Soil biodiversity

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Soil, a major compartment of

terrestrial ecosystems, represents a very particular ecosystem since it constitutes one of the most important reservoirs of biodiversity on the planet. Bacteria, fungi, springtails, insects, myriapods and many other organisms live and interact in the soil. This very heterogeneous biological richness is at the very origin of the functioning of the soil and of all the ecosystem services it provides to mankind, such as our food, our living space or our climate. Better characterizing it, better understanding it, can only help us to better manage it in order to safeguard it and perpetuate the treasure it constitutes for future generations.

1. A reservoir of biodiversity

We have all already turned over or seen soil turned over with a spade: we can easily distinguish the life that resides there, at least the visible part (the largest organisms), which is only a small part of the life that the soil harbors. Indeed, most of this diversity of organisms is invisible to our eyes because they are microscopic. The soil is thus one of the main reservoirs of **biodiversity**, since it hosts about a quarter of the total biodiversity (taxonomic diversity) of the planet [1]. Moreover, the number of "species" is several times higher than those observed on its surface. Biodiversity, a contraction of "biological diversity", refers to the variety of the living world. It is the diversity of all forms of animal, plant and microscopic life on Earth, and of all the relationships that species (of which we are part) have with each other and with their environment.

Several groups and a great diversity of organisms live in the soil: insects, mollusks, protozoa, algae, bacteria, fungi, *etc*. Soils have a very high level of heterogeneity, and an extremely large number of habitats, which also contribute to a high level of biodiversity, if the soil is in "good health". Indeed, the level of biological abundance and diversity can vary widely from one soil to another, depending on a variety of factors, including organic matter content, soil mineral composition (especially texture), pH and soil management practices. This biodiversity is not only very high in number, it can also be functional. Indeed, soil organisms maintain complex relationships with each other, but also influence the entire ecosystem by controlling the circulation of materials essential to plant life (carbon, nitrogen, phosphorus, potassium...) [2].

1.1. Who does what in the soil?

Biodiversity is "*the structural and functional variability of the diverse life forms that inhabit the biosphere, at increasing levels of organization and complexity: at the genetic, population, species, community and ecosystem levels*" [3] (see What is biodiversity? and

Biodiversity is not a luxury but a necessity). This definition highlights the need to understand and measure soil biodiversity in two aspects: the diversity of species and families (taxa) and the diversity of functions.

Taxonomic richness corresponds to the number of taxa (a taxon is a group corresponding to a level of classification of living organisms, such as a species or family) identified in the system under study. For an equal number of individuals, the more taxa present (species for example), the greater the diversity of a community. It is also usual to consider the **abundance** (number of individuals) of each taxon.

Functional biodiversity describes "who does what in the ecosystem" or "who is what" and not just "who is present" in a given community. Thus, to characterize functional diversity, it is necessary to assign or measure functions (nitrification, degradation of organic compounds...) or roles for each individual in a given community.

1.2. Soil organisms: from smallest to largest

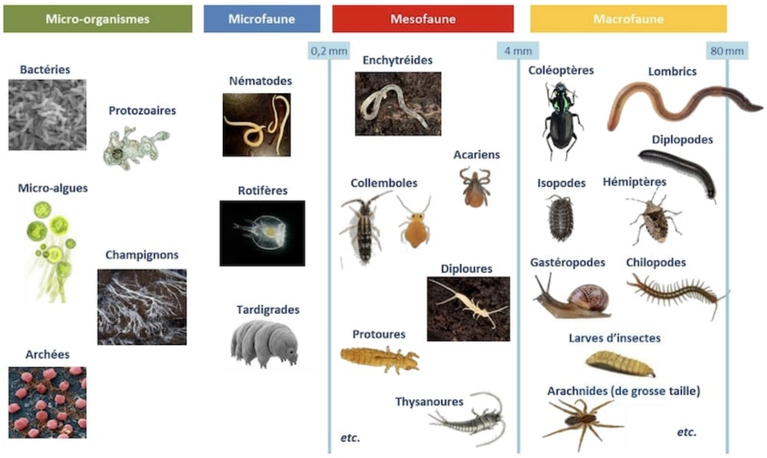

Figure 1: Diagram of the different groups of soil biodiversity classified by size. [Source: © Quentin Vincent - Study of abiotic, biotic and functional parameters and their interactions in neglected soils. PhD thesis - University of Lorraine - https://tel.archives-ouvertes.fr/tel-01896274/document]

Soil organisms are generally classified into four groups according to the size of the individuals: microorganisms (or microflora), microfauna, mesofauna and macrofauna. This classification reflects, among other things, the ability of different organisms to move through the soil pores (Figure 1) [4]. In addition, the upper flora (trees, shrubs, herbaceous plants) is involved through its root system, which represents a significant biomass and performs important functions in the soil.

The following sections detail the main groups of microorganisms and soil fauna. It should be noted that viruses are not considered as part of soil biodiversity because, although present in this environment and influencing the population dynamics of organisms, they are not living beings.

2. Soil micro-organisms

Soil **micro-organisms** are extremely abundant and of great taxonomic and functional diversity. They include bacteria, fungi, microalgae, archaea and protists [5]. The biological functioning of soils is strongly linked to microbial activity, which gives these microorganisms a major role in many soil functions as discussed below.

2.1. Bacteria

Bacteria are by far the most numerous and diverse soil microorganisms [6]. They come in a wide variety of shapes and sizes (mostly smaller than 2 µm). It is estimated that one gram of soil contains about one billion bacteria and between 2000 and 10000 bacterial species depending on their health status [7]. Metagenomic studies (reading DNA barcodes to characterize biodiversity) on different soils (grasslands, forests, arid soils, agricultural soils *, etc.*), have identified sequences belonging to *Proteobacteria (* 40%), *Acidobacteria* (20%) and *Actinobacteria* (13%) [8].

Bacteria play a key role in nutrient recycling, development (through the formation of symbioses), and soil structuring. They also contribute to the regulation of diseases, and to the depollution of contaminated soils. They interact in the rhizosphere of plants (region of the soil directly formed and strongly influenced by the association of roots and soil microorganisms) with which they can form **symbioses** with plants and they can also be **pathogenic**, both for animals and plants.

Bacteria play an essential role in the functioning of soils through their **mineralization** functions (mineralization of organic matter, oxidation-reduction of inorganic compounds, solubilization or precipitation of minerals, transformation of more or less recalcitrant organic compounds ...) [9]. They are thus at the base of the regulation of the main biogeochemical cycles of soils (carbon, nitrogen, phosphorus, sulfur...) and they are able to:

reduce sulfates to sulfites and sulfides (sulfate-reducing bacteria)

oxidize sulfur (*Thiobacillus* for example),

fix atmospheric nitrogen (diazotrophy alone or in symbiosis with plants),

produce nitrates (nitrifying bacteria),

make phosphorus available (by alkaline phosphatase for example) [9] *etc.*

In addition, some bacteria, especially those called PGPR (*Plant Growth Promoting Rhizobacteria*), have the **ability to develop symbioses with plants**, which allow them to increase the availability of nutrients for their growth.

Bacteria can also promote the decontamination of soils contaminated by heavy metals (known as trace metals or TMEs) [10] by modifying their availability, but they are mainly involved in the decontamination of organic compounds such as polycyclic aromatic hydrocarbons (PAHs) by mineralizing them at least partially.

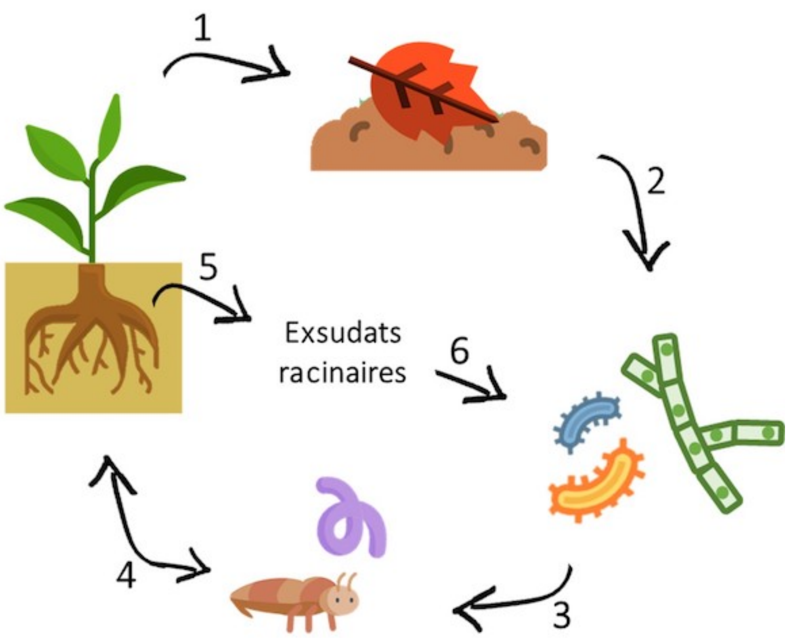

Figure 2. Simplified diagram of the microbial loop within the plant rhizosphere. [Source: © Quentin Vincent]

The biofilms that bacteria form in the soil constitute a very important quantity of microbial biomass that immobilizes large quantities of nutrients. Various processes such as predation of these microorganisms by protozoa, nematodes or micro-arthropods, can lead to the prolonged or rapid release of these immobilized and excess nutrients [11]. This remobilization of nutrients is thus termed the "**microbial loop"** [12], which is considered a primary control point for nutrient availability within the rhizosphere (Figure 2).

2.2. Fungi

Fungi are commonly classified into two groups: yeasts, which are unicellular, and fungi, which are multicellular and form branches called hyphae. These are the fine white filaments that we often see on the surface of the ground or leaves during a walk in the forest. These filaments constitute a very important biomass (several tons per hectare) and also an impressive network circulating through the soil over long distances: one square meter of meadow or forest soil contains several kilometers of hyphae.

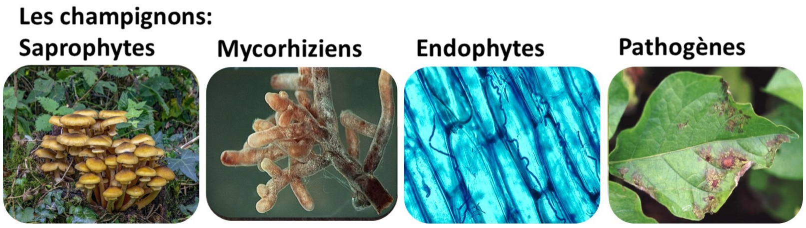

Figure 3. The four trophic modes of soil fungi [Source: royalty-free images - from left to right: Pixabay / Ellen Larsson, CC BY 2.5, via Wikimedia Common / Nick Hill, Public domain, via Wikimedia Common / No machine-readable author provided. Fk assumed (based on copyright claims), CC BY-SA 3.0, via Wikimedia Common]

The great diversity of fungi has led to their classification into taxonomic groups [13] with often complex Latin names, such as chytridiomycetes, glomeromycetes, basidiomycetes, ascomycetes, mucoromycetes (formerly zygomycetes). With respectively 56%, 31% and 10%, these last three groups represent almost all the fungal community of the soil. For practical purposes, fungi can also be classified according to their mode of feeding in the soil: **saprophytic, mycorrhizal, endophytic and pathogenic** [14] (Figure 3).

2.2.1. Saprophytic fungi

Figure 4: Saprophytic fungus living in a parasitic way on soil or plants (here Phellinus). [Source : © Quentin Vincent]

Saprophytic fungi (Figure 4) **feed on dead organic matter** (OM) already more or less decomposed or degraded by other organisms. These OMs provide them with nutrients that are predigested through the excretion of fungal extracellular enzymes. Saprophytes represent, in estimated numbers of organisms, about 44% of the fungal community, with little variation between different ecosystem types [13]. For fungi, too, a more functional classification has been developed: these are white, brown and soft rots [15]. These names are directly related to the decomposition of plant litter, which varies between species. This classification refers to visual characteristics of lignin degradation, and it should be noted that they are actually under the control of their capacity to degrade cellulose and hemicellulose, two major constituent elements of plants and therefore of their litter.

2.2.2. Mycorrhizal fungi

Mycorrhizal fungi **form symbiotic associations with plant roots**. These plant-fungus symbioses are extremely widespread and concern 80 to 90% of plant species [16]. In this mutually beneficial relationship, the fungus receives from the plant elements necessary for its growth such as sugars and vitamins. The fungus in turn absorbs various elements from the soil, including phosphorus, which it transfers back to the plant, thus considerably increasing the volume of soil explored by the plants for their growth.

There are two main groups of mycorrhizal fungi: ectomycorrhizal and endomycorrhizal. The **ectomycorrhizal** fungi form a network of hyphae (Hartig's network) on the surface of the roots of colonized plants. This forms a peripheral sleeve that serves as an exchange matrix between the plant and the fungus, and the latter is then able to insert itself between the plant cortical cells without being able to penetrate them. The plant hosts of these fungi are mainly of the shrub and tree type. More than 95% of ectomycorrhizae belong to the group of basidiomycetes [17].

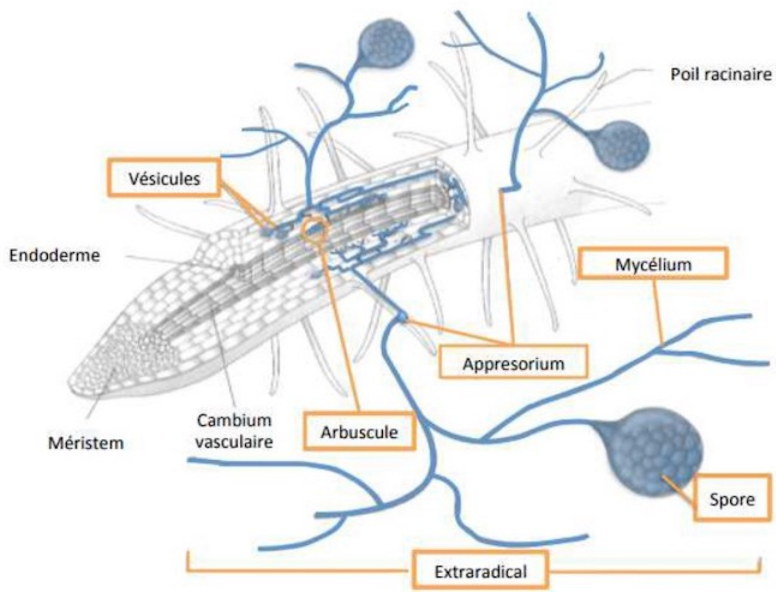

Figure 5. section of colonized root with the different endomycorrhizal structures. [Source: © J. André Fortin, Christian Plenchette, Yves Piché - MYCORHIZES - The Rise of the New Green Revolution]

Endomycorrhizal fungi form intracellular structures, with hyphae entering the root cells for close exchanges with the plant. There are 3 types of endomycorrhizae: ericoid, orchid and arbuscular. The hyphae of **arbuscular mycorrhizal fungi** (AM) form arbuscules in the cells of the root cortex, thus allowing direct exchanges between root and fungus. Extraradicular hyphae also grow several centimeters outside the root, exploring the surrounding soil, and bringing a multitude of spores (Figure 5) [18].

AM fungi (exclusively glomeromycetes) are obligate symbiotrophs since without the interaction with the host plant, which provides them with carbonaceous elements, they cannot complete their development cycle. For the plant, the main advantage is a better hydric and mineral nutrition, in particular in phosphorus brought by the fungus, which is most often translated by an increase of the plant biomass compared to a non-colonized plant.

2.2.3. Endophytic fungi

Endophytic (root) fungi have a way of life that is characterized by the **colonization of the internal structures of a plant in an asymptomatic way**. Indeed, these fungi take nutrients from the host without the latter showing signs of disease and remain entirely in the root tissues, unlike mycorrhizal fungi that colonize plants while developing in the rhizosphere. Endophytic fungi are overwhelmingly derived from ascomycetes and basidiomycetes, of which the three best known members are the DSE (*Dark Septate Endophytes*), Sebacinales and *Trichoderma* [19]. Like mycorrhizal fungi, endophytic fungi promote growth and resistance to abiotic stresses in the host plant.

2.2.4. Pathogenic/parasitic fungi

Pathogenic fungi can be primarily parasites of other fungi, animal pathogens or plant pathogens (phytopathogens) [20]. These soil-borne plant pathogenic fungi can **infect the roots**, or enter its vascular systems and colonize the entire organism by ascending the xylem vessels, although they mainly attack the aerial parts.

3. Soil fauna

If we take the image of observing the soil with a spade, we can easily distinguish animals of very different sizes: this is used to classify the soil fauna into four groups [21]: **microfauna, mesofauna, macrofauna and megafauna**. The soil fauna is defined as all the **animals that have at least part of their life cycle in the soil**. This fauna represents nearly **a quarter (23%) of the total diversity of living organisms** described to date [22] with very heterogeneous horizontal and vertical distributions. Thus, in the brown soils of temperate regions, the fauna is mainly located in the first 10 to 20 cm of the soil and its appendages (litter, dead wood, *etc.*).

3.1. The microfauna

Invisible to the naked eye, the microfauna is made up of individuals generally smaller than 200µm which **can therefore live in the capillary porosity of the soil**. Rotifers and tardigrades are part of the soil microfauna, but it is mainly protozoa and nematodes that make up the bulk of this microfauna. Indeed, the protozoa present an abundance varying from 100 to 1000 million individuals per square meter. This group is very diverse as well as their nutrition, but most protozoa can ingest particles and feed on bacteria. These organisms, like nematodes, live in the water film surrounding soil particles [23]. Approximately 30,000 species of nematodes are known to date, but this would only represent about 5% of the number of existing species. They are classified into five trophic groups: **bacterivores**, **fungivores**, **omnivores** (feed on bacteria and fungi), **phytoparasites** (parasites of plants), and **predators** (feed on other animals) [23]. Nematodes play a key role in the mineralization and decomposition of organic matter and in the regulation of microbial communities.

3.2. The mesofauna

The mesofauna (or micro-arthropods or meso-invertebrates) consists of animals with **a size of about 0.2 to 4 mm**. **Collembola** and mites are the two main representatives of this group. Protoures, diploures, thysanoures, enchytraides, and symphilic myriapods, are also part of the mesofauna but their abundance is much lower.

Collembola are probably the most abundant group of hexapods on Earth (up to 200,000 individuals per m-2 in uncultivated brown soils of temperate regions) and with a high diversity (about 8,000 known species, of which more than 2,000 in Europe (Figure 6). Collembola are essentially **decomposers**, feeding on mycelial hyphae and organic matter, and are therefore mainly found in soil and litter (dead leaves and wood). They thus play a major role in the decomposition process of the litter by micro-fragmentation and mixing of the organic matter.

Figure 6. Video of springtails on decaying wood. [Source: © Apolline Auclerc with the Direction du numérique de l'Université de Lorraine]

https://www.youtube.com/watch?v=EfQmlKoEjjE

Figure 7. The three modes of life in springtails. [Source: Epi-edaphic and hemi-edaphic springtails © Soizic Maillet - Eu-edaphic springtail © [Andy Murray, CC BY-SA 2.0](), via Wikimedia Commons]
** furca: abdominal appendage that allows the springtail to jump*

Springtails live for about 1-2 years in the soil and, like nematodes, are involved in the regulation of microbial populations. These small animals are able to adapt to their habitat, which is mainly reflected in morphological adaptations, which can be grouped into three modes of life: **epi-edaphic**, **eu-edaphic** and **hemi-edaphic** (Figure 7) (Read: [Collembola: actors of soil life]()).

With more than 48,000 species already described, mites colonize many habitats, especially those rich in organic matter (peat, decaying wood, litter, *etc.*). Like springtails, most mites contribute to the fragmentation of organic matter by producing fecal pellets and thus indirectly regulate microbial communities. Two orders of mites are generally distinguished: the **acariforms** and the **parasitiformes** [24]. Some are **predators** (mainly parasitiforms) and others are **parasites** (of plants or animals) or **decomposers** (mainly acariforms). Some species carry bacteria and fungi on their surface, thus contributing to their dissemination.

3.3. Macrofauna

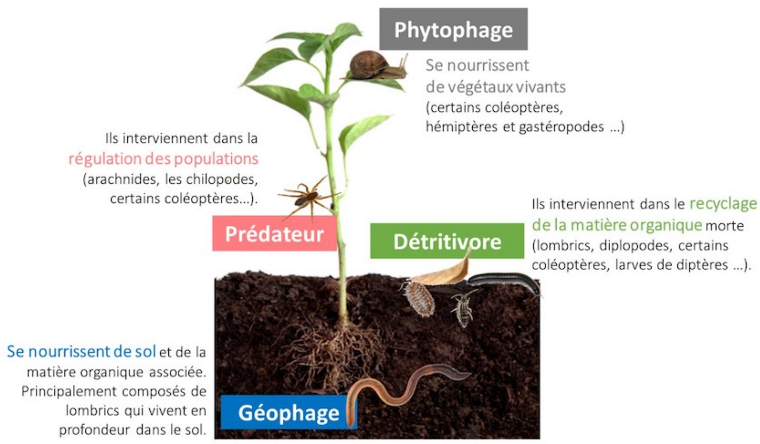

Figure 8. The four ecological groups of the macrofauna. [Source: © Quentin Vincent]

The **macrofauna** includes animals of about 4 to 80 mm. They are earthworms, larval and adult insects (mainly Hymenoptera, Coleoptera and Diptera (larvae)), myriapods, spiders, molluscs and crustaceans. These animals are also grouped according to their mode of nutrition; **predators**, **decomposers**, **geophagous** (feed on soil) and **phytophagous** [25] (Figure 8).

Another functional group, not related to a trophic group, is also often used; these are the "**soil engineers"** [26]. Soil engineers modify the soil environment through their construction activities (grubs, galleries, nests) that affect microbial diversity and activity. Soil engineers are mainly represented by earthworms (endogeous and anecitic) and ants. Earthworm species have been grouped into three categories:

endogeous (small geophagous worms living permanently in the first centimeters of soil in a network of horizontal galleries).

aneciques (a strange term for large saprophagous worms living in large galleries that can go down to a depth of 3 m, the "ploughmen" of the soil).

epigeneans (small red worms living in the litter and generally not digging galleries) [27].

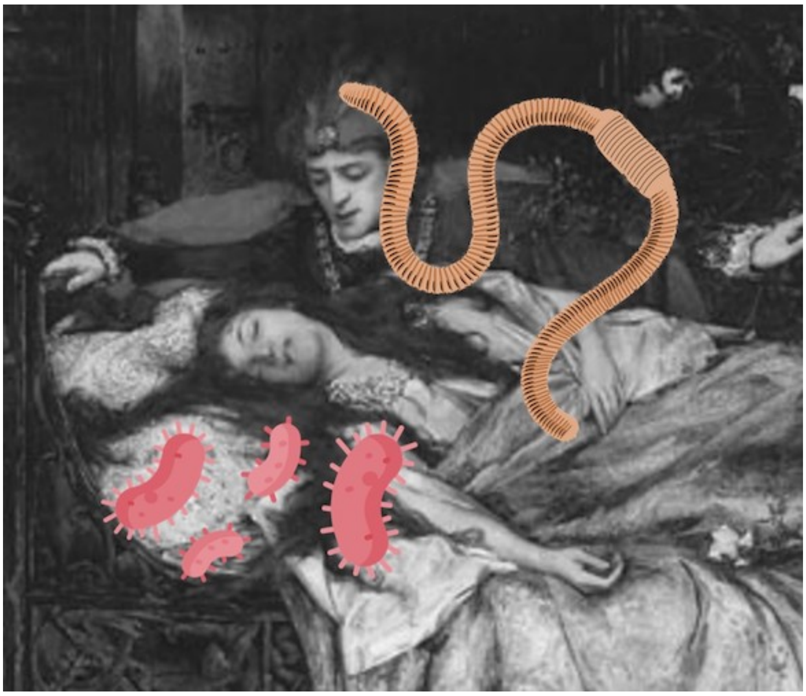

Figure 9. The Sleeping Beauty paradox [Source: © Henry Meynell Rheam, Public domain, via Wikimedia Commons]

Soil fauna, as a whole, plays a role as a vector for the dispersion and activation of microflora in the soil and also in the rhizosphere. Indeed, microorganisms are not very mobile and not very active in the soil, so they wait for other organisms such as fauna and plants, which will put them in the presence of organic substrates. This phenomenon is known as the "Sleeping Beauty Paradox" [28].

4. Measuring biodiversity

Over the past few decades, many **research programs** on soil biodiversity have sought to identify relevant indicators, to produce a comprehensive mapping and/or to identify soil uses influencing soil biodiversity.

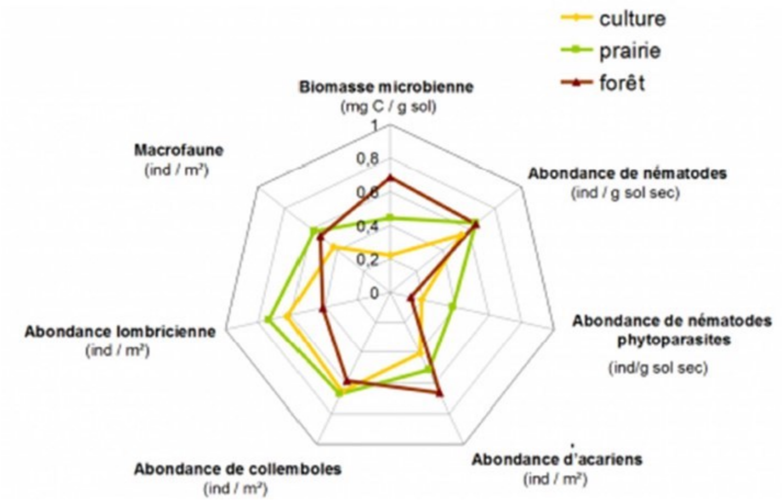

Figure 10. Measurement of biological indicators of soils subjected to 3 different uses (RMQS Bio-Div project) [Source: © Daniel Cluzeau et al. 2009 - RMQS Bio-Div program - https://ecobiosoil.univ-rennes1.fr/page/programme-rmqs-biodiv]

Among these, one cannot fail to mention the RMQS Bio-Div program (Réseau de Mesures de la Qualité des Sols) of Gis Sol, which aimed to create a reference system for soil quality. Indeed, there is very little reference data on soil biodiversity compared to physico-chemical data. One of the interests of this program was to multiply the indicators coming from several different biological groups (micro-organisms, micro-, meso- and macrofauna). The researchers involved have thus shown, among other major effects, **the influence of soil use** (here, forest, grassland and crop) on their biodiversity levels (Figure 10) [29].

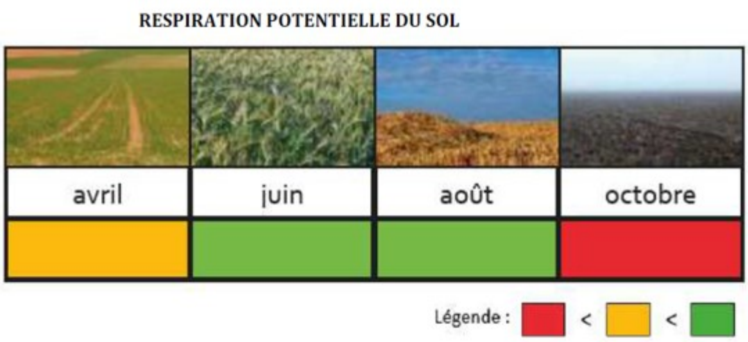

Figure 11. Seasonal variability the potential respiration of soil plots in conventional agriculture in 2016. Colors indicate significant differences between seasons. [Source: © Q.Vincent et al., 2019. Development of biological quality and soil organic carbon indicators for soil condition assessment in Wallonia: valorisation of the acquired knowledge and transfer to users (CARBIOSOL 5)]

The Bioindicator II program of ADEME (Agency for Ecological Transition) can also be cited since its main objective was to promote the development of methods for measuring biodiversity and soil functions, and the use of soil bioindicators to monitor their quality and assess the ecological risks related to their contamination. For example, the CARBIOSOL project of this research program has shown **variable effects of season** on relevant soil bioindicators, as shown in Figure 11 [30], with potential soil respiration. Potential respiration is the measure of the rate of mineralization of organic carbon to CO_2 during the decomposition of organic matter by microorganisms.

Among the methods of researching functional characteristics of organisms, the one called "**ecological traits and preferences**" is very relevant to describe the functions of communities. Thus, for example, a fungal community can be characterized by its capacity to mineralize different molecules (*e.g.* sugars, amino acids, polymers), or by its membership in a trophic group (*e.g.* saprophytes, symbiotics, endophytes, pathogens; see section 3.2). Or, an earthworm community can be characterized by the lifestyle of the different species or by the length of the individuals. It is in this context that the TEBIS (Traits Écologiques et Biologiques des organismes du Sol) network was created, in order to better characterize the ecological traits and preferences of soil organisms, as bioindicators in particular.

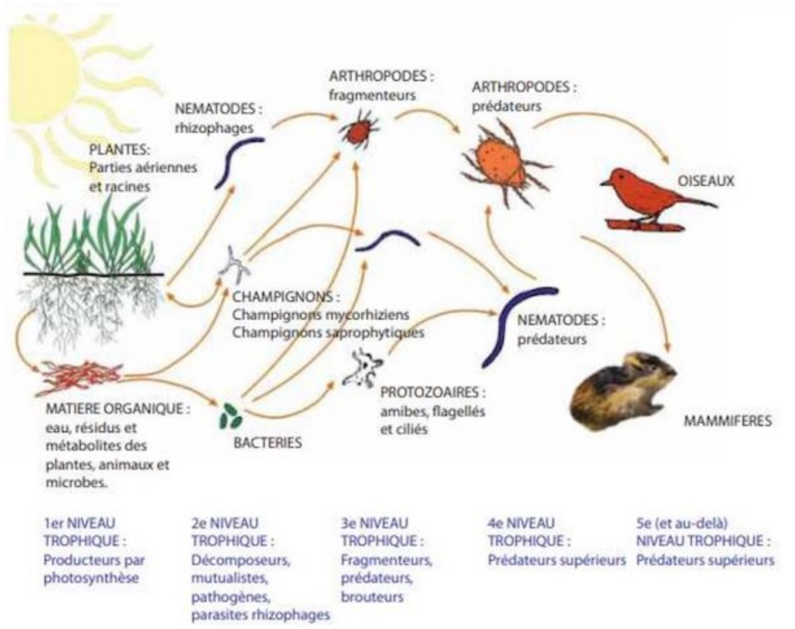

Figure 12. Schematic representation of a trophic chain in the soil [Source: © USDA- http://soils.usda.gov/sqi/concepts/soil_biology/soil_food_web.html]

Soil is a complex environment where organisms interact with their environment but also with each other: we speak of **biotic interactions** that largely control soil biodiversity [31]. Thus, when measuring the quality of a soil using biodiversity indicators, **biotic interactions must be taken into account**. Some researchers even invite to consider these biotic interactions as an integral part of biodiversity [6], in particular symbiotic relationships (mycorrhizae...), biotic interactions with strong reciprocal benefits. However, most of these biotic interactions are "predator-prey" relationships (Figure 12) [23].

This article has modestly attempted to show that the different biotic compartments of the soil interact with each other. Thus, by developing **simultaneous studies of different biotic compartments** of soils subjected to different uses and at different times, we will be able to have a more realistic view of the biodiversity of soils and the interactions between the different organisms in this ecosystem. Only this global approach studying the whole community (and not isolated biotic components) allows to consider all biological functions simultaneously [32], [33].

Messages to remember

A quarter of the total biodiversity of the planet is found in soils.

Soil biodiversity can be classified into 4 major groups: **micro-organisms, micro-fauna, meso-fauna, macro-fauna**. Plants can also be considered through their root system.

The different soil organisms(**taxonomic diversity**) have essential roles **(functional diversity**) in soil functioning.

The roles of these organisms in the soil are, for the most part, related to their **biological interactions** (prey-predator relationship, symbiosis etc.).

Many **factors** simultaneously modify the state of soil biodiversity, such as use, seasons, biotic interactions, *etc*.

Soil biodiversity must be **considered in a global way**, taking into account the close relationships and strong impacts between its different biological components.

Notes and references

Cover image. [Source : © A.Auclerc]

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