which the analysis of community structure, population dynamics and energy balance formed the core of the research. It is at this time that important and diverse studies on earthworms (Bouché, Lavelle), termites (Josens), protozoa (Pussard, Rouelle, Couteaux), microarthropods (Vannier, Athias) or insect larvae (Trehen, Deleporte) were published in France.

This research gradually split into two directions under the influence of schools of thought fed by different sources. One direction became increasingly interested in the role of biodiversity in soil functioning (considered mainly in terms of the mineralization of organic matter). It is largely based on experiments in microcosms popularized by the works of Setälä in Finland, followed by those of Heemsbergen and Berg in the Netherlands, and Hedde in France (e.g. [HED 07, HEE 04, MIK 02]). This line of research, which focuses on interactions between organisms, mainly through food webs, has produced a great deal of work since the 1980s [DER 94]. The indiscriminate use of microcosms, which represent the soil quite poorly, sometimes leads us to question the validity of the conclusions made, especially when these results are extrapolated on larger scales (e.g. plots and landscapes). However, this line of research describes in detail the organization of the microscopic or submicroscopic elements of the soil and emphasizes the occurrence of quite different patterns depending on whether the bacteria or fungi are the dominant primary decomposers, at the base of the trophic network [HUN 87].

The other direction, more inspired by soil science and ecosystem ecology, analyzed the interactions between organisms by taking into account the very special nature of the soil and the unique constraints that this environment exerts on the organisms that inhabit it. The concept of ecosystem engineers defined *a posteriori* [JON 94] is at the heart of this research. The types of interactions mostly mentioned by this research are: mutualism, predicted processes, the hydric functioning of the soil and all the functions and translation in soil ecosystemic services. Largely discussed by root specialists who have long described interactions and positive feedbacks in the rhizosphere (Coleman, Calot, Hinsinger, etc.), this approach applied to soil invertebrates has mainly, but not exclusively, been developed in France with the active participation of soil scientists. The strength and organization of soil science in France has provided very favorable conditions for these developments, with the support of well-targeted funding sources, in particular from the Ministry of Environment and INSU (Institut National des Sciences de l'Univers, CNRS). The work carried out in labs from different universities (Paris VI, XI and XII in particular, Rennes, Rouen, Montpellier, Nancy and Toulouse), the CPB (Centre de Pédologie Biologique) of Nancy, the Museum and the IRD (Institut de Recherche pour le Développement) led to a significant evolution of Dokuchaev's initial model [DOK 89], making it both more practical and detailed. The special nature of the soil as a habitat for organisms requires a broader conceptual framework that takes into account organisms, the structures they create in the soil and the processes (physical, chemical and biochemical) across the variety of spatial and temporal scales. The theory of self-organization, already widely used by physicists, chemists, sociologists and ecologists [PER 95], provides this global framework [LAV 16].

Progress in soil ecology has always been dependent on the advent of new technical options. The isotopic markers ^{13}C and ^{15}N have enabled the detailed exploration of flows between compartments; near-infrared spectroscopy (NIRS) has identified the origin of soil biogenic structures; molecular tools associated with the consideration of biological traits can now solve a large number of problems, from taxonomic resolution to the definition of diets and ecological functions of species.

1.2.2. *The root system of plants: the hidden side of plant ecology*

Roots, despite their essential roles in the functioning of plants, through the functions of acquisition of soil resources (water, nutrients), anchorage and reserves (especially in perennial plants), remain largely unknown compared to shoots. In addition, they play a key role in the functioning of ecosystems and the services they provide, in particular through their major impact on soil formation, biogeochemical cycles and provision of habitats for other soil organisms. They thus largely account for the status of ecosystem engineer [JON 94] held by plants.

Much of the research on root systems has focused on describing their highly diverse, but also plastic, morphology and architecture, as well as developing methodologies for observing these invisible below-ground organs if the soil is not previously excavated. The work of [KUT 60] and *Wurzelatlas* published in 1960 are the most complete in terms of describing architecture in a large number of plant species. However, models formalizing the rules for the construction of root architectures were only developed in the 1980s, with the work of Pagès in France, in parallel with that of Lynch in the USA. It is more recently that works based on the functional traits approach have been applied to the root compartment, mainly in grassland species (notably by Roumet at CNRS in Montpellier, as well as at INRA in Clermont-Ferrand and Toulouse) [ROU 16]. Given the invasive nature of the methods used to make comprehensive descriptions in the field, much of the knowledge of root systems is restricted to roots present in superficial soil horizons, in such a way that we have a truncated view, as pointed out in the meta-analyses conducted by [SCH 02]. French teams (Jourdan at French Agricultural Research Centre for International Development (CIRAD) and Pierret at The French Research Institute for Development (IRD)) have, however, led to pioneering work during the 2010s, in order to characterize deep roots and their importance [PRA 17]. These difficulties inherent to soil mean that much knowledge on roots is based on studies carried out in soil-less culture, with their associated limitations.

In terms of root–soil interactions, it was a German researcher, Hiltner, who was the first to define the rhizosphere in 1904, as the volume of soil around roots subjected to their activities [HAR 08]. He had shown that the rhizosphere was a hotspot of microbial activity; since then, a large part of research in this field has focused on understanding microbial ecology of this zone, especially in France on rhizobial and mycorrhizal symbiosis (in Dijon, Montpellier, Nancy and Toulouse, for example) and also on many other free-living communities in the root environment (in Cadarache, Dijon, Lyon, Nancy and Rennes, for example). These points are the subject of detailed developments elsewhere in this book (see Chapter 4). The work of Guckert and Morel in the 1970s pioneered the understanding of root exudation processes that are largely responsible for the rhizosphere effect, by stimulating the abundance and activities of the associated microbiota and by impacting its diversity. Work by Callot, Jaillard and Hinsinger in Montpellier, and Doussan in Avignon has also established that roots, through their multiple physiological activities, are capable of profoundly modifying chemical (pH in particular) and physical properties of the rhizosphere [HIN 09], even contributing to transformations in soil mineralogy, and thus to pedogenesis [HIN 13]. In addition to understanding the complex and multi-trophic interactions of the rhizosphere, the challenge is now to better understand how the plant roots of a plant community communicate and interact with one another (see Chapter 4), thus contributing to the frequently positive relationship observed between productivity and diversity within multispecies communities, such as in grassland agro-ecosystems, associated crops, agroforestry systems or mixed forests.

1.2.3. *Microorganisms: from tool development towards conceptual developments in ecology and evolution*

The study of soil has for a long time found it difficult to take into account soil microorganisms. These difficulties are associated with the very nature of microorganisms and the telluric environment in which they evolve.

Thus, microorganisms, as their name indicates, are of microscopic size, of the micrometric order for bacteria. It was not until Leeuwenhoek made improvements to the microscope in around 1670, which had been invented nearly 100 years before, that these bacteria could be visualized. However, the initial stages of soil microbiology date back to the 19th Century. The presence of microorganisms in soils was presumed following the work of Boussingault (1802–1887) showing that the degradation of humus may not be the only source of nitrogen in soils [BOU 97]. The role of microorganisms in the nitrification process was established by Schloesing (1824–1919) and Muntz (1846–1917), thus confirming Pasteur's hypothesis (1822–1895) on the microbial origin of nitrates. The isolation of microorganisms involved in nitrification was then carried out by Winogradsky (1856–1953) [WIN 49]. Biological fixation of nitrogen by bacteria in legume nodules was demonstrated in 1886 and a responsible bacterial agent was discovered by Beijerinck in 1888.

For a long time, analyses of soil microorganisms have been limited in their categorization to:

– morphological criteria, for example, for bacteria: rods (bacterium), bacilli (large rods with endospores), filamentous bacteria (sulfur bacteria) and sheathed bacteria, in which the cells are aligned in chains (ferrobacteria);

– physiological criteria associated with microbial activities in relation to geochemical cycles (e.g. for the nitrogen cycle, ammonifiers, nitrifiers, denitrificators, free atmospheric nitrogen fixers or symbionts) and their requirements (e.g. phototroph, chemotroph, autotroph, heterotroph).

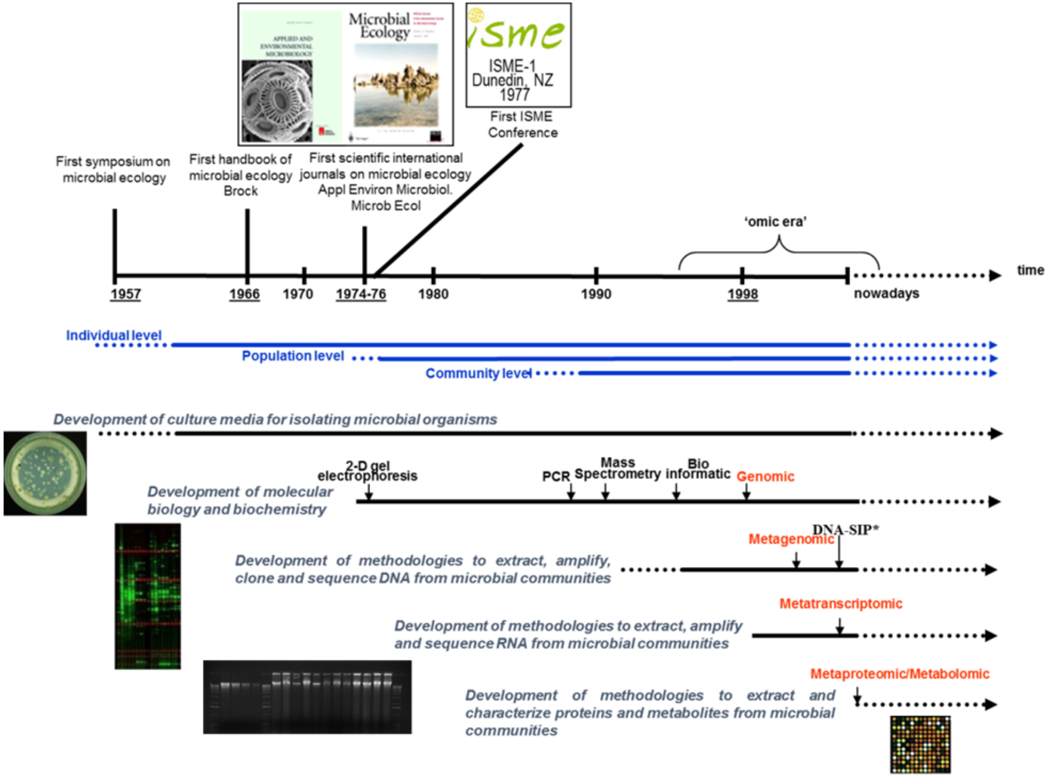

Figure 1.1. *Historical and step-by-step evolution of microbial ecology adapted from [MAR 07]. For a color version of this figure, see www.iste.co.uk/lemanceau/soils6.zip*

The corresponding microorganisms were analyzed following their cultivation on appropriate media [DOM 70]. At that time, a course on soil microbiology at the Pasteur Institute taught the corresponding methods [POC 62]. The research then focused on the development of favorable growing media (elective media) for the development of particular strains (see Figure 1.1) and on major functional groups without necessarily knowing the responsible organisms.

These elective growing media then made it possible, beginning in the 1970s, to analyze the diversity of strains on the basis of their activities and/or their trophic profiles (ability to use a range of organic compounds), enabling their taxonomic identification using dichotomous keys [STA 66]. At the same time, the first book on soil microbial ecology [DOM 70] and the first international journals of microbial ecology appeared (see Figure 1.1). In the 1970s and 1980s, advances in biochemistry (electrophoresis) and molecular biology (PCR) enabled the analysis of diverse populations, isolated on elective media, thus belonging to the same taxonomic group (community), at the molecular level by targeting repeated sequences (e.g. ERIC, BOX) and/or sequences with a taxonomic value (16S rDNA for bacteria) [LEM 95]. However, this isolation step represents a major bias since we now know that we are only able to cultivate a small fraction of soil-borne microorganisms, meaning that at that time we had a truncated vision of the microbial diversity. It was not until after further methodological developments were made with the extraction of soil DNA [MAR 01] that we realized the immensity of this diversity, which is around a million species of archaea and bacteria per gram of soil [TOR 02]. The analysis of the polymorphism of the DNA extracted from soil now makes it possible to theoretically access the full microbial diversity by avoiding the culturing step. It thus becomes possible to analyze all the microbial communities (metacommunities) and their genomes (metagenome) [PIV 15]. This path has been greatly favored by the spectacular reduction in the cost of DNA sequencing, thanks to the methodological developments generated by the leading sequencing programs of the human genome and gut microbiota.

The next step was to standardize the operating procedures of biodiversity analysis. It was then possible to compare soil biodiversity in various environmental situations (type of soil, climate, land use). The corresponding biogeographical studies have collectively enabled the identification of main environmental filters impacting microbial diversity with first the physical–chemical properties of soils (in particular pH) and then the type of land use

[RAN 13]. This research has also led to the establishment of databases of soil biodiversity according to the soil type and land use, which enables the interpretation of the results of soil biodiversity analyses, thus making it possible to determine the biological quality of these soils; as has long been possible with their physical–chemical properties [LEM 15].

In addition of the biodiversity description based on sequences with taxonomic values, it is also possible to target genes encoding activities involved in functions of agronomic interest (e.g. synthesis of the antibiotics involved in the suppression of diseases) and/or environmental interest (e.g. synthesis of N_2O reductase minimizing emissions of this powerful greenhouse gas). However, our knowledge of soil functional genes remains limited and extensive sequencing initiatives aim to better understand the biological functioning of the soil and to uncover new functional genes [VOG 09]. Important as they are, these functional genes only represent a genetic potential, and soil microbial ecology research aims to build a synthetic vision to improve our understanding of the biological functioning of soils and our ability to promote beneficial functions. For this purpose, it is necessary to relate the genetic potential of microbial diversity to its expression in terms of proteins and metabolites, then activities, functions and ultimately ecosystem services. In addition to the corresponding methodological developments (transcriptomics, proteomics and metabolomics, see Figure 1.1), this requires the use of equipped observatories (Environmental Research Observatories, ORE) to measure functions of agronomic and environmental interest and the corresponding ecosystem services (see Figure 1.2).

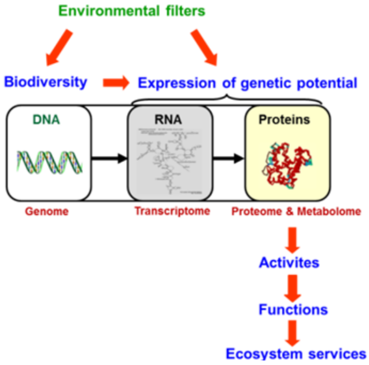

Figure 1.2. *Schematic representation of the relationship between biodiversity, expression of genetic potential, activities, ecosystem functions and services (adapted from [LEM 15]). For a color version of this figure, see www.iste.co.uk/lemanceau/soils6.zip*

After the major methodological advances achieved over the last decades in soil microbiology, which were essential considering the difficulty of its study, understanding the microbiological functioning of soils now requires conceptual developments in ecology and evolution such as those in plant and animal ecology studies. These approaches are beginning to be undertaken especially in biogeography studies (e.g. area–species relationship) and plant–microorganism interactions (e.g. holobionts, see Chapter 4).

1.3. Structure of this book

As mentioned above, soil ecology has its roots, as does above-ground ecology, in natural history. Some highly taxonomically rooted studies enable us to obtain information about a specific taxon, which can sometimes be extended to all taxa. This ecological approach applied to soils makes it possible to at least partially integrate the contributions from soil sciences (physics, chemistry, biochemistry). Through the improvement of observation and analysis methods (particularly, molecular ones) and the development of experimental approaches and modeling, an ecology connected with other soil-based disciplines is gradually emerging, which could in turn influence the ecology of above-ground environments.

In Chapter 2, "Diversity of Mechanisms Involved in Soil Ecological Interactions", we will see how ecology and soil sciences have converged and will continue to converge, due to a better integration of the interactions between the biotic and abiotic entities. On account of taxonomic inheritance in soil ecology, three chapters provide an overview of the interactions between major taxonomic groups (fauna, plants, microorganisms) and soil functioning. Chapter 6, "Soil Fauna: Determinants of Community Structure and Impacts on Soil Functioning", presents the different types of functional classifications of fauna as well as the resulting knowledge in terms of soil functioning and bioindication. The introduction to many ecological concepts and theories is presented in Chapter 3, "Biodiversity and Ecological Functioning of Soils". The reciprocal influences of plants and the biotic and abiotic soil components are presented in Chapter 5, "Interactions between Soil and Vegetation: Structure of Plant Communities and Soil Functioning". These three chapters combine methodologies and concepts specific to each major taxonomic group and others specific to all types of organisms. Chapter 4, "Plant–Microorganism Interactions in the Rhizosphere", focuses specifically on interactions between two major taxonomic groups, plants and microorganisms, with a focus on the plant organism interacting with microbial communities. The next two chapters provide general considerations on evolution and complex systems and analyze their implications for soil ecology research. Chapter 7, "Molecular Ecology of Soil Organisms: The Case of Earthworms", covers a model organism to illustrate the contributions of the theory of evolution and its methods in terms of species identification, knowledge of reproduction systems, analysis of gene flow, genetic variation within populations and phylogeography. Chapter 8, "Feedback Loops in Soils: Evidence and Theoretical Implications", presents a vision of soils as complex systems in which interactions and feedback loops are established with consequences in terms of eco-evolutionary dynamics, emerging properties and self-organization. Finally, Chapter 9, "Actions and Feedback: Consequences for Soil Management", offers a perspective on soil ecology research through eco-evolutionary dynamics and proposes a management method renewed by ecological engineering.

These chapters reflect the fact that soil ecology is entering a new era. Taxonomic approaches converge through the transversal conceptual framework proposed by ecology. In addition, the increasing importance of the contributions of the theory of evolution in soil ecology could strengthen the reconciliation of fields of research, which until now have been disconnected. Finally, molecular biology, which has become absolutely indispensable for the study of microbial communities, is progressing rapidly, leading to the development of new methodologies for studying other taxa.

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