3

Biodiversity and Ecological Functioning of Soils

3.1. Importance of biodiversity in the functioning of soils

3.1.1. *A diversity whose functional importance has been recognized late*

Soil is at the interface of four major terrestrial spheres (the atmosphere, hydrosphere, biosphere and lithosphere), which results in the interactions between these spheres. It is both an organic and a mineral environment, where dead organic matter constitutes a carbon reservoir, estimated at 1,500 billion tons, at least twice as much as that of biomass or in the atmosphere. However, it is also an environment containing the greatest diversity of terrestrial organisms, most of which, especially microorganisms, are linked to major biogeochemical cycles, and therefore to the functioning of soil and more generally to continental ecosystems [LAT 13].

As with other types of ecosystems, the need to understand the relationship between biodiversity and soil functioning is increasing alongside the magnitude of disturbances they experience. Interest in this topic, however, arose later than in other ecosystems, such as the oceans or visible (aerial) parts of terrestrial ecosystems despite the fact that the ecosystem services provided by soils are intrinsically linked to their biodiversity through multiple functions, such as the transformation of organic matter, the structuring and therefore the stability of the soil, the

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Soils as a Key Component of the Critical Zone 6: Ecology,
First Edition. Edited by Philippe Lemanceau and Manuel Blouin.

mitigation of pollution or the regulation of biological populations (see Figure 3.1).

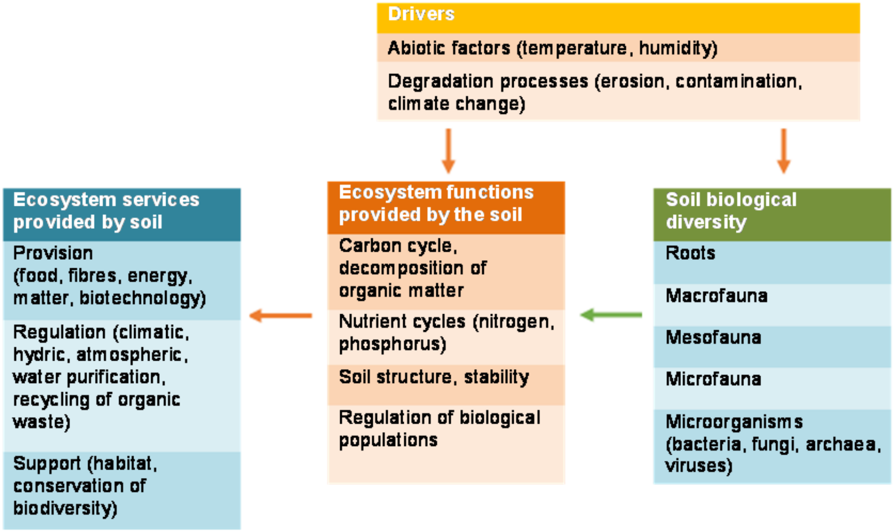

Figure 3.1. *Relationship between diversity, ecosystem functions and ecosystem services provided by soil under the influence of abiotic parameters and anthropogenic degradation processes. Ecosystem services are seen as the benefits that ecosystems provide to humans. Precise interactions between compartments are sometimes unclear, since all components of biodiversity potentially interact with one another and participate in soil functions. See also [MIL 05] and [ORG 16]. For a color version of this figure, see www.iste.co.uk/lemanceau/soils6.zip*

There are several potential explanations for the delayed interest of the scientific community in the relationship between soil biodiversity and functioning. First, soil has long been seen as a physical (support), chemical (fertility) and cultural resource (landscape aesthetics, philosophical and religious functions). Soil has also often been considered inexhaustible, the degradation of which has not often attracted attention in the past, except in cases of significant degradation (erosion in the case of the Dust Bowl in the United States in the 1930s or massive pollution in industrial accidents). This narrow functional point of view was also often limited to the soil surface, particularly due to practical reasons or to its relevance in agricultural practices such as plowing/tilling depth. Inclusion of the multiple functionalities and the diversity of deep soil is still a major scientific obstacle. While deep soils account for more than half of the total soil carbon stocks, the properties and dynamics of these stocks are largely overlooked [RUM 11]. However, cultural practices such as fertilization can, for example, lead to a differentiation of microbial communities in deep soils (by leaching) and not in superficial soils [LI 14].

Finally, the late realization of the importance of soil diversity is related to the very nature of this environment [LAT 13] where the study of ecological processes requires taking into account not only a very heterogeneous mixture of organisms and substrates but also heterogeneous physico-chemical conditions on very small scales. This increases the risk of distortion of the information obtained, and leads to the fact that soil is still often considered to be a “black box” [BAR 05]. This means that we can quite easily measure what goes in and out of this box (e.g. input of organic matter, CO_2 emission, leaching of nitrates), but the processes taking place within soil that generate these exchanges are still poorly understood. This is valid both for processes involved in regulating biogeochemical cycles and those affecting soil organisms.

Concerning biogeochemical cycles, it is difficult, if not impossible, to measure *in solum* the rapid degradation of a substrate at the very fine scale (µm) at which gases, solids and liquids mix. Microorganisms constitute the bulk of soil diversity. Their small size, their overwhelming diversity and the fact that the vast majority (probably >95%) cannot be easily cultured have for a long time been major obstacles to understanding their functioning. As a result, the extent of their diversity and functional importance in soils has only been appreciated with the relatively recent advances in molecular methods [TOR 02]. However, this cannot explain why larger organisms (invertebrates, earthworms, moles, etc. – see Chapter 6), most of which are considered to be ecosystem engineers, are poorly studied in terms of their diversity and influence on the functioning of soil [LAV 06]. Even for well-studied groups such as earthworms, there are still significant knowledge gaps with regard to their influence (positive, neutral or negative effects) on soil, their taxonomy and their behavior. These gaps may limit the use of worms for the management of soil ecosystem functions and services [BLO 13].

3.1.2. *Impact of biodiversity on soil functioning*

Due to its very slow formation, soil is a non-renewable resource. It is currently subject to severe disturbances, in particular because of its exploitation for the provision of many essential services to humans, such as the production of food and materials [LAT 13]. These disturbances may have a lasting impact on biodiversity within soil, which could, in turn, have deleterious effects on the overall budget of biogeochemical cycles such as the emission of greenhouse gases into the atmosphere [BAR 08]. Understanding the role of organisms in these cycles is therefore essential for understanding the stability of soil functioning in the face of global change. The stability of soil in the face of disturbances is determined by the balance between its resistance (ability to withstand changes) and its resilience (ability to return to the state it would have had if it had not been disturbed). This stability with respect to disturbances, such as pollution, climate change or land use, is dependent on all the components that make up this soil. For example, stability can be seen as the consequence of individual responses of soil organisms and their interactions. The links between biodiversity and stability can therefore be crucial, and several postulates from ecology suggest that ecosystem stability would increase with diversity – the ecological insurance theory [YAC 99] (see Figure 3.2). This stability can be discussed in terms of the diversity of organisms, as well as in terms of achieving ecosystem functions or services: this is called functional stability.

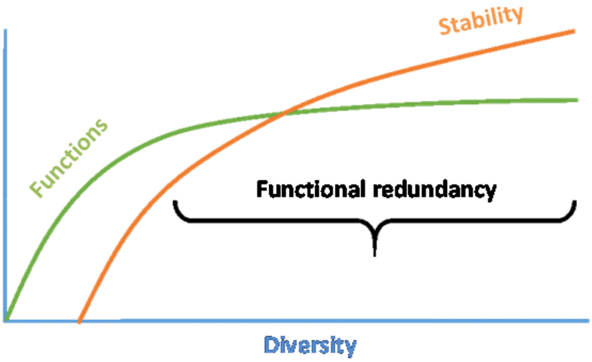

Figure 3.2. *A classic view of the relationship between diversity and functions taking into account ecological insurance (stability increases with diversity) and functional redundancy (functions reach a threshold where the increase in diversity no longer has an effect). For a color version of this figure, see www.iste.co.uk/lemanceau/soils6.zip*

These notions have been tested in soils, thanks to recent advances in different techniques. The development of genomic tools makes it possible to extract and massively sequence DNA, and thus to better estimate the diversity of soil organisms. The distribution and the involvement of these organisms in biogeochemical cycles can be understood through the use of stable isotope tracers (e.g. ^{13}C or ^{15}N), or the improvement of fine scale observations or 3-D visualization (e.g. X-ray tomography), or even modeling approaches. However, it is still difficult to reach a consensus on the links between biodiversity and biogeochemical cycles in soils, due to several difficulties:

– the disparity of scale between the process scale associated with soil organisms and the scale at which the overall outcome of these processes (e.g. that of a field, a landscape) is measured and modeled;

– difficulties in assessing the interactions between microorganisms (e.g. competition, predation) in soil, between microorganisms and macroorganisms (e.g. the effect of earthworms, plant roots), and between organisms and the physical environment (see section 3.2).

The latter observation is all the more constraining because soil organisms rapidly adapt to disturbances due to their high plasticity and rapid evolutionary dynamics [GRI 13]. This results in a high physiological and functional diversity that potentially increases the range of environmental conditions under which a function can be fulfilled. This in turn results in a strong functional redundancy (see Figure 3.2), which makes it even more difficult to predict the functioning of soil according to the environmental conditions (e.g. climate) [GOB 10]. Among the possible reasons for this strong functional redundancy: a common omnivore in an environment where it is difficult to choose one's prey, and low competition for resources; a strong preponderance of saprophagous organisms (consuming dead organic matter); extremely diverse metabolic pathways due to a very high diversity and the possibility of gene exchange between microorganisms; or a saturation of soils at a very fine scale in terms of organisms, nutrients or exoenzymes leading to strong interactions.

3.2. Main current research questions

Despite all the scientific obstacles mentioned above, there are some privileged lines of research and important developments of approaches and techniques to improve the understanding of the links between biodiversity, biogeochemical cycles and soil functioning.

3.2.1. *Biodiversity–function links impacted by abiotic parameters and disturbances*

Although a high level of functional redundancy appears to exist in soil organism communities, the functions performed will depend on several parameters, including the physiology or adaptation of these organisms, and the abiotic conditions (humidity, temperature, organic matter content, pH, salinity, texture, etc.). The adaptation of organisms in response to environmental changes can be expected to be strong in soils, particularly because of the importance of the microbial compartment, which is highly reactive and has a short generation time [WAL 12]. However, the literature shows that there is no general response to disturbances and that the level of stability seems to depend both on the context (type of soil), the type of disturbance (soil management, metallic or organic pollution, temperature, rainy events, etc.) and soil history [GRI 13]. The adaptation of communities therefore seems to be subject to different levels and thresholds of constraints [WAL 12]: the traits of a community can be governed by ecological trade-offs, and the adaptation of a community to a disturbance depends on the potential rate of change in community composition related to the rate of change in the environment.

Beyond these adaptive phenomena, and because of the difficulty of studying the black box, that is, the soil, in essence a very heterogeneous medium at a fine scale, it is not easy to understand why soil, in two different situations, expresses two different levels of function. This could be due to truly distinct communities that have *de facto* different metabolic capacities associated with different environmental conditions (ecological niches); it could also be the result of different physiological states of these communities (i.e. active or dormant organisms). Two major concepts emerge from this observation, both crucial and limiting for the ecology of soil organisms.

The first is the concept of dormancy, a state of cellular rest characterized by a very low metabolic activity, often in response to environmental stress conditions. This state of affairs greatly complicates the application of ecological theories to population dynamics that are often based on active individuals, in particular because techniques based on total soil DNA do not allow the distinction between dead, dormant, potentially active (responding quickly to better environmental conditions) and active organisms [BLA 13]. Given that in a typical soil without readily available substrates, active soil microorganisms seem to only make up between 0.1 and 2% of the total biomass, the analysis of the fractions that are active for the realization of the different soil functions seems particularly crucial for the future [BLA 13]. However, even if dormant organisms do not contribute directly to ecosystem processes at time t, they can become so at time t+1 due to fluctuations in environmental conditions, and are also important for the resilience of communities facing a disturbance [JON 10].

The second major concept is that of the ecological niche. Many biogeochemical processes in the soil occur at very small scales in which processes of gas and water transport and diffusion also take place. This creates a mosaic of microsites and gradients, resulting in varied habitats for soil organisms. Depending on the abiotic conditions, only some of these habitats may or may not be occupied. Due to the very heterogeneous distribution of resources in soils [ETT 02], the spatial distribution of organisms is therefore heterogeneous. They are distributed both over patches with low species richness and functional and biodiversity hotspots [FRA 07]. Finally, since the soil structure may vary over time [SIX 04], this also implies that the spatial distribution of organisms and/or of their habitat can change very rapidly [KUZ 15].

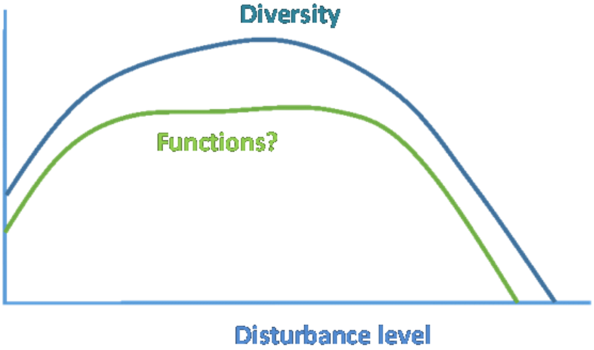

Figure 3.3. *The Intermediate Disturbance Hypothesis (IDH) is where species diversity is maximized when ecological disturbance is neither too rare nor too frequent due to the coexistence of organisms with different ecological strategies, thus ensuring stability of the ecosystem. For a color version of this figure, see www.iste.co.uk/lemanceau/soils6.zip*

Finally, the level of disturbance to soils is an important factor for diversity–function relationships. On the one hand, the higher the level of disturbance, the greater the potential impact on diversity and/or functions; however, disturbances could also increase diversity by increasing the number of ecological niches. Several alternative hypotheses have thus emerged, such as the Intermediate Disturbance Hypothesis (IDH) stating that species diversity is maximized when the ecological disturbance is neither too rare nor too frequent (i.e. at an intermediate level) (see Figure 3.3). The IDH could explain a higher level of biodiversity at intermediate levels of disturbance due to the coexistence of organisms with different strategies, thus ensuring the stability of the ecosystem [GRI 13].

3.2.2. *Biodiversity–functions and nutrient cycles*

All of the above considerations have mainly been tested in the study of the nutrient cycle and in particular the cycles of carbon, nitrogen and phosphorus (C, N, P). It would be long and tedious to detail here all the knowledge accumulated on these cycles and the possible relationships with the level of diversity, not only because the studies are extremely numerous (especially for carbon), but also because the results may be extremely heterogeneous depending on the environmental conditions (climate, pH, soil management, relationship with the vegetation cover, etc.). However, there are three types of results and major conceptual changes that have arisen over the last few decades.

First, global changes, especially climate and land-use changes, have become highly studied drivers, particularly for discussing carbon storage in soils and feedback loops with the atmosphere. For example, from the IPCC reports[1], we know that climate change will certainly affect many aspects of our daily lives by the middle and end of this century. This awareness makes climate and predictions of its evolution an important topic of the soil research agenda. Numerous studies seek to assess how biodiversity responds and can adapt to global change (see, for example, the recent Foundation for Research on Biodiversity’s prospective report [FON 15]), and these considerations are likely to increase with the establishment of the Intergovernmental Science and Policy Platform on Biodiversity and Ecosystem Services[2].

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[1] Group of intergovernmental experts on climate evolution, available at: https://www.ipcc.ch/.

[2] IPBES, available at: http://www.ipbes.net.

However, once again, soil can be seen as a poor relation, especially due to the measurement complexity and to the heterogeneity of this environment. Significant efforts are currently underway to understand, for example, along with changes in mean temperature and precipitation, how the nature of extreme events (droughts, intensive rainfall) associated with agricultural practices can modify the diversity and functioning of soil organisms associated with the carbon cycle [KAI 13, KAI 15], including at very small scales such as that of soil pores [RUA 11]. These issues are also at the heart of the 4 per 1,000 initiative (see Box 3.1) initiated in France and seeking to federate all public and private voluntary stakeholders in order to show that agriculture, and in particular agricultural soils, can play a crucial role in food security and climate change by storing more carbon. The answer to these questions, while exciting, is relatively complex. A simple question alone can sum up all the questions or antagonisms that are nested in this complexity: “What is a good soil?”: a soil that strongly mineralizes organic matter and thus provides plants with the nutrients they need for growth? Or a soil that mineralizes very little, which will be more unfavorable to plants, but will emit less greenhouse gases? One of the answers for agriculture will require better integration and better management of the root functioning of plants and varieties (rarely done so far). Indeed, plants in their rhizosphere can partially control soil organisms and their functions such as carbon mineralization and CO_2 production, but also other functions, such as those related to nitrogen loss and eutrophication [SUB 13].

The 4 per 1,000 initiative, launched in France, involves federating all the public and private voluntary stakeholders (states, communities, companies, professional organizations, NGOs, research establishments, etc.) within the framework of the Lima–Paris Action Agenda (LPAA). It aims to demonstrate that agriculture, especially agricultural soils, can play a crucial role in food security and in response to climate change. The official launch of the operation took place during COP21 on 1st December, 2015.

The 4‰ represents the annual growth rate of carbon stock in soils that would compensate for the current increase of CO_2 in the atmosphere. This growth rate is not a normative target for each country, but aims to illustrate that even a small increase in the soil carbon stock (agricultural, including grasslands and pastures, and forest soils) is a key factor in meeting the long-term goal of limiting the rise in temperature to + 2 °C. Beyond this threshold, the IPCC indicates that the consequences induced by climate change would be significant.

Based on sound scientific documentation, this initiative therefore invites all stakeholders to publicize or implement concrete actions on soil carbon storage and the type of practices to achieve this (agroecology, agroforestry, conservation agriculture, landscape management, etc.).

The aim of this initiative is to encourage stakeholders to engage in a transition to a productive, highly resilient agriculture, based on adapted soil management, creating jobs and income and thus bringing sustainable development.

Box 3.1. *The 4 per 1,000 initiative [4PE 17]*

A second major change is that current molecular tools make it increasingly possible to link soil biodiversity to their functions. Thus, some key functions of the nitrogen cycle, such as nitrification, have long been considered to be carried out by a limited number of organisms (some autotrophic bacteria – only capable of developing from mineral elements – carrying out the two stages of nitrification separately: oxidation of ammonium to nitrite, then nitrite to nitrate), which limited the application of the concept of functional redundancy for this function. In turn, it was discovered 15 years ago that the archaea (belonging to another kingdom of the living world) were not only able to achieve nitrification, but they also comprised of the majority in soils [LEI 06]. However, many authors question the role of archaea in nitrification, and suggest that their actual contribution to this function cannot be deduced from abundance and must be evaluated [HEI 15]. Finally, in 2015, when nitrification had always been considered as a two-step process catalyzed by oxidizing microorganisms, either ammonium or nitrite, the first organism (bacteria) capable of carrying out both steps was discovered [DAI 15]. These significant upheavals show how, for a key soil function studied for over a century, and even though it can lead to the production of N_2O (greenhouse gas 300 times more powerful than CO_2 and 12 times more powerful than methane) by the denitrification of nitrate, it soon became necessary to redefine the relationship between genes, diversity and realized functions, questioning which ecological niches could favor one or the other of these (new) nitrifying populations.

Finally, besides the three biogeochemical cycles (C, N, P) frequently studied in soils, there is a growing need in the scientific and practitioner communities to move towards a greater coupling between these cycles and also towards more stoichiometry (the study of the equilibrium of the chemical elements in the interactions and the ecological processes, as well as flows of energy and matter within the ecosystems). Indeed, most studies focus on carbon and the importance of CO_2 as a greenhouse gas (including in initiatives such as 4 per 1,000), while nitrogen and phosphorus are recognized as limiting elements and that soil organisms (e.g. bacteria and fungi) may have different stoichiometric constraints. Coupling the cycles, at least those of C, N and P, seems nevertheless crucial for evaluating the limitation of nutrients in soil ecosystem processes [CLE 07], including on a large scale where stoichiometry has been considered to be a powerful predictor of the bacterial diversity and composition at the regional scale [DEL 17].

3.2.3. *Development of approaches and techniques*

A number of approaches and techniques have enabled significant recent progress in the study of the relationship between diversity, ecosystem functions and ecosystem services provided by soil [LAT 13]. However, it is still difficult to understand the complex and rapid dynamics of populations or functions obtained *in situ*. One way to better understand what factors affect these dynamics is to better integrate soil biological compartments into the biogeochemical modeling of ecosystems. Another way is the use of controlled systems that allow, in particular, the study of microorganisms, microfauna (e.g. Collembola) or macrofauna (e.g. earthworms) under different environmental conditions. *In situ* projects on a very large scale also make it possible to observe the evolution of soil quality over the longer term under the effect of major natural factors (climate, for example) and of human activities. A systematic network of sites known as the “Soil Quality Monitoring Network” has been set up in France [RAN 13], in which the physico-chemical properties and the biodiversity of French soils is being studied at an unprecedentedly large spatial scale. On the so-called station scale (agricultural patch, forest patch, etc.), the recent development of automated measurements of climatic parameters and of the gases emitted by ecosystems suggests a better coupling between the dynamics of biogeochemical processes and organism diversity. Since 2002, this has been the case, for example, in France in Environmental Research Observatories (ORE), and in long-term Observations and Experimentation Systems for Environmental Research (SOERE) since 2009 [ALL 13].

Finally, despite these advances, one of the biggest challenges that remains is understanding the interrelations between soil organisms. Measurements of microorganisms can be one way to calculate critical thresholds of environmental conditions (e.g. precipitation levels, temperature increases) beyond which a modification of biodiversity or co-occurrence between organisms (simultaneous presence) could cause a decrease or cessation of the functions and services provided by soils. This will improve our understanding of how direct or indirect relationships between organisms are likely to influence the resilience and resistance of ecosystems and soils to disturbances [GRI 13].

There are still a number of challenges to overcome in order to achieve these goals (see Table 3.1). These challenges are both technical (e.g. the ability to preserve the samples prior to their analysis in the laboratory), methodological (e.g. to better appreciate the relationships between measurements *in situ* and in controlled environments) or simply material (e.g. the costs of mass sequencing). They have a negative impact on the possibility of resorting to systematic and repeated measurements under natural conditions, especially for regions where technical or financial resources are restricted (developing countries). Major challenges still to be overcome include the lack of knowledge about the functioning and ecology of certain groups of organisms, as well as the associated networks of interactions in soils. This is true for a number of soil microorganisms, because of the difficulty of cultivating them, but also for entire groups of organisms (e.g. viruses in soils are poorly understood, yet they can influence the ecology of microorganism communities through both their ability to transfer genes but also as a major cause of microbial mortality by cell lysis [KIM 08]; actinomycetes whose importance with regard to ecological functions is still debated, etc.). Finally, the development of more transdisciplinary approaches is also a challenge; soil ecology and its specialists are still not using sufficient modeling and evolutionary approaches [BAR 07].

Evaluation challenges	Tools	Obstacles	Expected benefits
Taxonomic diversity of the soil	Next Generation Sequencing (NGS); taxonomic determination	NGS costs; ability to preserve samples prior to analysis; lack of experts/guides for fauna, algae, viruses in the soil; almost no knowledge on deep soil (less than 30 cm)	Better communication on the importance of the functions rendered by the soil; best estimate of soil quality/fertility and resistance/resilience parameters
Functional diversity of the soil	Functional potential by evaluating the quantity of genes with particular functions (quantitative PCR – qPCR)	Ability to preserve samples prior to analysis; almost no knowledge on deep soil; weak to no knowledge of functional genes for a number of poorly studied (e.g. tropical) soils	Better estimate of greenhouse gas emissions and water biofiltration service; best estimate of soil quality/fertility and resistance/resilience parameters
Biogeochemical stocks and flows/functions/ services	Isotopes; elementary analyses; flux towers	Upscaling; difficulty in linking diversity to functions due to functional redundancy; some groups and compartments totally ignored (e.g. soil algae, deep soil); stoichiometry too limited to C, N or P	Better estimate of greenhouse gas emissions and water biofiltration service; best estimate of soil quality/fertility and resistance/resilience parameters
Environmental factors (water, T°, fire, herbivory, geology, vegetation patterns, ecosystem management, etc.)	Cartography; drones; weather stations; satellites, radar measurements; automated probes; humanities and social science approaches	Lack of expertise on the microbiota of certain ecosystems; automated stations unevenly distributed between ecosystems and biogeographic zones; not enough long-term manipulation; not enough links between humanities and social sciences, and so-called “hard” sciences	Water management and ecosystem management tips; communication to stakeholders; overall comparison

Table 3.1. *Challenges, tools, obstacles and benefits expected from current research on biodiversity–function linkages in soils*

3.2.4. *Awareness of the importance of biodiversity in the functioning of soils for human societies*

Together with the development of scientific techniques and approaches, an important awareness is currently associated with research questions relating to the links between soil biodiversity and its functioning. One of the drivers of this is the role of soil (the largest terrestrial stock of organic carbon) in the face of climate change. For example, the thawing of permafrost with global warming, and the resultant microbial decomposition of previously frozen organic carbon (releasing CO_2 or methane, potent greenhouse gases) is one of the most worrying potential feedbacks from terrestrial ecosystems to the atmosphere [SCH 08]. In addition, recognizing the role of soil biodiversity in agriculture, and in particular for fertility and the management of inputs (e.g. nitrogen), has recently developed exponentially as society transitions towards conservation agriculture and more rational systems. In this respect, taking biodiversity into account for the functions and services provided by soils is one of the drivers of new generations of farmers (whether they are working in very intensive systems or traditional agriculture), driving them towards collectively re-discussing the methods and consequences of these practices in order to optimize them.

All of this enthusiasm is accompanied by numerous publications aimed at the general public, decision-makers and stakeholders. These publications are initially found at the national level, at different levels of dissemination (see, for example, [EGL 10, GIS 11, LAN 15, STE 09]). Initiatives such as the 4 per 1000 or the RMQS mentioned above participate in this national dynamic. At the European level, the adoption of a Thematic Strategy for Soil Protection in 2007 by the European Parliament, which proposes guidelines for the protection and restoration of European soils[3], participates in this momentum and extends it. In addition, the European Commission has published a report on the relationships between soil biological diversity, functions, threats and tools for decision makers [TUR 10]. In this report, it is stated that "the consequences of the mismanagement of soil biodiversity have been estimated at more than $ 1 trillion a year in the world". This highlights the importance of more global initiatives, such as the Global Soil Biodiversity Initiative [GLO 17], multiple FAO reports or materials (e.g. [FAO 15a]) and 2015 as the International Year of Soil [FAO 15b]. It should be noted that the European Commission associated with the Global Soil

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[3] Available at: http://ec.europa.eu/environment/soil/three_en.htm.

Biodiversity Initiative has published the first World Atlas of Soil Biodiversity [ORG 16]. This open-access publication was also accompanied by the release of soil atlases on continental scales, such as the African Soil Atlas, a joint initiative of the European Union, the African Union and the United Nations [JON 13]. This initiative is well received as soil biodiversity in many geographical areas (e.g. Africa) and its ability to help ecosystems withstand climate change and improve agriculture are still poorly understood [WIL 16].

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Lata C., Barot Sébastien, Leloup J., Lerch T., Nunan N., Raynaud X.

Biodiversity and ecological functioning of soils.

In : Lemanceau P. (ed.), Blouin M. (ed.). Soils as a key component of the critical zone 6 : ecology. Londres : ISTE, Wiley, 2018, p. 39-56.

(Geosciences Series. Soils Set ; 6).

ISBN 978-1-78630-218-2