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Human societies rely on the vast diversity of benefits provided by nature, such as food, fibres, construction materials, clean water, clean air and climate regulation. All the elements required for these ecosystem services depend on soil, and soil biodiversity is the driving force behind their regulation. With 2010 being the international year of biodiversity and with the growing attention in Europe on the importance of soils to remain healthy and capable of supporting human activities sustainably, now is the perfect time to raise awareness on preserving soil biodiversity. The objective of this report is to review the state of knowledge of soil biodiversity, its functions, its contribution to ecosystem services and its relevance for the sustainability of human society. In line with the definition of biodiversity given in the 1992 Rio de Janeiro Convention[1], soil biodiversity can be defined as the variation in soil life, from genes to communities, and the variation in soil habitats, from micro-aggregates to entire landscapes.

→ **THE IMPORTANCE OF SOIL BIODIVERSITY**

Soil biodiversity organisation

Soils are home to over one fourth of all living species on earth, and one teaspoon of garden soil may contain thousands of species, millions of individuals, and a hundred metres of fungal networks. Bacterial biomass is particularly impressive and can amount to 1-2 t/ha – which is roughly equivalent to the weight of one or two cows – in a temperate grassland soil.

For the sake of simplicity, this report has divided the organisms and microorganisms that can be found in soil into **three broad functional groups** called chemical engineers, biological regulators and ecosystem engineers.

Most of the species in soil are microorganisms, such as bacteria, fungi and protozoans, which are the **chemical engineers** of the soil, responsible for the decomposition of plant organic matter into nutrients readily available for plants, animals and humans.

Soils also comprise a large variety of small invertebrates, such as nematodes, pot worms, springtails, and mites, which act as predators of plants, other invertebrates or microorganisms, by regulating their dynamics in space and time. Most of these so-called **biological regulators** are relatively unknown to a wider audience, contrary to the larger invertebrates, such as insects, earthworms, ants and termites, ground beetles and small mammals, such as moles and voles, which show fantastic adaptations to living in a dark belowground world. For instance, about 50 000 mite species are known, but it has been estimated that up to 1 million species could be included in this group.

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[1] "Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

Earthworms, ants, termites and some small mammals are **ecosystem engineers**, since they modify or create habitats for smaller soil organisms by building resistant soil aggregates and pores. In this way, they also regulate the availability of resources for other soil organisms since soil structures become hotspots of microbial activities. Moles for instance, are capable of extending their tunnel system by 30 cm per hour and earthworms can produce soil casts at rates of several hundreds of tonnes per ha each year.

Chemical engineers, biological regulators and ecosystem engineers act mainly over distinct spatio-temporal scales, which provide a clear framework for management options. This is because the size of organisms strongly determines their spatial aggregation patterns and dispersal distances, as well as their lifetimes, with smaller organisms acting at smaller spatio-temporal scales than larger ones. Thus, chemical engineers are typically influenced by local scale factors, ranging from micrometres to metres and short-term processes, ranging from seconds to minutes. Biological regulators and soil ecosystem engineers, on the other hand, are influenced essentially by factors acting at intermediate spatio-temporal scales, ranging from a few to several hundreds of metres and from days to years. This provides land managers with two distinct management options for soil biodiversity: direct actions on the functional group concerned, or indirect actions at greater spatio-temporal scales than that of the functional group concerned.

Factors influencing soil biodiversity

The activity and diversity of soil organisms are regulated by a hierarchy of abiotic and biotic factors. The main abiotic factors are climate, including temperature and moisture, soil texture and soil structure, salinity and pH. Overall, climate influences the physiology of soil organisms, such that their activity and growth increases at higher temperatures and soil moistures. As climate conditions differ across the globe and also, in the same places, between seasons, the climatic conditions to which soil organisms are exposed vary strongly. Soil organisms vary in their optimal temperature and moisture ranges, and this variation is life-stage specific, e.g. larvae may prefer other optima than adults. For instance, for springtails, the optimum average temperature for survival is just above 20 °C, and the higher limit is around 50 °C, while some bacteria can survive up to 100 °C in resistant forms. Soil texture and structure also strongly influences the activity of soil biota. For example, medium-textured loam and clay soils favour microbial and earthworm activity, whereas fine textured sandy soils, with lower water retention potentials, are less favourable. Soil salinity, which may increase near the soil surface, can also cause severe stress to soil organisms, leading to their rapid desiccation. However, the sensitivity towards salinity differs among species, and increased salinity may sometimes have positive effects, by making more organic matter available. Similarly, changes in soil pH can affect the metabolism of species (by affecting the activity of certain enzymes) and nutrient availability, and are thereby often lethal to soil organisms. The availability of phosphorus (P), for example, is maximised when soil pH is neutral or slightly acidic, between 5.5 and 7.5.

Soil organisms influence plants and organisms that live entirely aboveground, and these influences take place into two directions. Plants can strongly influence the activity and community composition of microorganisms in the vicinity of their roots (called the rhizosphere). In turn, plant growth may be limited, or promoted by these soil microorganisms. Added to this, plants can influence the composition, abundance and activity of regulators and ecosystem engineers, whereas these

species in turn can influence vegetation composition and productivity. Finally, soil organisms can induce plant defence responses to aboveground pests and herbivores and the aboveground interactions can feed back in a variety of ways to the biodiversity, abundance and activities of the soil organisms. In addition, within the soil food webs, each functional group can be controlled by bottom-up or top-down biotic interactions. Top-down effects are mainly driven by predation, grazing, and mutualist relationships. Bottom-up effects depend largely on competitive interactions for access to resources.

Services provided by soil biodiversity

Many of the functions performed by soil organisms can provide essential services to human society. Most of these services are supporting services, or services that are not directly used by humans but which underlie the provisioning of all other services. These include nutrient cycling, soil formation and primary production. In addition, soil biodiversity influences all the main regulatory services, namely the regulation of atmospheric composition and climate, water quantity and quality, pest and disease incidence in agricultural and natural ecosystems, and human diseases. Soil organisms may also control, or reduce environmental pollution. Finally, soil organisms also contribute to provisioning services that directly benefit people, for example the genetic resources of soil microorganisms can be used for developing novel pharmaceuticals. More specifically, the contributions of soil biodiversity can be grouped under the six following categories:

- **Soil structure, soil organic matter and fertility:** soil organisms are affected by but also contribute to modifying soil structure and creating new habitats. Soil organic matter is an important 'building block' for soil structure, contributing to soil aeration, and enabling soils to absorb water and retain nutrients. All three functional groups are involved in the formation and decomposition of soil organic matter, and thus contribute to structuring the soil. For example, some species of fungi produce a protein which plays an important role in soil aggregation due to its sticky nature. The decomposition of soil organic matter by soil organisms releases nutrients in forms usable by plants and other organisms. The residual soil organic matter forms humus, which serves as the main driver of soil quality and fertility. As a result, soil organisms indirectly support the quality and abundance of plant primary production. It should be underlined that soil organic matter as humus can only be produced by the diversity of life that exists in soils – it cannot be man-made. When the soil organic matter recycling and fertility service is impaired, all life on earth is threatened, as all life is either directly or indirectly reliant on plants and their products, including the supply of food, energy, nutrients (e.g. nitrogen produced by the rhizobium bacteria in synergy with the legumes), construction materials and genetic resources. This service is crucial in all sorts of ecosystems, including agriculture and forestry. Plant biomass production also contributes to the water cycle and local climate regulation, through evapo-transpiration.

- **Regulation of carbon flux and climate control**: soil is estimated to contain about 2,500 billion tonnes of carbon to one metre depth. The soil organic carbon pool is the second largest carbon pool on the planet and is formed directly by soil biota or by the organic matter (e.g. litter, aboveground

residues) that accumulates due to the activity of soil biota. Every year, soil organisms process 25,000 kg of organic matter (the weight of 25 cars) in soil in a surface area equivalent to a soccer field.

Soil organisms increase the soil organic carbon pool through the decomposition of dead biomass, while their respiration releases carbon dioxide (CO_2) to the atmosphere. Carbon can also be released to the atmosphere as methane, a much more powerful greenhouse gas than CO_2, when soils are flooded or clogged with water. In addition, part of the carbon may leak from soils to other parts of the landscape or to other pools, such as the aquatic pool. Peatlands and grasslands are among the best carbon storage systems in Europe, while land-use change, through the conversion of grasslands to agricultural lands, is responsible for the largest carbon losses from soils.

Although planting trees is often advocated to control global warming through CO_2 fixation, far more organic carbon is accumulated in the soil. Therefore, besides reducing the use of fossil fuels, managing soil carbon contents is one of the most powerful tools in climate change mitigation policy. The loss of soil biodiversity, therefore, will reduce the ability of soils to regulate the composition of the atmosphere, as well as the role of soils in counteracting global warming.

- **Regulation of the water cycle:** soil ecosystem engineers affect the infiltration and distribution of water in the soil, by creating soil aggregates and pore spaces. Soil biodiversity may also indirectly affect water infiltration, by influencing the composition and structure of the vegetation, which can shield-off the soil surface, influence the structure and composition of litter layers and influence soil structure by rooting patterns. It has been observed that the elimination of earthworm populations due to soil contamination can reduce the water infiltration rate significantly, in some cases even by up to 93%. The diversity of microorganisms in the soil contributes to water purification, nutrient removal, and to the biodegradation of contaminants and of pathogenic microbes. Plants also play a key role in the cycling of water between soil and atmosphere through their effects on (evapo-) transpiration.

    The loss of this service will reduce the quality and quantity of ground and surface waters, nutrients and pollutants (such as pesticides and industrial waste) may no longer be degraded or neutralised. Surface runoff will increase, augmenting the risks of erosion and even landslides in mountain areas, and of flooding and excessive sedimentation in lowland areas. Each of these losses can result in substantial costs to the economy. These costs can be linked to the need for building and operating more water purification plants, remediation costs, and ensuring measures to control erosion and flooding (e.g. the need to increase the height of dikes in lowland areas).

- **Decontamination and bioremediation**: chemical engineers play a key role in bioremediation, by accumulating pollutants in their bodies, degrading pollutants into smaller, non-toxic molecules, or modifying those pollutants into useful metabolic molecules (e.g. taking several months in the case of hydrocarbons, but much more for other molecules). Humans often use

these remediation capacities of soil organisms to directly engineer bioremediation, whether *in situ* or *ex situ*, or by promoting microbial activity. Phyto-remediation, which is indirectly mediated by soil organisms, is also useful to remove persistent pollutants and heavy metals.

Soil pollution is a major and acute problem in many areas of the EU, and all alternatives to bioremediation (physical removal, dilution, and treatment of the pollutants) are both technically complex and expensive. Microbial bioremediation is a relatively low-cost option, able to destroy a wide variety of pollutants and yielding non-toxic residues. Moreover, the microbial populations regulate themselves, such that when the concentration of the contaminant declines so does their population. However, to date, microbial bioremediation cannot be applied to all contaminants and remains a long-term solution. Microbial remediation differs from phyto-remediation in a way that it transforms the pollutant instead of accumulating it in a different compartment. The loss of soil biodiversity would reduce the availability of microorganisms to be used for bioremediation.

- **Pest control**: soil biodiversity promotes pest control, either by acting directly on belowground pests, or by acting indirectly on aboveground pests. Pest outbreaks occur when microorganisms or regulatory soil fauna are not performing efficient control. Ecosystems presenting a high diversity of soil organisms typically present a higher natural control potential, since they have a higher probability of hosting a natural enemy of the pest. Interestingly, in natural ecosystems, pests are involved in the regulation of biodiversity. Soil-borne pathogens and herbivores control plant abundance, which enhances plant diversity. Invasive exotic plants that are highly abundant may have become released from their soil-borne controls.

  Efficient pest control is essential to the production of healthy crops, and the impairment of this service can have important economic costs, as well as food-safety costs. Ensuring efficient natural pest control avoids having to use engineered control methods, such as pesticides, which have both huge economic and ecological costs. The use of pesticides, for instance, can be at the origin of a loss of more than 8 billion dollars per year due to environmental and societal damages. In natural ecosystems, the loss of pathogenic and root-feeding soil organisms will cause a loss of plant diversity and will enhance the risk of exotic plant invasions. Changes in vegetation also influence aboveground biodiversity. Loss of this ecosystem service, therefore, will cause loss of biodiversity in entire natural ecosystems.

- **Human health**: soil organisms, with their astonishing diversity, are an important source of chemical and genetic resources for the development of new pharmaceuticals. For instance, many antibiotics used today originate from soil organisms, for example penicillin, isolated from the soil fungus *Penicillium notatum* by Alexander Fleming in 1928, and streptomycin, derived in 1944 from a bacteria living in tropical soil. Given that antibiotic resistance develops fast, the demand for new molecules is unending. Soil biodiversity can also have indirect impacts on human health. Land-use change, global warming, or other disturbances to soil

systems can release soil-borne infectious diseases and increase human exposure to those diseases. Finally, disturbed soil ecosystems may lead to more polluted soils or less fertile crops, all of which, if they reach large proportions, can indirectly affect human health, for example through intoxication of contaminated food or massive migrations.

Loss of soil biodiversity, therefore, could reduce our capacity to develop novel antibiotic compounds, it could enhance the risk of infectious diseases, and it could increase the risk for humans to ingest toxic or contaminated food.

The economic value of soil biodiversity

In order to allow for performing cost-benefit analyses for measures to protect soil biodiversity, some economic estimates of the ecosystem services delivered by soil biodiversity need to be provided. Several approaches exist. The valuation can be based on the prices of the provided final products, such as food, fibres or raw materials, or be based on the stated or revealed preference. The stated preference methods rely on survey approaches permitting people to express their willingness-to-pay for (or willingness-to-accept) the services provided by biodiversity and its general contribution to the quality of life (e.g. aesthetical and cultural value, etc.). Alternatively, cost-based methods can be used, in which the value of a service provided by biodiversity is evaluated through a surrogate product. Thus, the 'damage avoided' cost can be estimated, for instance, which is the amount of money that should be spent to repair the adverse impacts arising in the absence of a functioning ecosystem (e.g. in the case of soil biodiversity, the cost of avoided floods). For instance, the consequences of soil biodiversity mismanagement have been estimated to be in excess of 1 trillion dollars per year worldwide.

➔ CURRENT THREATS TO SOIL BIODIVERSITY

Soil degradation

The majority of human activities result in soil degradation, which impacts the services provided by soil biodiversity. Soil organic matter depletion and soil erosion are influenced by inappropriate agricultural practices, over-grazing, vegetation clearing and forest fires. It has been observed, for example, that land without vegetation can be eroded more than 120 times faster than land covered by vegetation, which can thus lose less than 0.1 tonne of soil per ha/y. The activity and diversity of soil organisms are directly affected by the reduction of soil organic matter content, and indirectly by the reduction in plant diversity and productivity. Inappropriate soil irrigation practices may also lead to soil salinisation. When salinity increases, organisms either enter an inactive state or die off. An important portion of European soils have high (28%) to very high (9%) risks of compaction. Soil compaction impairs the engineering action of soil ecosystem engineers, resulting in further compaction. This has dramatic effects on soil organisms, by reducing the habitats available for them, as well as their access to water and oxygen. Even more dramatic for soils, sealing caused by urbanisation leads to a slow death of soil communities, by cutting off all water and soil organic matter inputs to belowground communities, and by putting pressure on the remaining open soils for performing all the ecosystem services.

Land use management

Grassland soils are the soils that present the richest biodiversity, before forests and cropped or urban lands. Within rural lands, soil biodiversity tends to decrease with the increasing intensification of farming practices (e.g. use of pesticides, fertilisers, heavy machinery). However, not all soil management practices have a negative impact on soil biodiversity and related services. While in general chemical treatments and tillage aimed at improving soil fertility trade off with soil carbon storage and decontamination services, in contrast mulching, composting and crop rotations all contribute to improve soil structure, water transfer and carbon storage.

Europe has experienced drastic land-use changes throughout its history, which have shaped the communities of soil organisms found today. Fast and rapid land-use changes are still occurring today, towards increased urbanisation and intensification of agriculture, but also towards forest growth. Soil biodiversity can only respond slowly to land-use changes, so that ecosystem services under the new land uses may remain sub-optimal for a long time (e.g. reduced decomposition of soil organic matter). Land conversion, from grassland or forest to cropped land, results in rapid loss of soil carbon, which indirectly enhances global warming. It may also reduce the water regulation capacity of soils and their ability to withstand pests and contamination. The current urbanisation and enlargement of cities creates cold spots of soil ecosystem services, and one of the challenges is to free soils in urban environments, for example by semi-opening pavement, green roofs and by avoiding excessive soil sealing and a much stronger focus on the re-use of land, e.g. abandoned industrial sites (brownfield development).

Climate change

Global climate change is already a well-known fact and it is expected to result in a further increase of 0.2°C per decade over the next two decades, along with a modification in the rate and intensity of precipitations. As such, climate change is likely to have significant impacts on all services provided by soil biodiversity. It will typically result in higher CO_2 concentrations in the air, modified temperatures and precipitation rates, all of which will modify the availability of soil organic matter. These changes will thus significantly affect the growth and activity of chemical engineers, with implications for carbon storage, nutrient cycling and fertility services. For this reason it is of particular relevance that the 2009 (recently adopted) EU White Paper establishes a framework for action to strengthen the EU's resilience to cope with the impacts of a changing climate. Water storage and transfer may also be affected through a modification of plant diversity and of the engineering activity of soil organisms. Climate change may also favour pest outbreaks and disturb natural pest control by altering the distributions or interactions of pest species and of their natural enemies, and potentially desynchronising these interactions.

Chemical pollution and Genetically Modified Organisms (GMOs)

The pollution of European soils is mostly a result of industrial activities and of the use of fertilisers and pesticides. Toxic pollutants can destabilise the population dynamics of soil organisms, by affecting their reproduction, growth and survival, especially when they are bio-accumulated. In particular, accumulation of stressing factors is devastating for the stability of soil ecosystem services. Pollutants may

also indirectly affect soil services, by contaminating the belowground food supply and modifying the availability of soil organic matter. The impacts of pollutants are not distributed equally among the three functional groups and depend on the species considered, as well as on the dose and exposure time to the pollutant. For instance, microorganisms, which have a very short reproduction time, can develop fast resistance to toxic chemicals and the sensitivity of nematodes to pentachlorophenol after 72 hours of exposure can be 20 to 50 times higher than their sensitivity to cadmium. The exposure of earthworms on the other hand is highly dependent on their feeding preferences, and on their ability to eliminate specific pollutants. Therefore, for each chemical pollutant and species considered, a specific dose-response curve should be determined. Holistic approaches, that investigate the impacts of chemical pollutants on soil ecosystem functioning as a whole are still lacking and only recently started to be covered in ecological risk assessments. However, significant impacts can be expected on nutrient cycling, fertility, water regulation and pest control services.

Genetically modified crops may also be considered as a growing source of pollution for soil organisms. Most effects of GMOs are observed on chemical engineers, by altering the structure of bacterial communities, bacterial genetic transfer, and the efficiency of microbial-mediated processes. GMOs have also been shown to have effects on earthworm physiology, but to date little impacts on biological regulators are known. The available information suggests that GMOs may not necessarily affect soil biodiversity outside the normal operating range, but this issue clearly has been not explored in detail yet.

Invasive species

Exotic species are called invasive when they become disproportionally abundant. Urbanisation, land-use change in general and climate change, open up possibilities for species expansion and suggest that they will become a growing threat to soil biodiversity in the coming years. Invasive species can have major direct and indirect impacts on soil services and native biodiversity. Invasive plants will alter nutrient dynamics and thus the abundance of microbial species in soil, especially of those exhibiting specific dependencies (e.g. mycorrhiza). Biological regulator populations tend to be reduced by invasive species, especially when they have species-specific relationships with plants. In turn, plant invasions may be favoured by the release of their soil pathogen and root-herbivore control in the introduced range. Soil biodiversity can serve as a reservoir of natural enemies against invasive plants. Setting up such biological control programmes could save billions of euros in prevention and management of invasive species.

➔ **POTENTIAL SOLUTIONS**

Indicators and monitoring schemes to track soil biodiversity

Establishing the state of soil biodiversity and assessing the risks of soil biodiversity loss, requires the development of reliable indicators, so that long-term monitoring programmes can be set up. Such indicators need to be meaningful, standardised, and easily measurable. To date, no comprehensive indicator of soil biodiversity exists, that would combine all the different aspects of soil complexity in a single formula and allow accurate comparisons. However, there exist a host of simple indicators that target a specific function or species group, and many of which are based on ISO (International Organization for Standardization) standards. Although widely accepted reference sets of indicators, reference ecosystems and

standardised sampling protocols are missing, much is to be expected from the use of novel molecular tools in assessing and monitoring soil biodiversity.

The lack of awareness of the importance of soil biodiversity in society further enhances the problem of the loss of ecosystem services due to loss of soil biodiversity. So far, budgets spent on schemes for monitoring soil biodiversity remain insufficient. The cost of the monitoring scheme is often estimated as extremely expensive, but when we consider the cost per hectare it is often less than one euro. While several regional monitoring programmes have been developed in the recent years, no consensus exists on their scope, duration, or on the parts of the soil system that they represent, which makes their results difficult to compare. The Environmental Assessment of Soil for Monitoring (ENVASSO project)[2] is the first attempt to develop a comprehensive and harmonised soil information system in Europe. It offers a set of minimum reference indicators for soil biodiversity that can constitute a standard against which future monitoring schemes should be developed. Such activities need to be integrated with programmes that study the relationship between soil biodiversity and the resulting ecosystem services.

Existing policies related to soil biodiversity

To date, no legislation or regulation exists that is specifically targeted at soil biodiversity, whether at international, EU, national or regional level. This reflects the lack of awareness for soil biodiversity and its value, as well as the complexity of the subject. Several areas of policy directly affect and could address soil biodiversity, including soil, water, climate, agricultural and nature policies. However, currently, soil biodiversity is only indirectly addressed in a few Member States through specific legislation on soil protection or regulations promoting environmentally-friendly farming practices.

Given the differences among belowground and aboveground biodiversity, policies aimed at aboveground biodiversity may not do much for the protection of soil biodiversity. In contrast, the management of soil communities could form the basis for the conservation of many endangered plants and animals, as soil biota steer plant diversity and many of the regulating ecosystem services. This aspect could be taken into account or highlighted in future biodiversity policies and initiatives, such as the new strategy for biodiversity protection post-2010.

To promote soil biodiversity protection, an EU dimension would offer several benefits. It should focus on the main drivers of soil biodiversity loss, namely land use and climate change, in order to provide long-term sustainable solutions. In addition, attention should be paid to clarifying the linkages between soil biodiversity, its functions, and the impacts of human activities, by estimating the economic value of its services. To this end, the development of monitoring schemes would allow quantifying and communicating on the changes in soil biodiversity and their impacts. This is crucial in order to improve awareness on the central role of soil biodiversity and for developing capacity-building among farmers to promote biological management. The introduction of mandatory monitoring requirements could contribute, as has happened in other fields (e.g. the requirements for the monitoring of surface water status under the Water Framework Directive), to triggering the development of adequate indicators and

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[2] ENVASSO website: www.envasso.com/content/envasso_home.html; last retrieval 23/12/2009.

monitoring methodologies. In this regard, the EU proposal for a Soil Framework Directive[3] presented by the European Commission in 2006 provides the legislative framework for introducing specific monitoring requirements.

For the future, more attention should be given to developing and refining existing soil biodiversity and ecosystem management opportunities under different land uses and socio-economic conditions, and to integrating those strategies within the existing bodies of legislations (e.g. cross compliance, Habitats Directive, etc.).

→ **WHAT WE DON'T KNOW**

Several knowledge gaps exist on components of soil biodiversity, and **new groups of soil organisms** having potentially high ecological significance (e.g. Archaea) have only recently been considered as having specific functions in soil ecosystems.

In addition, no consistent relationships between soil species diversity and soil functions have been found to date, implying that more species do not necessarily provide more services. This is because several species can perform the same function. Indeed, the services provided by soil and soil biodiversity should not be considered in isolation, but rather as different facets of a set of highly associated functions performed by soil biota. Such a holistic knowledge of soil is currently lacking and we do not yet have an exact understanding of the potential interlinkages among services.

Another factor of uncertainty is that sometimes even the mechanisms underlying one specific service are not perfectly understood. For instance, it is not yet known exactly how biodiversity can control pest spread or how to quantify the final impacts of soil biodiversity disturbance to human health, even if it is observed that a qualitative relationship exists. Finally, an economic evaluation of these services would be useful, but a homogeneous approach to perform this evaluation is not yet available.

Regarding the factors influencing soil biodiversity, a number of experimental difficulties still need to be solved (e.g. how to reproduce natural conditions in laboratory models appropriately) and more information needs to be collected, especially for some classes of organisms (e.g. the effect of pH on nematodes).

Finally, regarding threats, more research is needed to estimate the impacts on soil organisms and functions. Individual studies focused on local soil ecosystems will be indispensible to develop a global view and to measure the effects on soil biodiversity appropriately. In addition, there is now a clear need for further studies on potential interactions among threats (e.g. how climate change influences the impacts of chemical pollution).

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[3] www.ec.europa.eu/environment/soil/index_en.htm.

- One hectare of soil contains the equivalent in weight of one cow of bacteria, two sheep of protozoa, and four rabbits of soil fauna (p. 47, 55, 58).

- There are typically one billion bacterial cells and about 10,000 different bacterial genomes in one gram of soil (p. 49).

- Every year, soil organisms process an amount of organic matter equivalent in weight to 25 cars on a surface area as big as a soccer field (p. 35).

- Only 1% of soil microorganism species are known (p. 31).

- Some nematodes hunt for small animals by building various types of traps, such as rings, or produce adhesive substances to entrap and to colonise their prey (p. 50).

- Some fungi are extremely big and can reach a length of several hundred metres (p. 49).

- Some species of soil organisms can produce red blood to survive low oxygen conditions (p. 55).

- Some crustaceans have invaded land (p. 66).

- Termites have air conditioning in their nests (p. 64).

- Bacterial population can double in 20 minutes (p. 112).

- The fact to be ingested by earthworms or small insects can increase the activity of bacteria (p. 91).

- Soil bacteria can produce antibiotics (p. 113).

- Bacteria can exchange genetic material (p. 37).

- Soil microorganisms can be dispersed over kilometres (p. 73).

- Some soil organisms can enter a dormant state and survive for several years while unfavourable environmental conditions persist (p. 48).

- Fungal diversity has been conservatively estimated at 1.5 million species (p. 49).

- Earthworms often form the major part of soil fauna biomass, representing up to 60% in some ecosystems (p. 62).

- Several soil organisms can help plants to fight against aboveground pests and herbivores (p. 108).

- Ninety per cent of the energy flow in the soil system is mediated by microbes (p. 46).

- The elimination of earthworm populations can reduce the water infiltration rate in soil by up to 93% (p. 100).

- Moles are very common, and can be found everywhere in Europe, except in Ireland (p. 67).

- Moles need to eat approximately 70% to 100% of their weight each day (p. 68).

- Moles can paralyse earthworms thanks to a toxin in their saliva. They then store some of their prey in special 'larders' for later consumption – up to 1,000 earthworms have been found in such larders (p. 68).

- The improper management of soil biodiversity worldwide has been estimated to cause a loss of 1 trillion dollars per year (p. 114).

- The use of pesticides causes a loss of more than 8 billion dollars per year (p. 110).

- Soils can help fight climate change (p. 99).

Contents

*All words in green are defined in the glossary.

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Acronym	Definition
AOB	Ammonia Oxidising Bacteria
BBSK	Biological Soil Classification Scheme
BIOASSESS	BIOdiversity ASSESSment tools project
BISQ	Biological Indicator System for Soil Quality
BSQ	Biological Soil Quality
CAP	Common Agricultural Policy
CBD	Convention on Biological Diversity
CC	Climate Change
CDC	Center for Disease Control and Prevention
CITES	Convention on International Trade in Endangered Species
COP	Conference of Parties
DNA	DeoxyriboNucleic Acid
DSQN	Dutch Soil Quality Network
EAP	Environment Action Programme
EC	European Commission
ECCP	European Climate Change Programme
EFSA	European Food Safety Authority
EMAN	Ecological Monitoring and Assessment Network
EMI	Eco-Morphological Index
ENVASSO	Environmental Assessment of Soil for Monitoring
ERA	Ecosystem Risk Assessment
ERC	Ecotoxicologically Relevant Concentration
EU	European Union
FAO	Food and Agriculture Organisation
FP	Framework Programme
GAEC	Good Agricultural and Environmental Conditions
GHG	GreenHouse Gases
GISQ	General Indicator of Soil Quality
GMO	Genetically Modified Organism
IBQS	Biotic Indicator of Soil Quality
ISO	International Organisation for Standardisation
MEA	Millennium Ecosystem Assessment
MS	Member States of the EU
NAPs	National Action Programmes
NOR	Normal Operating Range
ONF	French National Forest Office
PCB	PolyChlorinated Biphenyl
PCR	Polymerase Chain Reaction
QBS	Biological Quality of Soil
RENECOFOR	National network for the long term tracking of forest ecosystems (*Réseau National de suivi à long terme des ECOsystèmes FORestiers*)
RIVPACS	River Invertebrate Prediction and Classification System

Acronym	Definition
RMQS	Soil Quality Measurement Network
SACs	Special Areas of Conservation
SARS	Severe Acute Respiratory Syndrome
SBSTTA	Subsidiary Body on Scientific, Technical and Technological Advice
SOC	Soil Organic Carbon
SOILPACS	Soil Invertebrate Prediction and Classification Scheme
SOM	Soil Organic Matter
SPAs	Special Protection Areas
SPU	Service Providing Unit
TWINSPAN	Two-Way INdicator SPecies ANalysis
UBA	German Federal Environmental Agency

Anabolic reaction is a chemical reaction which involves building complex molecules from simpler molecules and using energy.

Anecic earthworms build permanent, vertical burrows that extend deep into the soil. This type of worm comes to the surface to feed on manure, leaf litter, and other organic matter. This class of earthworms, such as the night-crawlers, *Lumbricus terrestris* and *Aporrectodea longa*, have profound effects on organic matter decomposition and soil structure.

Autotroph organisms produce complex organic compounds from simple inorganic molecules using energy from light (by photosynthesis) or performing inorganic chemical reactions. In this latter case they are called chemotrophic organisms. Autotroph organisms, such as plants or algae, are primary producers in the food chain.

Biome is the biggest unit of ecosystem categorisation. It is a complex biotic community characterised by distinctive plant and animal species, and maintained under the climatic conditions of the region. For example, all forests share certain properties regarding nutrient cycling, disturbance, and biomass, which are different from the properties of grasslands.

Bioturbation is the displacement and mixing of soil particles. In soil ecosystems bio-turbation is mainly performed by earthworms and gastropods, through infilling of abandoned dwellings, burrowing, displacement, mix, ingestion and defecation of soil.

Catabolic reaction is a reaction that breaks macromolecules into constituent simpler sub-units.

Commensalism is a class of ecological relationships between two organisms where one benefits and the other is not significantly harmed or benefited.

Community is any combination of populations from different organisms found living together in a particular environment; essentially the biotic component of an ecosystem.

Cryptobiosis is an ametabolic state of life entered by an organism in response to adverse environmental conditions such as desiccation, freezing, and oxygen deficiency. In the cryptobiotic state, all metabolic procedures stop, preventing reproduction, development, and repair. An organism in a cryptobiotic state can essentially live indefinitely until environmental conditions return to being hospitable. When this occurs, the organism will return to its metabolic state of life as it was prior to the cryptobiosis.

Cyst is the resting or dormant stage of a microorganism, usually a bacterium or a protist, that helps the organism to survive unfavourable environmental conditions. It can be thought of as a state of suspended animation in which the metabolic processes of the cell are slowed down and the cell ceases all activities like feeding and locomotion.

Diapause is a physiological state of low metabolic activity with very specific triggering and releasing conditions. This state of low metabolism is neurologically or hormonally induced. Diapause occurs during determined stages of life-cycles, generally in response to environmental stimuli. Once diapause has begun, metabolic activity is suppressed even if favourable conditions for development occur. It can be defined as a predictive strategy of dormancy.

Dormancy is a period in an organism's life cycle when growth, development, and (in animals) physical activity is temporarily suspended. This minimises metabolic activity and therefore helps an organism to conserve energy. Dormancy tends to be closely associated with environmental conditions.

Ecosystem is a complex set of connections among the living resources, habitats, and residents of an area. It includes plants, trees, animals, fish, birds, micro-organisms, water, soil, and people. It is an ecological community which, together with its environment, functions as a unit.

Ecosystem process comprises the physical, chemical and biological events that connect organisms and their environment.

Ecosystem function is the collective intraspecific and interspecific interactions of the biota, and between organisms and the physical environment, giving rise to functions such as bioturbation or organic matter decomposition.

Ecosystem service is the benefit that is derived from ecosystems. This comprises provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational and cultural benefits; and supporting services such as nutrient cycling that maintain the conditions for life on Earth.

Endogeic earthworms forage below the soil surface in horizontal, branching burrows. They ingest large amounts of soil, showing a preference for soil that is rich in organic matter. Endogeics may have a major impact on the decomposition of dead plant roots, but are not important in the incorporation of surface litter.

Enzymes are molecules (mostly proteins) that catalyze chemical reactions within living cells.

Epigeic earthworms are those that live in the superficial soil layers and feed on undecomposed plant litter.

Eukaryote is an organism whose cells contain a nucleus enclosed within a nuclear membrane and complex structures called organelles. Most living organisms, including all animals, plants, fungi, and protists, are eukaryotes.

Eusocialty is a term used for the highest level of social organisation among organisms of the same species in a hierarchical classification. Eusocial organisms (mainly invertebrates) have certain features in common: reproductive division of labour, overlapping generations and cooperative care of young. The most common eusocial organisms are insects including ants, bees, wasps, and termites, all with reproductive queens and more or less sterile workers and/or soldiers.

Free radicals are molecules, atoms or ions having unpaired electrons and thus being extremely reactive.

Functional group is a group of species with comparable functional attributes.

Habitat is the area or the environment where an organism, an ecological community or a population normally lives or occurs, e.g. a marine habitat.

Heterotroph organisms use organic substrates to obtain its chemical energy for its life cycle. This contrasts with autotrophs such as plants, which are able to use sources of energy such as light directly, to produce organic substrates from inorganic carbon dioxide. Heterotrophs are known as consumers in food chains, and obtain organic carbon by eating other heterotrophs or autotrophs. All animals are heterotrophic, as well as fungi and many bacteria.

Humus refers to any stable organic matter in soil that will not be further decomposed.

Hyphae are long, branching filaments of a fungus. Hyphae are the main mode of vegetative growth in fungi and are collectively called a mycelium.

Infectivity is the feature of a pathogenic agent that exemplifies the capability of entering, surviving, and multiplying in a susceptible host, leading to a disease.

Invasive species are exotic species which become disproportionally abundant in their new environment.

Microarthropods are small invertebrates (< 2 mm) in the phylum Arthropoda. The most well known members of the microarthropod group are mites (Acari) and springtails (Collembola).

Mutualism is a biological interaction between two organisms, where each individual derives a fitness benefit (e.g. survival or food provisioning).

Mycelium is the vegetative part of a fungus, consisting of a mass of branching, thread-like hyphae.

Mycorrhiza is a symbiotic association between a fungus and plant roots. The fungus colonises the roots of the host plant, either intracellularly or extracellularly. This association provides the fungus with relatively constant and direct access to glucose and sucrose produced by the plant in photosynthesis. In return, the plant gains the use of the mycelium's very large surface area to absorb water and mineral nutrients from the soil, thus improving the mineral absorption capabilities of the plant roots. Since both involved organisms benefit from the interaction, it is defined as a mutualistic association.

Nematodes are roundworms (see section 2.1.2)

Parasitism is a type of symbiotic relationship between two different organisms where one organism, the parasite, takes some advantages from another one, the host.

Parthenogenesis is an asexual form of reproduction found in females where the growth and development of embryos occurs without fertilisation by a male.

Primary production is the production of organic compounds from atmospheric or aquatic carbon dioxide, principally through the process of photosynthesis, and less often through chemosynthesis.

Prokaryotes are organisms characterised by the absence of a nucleus separated from the rest of the cell by a nuclear membrane and by the absence of complex membranous organelles.

Protists are a diverse group of eukaryotic microorganisms, including amoeba, algae and molds.

Provisioning services are a class of ecosystem services providing goods such as food, water, construction material, etc.

Regulating services are a class of ecosystem services which provide the regulation of ecosystem processes, such as water flux, climate control, pest control, etc.

Resilience is the capacity of an ecosystem to stand negative impacts without falling into a qualitatively different state that is controlled by a different set of processes.

Rhizosphere is the zone around plant roots which is influenced by root secretion and by the root-associated soil microorganisms.

Rizhobium is the group of bacteria that forms symbiotic associations with leguminous plants and which is responsible for fixing atmospheric nitrogen into a form that can be used by plants.

Supporting services are a class of ecosystem services providing indispensable processes such as nutrient cycles and crop pollination.

Symbiosis refers to a close and long term interaction between two species of organisms in which both species obtain a substantial benefit.

Taxon is a group of (one or more) organisms, which a taxonomist adjudges to be a unit. Usually a taxon is given a name and a rank, although neither is a requirement, and both the taxon and exact criteria for inclusion are sometimes still subject to discussion.

Vascular plants (also known as tracheophytes or higher plants)**:** are those plants which have lignified tissues for conducting water, minerals, and photosynthetic products through the plant.

FIGURES

TABLES

BOXES

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1. INTRODUCTION

1.1.   CONTEXT AND OBJECTIVES

This report endeavours to fulfil a double commitment on behalf of the European Commission (EC), regarding soil and biodiversity protection. With 2010 being the International Year of Biodiversity, and the European Union (EU) seeking to play a pioneering role in halting biodiversity loss, growing attention has been paid over recent years to improve our assessment of biodiversity in the EU, and to evaluate the services that biodiversity provides to human societies. In parallel, the EC - increasingly aware that soil is a vital and non-renewable resource that is increasingly threatened but overlooked by policy - recently adopted a Thematic Strategy on the Protection of Soil[4]. The aim of this strategy is to provide guidelines for a holistic approach to soil protection at the EU-level.

With the realisation that greater biodiversity is present inside the soil than on it, and that this soil biodiversity is responsible for providing many of the ecosystem services on which human society relies, the protection of soil biodiversity stands as a key element in achieving the objectives of the Soil Thematic Strategy, while contributing to halting the loss of biodiversity as a whole. Today however, soil biodiversity is one of the most hidden and least well-known components of biodiversity, and its role remains largely unknown to the broad public and to decision-makers (Wolters 2001). Moreover, in the view of global biodiversity loss, the question arises as to what the current risks of soil biodiversity loss are, and how soil biodiversity can be restored, protected and conserved. Considering the specific nature of soil biodiversity as compared to that of aboveground biodiversity, solutions known for aboveground conservation and restoration practices may not always be simply transferable to soils.

Although much remains to be uncovered about soil organisms, soil ecologists have made tremendous progress over recent years, such that the roles and functions of soil organisms can be assessed. The objective of this report is thus to review the state of the knowledge of soil biodiversity, its functions, its contribution to ecosystem services, and its relevance for the sustainability of human society. In line with the definition of biodiversity given in the 1992 Rio de Janeiro Convention, soil biodiversity can be defined as the variation in soil life, from genes to communities, and the variation in soil habitats, from micro-aggregates to entire landscapes. In this report, soil encompasses both the mineral layers and the litter, and soil biodiversity is understood as the diversity of organisms that spend and can complete their entire life in the soil. Although many species are also part-time soil residents (insect larvae, beetles, mound-building insects, burrowing vertebrates), strict soil dwellers already represent a prodigious diversity of life. Moreover, they are the less known and less cared for component of global biodiversity, and as such are often overlooked.

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[4] COM(2006) 231, 22.9.2006 (www.ec.europa.eu/environment/soil/index_en.htm).

The purpose of this report is to provide the background and tools for policy-makers to take decisions that can help sustain soil biodiversity and functions. The report may also provide researchers with directions where their efforts need to be concentrated so as to fill gaps in knowledge. To this end, the first step is to describe soil biodiversity organisation and functions. The second step is to understand the importance of soil biodiversity to human society, by showing how these functions contribute to the provision of ecosystem services. This is followed by an analysis of the current and future threats to soil biodiversity (soil degradation processes, land management, climate change, biological invasions, pollution), so as to assess the risks faced by soil organisms and humans. Given this background, available tools for decision-makers are analysed, in terms of monitoring, management practices, or existing policies and regulations.

In order to make sense of the extreme diversity of soil biota, and to highlight the importance of soil biodiversity to human societies, it has been chosen to group soil organisms according to three all-encompassing ecosystem functions: transformation and decomposition, biological regulation, and soil engineering. Each of these functions can be performed by a characteristic assemblage of soil organisms, or functional group. The main benefit of this functional grouping is that it allows a better understanding of how activities vary over distinct spatio-temporal scales and how each functional group contributes to the provision of services.

1.2.   WHAT IS SOIL BIODIVERSITY?

Biodiversity is considered to comprise all biological variation from genes to species, up to communities, ecosystems and landscapes (MEA 2005). Soil biodiversity is the variation in soil life, from genes to communities, and the variation in soil habitats, from micro-aggregates to entire landscapes. As many species have overlapping functions, there is less functional biodiversity than taxonomic diversity.

The sheer diversity found in soils has contributed to make soil ecologists precursors in many ways. They approached soil biodiversity from a functional perspective much earlier than aboveground ecologists. However, difficulties remain, since compared to the aboveground world, soils are an extremely heterogeneous habitat, and considering the small size of many organisms, processes and interactions take place at scales that are unimaginably small from a human perspective.

1. 2. 1.   ABOVEGROUND VERSUS BELOWGROUND BIODIVERSITY

➔ SOIL BIODIVERSITY IS HUGE

Soils are the habitat and resource for a large part of global biodiversity: over one-fourth of all living species on earth are strict soil or litter dwellers (Decaens, Jimenez et al. 2006). They are home to a prodigious diversity of life, which can often be several orders of magnitude greater than that present aboveground or in the canopy of rainforests (Heywood 1995; Decaens, Jimenez et al. 2006). One square metre of land surface may contain some ten thousand species of soil organisms, whereas aboveground biodiversity is some orders of magnitude lower (Schaefer and Schauermann 1990; Wardle, Bardgett et al. 2004).

Microorganisms such as algae, bacteria and fungi form the majority of the soil biomass (Figure 1-1). One teaspoon of soil contains several thousands of microbial species,

several hundred metres of fungal hyphae, and more than one million individuals (Schaefer and Schauermann 1990; Wardle, Bardgett et al. 2004). Indeed, as can be seen in Table 1-1, microbial species are still largely unknown. This is one of the major differences between aboveground and belowground biodiversity.

Table 1-1: Estimated global number of aboveground and belowground organisms (adapted from De Deyn and Van der Putten 2005 and Wall et al. 2001)

Group	Organisms	Known	% Known
Plants	Vascular plants	270000	84%
Macro-fauna	Earthworms	3500	50%
Meso-fauna	Mites	45231	4%
	Springtails	7617	15%
Micro-fauna	Protozoa	1500	7.5%
	Nematodes	25000	1.3%
Microorganisms	Bacteria	10000	1%
	Fungi	72000	1%
Marine species	All marine organisms	230000	30%[5]

Soils also comprise a large variety of invertebrates, such as earthworms, mites, spiders, beetles, ants and termites (Figure 1-1), as well as litter-inhabiting arthropods such as millipedes, centipedes and wood lice. But the best-known soil inhabitants may well be the small mammals, such as moles and voles which can show fantastic adaptations to living in a dark belowground world (Figure 1-1).
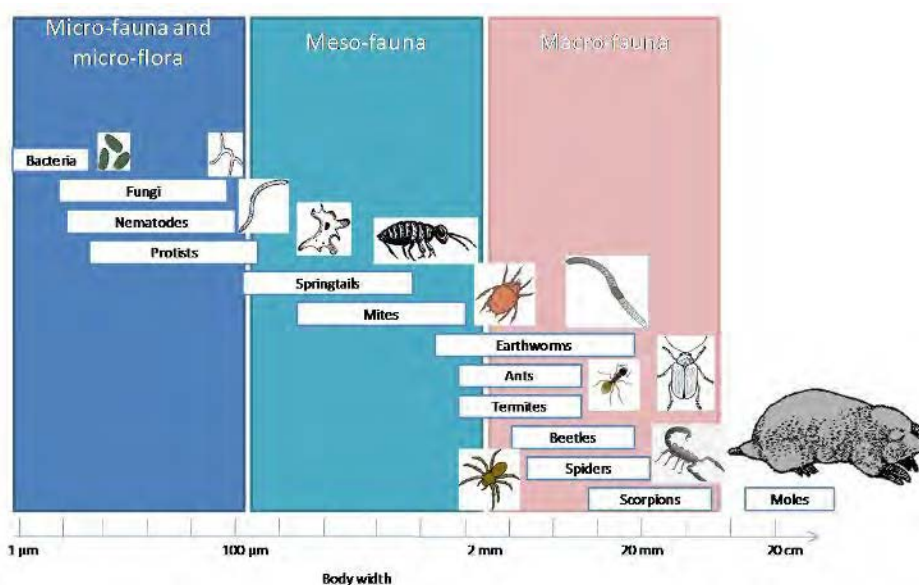
Figure 1-1: Main soil inhabitants, by size

→ SOIL ORGANISMS ARE PROFOUNDLY INVOLVED IN ALL SUPPORTING ECOSYSTEM SERVICES

When soil organisms eat, grow, and move, they perform essential services for ecosystems, as well as for human society (Figure 1-2). Among the key ecosystem services mediated by soil biota are the transfer, storage, and provision of clean ground water, the storage of carbon and the prevention of trace gas emissions crucial for climate control, as well as the provision of nutrients and pest and pathogen regulation, supporting plant growth and aboveground biodiversity. In fact, soil biota are involved

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[5] Source : Census of marine life

in the provision of all the main supporting and regulating services, and the current rate of soil destruction, sealing and other threats due to the misuse of soil by humans, is threatening the sustainability of human life on earth. Soil is also a treasure chamber for biodiversity, which can generate new opportunities for developing novel medicines. Therefore, the responsible management of soil and its biodiversity is pivotal to sustaining human society.

SUPPORTING SERVICES
- Decomposition
- Nutrient cycling
- Soil formation
- Primary production
- Water cycling

PROVISIONING SERVICES
- Food
- Freshwater
- Fuel
- Wood, fibre
- Genetic resources
- Medicines, pharmaceuticals

REGULATING SERVICES
- Climate regulation
- Water regulation
- Disease regulation
- Pest regulation
- Water purification
- Erosion regulation
- Air quality regulation

CULTURAL SERVICES
- Aesthetic
- Spiritual
- Educational
- Recreational

Figure 1-2: Contribution of soil biodiversity to the provision of ecosystem services (highlighted services)(adapted from (MEA 2005)

→ SOIL BIODIVERSITY DRIVES MANY ABOVEGROUND PROCESSES

Most of the phenomena that are observed in the visible, aboveground world are steered directly or indirectly by species, interactions, or processes in the soil (Wardle 2002; Bardgett, Bowman et al. 2005). With the exception of fish, all the food that we eat, the air that we breathe, clothes that we wear, and construction materials that we use, are directly or indirectly linked to soil. This is why soil biodiversity is so pivotal for life on earth. Soil biota can regulate the structure and functioning of aboveground individuals and communities directly, by stimulating or inhibiting certain plant species more than others. Alternatively, soil organisms can regulate aboveground communities indirectly by altering the dynamics of nutrients available to plants. These indirect effects tend to involve less specific interactions and occur over longer durations than the direct regulations (Van Der Putten 2003, Wardle et al. 2004).

→ SOIL AS A HETEROGENEOUS HABITAT

Soil is an extremely heterogeneous habitat, which is not uniformly occupied by soil organisms. Soil microorganisms actually only represent 0.1% of soil by mass, and occupy less than 5% of the total soil volume (Ingham, Trofymow et al. 1985). Soil consists of a mosaic of inorganic minerals resulting from rock weathering, and organic material that is partly decomposed product of plants and other organisms (Box 1).

Soil microorganisms live within the pores left between soil particles, free or attached to surfaces, such as in water films surrounding soil particles (Stotzky 1997). The pore space can be of various shapes and sizes, depending on the texture and structure of the soil. Texture characterises the relative importance of clay (<5 μm), silt (5-50 μm) and sand particles (>50 μm). The smaller the particles, the more space they leave between them that can be filled by water and/or soil organisms. Indeed, a high density of small pores can result in less water availability for plants and small animals due to the intrinsic physical properties of water. For instance, clay soils have many small particles which make them more porous, whereas sandy soils have coarser particles. Accordingly, the surface area of pore space can exceed 24,000 m² in 1 g of clay soil, and this area decreases as the silt and sand contents increase (Gardi 2009). Soil texture also largely determines other soil characteristics, such as pH and organic matter content. Given the poor water retention capacity of sandy soils, nutrients and lime will be easily washed out, making these soils more acidic. Moreover, clay minerals can form aggregates with the humic compounds in the soil, thereby protecting organic material and affecting its availability in the soil. Soil organisms also directly modify soil architecture, creating further habitats within the pores, by building networks of solid structures.

> **Box 1: Soil Organic Matter and biological activity**
>
> Soil organic matter (SOM) is any component that contains carbon compounds from living organisms. Typically, the largest component of soil organic matter (up to 85%) is litter, the dead or decaying material mainly from plants. Living roots can make up another 10% of SOM, while soil organisms make up the remainder.
>
> Plant residues contain 60-90% moisture, while dry-matter consists mainly of carbon, oxygen, hydrogen, and small amounts of sulphur, nitrogen (N) and phosphorus (P). Every year, soil organisms process 25000 kg of organic matter per soccer field. These nutrients are very important for soil fertility. Approximately half of SOM can be decomposed to its elemental form (the active SOM), while the remaining fraction, also known as humus, is more resistant to decomposition and accumulates in soil (the inactive SOM). SOM is a critical component of the soil habitat: by providing resources in the form of nutrients available to plants, it often constitutes hotspots of soil activity and is fundamental in maintaining fertile and productive soils (Tiessen, Cuevas et al. 1994; Craswell and Lefroy 2001). SOM is also an important 'building block' for the soil structure, contributing to soil aeration, and enabling soils to absorb water and retain nutrients. Soil organisms can also use SOM to bind soil particles together in aggregates, thereby modifying soil structure and creating new habitats. Moreover, given that soil comprises the largest pool of organic terrestrial carbon, understanding SOM dynamics is also pertinent to climate change concerns and greenhouse gas mitigation efforts (Cole 1996). SOM can serve as a buffer against rapid changes in soil pH, and the CO_2 storage as soil organic matter contributes to climate control.

The pore space can be either air-filled or water-filled, which limits the movements of soil organisms, since some may be strictly terrestrial and others strictly aquatic. The portion of pores that is filled with water or with air depends on the soil water content, with small pores being filled with water for longer periods than large pores.

The overall architecture of the pore network determines the type and abundance of soil organisms that can live there. Given the scale of soil organisms (μm to cm) and total soil porosity (30-60% in the upper layers of most soils), there is actually a huge amount of habitable space. Each pore can be seen as an island where life is possible, separated from other suitable habitats by a hostile mineral and rock matrix. The labyrinthine nature of the pore networks defines where organisms can move and the size of the pores where prey and organic matter can afford physical protection.

Soil heterogeneity changes with the depth. The topsoil, or outermost 5-20 cm of soil, typically concentrates the majority of plant roots, most nutrients and organic matter, and therefore most biological activity (Box 1). In contrast, very little biological activity is known in the more densely packed subsoil below, because of the limited oxygen availability and less organic substance etc.

→ **SOIL BIODIVERSITY IS DIFFICULT TO CHARACTERISE**

To unravel the nature of belowground diversity has proven a challenging task. However, in the last decade, significant progress has been made, and new techniques have allowed exploring soil in a way that was not previously possible. For instance, communities of archeal bacteria are only starting to be explored but may be the main actors in the decomposition process (Leininger 2006). However, most soil biodiversity is not visible to the naked eye, and many soil species are still unknown (Table 1-1). Potentially as much as 99% of global soil bacterial and nematode species are still unknown (Wall, Virginia et al. 2000). Notably though, soil biodiversity is better known in Europe than those global numbers suggest. But even when they are known, the basic biology, ecology and distribution patterns of soil organisms often remain unknown (Fragoso, Kanyonyo ka Kajondo et al. 1999). The reasons for this are partly methodological, and partly intrinsic to the nature of soil biodiversity.

Distinguishing between different species of microorganisms can be challenging, despite the progresses made by using molecular techniques (e.g. DNA - DeoxyRibonucleic Acid-microarrays), which have allowed determining unculturable microorganisms. Today, less than 1% of microorganisms can be cultivated and/or characterised (Torsvik and Ovreas 2002). Although the morphological identification of species under the microscope has been replaced at least in part by molecular methods involving DNA or phospholipids analyses, most methods actually characterise entire communities rather than single species. Moreover, even with molecular methods, rare species or groups having lower DNA concentrations may not be detected (Borneman and Hartin 2000). For these reasons, progresses are still needed to have a precise knowledge of soil community microbial compositions. The characterisation of soil metagenome is currently underway and may yield important information on microbial diversity. However, one problem can arise with the extraction of DNA. It is suggested that the indirect method can give larger fragments than the direct method, and for this reason is suitable for the characterisation of soil metagenome. However, the extracted DNA may not be representative of the indigenous soil DNA (Bakken 2006).

The species concept is more complicated in soil than in aboveground ecosystems. Indeed, the rate of evolution of microorganisms is much faster than that of most aboveground organisms, and species identity is thus much harder to determine.

Aboveground, most organisms depend on sexual reproduction to create new genetic information and evolve. In contrast, microorganisms are present in the soil in much larger numbers compared to aboveground, and they can reproduce asexually (Box 2) at much faster rates, as short as 20 minutes. This enhances their potential for accumulating mutations and thus for adaptation compared to slower sexually reproducing species. Microorganisms are also able to gain new genetic information in their DNA without sexual reproduction, by horizontal gene transfer (see Box 2). This potential is actually increased, for example in soils that are rich in clay or humic molecules, which can protect nucleic acids from degradation, thus enabling them to be taken up by bacterial cells (Nannipieri 2002). This begs the question as to whether species estimates such as those presented in Table 1-1 are at all meaningful for microorganisms.

Box 2: Vertical and horizontal gene transfer

Vertical gene transfer: In the majority of living organisms, gene transfer occurs vertically from parental organisms to the offspring. This transfer can occur through sexual reproduction, if the genetic information of the two parents is recombined into the offspring, or through asexual reproduction, where the parental genetic information is simply replicated into the offspring. In both cases, errors in copy (or mutations) can occur, which offer a basis for adaptation, whereby mutations that favour the survival or reproduction of the offspring will be selected.

Horizontal gene transfer: In some cases an alternative path, the so called horizontal gene transfer, can take place. In this case, an organism incorporates genetic material (DNA) from another organism without being its offspring. All bacteria can perform horizontal gene transfer.

There are three main mechanisms through which horizontal gene transfer can occur:

- **Transformation:** a living bacterial cell uptakes and integrate foreign genetic material from surrounding dead bacteria cells

- **Transduction:** a virus transfers DNA between two bacteria. The new DNA is integrated in the DNA of the receiving cell.

- **Conjugation:** a living bacterial cell makes a copy of a portion of its DNA and transfers this genetic material to other unrelated bacteria through cell-to-cell contact. This additional genetic material may confer survival advantages to its host (e.g. providing resistance to antibiotics).

The transformation process can be important in soil since extracellular DNA adsorbed by soil particles and protected against degradation can be used for transforming competent bacterial cells (Pietramellara 2009). This means that DNA from a previous microorganism or from a spatially distant microorganism can be used by competent bacterial cells.

Mechanisms of horizontal gene transfer in bacteria
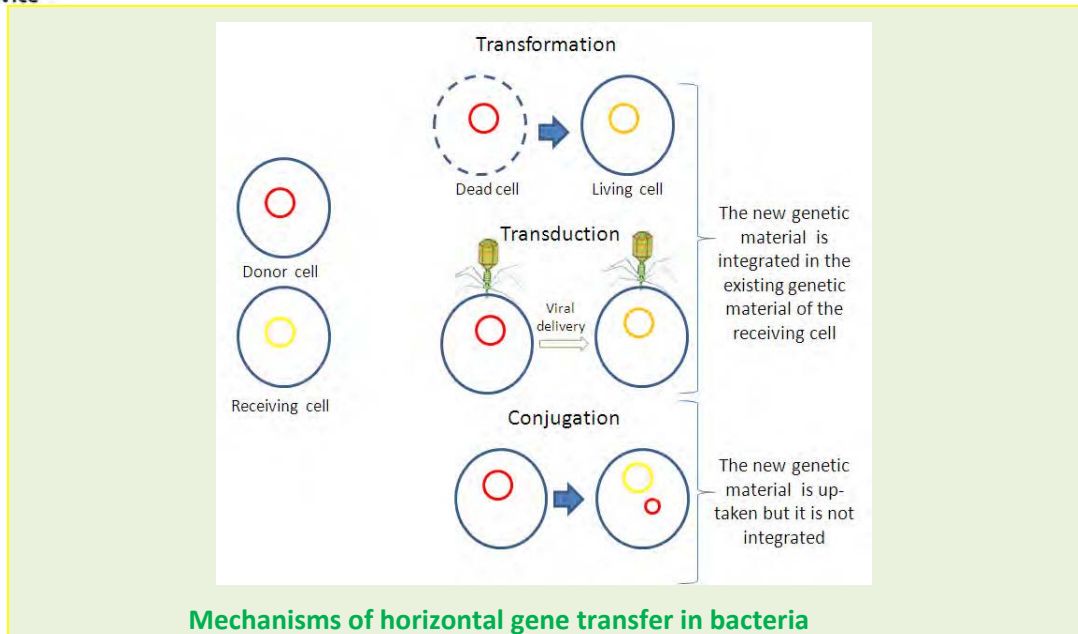
→ **SOIL COMMUNITIES ARE EXTREMELY DYNAMIC IN SPACE AND TIME**

Spatial structure

Soil organisms are not uniformly distributed through the soil, but species are found where they can find a suitable habitat: most species are concentrated around roots and in the litter-rich top layer. These habitats are shaped by processes acting at nested spatial scales. At the scale of entire landscapes, climate and soil texture set an envelope of possible habitat conditions. At an intermediate ecosystem level, variable factors influenced by land use and management, such as soil pH and organic matter content, determine the prevailing conditions of the habitat. Locally, litter quality and nutrients interact with these habitat factors to determine the specific local soil condition (Figure 1-3).

Population processes, such as dispersal, reproduction and competition, or small scale succession processes are also influenced by soil heterogeneity and together they are major determinants of the spatial distribution of soil organisms (Ettema and Wardle 2002). Biotic activity in soil often seems concentrated. In combination with soil heterogeneity, the limited dispersal ability of soil biota means that soil organisms have a limited active mobility in the soil matrix, usually not more than micrometres to centimetres. Reproductive strategies may also lead to aggregations of individuals, for instance for egg-laying species through clumped egg distributions, or for other species because of their small size and limited dispersal ability (e.g. bacterial colonies). However, soil organisms can sometimes become passively dispersed from few metres to thousands of kilometres by wind, water, or other vectors.
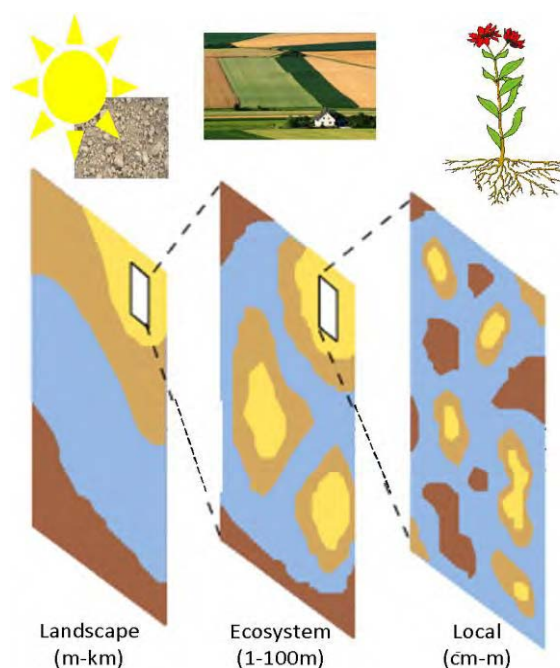
Figure 1-3: Spatial structure of soil communities over three nested spatial scales, adapted from (Ettema and Wardle 2002)

Temporal structure

The lifetimes of soil organisms can vary from a few minutes to hundreds of years (Figure 1-4). This is because some soil organisms are capable of entering a dormancy, which can last up to several years, during which they are literally 'asleep'. This confers them the enviable ability to travel in time, and to survive disturbances, absence of suitable hosts/habitats, and other adverse conditions.

The activity of soil organisms depends on whether a species finds suitable resources available. In general, the activity of soil organisms is regulated over three main temporal scales. As for aboveground biodiversity, over large to intermediate time scales the successional dynamics of entire ecosystems (tens to thousands of years) and the seasonal changes in vegetation productivity (months), influence the type of resources available to soil organisms, and therefore which species are active and which are not. This reflects the tight coupling between plants, microbes and other soil organisms. This tight coupling between plants and soil organisms is also revealed by pulses of nutrient release, driving the local activity of soil communities.

1.3.   ISSUES FOR THE CONSERVATION OF SOIL BIODIVERSITY

Global biodiversity is declining at unprecedented rates, and conservation efforts have become intensified in recent years to prevent, or counteract this loss. Currently however, most conservation efforts and knowledge are focused on aboveground diversity. Soil animals represent only 1% of the IUCN (International Union for Conservation of Nature) red-listed species, and only eight soil species have CITES (Convention on International Trade in Endangered Species) protection worldwide (three scorpions, four spiders, and one beetle), despite the fact that soil biota represents almost one fourth of all species on earth (Decaens, Jimenez et al. 2006).
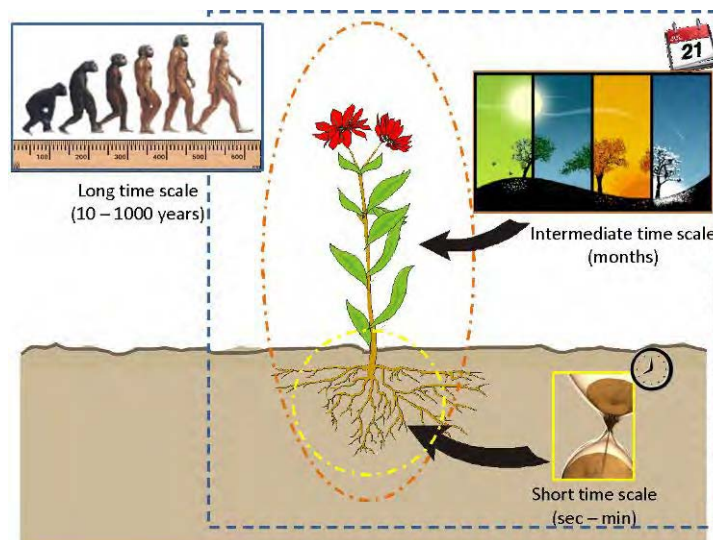
Figure 1-4: Temporal structure of soil communities over three nested time scales

→ CONSERVATION STATUS OF SOIL BIODIVERSITY

There is little data on the extinction of soil organisms as opposed to aboveground organisms. However, in a recent EU-wide sampling of macro-fauna (earthworms), over half of the species identified were rare, and found only once or twice across the different sites (Watt 2004). The disappearance of large endemic earthworm species has also been reported in the South of France (Abdul Rida and Bouché 1995), and many more earthworm extinctions have been reported in the tropics, such as the disappearance of the Acanthodriline earthworms in South Africa (Ljungström 1972) or of the giant 2-metre-long earthworm *Rhinodrilus fafner*. Overall, the results from some of the few attempts at monitoring the status of soil populations point to a decline in populations as the intensification of soil use increases (Ruiz Camacho 2004). Rarity may also be a consequence of the growing homogenisation of European landscapes due to urbanisation, similar agricultural practices, economic conditions, technical means, and choices in environmental planning. The effects of such homogenisation have been observed for aboveground biodiversity. For instance, it has been observed that urbanisation might cause a homogenisation of bird species present in EU countries, by decreasing the abundance of ground nesting bird species and bird species preferring bush-shrub habitats. Indeed no specific work has been carried out on soil biodiversity homogenisation. Soil species with broader habitat tolerances may be selected at the expense of species with specific habitat requirements that are unable to adapt to change and remain isolated in natural habitat fragments.

Although many species living in soil are in danger, their extinctions are probably completely unnoticed and the databases and tools to monitor this do not yet exist.

→ CURRENT RISKS TO SOIL BIODIVERSITY

Today, disturbance regimes are changing drastically under the combined effects of climate change, biological invasions, and direct human modifications of the environment. However, it remains very difficult to assess and predict how soil communities will respond to these disturbances.

Contrary to common belief, disturbances do not necessarily lead to long-term biodiversity loss. In many cases, moderate (intermediate) disturbances can actually be a positive force, enabling species co-existence, and thus increased biodiversity (Box 3).

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Box 3: Impact of disturbances on soil biodiversity

Environmental variability is an integral part of the dynamics of ecosystems, and some disturbances are inevitable. For instance, seasonal variations are within the normal range of disturbance for many organisms. However, climate change may intensify these seasonal disturbances, stretching the limits more towards those of extreme events, such as for example the severe summer droughts to which large parts of Europe has become exposed more frequently during the past decade. Such **unpredictable natural or anthropogenically-induced disturbances** (e.g. droughts, storms, fires, habitat fragmentation, the use of pesticides, fertilisers or tillage) alter the habitat of organisms and the functioning of the ecosystem, especially when these stresses build up simultaneously (Griffiths, Ritz et al. 2000).

Disturbances can have opposite impacts on ecological communities: on one hand, they are often recognised as the main drivers of biodiversity loss, while on the other hand, they are increasingly acknowledged to be one of the mechanisms promoting the co-existence of species. This apparent contradiction is solved by the **Intermediate Disturbance Hypothesis**, arguing that biodiversity is highest when disturbance is intermediate. The main idea is that with low disturbance, competitive exclusion by the dominant species arises, whereas with high disturbance, only species tolerant to the stress can persist.

One aim of conservation is to maximise the stability of ecosystems in response to disturbances. This stability can be seen as the **resistance** of the ecosystem to change, whereby ecosystems are able to continue to function without change when stressed or disturbed. Another component of stability is the **resilience** of an ecosystem to change, that is, its ability to bounce back and recover after a disturbance. Resilience thus can explain how long a system will take to recover after a disturbance. Communities with high resilience may return almost immediately to their original state, whereas communities with low resilience may take years to return their original state.

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This is because a disturbance, while it may lead to the disappearance of some species, opens up niches or resources for other organisms to use. Moreover, an identical disturbance event can lead to very different outcomes in different soil communities, as species and communities exhibit distinct resistance and resilience to stress (Box 3). Thus the same disturbance event can have very little effect on some systems (high resistance and high resilience), while it may dramatically affect others although they may be able to recover very fast (low resistance and high resilience). Finally, the influence of a disturbance on a community depends strongly on its frequency, intensity, and on whether it is interacting with other disturbances (e.g. land-use change involves physical disturbances or the use of fertilisers and pesticides). Accordingly, predicting the impacts of disturbances for soil ecosystem functioning and services is complicated. Soil food webs are very complex, and many functions in soil are carried out by more than one species, in what is called functional redundancy. Given this functional redundancy, it could be thought that species may become extinct without any repercussions on the provision of soil services. But in fact, due to the highly integrated nature of soil food webs, any intervention that disturbs one function will inevitably affect the dynamics of others. Today, several lines of evidence point to the fact that ensuring high soil biodiversity has an insurance effect (Box 4).

Box 4: Functional redundancy: myth or reality?

Although there are many reasons to protect biodiversity for its intrinsic value, conservation efforts are increasingly justifying biodiversity conservation for the functions, or services, it provides. In this case, a major question is whether all species are important for soil ecosystem functioning.

To date, no consistent relationship between soil species diversity and soil functions has been found (Bardgett 2002; Bardgett 2005), implying that more species do not necessarily provide more services. This is because several species can perform the same function. Thus, according to the 'redundant species' hypothesis, only a minimum number of species is necessary for soil ecosystems to function (Naeem, Thompson et al. 1995) and the loss of a functionally redundant species would have little impact on the quantity or quality of the service provided (Naeem, Thompson et al. 1995; Hunt and Wall. 2002).

Other theories pertain that the fact that many soil species may appear functionally 'redundant' is rather related to our lack of understanding of soil systems (Wolters 2001). Indeed:

- **Not all functions exhibit redundancy,** some species may be the only ones able to perform their function. For instance, many species are involved in the decomposition of organic matter, and the loss of one of these species may not necessarily have a direct negative effect on the functioning of the ecosystem. In contrast, the breakdown of some toxic chemicals may only be performed by a single species of bacteria, in which case, the loss of this species means a complete loss of the function in the ecosystem. Nitrification (that is the transformation of nitrite into nitrate) is also performed by very few microorganisms.

- **Redundancy is highly context-dependent,** for instance, while two species of bacteria may appear to perform the same decomposition function, they may not perform it under the same range of conditions, or at all times. For example, one species could become inactive under heat stress whereas the other could still be functioning perfectly, or may even show increased activity.

- **Soil organisms can contribute to more than one function,** for example, many species of fungi and bacteria that are responsible for most of the transformation and decomposition processes also contribute, albeit to a lesser extent, to soil structure modification. Moreover, because of the integrated nature of soil food webs, some 'redundant' species may gain functional significance by regulating the activity of a functionally important species. Thus, species that are redundant for one function may play a key functional role elsewhere in the food web.

Therefore, according to the 'insurance hypothesis', it seems that there are many ways in which current, apparently redundant, diversity may have a function under future, unpredictable conditions. Given that we still know little about the role of single species, and according to the precautionary principle, it may thus be important to preserve this biodiversity for insurance purposes and not put our future at stake by reducing the insurance value of the biodiversity capital. This is also consistent with the principle of 'no net loss of biodiversity' (whether in the quantity or quality of the functions provided), advocated by the Convention on Biological Diversity.

When including a wider range of processes that take place into soil, soil biodiversity may best be considered by focusing on functional groups, which are fewer in number than the feeding groups of soil organisms that are distinguished in soil food web models (Box 5). These functional groups play a major role in ecosystem functioning, and therefore in the provision of ecosystem services. They may be defined as a set of species that have similar effects on a specific ecosystem-level biogeochemical or biophysical process.

Since classifications can be based on different criteria, and even between functional approaches various levels of aggregations are being used (Lavelle 1997; Swift, Izac et al. 2004; Barrios 2007; Kibblewhite 2008), in this report, it has been decided to group soil organisms according to three all-encompassing ecosystem functions: transformation and decomposition, biological regulation, and soil engineering. Each of these functions can be performed by a specific assemblage of soil organisms, or functional group:

- **Chemical engineers** (transformers and decomposers): organisms responsible for carbon transformation through the decomposition of plant residues and other organic matter, and for the transformation of nutrients (e.g. nitrogen, phosphorus, sulphur)
- **Biological regulators**: organisms responsible for the regulation of populations of other soil organisms, through grazing, predation or parasitism, including soil-borne pests and diseases.
- **Ecosystem engineers**: organisms responsible for maintaining the structure of soil by the formation of pore networks and bio-structures, and aggregation, or particle transport.

This classification may seem an oversimplification; however it has proven to be a good communication and analytical tool. The main benefit of this grouping is that the activities of the different functional groups can actually be mapped over a series of nested spatio-temporal scales ranging from small scale/short-term to large scale/long-term processes (Figure 2-2 and Box 5). This is because most soil organisms are influenced by the environment, according to their size and dispersal capacity. Thus chemical engineers are essentially composed of microorganisms, influenced mainly by local scale factors, although they are also susceptible to rare long distance/time travel events (passive dispersal, dormancy). Biological regulators tend to be largely composed of meso-fauna, while ecosystem engineers tend to be mostly macro-fauna, both of which are thus influenced by local as well as larger scale spatio-temporal processes (landscape scale and years). Thus this functional approach is a useful way to look at functions and provides a clear framework for management options (e.g. choose among direct action on the functional group affected or indirect action at higher spatio-temporal scales than that of the functional group affected).

It is important to highlight that the classification into functional groups is indicative of the most characteristic role of an organism, but is not rigid. For example, some biological regulators or chemical engineers (e.g. through the secretion of sticky proteins) can also act as ecosystem engineers (Figure 2-1). Similarly, many plant pests, such as herbivorous insects and nematodes are controlled at least in part by microbial

enemies. And while bacteria are chemical engineers given that their digestive capacities are greatly developed, they can also exert some limited disease control and some ecosystem engineering, at their scale of space (Young and Crawford 2004). On the other hand, earthworms that are clearly identified as ecosystem engineers, have some limited ability to digest organic matter with proper enzymes (Lattaud, Mora et al. 1999).
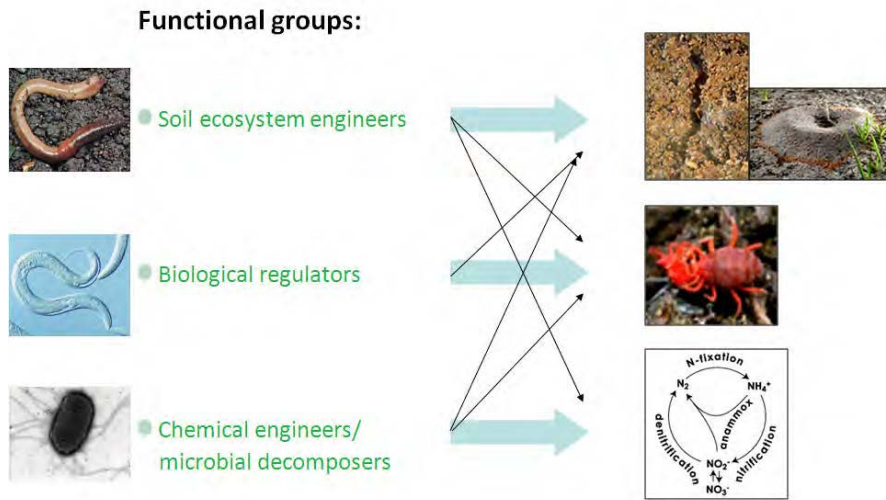
Figure 2-1: Possible cross among functional groups
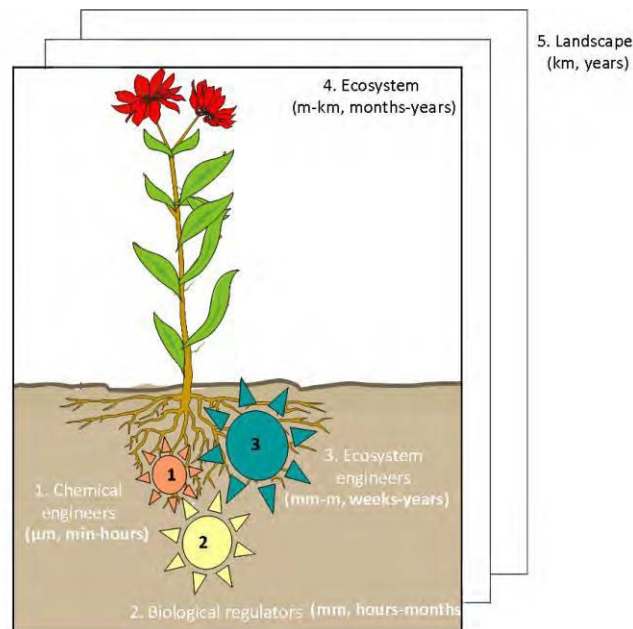
Figure 2-2: Functional organisation of soil communities over five nested spatio-temporal scales of action. The size of the wheels represents the spatio-temporal scale.

In this section, the description, biology, and functions of the main organisms in each functional group are briefly presented according to their main tasks in the soil (e.g. soil

formation) without taking into consideration other potential functions not related to soil ecosystems (e.g. pathogens for humans). Both the biotic and the abiotic factors influencing their ecology are also discussed. It is also important to clarify that, for the sake of simplicity, only the main types of soil organisms of each functional group have been described in this section. Organisms that are less clearly related to the highlighted functions (e.g. archea and viruses for chemical engineers, or millipedes, centipedes, beetles, caterpillars, enchyatreids, scorpions etc. for the other functional groups) are not explained in detail and have been briefly mentioned where relevant.

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Box 5: Food web approach

Historically, the study of soil biodiversity started with a mapping of the soil food webs, perhaps because the most fundamental integrating feature of soil communities is that of the feeding relationships between organisms. The figure below shows how the soil food web details the chain of energy transfer in the soil, which is based on grouping organisms in feeding guilds, according to their trophic role and food preferences (Hunt and Moore 1988, De Ruiter et al. 1995). In a simplistic fashion, the soil food web can be seen as fuelled by plants and photosynthetic bacteria that fix the carbon from the atmosphere through photosynthesis. Other soil organisms then obtain their energy by decomposing the plant residues and organic compounds found at the bottom of the food web, or by consuming other organisms. Throughout this process, nutrients are converted from organic to inorganic form and made available to plants and other soil organisms.
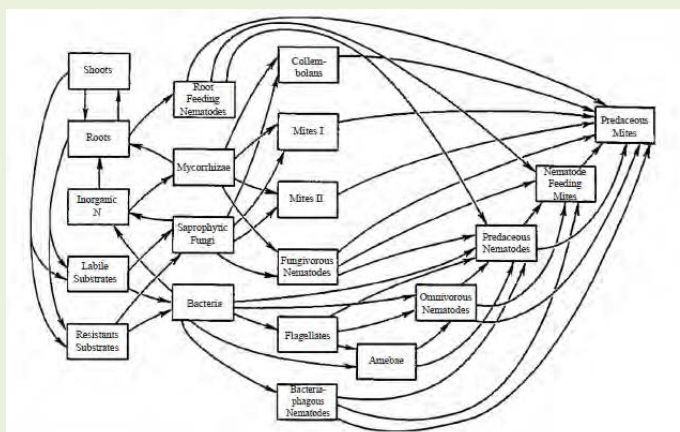
Example of a soil food web (Hunt, Coleman et al. 1987)

While the soil food web approach has been useful for understanding nutrient cycling and energy flows in soil communities, it has a limited capacity to explain other ecosystem processes. Indeed, by focusing exclusively on feeding, it overlooks other important processes not based on feeding relationships, such as soil structure development, parasitism and pathogenesis. Moreover, trophic groupings subsume a significant variation in functional behaviour, which is not made explicit in the food webs. Furthermore, the structure of the food web relies on biomass and species composition, whereas activity provides a better understanding of soil biological function. However, considering the questions addressed, the food web approach has provided a valuable contribution to place the feeding guilds and their roles in the soil in a structured and population-dynamical perspective, as well as a good entrance into functional soil biodiversity.

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2.1.   FUNCTIONAL GROUPS

2. 1. 1.   CHEMICAL ENGINEERS: MICROBIAL DECOMPOSITION AT THE BASIS OF THE FOOD WEB

Chemical engineers are responsible for the chemical processes at the first level of the food web and encompass all the organisms that decompose organic matter through catabolic and anabolic reactions. Microorganisms, or the smallest soil organisms, such as bacteria and fungi, are by far the most important contributor to this group, since over 90% of the energy flow in the soil system is mediated by microbes[6] (Coleman and Crossley 1996; Nannipieri and Badalucco 2003). Also viruses are common in soil. This category of microorganisms, which represent a large and highly heterogeneous group, can infect all types of living cells, from bacteria to large animals.

→ BACTERIA

What are they?

Bacteria are unicellular organisms which display a wide diversity of shapes and sizes. While they are usually smaller than 2 µm, they can range from 0.5 to 5 µm, be either spherical or rod-shaped, and occur in isolation or in various types of aggregations (Figure 2-3).
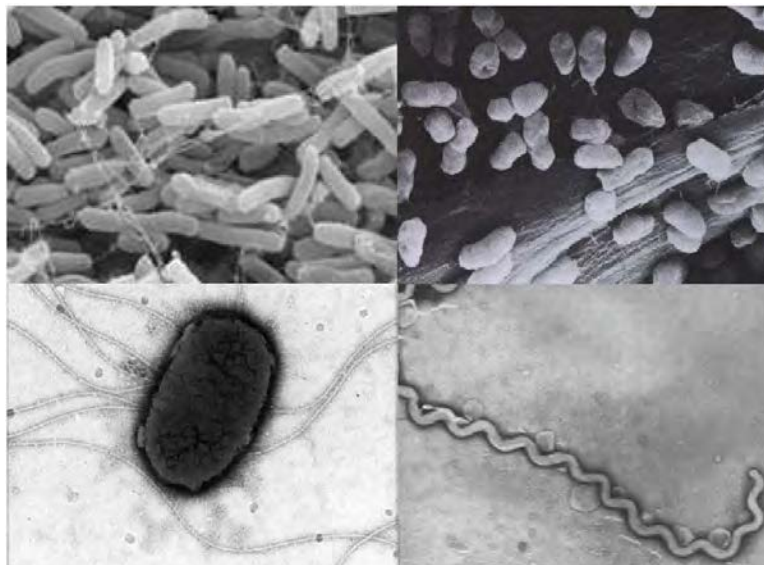
Figure 2-3: Examples of soil bacteria (body size: 0.5-5 µm)[7]

This extensive array of morphologies reveals a prodigious diversity. Bacteria are probably the most species rich and the most abundant array of organisms on earth (Torsvik and Ovreas 2002). It is estimated that 4 to 6 X 10^{30} of bacteria may live on the earth, with the large majority (about 92%) living in the soil and its subsurface (Whitman, Coleman et al. 1998).

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[6] Some data supporting this assumption were already presented in the International Biological Programme in the 70s: www7.nationalacademies.org/archives/International_Biological_Program.html; last retrieval 6/09/09

[7] Picture in K. Ritz presentation COP9 Soil biodiversity event in Bonn, May 22nd 2008

There are typically a billion bacterial cells and about 10,000 different bacterial genomes in one gramme of soil (Torsvik, Ovreas et al. 2002). Bacterial biomass is also impressive and can amount to 1-2 t/ha – which is equivalent to the weight of one cow – in a temperate grassland soil (Killham 1994), that is to say 3 to 5% of total soil organic matter content. Some bacteria (Actinobacteria) form branching filaments resembling fungal mycelium. A few of them are pathogens while others are common in soil where they decompose organic matter. Actinobacteria form a wide range of antibiotics and are able to degrade many toxic pollutants. Another type of soil bacteria, called cyanobacteria, are autotrophic organisms and use photosynthesis to produce carbohydrates. The typical smell of freshly moistened soil or compost is due to a protein called geosmin produced by these organisms.

Where do they live?

Bacteria are aquatic organisms that live in the water-filled pore spaces within and between soil aggregates.

Most bacteria are unable to move and attach to the surface of mineral or organic particles, forming dense mats of cells called bio-films (Donlan 2002). These aggregations of cells contain multiple species of bacteria and can display complex arrangements or secondary structures such as micro-colonies and networks of channels. Since they cannot move, their dispersal is dependent on water movement, root growth or the activity of soil and other organisms (Lavelle and Spain 2001).

Not all bacteria are fixed to structures, some types can move actively by using a flagella, bacterial gliding, twitching motility or changes of buoyancy (Bardy, Ng et al. 2003). Indeed, movements are of the order of microns and do not provide enough mobility to shift from a habitat to another.

Still, movements are highly limited and over 90% bacteria in soil are inactive because they have not been able to move towards an organic substrate to use (Lavelle 2002)(Box 6).

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Box 6: The Sleeping Beauty paradox

Microorganisms are the main decomposers, responsible for over 90% of the mineralisation occurring in soils (Lavelle & Spain 2001) and able to decompose any kind of natural substrate. In optimal laboratory conditions, individuals can multiply extremely fast, tremendously increasing their biomass in short periods of time (in the order of days). However, in nature, the turnover time of microbial biomass generally varies between 6 and 18 months, that is 1,000 to 10,000 times slower than under laboratory conditions. This indicates that in nature, micro-organisms are inactive most of the time. This inactivity may be due to starvation, resulting from their inability to move towards new substrates once their immediate surroundings are exhausted. The apparent contradiction between laboratory and field observations has been named the 'Sleeping Beauty paradox' (Lavelle, Lattaud et al. 1995). The 'Prince Charming' of the story is any macro-organism, including plant roots, or physical process that may bring microorganisms in contact with new substrates to decompose, thereby activating them.

Importantly, earthworms provide the suitable temperature, moisture and organic resources within their guts for microbes to be activated (Brown, Barois et al. 2000). This makes the activation process more complex than tillage, and tillage is not relevant for such an activation of bacteria.

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What do they do?

As such, the activities of bacteria are directly dependent on relatively high soil water contents (Killham 1994; Lavelle and Spain 2001).

Bacteria are able to perform an extremely wide range of chemical transformations (see the end of this section also).

Bacteria also exhibit an extremely wide array of metabolic traits, which can be grouped in two main categories. Heterotrophic bacteria use organic carbon as their source of carbon. Autotrophic bacteria are particularly important in nitrogen cycling (Box 8). Some bacteria form symbiotic relationships, or permanent beneficial partnerships with plants. The principle of these symbiotic relationships is based on plants providing bacteria with simple carbon compounds from their roots, while bacteria fix nitrogen from the air in a form plants can use (Box 7). The best-known example of these is the symbiotic association between rhizobia and legumes. Some bacteria are highly specific and can only form associations with one host plant. This is the case of soy bean plants for instance. In contrast, other bacteria such as *Bradyrhizobium* can form symbiotic associations with both lupins and serradella. Other bacteria form symbiosis with animals such as those living in nephrids of earthworms and help in recycling of nitrogen. Others grow on the surface of fungal mycelium (e.g. mycorrhiza helper bacteria) or inside the fungal mycelium.

How do they reproduce?

Bacteria grow and divide extremely rapidly, potentially doubling population in a few minutes (Eagon 1962).

The second remarkable characteristic of this group is that it can use horizontal gene transfer (Box 2). Soil bacteria can uptake proteins and DNA directly from the soil (Khanna and Stotzky 1992). This is based on the capacity of soil to adsorb important biological molecules, such as proteins and DNA, while allowing them to maintain their activity. By taking up those molecules, bacteria can diversify and evolve very fast.

How long do they live?

Some bacteria are also able to survive through extreme physical and chemical stresses, such as high levels of UV light, heat, pressure or desiccation by entering a form of dormant stage. They do so by forming highly resistant dormant structures called endospores, which show no detectable metabolism. Bacteria can remain viable for years in that form, and be passively transported over long distances, giving them the enviable capacity to travel through time and across the planet.

➔ **FUNGI**

What are they?

Fungi are an immensely diverse group of organisms and are among the oldest and largest organisms on earth, encompassing a huge range of forms, from microscopic single-celled yeasts to complex structures such as rhizomorphs, fungal mats or fruit-bodies (Figure 2-4). Most fungi are invisible to the naked eye, living for the most part in soil, dead matter, and as symbionts of plants, animals, or other fungi. In the large majority of cases, fungi grow as thread-like multi-cellular microscopic filaments called hyphae (Figure 2-5). These filaments can assemble and intertwine into more complex macroscopic structures to form a mycelium, such as the mould on fruits. Fungi with their hyphae can explore soil, whereas the central body remains in one microhabitat,

differently from bacteria which has to move to explore microhabitats different from the original one.
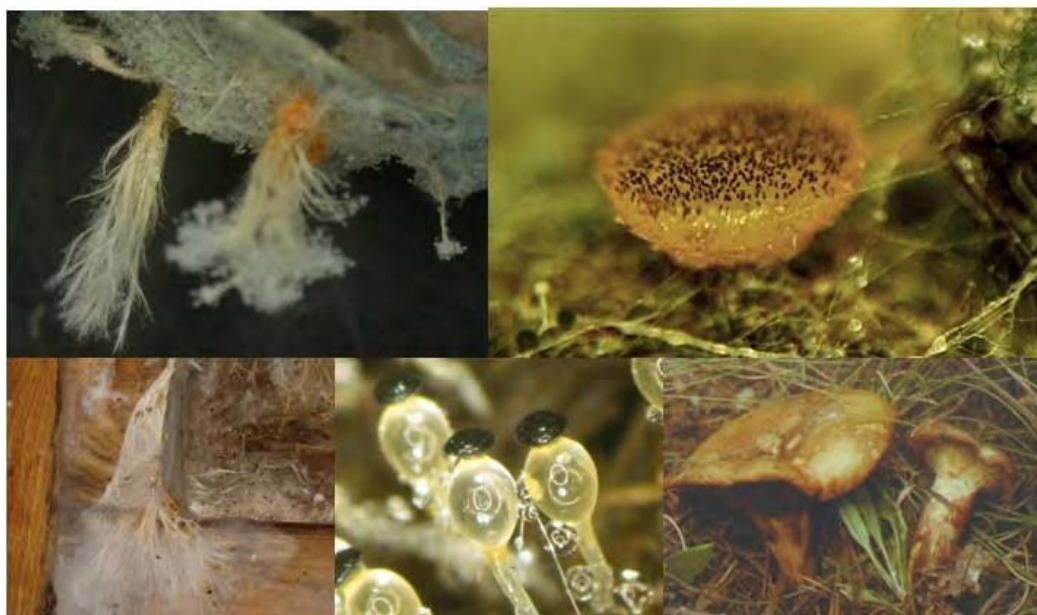
Figure 2-4: Examples of diversity in soil fungi[8]

Figure 2-5: Cells and hyphae of the dimorphic fungus *Aureobasidium pullulans* (fungal hyphae diameter: 2-10 μm)[8]

Currently, over 80 000 species of fungi described may live in soil at least part of their life, but many more remain to be discovered. The magnitude of total fungal diversity has been conservatively estimated at 1.5 million species (Hawksworth 1991). One gramme of soil can contain as much as one million individual fungi, while the fungi biomass in temperate soil can amount to 2-5 t/ha (Killham 1994). However, detecting which fungi are present in a soil is not an easy task, since many cannot be grown in cultures or are present only as spores or mycelium (as opposed to visible fruit bodies above the soil). Some mycelia are extremely long and can reach up to 200 m per gramme of soil (Bardgett 2005).

[8] Courtesy of Katarina Turnau

Where do they live?

With their hyphae, fungi push their way between soil particles, roots and rocks. Fungal hyphae have a high surface area to volume ratio, which makes them specifically adapted to growth on solid surfaces and within substrates, since they can exert large mechanical forces.

However, some fungal species also grow as single cells, usually in aquatic environments, such as water-filled pores.

What do they do?

Like animals, fungi need organic substrates to obtain carbon for growth and development. They are heterotrophic organisms that have evolved a remarkable metabolic versatility that allows many of them to use a large variety of organic substrates for growth, which would otherwise remain locked up in dead plants or animals. Some fungi live on dead or decaying organic matter, breaking it down and converting it to forms which are available to higher plants. Others are dependent on complex organic substances for carbon, breaking up sugars, starches, or lignin and cellulose in wood.

Specialised fungi can be pathogenic for the tissues of plants or to other fungi, while others form mutually beneficial relationships with plants, or mycorrhizal associations, by assisting in direct nutrient supply to the plants (Box 8). Mycorrhizal associations occur on almost all terrestrial plants and their specificity varies widely. Whilst many mycorrhizal fungi can form associations with many different host plants, others are either host-specific or severely host-limited. In addition, a single plant host may support a number of different mycorrhizal fungi within a single rhizosphere (Perotto, ActisPerino et al. 1996). Moreover, some fungi (very common in soil) hunt for small animals such as nematodes or amoebae. These fungi build various types of traps such as rings, or produce adhesive substance to entrap and to colonise the prey.

Box 7: The role of chemical engineers in the nitrogen cycle

The process of decomposition of organic materials is a gradual and complex process, which has taken place since life first appeared on our planet. In this process, chemical engineers feed upon decaying organic materials and convert the organic nitrogen back to mineral nitrogen. Under predominantly anaerobic conditions, denitrifying bacteria convert nitrate into atmospheric nitrogen. This nitrogen can then be fixed by free-living or symbiotic bacteria, thereby contributing to plant nutrition.

First, bacteria or fungi convert the organic nitrogen from decaying animals or plants to ammonium ($NH4^+$), in a process called **ammonification**. A number of microorganisms are able to perform this first mineralisation step. Moreover, plants and microbes may use organic nitrogen forms, thereby bypassing this mineralisation step (Nannipieri 2009). The direct uptake of low molecular weight organic compounds, such as amino acid, by soil microorganisms, is called "direct route" (Manzoni 2008). This is probably of most importance in N limited ecosystems, such as the arctic and alpine regions, but also potentially in low productivity agricultural sites (e.g. grasslands).

After ammonification, the chemical processes are conducted by specialist groups of bacteria. The **nitrification process** is conducted by small specialist groups of chemotrophic bacteria, called Ammonia Oxidising Bacteria (AOB), which convert this ammonia to nitrites (NO_2^-) that are toxic to plants. Other groups of bacteria oxidise these nitrites into nitrates (NO_3^-), which present no harm, and are useful for to plant

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growth. Some bacteria can also reduce nitrate or nitrite to nitrous oxide under anoxic conditions. Plants can absorb ammonium (NH_4^+) or nitrate (NO^{3-}) ions from the soil via their root hairs, or through mutualistic relations with rhizobium bacteria (see Box 8). Plants infected by mycorrhizal fungi can use both low (amino acids, amino sugars and peptides) and high molecular weight organic (proteins) N compounds as N sources (Schimel 2004). In many ecosystems, the critical process is not N mineralization but the depolymerization of N-containing compounds due to the activity of enzymes, such as extracellular proteases released by microorganisms. Thus, soil chemical engineers contribute directly to soil fertility. Alternatively, for the nitrate that is not absorbed by plants, **denitrification** can take place. Denitrification is the reduction of nitrates back to nitrogen gas into the atmosphere (N_2). Denitrification is performed by the action of some bacteria in anaerobic conditions. These bacteria do not require air for their activity, but use nitrogen in the place of oxygen during respiration. Intermediate compounds in denitrification process are NOx compounds with powerful greenhouse effects.
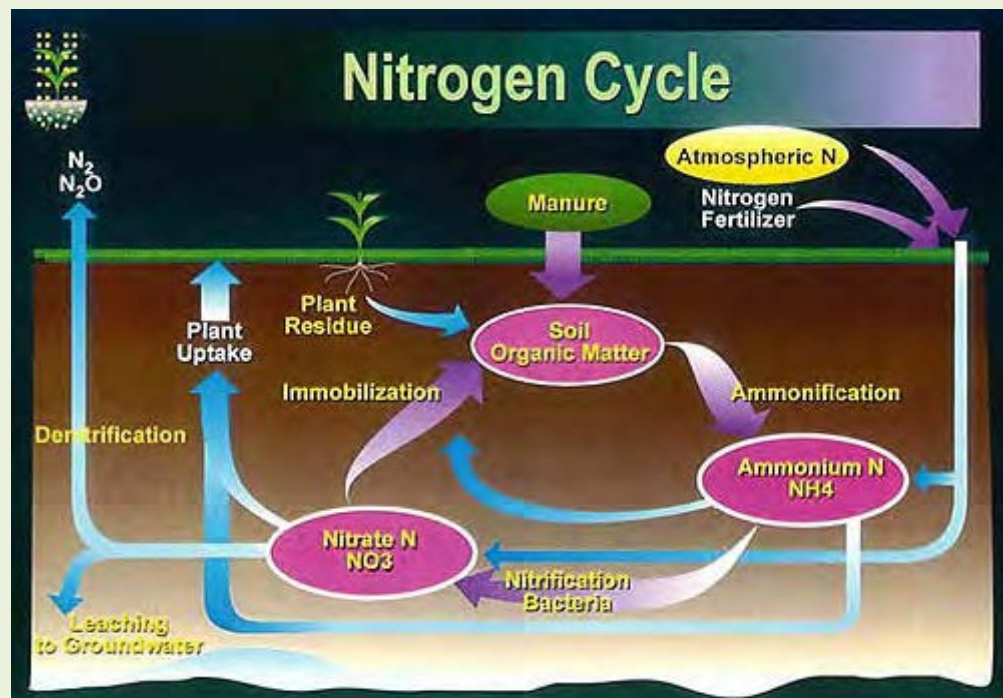
The soil nitrogen cycle

Image from: www.soilsensation.net/images/nitrogen_cycle_orig.jpg

How do they reproduce?

Fungi can reproduce via both sexual and asexual reproduction through spores produced in specialised reproductive structures. Some species have lost the ability to form reproductive structures, and propagate solely by vegetative growth.

How long do they live?

The life span of fungi is difficult to define, especially for the species that grow clonally. Some fungi, like Armillaria, can become very large (hectares) and live for many years.

Chemical decomposers can carry out many biological reactions and are involved in all major soil processes, ensuring a large part of soil biological activity. The main role of chemical decomposers in soil is the breakdown of organic matter into nutrients readily available to plants, and therefore animals and humans. They do so in a process called catabolism, through which large molecules are broken down into smaller units.

Chemical decomposers are involved in all the catabolic reactions contributing to the breakdown, transformation and mineralisation of carbon and nitrogen in soils. Most commonly, decomposition occurs in the presence of oxygen near the soil surface. Microorganisms use enzymes to oxidise the organic compounds. This process releases energy and carbon, nitrogen and phosphorus for their growth. The carbon is used as a source of energy, which is burnt up and respired as CO_2. The first compounds to be broken down are those that have simple cellular structures, such as amino acids and sugars. Cellulose in leaves, wax and phenols have more complex structures, characterised by strong chemical bonds, and take longer to be decomposed. Lignin in woody parts is the slowest compound to be decomposed. Fungi in general can decompose more recalcitrant material than bacteria.

The mineralisation to carbon dioxide and nutrients readily available to plants can take more or less time. Organic molecules may still undergo several oxidations reactions before the nitrogen, phosphorus and sulphur are converted to ammonium (NH_4^+), phosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) which plants can use.

The main function of chemical decomposers is to extract the nutrients from decaying organic material in the form of ions that can then be absorbed by plants. Indeed, nitrogen is essential and limiting for plant growth, since it is needed for incorporation into amino-acids, nucleic acids, and chlorophyll. The different steps of the nitrogen cycle and its main actors are detailed in Box 7.

In anaerobic conditions (without oxygen), microorganisms reduce nitrogen to organic acids and ammonia.

Some organisms included in other functional groups, like for example earthworms or large arthropods, can also contribute to the decomposition of organic matter. They shred the organic matter chewing up dead plants (see also section 2. 1. 3).

Importantly, some microorganisms included in the microbial decomposer group can also play a role as ecosystem engineers. For example, some species of fungi produce a glycoprotein called glomalin which play an important role in soil aggregation due to its sticky nature (Rillig 2004; Purin 2007).

Box 8: Mutualism

Mutualism is a biological interaction between two organisms of different species, where each individual derives a fitness benefit, for example protection for predators or food resources. In soil ecosystems there are many mutualistic interactions, often involving soil microorganisms. Here, two characteristic examples are provided of mutualistic relationships between bacteria, fungi and plants, which often increase the tolerance of plants to various stresses: rhizobia and mycorrhiza.

Bacteria and leguminous plants (Rhizobia): Root exudates stimulate the multiplication of free-living rhizobia bacteria. A bacterial colony typically develops on a root hair, which then begins to curl, and the cell is penetrated by the bacteria. The plant then encloses the multiplying bacteria by laying down a cell wall, forming an infection thread that may grow the nodule. In this association, rhizobium produces ammonium, thereby allowing plants to absorb nitrogen in the easiest route possible (compared to nitrate), since ammonium can be directly incorporated into proteins, without the need for any further chemical reactions. Importantly rhizobia cannot fix nitrogen without the plant and the plants cannot absorb nitrogen without the rhizobia, so these organisms need each other to survive. Sometimes rhizobia nodules can be red, due to a protein called Leghaemoglobin, which serves to fix surplus oxygen in the root. This protein is similar to our blood haemoglobin.

Root nodules created by rhizobium bacteria[9]

Fungi and higher plants (Mycorrhizal fungi): A similar type of mutualism occurs in the roots of higher plants with fungi. Higher plants and trees (gymnosperms, angiosperms) present mycorrhiza, which is an intimate mutualism between fungus and root tissue. The mycorrhizal fungi gain constant and direct access to the carbohydrates produced by plants during photosynthesis. In turn, the fungi actually form a network of filaments that grow in and around the plant root, thereby enabling the plants to use the large surface area of mycelium to improve their mineral absorption capacity. Plants can access nutrients and water that they may not have been able to reach otherwise. Three main types of mycorrhizal associations exist. In free-living associations between plants and fungi, usually on the roots of trees, the mycorrhiza form tightly matted sheaths (arbuscular mycorrhiza).

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[9] Image from: www.morning-earth.org/graphic-E/BIOSPHERE/Bios-C-PlantsNew.html

Microorganisms are not distributed randomly in the environment. They usually occur in colonies and bio-films, caused by two main biological factors: the location of food sources and the specific reproduction processes of the microorganisms

At the micro-scale, active chemical decomposers are usually found in 'hotspots' of increased biological activity, probably reflecting the micro-distribution of available substrate and inhabitable pore space (Nunan, Wu et al. 2002), which can be mediated by soil engineers (Beare, Coleman et al. 1995). Indeed, only a few microhabitats have the right set of conditions to allow microbial life, such as aggregates and pores with different physico-chemical properties from the bulk of the soil, zones with accumulated organic matter or animal manures, or in the soil immediately around plant roots (the rhizosphere) (Kowalchuk, Buma et al. 2002) (Grundmann and Debouzie 2000; Nannipieri, Ascher et al. 2003).

Large-scale spatial patterns of microbial distribution are also detected, both horizontally and vertically. Vertically, large scale aggregations in the subsoil may be due to nutrient transport through the soil profile: the distribution of flow paths regulates the supply of nutrients and thus the distribution of bacterial communities (Nunan, Wu et al. 2002) and the presence of plant roots, which provide nutrient-rich resources for microbial growth. Horizontally, spatial aggregations in the top-soil at larger scales may instead be determined by variations at the landscape level (Robertson, Klingensmith et al. 1997; Smith, Halvorson et al. 2002). However, in between the micro- and large-scales, it is not always clear whether some microbial patterning exist. Some studies find no spatial structure at intermediate scales (0.1 – 1m)(Nunan, Wu et al. 2002), while others do, possibly reflecting the different scale of influence of individual arable plants, and earthworm species on microbes (Rossi, Lavelle et al. 1997; Saetre and Baath 2000; Jimenez, Rossi et al. 2001).

The time-table of microbial metabolism is also important to consider with typical turnover rates in soil of 0.2-6 years for the soil microbial biomass compared to the much longer turnover time for organic material, depending on what type of litter has been produced by the plants. Importantly, within the same spatial scale, microorganisms can present a high temporal variability in their activity rate due to the presence of both active and resting cells (Felske and Akkermans 1998).

2. 1. 2. BIOLOGICAL REGULATORS

Biological regulators act as regulators of microbial activities, mainly through grazing but also through parasitic or mutualistic interactions with other microbes or invertebrates. These interactions control the abundance of populations in the soil food webs, together with the resource supply as made available by the chemical engineers. They are composed of a diverse group of organisms, comprising protists, nematodes, and microarthropods. They also contain pathogenic and parasitic/herbivorous regulators of plant abundance. Moreover, the class of enchyatreids, also called 'pot worms', play a role of biological regulators activating microflora, and occasionally, especially in soil with no earthworms, of soil engineers (Box 9).

Box 9: Enchyatreids

Pot worms are small white creatures commonly found in European soils and best known as fish food to most of us. Scientifically, they are known as Enchytraeids and are segmented relatives of the earthworm. This group also includes aquatic species, such as ice worms. With body sizes ranging from 1 to 50 mm, they are much smaller than other earthworms, and barely visible to the naked eye.

Pot worms feed on the same type of litter as earthworms. Their diet is mainly composed of bacteria, fungus and organic matter. They are also known to prey on nematodes. They are efficient at aerating soil and at breaking down some organic materials. Enchytraeids have a wide tolerance to water, but have little adaptation to drought. They prefer an acid environment that is moist, and may migrate up and down daily in response to changes in soil moisture. Accordingly, they reach their greatest abundance in the moist temperate soils. Some Enchyatreids can even be found under snow and glacier ice, and they are common in the sub-arctic. However, although some species can thrive in higher temperatures, many are seriously affected and may die off at annual means above 16 °C. Some species have the surprising ability to produce red blood to survive low oxygen conditions.

Enchytraeids are hermaphroditic, which means that each individual possesses both male and female reproductive organs, although some species can reproduce through parthenogenesis and asexually by fragmentation and also by self-fertilization in a cycle of about 20 days.

A typical enchyatreid worm

➔ **PROTISTS**

What are they?

Protists are a diverse group of unicellular eukaryotes, typically ranging from 10–50 μm, but sometimes reaching lengths of 1 mm (Figure 2-6). They are the smallest organisms within biological regulators, and can reach densities of about 10^6 cells per gramme of soil. In one hectare of soil, the equivalent in weight of 2 sheep of protists can be found.

Where do they live?

Protists need bacteria and fungi to feed on, and the water around soil particles to live and to move in, so that besides food, moisture is critical for their survival. They live in the water layer around soil particles.

Figure 2-6: A typical soil protist (body size: 2-200 μm)[10]

Protists can be classified according to the way they move. Ciliates move by beating their cilia like tiny oars, amoebae move by extending parts of their cells as pseudopods, and flagellates swim by waving their flagella like a whip. Protists have a high dispersal potential due to their capacity to live in resistance forms which can be passively transported by wind and/or water floods for several kilometres.

What do they do?

Protists control bacteria populations. To kill their prey, protists surround it and engulf it in their cytoplasm, digesting it in stomach-like compartments called vacuoles.

How do they reproduce?

Asexual reproduction is their most common form of reproduction, through division in two identical (binary fission) or multiple daughter cells (multiple fission). But in cases of environmental stress, sexual reproduction is also possible, usually as a means to recombine genetic information.

How long do they live?

During their life cycle, protists can have proliferative stages and dormant stages (e.g. cysts). In the dormant form, protists can survive extreme environmental conditions, and for long periods without access to nutrients, water, or oxygen. Protists are also able to spread fast and differently according to the environmental conditions.

➔ **NEMATODES**

What are they?

The other main component of biological regulators is roundworms or nematodes. Nematodes are tiny worms of about 0.5-1 mm in length which are common in soils everywhere (Figure 2-7). They can reach densities of 10-50 individuals per gramme of soil and have successfully adapted to almost every type of environment, even the most extreme ones such as Antarctica and deep sea oceanic trenches.

Nematodes are, in general, some of the most diverse groups of species, with over 80 000 nematodes species already described, but a total 500 000 species estimated (Bongers and Bongers 1998).

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[10] Image from: www.blm.gov/nstc/soil/protozoa/index.html

Figure 2-7: *Caenorhabditis elegans*, a soil nematode used as a model in genomic research (body size: 500 μm)[11]

Where do they live?

Nematodes are common in almost any soil, but they prefer somewhat coarser textured, porous soils. They move in water films inside pore spaces, except in the smallest pore spaces, which are not accessible for them. They tend to have a limited dispersal capacity of a few centimetres, although some nematodes can migrate up to a metre per year. They also have capacity of passive dispersal by wind, or attached to animals.

What do they do?

Nematodes are ubiquitous on earth due to their high adaptability. They are important components of soil food webs (Coleman 1984) and can be classified according to their feeding habits (Yeates 2009). Some species feed on algae, others on bacteria, fungi or plant roots. Other species still are predatory, and feed on other nematodes and protists, while some are omnivores and will eat any of the above. This diversity in feeding habits is important for agriculture: the production of some predating nematode species in fermenters is an established tool in biological plant protection

Their hunting technique depends on their diet. Fungal-feeders puncture the cell wall of fungi to suck their contents, whereas predatory nematodes attach themselves to the cuticle of other nematodes, scraping it away until their internal body parts can be extracted.

Nematodes are concentrated where their main preys occur. Thus the occurrence of bacterial and fungal-feeding nematodes is related to where the bacteria and fungi are located in the soil. Root-feeders are concentrated around roots of stressed or susceptible plants.

How do they reproduce?

Most nematodes have sexual reproduction, and important phenotypic differences exist between males and females, with males usually much smaller than females. Some species are hermaphroditic, and keep their self-fertilised egg inside the uterus until it hatches. Sometimes, the juvenile will cannibalise its parent.

Some species are parasitic and spend a part of their life cycle inside a host, other species are free-living. The life cycle is pretty simple in free-living nematodes, where

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[11] Image from: www.idw-online.de/pages/de/image46368

the larvae hatch from eggs, eventually growing into adults. In contrast, the life cycle is often much more complicated for parasitic species, where individuals pass through several juvenile stages before becoming adult.

How long do they live?

Similarly to protists, nematodes have the capacity to become dormant, in a desiccated state, when the conditions are not suitable for them anymore, such as in hot and dry conditions. Thanks to this ability, some specimens have been found to continue to live after 40 years in a slide collection.

→ **MICROARTHROPODS**

What are they?

Microarthropods are small invertebrates that rely on an external skeleton for body structure. They range in size from microscopic to a few millimetres, and include small insects, such as springtails, as well as some spiders and mites. Springtails (Collembola) is the only insect without wings and have a segmented body of 0.2-6 mm with specialised appendages, including a spring-like tail used for jumping (Figure 2-8).

Mites (Acaridae) are the most abundant arthropod living in soil. Their density in forest soils can reach hundreds of thousands of individuals per square metre, whereas mites often go un-noticed because of their small size (most are a few tens of µm)(Petersen H and Luxton 1982). About 50 000 mite species are known, but it has been estimated that up to 1 million species could be included in this group. In one hectare of soil, the equivalent in weight of four rabbits of soil fauna can be found.

Figure 2-8: Example of springtails (*Collembola*) (body size: 0.2-6 mm)[12]

Figure 2-9: Examples of the common red mite and predatory mite eating a springtail (body size: 0.5-2 mm)[13] and other soil microarthropods

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[12] Image from: www.amentsoc.org/insects/fact-files/orders/collembola.html
[13] Image from: www.prairieecosystems.pbworks.com/Dennis-NaturalistGuide

Where do they live?

This class of organisms have limited burrowing ability and generally live in surface litter or confined in the topsoil. Due to their small size, most species are capable of squeezing through small pore spaces and root channels.

Most have limited mobility. Springtails usually live in aggregations, and have a gregarious behaviour driven by secreted pheromones that helps single individuals avoid non favourable (e.g. dry) habitats. Mites are highly heterogeneous and, depending on the species, their habitat and ecology can be extremely different.

What do they do?

Microarthropods can have varied feeding habits. Most soil-dwelling microarthropods are herbivores, fungal feeders, or predators. The predators eat nematodes or other microarthropods. Some of them are generalists, feeding on several prey types, whereas others are specialists, hunting only a single prey type. Springtails and mites for instance mostly eat decaying vegetation associated bacteria and fungi. They are however also known to occasionally eat nematodes or other micro-invertebrates (Figure 2-9).

How do they reproduce?

Microarthropods mostly reproduce sexually. However, in springtails, reproduction can be sexual (through spermatophores) or via parthenogenesis (without fertilisation by a male). Some mite species are parasites and are dependent on the interaction with a host to complete their life cycle.

Some microarthropods can present a complex life cycle with multiple life stages, such as larvae and nymphs.

How long do they live?

Usually, in European temperate regions, they would have one or two generations per year. However, most microarthropods are capable of cryptobiosis, a state of suspended metabolism, which enables them to survive extremes of temperatures or dryness that would otherwise be lethal.

➔ **FUNCTION**

Biological regulators act as integrators of the food web, linking the lower functional level of chemical engineers in space and time, and regulating their dynamics (by feeding and contributing to the dispersion of microbes), mainly through predation and through modulating their activation during the digestion process (Neutel 2007)(Swift 1979). The microbial activity continues in faecal pellets that the invertebrate occasionally re-ingests taking advantage of the substrates released by microbes.

Moreover, parasitic and mutualistic actions of biological regulators directly regulate the abundance and the activity of chemical engineers through top-down effects. At low densities, predators stimulate the growth rates of their prey populations (e.g. bacterial feeders stimulate bacterial growth), but at high densities they reduce the populations of their prey. Predation often suppresses microbial populations more than resources, such that food resource availability is not a limiting factor for them anymore. This regulation can induce cascading effects on the abundance, biomass, or productivity of the lower trophic levels. However, predatory regulation is highly context sensitive. Therefore, its effects can change substantially in the face of disturbances, since food webs are highly dynamic and open entities, that can change in species attributes,

composition and dynamics (de Ruiter, Wolters et al. 2005). This applies even more to some other functions, such as parasitism, or plant pathogenesis, where specificity is much higher. Parasites and pathogens contribute not only to the regulation of species abundance, but also to the regulation of biodiversity.

Protists and nematodes, through their predatory action help disperse both organic matter and decomposers in the soil, and play a role in fragmenting organic matter and increasing its surface area for microbial attack (Anderson, Coleman et al. 1981; Griffiths, Ritz et al. 1994). In this way, they indirectly contribute to increasing the availability of nutrients that would otherwise remain immobilised in the microbial biomass (Ingham, Trofymow et al. 1985). Evidence exists that increased complexity in the food web may sometimes accelerate nutrient mineralisation (Couteaux, Mousseau et al. 1991; Setala and Huhta 1991; Setala, Tyynismaa et al. 1991), which may then promote productivity.

Moreover, the action of the biological regulators can influence aboveground biodiversity. Indeed, through their effects on plant presence and plant chemistry, biological regulators also influence interactions between plants and aboveground pests and diseases (Scheu 2001; Van der Putten, Vet et al. 2001). Therefore, this functional group is also central in the development of semi-natural ecosystems, sustainable agriculture and forestry, by indirectly influencing plant abundance, invasive species outbreaks, and plague and pests outbreaks in crop systems.

→ SPATIO-TEMPORAL SCALE

The distribution of biological regulators in ecosystems and entire landscapes follows gradients in soil type, water availability and cultivation practices. For example, the distribution of springtails in agricultural landscape can follow large-scale soil carbon gradients and type of land cultivation (Fromm, Winter et al. 1993). Likewise, the distribution of nematodes can often also be explained by land management and soil disturbance. For instance, a model showed that when the availability of resources is fluctuating, the distribution of nematodes mainly depends on the ability of species to re-colonise resource-rich patches from neighbouring patches (Ettema, Rathbun et al. 2000).

However, further spatial patterns in the composition of biological regulators can be found at slightly smaller spatial scales within ecosystems. For example, an aggregated spatial pattern (6-80 m) of nematodes was observed in an agricultural soil, despite the homogenising effect of monoculture (Robertson and Freckman 1995). These results suggest that important soil food web components can be strongly patterned at sub-hectare scales. That this patterning is maintained in an ecosystem subjected to the homogenising influences of annual soil tillage and a monoculture plant population is remarkable, and suggests that such patterning may be even more common in less-disturbed sites. The inclusion of these patterns in studies on ecosystem processes and soil community dynamics may significantly improve soil trophic models and our understanding of the relationship between soil populations and ecosystem functions.

At the smallest spatial scales, biological processes and soil structural and chemical heterogeneity are the main structuring agents. For example, ecological conditions which look uniform from the perspective of our own eyes are not perceived as such by for example amoebae (a protist).

Over larger spatial scales, passive dispersal can play a huge role. For instance, the same species of springtails can be found all over the Arctic zone (K. Hedlund, personal

communication), nematodes and protists are known to have large bio-geographical distributions and earthworms can be passively dispersed by human activities.

At a given time, only a small subset of species is biologically active: only the species capable of using the resources currently available. Thus the activity of biological regulators tends to follow pulses: their growth and reproduction usually follows seasonal patterns of resource abundance, but as soon as conditions become inadequate, they then have the ability to survive long periods in resistant, resting stages. For instance, for bacteria-feeding protists and nematodes, growth is generally at its maximum during the first weeks following addition of organic material to soil (Christensen, Griffiths et al. 1992). Then the majority of soil protists enter in a resting phase, forming cysts (Figure 2-10) (Ekelund and Ronn 1994), while other members of the soil biota, like for example, microarthropods, even if they do not form such resting recognizable forms, may also have periods without activity, as eggs or nymphs. In conclusion then, when resources are scarce, many biological regulators are able to tune their activity in time rather than disperse in space.
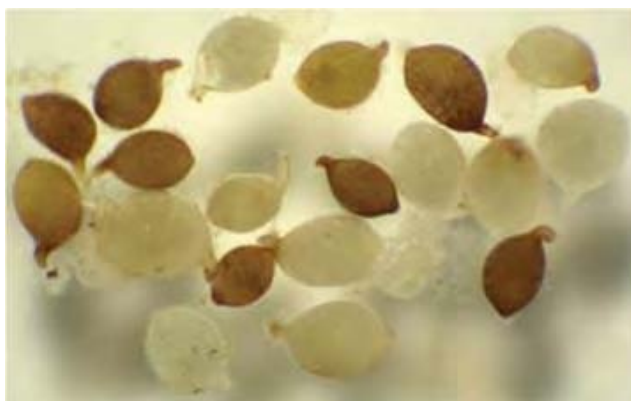
Figure 2-10: Cysts of nematodes (size: µm-mm)[14]

2. 1. 3.   SOIL ECOSYSTEM ENGINEERS

Ecosystem engineers are organisms that modify environmental conditions for other organisms through their mechanical activities (Jones 1997). Soil ecosystem engineers have the ability to build resistant organo-mineral structures and pores by moving through the soil and mixing the soil, in process known as bioturbation. Earthworms, termites, ants and roots have been identified as the most important soil engineers (Lavelle, Bignell et al. 1997).

However, soil engineers also include many other invertebrates, such as millipedes, centipedes, beetles, caterpillars, and scorpions, which may be more or less responsible for soil formation function. Engineers can also include some vertebrates which are part-time soil residents and primarily dig the soil for food or shelter, such as voles, snakes, lizards, mice, rabbits, etc. (Box 10). Soil organisms included in other functional groups can also play a relatively minor role in soil engineering. Bacteria and fungi also play a role in soil structure formation, for example arbuscular mycorrhizal fungi exude compounds that enhance soil aggregate formation and fungal mycelia have been shown to physically enmesh aggregates and to bind them together.

Box 10: Burrowing mammals

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[14] Image from: www.ipm.iastate.edu/ipm/icm/2007/7-30/nematode.html

Most burrowing mammals, with the exception of moles, are only part-time soil residents. They may include large creatures such as badgers and small ones such as shrews. They typically dig burrows and tunnels underground to gain protection from predators and weather extremes. Territorial species may maintain a set of burrow systems, whereas others such as badgers dig many burrows that are not maintained.

Their digging mixes topsoil with litter and faeces. This helps fertilise the soil and buries soil organic matter, which benefits many plants and soil microorganisms. Their burrows and tunnels also allow water from heavy storms to rapidly infiltrate the soil, rather than runoff. Moreover, the burrow systems aerate the soil, providing oxygen around plant roots. They may also bury seeds, thereby promoting plant dispersal and growth.

European badger emerging from burrow[15]

→ EARTHWORMS

What are they?

Earthworms range from a few millimetres to several tens of centimetres and they are basically a long digestive system in the shape of a tube (Figure 2-11).

Earthworms often form the major part of the soil fauna biomass, representing up to 50% of the soil fauna biomass in some temperate grasslands, and up to 60% in some temperate forests.

Figure 2-11: *Lumbricus terrestris* (anecic earthworm, size range: 0.5-20cm)[16]

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[15] Image from: www.badger-watch.co.uk/gallery/images/Badger.html
[16] Image from: www.ync.ca/bronze%20level%20guide/nd_worm_watch.htm

Several thousands of earthworm species, grouped into five families, are distributed all over the world. In Europe, but also North America and Western Asia, the most common worms belong to the family *Lumbricidae*, which has about 220 species.

Where do they live?

Earthworms are burrowing creatures, ingesting soil and expulsing it either at the soil surface or in the space that they have just emptied by soil ingestion. They travel in their burrows by muscular contractions which alternately shorten and lengthen their body, aided in their progression by the secretion of lubricating mucus. In this way they can move for several metres.

What do they do?

Earthworms play a major role in soil functions like the decomposition of organic matter. They are herbivores and can be divided into three main ecological categories: (1) the epigeic or leaf litter-/compost-dwelling worms, (2) the endogeic worms that live in the topsoil and also feed in the soil, mostly on plants, and (3) the anecic worms that spend most of their time in the soil, in the semi-permanent deep burrows they construct, but which feed on the surface litter that they generally mix with soil. Epigeic worms have little impact on soil structure, and anecics and endogeics are responsible for most engineering work, through their burrowing and mixing activities.

Moreover, the gut of earthworms is actually a very active microbial reactor with specific environmental conditions that selectively awake dormant soil microorganisms. Therefore, as a result of their microbial activity, earthworm casts exhibit high relative concentrations of nutrients, such as NH_4^+ and P.

How do they reproduce?

The majority of earthworms are hermaphrodites, which means that each individual possesses both male and female reproductive organs. Despite this peculiarity, earthworms still mate, in order to exchange sperm with which they will then inject their own eggs. A minority of species can also reproduce by parthenogenesis (asexual reproduction) which gives them significant advantages in colonising new environments and being occasionally invasive species.

How long do they live?

It generally takes about one year for earthworms to develop to the adult stage, although only a relatively small proportion (20 to 30%) make it to this stage. Some large deep soil living species may live several years.

→ **TERMITES**

What are they?

Termites are small insects, measuring around 0.5-2 cm in size, depending on their cast and on the species (Figure2-12). All termite species are highly social and live in colonies of up to one million individuals.

Although they are most common in tropical environments, termites can live just about anywhere as long as the ground does not completely freeze in the winter. But while almost 3 000 species of termites have now been identified, less than ten species occur in natural habitats in Europe, and only a few of these live in soil.

Figure2-12: European termite (termite's average body size: 0.3-0.7 cm)[17]

Where do they live?

Subterranean termites live and breed in soil, sometimes several metres deep - although some colonies may build nests inside fallen trees or in other aboveground locations.

The nests of termites are elaborate structures made using a combination of soil, mud, chewed wood/cellulose, saliva, and faeces that create a protected living space and optimal humidity through water condensation. Inside the nests, a network of tunnel-like galleries provide the possibility to move through the nest structure and ensure air-conditioning and control the CO_2/O_2 balance (Abe 2000).

Neither individual termites nor colonies normally travel long distances as they are constrained to live within their territorial border or within their food materials.

What do they do?

Termites are major detritivores, which play a crucial role in the soil food web. They are able to degrade cellulose, a complex sugar molecule that gives trees and shrubs their structure. Cellulose cannot be digested by most other organisms, including humans. Termites feed mostly on cellulose from dead plant material, such as wood and leaf litter, but also on animal dung (Lavelle and Spain, 2001).

Some termites are also soil-wood feeders and soil feeders, which means that they ingest a high proportion of mineral material. Their nutrition derives mainly from well-decayed wood and partly humified soil organic matter.

Another group of termites, in some areas of the world, grow fungi in their nests on macerated plant material cakes (fungus-growing termites).

How do they reproduce?

Termites are eusocial insects living in organised colonies comprising casts, or sets of different looking individuals designed to perform definite tasks. Colonies start with a queen and her king, but at their maturity, they can reach several hundred to several million individuals. The queen is the central and largest individual in the colony, whose function is to produce 10-20 eggs in the early stages of a colony, but up to several thousand eggs per day after several years. Meanwhile, thousands of workers are toiling around, tending to the queen, building and maintaining the nest, gathering food or feeding the young larvae. A handful of soldiers, with large heads and powerful jaws, are posted outside the nest, to guard the nest and the colony.

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[17] Image from: www.uky.edu/Ag/Entomology/ythfacts/bugfun/riddlans.htm

How long do they live?

Termites typically live a few weeks with the exception of the royal couple that may live for years.

→ **ANTS**

What are they?

Like termites, ants are small social insects, ranging in size from 0.75 to 52 mm, which live in colonies. Ants thrive in most ecosystems and have colonised almost every place on earth. Their success may be attributed to their extraordinarily diverse range of life strategies and their ability to modify habitats and tap resources (Figure 2-13).

Figure 2-13: *Lasius neglectus* ants, recently invading Europe (2.5-3 mm) [18]

To date, more than 12 000 species of ants have been described, but Europe is one of the less diverse regions, hosting less than 200 ant species (Hoelldobler and Wilson 1990).

Where do they live?

Ants live in underground nests that consist of a series of underground chambers, connected to each other and to the surface by small tunnels. Inside the nest, there are rooms for nurseries, food storage, and mating (Box 11).

What do they do?

Most ants are generalist predators, scavengers and indirect herbivores, but a few have evolved specialised ways of obtaining nutrition (e.g. by raising other insects or fungi within their nests) (Wilson and Holldobler 2005).

Ants display an extraordinarily diverse range of life strategies, including mimetic, commensal, parasitic, and mutualistic interactions with other species. Moreover, within ants of the same or of different species, very complex communicative, competitive and cooperative interactions may exist.

Some species of ants in the temperate and boreal forests of Eurasia have been observed to build large parts of their nests aboveground, using organic materials collected from the surrounding soil, thus increasing the spatial heterogeneity of soil for water and available nutrients, as well as tree growth (Jurgensen, Finer et al. 2008).

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[18] Image from:
www.m.gmgrd.co.uk/sbres/367.$plit/C_67_article_2040546_body_articleblock_0_bodyimage.jpg

> ### Box 11: Ant gardens
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> Some species of ants in the Tropics can create huge nests which are amazingly well-integrated into the local vegetation: the ant gardens. The nests contain large quantities of humus and thus form a good environment for seed germination. In fact, ants continuously carry seeds into the nest, and those seeds then germinate and become plants contributing to maintain of the overall nest structure. In addition to its structural role, the presence of vegetation is important as a source of food for ants. In turn, ants ensure the dissemination of the plant seeds. The nest size progressively increases, in parallel with the plant growth. Different species of ants and arthropods can progressively be integrated in the garden, creating a veritable micro-ecosystem (Corbara 1999).
>
>
>
> **Ant garden (Corbara 1999)**

How do they reproduce?

Like termites, ants are eusocial insects living in colonies, with different casts of individuals. Ants emerge from an egg and develop by complete metamorphosis with the larval stages passing through a pupa stage before developing as an adult. Depending on the species and the age of the colony, colonies can count a handful of individuals to millions of individuals.

How long do they live?

The life span of ants is extremely variable depending on the considered species. It can range from a few months to several years.

→ ISOPODS

What are they?

Isopods form a very heterogeneous and ubiquitous group of crustaceans (more than 10 000 species). They have a segmented body and range in size from 0.5 mm to several tens of centimetres (Figure 2-14).

Figure 2-14: Isopods (1-10 mm)[19]

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[19] Image from: www.morning-earth.org/graphic-E/BIOSPHERE/PLANTIMAGE/SOIL%20LIFE/sowbug24

Where do they live?

Many of them live in the aquatic environment, but members of the suborder *Oniscidea* (about 5 000 species) are fully terrestrial and may typically leave in litter layers (e.g. sowbugs and pill bugs). These are by far the most successful group of crustaceans to invade land.

What do they do?

Isopods usually have a detritivorous feeding regime, and act as ecosystem engineers at producing sometimes rather stable faecal pellets. They can occasionally be very important ecosystem engineers, mainly in desert areas (Yair 1995). Isopods can display a range of feeding habits, some being herbivores, detritivorous, carnivores or parasites.

How do they reproduce?

Isopods reproduce through sexual reproduction.

How long do they live?

The average life span of most isopods is about 2 years but some have lived as long as 5 years.

➔ **MOLES**

What are they?

Moles are small mammals with a hairless, pointed snout in front of the mouth opening and cylindrical bodies measuring about 15 cm in length. They are fantastically well adapted to underground burrowing, with small covered eyes, no external ear, and very wide, broad forefeet (Figure 2-15).

Figure 2-15:- European mole[20]

Moles are very common, and can be found everywhere in Europe, except Ireland[21]. They are present in most habitats where the soil is deep enough to allow tunnelling and are not able to maintain existence in hard, compact, semi-arid soils such as in coniferous forests.

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[20] Image from: www.cornwallwarrener.co.uk/Moleman_devon_cornwall.html

[21] During the last ice age, most parts of Ireland were covered, as was Britain, and as the ice retreated animals from the south moved northwards. Moles they did not get into Ireland because the sea level rose too quickly.

Where do they live?

Moles spend almost all their lives underground in an extensive system of permanent and semi-permanent tunnels. The permanent deep burrow system forms a complex network that can cover hundreds of metres, at varying depths in the soil. The permanent tunnels are used repeatedly for feeding over long periods of time, sometimes by several generations of moles. This is also where moles build their nest, usually one or more spherical nest chambers, each lined with a ball of dry plant material.

However, most of the underground network of a mole is usually made up of shallow 3-4 cm diameter tunnels that range over its hunting grounds. These surface tunnels are usually short-lived and may not be used again or only re-traversed at irregular intervals.

Moles make their home burrows in high, dry spots, but they prefer to hunt in soil that is shaded, cool, moist, and populated by worms and grubs. Thus surface tunnelling typically occurs in newly cultivated fields, in areas of light sandy soil and in very shallow soils, where prey is concentrated just below the surface. The deepest tunnels are used most in temperature extremes, such as in times of drought and low temperatures.

What do they do?

Moles are predators, feeding primarily on earthworms, but also on other small soil invertebrates, such as insect larvae in the summer. They have very large food requirements, and need to eat from 70% to 100% of their weight each day. This requires them to move extensively in the search of prey, shearing the soil with their forefeet and scooping it to the surface to form a molehill. They are capable of extending their tunnel system by 30 cm per hour in this way.

They catch their prey either by trapping or hunting: they can collect the prey that have fallen through their tunnels or chase and dig them out. Once caught, they can paralyze earthworms thanks to a toxin in their saliva. They then store some of their prey in special 'larders' for later consumption – up to 1000 earthworms have been found in such larders.

How do they reproduce?

Males and females are solitary for most of the year, occupying exclusive territories. With the start of the breeding season males enlarge their territories, tunnelling over large areas in search of females. A litter of 3 or 4 baby moles is born in the spring and disperses from their mother's nest after approximately a month and a half. Dispersal takes place aboveground and is a time of great danger.

How long do they live?

Most moles don't live beyond 3 years but can live up to 6 years. Their main predators are owls, buzzards, stoats, cats and dogs but vehicles and humans also kill many.

→ **PLANT ROOTS**

Roots are one of the main ecosystem engineers. The amount of roots present in the soil can be almost as large as, or even larger than, the amount of aboveground plant biomass (Figure 2-16).

What are they?

Roots are the part of the plant that typically lies belowground and anchors the plant to the ground, while absorbing nutrients and moisture from the soil. The first function is generally performed by short lived thin roots whereas anchoring is performed by perennial large long lived roots. Root systems can vary in shapes and sizes. They can be shallow or deep, and comprise coarse roots (> 2mm) that are perennial organs equivalent to tree branches, and fine roots which are short lived organs specialised in water and nutrient uptake. Roots will generally grow in any direction where suitable conditions of aeration, mineral nutrients and water availability exist.

Figure 2-16: Excavated root system[22]

What do they do?

The two major functions of roots are the absorption of water and inorganic nutrients, and the anchoring of the plant body to the ground. Roots often participate in the storage of food and nutrients and they can produce, or store chemicals that are used in defending plants against plant-feeding enemies.

The region of soil immediately adjacent to and affected by plant roots (about 2 mm) is called the rhizosphere: it is a very dynamic and species rich environment. This is because roots draw nutrients and water to the plant, while exuding organic compounds, which together makes the environment of the rhizosphere very different from the rest of the soil. Soil microorganisms feed on these so-called root exudates, thereby attracting larger soil organisms to feed on them. The concentration of soil organisms can be up to 500 times higher in the rhizosphere than in the rest of the soil.

Moreover, the roots of many plant species enter into symbiosis with certain fungi or bacteria (Box 8), which can promote the acquisition of nitrogen, phosphorus and water.

How long do they live?

Plant roots are highly dynamic; root hairs live only a couple of days at maximum, while other parts may turn over in a couple of days or weeks. Only the larger anchoring roots can become as old as the plant itself.

→ **FUNCTION**

Contrary to biological regulators, the effect of ecosystem engineers mainly develops through non trophic relationships. At the heart of the soil engineering concept is the ability of ecosystem engineers to move through the soil and to build organo-mineral structures with specific physico-chemical properties (Lavelle 1997; Hedde, Lavelle et al. 2005; Mora, Miambi et al. 2005). Ecosystem engineers thus alter ecosystem dynamics

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[22] Photo by Keith Weller, Ag Research Magazine

through these structures, directly, by modifying or creating habitats, or indirectly, by regulating the availability of resources for other species (Jones, Lawton et al. 1994).

Some organisms included in the other two functional groups can also act as ecosystem engineers. Aside from their main function in decomposition, soil-microorganisms also play other minor roles of engineering in the soil. For instance, bacteria and fungi can produce (exude) a sticky substance in the form of polysaccharides (a type of sugar) or proteins that help bind soil particles into small aggregates, conferring structural stability to soils. Thus, chemical engineers can contribute to the soil engineering function. However, in general their effect is less marked than that originated by ecosystem engineers.

Similarly to chemical engineers, the largest biological regulators (springtails and mites) also have an engineering function. They can produce structures from organic matter where microbes can live and function. These structures can be produced either by altering microbial decomposition rate through grazing and excretion of nutrient rich faeces contributing to the formation of the structures (Cole 2002). Although the impact of faeces on soil physical properties is limited, these structures may alter the spatio-temporal patterns of decomposition and mineralisation. While mineralisation may be enhanced in short periods inside those structures, in the longer term, the aeration and water storage may be limited, resulting in an important decrease of mineralisation (Toutain, Villemin et al. 1982). In addition, these structures may leach organic acids that affect, in the long term, soil functioning.

Main types of structures created by ecosystem engineers

Three main groups of structures are commonly found in European soils, and exhibit different physico-chemical properties from the surrounding soil.

- Earthworm casts

Earthworms ingest soil and leaf tissue to extract nutrients and then excrete casts, or small faecal pellets ranging in size from a few millimetres to several centimetres in diameter. Typically, granular casts are very small and formed by isolated faecal pellets and are generally produced by epigeic worms, whereas globular casts are larger and normally produced by endogeic or anecic earthworms. They comprise an accumulation of oval-shaped pellets which coalesce to form large structures.

- Earthworm tunnels

Earthworms construct galleries through their movements in the soil matrix. Each time they pass through the gallery they coat its walls with mucus. These galleries may be filled with casts and contribute both to macro-pore formation or eventually micro-aggregate formation.

- Termite mounds / Ant heaps

In their building activities, termites process high quantities of material and transport small particles from the deeper to the upper soil horizons. Thus their mounds exhibit different soil properties as compared with surrounding soil. Similarly, through their nest-building activities, ants can incorporate a lot of organic matter and nutrients into the soil. All these activities contribute to the mixing of soil and the formation of soil aggregates.

Habitat modification and creation

Ecosystem engineers are primarily physical engineers, building resistant soil aggregates and pores that serve as habitat for all smaller soil organisms (Box 12). In that way, ecosystem engineers greatly enhance the amount of habitat available for other soil organisms. However, they operate some degree of selection, as they may decrease the number of plant parasitic nematodes through a stimulation of the plant's natural defences, and also remove a significant proportion of the surface leaf litter with significant – although sometimes positive – effects on litter arthropod communities (Marinissen and Bok 1988; Loranger, Ponge et al. 1998). For instance, the effect of earthworms on aggregate formation results from the net outcome of their feeding and burrowing activities. Earthworms create macro-pores through their tunnelling activities and ingest soil particles and organic matter, mixing these two fractions together and expulsing them as surface or subsurface casts. They can thus produce casts at rates of several hundreds of tonnes per ha, with maximum values well above 1,000 tonnes in tropical savannas (Lavelle 1978). These casts can then form stable aggregates as long as they experience a drying cycle (Shipitalo M J and Protz R 1989; Blanchart, Albrecht et al. 1999; Blanchart, Albrecht et al. 2004).

Through their activity, soil engineers modify the soil aggregation rate and porosity, having impacts on associated hydraulic properties (Barros et al. 2001, Lavelle et al. 2001). Engineers generally maintain high levels of aeration and porosity of soil through the formation of structures such as burrows, tunnels, galleries, casts, mounds etc. and by increasing the proportion of stable aggregates in the soil and thus stable inter-aggregate porosity. For instance, the large vertical galleries of anecic earthworms facilitate the flow of water through the soil profile, increasing the transport of water and nutrients leaching into the deeper soil layers (Neirynck, Mirtcheva et al. 2000). Similarly, ant nests have been shown to affect water infiltration rates and soil organic matter content (Hoelldobler and Wilson 1990).

Regulation of resources

The structures created by the activity of soil engineers are privileged sites for a number of soil processes (mineralisation, de-nitrification, nitrogen-fixation, water and air infiltration), becoming hotspots of diversity and litter transformation where nutrient availability is increased (Lavelle et al. 1997).

Litter transformers such as isopods or *Myriapoda Diplopoda*, consume dead plants and produce organic aggregates in the form of faecal pellets a few tenth of millimetres in size (Brethes, Brun et al. 1995). These faecal pellets are moister and higher in nutrients than the surrounding soil, which favours their colonisation by chemical engineers. Five to 25% of the whole soil micro-flora can be found close to the surface of galleries, which only represents 3% of soil volume (Lavelle and Spain 2001). These structures serve as incubators for microbial digestion and do not usually last very long, since they are usually ingested back by the worms. They may alter the timing and spatial pattern of microbial decomposition. As a consequence, ecosystem engineers can greatly enhance the mineralisation of nitrogen and can simulate other nitrogen transformation such as denitrification.

Moreover, since earthworms can consume and incorporate large amounts of organic matter into the soil, they have important effects on the dynamics of soil organic matter and soil physical processes at different spatio-temporal scales (Decaëns, Jimenez et al. 1999).

The activity of ecosystem engineers also generally results in improved soil fertility and plant production (Scheu 2001), through its indirect effect on the activity of chemical engineers and nutrient cycling as well as direct effects on plant physiology (Blouin, Barot et al. 2006). Indeed, experiments show that a decline in the abundance and diversity of local invertebrate engineer communities, may have occasionally detrimental impacts on soil functioning when an invasive earthworm compacting species transforms the whole surface soil into a continuous layer of compacted soil that creates lethal anaerobic conditions for plants roots (Chauvel, Grimaldi et al. 1999). Similarly, the tunnelling efforts of termites help to aerate soils, which can result in patchy changes/improvements to soil composition and fertility, by allowing water transport for instance.

Box 12: Soil aggregates

Soil particles can be bonded together in larger structural units called aggregates. These aggregates fit more or less closely together, creating spaces of many different sizes providing habitats for other soil organisms, and able to store air, water, microbes, nutrients and organic matter. Typically, micro-aggregates (< 250 μm) are bound together by temporary agents, such as roots and fungal hyphae, or transient agents, such as microbial polysaccharides, to form macro-aggregates (> 250 μm).

Ecosystem engineers are one of the main actors influencing aggregate dynamics. For example, earthworms affect the ratio of macro- to micro-aggregates by ingesting and expulsing aggregates of various sizes during their tunnelling and feeding activities. The casts they expulse are rich in organic matter, and although these casts are not stable when they are freshly formed and wet, the mix of organic matter, mucus and soil can make them highly stable casts upon drying.

A second important mechanism of macro-aggregate formation is through the activity of roots and chemical engineers. Active growing roots and fungal hyphae can initiate macro-aggregate formation by enmeshing fine soil particles and binding them together (e.g. through secretion of sticky proteins). Microbial or root exudates, composed of long and flexible polysaccharides bind them together in stable aggregates that can resist decomposition.

The formation and breakdown of aggregates directly influences the dynamics of soil organic matter. Aggregates physically protect SOM from microorganisms and microbial enzymes and influence microbial turnover. For example, earthworms may stabilise SOM through the incorporation and protection of organic matter in their casts (Martin 1991; Guggenberger, Thomas et al. 1996; Bossuyt, Six et al. 2004; Bossuyt, Six et al. 2005).

The stability of aggregates is crucial, since unstable aggregates are unable to withstand pressure and compaction, thereby leading to poor water infiltration and aeration. The stability of macro-aggregates can only be maintained if there is a continuous replenishment of organic matter to replace the binding agents that are constantly being degraded by soil organisms. Aggregate stability is a particularly serious problem in soils that have a high proportion of sand and silt: as aggregates break open, sand, silt and clay particles are released and washed up into soil pores, preventing further water infiltration. This process is called 'soil crusting', and effectively seals the soil surface, promoting erosion.

Soil ecosystem engineers create structures that may persist much longer than the organisms that have produced them (Blanchart, Lavelle et al. 1997; Le Bayon and Binet 1999), which means that this functional group mostly influences soil processes at a large temporal scale. For instance, the casts of earthworms can last half a year to a year, whereas termite nests may last for much longer periods still (Decaëns et al. 2000).

In space, the distribution of earthworms, for example, is spatially structured forming patches of several metres in diameter in most ecosystems. This pattern seems to be the result of two possibly coordinated processes, one related to demographic patterns (juveniles having more aggregated distributions) and the other related to successions in the soil environment. For example 'compacting species' feed on small soil aggregates and 'de-compacting' species follow, once the former group has eaten up small aggregates and moved towards patches where de-compacting species have just transformed large aggregates into smaller ones (Blanchart, Lavelle et al. 1997; Barot, Rossi et al. 2007).

When considering the chemical processes performed or facilitated by soil engineers, opposite effects have been observed at different spatio-temporal scales. For example, at a fine scale termites and earthworms accelerate mineralisation through their digestion of organic material, but at a larger scale, the mineralisation of the organic material forming the nest is not possible for several years, until the colony dies. This provides a capability to regulate processes at fine discrete temporal and spatial scales.

2. 1. 4. SUMMARY OF THE CHARACTERISTICS OF THE DIFFERENT FUNCTIONAL GROUPS

The table below presents a scheme of the soil organisms' characteristics.

Table 2-1: Summary of the characteristics of the three soil functional groups

Characteristics	Chemical engineers	Biological regulators	Ecosystem engineers
Main Organisms	Bacteria, fungi	Protists, nematodes, mites, springtails (Collembola)	Ants, termites, earthworms, plants roots
Function	Organic matter decomposition, mineralisation + nutrients release, pest control, toxic compounds degradation	Regulation of microbial community dynamics, faecal pellet structures, mineralisation, nutrient availability regulation (indirect), litter transformation and organic matter decomposition	Creation and maintenance of soil habitats; transformation of physical state of both biotic and abiotic material, accumulation of organic matter, compaction of soil, de-compaction of soil, soil formation
Body size	0.5-5 µm (bacteria) 2-10 µm (fungal hyphae diameter)	2-200 µm (protists) 500 µm (nematodes) 0.5-2 mm (mites) 0.2-6 mm (springtails)	0.1-5 cm (ants) 0.3-7 cm (termites) 0.5-20 cm (earthworms)
Density in soil	10^9 cells/g of soil (bacteria) 10 metres/g of soil (fungal hyphae)	10^6 g/soil (protists) 10-50 g/soil (nematodes) 10^3-10^5 per m^2 /soil(mites) 10^2-10^4 m^2/soil (springtails)	10^2-10^3 m^2/soil (ants) 10-10^2 m^2/soil (earthworms)

Characteristics	Chemical engineers	Biological regulators	Ecosystem engineers
Scale of spatial aggregation	From 1 to $10^2 \mu m$	cm (protists) Tens of metres (nematodes) Hundred of metres (springtails, termites)	cm-m (ants, termites, earthworms)
Scale of active and passive dispersal	μm (active); no limit (passive)	From mm to hundred of metres (protists) From mm to m (protists) From mm to metres (springtail and mites)	1 to 100 m (earthworms) up to 1000 m social insects
Scale of resources use	1 to $10^2 \mu m$ (bacteria) μm- metres, occasionally up to km (fungal hyphae)	100 μm to a few mm (nematodes) mm to cm (mites, springtails)	same scales
Ability to change the environment	Highly restricted to micro environments	Intermediate	High
Resistance to environmental stresses	High (cysts, spores)	High (Protist, nematodes) Intermediate (meso-fauna)	Low

2.2.   FACTORS REGULATING SOIL FUNCTION AND DIVERSITY

The activity and diversity of soil organisms are regulated by a hierarchy of abiotic and biotic factors. Abiotic factors tend to be large scale phenomena, while biotic factors tend to act at smaller scales. Biotic factors include all the biological interactions in the soil ecosystem and tend to be more local, involving phenomena such as:

- competition,
- predation,
- grazing,
- mutualism
- symbiosis
- infectivity

Abiotic factors[23] include:

- climate (temperature, moisture)
- pH
- salinity
- soil structure
- soil texture

Both biotic and abiotic factors can have direct and indirect impacts on soil functional groups. We consider a direct impact when the biotic or abiotic factor modifies directly the physiology and/or ecology of soil organisms (e.g. temperature has a direct effect on

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[23] All the abiotic factors influence the efficiency of the decomposition of organic matter and nutrient availability

earthworm physiology). An indirect impact occurs when the sensitivity to the biotic or abiotic factors depends on the alteration of a secondary parameter (Figure 2-17).

The influence of temperature and moisture on local vegetation, for example, can lead to indirect impacts on soil organisms: plants indirectly affect both invertebrate and microbial soil communities, by regulating the quantity, quality and distribution of organic resources (Lavelle, Blanchart et al. 1993). In turn, soil organisms have feedback interactions on plants, which further influence the composition and productivity of the vegetation, and ultimately affect the organisms operating at larger spatial scales, such as aboveground vertebrate herbivores (Bardgett and Wardle 2003). These soil-plant interactions also can have larger scale effects, such as on the local (micro-) climate via altered precipitation and on global atmospheric conditions through the storage or release of greenhouse gases. Therefore, the soil and soil organisms are an important component of the global cycles of carbon, nitrogen and water and their action is regulated by aboveground-belowground interactions (Figure 2-18).
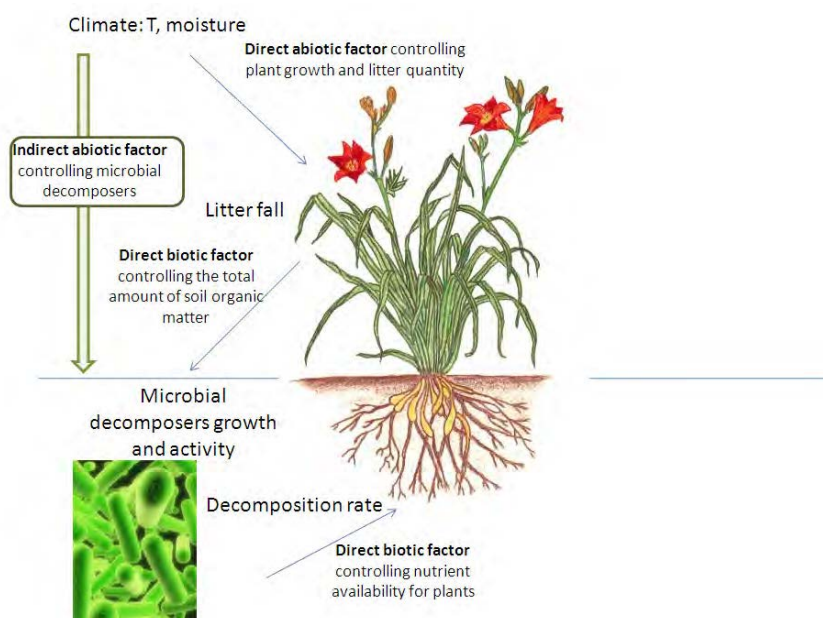
Figure 2-17: The indirect impact of climate on chemical engineers through altering plant productivity and litter fall. T=temperature

In the first part of this section the main abiotic factors (climate, temperature, moisture, salinity, pH, soil texture and land uses) affecting each functional group are presented. In the second one the main biotic interactions between the three functional groups are described.

2. 2. 1.   ABIOTIC FACTORS

In this section we present the main natural abiotic factors regulating the ecology of the three functional groups of soil organisms previously defined. For each functional group, we consider the impacts of:

- climate, temperature and soil moisture
- soil texture and structure
- salinity
- ph
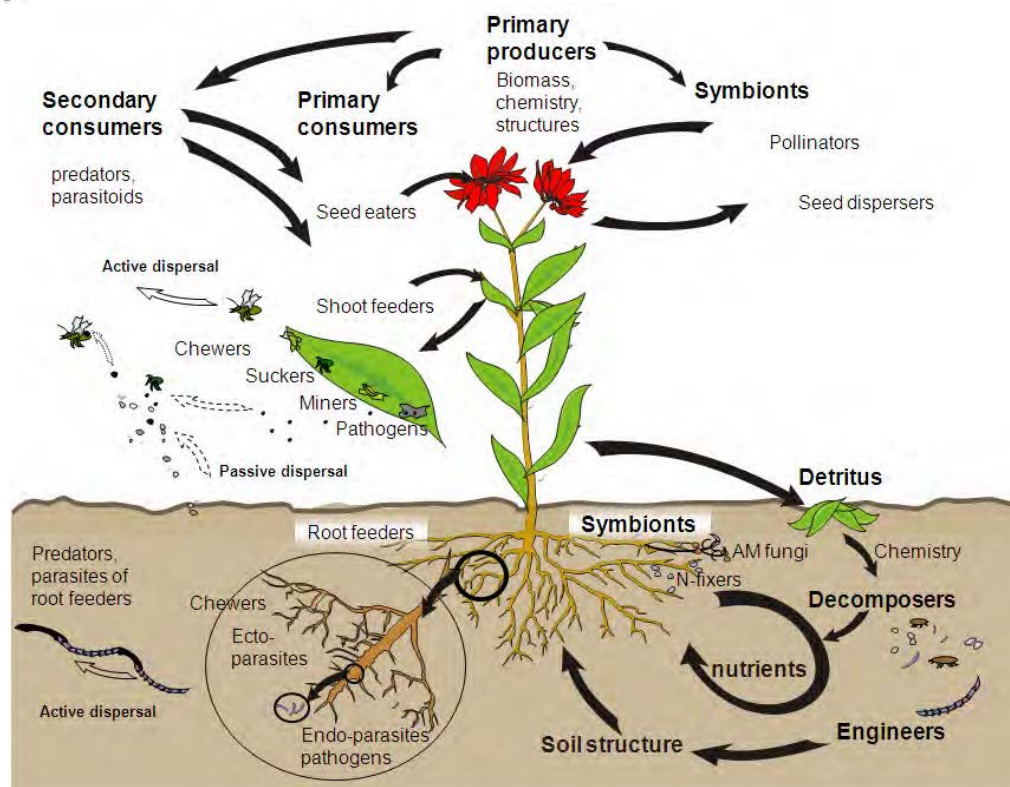
Figure 2-18: Interdependency of aboveground and belowground biodiversity. Adapted from (De Deyn and Van der Putten 2005)

It is worth highlighting that, regarding the ecosystem engineers, the majority of available information on factors regulating ecosystem engineers' ecology is on earthworms.

→ CLIMATE, TEMPERATURE AND SOIL MOISTURE

Abiotic regulations by climate are large scale determinants of microbial activities. The overall effect of climate on soil microorganisms can be perceived through the seasonal dynamics of microbial populations. These dynamics are due to the fact that **growth**, **activity** and **composition** of microbial communities are sensitive to the two main factors regulated by climate: temperature and moisture. Growth and activity rates are individual characteristics of microbial communities and may vary independently. This means that climatic conditions favouring a high level of microbial activity do not always facilitate a high microbial growth and associated increased biomass.

In general, a rise in atmospheric temperature corresponds to a rise in microbial activity. Thus typically, microbial growth and activity generally decrease in winter time, due to the decreased temperature. However, such expected seasonal dynamics may change in specific soil ecosystems, e.g. in tundra soils, microbial biomass is at its maximum in late winter time when temperature is low (Schadt, Martin et al. 2003). Thus, even if there is in general a positive correlation between temperature and microbial growth and activity, responses to temperature can also depend on the species of chemical engineers present in the microbial community and on the considered temperature range. Extremely high temperatures, in general, are deleterious for many microorganisms. Indeed, some species of chemical engineers may survive such adverse conditions by entering survival inactive forms, which may resist high temperatures

better than active individuals. It is worth highlighting that actually much uncertainty exists about how reactive different microbial groups (and fauna) are to temperature, e.g. some studies show no response of microbial to elevated temperature, or only weak relationship between mean annual temperatures and densities of microbial biomass (Wardle 2002).

The seasonal changes observed in soil microbial activity are also often associated to modifications in chemical engineers community composition. In general, fungi dominate during winter while bacteria are more active in the summer (Lipson and Schmidt 2004). This leads to yearly cycles in the activity of the various groups of soil within the functional group, which are important for the regulation of both the concentration and the availability of nutrients in the soil. Such changes in the composition and activity of chemical engineers community also mean that biotic interactions between chemical engineers and plants are not constant during the growing season (Bardgett 2005). For example, in Alpine meadows the microbial mediated N-immobilisation is at its maximum in autumn and winter when the local vegetation is in a senescent phase (Figure 2-19).
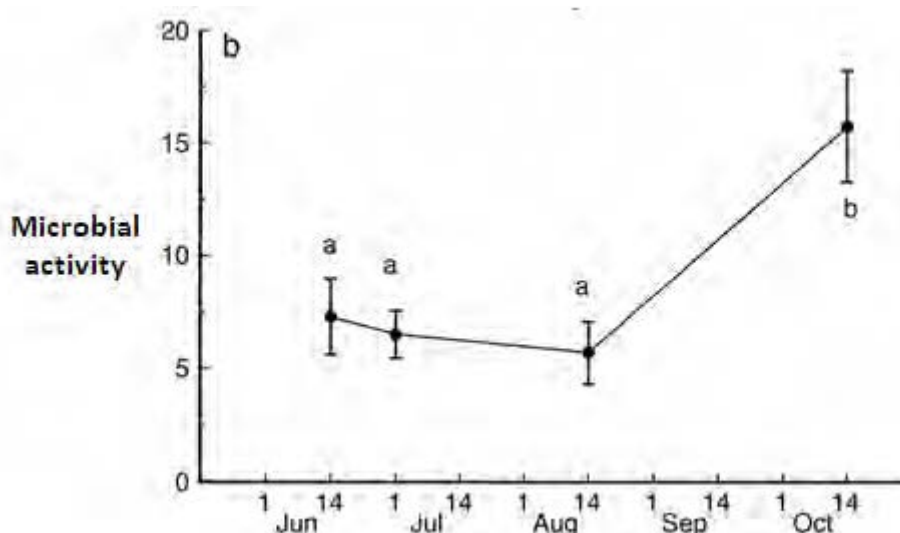
Figure 2-19: Monthly variation of microbial activity in Alpine meadows (Jaeger, Monson et al. 1999)

Conversely, immediately after snow melting, plants are more active and become dominant competitors in nitrogen up-taking (Jaeger, Monson et al. 1999).

Soil moisture can have both direct and indirect impacts on chemical engineers. Soil moisture directly influences the physiological status of bacteria (Harris 1980) and may limit their capacity to decompose various types of organic compounds. The soil moisture values for an optimal microbial activity vary depending on the basis of soil type and microbial community composition (Prado 1999). Soil moisture also indirectly influences microbial community growth, activity, and composition through the modification of the quality and the quantity of plant litter production. This can affect plant-microbes and engineers-microbes interactions. Microbes generally keep significant activities when plants are no longer able to be active. This is because their small size allows them to use water from the very small pores in which they live; this water being contained in small sized pores is very strongly retained by surface tension forces to pore walls. Plants cannot exert suctions beyond a certain value while

microbes that live in the water do not need to exert such strong pressures to obtain water.

Soil moisture can also indirectly influence a number of physical and chemical properties of soil, such as redox potential, pH, oxygen and carbon dioxide levels (Tiwari 1987), which can in turn influence the microbial population and overall activity.

In summary, variations in soil temperature and moisture can have strong direct impacts on chemical engineers and indirect impacts through influencing the plant-microbe interactions in the rhizosphere or soil properties (Dijkstra and Cheng 2007). Indeed, there are no general trends for these impacts, because they are strongly dependent on the considered microbial species, community structure and local soil characteristics. Thus, in a perspective of climate change, it is difficult to estimate the impacts on soil chemical engineers and individual studies focused on local soil ecosystems will be indispensible to develop a global view and appropriately measure the effects on soil biodiversity.

Temperature and moisture are also important determinant of biological regulators community structure and functioning. The main effects have been observed on nematodes and microarthropods, and are extremely important to estimate the impact of average temperature increase, due to climate change or other more local impacts, such as fires.

The sensitivity of nematodes to temperature and soil moisture (Ruess, Michelsen et al. 1999; Hoschitz and Kaufmann 2004) depends on their metabolic state. This class of organisms has a different strategy of survival in extreme environmental conditions and can form cysts or enter dormant stages allowing them to survive to the most extreme soil temperature and moisture changes (Wall and Virginia 1999; McSorley 2003). Thus, for example, *Steinernema Carpocapsae* can survive at 5°C in a dormant state. When extreme conditions occur in the reproductive period, juvenile nematodes can be gradually released from maternal eggs. This provides a temporal distribution of juvenile nematodes through the reproductive season and an insurance of a minimum survival even in adverse conditions, such as summer droughts (Van der Stoel and Van der Putten 2006).

The effects of high temperatures and droughts on nematodes are mainly dependent on how they influence soil moisture. In particular, the thickness of water films on soil aggregates surface is a key regulating factor. The sensitivity to soil moisture is of course dependent on the considered biogeographical zone and on the original hydrological conditions. In arid ecosystems such as deserts, for example, nematode survival is highly dependent on soil moisture, while in temperate zones (e.g. temperate grasslands) their survival is unlikely to be at stake, unless soils dry out completely (Papatheodorou, Argyropoulou et al. 2004; Strong, De Wever et al. 2004).

Temperature and soil moisture are also two of the most important abiotic factors regulating the biology of microarthropods (springtails and mites) and influencing the seasonal patterns of their population abundance (Cassagne, Gers et al. 2003; Roy and Roy 2006). The optimum average temperature for survival is just above 20 °C while the higher limit is around 50 °C (Vannier 1994). In general, species that live on the litter surface can tolerate higher temperatures than species living further down in the soil. Most springtails and mites have been reported to have their lethal temperature limits quite high, between 35 and 40 °C (Choudhuri 1963). Of course, species living in warm areas have a higher resistance to high temperature as compared to species living in temperate and cold areas. Temperature can also influence both springtails

development (through degrees days) and reproduction rates with important impacts on population growth (Diekkruger and Roske 1995; Choi and Ryoo 2003).

Similar to temperature, soil moisture can influence the reproduction and locomotion of springtails. In general, higher population densities of springtails are observed at increased humidity rates (Sjursen and Holmstrup 2004).

Closely related microarthropods species can differ in temperature tolerance and soil moisture sensitivity; each species seems to require quite specific temperature and moisture conditions (Christiansen 1964). In addition, thermo-tolerance varies depending on the developmental stages (Chown 2004). For example, like most species in the planet, juvenile springtails are more sensitive to heat than adults (Choudhuri 1963). Thus, when evaluating the impacts of climate variability on this functional group, the eventual difference in temperature and soil moisture sensitivity of different species should be considered for mature, as well as for the previous developmental juvenile stages.

Finally, climate can strongly influence the physiology of earthworms, through altering the soil temperature and moisture. Several studies report a seasonal variation in the growth and activity of earthworms in response to changes in temperature and soil moisture. Earthworms often lose weight, increase their burrowing activity, or enter into quiescence or diapause when soils are too dry (Booth, Heppelthwaite et al. 2000; Holmstrup 2001). In contrast, growth is favoured in soils with high levels of moisture and high temperatures. In the case of *Lumbricus terrestris*, for example, the optimum temperature and soil water potential for food consumption are about 22 °C and 7 kPa, respectively. These results suggest limited burrowing and more intensive feeding in wetter soils, through a greater consumption of soil and organic substances, while slightly drier, non-compacted soils favour tunnelling and exploration in the soil profile (Bolton and Phillipson 1976; Scheu 1987; Daniel 1991).

Such considerations are crucial for the conservation of soil biodiversity in a context of climate change. Soil moisture is one of the factors susceptible to be strongly altered. In particular, the higher frequency of droughts forecasted, could be a serious threats to earthworm communities, altering their feeding rate, their growth and their overall function of soil engineers.

→ SOIL TEXTURE AND STRUCTURE

The ecology of soil chemical engineers can be influenced by soil texture and soil structure. These two factors are critical determinants of microbial activity, because they control the protection and the availability of organic matter, which is the main resource of nutrients for this functional group. Depending on soil properties, microbes may have a more or less easy access to organic matter, and in unfavourable textural and structural conditions they can starve in the vicinity of high resource patches.

Some textural classes of soils favour microbial biomass and diversity more than others. Microbial biomass tends to be higher in clay rich and volcanic ash soils than in sandy soils (Sparling 1997). Interestingly, the effects of soil structural properties on organic matter availability, and the subsequent microbial activity rates are also strongly influenced by soil texture. For example, in loam and clay rich soils, the disruption of soil structure enhances nitrogen mineralisation more than in sandy soils (Hassink 1992), leading to a increased microbial activity.

Thus, both soil textural class and structure can impact this functional group. As a consequence such properties and the local chemistry of soil organic matter are

considered one of the best predictors of microbial activity (Grandy, Strickland et al. 2009). Some authors (Lauber, Strickland et al. 2008) have even shown that specific changes in soil properties can be used to predict changes in microbial community composition across a given landscape. These findings suggest that more detailed analyses of soil properties will enable identification of significant predictors of soil microbial distribution.

Soil properties, such as texture and structure, and land use can also have strong impacts on the ecology of all biological regulators. Regarding nematodes, the influence of soil structure on their biology is expected, since these organisms live in water-filled pores and in water films around soil particles. Soil porosity and aggregation rates play a crucial role in regulating the distribution of nematodes within the soil matrix. A positive correlation between larger pores and nematode biomass was found, for example, in grasslands (Hassink, Bouwman et al. 1993), probably because soil structure influences how soil microbial biomass is protected, which in turn affects the resource availability for bacterial feeding and fungal feeding nematodes (Griffiths and Young 1994).

Soil textural categories have both direct and indirect impacts on biological regulators. Direct effects of soil texture on physiology of nematodes have been observed, but vary among species. Reproduction of some species for example (e.g. the root knot nematode *Meloidogyne Incognita*), is greater in coarse-textured soils than in fine-textured soils, whereas for other species (e.g. *Rotylenchus Reniformis*) reproduction is favoured in loamy sand with intermediate percentages of clay and silt (28%) (Koenning 1996). Indirect effects of soil texture are rather link to the effects on soil moisture. Soil moisture is influenced by soil water retention capacity which is in turn associated to the textural class. Such indirect impacts on soil moisture can influence nematode abundance and community composition (Koppenhofer, Kaya et al. 1995).

Soil texture also influences the biomass of larger sized organisms, including some genera of microarthropods such as springtails and mites. The interactions of microarthropods with their prey are favoured by large pore sizes. Thus, the abundance of microarthropods is higher in coarse than in fine-textured soils and soil compaction reduces microarthropod abundance (Didden 1987; Heisler 1991; Heisler and Kaiser 1995) (see also section 4.).

Finally, soil texture can also strongly affect the total biomass of soil earthworms. Medium textured (loamy) soils with high silt contents are favourable environment for earthworms and facilitate a high population density and biomass. In contrast, sandy soils are a less appropriate environment because they present too low water retention potentials and the sharp shape of sand particles can cause the abrasion of the body surface of earthworms. Clay soils have a more favourable water retention potential than sandy soils and a smoother texture. However, the average temperature of clay soils makes them less appropriate for earthworms than the medium textured ones (Kainz 1991).

Similar to what happens for biological regulators, soil texture can also regulate the biotic interactions between earthworms and microbial organisms. In particular, differences in habitat conditions (e.g. water regimes) and in the distribution of resource availability in clay and sandy soils may influence the vertical distribution of earthworm activity leading to indirect effects on microbial biomass. In deeper layers of clay soil, for example, earthworm activity increases the transport of crop residue into the subsoil (Hendrix, Peterson et al. 1998).

The relationships between the abundance and activity of earthworms, and soil texture are not general and vary depending on the species considered. In addition, the influence of soil texture depends on the eventual effect of other environmental factors or threats (e.g. tillage) which can alter the relation between the number of earthworms and soil properties. As most earthworm studies have been conducted with absent or reduced tillage, these results are in general quite well related to soil textural properties (Nuutinen, Pitkanen et al. 1998; Klok, Faber et al. 2007; Joschko, Gebbers et al. 2009). In conclusion, we can say that soil properties such as soil texture induce the basic abundance pattern of earthworms in agricultural soils which can be further modulated by management practices such as tillage (Fox 2004).

→ SALINITY

Most studies investigating the effects of salinity on microbial diversity and functioning are laboratory-based and difficult to extrapolate to field conditions. This is in general valid when studying the impacts of salinity on soil organisms, thus not limited to chemical engineers.

In open fields, a modification of soil salinity often occurs near the surface, in the top soil, where both organic matter and soil microbial activity are typically concentrated. As a consequence, changes in soil salinity could directly and indirectly affect microbial activity. The direct effect of salinity is to alter microbial physiology, while the indirect effect is done through a modification of organic matter solubilisation and availability of nutrients.

Only few studies have analysed the effects of salinity on soil chemical engineers, and often show contradictory results (e.g. in some studies a high salinity is shown to favour microbial biomass while in others salinity is rather deleterious) (Laura 1973; Laura 1976; Sarig, Roberson et al. 1993; Nelson, Ladd et al. 1996). This may be due, at least in part, to the complex interactions between direct and indirect impacts of salinity on this functional group. In principle, an increased salinity has a negative effect on microbial osmotic capacity and survival. However, it is also possible that, in specific conditions, soil organic matter becomes more soluble at high salinity, and the increased availability of nutrients may reduce the effects of osmotic stress on microbes (Wong, Dalal et al. 2008) (Figure 2-20). Moreover, different microbial communities can present specific sensitivity to salinity and consequently different decomposition efficiencies in salty conditions (Rietz and Haynes 2003). This kind of effects could partly explain the observed contradictory results.
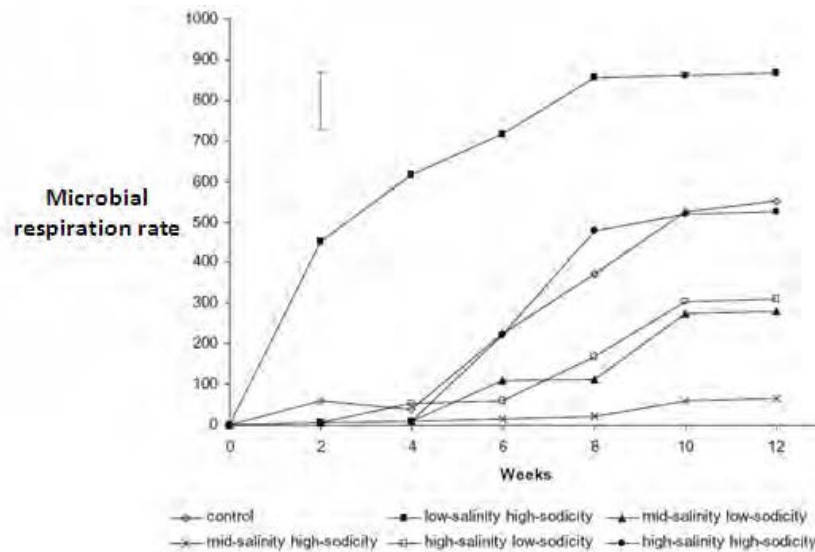
Figure 2-20: Soil microbial respiration at different salinity and different levels of available sodium (sodicity). Respiration rate are higher at high than at medium salinity, due to a compensatory effect on organic matter solubility. Salinity varies from 0.5 to 30 (soil electrical conductivity) (Wong, Dalal et al. 2008)

Salinity can also influence the viability of biological regulators. In particular, nematodes can be highly sensitive to salinity variations. When exposed to high salinity, nematodes may undergo osmobiosis which is a dehydration response to the osmotic stress. Individual nematodes species present different tolerance to salinity and their spatial distribution may reflect the differential sensitivity to salt.

Salinity may affect nematodes population density through a modification of their development, survival, and capacity to infect plants. Inter-species sensitivity is so variable that the impacts may vary even within the same category of species. In the case of plant parasitic nematodes, for example, some species are neutral to a salinity increase while other species show an impaired development and ability to infect plants (Thurston, Ni et al. 1994). In specific environments, like the dry valleys of Antarctica, a number of studies have shown that soil salinity is a key factor in explaining the abundance and community structure of soil nematodes (Freckman and Virginia 1997; Courtright, Wall et al. 2001; Barrett, Virginia et al. 2004).

High salinity leads to the desiccation of springtails. Owing to their physiological characteristics (they absorb water and ions from the soil), springtails are particularly sensitive to salt stress. Thus, soil salinity may have a profound effect on the hydration of these organisms. Reproduction of springtails was significantly impaired at intermediated values of salinity (measured as electrical conductivity: 1.03 dSm-1) while absolute cessation of reproduction occurred at high salinity (1.62 dSm-1)(Owojori 2009)(Figure 2-21).
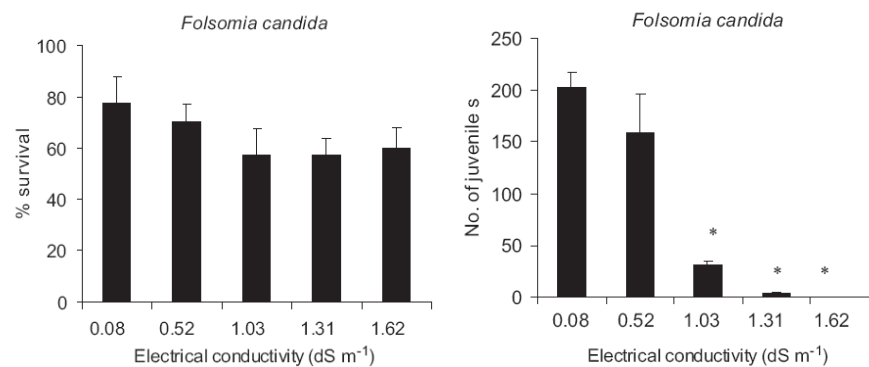
Figure 2-21: Survival and reproduction of a species of springtails (*Folsomia candida*) exposed to natural soils of varying salinity (measured as electrical conductivity) for 4 weeks under controlled laboratory conditions

Finally, survival and reproduction of earthworms can be strongly affected by salinity. For the species *E. fetida*, for example, a salinity corresponding to an electrical conductivity (EC) of 1. 03 dSm^{-1} is already lethal after few days of exposure (Figure 2-22).
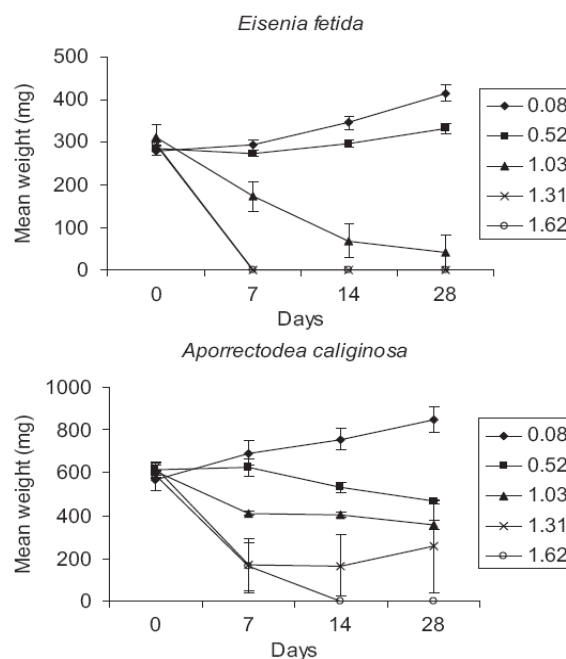
Figure 2-22: Growth of two earthworms species (*Eisenia fetida* and *Aporectodea caliginosa*) exposed for 4 weeks in soils of varying salinity under controlled laboratory conditions (Owojori 2009)

However, to date, most data have been collected in artificial soils and may under- or overestimate effects in natural soils (Robidoux and Delisle 2001). In fact, the bioavailability of salts is not the same in natural and laboratory conditions. In general, salt toxicity is lower in natural soil, probably because of the absorption of salts with the organic matter (Table 2-2).

These experimental difficulties, valid for all functional groups, leave the question open about how soil organisms in general respond to salinisation.

Table 2-2: Comparison of salt toxicity for the earthworm *Eisenia Fetida*, in natural and artificial soils (Robidoux and Delisle 2001)

Salt	Toxicity (LC_{50}[24]) – artificial soil	Toxicity (LC_{50}) – natural soil
Sodium Chloride	3.2	17.2
Calcium Magnesium Acetate	14.8	35.8

When considering the impacts of high salinity on earthworms, the fact that a high salinity may favour the bioavailability of metal contaminants and consequently their toxicity, should also be taken into account. This process could affect the survival of all soil organisms, but in particularly of earthworms, which are extremely sensitive to metal contaminants, however with large interspecies variations.

→ **PH**

Changes in soil pH can affect the soil chemical engineers through a direct effect on their survival, as well as through a modification of their metabolism. In fact, several enzymes whose activity is crucial for the regulation of microbial metabolism, such as nitrogenase, are dependent on soil pH. Moreover, the solubility of nutrients and the ionisation of mineral elements are also regulated by pH values.

Phosphorus (P) availability, for example, is strongly influenced by soil pH. Availability of P is maximised when soil pH is between 5.5 and 7.5. Acid soil conditions (pH < 5.5) cause dissolution of aluminium and iron minerals which precipitates with solubilised P and rend it unavailable. Basic soil conditions (pH > 7.5) cause excessive calcium to be present in soil solution which can precipitate with P, again decreasing P availability. The optimum for P availability is then a neutral to slightly acidic pH.

As for chemical engineers, soil pH is one of the abiotic factors susceptible to influence biology and activity of biological regulators. Regarding nematodes, little information is available and is often contradictory. As for other parameters, the sensitivity of nematodes to soil pH, both in terms of survival and activity, depends on the considered species and could be correlated to other environmental factors (Crommentuijn, Doodeman et al. 1994; Spurgeon and Hopkin 1996; Korthals, Smilauer et al. 2001). A correlation, for example, has been demonstrated between pH and copper related toxicity. The effect of copper contamination is generally enhanced with decreasing soil pH. The effect of pH on heavy metal availability in soil depends on the fact that by increasing the pH usually heavy metals precipitate as hydroxides. Species composition and the abundance of trophic groups are in general more sensitive than the total number of nematodes.

Soil pH is considered a key factor determining species diversity of microarthropods communities, including springtail and mites. Regarding springtails, an increase of population density and local diversity in relationship to soil acidity has been reported. Springtails have inherited specific physiological characteristics following the adaptations during their evolutionary path that allow them to choose the top of the acidic soils as a particularly favourable environment (Loranger 2001). In the case of mites, response to pH is less clear than for other groups (van Straalen 1998). Mites prefer neutral pH in laboratory conditions (Bedano, Cantu et al. 2005). However, similarly to what has been observed for nematodes in natural environments, the response of a species of microarthropods to soil pH can be strongly dependent on the environmental context (presence of toxic compounds, type of vegetation, etc.).

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[24] LC_{50} is defined as the concentration of a chemical that will kill half of the considered population. Thus a high level of LC_{50} corresponds to a low toxicity.

In conclusion, the results on pH sensitivity of soil microarthropods obtained in laboratory conditions are only indicative for field extrapolations. The local environmental context and the individual sensitivity of the analysed species should always be considered in the evaluation. This is valid for biological regulators, but also for the other soil functional groups.

Similarly to what has been observed for biological regulators, soil pH governs the uptake of toxic compounds by soil engineers thus modifying their sensitivity to pollutants. This could impact a number of earthworm physiological parameters, including reproduction rate. Earthworms, in general, have higher biomasses and diversities at neutral pH (Figure 2-23) although a comparison among temperate and tropical patterns showed a relatively better tolerance (one pH unit) of tropical species to acidification as compared to temperate ones (Lavelle et al. 1995).
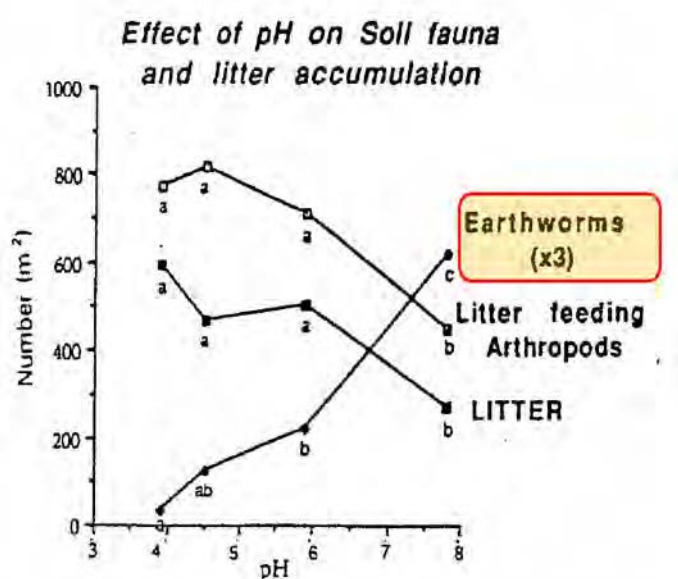
**Figure 2-23: Effect of soil pH on earthworms in temperate soils
(Lavelle and Faille, unpublished data)**

2. 2. 2. BIOTIC INTERACTIONS

Within soil food webs, functional groups can be controlled by bottom-up or top-down biotic interactions. In general, bottom-up interactions are those that involve resource uptake at a bottom level having impacts at an upper level. This can be fresh root material in the case of plant feeders, dead roots, root exudates and litter in the case of primary decomposers or preys in the case of secondary decomposers and predators. Top-down effects are mainly driven by predation: predation performed by an organism at upper level of food web can have impacts on organisms at lower levels. Both bottom-up and top-down control involve competition for resources (Rassman et al. 2005, Piskiewicz et al. 2009). After many years of debate, the current view is that most species can be controlled by both bottom-up and top-down effects, which may change dynamically over time (Moore et al. 2003)

Here, the main bottom-up and top-down biotic interactions between the three soil functional groups are presented.

→ ABOVEGROUND/BELOWGROUND INTERACTIONS

Despite being separated in space, aboveground and belowground organisms influence each other, both directly and indirectly. For instance, large herbivores feeding aboveground can have strong indirect impacts on soil belowground communities (Box 13). Similarly, plants, as primary producers possessing belowground (roots) and aboveground (leaves, stems and flowers) organs, play a direct role in linking above and belowground organisms (Van der Putten, Vet et al. 2001; Wardle 2002). The main biotic interactions among plants and soil functional groups are presented below.

Box 13: The feedback effect of large herbivores feeding

The majority of research works on the impacts of herbivore feeding activity are focused on plant community structure or biodiversity. However, herbivores may also have positive or negative indirect effects belowground, on soil organisms and cycling of nutrients. For instance, acceleration of nutrient cycles occurs when herbivores promote the supply of labile substrates to soil as faeces and/or root exudates, which stimulates soil decomposer activity, rates of nutrient mineralization, and uptake of nutrients by grazed plants (Bardgett and Wardle 2003). In contrast, deceleration of nutrient cycling occurs when selective feeding on nutrient rich plant species leads to the dominance of plants that produce poor quality litter, or when herbivory induces the production of secondary metabolites in foliage which reduce litter quality and decomposability. Moreover, in extensively grazed conservation meadows, a long-term exclosure study, has demonstrated that large herbivores influenced soil biodiversity through altering vegetation composition (Veen et al. 2009).

Herbivores grazing can also heat up the soil, stimulating ant activity. The ants bring up fresh soil from deeper layers, which contain less nematodes and microorganisms. As a result, soil on ant mounds becomes more appropriate for plants that are normally sensitive to soil nematode and microbial pathogens. Such biotic interactions, depending on the context, can finally create mosaics of plant diversity (Blomqvist et al. 2000).

Plants and chemical engineers

Interactions between plants and chemical engineers have an important role in plant community development, plant diversity, nutrient cycling and in the maintenance of overall soil structure. The interactions between plant roots and microorganisms are important and they occur through a molecular crosstalk. These interactions can be beneficial, detrimental and neutral. Plant-microorganism feedback interactions are case sensitive and depend on plant species, plant taxonomic (or functional) groups and site-specific differences in soil properties (Bezemer, Lawson et al. 2006). This means that the key interactions may be context-dependent, but that plant-soil interactions generally play a major role in regulating aboveground biodiversity and ecosystem functioning.

In general, plants may strongly affect soil microbial community composition (Grayston, Wang et al. 1998; Miethling, Wieland et al. 2000) since the abundance, activity and composition of bacterial communities in the rhizosphere vary according to vegetation diversity, depending mainly on the biochemical diversity of their root exudates (Lavelle, Lattaud et al. 1995; Wardle, Bonner et al. 1999).Vice versa, in many soil ecosystems, plant growth is limited by the amount of nutrients released by bacteria and fungi, such as NH_4^+, which depends on the microbial driven decomposition rate.

In the perspective of climate change, any modification of atmospheric CO_2 concentration would influence this relationship through altering plant growth and productivity, hence the quality and quantity of organic substrates   entering soil as

exudates and litter, thus finally influence the availability of substrate for decomposer microorganisms (Figure 2-24)(Zak, Pregitzer et al. 2000) and can have either positive or negative influence on the nutrient mineralisation. The increase in the atmospheric CO_2 concentration would stimulate the photosynthetic activity of certain species of plants and thus could affect the microbial functions in the rhizosphere which are generally carbon-limited. This would happen indirectly through modifying root deposition. Other indirect effects caused by the greater soil carbon allocations concern the enhancement of soil structure and the increase in the plant uptake of nutrients and water. This could cause a decrease in the amount of available nitrogen with competition between plants and microorganisms, favouring microorganisms and provoking a decrease in plant growth. Apparently, the different results on activity, composition and size of soil microflora and on the interaction between microorganisms and plants and microorganisms and fauna depend in fact on the different plant-soil systems studied having different intrinsic characteristics and the different techniques used having different sensitivities. Mycorrhizal infections of plant roots under elevated CO_2 concentration, for instance, are generally stimulated due to the increase in the carbon allocation rates to roots. However, future research should address the central role of mycorrhiza in the context of global change, as they appear to be a keystone in the CO_2 –related response.
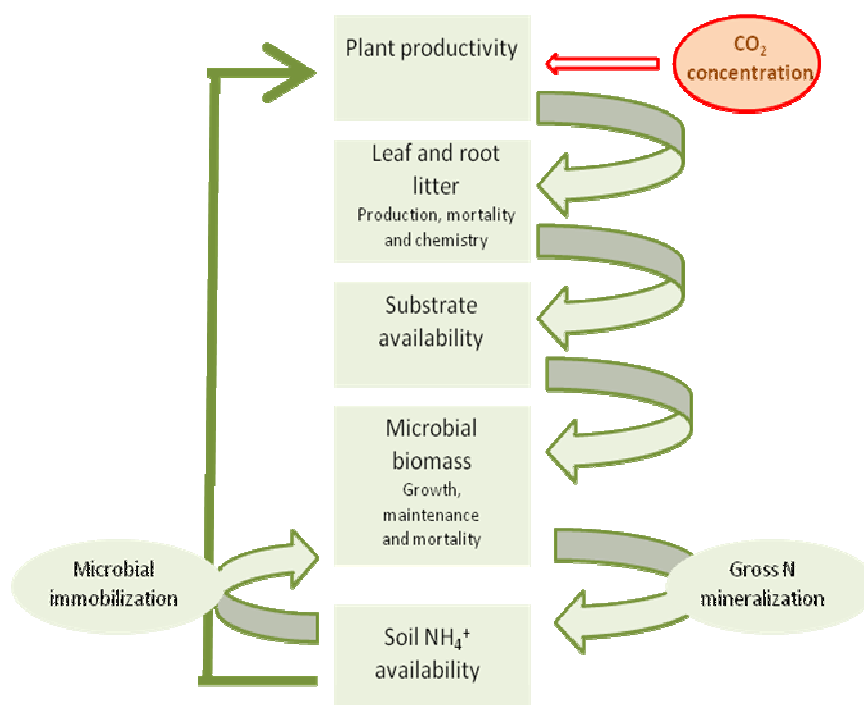
Figure 2-24: A conceptual model illustrating the links between plant productivity and microbial activity in terrestrial ecosystems (adapted from (Zak, Pregitzer et al. 2000))

Plants can also set up mutualistic interactions with fungi. The majority of vascular plants are associated with mycorrhizal fungi. The plants through this interaction benefit from an increased capacity to extract phosphorus, water or other nutrients from the soil, whereas the fungi obtain carbohydrates from the plants in return (Box 8). The relationship between plants and soil fungi can also regulate the spatial patterning of a plant community, for example in temperate forests plant-pathogenic soil fungi actively contribute to tree spacing by killing off saplings in the vicinity of the parent trees (Packer and Clay 2000).

In brief, the physiological activities of both plants and soil microbial communities and their interactions control the flow of nutrients, such as carbon and nitrogen in terrestrial ecosystems.

Plants and biological regulators

The biotic interactions between the biological regulators and the ecosystem engineers are, to our knowledge, limited to the parasitic interactions between nematodes and plant roots. Root-knot nematodes and cyst nematodes for example, are obligate pathogens of numerous plant species feeding exclusively on the cytoplasm of living plant cells. These organisms cause dramatic changes in the morphology and physiology of their hosts and a number of plant processes are altered by nematodes as they establish their specialised feeding cells. Thus, plant-parasitic nematodes can devastate a wide range of crop plants, causing huge economic losses in agriculture each year.

Plants and ecosystem engineers

Similarly to chemical engineers, ecosystem engineers may also have an important influence on plant community structure by altering plant nutrition. This influence can be direct or indirect (Figure 2-25).
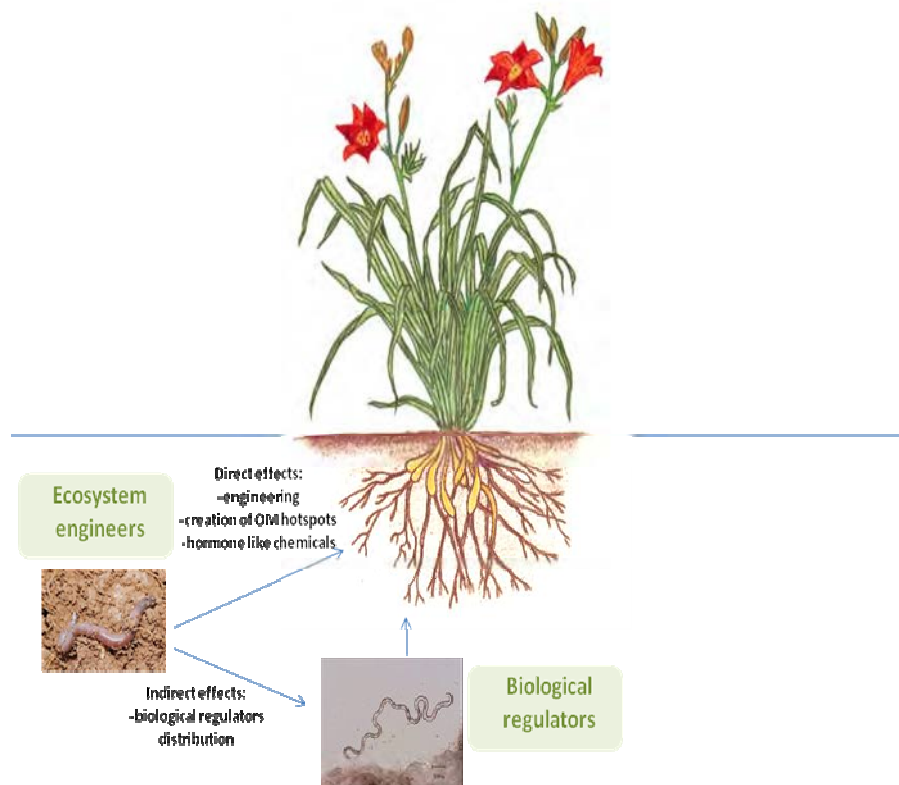
Figure 2-25: Direct and indirect effects of ecosystem engineers on plants

Ecosystem engineers can directly determine the plant community structure through their engineering action, the creation of organic matter hotspots, or through the release of active compounds. Earthworms, for instance, may actually influence plant health and defence through the production of hormone like products (Bezemer, De Deyn et al. 2005; Blouin, Zuily-Fodil et al. 2005) while termite mounds, ant mounds and gopher mounds in different region of the world can locally determine the vegetation type and favour specific plant species which can be extremely different from those in the surrounding landscape (Hobbs and Mooney 1985; Spain and McIvor 1988;

Blomqvist, Olff et al. 2000). Interestingly, food choice experiments show strong termite preferences in favour of the plant species growing on their own nest. Therefore, there is a clear agreement between plant preferences for soil altered by termite activity and termite preferences for plant species favoured by their engineering action (Konaté 1998). In addition, ecosystem engineers benefit from the plant roots to stabilise their nest and of the presence of nectar as a food source. Thus, in some cases, the biogenic structures produced by ecosystem engineers, in addition to the direct advantages, could also have indirect positive effects on their fitness.

The spatial patterning of the activity of soil engineers can also have important effects on the growth of individual plants due to the creation of organic matter hotspots. The amount of nutrients, such as phosphorus and nitrogen for example, is higher in earthworm casts and burrows than in the surrounding soil (Heine and Larink 1993) creating hotspots of resources which are available for roots growth. The capacity to locate such nutrient enriched patches and the optimal patch size varies among plant species (Campbell, Grime et al. 1991; Hutchings 1994), which cause ecosystem engineers to selectively favour or disfavour plant species, which will alter their competitive balance and, therefore, plant diversity and community composition.

Ecosystem engineers can also have an indirect effect on plants through a modification of the spatial distribution of biological regulators. This phenomenon has been observed, for example, in the Netherlands, where ants in semi-natural grassland soil bring fresh subsoil to the surface, which provides the plants with a substrate that is free of plant-parasitic nematodes. This condition favours the grass (red fescue*: Festuca rubra*) over sedge (sand sedge: *Carex arenaria*). After a while, the soil becomes colonised again by plant-parasitic nematodes, which results in the replacement of the grass by the sedge (Olff, Hoorens et al. 2000).

Aboveground-belowground interactions through plant defensive chemistry

Plants have a variety of chemical defences that often increase in concentration following attacks by herbivores. Such induced plant responses can occur aboveground, in the leaves, and also belowground in the roots (e.g. release of toxic compounds). Soil organisms can also induce defence responses aboveground and vice versa.

The effects of belowground organisms on aboveground plant defence can be direct or indirect. Several soil organisms (nematodes, mycorrhizal fungi, etc.) which pass a part of their life cycle in association with plant roots can directly influence the release of defence molecules in the aboveground parts of the plant, thus finally changing the plant defence efficiency against aboveground pests and herbivores. Alternatively, indirect defence involves the attraction of the enemies of the herbivores and pests, as, when they are fed upon, plants emit volatile compounds that are attractive for herbivores and pest enemies.

Similarly to belowground organisms, aboveground herbivores can influence belowground plant defence responses. Plant feeding by caterpillars, for instance, caused a decrease in toxic molecules capable of reducing the growth of pathogenic fungi in ragwort roots. Indeed, the effects of aboveground organisms on belowground plant defences, even if less severe that the opposite effects, can significantly alter the soil community composition (Poveda, Steffan-Dewenter et al. 2003; Bezemer and van Dam 2005).

→ **BELOWGROUND/BELOWGROUND INTERACTIONS**

Chemical engineers and biological regulators

Biological regulators can modulate microbial activity by regulating their number, mainly through grazing. In fact, several species of protists, as well as bacterivorous nematodes, graze on bacteria. Thus, the biomass of methanotrophic bacteria is partly determined by the grazing activity of local protists (Murase and Frenzel 2008). Similarly, food web studies in a range of soil systems have shown that the availability of mineralised nitrogen for vegetation is dependent for approximately one third on the predation of microbes, which releases mineral nutrients that become available for plant uptake (Clarholm 1985). For instance, protists can modify the composition of microbial communities of the rhizosphere through grazing on selected plant growth promoting rhizobacteria (Bonkowski 2002). Nitrogen and phosphorus mineralisation rates can also be regulated by grazing on soil fungi (Ingham, Trofymow et al. 1985). Effects of grazers become evident when they are selectively omitted. For example, the elimination of nematodes reduce the overall nutrient mineralisation and consequently causes a decrease in both nitrogen and phosphorus uptake by wheat (Hu, Li et al. 1998).

However, biological regulators may also stimulate and shape microbial activities through more complex mechanisms. For instance, during the grazing process a number of nutrients and stimulating compounds become more available for microorganisms thus favouring their growth (Swift M J, Heal O W et al. 1979; Ratsak, Maarsen et al. 1996). Moreover, the migration of nematodes creates porosity and improves the ventilation in soils, enabling the transport of previously unavailable nutrients to microbes. In addition, root-feeding nematodes affect the quantity and quality of rhizosphere deposit, inducing plants to produce secondary protection substances (Kerry 2000), which have an impact on microbial diversity. Finally, biological regulators can promote the heterogeneity of the micro-environment and thus the diversity of microorganisms (Ritz, Griffiths et al. 1997). On the other hand, microorganisms can inhibit the reproduction of biological regulators in the rhizosphere. Some species of fungi, for example, produce chemicals that may inhibit the hatching of eggs and the mobility of juvenile nematodes (Kerry 2000).

The local effects of biotic interactions among chemical engineers and biological regulators vary locally, depending on several factors, including (Bardgett and Chan 1999):

- Chemical engineers and biological regulators local species composition
- Selective grazing: micro-predators may prefer some microbial species to others. Bacteria-feeding nematodes, for example, prefer to graze soil bacteria which are in suspension, while protists prefer to graze larger and rapidly growing bacteria. As a consequence, the feeding rate of micro-fauna can change the competition advantage among different types of microbial communities, and may offer a growth dominant condition for fungi via grazing on bacteria. Thus, through a selective grazing, protists and nematodes could strongly affect the structure and the functioning of the soil microbial community.
- Local soil physicochemical characteristics: C/N ratio, organic matter content, pH, etc.

Soil microbes can also act as antagonists to pathogens (protection from pest), or as pathogens to plants or other soil organisms, thereby contributing to the biological regulation function (see also section 3.6).

Chemical engineers and ecosystem engineers

Soil ecosystem engineers select and regulate the communities and activities of chemical engineers that inhabit their functional domains (Lavelle, Bignell et al. 1997) through a direct action on their ecology or through an influence on biological regulators that operate food web regulations inside these domains (Marinissen and Bok 1988; Loranger, Ponge et al. 1998; Decaens, Jimenez et al. 1999). They can have predatory or mutualistic interaction with chemical engineers.

The mutualistic relationships are developed with the microorganisms that pass through their gut thanks to the ingested soil and in the biogenic structures which they build thereafter. The selective reactivation and incubation of microbes within the earthworm's gut causes a crucial first step of activation in the organic matter decomposition process. In soils that have been experimentally treated with earthworms, for example, soil microbial biomass is reduced, while the metabolic activity of earthworms is increased (Scheu 1992). A similar effect also occurred with termites and ants (Abbadie and Lepage 1989; Dauber and Wolters 2000; Petal, Chmielewski et al. 2003; Brauman, Daily et al. 2007).

Generally predominant mutualistic relationships among chemical engineers and ecosystem engineers may turn into or occasionally comprise predation. The ecosystem engineers grazing on fungi, for example, can modulate the fungal growth in both positive and negative ways depending on the grazing intensity (e.g. the hyphal length of a fungus is greatest when subjected to intermediate intensities rather than low or high intensities of earthworm grazing)(Wardle 2002).

Another common mutualistic interaction among fungi and plants are mycorrhizal fungi and rhizobia

2.3. CONCLUSIONS

The **high diversity** of soil organisms is reflected in the vast range of functional roles that they perform. As has been seen, soil organisms can be broadly separated into **three main functional categories**: chemical engineers, biological regulators, and ecosystem engineers, **living and acting at different spatio-temporal scales**.

As stated at the beginning of the chapter, it should be noted that the three functional groups presented here do not cover all the soil organisms present in soil, but only the key ones which are considered to have a major functional role. In addition, it is worth stressing that several knowledge gaps exist on components of soil biodiversity, and that **new groups of soil organisms** with potentially high ecological significance (e.g. Archaea) have only recently been considered as having specific functions in soil ecosystems. Thus, the classification proposed here should be regularly reviewed in the light of the constantly evolving scientific findings on soil organisms.

As has been seen in section 2.2, a **hierarchy of both biotic and abiotic factors** govern the composition and activity of the soil community **at different spatial/temporal scales**. Among the abiotic, temperature, moisture, pH, salinity and some soil characteristics are the main factors to consider, while the key biotic interactions for the soil ecosystem functioning occur between the three functional groups and are often bi-

directional. The role of these biotic and abiotic factors in driving functions will be **biome/habitat specific**, and will also vary depending on geographical parameters (e.g. topography) and, of course, **depending on the species considered**. Moreover, within the same species, the same factor (e.g. temperature) can have different effects, depending on the **developmental stage** or the **life history traits** for a single individual. Finally, depending on the context, abiotic factors could control biotic factors, or vice versa. Thus, in order to better understand the influence of a range of biotic and abiotic factors on soil ecosystems, a **case-based approach**, analysing the effects of determinate conditions (e.g. climatic scenarios) on the key species of a specific soil ecosystem should be taken. In general, when considering the influence of regulating factors, an **above-below ground perspective** taking into account what is occurring above ground (e.g. the presence of mammal herbivores) should be a priority, and the potential for such interactions to influence soil functions should always be considered. Thus, in conclusion, *in situ* field studies, even if more difficult to carry outwill be more informative regarding the real influence of interacting abiotic and biotic regulating factors on soil ecosystems (e.g. above-below ground interactions), while laboratory studies will be more easily performed to obtain information on the impacts of a specific biotic or abiotic factor on a single species.

→ MAIN RESEARCH GAPS

- **Function of new groups of soil organisms (e.g. archea)**
- **More evidence on the relationship between soil diversity and soil functions**
- **Deeper knowledge on mechanisms underlying a specific function**
- **How abiotic and biotic factors influence soil organism mediated functions through the modification of single species biology**
- **More data on the impacts of a specific factor on an individual species (e.g. salinisation on nematodes).**

3. SERVICES PROVIDED BY SOIL AND RELATED BIODIVERSITY

3.1. INTRODUCTION

As discussed in the previous chapter, the community of organisms living in soil carries out a very broad range of biochemical and biophysical processes that regulate the functioning of the soil itself and that can also affect the neighbouring ecosystems. Many of these functions also provide essential benefits to human society. Most of these services are supporting services, or services that are not directly used by humans but which underlie the provisioning of all other services. These include for instance nutrient cycling and soil formation. In addition, soil biodiversity is involved in all the main regulatory services, namely the regulation of atmospheric composition and climate, water quantity and quality, pest and disease incidence in agricultural and natural ecosystems, and human diseases. Soil organisms may also control, or reduce environmental pollution. Finally, soil organisms also contribute to provisioning services that directly benefit people, for example the genetic resources of soil microorganisms can be used for developing novel pharmaceuticals.

Each function may contribute to services either directly or indirectly. For instance, nutrient cycling clearly underlies crop production, while soil engineering affects water storage and transfer, and soil biodiversity offers a reservoir of species which may contribute to pest control, decontamination, or to the development of new medicines. Other functions performed by soil and soil biodiversity contribute more indirectly to human well-being, such as soil organic matter decomposition which contributes to carbon storage and climate control. A key question is thus the definition of the relationships between soil, soil biodiversity and the ecosystem goods and services which are derived from its functions.

The six main ecosystem services related to soil and to soil biodiversity considered in this study are:

- **Soil organic matter recycling and fertility**, including soil formation: a basic function that supports nutrient cycling and primary production which then contributes to biomass production
- **Regulation of carbon flux and climate control** via the carbon storage
- **Water cycle regulation,** infiltration, storage, purification, transfer to aquifers and surface effluents, erosion prevention and regulation of flows in effluents (flooding or drying out of rivers)
- **Decontamination and bioremediation:** a chemical and physical neutralisation of contaminants
- **Pest control:** biological control of pests and pathogens of plants, animals and humans.
- **Human health:** this includes both direct (e.g. provisioning of pharmaceutical molecules) and indirect services (e.g. avoided impacts linked to the non-provisioning of the above mentioned services)

In the definition of these six services, for the sake of simplicity and to avoid double-accounting, several sub-services has sometimes been grouped into one service. The

following table show the comparison among our grouping and the services defined in the Millennium Ecosystem Assessment (MEA) report. For each identified service, the soil organisms and the related processes underlying the service's provision, as well as its utility for human society, will be presented.

Table 3-1: Comparison of the services classification of this report with MEA nomenclature

This report	MEA nomenclature	Category of service
Soil organic matter recycling and fertility, including soil formation	Decomposition, nutrient cycling, soil formation, primary production, erosion regulation	Supporting and Provisioning
Regulation of carbon flux and climate control	Climate regulation	Regulating
Water cycle regulation	Water regulation and water purification	Regulating
Decontamination and bioremediation	-	Regulating
Pest control	Diseases regulation	Regulating
Human health	Diseases regulation	Regulating

3.2. SOIL ORGANIC MATTER RECYCLING, FERTILITY AND SOIL FORMATION

Soil fertility can be defined as the ability of soils to support plant growth by ensuring the adequate recycling of organic matter and nutrients. The contribution of soil organisms to soil fertility can thus be decomposed into its supporting and provisioning services:

- **Supporting services** such as nutrient cycling and decomposition of organic matter, that support life and other ecosystem services such as plant production and soil formation. Soil formation or pedogenesis is the process by which soil is created.
- **Provisioning services** such as production of crop or plant biomass, also called primary production (Figure 3-1), that provide goods to society.

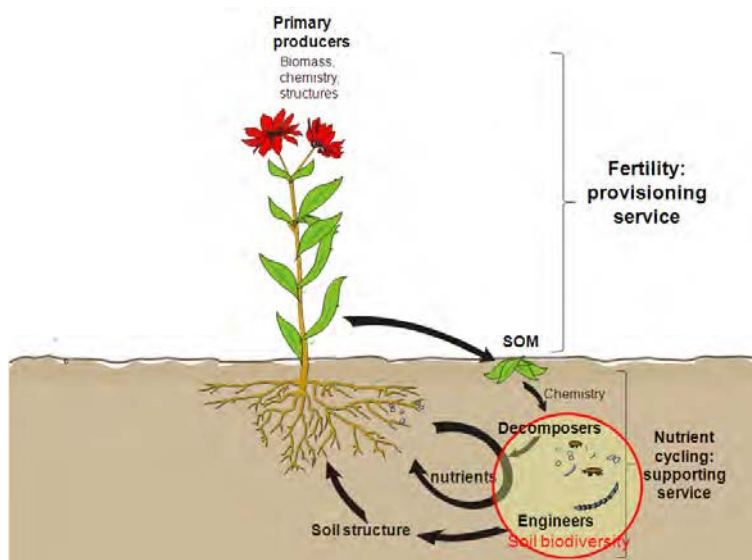**Figure 3-1: Relationship between soil organic matter cycling (supporting service) and fertility services (provisioning service)**

➔ **SUPPORTING SERVICES**

Soil biodiversity drives two main supporting services which are interwoven: organic matter decomposition and nutrient cycling. Soil biotas decompose dead organic matter resulting in the formation of more complex organic matter called humus (Box 1) that participates in general soil formation and quality maintenance through its specific properties (cation retention, hormone like effects on plants, water retention, and stabilisation of soil aggregates). Humus is an important buffer, reducing fluctuations in soil acidity and nutrient availability. Thus, the organisms living in and on the soil can contribute to the formation of distinct humus giving rise to distinguishable soil types. For instance, coniferous forests have acidic leaf litter and, with the help of local soil organisms, form what are known as inceptisols, while mixed or deciduous forests leave a larger layer of humus, changing the elements leached and accumulated in the soil, forming what we call the alfisols.

Although chemical engineers are the main actors of organic matter decomposition, all three functional groups are involved in organic matter recycling. As a consequence, organic matter recycling is regulated in a very complex manner, by all the biotic and abiotic factors controlling the ecology of soil organisms (section 2.2).

➔ **PROVISIONING SERVICES**

Plants are primary producers able to produce biomass from inorganic compounds, and their products are often referred to as primary production. Photosynthesis is the main chemical process through which plants produce organic compounds (the primary production) from the fixation of atmospheric CO_2:

CO_2 + H_2O (water) + *light* = CH_2O + O_2
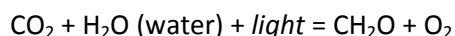
The molecule obtained by the fixation of CO_2 is generally called reduced carbohydrate. Importantly these simple molecules produced by plants can be used to synthesise more complex molecules such as lipids or proteins. Alternatively the reduced carbohydrates can be consumed by plants to obtain energy for their growth.

In addition to photosynthesis, plants absorb ions made available by soil organisms via their roots, or through mass flow and simple diffusion. The mineral ions absorbed by the plant travel from the roots to the growing parts where they are integrated to form new indispensable molecules for the plant.

Both the abundance and the quality (i.e. nutritional quality) of primary production are intricately linked to the diversity of functions performed by soil fauna and flora, since the functional groups contribute to the availability of nutrients and to the soil structure, two crucial parameters for plant growth. However there are little data to quantify this linkage.

3. 2. 2.   **WHY IS THIS SERVICE IMPORTANT TO HUMAN SOCIETY?**

Soil fertility and nutrient recycling are evidently important to human society for several reasons. First of all, this service is indispensable for food production and more generally for all forms of agriculture and forestry. Plants take up the non-mineral nutrients — carbon, hydrogen and oxygen — from air and water, while the soil plays a role in providing them with the mineral nutrients essential for their growth. This service is also important through the deleterious impacts that its improper

management may bring, such as eutrophication of water bodies by effluents and air pollution (Lavelle, Dugdale et al. 2005).

Plants provide products (ecosystem goods) that are important for the development of human society. The most evident of these is food, in the form of fruits and vegetables and other derived food products (e.g. vegetal oils). All of these products provide vitamins, mineral elements, proteins, lipids, oligo-elements, fibres and sugars which are crucial for the human diet. But the plant-derived products are not limited to food. A large spectrum of additional products, ranging from energy to genetic resources, is provided by primary producers. To cite some examples: textile fibres, wood, fuel (e.g. biofuel), and a large quantity of active molecules used in pharmaceuticals. Thus, the provision of the soil fertility and nutrient recycling service is crucial for human society and its impairment would have important impacts on our development.

In addition, primary producers (plants) release oxygen into the atmosphere and through the process of evapo-transpiration, which is the sum of evaporation and plant transpiration from the soil surface to atmosphere. The primary producers partly regulate the movement of water to the air, which is an essential step in the water cycle and local climate regulation (Figure 3-2). Thus, this service is indirectly linked to the water and climate regulation services discussed later in this chapter.
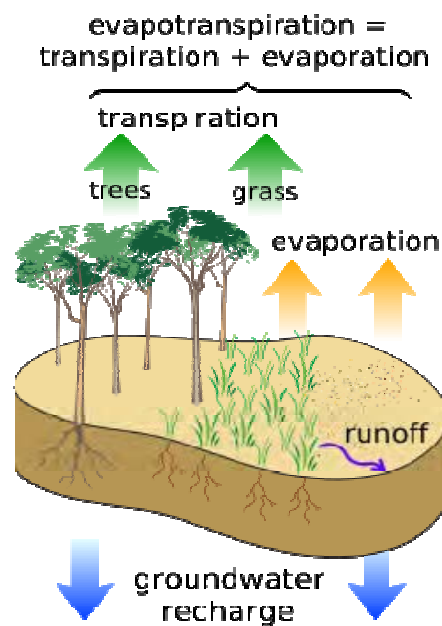
Figure 3-2: The sum of transpiration and evaporation from earth's surface give rise to the evapo-transpiration process[25]

3.3.   REGULATION OF CARBON FLUX AND CLIMATE CONTROL

Soil biological processes driven by soil biota can have an important effect on the global carbon cycle. This is because **soils are both a sink and a source of carbon**. Soil stocks carbon mainly in the form of soil organic matter and releases carbon in the form of carbon dioxide (CO_2) formed during the decomposition of soil organic matter. The soil carbon pool is thus in a dynamic equilibrium of inputs and outputs (Figure 3-3). Soil is the second largest global carbon pool, estimated to contain about 2500 Gt of carbon to

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[25] Image from: www.answers.com/topic/evapotranspiration

one metre depth, and with vegetation contains some 2.7 times more carbon than the atmosphere (Woodward 2009).

Soil carbon stock can be organic or inorganic. If we consider the soil inorganic pool included, the soil pool contains three times as much carbon as the atmosphere. The carbon stored in aquatic, especially marine systems, contains more carbon than soil and air together.
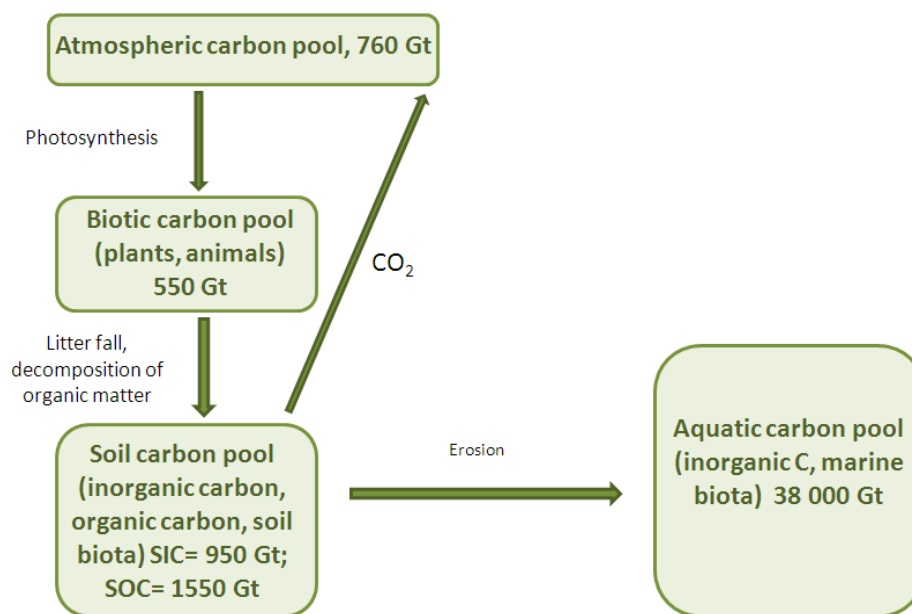
Figure 3-3: Input and output of soil carbon

The carbon output is mainly in the form of carbon dioxide (CO_2), which is one of the main greenhouse gases (GHG) contributing to global warming. In addition to CO_2, soil biota can also control fluxes of other GHGs, such as methane (CH_4), which is produced during the carbon cycle, and nitrous oxide (N_2O) which is produced as part of the nitrogen cycling (Box 7). While these gases represent much smaller fluxes than those of CO_2, they are much more potent than carbon dioxide as a greenhouse gas (21 times and 310 times, respectively).This process, together with the GHG released by human activity, contributes to global warming.

Thus, through their capacity to stock carbon, soils can act as a buffer compartment in a context of climate change. A good carbon storage capacity of soils could be one of the tools for climate change mitigation, especially because of its immediate and low cost availability. However, the limited magnitude of its effect and especially its potential reversibility, for example due to converting grassland into arable land, should be kept in mind (Schils 2008). Moreover, the soil carbon pool is itself susceptible to warming, causing enhanced carbon loss to atmosphere and carbon cycle feedback (Huntingford 2000).

3. 3. 1.   WHICH PROCESS IS RESPONSIBLE FOR THE DELIVERY OF THIS SERVICE?

The regulation of carbon flux is a process driven by soil biota. The global soil organic carbon pool is estimated at 1550 Giga tonnes (Gt), 73-79 Giga tonnes of which (around 5%) are stored in Europe (Schils 2008). Soil organic carbon is the main fraction of the soil carbon pool. The soil organic carbon pool is mainly formed by soil biota and accumulated organic matter (e.g. litter, aboveground residues).

Soil organic carbon is gained through the decomposition of organic matter leading to humification of lignin, cellulose and other organic compounds by soil microorganisms (Figure 3-4). A part of the organic matter is mineralised in the inorganic carbon pool. Thus, all the soil organisms involved in organic matter decomposition play a key role in the delivery of this service.
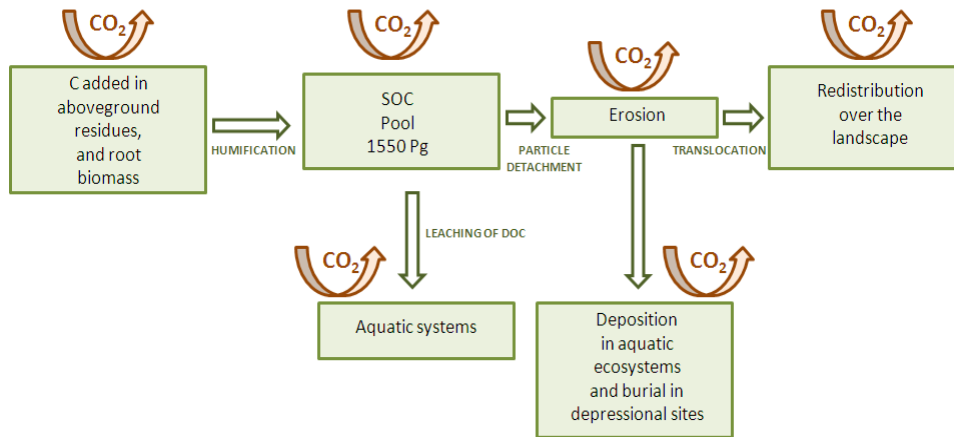
Figure 3-4: Processes affecting soil organic carbon (SOC) dynamics. DOC= dissolved organic carbon - - adapted from (Lal 2004)

Soil organic carbon can be lost in the form of CO_2. The CO_2 released during the respiration of soil organisms involved in the various soil organic matter decomposition processes is widely thought to be one of the most important sources of CO_2 to the atmosphere. The size of this flux is 55 Gt per year (Schils 2008). Indeed, feedback between soil organic carbon and atmospheric CO_2 is a process which is not fully understood yet. In addition to this loss in gaseous form, soil carbon equilibrium can be altered by other processes. Soil particles containing both organic and inorganic carbon can be detached from the soil matrix and transported away, being redistributed in the landscape or deposited in aquatic ecosystems. Carbon can also leach from soil to water.

All these processes are influenced by soil texture, biomass, level of disturbance, soil structure, nutrient cycling, profile characteristics, and climate. Thus, some types of soils, having different textures or land uses can store more carbon than other types: in Europe, for example, peat land soils store 20% of the total carbon stored in EU soil. Indeed, the published literature shows large variations in the amounts of carbon accumulated in different soil categories. Grassland soils were found in all studies to generally accumulate carbon. However, the studies differ on the amount of carbon accumulated. In one study, the sink estimate ranged from 1 to 45 million tonnes of carbon per year and, in another study, the mean estimate was 101 million tonnes per year. Croplands were found to act as a carbon source, but estimates are highly variable. In one study they were estimated to be a carbon source equal to 39 million tonnes per year, while in another study, croplands in Europe were estimated to be losing up to 300 million tonnes of carbon per year. The latter is now perceived as a gross overestimation. Forest soils generally accumulate carbon. Estimates range from 17 to 39 million tonnes of carbon per year with an average of 26 million tonnes per year in 1990 and to an average of 38 million tonnes of carbon per year in 2005. It would seem that on a net basis, soils in Europe are on average most likely accumulating carbon. However, given the very high uncertainties in the estimates for cropland and grassland, it would not seem accurate and sound to try to use them to aggregate the data and produce an estimate of the carbon accumulation and total carbon balance in

European soils (Schils 2008). Thus, precise future estimations are difficult to extract from the literature, given the number of uncertainties, including the dynamic trends in land-use change in Europe. Given the political importance of the management of soils for carbon storage, some recent works have estimated the potential for agricultural soils to sequester more carbon through changes in management, and this has been recently considered in the context of different biological strategies for C sequestration (Woodward 2009).

In any case, any activity altering the input of organic matter to soil (e.g. conversion from natural to urban landscape), modifying organic matter decomposition by soil organisms, or that favours erosion or leaching, can have significant impacts on the delivery of the carbon storage service of soils (see also section 4.).

In Europe, for example, the largest emissions of CO_2 from soils are resulting from land-use change (e.g. from grassland to agricultural fields) and the related drainage of organic soils. This is due to the fact that land-use changes modify soil conditions (e.g. oxygen concentration) and thus activate soil biota mediated production of CO_2. In the pre-industrial era, soils were one of the major sources of atmospheric CO_2 mostly due to land-use change (e.g. conversion of natural environments into agricultural land). However, in the industrial era, carbon emitted by soil represents only half of the quantity emitted by fossil fuel combustion (Table 3-2).

Table 3-2: Estimates of pre- and post-industrial losses of carbon from soil and emission from fossil-fuel combustion, overall estimation in the word (Lal 2004)

Source	Carbon emissions (Gt)
Pre-industrial era	
Land-use conversion	**320**
Fossil fuel combustion	**0**
Post-industrial era (since 1850)	
Land-use conversion (total)	**136 $\pm$ 5**
Soil cultivation	78 $\pm$ 12
Erosion	26 $\pm$9
Mineralisation	52 $\pm$ 8
Fossil fuel combustion	**270 $\pm$ 30**

3. 3. 2. WHY IS THIS SERVICE IMPORTANT TO HUMAN SOCIETY?

The service of regulating climate through regulating GHG fluxes is very important to human society. Even relatively small changes in the CO_2 flux between soil and the atmosphere, for example, could have a significant impact on climate. A perturbation of climate stability can lead to several deleterious effects for human society. Direct effects could be to affect human health, water resources, crop productivity, food resources and security. Indirect effects could be to disturb social equity, governance, production and consumption patterns and population growth (IPCC 2007). In addition, a deregulation of climate due to an impaired GHG flux in soils may strongly affect all other natural ecosystems leading to losses in global ecosystem services.

3.4. REGULATION OF THE WATER CYCLE

Soil water regulation services include the capacity to infiltrate water, store it underground, as well as regulate its flux and purity in a balanced way in order to keep water quality and quantity.

Rainfall, snow, and dew, are the main sources of water reaching soil. Water reaching the soil surface can follow different paths (Figure 3-5):

- infiltration and/or surface run-off
- interflow below the soil surface
- evaporation and root uptake, followed by evapo-transpiration by plants
- deep percolation to groundwater
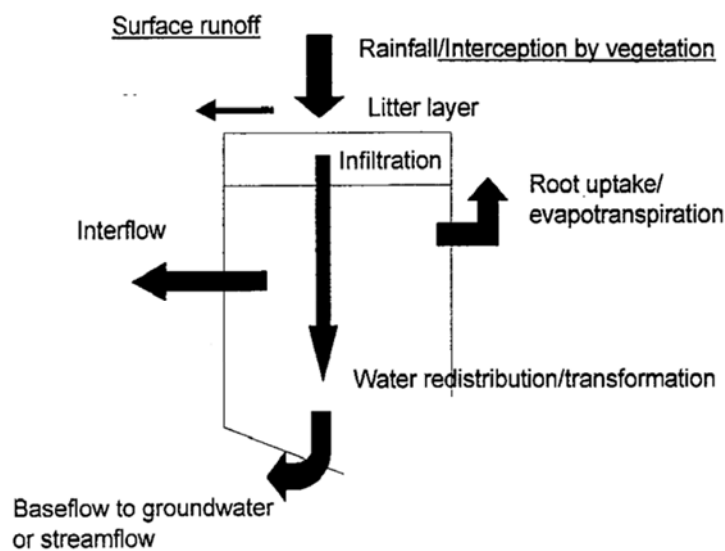
Figure 3-5: Water pathways in soil (Bardgett, Anderson et al. 2001)

The majority of processes linking soil properties and soil biodiversity to water control services have been qualitatively described, but precise quantification of these direct and indirect relationship are lacking (Bardgett, Anderson et al. 2001).

→ **WATER INFILTRATION**

When water reaches the soil, it can infiltrate underground or run-off along the soil surface. The choice between these two options depends on the quality of the soil matrix which is in turn determined by soil properties, including biodiversity. Apart from some algal crusts in the Arctic ecosystem that block water infiltration, the majority of soil organisms have a positive impact on the infiltration rate. For example, soil engineers such as earthworms and termites can significantly increase infiltration rates through soil by creating macro-pores and channels. Thus, for example, **the elimination of earthworm populations due to soil contamination can reduce water infiltration rate up to 93%** (Clements 1982).

In addition to earthworms, ants and termites can affect water infiltration rates. Underground aquifers can be recharged by the water flow passing though nest galleries, particularly in arid environments. For example, the elimination of small populations of a species of termite in the Chihuahuan Desert resulted in a modification of surface run-off pattern and infiltration (Bardgett, Anderson et al. 2001). Other organisms can also have indirect effects on water infiltration rates through modifying the quantity and quality of soil organic matter.

Another major factor controlling the water infiltration rate in soil and its capacity for water retention is the surface of ground covered with plants or plant litter. The vegetation quality and distribution in the soil matrix is regulated by soil characteristics and soil biodiversity which, as we have seen, ensure the appropriate functioning of the ecosystem, providing the conditions for plant growth.

The presence of vegetation can regulate the quantity of water reaching the soil by protecting it with leaves, capturing the water and structuring the soil with underground roots. The result of this action is that water is kept locally and can pass through into underground reserves. When vegetation is limited or absent, water will run off, instead of going underground, enhancing the erosion of soil particles. Plant roots prevent that soil particles from being washed away with water flows, keep soil macro-aggregates together and avoid landslides.

In the case of deforestation, the run-off and the associated risk of erosion are increased, while the water infiltration rate is decreased (see also section 4. 2. 1). Thus, a healthy soil sustaining plant growth is also particularly important to avoid erosion (Ineson et al. 2004). **In the USA, for example, it has been observed that land without vegetation can be eroded 123 times faster than land covered by vegetation**, which lost less than 0.1 ton of soil per ha/yr. In Utah and Montana, in cases where the amount of ground cover decreased from 100% to less than 1%, erosion rates increased approximately 200 times (Pimentel and Kounang 1998)(Figure 3-6).
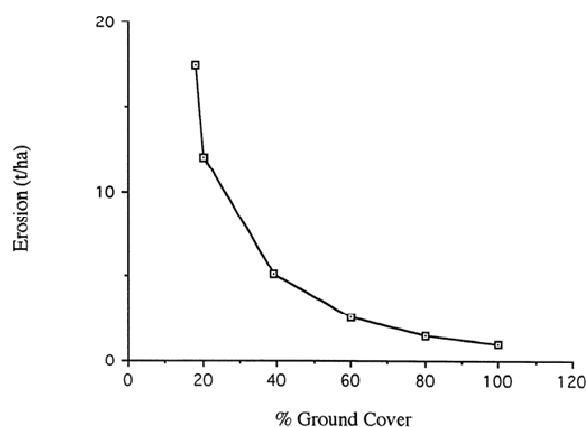
Figure 3-6: Soil erosion rates related to percentage of ground cover in Utah and Montana (Pimentel and Kounang 1998)

As a consequence, the frequency and the intensity of run-off, flooding, and aquifer recharge can be strongly influenced by changes in land cover. This includes, in particular, alterations that change the water storage potential of the system, such as the conversion of wetlands or forests into croplands, or the conversion of croplands into urban areas.

➔ WATER PURIFICATION

The infiltration of water through the soil is also an important part of water purification. Contaminants and pathogenic microbes (e.g. some forms of bacteria and viruses) can then be absorbed on the surface of soil particles during this infiltration, resulting in cleaner and safer water. Several physico-chemical processes take place during the water infiltration: sedimentation, precipitation, oxidation-reduction, sorption-

desorption, ion-exchange and biodegradation of contaminants. The ability of soil to perform these functions depends on its texture, salt content, humus content and richness in microorganisms located in the subsurface. All these factors are, at least partly, dependent on soil characteristics, including soil biodiversity.

➜ WATER STORAGE AND TRANSFER

Once infiltrated, water is redistributed underground. This redistribution is highly dependent on soil porosity, which in turn is influenced by the activity of ecosystem engineers. The existence of pores of different sizes allows water to be retained at different tensions (the smaller the size of the pore, the greater the force with which it is retained in soil) providing plants with a continuum of water resources as soil dries (Bardgett, Anderson et al. 2001).

In addition, the productivity and composition of plants can also influence water transfer, by controlling the rate of evapo-transpiration of water, from the soil to the atmosphere. Thus, water movement is indirectly regulated by plant and root biomass distribution, which are both partly dependent on soil biodiversity. For example, when a root-feeder, such as a nematode, alters the plant growing rate, this will influence the overall evapo-transpiration rate and water movement (Figure 3-7).
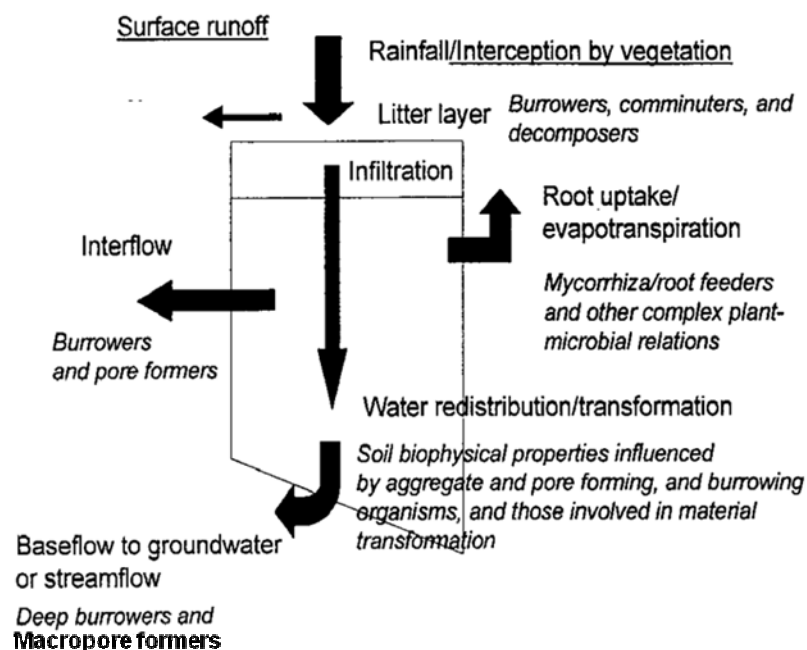
Figure 3-7: Scheme of the role of soil properties and biodiversity in soil water pathways (Bardgett, Anderson et al. 2001)

3. 4. 2.   WHY IS THIS SERVICE IMPORTANT TO HUMAN SOCIETY?

Water quality and quantity are essential to human life, and most of it comes from underground sources. Thus if the groundwater quality is degraded because of impairment in soil functioning, all the degradable pollutants will not be degraded or neutralised. As a consequence, the need for water treatment facilities will increase. If the groundwater quantity is reduced following impairments in soil regulation of rainfall infiltration and storage, the underground reservoirs of drinking water indispensable in periods of droughts will be impaired. In addition, the surface run-off will be increased

leading to a higher frequency of peak flows and flood risk. Such stronger run-off will then result in higher erosion rates and an increased accumulation of sediments in flood water. An increased quantity of sediments transported by flood waters will in turn result in a higher risk for human health (Ebi, Kovats et al. 2006). Obviously, a degradation of water quality and a decrease in quantity could also have deleterious impacts on human wellbeing and quality of life, and in the more extreme scenario, affect human health. Additional negative impacts resulting from the impairment of the water regulation service include eutrophication of water bodies, sedimentation of gravel-bedded rivers, loss of reservoir capacity, and muddy flooding of roads and communities.

Thus, maintaining an efficient water regulating service will avoid important costs for the construction and the operation of water purification plants and remediation to prevent the drying out of streams as well as to ensure flood control. First attempts to economically evaluate the value of healthy ecosystems providing a good water quality have been performed. Since 1997, there is a worldwide trend to organise systems for payment of water services, in which people living in the higher parts of water catchments where water is stored and purified get subsidies from people from low lying areas (urban and industrial areas) to maintain ecosystem in good health and hence, water services (280 000 ha enrolled a cost of $30 million)(MEA 2005).

3.5.   DECONTAMINATION AND BIOREMEDIATION

Soil is a natural sink for pollution. Soil contamination is deleterious for both the environment and for human health. However, soil-related processes can mitigate the impacts of pollution on the environment and human health through modification and control of their chemical fate and behaviour, thus limiting the transfer of pollutants to other media. This service is called decontamination or bioremediation. Natural occurring bioremediation can be enhanced by human intervention, called human-driven bioremediation. This is often applied to try to return a contaminated area back to its pristine state. However, this is in general a very long-term process, which in some cases is not possible where the contaminant loads are too large or the risks too high.

Bioremediation can be performed using:

- microbes (most cases) which transforms organic compounds
- plants which can accumulate a pollutant and facilitate its removal from soil matrix (phytoremediation)

Bioremediation can ensure, for example, the partial decontamination of an aquifer once the pollution source has been removed or when hotspots of pollution have been treated. A number of frequently encountered pollutants, such as chlorinated hydrocarbons, benzene, toluene, xylene, and ethyl benzene can be removed through natural soil decontamination. Other components such as inorganic molecules and pesticides can also be remediated by soils, while heavy metals can be chemically neutralised into inactive forms by chelation processes, accumulated in plants and removed from the sites (Table 3-3). Indeed, several pollutants such as persistent organic pollutants (e.g. dioxins) cannot be decomposed by soil microorganisms. Moreover, soil microorganisms can also be intoxicated by dangerous substances in the soil. Therefore it is necessary to take into account the toxicity to soil organisms as part of the risk assessment of contaminated sites.

Table 3-3: Some contaminants that can be bio-remediated and their potential sources

Class of pollutants	Examples of potential sources
Chlorinated phenol	Timber treatment
Pesticides	Agriculture, pesticide manufacturing
Chlorinated solvents	Drycleaners
Polychlorinated biphenyls	Power stations, electrical manufacturing
BTEX	Port facilities, airports, gas work sites
PAHs	Engine works, oil production and storage

The overall service is ensured by both biotic and abiotic soil properties and depends on local geology, hydrology and ecological communities. Both biological and physico-chemical processes underlie the provisioning of this service.

The biological processes involved in bioremediation include:

- **Bioavailability:** the fraction of a total amount of a chemical present in a specific environmental compartment that, within a given time span, is either available or can be made available for uptake by (micro)organisms or plants, from either the direct surroundings of the organisms or the plant or by ingestion of food.
- **Bioaccumulation:** the ability of soil organisms to incorporate pollutants and to cumulate them within the organism
- **Biological degradation:** is the capacity of living organisms to modify the chemical fate of a pollutant into smaller, non toxic molecules (e.g. CO_2)
- **Metabolisation:** is the ability of a living organism to modify a chemical pollutant and obtain useful metabolic molecules.

In addition to these biological processes, a number of physico-chemical processes are involved in decontamination, including:

- **Abiotic degradation** (e.g. photodegradation, hydrolysis)
- **Dilution**
- **Dispersion**
- **Radioactive decay**
- **Absorption of contaminants.**

3. 5. 1. WHICH PROCESS IS RESPONSIBLE FOR THE DELIVERY OF THIS SERVICE?

The microorganisms included in the group of chemical engineers play a key role in the four biological processes mentioned above. However the overall process of biodegradation of a compound is often a result of the actions of multiple organisms. Effects of biological controllers and ecosystem engineers which are the proximate determinants of microbial activities are also likely to play a great role in microorganism performances.

The microorganisms performing bioremediation may be:

- indigenous to a contaminated area (natural bioremediation)
- indigenous from a non contaminated area and transported on site (human-driven bioremediation)
- selected in a laboratory and transported to the contaminated site (human-driven bioremediation)

In order to have an effective bioremediation, microorganisms must enzymatically attack the pollutants and convert them to harmless products. As a consequence, all factors influencing their survival, growth and activity rate can have an impact on the

efficiency of bioremediation. Thus, human-driven bioremediation often involves the manipulation of environmental parameters to allow pollutants degradation to be more efficient. Of course the optimal environmental parameters depend on the pollutant to be treated and the specific microorganism used.

Bioremediation can be performed *in situ*, which means directly in the polluted area or *ex situ* which means that the contaminated soil is transported elsewhere to be treated. The *in situ* strategies are in general less expensive and provoke a minor disturbance to local ecosystems than *ex situ* strategies, because the human alteration of the local ecosystem is lower (Box 14).

Box 14: A successful example of bioremediation

A well-known example of bioremediation is the microorganisms mediated cleaning after the large accidental oil spill by the tanker Exxon Valdez in Alaska in March 1989. The accident spilled approximately 41 000 m^3 of crude oil and contaminated about 2 000 km of coastline. Bioremediation was the main strategy used in this case. Nutrients and fertilisers to enhance bacterial growth were applied on the surfaces of contaminated sand and sediments. This resulted in a fivefold increase in the rate of oil degradation due to enhanced bacterial activity (Bragg 1994) and, finally, in an efficient site remediation.

Bioremediation using microorganisms can sometimes be ameliorated by the presence of earthworms, due to their regulative action on microbial activity and distribution in the soil (Table 3-4). However, due to the earthworms' high sensitivity to certain pollutants, this is valid only in the case of pollutants which are not lethal for them.

Table 3-4: PCB (Polychlorinated biphenyl) removal in treated soils after 18 weeks in the presence and absence of earthworms -adapted from (Singer 2001)

Soil depth	% PCB removed (g-1 soil)	
	Earthworms	No earthworms
0-2	67	58
2-6	39	44
6-20	53	43
total	52	45

Soil organisms can also affect important soil characteristics such as porosity, pH and organic matter content, that have an indirect effect on pollutants decontamination (Bennett, Hiebert et al. 2000). In addition, a number of chemicals secreted by bacteria and fungi can influence desorption (contrary process of absorption) and the removal of metals and hydrocarbons from the soil matrix. Using a fungus, for example, a maximum solubilisation of 68% for copper for a medium containing potato peels was achieved (Mulligan and Kamali 2003).

Remediation by plants is called phyto-remediation. In the case of phyto-remediation the link between the service and soil biodiversity is indirect compared to microbial mediated bioremediation, for example because soil biodiversity plays a role in regulating plant abundance and distribution. This process is particularly useful to remove metal pollutants and widespread residual organic compounds from soil and water. Plants are efficient in accumulating and immobilising persistent pollutants. Several strategies of phyto-remediation exist: phyto-extraction, phyto-transformation, phyto-stabilisation, phyto-degradation, phyto-volatilisation and rhizo-filtration (Table 3-5). A combination of these processes can occur in nature.

Table 3-5: Strategies of phyto-remediation

Strategy	Mechanism
Phyto-extraction	Uptake pollutant in the plant (e.g. metal), removal of the plant
Phyto-transformation	Uptake pollutant in the plant (e.g. organic pollutant), degradation within the plant. High above biomass production and/or pollutant translocation to the above plant biomass is required to make a phytoremediation approach successful.
Phyto-stabilisation	Root exudation provokes the precipitation of metals into stable organic forms (Phytostabilization of metals *in situ* accompanies frequently the bioremediation approaches)
Phyto-degradation	Enhancement of the microbial degradation in the rhizosphere
Rhizo-filtration	Uptake of pollutant in plant roots (e.g. metal)
Phyto-volatilisation	Evapo-transpiration of pollutant (e.g. mercury)

All the abiotic processes involved in soil decontamination and their efficiency are determined by the physico-chemical properties of soil surface, soil porosity, the chemical properties of pore-water compartment, and, of course, the physico-chemical properties of the pollutants (e.g. behaviour of organic and inorganic molecules may be significantly different in the soil matrix). The presence of surface active fractions such as organic matter, possessing high surface areas and charges can, for example, facilitate oil retention in the soil matrix. All these physico-chemical properties are directly or indirectly linked to soil properties and biodiversity. For example, earthworms and microbes are key actors in the determination of soil aggregation and porosity. Similarly, microbial activity can locally alter soil pH, affecting soil aggregation and its capacity to absorb contaminants.

Therefore, a high diversity and biological activity within soils, especially at the level of chemical engineers, but also in the case of ecosystem engineers, is indispensable to ensure this crucial service through a direct influence on soil biotic degradation processes and an indirect influence on soil abiotic degradation processes of pollutants.

3. 5. 2. WHY IS THIS SERVICE IMPORTANT TO HUMAN SOCIETY?

Three alternatives exist to bioremediation: physical removal of pollutants, dilution, and treatment. However, soil clean-up is, in general, a difficult operation with very high costs. The European Environment Agency has estimated the total costs for the clean-up of contaminated sites in Europe to be between 59 and 109 billions of Euros (EEA 2000). Bioremediation is the cheapest option for soil decontamination.

The natural capacity of soil to decontaminate has permitted to restore numerous sites (Bragg 1994). This extremely important service has thus been the object of extensive studies. A number of bacteria, fungi (including mycorrhizae) and plants have been tested to evaluate their decontamination capacity. Bioremediation using microorganisms presents some general benefits:

- It is useful for the complete destruction of a wide variety of contaminants, rather than simply transferring them among natural media (e.g. pollutants transfer from soil to water or atmosphere)
- The residues for the treatment are usually non-toxic products and include carbon dioxide, water, and cell biomass
- It is a natural process generally perceived by the public as an acceptable method for waste treatment
- In most cases, when the contaminant is degraded, the bio-degradative microbial population declines
- The transport of waste is limited when *in situ* strategies are chosen

- It is a relatively low-cost option

However, natural soil decontamination is often not sufficient to restore a polluted site completely, since natural biodegradation processes are in general very slow (several decades), soil organisms cannot break down some pollutants, and sometimes the contaminant load is too large. This extremely important service has thus some limitations:

- It does not apply to all contaminants, e.g. to some hydrophobic organic compounds
- It is very slow and sometimes the risks and the exposure to dangerous substances do not allow for such long techniques
- It may not work if the contaminant load is too significant (see section 5.5.1)
- In some cases, the properties of the biodegradation products are not known well enough to be sure that their nature is not more toxic than the original molecule
- There is a difficulty in controlling all the environmental conditions for an optimal bioremediation
- More research is needed to improve treatments for soil contaminated by complex mixtures of pollutants
- It is a long term treatment, compared to alternative strategies, and thus it requires the monitoring of the contamination (which may increase the costs of such technologies)
- It is rarely 100% efficient in the elimination of pollutants. Regulatory uncertainty remains regarding acceptable performance criteria, e.g. can an efficiency of around 70% in the pollutant removal be acceptable and is the site then defined as completely decontaminated?

Understanding the categories of chemicals that can be biodegraded and the responsible biotic and abiotic transformation processes underlying natural attenuation is crucial to ensure the development of bioremediation, due to its potential of efficient and inexpensive soil cleaning. However, natural soil decontamination is often not sufficient to restore a polluted site completely, since natural biodegradation processes are in general very slow (several tens of years).

In the case of plants, 400 species capable of accumulating metals have been reported (Yang 2004). After sufficient plant growth and metal accumulation, the aboveground portions of the plant are harvested and removed, resulting in the permanent removal of metals from the site. Phyto-remediation is preferentially used in the following conditions:

- Very large field sites
- Sites with a low concentration of contaminants
- As the final step of a decontamination procedure

There are some limitations:

- Long duration of time (and thus long term monitoring of the contamination)
- Potential contamination of the vegetation and food chain (when the pollutant is not degraded within the plant or when the plant is not removed)
- Difficulty in establishing and maintaining vegetation in heavily polluted sites.

In conclusion, the application of bioremediation using either microorganisms or plants is feasible and relatively cheap. However, the option of transforming the pollutants through microbial conversion seems preferable to the option of bio-accumulating the pollutant into a plant, thus leading to a simple transfer from one ecosystem to another medium. Setting a bioremediation protocol in a contaminated site requires excellent knowledge of the nature and distribution of the pollution as well as of the local soil organisms and plants. Different levels of cleaning up can be reached, depending on the case, but to date precise criteria that define the quality of bioremediation are still lacking.

3.6. PEST CONTROL

Biological pest control is the natural or human-influenced ability of natural competitors, predators or parasites, to act as biological control agents for pest species. This control can be through top-down or bottom-up mechanisms. Top-down pest control occurs when a predator controls the structure/population dynamics of a species within the ecosystem. Bottom-up control in ecosystems occurs when the nutrient supply controls the development of species. Evidences from natural systems show that the low diversity of an ecosystem is associated with a higher vulnerability to pests, due to altered top-down and bottom-up control mechanisms. In agricultural fields, for example, the soil functioning is modified and, as a consequence, its equilibrium can be altered leading to outbreaks of crop pests. Thus, the natural biological pest control service can be used as an alternative to pesticides. Biological pest control strongly influences the provisioning services as well, because it promotes primary production: diseased crops do not produce food or fibres as efficiently as healthy crops.

3. 6. 1. WHICH PROCESS IS RESPONSIBLE FOR THE DELIVERY OF THIS SERVICE?

Soil biodiversity ensures pest control by acting both directly on belowground pests, and indirectly on aboveground pests (Figure 3-8). In ecosystems presenting a high diversity of soil organisms, harmful microbes or nematodes attacking crops are less aggressive, as their effects are diluted in larger communities (Altieri and Letourneau 1982; Lavelle, Bignell et al. 2004). In addition, vegetation diversity (aboveground diversity), which is in part regulated by soil biodiversity, favours aboveground pest control through supporting natural insect communities and some plant species that are specific targets for pests, thus alleviating the pest charge on other plants.
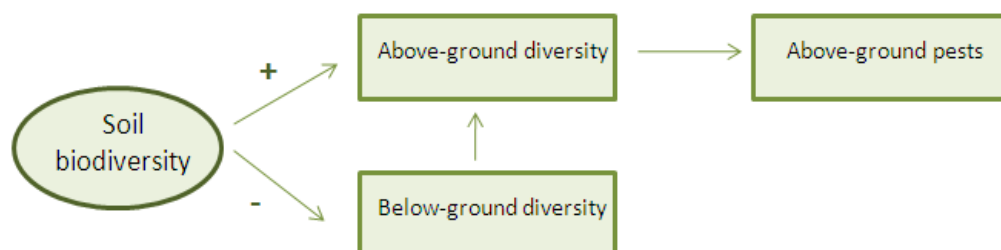

Figure 3-8: Soil biodiversity regulates the aboveground and belowground pests

In natural communities, the size of populations is mainly regulated by the presence of other organisms. Pests spread occurs either when top-down or bottom-up controls are not efficient enough. Soil biodiversity can influence both top-down and bottom-up effects:

- **Top-down pest control:** a typical top-down control mechanism is, for example, an induced enhancement of the natural enemies. This strategy has been applied by Settle et al. (1996) who demonstrate how organic inputs in rice fields, by maintaining high levels of decomposer communities, maintain constant levels of generalist predators[26] that feed on pest species. Whenever an insect pest arises, control is immediately triggered as generalist predators are already present. The idea is thus to favour the resources needed by the pests' natural enemies.

  Possible strategies to enhance the natural top-down effects include improving the availability of alternative foods preferred by the natural enemies, facilitating the creation of a microclimate in which natural enemies may over-winter or seeking refuge from factors such as environmental extremes or pesticides, etc. In addition, the temporal availability of such resources may be manipulated to encourage early season activity of natural enemies. Finally, the spatial arrangement of such resources to enhance natural enemy activity within the crop must be considered.

- **Bottom-up pest control:** bottom-up strategies act directly on the resources available for pests. In practice, the density of invasive predators can be controlled by limiting their resources at the base of the food web.

Several studies show that pest control relationships within the food web depend on general soil biodiversity, rather than on the presence of a specific species of soil organisms. For specific soil-borne crop enemies, such as for example the cereal root-pathogens and the root knot nematodes, it seems that there should be specific microbial enemies that play a key role in controlling the pest (Kerry 1998). However, recent multi-disciplinary approaches have shown that there is in fact a wide range of control factors for this kind of pest, which all play a role in their suppression (van der Putten, Cook et al. 2006). Similarly, it has been observed in the case of the pea aphid pest, that when three of its enemies were present, the pest was suppressed more than predicted from the summed impact of each enemy species alone (Cardinale 2003).

Threats to soil biodiversity can alter soil community structure and internal food web interactions. This results in deleterious impacts on the ecosystem's self-regulation properties and favours pests. However, if relatively simple precautions are taken to maintain some diversity surrounding the crops, pest invasion can be controlled. Some evidence indicates the importance of the ground cover vegetation or of the adjacent wild vegetation to protect crops from pests. Specific types of weeds, for example, can harbour and support beneficial arthropods species capable to fight pest populations (Boatman 1994). In general, the more diverse and stable the agro-system, the more stable the insect community.

In conclusion, in a diverse ecosystem, the species present cover all the available ecological niches and use the resources available in an optimal way (Elton 1958). This balance impedes the development of pests and invasive species (Altieri 1994). Thus, keeping a high bio-diverse ecosystem is an important part for a good defensive strategy, at least for generalist pest species.

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[26] A generalist predator is a type of pest that attack a wide range of plants and it is not specific to one type of crop (e.g. Aphis gossypii).

The provision and the regulation of primary production is one of the most important services ensured by soils. The service of pest regulation is indirectly related to the primary production, since such a control avoids the loss of plants and plant products. Understanding the importance of this service is thus evident for everybody: diseased crops don't provide food and fibres. A loss of plants and of their products due to a pest invasion could not only dramatically affect human health through a loss of crops yields and consequently food resources, but also seriously impair the economic, scientific and cultural development through the elimination of all the plant derived products. For example, the value of potato crops which are at risk from Colorado beetle in UK is about 322 millions of Euros[27]. The importance of this regulatory service for human society is thus obvious (Table 3-6, Table 3-7, Figure 3-9). Moreover, the human-driven pest control is one method which can be used to reduce the need for large scale applications of broad spectrum pesticides. This category of pesticides can be highly problematic as they often act on insects which are beneficial to crops as well as harmful insects. It has been demonstrated that the use of pesticides can be at the origin of huge economic cost: a loss of more than 8 billions of dollars per year for the United States (Pimentel 2005). To that the ecological costs should be added. In conclusion, the appropriate functioning of this service is crucial from both an environmental and an economic point of view.

Figure 3-9: Signs of pest damage: Healthy potato foliage (left) and pest-infested potato plants (right)

Table 3-6: Major pest in potatoes

Pest	Type of damage
Aphids (aboveground pest)	Aphids damage potatoes primarily by spreading plant diseases. Occasionally, aphids become so abundant that their feeding weakens the plants.
Beet Leafhopper (aboveground pest)	Leafhoppers feed by sucking sap from the plant causing a damage of the leaves. They are also responsible for transmitting the curly top virus.
Cutworms (aboveground pest)	Cutworms may cut off the stems of young plants and feed on foliage and tubers.
Flea Beetles (aboveground pest)	The beetles feed on leaves and stems resulting

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[27] www.statistics.defra.gov.uk/esg/evaluation/planth/annex1_3.pdf Last retrieval : 21/08/09

Pest	Type of damage
	in many small holes in the leaves. The larvae feed on roots, underground stems, and tubers.
Potato Psyllid (aboveground pest)	Damage is caused by a toxin that the immature produce when they feed. The toxin causes a plant response known as psyllid yellows. Symptoms include an upward curling of leaflets nearest the stem on the top part of the plant.
Potato Tuberworm (belowground pest)	The typical damage results from larvae mining in the tubers.
Potato cyst nematodes (belowground pest)	Infest potatoes roots causing a decrease in growth

Table 3-7: Major aboveground pests and diseases of raspberry in Europe: their damage, distribution and importance[28]

Common name	Type of damage	Distribution in Europe	Importance
Large Raspberry Aphid	Virus Vector/Foliage	Widespread/Northern	*****
Small Raspberry Aphid	Virus Vector/Foliage	Widespread/Southern	**
Rubus leafhoppers	MLO Vector	Localised	*
Common Green Capsid	Foliage	Localised	*
European Tarnished Bug	Foliage/Flowers	Widespread/Northern	*
Raspberry Beetle	Flowers/Fruit/Contaminant	Widespread/Throughout	*****
Clay-coloured Weevil	Buds/Foliage	Localised/Northern	***
Strawberry Blossom Weevil	Buds/Flowers	Localised/Southern	**
Raspberry Cane Midge	Canes (Midge Blight)	Widespread/Throughout	*****
Raspberry Moth	Buds	Localised/Northern	***
Double Dart Moth	Buds	Localised/Scotland	***
Two-Spotted Spider Mite	Foliage	Widespread	****
Raspberry Leaf and Bud Mite	Foliage	Widespread but sporadic	***
Large Raspberry Aphid	Virus Vector/Foliage	Widespread/Northern	*****

3.7.   HUMAN HEALTH EFFECTS

Human health is here defined as the sum of complex interactions between the genetic characteristics of individuals and their environmental exposure to infectious or toxic agents. Soil processes driven by soil biota can impact human health in two main ways. First, soil organisms may be a source of new medicines, and a decrease of soil biodiversity could directly impact this service. Second disturbances to soils and related biodiversity through land-use changes can potentially have non negligible indirect impacts on human health.

With their richness in microorganisms, soils are an important source of chemical and genetic resources for the development of pharmaceuticals (Box 15). In 1944, for instance, streptomycin, an antibiotic used to treat a number of infectious diseases, was isolated from a bacteria living in tropical soil. Another very well known example is the history of penicillin which has been the first pharmaceutical isolated from soil fungi in

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[28] www.scri.ac.uk/scri/file/individualreports/1999/29ICM.PDF; last retrieval 15 June 2009

1928. In the laboratory of Alexander Fleming, a culture of staphylococcus bacteria was contaminated with this soil fungus *Penicillium notatum*. Fleming observed that the fungus inhibited the growth of the infectious bacteria next to it. He deduced that something from the mould must be killing them, and shortly thereafter he isolated penicillin.

All the current and future studies on microbial produced antibiotics and fungicides can be useful to find new therapeutic molecules (Box 15) and help in fighting microbial resistance of human pathogens to currently used antibiotics. In the last years, a phenomenon of microbial breaking of resistance has been observed, increasing so rapidly that new drugs that were wonderful 20 years ago now turn out to be useless (Taubes 2008). This happens because bacteria have two main properties:

- They divide very fast (in average every 20 minutes) and their capacity to genetically evolve in order to respond to an environmental stressor is consequently extremely high.
- Any genetic information (e.g. the one coding for antibiotic resistance) can very fast spread from one bacterium to another.

Such bacterial characteristics can be very dangerous for human health. In 2002, for example, the U.S. Center for Disease Control and Prevention (CDC) estimated that at least 90 000 deaths a year in the United States could be attributed to bacterial infections, more than half caused by bugs resistant to at least one commonly used antibiotic. For this reason, the medical community is always looking for new antibiotics. In this context, maintaining an ecosystem in a good status and rich in biodiversity could be a guarantee to keep a huge source of pharmaceuticals available.

Soils and related biodiversity can also have indirect impacts on human health. Below some examples are provided to illustrate how an alteration of soils and related biodiversity can be associated to such health impacts.

Land-use changes, which result in a disturbance of soils and a loss of biodiversity, such as urban expansion, deforestation, or agricultural development have been correlated to an increased incidence of human infectious diseases (Table 3-8) (Patz et al. 2000). For example, in the United States, agricultural practices altering watersheds and freshwater flows could be linked to an increased soil-borne infectious diseases rate (Chua, Goh et al. 1999; Rose, Epstein et al. 2001). Such a correlation, depending on the considered case, could be explained by alteration of soil biodiversity which is always associated to the equilibrated functioning of the soils. The soil-borne infectious diseases, being caused by a microorganism living its entire life cycle or a part of it within the soil, are of course impacted by any soil and biodiversity disturbance. A change in the soil equilibrium can be at the origin of important changes in soil pathogens survival, growth, infectivity, and distribution. As a consequence, the human exposure rate may be consequently modified, leading to unexpected disease spreads.

Box 15: New antibiotics and fungicides emerging from soil biodiversity

Soil biodiversity may include a wealth of novel compounds that humans can use as bactericides or fungicides. In the soil, these compounds are typically produced by bacteria and fungi to fight other microbes. For instance, the release of these compounds can suppress competitor microbial species and increase resource availability for the producing species (de Boer 2007).

New species, or even entire new genera, of soil microbes are continuously being discovered. As a consequence, new survival strategies revealing previously unknown

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mechanisms of microbial control and new molecules are also continuously discovered. For example, it has been recently observed that the newly found soil bacterial genus Collimonas can inhibit soil fungal growth (Hoppener-Ogawa, Leveau et al. 2009). There is then a huge potential in soil organisms as a source of new pharmaceuticals.

Several methods are currently being developed to screen the genetic pools of microorganisms and to facilitate the discovery of new pharmaceutical potentials. Metagenomics approaches enable to screen microbial DNA for loci involved in the production of antibiotics or fungicides. These screening methods are applied, for example, to unravel which microbial products could be involved in making soils suppressive to plant pathogens (van Elsas, Speksnijder et al. 2008). However, the characterisation of soil metagenome is still under way and presents some technical difficulties (e.g. the extraction of DNA and the fact that due to soil heterogeneity the extracted DNA is not the total present in the soil sample and thus cannot be representative of the indigenous soil DNA)(Bakken 2006).

Table 3-8: Agents and infectious diseases caused by a soil pathogens and having a suspected or known links to land-use change (Patz, Daszak et al. 2004)

Agent/Infectious disease:
Lyme disease
Meliodiosis
Anthrax
Hookworm
Coccidioidomycosis

Disturbance of soils and related biodiversity may also alter food and water quality, and thereby indirectly impair human health.

More indirectly, a disturbance of soil functioning and biodiversity may affect associated services, such as fertility, which are essential for human survival. This could result in massive human migrations, which can have important implications for the spread of infections, children mortality, nutrition, and mental illness. In addition, immigrants can then act as vectors carrying infectious disease from their original area to new countries. This has been, for example, the case for SARS (Severe Acute Respiratory Syndrome), tuberculosis and hepatitis B (Loutan, de Haan et al. 1997).

In conclusion, soil biodiversity, through ensuring a continuous regeneration of genetic resources for the creation of new pharmaceuticals and well functioning soils, can participate in the protection of human health. From a holistic point of view, any factor affecting soil biodiversity could directly or indirectly have deleterious impacts on human health.

3.8. ECONOMIC VALUATION OF BIODIVERSITY

Putting a value on biodiversity is no easy task. But in order to enable costs benefit analyses of measures to protect soil biodiversity, some economic estimates of the ecosystem services it delivers need to be provided. In 1995, a team of ecologists and economists estimated the value of biodiversity to the global economy as being in the region of $US 33 trillion annually (Costanza 1997). However, this estimate has been defined as a "minimal estimate" by its own creators.

Thus, more recently, the "Service Providing Unit" (SPU) concept was developed, which aims to assess the cost of the loss of a unit of biodiversity (Luck 2003). The crucial point made in this approach is that changes in key characteristics of populations or

communities due, for example, to anthropogenic pressures, have implications for service provision. Such changes need to be quantified to understand their implications fully. The SPU concept permits to estimate the value of the marginal product of biodiversity, or the contribution of the ecosystem to the incremental production of goods, services and human welfare at any one point of time. It is therefore a useful tool for policy makers. As explained in the following Box, other attempts to provide decision-making tools for policy makers have been made in the context of The Economics of Ecosystems and Biodiversity (TEEB) study.

There are two main approaches to assess the value of biodiversity, depending on the type of economic value considered:

- **Production value:** production function approach, where a part of the valuation is based on the prices of the provided final products such as food, fibres or raw materials. Thus, soil services performed by various soil species, for example, will contribute to the quality and the quantity of crop production, and thus to its final price.

- **Utility value:** based on the stated or revealed preference. The stated preference methods rely on survey approaches permitting people to express their willingness-to-pay for (or willingness-to-accept) the services provided by biodiversity and its general contribution to the quality of life (e.g. aesthetical and cultural value, etc.). In the revealed preference method this utility is assessed through market associated values, such as, for example, the cost of a travel to a touristic natural area.

Alternatively, cost-based methods can be used, in which we evaluate the value of a service provided by biodiversity through a surrogate product. Thus we can estimate:

- The 'replacement cost' which is the cost that would be spent to replace the ecosystem services that are provided by biodiversity (e.g. in the case of soil biodiversity, the cost of fertilisers or pesticides).
- The 'damage avoided' cost is the amount of money that should be spent to repare the adverse impacts arising in the absence of a functioning ecosystem (e.g. in the case of soil biodiversity, the cost of avoided floods)
- The 'preventive expenditure' is the amount of money that would need to be spent to avoid the costs of impacts. One example for soil biodiversity pest control service, for example, would be the additional cost of water purification needed to remove pesticide residues.

One of the main difficulties for applying these methods is that the share of the total value due to soil biodiversity has yet to be established, since it cannot be assumed that it is 100 per cent. In particular, it is often very difficult to separate the contribution of aboveground diversity from that of soil biodiversity, even if some attempts exist. As shown in the following table, the consequences of such impropriety have been estimated to be in excess of US dollars 1 trillion per year worldwide (Pimentel, 1997).

<div style="border:1px solid green; padding:10px;">

Box 16: The TEEB study[29]

Following the meeting of the environment Ministers of the G8 countries and the five

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[29] www.teebweb.org ; last retrieval 14/12/2009

major newly industrialising countries that took place in Potsdam in March 2007, the German government proposed a study on 'The economic significance of the global loss of biological diversity' as part of the so-called 'Potsdam Initiative' for biodiversity. This initiative gave rise to **The Economics of Ecosystems and Biodiversity (TEEB) study.** The initiative is a major international initiative to draw attention to the global economic benefits of biodiversity.

The TEEB study aims to:

- Integrate ecological and economic knowledge to structure the evaluation of ecosystem services under different scenarios.

- Recommend appropriate valuation methodologies for different contexts.

- Examine the economic costs of biodiversity decline and the costs and benefits of actions to reduce these losses.

- Develop "toolkits" for policy makers at international, regional and local levels in order to foster sustainable development and better conservation of ecosystems and biodiversity.

- Enable easy access to leading information and tools for improved biodiversity practice for the business community – from the perspective of managing risks, addressing opportunities, and measuring impacts.

- Raise public awareness of the individual's impact on biodiversity and ecosystems, as well as identifying areas where individual action can make a positive difference.

In the context of TEED, a 'policy toolkit' providing guidance for policy-makers, covering subsidies and incentives, environmental liability, new market infrastructure, national income accounting, cost-benefit analysis, cost-effectiveness analysis, and methods for implementing Payment for Ecosystem Services (PES) and Access and Benefits Sharing (ABS), has been elaborated.

Support for TEEB continues to grow and, in April 2009, the G8+5 Environment Ministers signed the Carta di Siracusa which further supports the work of TEEB as a vital component of addressing the increasing depletion of ecosystems and biodiversity. The final synthesis and presentation of TEEB are expected in October 2010.

Table 3-9: Total estimated economic benefits of biodiversity with special attention to the services provided by soil biodiversity (modified from Pimentel et al. 1997)

Service /Activity	World economic benefits (x US dollars 10^9 per year)
Organic matter cycling/waste recycling	760
Soil formation	25
Nutrient cycling	90
Bioremediation	121
Pest Control	160
Fertility/ pollination	200
Wild food	180
Biotechnology industry	6
Total	1542

Some attempts of estimations at the national level also exist. An Irish report, for instance, recently estimated the value of soil fertility and nutrient cycling in the country at Euros 1 billion per year (Bullock 2008). Soil biodiversity is essential to the provision of this service, but so is aboveground biodiversity through, for instance, pollination. When, in the case of specific crops, the importance of pollination is greater, the value attributed to this ecosystem service can be further raised.

Similarly, in Ireland, the baseline value of pest control, which is at least partly due to soil biodiversity, has been estimated at 20 million per year. This is before savings on pesticides which could reach perhaps a further Euros 2 million (Bullock 2008). Moreover, several attempts have also been made to assess the value of primary production in different ecosystems such as forests, agricultural fields, etc. (Table 3-10). Primary production is highly, but not exclusively dependent on soil biodiversity, thus the contribution of soil biodiversity to this service remains uncertain.

Table 3-10: Marginal value of provisioning services (cost of policy inaction) by forest biome, adjusted for profits (Braat 2008)

Forest biomes	Cost of policy inaction in EU (2007Euros /ha/year)
Boreal	246
Warm mixed	14
Temperate mixed	99
Cool coniferous	107
Temperate deciduous	142

Carbon storage depends on soil biodiversity, but also on the storage capacity of aboveground plants. An evaluation of the cost of policy inaction for different forestry biomes, demonstrating the scale of the potential losses of carbon storage from land-use changes, is available (Table 3-11).

Table 3-11: Marginal value of carbon sequestration (cost of policy inaction) by forest biome, projections in 2050 - Lower bound estimates (Braat 2008)

Forest biomes	Cost of policy inaction in EU (2050Euros /ha/year)
Boreal	864
Warm mixed	2126
Temperate mixed	1373
Cool coniferous	864
Temperate deciduous	1179

An estimation of the carbon stock in grassland soils has been calculated for France and evaluated at Euros 320 /ha per year. For French forests, a similar estimation gives a value comprised between Euros 22 and Euros 150 /ha per year. However, this last value comprises, but is not limited to soil carbon storage (Chevassus-au-Louis 2009).

3.9. CONCLUSIONS

The services provided by soil can be grouped into six main service categories which have been estimated by the authors of the report to be the most related to soil biodiversity: soil fertility, carbon flux and climate regulation, water regulation, decontamination, pest control and human health. Each service can be ascribed to specific functions and processes performed by soil organisms. The table below summarises the main roles of each of the functional groups in providing soil services.

Table 3-12: Conclusive scheme summarising the relationship between soil functional groups and soil services

Soil services	Chemical engineers	Biological regulators	Ecosystem engineers
Soil fertility and nutrient cycling, soil formation	Mineralisation of all substrates; Nitrogen fixation and nutrient assimilation by plants (mutualism)	Control on microbial activities	Influence pathways through creation of habitats and selective activation
Water regulation	Limited creation of micro-porosity (fungal micro tubules; micro aggregates and consolidation of macro-aggregated structures)	Control on microbial activities	Regulation of macro-aggregation (compacting and de-compacting functions); regulation of porosity
Carbon flux and climate regulation	Organic matter decomposition Synthesis of recalcitrant components GHG emissions	Control on microbial activities	Sequestration of organic matter in stable compact structures; Maintenance of aerobic conditions
Decontamination	Transformation into less toxic forms, neutralisation (chelation processes)	Control on microbial activities	Stimulation of release in easily assimilated forms by microorganisms Sequestration into micro-sites (stable macro-aggregates)
Pest control	Control of fungal and bacteria diseases	Control/spread of fungal diseases Community level control	Control of plant parasitic nematodes Food for generalist predators
Human health	A stable microbial community helps in controlling the spreading of eventual pathogens for humans. Chemical engineers are also a source of new pharmaceutical molecules.	Control on microbial community	Contribute to water quality and in general to soil formation and maintenance, which prevent natural disasters (flood, landslides, etc.)

The table highlights the general trends, but it is important to highlight that precise links between soil biodiversity and services are not always clearly identified. It can be very difficult to distinguish among services provided by soil in general and services provided specifically by soil biodiversity. In addition, to date, no consistent relationships between soil species diversity and soil functions have been found (Bardgett 2002, Bardgett 2005b), implying that more species do not necessarily provide more services. This is because several species can perform the same function (Box 4). Moreover, the relative contribution of the different groups of soil biota to specific functions varies across biomes, habitats and land uses.

In addition, services are often interlinked, such that pest control will contribute to fertility for instance, whereas other services may trade off against each other. Therefore, the services provided by soil and soil biodiversity should not be considered in isolation, but rather as different facets of a set of highly associated functions performed by soil biota. Such a holistic knowledge of soil is currently lacking and we do not have an exact understanding of the potential interlinkages among services.

Another factor of uncertainty is that sometimes, even the mechanisms underlying one specific service are not perfectly understood. For instance, we do not know exactly

how biodiversity can control pest spread or how to quantify the final impacts of soil biodiversity disturbance to human health, even if we observe that a qualitative relationship exists.

Thus, additional knowledge is needed regarding the biological mechanisms underlying services and the quantification of their dependence on soil biodiversity. There is a clear need to develop approaches that identify and quantify changes in ecosystem dynamics and their implications for ecosystem services and to understand the links between species population dynamics (e.g. changes in population density and distribution) and service provision. Finally, a precise economic evaluation of these services would be useful, but a homogeneous approach to perform this valuation is not yet available, even if some attempts exist at both global and national levels.

→ **MAIN RESEARCH GAPS**

- **Quantify the benefits of the services provided by soil ecosystems**
- **Assess the economic value of the services delivered by soil ecosystems**
- **Quantify the relationship between soil processes, soil biodiversity and services**
- **More knowledge on the potential inter-linkages among services**
- **Understand the links between species population dynamics**

4. DEALING WITH THREATS TO SOIL BIODIVERSITY

4.1. INTRODUCTION

European soils are a widely used resource, submitted to a number of relatively well identified threats (ENVASSO 2008). Soil biodiversity can be threatened by **soil degradation processes**, such as erosion, organic matter depletion, salinisation, sealing and compaction; and several major **threats**, including land-use change, climate change, chemical pollution, GMOs, and invasive species. As shown in Figure 4-1, each of these threats can act **directly** on soil biodiversity (e.g. chemical pollution) or **indirectly**, through one of the soil degradation processes (e.g. land-use change can affect soil biodiversity by favouring erosion).

In this chapter, the above-mentioned degradation processes are first defined, with a description of the natural and human-driven process driving them, and a discussion of their distribution in Europe. The specific impacts of each threat on soil biodiversity are then presented, by looking at their effects on functional groups and related services.
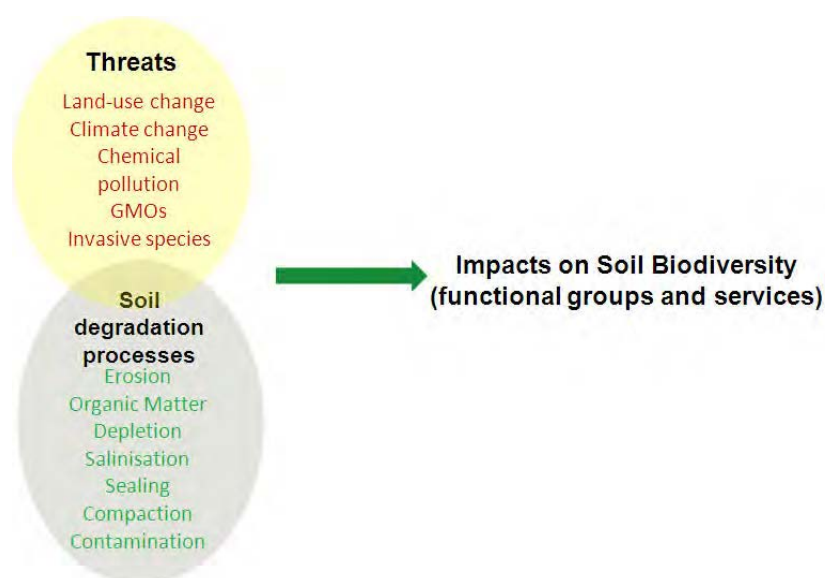

Figure 4-1: Schematic representation of the approach used to present the threats to soil biodiversity

4.2. SOIL DEGRADATION PROCESSES

Soil degradation is a very common feature in Europe and worldwide. Although the quality of managed soils may be improved by cultivation, the majority of human activities (e.g. intensive agriculture, tourism, occupation of land, etc.) reduce soil quality directly or indirectly by soil degradation. Soil degradation can alter productivity, soil functioning, and all related services. The impacts of the five main soil degradation processes on soil biodiversity are detailed below.

Soil erosion is normally a natural process occurring over geological time scales, and consists of the removal of the land surface by physical forces leading to a progressive exposition of underlying rocks. Erosion first removes organic and fine-textured particles from the soil surface, and then moves the deeper soil particles to water effluents or wind that transport them away from the landscape. The main natural drivers of erosion are water and wind action, which scratch, detach, and/or move soil from one point to another, sometimes thousands of miles away. Soil biota may contribute to erosion processes, especially when larger soil engineers deposit thin unstable aggregates on the soil surface (Blanchart, Albrecht et al. 2004; Cerda and Jurgensen 2008). These earthworm deposits may trigger soil creeping and the transfer of smaller particles towards deeper soil layers (Nooren, Vanbreemen et al. 1995).

Natural soil erosion can be significantly accelerated by anthropogenic activity. Practices that involve deforestation, exposing bare soil to water and wind, the use of deep tillage or mineral fertilisation enhance water run-off and wind action, which triggers erosion (Lal and Kimble 1997; Heisler, Rogasik et al. 1998). Factors such as soil characteristics and climate (e.g. long drought periods followed by heavy precipitation), can also favour the acceleration of human-driven erosion. Each year, in the world 75 billion metric tonnes of soil are removed from the land by wind and water erosion, most of it coming from agricultural fields (Myers 1993). Eroded soil can result in the filling of lakes, reservoirs and rivers with soil particles. In addition, soil erosion can promote the diffusion of soil and water pollution and destroy natural habitats.

The direct effect of erosion is the degradation of the upper layer of the soil and the decrease of soil organic matter content. As a result, the nutrient availability for soil organisms is diminished, their biomass is reduced, and probably their diversity also (Pimentel, Harvey et al. 1995)(Figure 4-2).
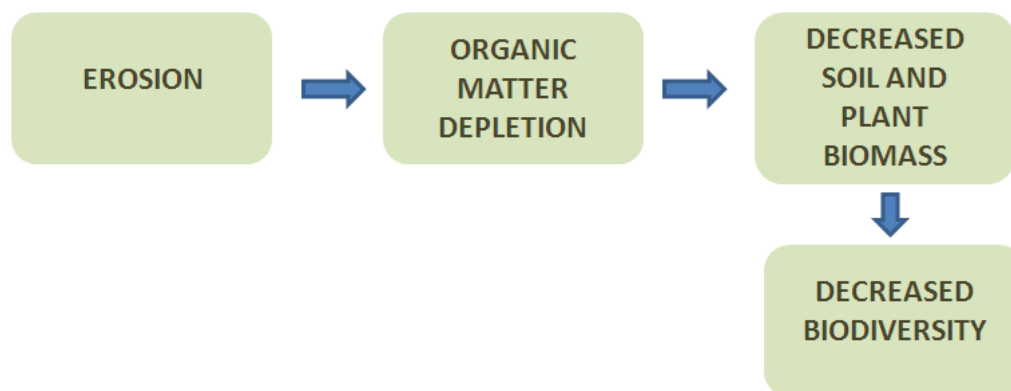

Figure 4-2: Relationship between soil erosion, biomass, and biodiversity

Erosion can also have indirect effects on soils and their services, through reducing plant diversity, standing biomass and productivity. For instance, erosion can reduce soil carbon storage, since reduced plant growth means less carbon input to soils. In addition, erosion leads to enhanced carbon emissions due to breakdown of soil structure and exposure of carbon in aggregates. In turn, erosion-induced reductions in plant diversity and abundance can reduce soil biodiversity. For instance, by reducing plant diversity, erosion significantly reduces the stability and of grassland ecosystems. In experiments on nutrient-poor sandy soils, the decrease in plant diversity made the grassland less resistant to drought, thereby reducing total plant biomass (Tilman and Downing 1994). This may reduce soil biodiversity.

Different impacts of erosion on soils are in fact correlated and it is difficult to separate them. The loss of soil organic matter triggered by soil erosion, for example, reduces water storage capacity and promotes water run-off. This leads to a decrease in soil nutrient levels causing a reduction in the number and overall biodiversity of soil biota (Figure 4-3).
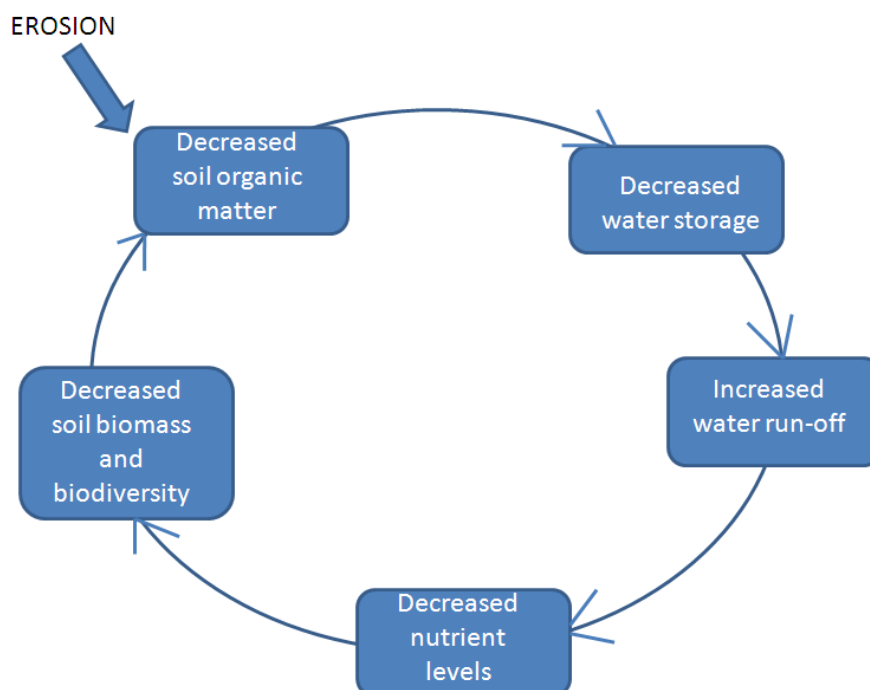

Figure 4-3: Example of interactions between direct and indirect erosion impacts

Currently, erosion affects 46.3% of European soils, although at variable intensities. Overall, soil erosion rates in Europe were estimated to average 17 tonnes/ha/year, greatly exceeding the rate of soil formation of about 1 tonne/ha/year (Barrow 1991). In Europe, soil erosion is mainly due to inappropriate agricultural practices, deforestation, overgrazing, forest fires and construction activities. Soil losses through water run-off are also significant (Figure 4-3). Some particularly heavy storms can cause losses of 20 to 40 tonnes/ha, which is 20 to 40 times greater than natural soil renewal. Under climate change, when there will be an increase in extreme climatic events, it is expected that soil erosion problems will further increase.

The Mediterranean region is particularly sensitive to erosion because of its climatic conditions and the nature of its soils. In this area, long droughts are often followed by heavy precipitation events which accelerate the erosion of fragile soils. In some Mediterranean areas, erosion is irreversible and no more soil is left. In the north of Europe, the situation is slightly better. Soil erosion in this area is less aggressive because rainfall events are more evenly distributed over the year.
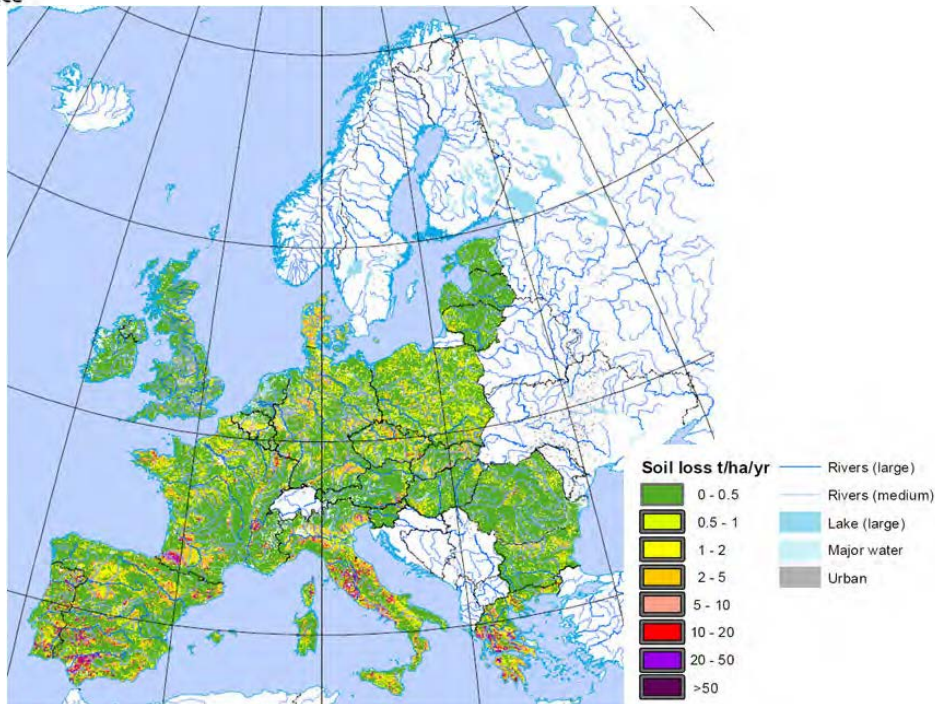
Figure 4-4: Estimated soil erosion by water in Europe (source: Pan-European Soil Erosion Risk Assessment PESERA)[30]

4. 2. 2. ORGANIC MATTER DEPLETION

The critical quantity of organic matter ensuring an optimal soil fertility has not yet been defined (Korschens, Weigel et al. 1998). These thresholds will be highly context-dependent (Box 1). Natural processes that determine the quantity of soil organic matter include:

- **Climate**. Climate driven factors such as temperature, precipitation, wind or rain intensity can contribute in the distribution of soil organic matter in the landscape.
- **Land cover and/or vegetation type** mainly influence litter quantity
- **Topography**: slope and aspect have an influence on organic matter accumulation.

Anthropogenic processes that influence soil organic matter include:

- **Conversion of (semi-)natural ecosystems to agriculture and changes in land use (e.g. conversion of arable to grassland).** For instance, the conversion of natural to agricultural ecosystems usually causes depletion of 50 to 75% of the previous soil carbon pool.
- **Deep ploughing** leads to organic matter dilution within soil. Agricultural ecosystems generally contain less soil organic carbon (SOC) than their potential capacity because of the severe losses due to accelerated erosion and leaching (Lal 2005) and because of the increased respiration rate in ploughed soils, due to the enhanced aerobic status of deeper soil layers.
- **Soil erosion**
- **Leaching of nutrients from soil to water** (e.g. due to excessive irrigation)

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[30] www.eusoils.jrc.ec.europa.eu/ESDB_Archive/pesera/pesera_download.html; last retrieval 27/08/09

- **Artificial removal or decrease of litter** due to land conversion (e.g. deforestation)
- **Forest fires**
- **Over-grazing**

As an important source of soil fertility and soil structure (Box 1), SOM depletion leads to a decrease in soil fertility and in soil biota biomass with significant consequences for biodiversity. Such impacts are the same as those for soil erosion discussed above.

A large fraction of European soils (45%) has very low organic matter content, between 0 and 2% (Citeau 2008). Southern Europe suffers from organic matter depletion due to its warm climate which favours the activity of chemical engineers, and therefore the organic matter decomposition. Indeed, some warm areas of France and Germany are also affected by this type of soil degradation (Figure 4-5).
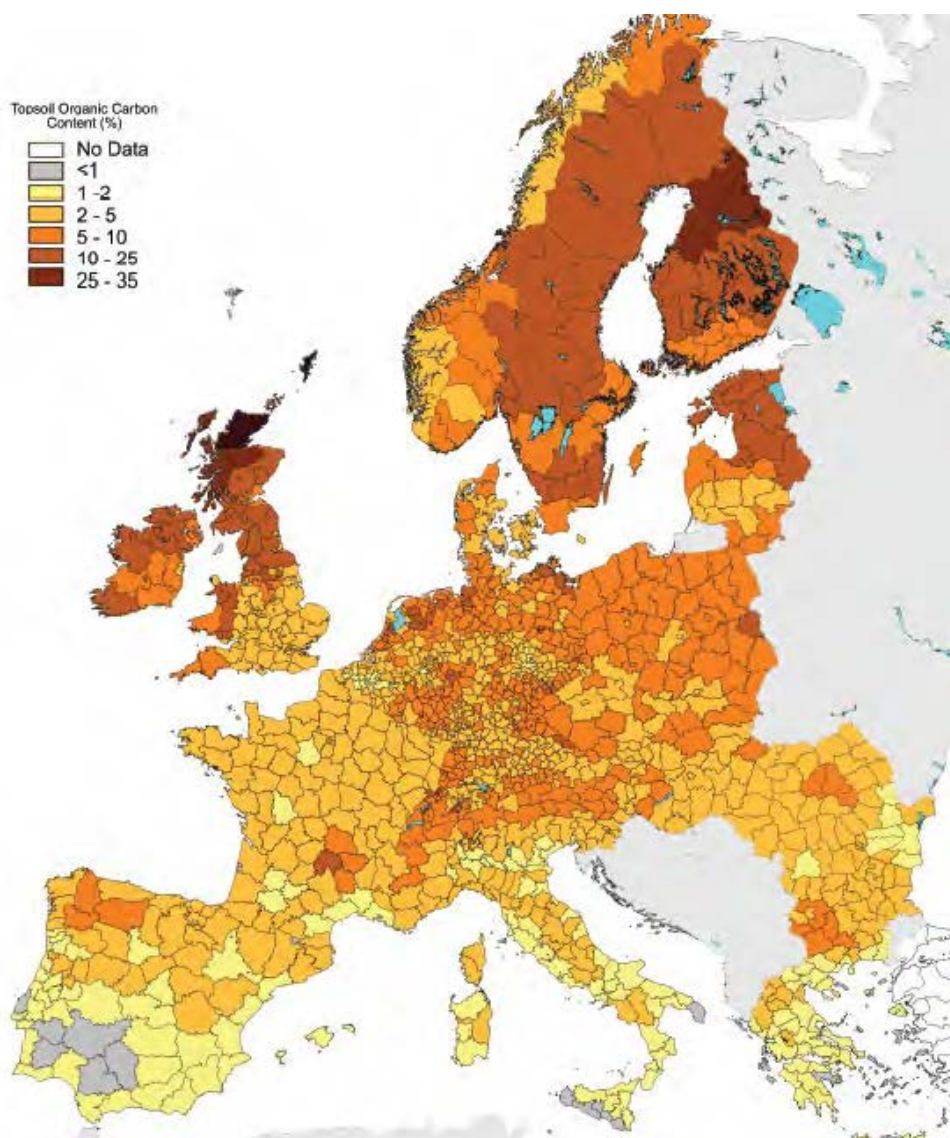

Figure 4-5: Organic carbon content in European soils[31]

Salinisation is the accumulation of water-soluble salts in the soil. This process can be natural or human-induced. In general, inappropriate irrigation practices, such as use of saline water and/or soil characteristics which inhibit salt washing are at the origin of the problem. Soil salinisation can also be triggered by the over-exploitation of groundwater in coastal areas, which leads to the infiltration of salty marine water. Moreover, marine storms can potentially increase soil salinisation in coastal areas.

As soil salinity is one of the key factors controlling the ecology of soil organisms, high salt concentration can affect the overall metabolism of plants and soil biota included in the three functional groups. Many bacterial species have optimal salinity concentrations and enter a dormant state (dormancy) if the optimal range is exceeded, resulting in inactive states. Both biological regulators and ecosystem engineers are in general extremely sensitive to salinisation. In the majority of cases, salinisation causes a strong decrease in plant growth and crop productivity, so that salinisation may lead to desertification and loss of soil biodiversity (Box 17).

Salinity is a global threat for soils. In Europe, between 1 and 3 million hectares are affected by this degradation process. The Mediterranean region, Spain, the Caspian Basin and the Carpathian Basin are the most affected areas (Figure 4-6).
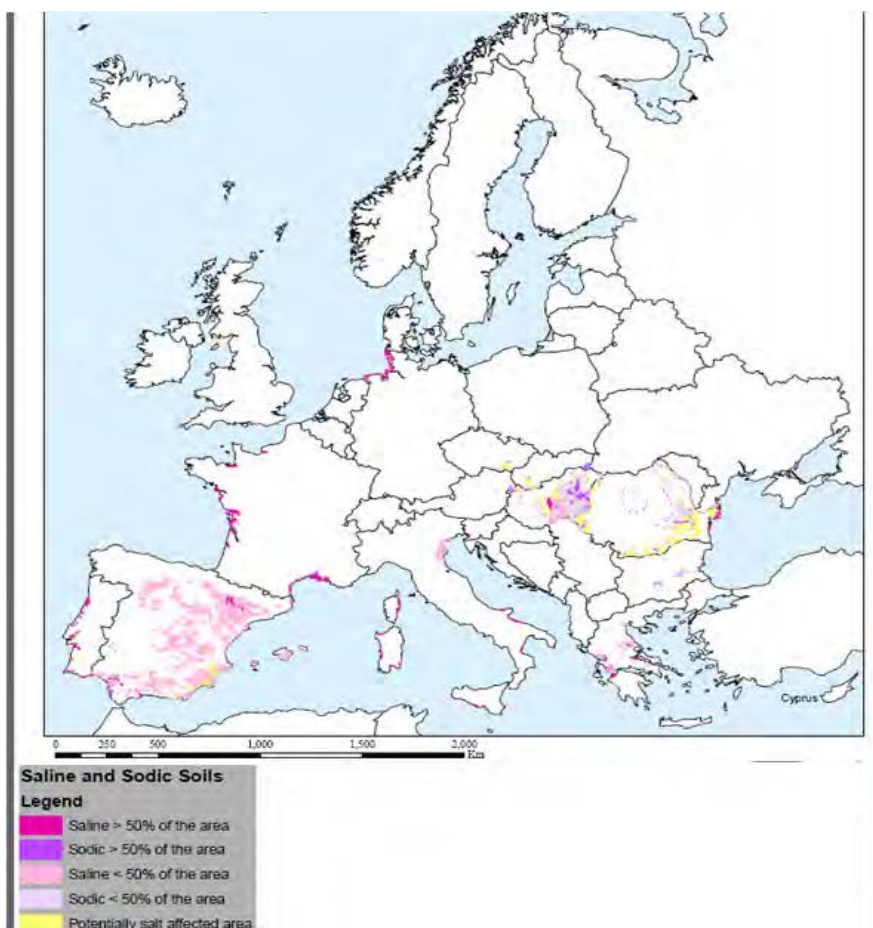

Figure 4-6: Salinity in European soils[32]

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[32] www.eusoils.jrc.ec.europa.eu/library/themes/Salinization/; last retrieval 31/08/09

Box 17: Desertification and biodiversity

Due to excessive erosion or salinisation or both, land degradation may reach the point of irreversibility, i.e. desertification. Desertification is a form of land degradation in arid, semi-arid and dry sub-humid areas, resulting from various factors, including climatic variations and human activities. Desertification most frequently results from the mismanagement of biodiversity: overexploitation of vegetation cover leading to topsoil erosion and hence reduced productivity, or improper water use resulting in salinisation. This affects not only crops but also rangeland and soil biodiversity. The final effect is the loss of natural ecosystems. When the overexploitation of rangeland results in desertification, the effects on biodiversity are first expressed in the direct loss of plant species and the animals associated with them, and later in the loss of topsoil and the potential for rehabilitating biodiversity. These biodiversity losses, both in goods and services, further exacerbate desertification in the affected areas.

4. 2. 4. COMPACTION

Soil compaction is a type of physical degradation due to the reorganisation of soil micro and macro aggregates, which are deformed or even destroyed under pressure. Compaction results in poor drainage, sub-surface gleying, etc. Soils can be naturally compacted at various degrees, and their natural compaction rate can be further increased by trampling or heavy machinery. The sensitivity of soils to compaction depends on soil properties, such as texture and moisture, organic carbon content, and on several external factors such as climate and land use.

The direct impact of soil compaction is the formation of a unique, uniform layer of soil. Within this compacted layer, the access for soil engineers, water and oxygen is much harder than in the original non-compacted soil matrix. This causes for instance altered root dimensions and distribution, leading to a modification of their engineering action and a decrease in plant growth. This has been observed for example in the case of corn where the proportion of deep roots is strongly decreased in the compacted area (Whalley, Dumitru et al. 1995) (Figure 4-7). The macropores created by plant roots and ecosystem engineers are the most vulnerable to soil compaction. A loss in macro-porosity significantly reduces the total soil aeration and water infiltration rate, having several impacts on soil organisms. Obstructed water infiltration results in water run-off and erosion.

The first direct impact caused by soil compaction and the consequent reduction of soil porosity is the reduction of available habitats for soil organisms. This affects in particular soil organisms living in surface areas, such as earthworms. Any compaction damages the earthworm tunnel structure and kills many of them.

Alteration of soil aeration and humidity status due to soil compaction can seriously impact the activity of soil organisms. Oxygen limitation can modify microbial activity, favouring microbes that can withstand anaerobic conditions. This alters the types and distribution of all organisms found in the rest of the soil food web. In addition, both laboratory and field observations have shown that compaction can significantly reduce the numbers of microarthropods involved in biological regulation, as shown in Table 4-1. The degree of impact varies with both the type of micro-arthropod and soil. Although micro-arthropod populations may recover, this can take several months.