Soils are increasingly under pressure and so are the organisms living in them. Intensive agriculture, loss of aboveground biodiversity, soil erosion and land degradation are among the most relevant threats to soil life. We can protect soil creatures by taking specific actions. No-tillage, diversification of crops, increasing reforestation and greater use of natural amendments are examples of interventions that may promote life in soils. People need to know about the fascinating world belowground and understand its value. The Global Soil Biodiversity Atlas presents the often neglected protagonists in the environment that surrounds us all.

Soil is an extremely complex system resulting from the essential interactions between inert and living components. Soils host a myriad of soil organisms ranging in size from a few micrometres to several centimetres, from the microscopic bacteria and archaea to the “giant” earthworms and moles. All these organisms are distributed over space and time, and each ecosystem and season has its unique soil community. Soil organisms interact to provide essential ecosystem services to human beings and the environment, ranging from supporting plant growth to the regulation of climate.
Supporting the EU Biodiversity Strategy and the Global Soil Biodiversity Initiative: preserving soil organisms through sustainable land management practices and environmental policies for the protection and enhancement of ecosystem services.
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Soil biodiversity data

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Soil is alive! Soil is home to millions of different organisms: from microorganisms, such as bacteria and fungi, to macrofauna, such as insects and earthworms. Also, several mammals have a strong link to soil. Organisms living in the soil are many, amazing, smart, important and unique. Soil biodiversity is full of incredible stories. The first ever Global Soil Biodiversity Atlas presents you with an exceptional overview of life living in soils. (LD, AM, GF)
Preface

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2015 was the United Nations International Year of Soils and, for the first time, soils and the life within them were in the spotlight globally. We are pleased therefore, that an international group of experts and scientists from the European Commission’s Joint Research Centre (JRC), in close collaboration with colleagues from the Commission’s Directorate-General for the Environment and the Global Soil Biodiversity Initiative, have produced the first ever Global Soil Biodiversity Atlas.

Soils are vital for human survival and underpin many sectors of our economy. It is estimated that 99 % of the world’s food comes from the terrestrial environment. But soils are also home to over a quarter of global biodiversity. Millions of soil-dwelling organisms promote essential ecosystem services – from plant growth to food production. They support biodiversity, benefit human health, promote the regulation of nutrient cycles that in turn influence climate, and represent an unexplored capital of natural resources.

Our knowledge of soil life is growing continuously, thanks to recent technological advances and awareness of its value. However, it is estimated that only 1 % of soil microorganism species have been identified. Therefore, understanding the highly complex and dynamic life below ground remains one of the most fascinating challenges facing scientists today. A clearer picture of our soils will allow us to better understand environmental and global climate change processes whilst also exploring possible adaptation strategies.

Pressures on soil organisms are well known. An ever increasing global population, and increased demand for food and fibre lead to intensified agriculture, greater use of fertilisers and pesticides, as well as monocultures. Unsustainable agricultural practices, climate change, soil erosion and loss of aboveground diversity all negatively affect organisms that live in soil. To develop actions that will preserve soil life, we need to better understand the consequences of the loss of soil biodiversity.

The Global Soil Biodiversity Atlas raises awareness of the role of soil organisms in sustaining life on our planet, and presents the latest research on soil biodiversity. It is also a major contribution to the EU target of halting the loss of biodiversity and ecosystem services in the EU by 2020, and the goals of the 2030 Agenda for Sustainable Development on sustainable food production and fighting land degradation.

This impressive publication marks a crucial step towards a global coordinated effort to assess life below ground, and highlights the need to improve soil conservation and the diversity of life within it.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

The Global Soil Biodiversity Atlas, with its very engaging and pedagogical presentation, provides non-specialists with access to a vast body of knowledge on the richness and extent of life beneath our feet. It will contribute to raising awareness about the importance of soil biodiversity for the functioning of our ecosystems, our ecosystem services and ultimately human well-being. This atlas will also represent a relevant contribution to the work carried by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

The IPBES was established in 2012 as a mechanism to provide policy relevant knowledge on biodiversity and ecosystem services response to requests from policy makers. Its membership currently includes 124 governments.

In 2015, the IPBES initiated an assessment of land degradation and restoration in response to requests from governments and other stakeholders, including the United Nations Convention to Combat Desertification (UNCCD). This assessment will be launched in early 2018. It will review the benefits of avoiding degradation: the concepts and perceptions of land degradation and restoration, according to different worldviews; indirect and direct drivers of degradation processes; the nature and extent of land degradation processes, and the resultant loss or decline in biodiversity and ecosystem structure and functioning; and the impact of changes in land degradation and restoration on the delivery of ecosystem services and human well-being. It will also assess the effectiveness of interventions intended to prevent, halt, reduce and mitigate processes of land degradation and to rehabilitate or restore degraded land and a range of development scenarios, including the consideration of different response options and their implications for land degradation regionally and globally. Finally, guidance will be provided to decision makers on how to address land degradation problems and implement restoration strategies at various levels and scales.

The IPBES is currently performing four regional assessments of biodiversity and ecosystem services in Africa, the Americas, Asia Pacific, Europe and Central Asia. Experts involved in these assessments include, of course, specialists of soil biodiversity. If approved by its Plenary in February 2016, the IPBES will begin a global assessment of biodiversity and ecosystem services, almost 15 years after the Millennium Ecosystem Assessment, to be released in 2019. This assessment will form a contribution to the report of the Convention on Biological Diversity on the implementation of the Strategic Plan 2011-2020 and its 20 Aichi Targets.

By contributing to a better understanding and appreciation of soil biodiversity, this atlas will complement the work of the IPBES, and contribute to our common ultimate goal, which is to better value and protect our biodiversity.

Global Soil Biodiversity Initiative

Our age is one of rapid change, incredible discoveries and big science that revolutionise our understanding of how the world around us works. This first global compilation of soil biodiversity focuses on the rapid acceleration of our knowledge and how this dazzling and spectacular world beneath our feet (from bacteria, through fungi, nematodes, mites, ants and earthworms to recognisable animals such as moles, gophers and reptiles) works together, mostly unseen, to provide us with benefits necessary for life. As with other big science initiatives, the newly launched Global Soil Biodiversity Initiative (GSBI) builds on previous successful national and international programmes: the Human Genome Project, The Brain-mapping Project, the Census of Marine Life, the newer Future Earth sustainability research project, and the SCOPE (Scientific Committee on Problems of the Environment) programme of the International Council for Science. These collaborations fostered new thinking, integration of biodiversity and ecosystem science, recognition of ecosystem services, and the importance of the fusion of molecular, species, and ecosystem information to fully encompass biodiversity.

The White Paper produced from the inaugural GSBI meeting in 2012 in London reiterated that ‘Earth’s soils are living, dynamic interfaces’ and that ‘Soil organisms are critical for the maintenance of ecosystem services, such as primary productivity, stable soil structure, regulating pathogens and parasites of plants, animals and humans, and ensuring a functioning and productive soil system’. Despite this, soil biodiversity is usually left out of policy decisions, is often overlooked in big evolution and ecology endeavours, and most people are unaware that life as we know it depends on this biodiversity. This reflects our fragmented knowledge of soil biodiversity globally, which is surprising considering its significance. This is not the biodiversity at the bottom of deep ocean trenches, rather it is the very accessible biodiversity in the upper layer of that ‘cold, rocky scum of continent carrying tectonic plates’ that is humanity’s home.

This first ever Global Soil Biodiversity Atlas (GSBA) is the first major product of the Global Soil Biodiversity Initiative and is the result of a partnership with the European Commission’s Joint Research Centre (JRC). Modelled on the European Atlas of Soil Biodiversity, it is an exciting collaboration with contributions from experts in soil biology and ecology from all over the world. The GSBA highlights soil as a habitat for an enormous, but largely unknown, diversity of soil-dwelling organisms that keep both the human population and the planet alive. At its most fundamental, it is a series of amazing photos, maps, charts, tables, statistics, and shared information that scientists, educators, policy makers, and non-specialists alike can use as a toolkit for knowing and understanding soil biodiversity globally. Ultimately though, this atlas is a precursor of the GSBI vision – a multi-dimensional data visualisation tool that demonstrates the complexity of soil biodiversity, its link to ecosystem science and its critical role as a future global resource for all of society.

Key messages

- Soil is an important habitat for thousand millions of organisms.
- Soil biodiversity is extremely diverse in shapes, colours, sizes and functions.
- Soil biodiversity is globally distributed, from deserts to polar regions through grasslands, forests, urban and agricultural areas.
- Soil biodiversity supports many services essential to human beings: plant growth, water and climate regulation, and disease control, among others.
- Soil biodiversity is increasingly under threat due to several pressures acting on soils.
- Interventions to reduce the impact of threats to soil biodiversity are available and should be widely adopted.
- Policies to protect and value soil biodiversity are still at an early stage and need to be further developed.
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Soil is a natural resource comprised of solids (minerals and organic matter), liquids and gases that is found on the land surface, occupies space, and is characterized by one or both of the following horizons, or layers, that are distinguishable from the initial material as a result of additions, losses, transfers, and transformations of energy and matter and the ability to support rooted plants in a natural environment. (AB, BHR, TS, USDA, WDNR, USDA/NRCS)
Scope of the atlas

‘Essentially, all life depends upon the soil …
There can be no life without soil and no soil without life: they have evolved together.’


Soil is composed of living organisms, minerals, organic matter, air and water, and performs a number of key environmental, social and economic services that are vital to life. Supplying water and nutrients to plants, at the same time soil protects water supplies by storing, buffering and transforming pollutants. Soil is an incredible habitat, and it also provides raw materials, preserves our history and reduces the risk of floods. Without soil, the planet as we know it would not function.

However, the importance of soil and the multitude of environmental services that depend on soil properties are not well understood by society at large. Part of the problem is that, with an increasingly urban society, many people have lost contact with the processes that lead to food production. Most people expect to find food on the shelves of supermarkets and have limited or even no appreciation of the roles played by soil. Concepts such as nutrient cycling and organic matter management, that are critical to soil fertility and food production, are a mystery to most of us.

There is very little dialogue between the soil science community and the general public. The majority of soil-related information is geared toward university-level or scientific journals – normally beyond the reach and understanding of the general public. This results in a lack of material to help interested stakeholders appreciate the value of soil and to guide them in preserving this precious resource.

As a consequence, soil tends not to feature in the minds of the public or politicians. However, soil experts are becoming increasingly aware of a greater need to inform and educate the general public, policy makers, land managers and other scientists of the importance and global significance of soil. This is particularly true for soil biology and biodiversity.

The first section aims to provide an overview of the factors that determine the main characteristics of the habitat by describing the key soil-forming factors and how soils vary on a global scale, while the second section presents a visual introduction to, and description of, the main groups of soil organisms. Given the astonishing levels of variation of life present in soils, it is impossible to present a complete overview of all soil biodiversity in this publication (just listing all of the known species of bacteria found in soils could take up many hundreds of pages). Starting with the smallest organisms, namely bacteria, and working up through the taxonomic groups, from fungi and nematodes to the insects and mammals that we are more familiar with, this section gives a taste of the breadth of different types of organisms which live, usually unnoticed, beneath our feet.

The third section describes the patterns of soil biodiversity from micro to global scales, both geographically by specific ecosystems and in time. The fourth, fifth and sixth sections are linked in explaining how soil biota drive ecosystem services; how ecosystem services are under threat from a range of pressures, such as land use and climate change, and what measures may be taken to protect soil organisms and the benefits they provide to society.

The final section outlines a series of policy, education and outreach initiatives to support soil biodiversity management and conservation. The atlas also contains a supporting glossary and suggestions for further reading.

The atlas is an activity of the Global Soil Biodiversity Initiative, which was launched in September 2011 to develop a coherent platform for promoting the translation of expert knowledge of soil biodiversity into environmental policy and sustainable land management for the protection and enhancement of ecosystem services (see Chapter IV).

The Global Soil Biodiversity Atlas was targeted as a contribution to the International Year of Soils 2015 and is a follow up to the highly acclaimed European Atlas of Soil Biodiversity, which was published by the European Commission as a contribution to the 2010 International Year of Biodiversity. By providing a global perspective on soil biodiversity and related issues, the atlas discusses the steps being taken to increase our appreciation of soil biodiversity and the development of measures to protect this vital resource.

To many people soil appears as solid ground. However, all soils contain space for life, from pores and cracks to burrows and root systems. (EM)

A fungus emerges from the soil. The soil that lies beneath our feet is teeming with life. Much of it is unknown and beyond the comprehension of most. Soil is the living shell of planet Earth. (WJ)

Vascular plants

<table>
<thead>
<tr>
<th>Organism size</th>
<th>Group</th>
<th>Known species</th>
<th>Estimated species</th>
<th>% described</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macrofauna</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Earthworms</td>
<td>7000*</td>
<td>500000</td>
<td>25 %</td>
<td></td>
</tr>
<tr>
<td>Ants</td>
<td>14000</td>
<td>25000 - 30000</td>
<td>60 - 50 %</td>
<td></td>
</tr>
<tr>
<td>Termites</td>
<td>2700</td>
<td>51000</td>
<td>87 %</td>
<td></td>
</tr>
<tr>
<td>Mesofauna</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mites</td>
<td>40000*</td>
<td>100000</td>
<td>55 %</td>
<td></td>
</tr>
<tr>
<td>Collembolans</td>
<td>8500</td>
<td>50000</td>
<td>17 %</td>
<td></td>
</tr>
<tr>
<td>Microfauna ad microorganisms</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematodes</td>
<td>20000 - 25000*</td>
<td>1000000 - 10000000*</td>
<td>0.2 - 2.5 %</td>
<td></td>
</tr>
<tr>
<td>Protists</td>
<td>21000</td>
<td>700000 - 7000000*</td>
<td>0.03 - 0.3 %</td>
<td></td>
</tr>
<tr>
<td>Fungi</td>
<td>97000</td>
<td>1500000 - 5100000*</td>
<td>19 - 65 %</td>
<td></td>
</tr>
<tr>
<td>Bacteria</td>
<td>15000</td>
<td>&gt;10000000</td>
<td>&lt; 1.5 %</td>
<td></td>
</tr>
</tbody>
</table>

Known and estimated number of species of soil organisms and vascular plants organized according to size. Values of estimated diversity comply with the published literature, and are supported by expert judgement. Asterisks indicate numbers of species that live in the soil (updated from Barrios, Ecological Economics, 2007). (1.2)

<table>
<thead>
<tr>
<th>Organism size</th>
<th>Group</th>
<th>Known species</th>
<th>Estimated species</th>
<th>% described</th>
</tr>
</thead>
</table>

| Earthworms | 7000 | 500000 | 25 % |
| Ants | 14000 | 25000 - 30000 | 60 - 50 % |
| Termites | 2700 | 51000 | 87 % |

Organism size Group Known species Estimated species % described

The Global Soil Biodiversity Atlas was targeted as a contribution to the International Year of Soils 2015 and is a follow up to the highly acclaimed European Atlas of Soil Biodiversity, which was published by the European Commission as a contribution to the 2010 International Year of Biodiversity. By providing a global perspective on soil biodiversity and related issues, the atlas discusses the steps being taken to increase our appreciation of soil biodiversity and the development of measures to protect this vital resource.

Earthworms enhance soil productivity by mixing the upper soil layers, which redistribute material and aerate the soil and increases surface water infiltration. Earthworms increase crop yields by 25 %, on average.
What is soil?

The term ‘soil’ means different things to different people. To the vast majority living in cities, soil is simply the ‘dirt’ or ‘dust’ to be cleaned from their hands or the vegetables that they buy to eat. However, to the majority of gardeners or farmers, soil is the uppermost surface of the Earth that is cultivated and nurtured to produce crops. To the engineer, it is the ‘overburden’ or the unwanted loose material that needs to be removed to provide a more stable foundation upon which to build. To the climate change modeller, it is both a storehouse and source of carbon, and to the hydrologist, soil is a buffer that stores rain, thus alleviating floods and providing drinking water as well as base flow for rivers. Finally, to the botanist, it is a fascinating habitat teeming with life.

In fact, soil is all of these things. Soil is the living, breathing skin of our planet. Soil is the result of the interactions between the atmosphere (as governed by climate), the biosphere (local vegetation, animal activities, including those of humans) and the geosphere (the rocks and sediments that form the upper few metres of the Earth’s solid crust). Those of us who study soil have a definition for it. We say ‘soil is any loose material on the surface of the Earth that is capable of supporting life’ and these life-supporting functions have been understood from the earliest times.

*A notion that destroys its soils destroys itself.*


What is soil made of?

All of us have come into contact with soil at some point in our lives and most people are familiar with such terms as clay, silt, sand or peat. In reality, soil consists of a mixture of non-living materials and living organisms that represent the products of weathering and biochemical processes. Rocks are weathered into individual grains, while decaying vegetation and living organisms undergo weathering and biochemical processes. Rocks are weathered into soil particles which are then transported by water and wind, which finally settle on the surface of the Earth. Soil is the result of the interactions between living and non-living materials.

The look and feel of soils

- **Texture** describes the size and type of mineral particles that make up the soil and are characterised according to their diameter. They range from gravel (>2 mm), sand (0.02-0.063 mm), silt (0.002-0.004 mm) to clay (<0.002 mm). Texture can be estimated by rubbing soil between your fingers. Clay soils will feel smooth while sandy soils are gritty.
- **Structure** refers to the arrangement of these soil particles into larger aggregates or clumps, of different sizes and shapes and the pore spaces that are left between them. It is into these spaces that root hairs grow and from which they extract water and oxygen.
- **Organic materials** are defined as materials derived from living organisms that are dead or dying, which make up the soil’s organic matter. It is these materials that contribute to the soil’s fertility and productivity.

The soil in profile

In most cases, if we dig a hole into the ground and look at the vertical section of soil that is revealed, we will notice a number of different layers, roughly parallel to the surface. These layers are referred to as ‘horizons’ and are the result of a range of geological, chemical and biological processes that have acted upon the parent material over the lifetime of the soil (see pages 20-25). Relatively young soils, such as those on river sediments or sand dunes or volcanic ash, may have indistinct or even no horizon formation. As age increases, horizons tend to be more apparent (there are exceptions, such as in deeply weathered tropical or permafrost-affected soils).

Most soils usually exhibit three or four horizons (there can be more or less). Horizons are generally described by their colour, texture, structure, organic matter and the presence of carbonates. More detailed characteristics can be measured in the laboratory. Some soils show a gradual change from one horizon to another, while other soils may possess horizons that have markedly different characteristics to each other.

The identification and quantitative description of horizons are important aspects of studying soils. Most soils conform to a similar general pattern of horizons and in soil science, major horizons are usually denoted by a capital letter as a means of shorthand and easy communication (typically followed by several alphanumerical characters to denote a characteristic feature). (3)

Know your A, B, C, ...

When a vertical section of the soil is examined, the thin uppermost layer normally contains the undecomposed or slightly decomposed remains of plants living on the surface of the soil. This layer is called an organic horizon and is referred to by the letter ‘O’. The O horizon is not saturated with water for prolonged periods and its mineral content is very low. Where the accumulations of organic material on the soil’s surface are saturated with water for prolonged periods, this is referred to as an H horizon. Organic matter in both the H and O horizons may be further divided into the following: 1) slightly decomposed – plant remains are visible to the naked eye; 2) an intermediate phase where decomposition is more advanced but plant remains are still visible; 3) a completely decomposed organic layer on top of the mineral soil.

Beneath the O horizon, a dark horizon containing a mixture of organic and mineral material can be recognised, which is referred to by the letter ‘A’. The A horizon is the topsoil, which contains most of the organic material within the soil, hence its darker colour. It is the engine room of the soil where most of its biological and chemical activities occur (e.g. biomass growth, dead litter and root decay and release of nutrients, formation of organic acids and their reactions with minerals, etc.). If the topsoil layer is removed by erosion or human activity, most of the soil’s ecological potential goes with it. While the topsoil layer will regenerate over time, if left undisturbed it may take hundreds of years for its full original potential to be restored.

Below the topsoil (O and A horizons) lies the mineral subsoil containing one or more brighter coloured layers that are referred to by the letter ‘B’. In most soils, the B horizon contains much less organic material than topsoil (often making it lighter in colour); however, this horizon is still exploited by plant roots and soil organisms that use the stored water, air and nutrients.

Brownish, yellowish or reddish soils originate from oxides (very often iron) formed by the weathering of minerals, whereas greyish or bluish tones can result from chemical reactions in waterlogged conditions. Towards the base of the subsoil, the soil structure gradually becomes less apparent as the factors affecting its development decrease in influence.

Eventually, a layer is reached where the influence of soil-forming processes is less apparent. This layer is referred to by the letter ‘C’. This horizon is often referred to as the parent material. The characteristics are usually very different to the A and B horizons and may contain weathered blocks of the underlying geological substrate. The W horizon basically denotes the layer of hard bedrock underneath the soil. Soils formed in situ will exhibit strong similarities to this layer.

Soils formed predominantly from the decaying remains of plants are referred to as peat and do not reflect the standard A-B-C arrangements of mineral soils. Horizons in organic soil tend to reflect the degree of decomposition or inputs of mineral material.

Soil – it’s amazing!

- **Soil makes up the outermost layer of our planet, while topsoil is the most productive and biologically active soil layer.**
- **A typical mineral soil sample is 4% minerals, 25% water, 25% air and 5% organic matter.**
- **Soil has varying amounts of organic matter (living and dead organisms). It is estimated that 5-10 tonnes of annual life can be found in one hectare of temperate grassland soil.**
- **Ten tonnes of topsoil spread over one hectare is only a few mm thick, but it can take more than 500 years to form 2 cm of topsoil.**
- **Soils are generally around 1 – 2 m deep. However, some soils are very shallow (just a few centimetres) while soils found on old, stable land surfaces are much, much deeper. The Philippine Palaeo is claimed to be 190 m deep.**
- **New soil material is continuously deposited by rivers, volcanoes and wind on the Earth’s surface. While soils in glaciated regions are relatively young, older, more weathered soils can be found closer to the tropics. The three thousand million year old Néwé Paleosol in South Africa is the world’s oldest soil deposit.**
Where do soils come from?

Soil-forming factors

As can be seen from the pictures on this page, the appearance and characteristics of soils can vary considerably from place to place. The next few pages of the atlas will outline the main soil-forming factors and illustrate how they dictate the properties of a particular soil.

The Russian scientist Vasily Vasilievich Dokuchaev is commonly regarded as the father of pedology, the scientific discipline concerned with all aspects of soils. He was the first person to articulate that geographical variations in soil characteristics were related to climatic, topographic conditions, time and vegetation as well as geological factors (parent material). His ideas were further developed by a number of soil scientists, including Hans Jenny who, in 1941 [4], established a mathematical relationship that states that the observed properties of soil are the result of the interaction of many variables, the most important of which are parent material, topography or position in the landscape, climate, living organisms/soil biodiversity, human activities and time (see following pages). According to this relationship, variations in living communities, parent material, climate or the age of the soil will result in specific soil characteristics.

For example, the weathering of solid bedrock through processes such as heating-cooling or freeze-thaw cycles (determined by topography and climate) produces a matrix of rock fragments (also known as regolith). Furthermore, weathering leads to the production of finer structures containing crystalline minerals that have been liberated from the rock. These fine-textured materials provide ideal conditions for seeds to germinate and lichens, mosses and higher plants to become established. The growth of vegetation is supported by the decomposition of minerals into simple molecules or compounds that act as plant nutrients. As plants become established, dead leaves will fall on the surface and decay to form thin organic layers, which in turn, support the next cycle of plant growth by returning the nutrients to the soil. Over time, the parent material is buried by more and more organic matter that has been dragged from the surface into the soil. Such soils occur in climates with an annual and seasonal rainfall of 450-600 mm, cold winters and relatively short, hot summers (e.g. North American prairies, Euranian steppes). In colder areas, the surface horizon can be as much as two meters deep. Due to the low rainfall, lime is not leached from these soils, making them some of the most naturally fertile soils on the planet. (EM)

This fine-textured soil from Australia with high levels of swelling and shrinking, clay minerals. Initially derived from the weathering of basic rocks, such as basalt, the clays were later redeposited in still water conditions. The dark colour indicates that iron is virtually absent from this soil. Note the cracks on the surface (0-15 cm) that result from shrinking and swelling in wet and dry conditions. (SD)

A shallow, stony soil from South America overlaying hard rock, reflecting very recent soil formation. This is the most widespread soil type on the planet, such soils are particularly common in mountain areas, notably in Asia, South America, northern Canada, Alaska and in the Saharan and Arabian deserts. However, they are unsuitable for agriculture because of their inability to hold water. They are generally used for extensive grazing or to support natural woodlands. (AN)

Much more information on soil-forming processes can be found in most general soil text books (see pages 172-173).
Soil-forming factors – Parent material

Parent material refers to the substance from which the soil has been derived. While in most cases it is of geological origin, parent material can also be organic. The nature of the parent material can have a profound influence on the characteristics of the soil. For example, the texture of sandy soils is determined largely by the presence of quartz grains in the parent material, which, in turn, controls the movement of water through the soil. The mineralogy of the parent material is mirrored in the soil and can determine the weathering process and control the natural vegetation composition. For example, lime-rich soils are generally derived from calcareous rocks (e.g. limestone and chalk) or sediments derived from such deposits. In turn, lime-rich soils can offset the development of acidic conditions but may not support organisms and plants that are not tolerant of alkaline soil conditions (e.g. rhododendrons).

Three types of parent material are recognised: 1) unconsolidated deposits that have been transported by ice, water, wind or gravity; 2) weathered materials directly overlaying consolidated hard rock from which they originate; 3) organic material composed of decaying or partially decayed plant remains. In the former two cases, the parent material can be weathered through physical destruction of rock (freezing or drying cycles) or chemical reactions (dissolution of elements). Weathered parent material is often referred to as saprolite.

While the forces created by the expansion and contraction of minerals, induced by daily temperature variations, cause rocks to shatter and exfoliate (especially in hot deserts), in most cases water is the dominant agent in weathering processes. Water can cause rocks to shatter through repeated freezing and thawing of water trapped in rock cavities. Water also initiates solution and hydrolysis (the destruction of a compound through a reaction with water that produces an acid and a base) that liberate minerals contained within the rock. Water also supports life which, in certain situations, is a major contributor to the weathering process. Plant roots can cause physical weathering as they grow and expand inside cracks in the rocks. Roots and decaying vegetation also produce organic compounds such as solvents, acids and alkalines that enhance the actions of percolating rainwater.

The degree of weathering depends on a number of environmental factors, such as temperature (determined by climate, exposure and altitude), the rate of water percolation (determined by texture, relief, climate), the presence of oxygen (again texture and altitude), the rate of water percolation (determined by parent material (for example, quartz is much more stable than olivine). Weathering of minerals continues in the soil following a sequence from the least to the most stable minerals. Minerals undergo changes that cause the formation of secondary minerals and other compounds that are soluble in water (to varying degrees).

Soil is considered organic if it contains more than 20 % of organic matter. By contrast, mineral soils contain less than 20 % organic matter but can possess organic surface horizons.

What is a rock?

- A rock is a naturally occurring solid material with a distinctive mineral composition. There are three basic types of rock: igneous, sedimentary and metamorphic.
- Igneous rocks form from molten material. They include rocks, such as basalt, that are ejected from volcanoes and granite, which is formed by magma that solidifies far underground. They are generally categorised by the size of their crystals and the presence of the mineral quartz.
- Sedimentary rocks are formed by the deposition of weathered rock fragments by wind or water. Shales are deposited on ocean floors. Conglomerates and sandstones are resistant fragments of other rocks deposited by rivers, while limestone and chalk are created through the precipitation of calcium carbonate in oceans. Fossils are found in sedimentary rocks.
- Metamorphic rocks are igneous or sedimentary rocks that have been transformed by intense heat, pressure or the intrusion of fluids resulting in changes in mineralogy and structure. Examples include marble (from limestone), slate (from shale) and gneiss (from granite).

Surface Geology

- No Data (ND)
- Unconsolidated Sediments (SU)
- Siliciclastic Sedimentary Rocks (SS)
- Mixed Sedimentary Rocks (SM)
- Carbonate Sedimentary Rocks (SC)
- Evaporites (EV)
- Pyroclastics (PY)
- Metamorphic Rocks (MT)
- Acid Plutonic Rocks (PA)
- Intermediate Plutonic Rocks (PI)
- Basic Plutonic Rocks (PB)
- Acidic Volcanic Rocks (VA)
- Intermediate Volcanic Rocks (VI)
- Basic Volcanic Rocks (VB)
- Ice and Glaciers (IG)
- Water Bodies (WB)
Soil-forming factors – Topography

The shape of the land surface, also referred to as relief or topography, is a key soil-forming factor as it has an important influence on local climate, vegetation and the movement of water. Mountains can affect the amount and intensity of precipitation and vegetation growth on a large scale, whereas locally, the angle or slope of the ground controls drainage and movement of materials. Even small variations in elevation can be important in flat lands. River terraces or small depressions can lead to localised improved drainage or waterlogging, respectively. Micro-topography can be particularly important if saline groundwater occurs close to the surface as it will affect evaporation rates.

The position of soil in the landscape is very important. Generally, soils found at the top of a slope tend to be freely draining, while those at the foot of a slope or on the floor of a valley are often poorly drained. In some cases, the water table may be near to or at the surface. In this case, different soils may form on the same parent material, under the same climate and even vegetation type (e.g. a grass-covered slope). Soils occurring on the middle of slopes receive sediment and solutions from higher up but, at the same time, lose material to soils below. In these cases, the actual shape of the slope is important as smooth, irregular, convex or concave slopes will result in different soil characteristics.

The map on the right shows the variation in elevation of the land surface in metres above sea level. The map is based on measurements taken by a specially modified radar sensor carried on board the NASA Space Shuttle as it orbited the planet [6].

The light turquoise and dark orange colours represent areas below or just above sea level, respectively. The low-lying salt lakes of North Africa, the Caspian Sea and the Dutch coast are particularly evident. In fact, the lowest point in the world is the Dead Sea on the Israel-Jordan border, which is -411 metres below sea level.

The dark orange areas show the extent of landscapes with low elevation and relief. These include the wetlands of Siberia, much of northern and central Eurasia, the Amazon and Paraná-Paraguay Basins in South America and the coastal lands around the Gulf of Mexico and Hudson Bay, which are generally flat or only gently undulating. Light orange denotes the high plains where the landscape will begin to show evidence of soil erosion on steeper slopes (eastern and central North America, northern Africa and large parts of Australia).

The yellow colours represent upland regions which, in some places, give way to mountainous areas (green). The Rocky Mountain Range, Greenland, the Alps, the Atlas Mountains of North Africa, the Anatolian Plateau and Zagros Mountains in the Middle East, the Southern Highlands in Tanzania and Mongolia are clearly visible. The highest elevations on the planet (dark blue) are found in the Himalayas where Mount Everest reaches a height of 8 848 metres above sea level. High mountain peaks are also present in the South American Andes (Mount Aconcagua, 6 962 m).

In addition to drainage, rainfall and solar radiation, another key factor for soil formation is temperature. While modified by latitude, proximity to the sea and some meteorological conditions known as inversions, ambient temperature generally drops with increasing elevation. This reduction in temperature is known as the lapse rate and, as a rule, temperature drops between 5 and 10 °C/1 000 m depending on air humidity; lusher normal atmospheric conditions, a value of 6 °C/1 000 m is usually quoted.

Soils on sloping ground – the Catena

- Catena comes from the Latin word for chain and describes the sequence of soils down a slope.
- On sloping ground with consistent parent material, the influence of relief dominates other soil-forming factors.
- The theory of the catena originates from a soil reconnaissance survey that was carried out by an agricultural officer, Geoffrey Milne, in what is now Tanzania during 1935-1936.
- He realised that the soils running from the crest of a hill to the floor of the swamp in the valley below differed somewhat from its neighbours and that the same soil types were occurring in the same landscape setting. This accelerated the production of soil maps.
- Interestingly, local farmers had an indigenous yet sophisticated understanding of the role of topography in determining soil characteristics.
- Milne’s initial ideas were set out in a ground-breaking paper that was published in 1947 [7]. He became one of the outstanding figures in international soil science and his concept provided the foundation for soil surveying all over the world.
Soil-forming factors – Climate

Climatic zones

Soil formation depends enormously on the climate as temperature and moisture levels affect weathering processes and biological activity like evapotranspiration, leaching or saturated soils can occur. When the opposite is true, salts can rise to the surface. Chemical weathering is very active in areas with high temperatures and high humidity, while physical weathering dominates in hot, dry desert regions.

About 36% of the Earth’s land surface is located within the Tropical Belt, where temperatures are warm all year round (generally 25°–28°C) and lack extreme seasons. In countries south of the Equator, the seasons are the opposite to the countries that lie north of the Equator. The broad climatic patterns are driven by ocean currents, weather systems, distance from the sea and topography (mountain chains often act as climatic barriers). The following five main climatic groups can be distinguished:

(A) Tropical: characterised by constant high temperatures, with all 12 months of the year having an average temperature of 18°C or higher, with little or no seasonality. It is subdivided into tropical rainforest climate (Af) where all months have an average precipitation of at least 60 mm, and generally occurs within 5°–10° latitude of the Equator, tropical monsoon (Am), tropical wet and dry or savannah (Aw). Sometimes As is used in place of Aw if the dry season occurs during the time of higher sun and longer days.

(B) Dry (arid and semiarid): where actual precipitation is less than a threshold value equal to the potential evapotranspiration. Subdivided into desert (BW) when the annual precipitation is less than 50% of this threshold and steppe (BS) if in the range of 50–100 mm. A third letter (a, b, or n) can be included to indicate temperature characteristics (see map legend at top right). Additionally, a fourth letter can be specified to indicate if either the winter or summer is ‘wetter’ than the other half of the year.

(C) Temperate: characterised by an average temperature above 10°C in the warmest months (April to September in the Northern Hemisphere), and a coldest month average between -3°C and 18°C. In this group, the second letter indicates the precipitation pattern: w indicates dry winters, s indicates dry summers and f indicates significant precipitation in all seasons. The third letter indicates the degree of summer heat where a indicates that the warmest month average temperature is above 22°C with at least four months averaging above 10°C, b indicates that the warmest month averages below 22°C, but with at least four months averaging above 10°C, while c means three or fewer months have mean temperatures above 10°C. Subdivided into dry-subtropical or Mediterranean (Csa/Csb), humid subtropical (Cfa, Cfb, Cfc), continental temperate or oceanic (CfC, Cfc, Cwb), temperate highland tropical climate with dry winters (Cwb, Cwc), maritime subarctic climates or subpolar oceanic climates (CfC) and dry-submarine maritime subarctic climates (Csc).

(D) Continental: characterised by an average temperature above 10°C in the warmest months and a coldest month average of below -3°C. Usually found in the interiors of continents and on east coasts north of 40°N. In the Southern Hemisphere, group D climates are extremely rare due to the smaller land masses in the middle latitudes and the almost complete absence of land at 40°–60°S. The second and third letters are used as for group C climates, while a third letter d indicates three or fewer months with mean temperatures above 10°C and a coldest month temperature of below -38°C. Subdivided into hot summer continental climates (Dfa, Dfa, Dsa), warm summer continental or hemiboreal (Dfb, Dfw, Dsb), continental subartctic or boreal (taiga) climates (Dfc, Dfc, Dwc) and continental subarctic or boreal (taiga) climates (Dsc, Dsc, Dsc) and continental subarctic climates with extremely severe winters (Dfd, Dwd, Dsd).

The Tropics

- The Tropics denote the area on the Earth where the sun is directly overhead at least once during the solar year. It is limited by the Tropic of Cancer, at approximately 23°26′16″ N, and by the Tropic of Capricorn, at 23°26′16″ S, which marks the points where the sun is directly overhead during the summer solstice (June 21st and December 21st, respectively).
- The term ‘tropical’ is sometimes used in a general sense to denote a climate that is generally warm and most of the year round and where there is often lush vegetation. However, in a strict sense, a tropical climate is not wet and all months have an average temperature >18°C.

(E) Polar and alpine: characterised by average temperature below 10°C throughout the year. Subdivided into tundra (ET) and ice cap (EF) where in the latter all 12 months have average temperatures below 0°C. Occasionally, a third, lower-case letter (w, s, f – see group C) is added to ET climates to indicate precipitation patterns. Seasonal precipitation levels are almost never attached to ET climates due to the difficulty in distinguishing between falling and blowing snow, as snow is the sole source of moisture in these climates.

Annual temperature range

Temperature and fluctuations in temperature have an important influence on soil-forming processes. The map below shows the annual temperature amplitude based on the difference between the mean temperatures of the warmest and coldest months.

What controls climate?

• Climate classification systems, like Köppen-Geiger (8), organise the world’s climate on the basis of meteorological patterns. These are controlled by:
  - latitude which influences the seasonal range of solar intensity, and evaporation as it is temperature dependent;
  - land heating/cooling faster and more intensely than water; therefore, continental locations have a larger seasonal temperature range than maritime locations. Maritime locations often have more precipitation;
  - geographic location, since issues such as prevailing winds influence local climate;
  - temperature, which generally decreases with altitude. Mountains also affect precipitation patterns;
  - ocean currents which play a critical role, as sea-surface temperature influences air temperature. Evaporation rates are generally higher where sea-surface temperature is higher;
  - atmospheric pressure patterns and resulting winds, which influence advecting temperature and moisture, cause areas of convergence and divergence and influence mid-latitude storms.

How does climate affect weathering?

• Weathering is the breaking down of rocks and minerals.
• Physical weathering is accentuated in very cold or very dry environments, while chemical reactions are most intense where the climate is wet and hot. Both types can occur together and each tends to accelerate the other.
• Studies have shown that tropical weathering rates, where temperature and moisture are at their maximum, are 3.5 times higher than the rates found in temperate environments.
• When water freezes, its volume expands by 11%, which can create incredibly high pressures in confined spaces.
• Heating and cooling of rocks causes minerals to expand and contract at different rates. These stresses eventually cause rocks to crack, often by a process known as exfoliation where the outer layers just peel away. Moisture and frost can mitigate these effects.
• Carbon dioxide dissolved in rainwater produces a weak carbonic acid, which can cause weathering of the rocks on which it falls.
Temperature

The map shows the patterns of mean annual air temperature across the world. The highest temperatures (dark red colour) occur in Montana and along the coast of the Red Sea. The highest shade temperature ever recorded in the world was 58°C at Al Azniyah, Libya, on September 13, 1922. However, summer temperatures in many parts of the world often reach 46°C or higher almost every day. In fact, the daily temperatures in the Danakil Depression of Ethiopia and the Eritrean lowlands are consistently higher than 40°C and can regularly reach 50°C. During the night, temperatures may drop sharply. Several deserts show large seasonal temperature ranges.

Temperatures measured directly on the ground may significantly exceed air temperatures. A ground temperature of 93.9°C was recorded in Furnace Creek, Death Valley, California, USA in July 1972, which may be the highest natural surface temperature ever recorded. More recently, satellite measurements of ground temperature taken with the MODIS infrared spectroradiometer on the Aqua satellite recorded a maximum temperature of 70.7°C in the Lut Desert, Iran. However, these measurements are lower than the maximum point surface temperature as they reflect averages over large areas and include atmospheric attenuation, or gradual loss of intensity. Researchers have calculated that the theoretical maximum possible ground surface temperature should be between 90 and 100°C for dry, darkish soils of low thermal conductivity.

To many people's surprise, temperatures near the Equator are not excessively high, with average daily temperatures being a constant 24-27°C throughout the year. Extensive cloud cover and heavy rainfall prevent temperatures from rising much higher than 33°C. The diurnal temperature change (i.e. between day and night) is usually between 2°C and 5°C, which is greater than the annual temperature range of 2°C.

The coolest regions (light grey and purple) are, as expected, in the Arctic and in the high mountain ranges. The lowest temperature ever recorded on Earth was −89.2°C at Vostok Research Station, Antarctica, although a temperature of −93.2°C was measured by the Landsat 8 satellite for an unnamed Antarctic plateau on August 10th, 2010.

Is precipitation only about rain?

- Precipitation is any product of the condensation of atmospheric water vapour that falls under gravity.
- The main forms of precipitation include drizzle, rain, sleet, snow, graupel (soft hail or snow pellets) and hail.
- Precipitation occurs when a portion of the atmosphere becomes saturated with water vapour, so that the water condenses and precipitates.
- Fog, mist and dew are not considered as precipitation. While low compared to rain, their contribution can be significant ecologically, especially in and climates. Dew is also a habitat for plant pathogens, such as the potato Phytophthora infestans (see page 37), which infects potato plants.

Precipitation

The map below shows the pattern of mean annual precipitation (millimetres of rainfall and the water equivalent of snowfall). Climate classification systems, such as Köppen-Geiger, use average annual rainfall to help differentiate between climate regimes. Precipitation is measured using rain and snow gauges; however, rainfall can also be estimated by weather radars and satellites.

Rainfall is distributed very unevenly across the planet. Many areas receive either too much rain or too little. In parts of the west coast of Africa, for example, annual rainfall averages more than 3,000 mm. In the city of Monrovia, Liberia, more than 1,000 mm of rain falls on average during the month of June alone. By contrast, more than half of Africa receives less than 500 mm of rainfall yearly, while rain may not have fallen for many years in some parts of the Atacama Desert or Arabian Peninsula. The wettest place in the world is Cherrapunji, situated on the southern slopes of the Eastern Himalaya in India, with an average annual rainfall of 11,430 mm. The highest recorded rainfall in a single year was 22,987 mm in 1861. In the tropical rainforest climate, all 12 months have an average precipitation of at least 60 mm. In relation to soil formation, humid conditions lead to more chemical weathering, higher levels of organic matter and leaching of minerals and organic matter. Heavy or prolonged rain can lead to soil erosion and saturated soils. A lack of rain will give rise to the development of crusts and accumulation of salts.

Antarctica is the driest continent. The globally averaged annual precipitation over the whole Earth has been estimated at 990 mm but drops to 715 mm over all land masses. Prolonged and widespread droughts, such as those found in the Sahel regions of Africa in 1973, can cause much suffering and social unrest. Changes in precipitation patterns can also have a marked effect on soil organisms.
Soil-forming factors – Climate

Soil temperature regimes

Soil temperature is an important attribute and key environmental factor in determining soil-forming processes, the natural distribution of plants and the control of biological processes in the soil. Soil temperatures above or below critical limits severely inhibit seed germination, even if there is adequate soil moisture. The life cycles of many soil-borne pests and diseases are controlled by soil temperature. The temperature of the subsoil lags behind air temperature, commonly by one to two months. The length of lag depends on climate, shade, aspect, the thickness of the organic layer and the thermal conductivity and heat capacity of the soil (governed by factors such as mineralogy and porosity, i.e. how well the soil absorbs water). The map on the right shows the pattern of the main soil temperature regions across the world (for a depth of 50 cm). The classes are:

- Gelic: from the Latin gelane, to freeze. These soils are associated with permafrost and have a mean annual soil temperature (MAST) at or below 0 °C. Gelic soils can be further divided into Pergelic (MAST between −4 °C and −10 °C) and Hypergelic (MAST < −10 °C).
- Cryic: very cold soils but no permafrost. MAST between 0 °C and 8 °C.
- Frigid: soils are warmer in summer than in the cryic regime, but their MAST is still between 0 °C and 8 °C and the difference between mean summer and winter soil temperatures ≥ 6 °C.
- Mesic: MAST is 8 °C or higher but lower than 15 °C; the difference between mean summer and winter soil temperatures ≥ 6 °C.
- Thermic: MAST ≥ 15 °C but lower than 22 °C; the difference between mean summer and winter soil temperatures ≥ 6 °C.
- Hyperthermic: MAST ≥ 22 °C and difference between mean summer and winter soil temperatures ≥ 6 °C.
- Megathermic: MAST ≥ 28 °C

The prefix ‘iso-’ indicates that the difference between mean summer and mean winter soil temperatures is lower than 6 °C.

Soil moisture regimes

Soil moisture regimes affect soil formation and the use or management of soils. Soil moisture regime classes include:

- Aquic: soil is saturated with water long enough to cause anaerobic conditions (not visible on the map).
- Interfrost: cold winters where soil moisture freezes for several months of the year. Can have snowfall.
- Xeric: arid climate, usually dry. Irrigation required for crop production.
- Udic: humid climate. Soils usually moist all year round; therefore, irrigation is not generally required for crop production.
- Hyperic: very cold soils but no permafrost. MAST between 0 °C and 8 °C and the difference between mean summer and winter soil temperatures ≥ 6 °C.
- Permafrost: soil material remains below 0 °C for two or more years in succession. Water occurs predominantly as ice in the form of lenses, veins, crystals and wedges.
- Periglac: cold winters where soil moisture freezes for several months of the year. Can have snowfall.

Soil moisture estimated from satellites

In the map below, blue areas denote low soil moisture or lack of vegetation, such as in deserts, while red areas are forested. In-between colours denote subtle differences in soil moisture levels.
Soil-forming factors – Living organisms

All plants and animals (from microorganisms to humans) affect soil formation. Living organisms add organic matter – a key component of soil – through the breakdown of litter, decomposition of dead roots and the conversion of compounds exuded (i.e. released) from living roots (see pages 33-35, 38-41). Facilitate chemical exchanges between roots and the soil to produce essential nutrients. Both animals and plants allow moisture and gases to seep into deeper layers along burrows and root channels. Humans can impact soil formation through land management practices that disturb natural processes and change the chemical and physical characteristics of the soil.

Cultivation practices and burrowing animals mix soil from different horizons, especially from the organic-rich surface layers. The nature of biological activity in the soil is governed by climate, topography and soil characteristics, such as depth, texture, structure and chemistry (e.g. pH and salinity).

Ecoregions and biomes

Ecoregions can be defined as relatively large units of land or water containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change. The limits of ecoregions generally follow continental boundaries or major barriers to plant and animal distribution (such as the Himalayas and the Sahara).

Ecoregions are classified by the presence of biomes, which are major plant communities determined by rainfall and climate. Forests, grasslands (including savannah and shrubland) and deserts are distinguished by climate (e.g. tropical, subtropical and temperate) and water conditions. In addition, forests are divided into conifers, broadleaf or mixed.

Land cover

The term ‘land cover’ is used to describe the physical material at the surface of the planet. While predominantly vegetation, it can also include ground water or artificial surfaces. Depending on the scale of observation and complexity of the cover type, the eventual classification may be a mixture of the above. It is important to distinguish between the terms ‘land cover’ and ‘land use’. For example, a land cover of mixed shrubs and grass could be used as a park, an orchard or savannah.

The map below shows the principal types of land cover in 2012 as mapped by satellites orbiting the Earth. The map shows that equatorial regions are covered by extensive forests, which merge to the north and south with open woodland and increasing grasslands or savannah.

Mid-latitudes are characterised by aridity giving rise to bare or sparsely vegetated areas. More temperate climates display a mosaic of croplands and forests that indicates the human alteration of natural vegetation patterns. Northern latitudes show mixed and conifer forests, which give way to the open shrubland of the tundra. At this scale, only the largest urban areas are visible. While trees cover around 27 % of the planet, it is estimated that around three-quarters of the Earth’s vegetated surface have been altered by prolonged human activities (see pages 18-19).
Originally, human settlement was closely dependent on climate, the availability of water, the length of the growing period and the presence of fertile soils for crops and fodder. As a consequence, the urban pattern and infrastructure network that is visible today reflects the areas that match these conditions. The map on the right shows global population density (technically this is the estimated number of people living within one square kilometre). This map denotes where people are concentrated; from the less populated white areas to the densely populated red and purple regions. Population density is generally very low in arid, cold and mountainous regions while the Nile Delta, the Ganges Plain and the Far East are amongst the most densely populated areas on the planet. Average global population density (excluding Antarctica) is estimated at around 50 people/km². However, over half of the land surface is inhospitable. The most densely populated region is the North Indian River Plain with 1 000 people/km².

Soil-forming factors – Human activities

Long-term global population growth is difficult to predict. Projections from the United Nations show a continued increase in population in the near future with a steady decline in population growth rate. The graph shows estimates of the total world population to 2100 based on the projections of total fertility and life expectancy at birth. Global population is expected to reach between 8.3 and 10.9 thousand million by 2050. Increased pressure on land resources in relation to drivers such as urbanisation, climate change and food security will affect soil processes. (UNEP) [16]
Soil-forming factors – Time

While soils are formed through the combined effect of physical, chemical and biological processes which operate over hundreds or thousands of years, these factors rarely remain constant. Time determines the duration for which a set of factors is active. Over geological timescales, new sources of parent material can be introduced to the landscape while changes in global climate patterns are usually accompanied by changes in sea-level, erosion and deposition regimes, vegetation patterns and the shape of the landscape. Over much shorter timescales (100–1000 years), major changes can occur in the amount and nature of biological activity or hydrological conditions within a soil. Even annual fluctuations in weather patterns (e.g. drought or above-average rainfall) or changes in the use of the land (conversion of forest to agriculture) can change the nature of soil-forming factors that can either lead to an increase in the rate of soil formation or to the destruction, or even complete removal, of the soil. Given constant environmental conditions, all soils must eventually tend toward a state of equilibrium or maturity where the rate of soil formation is equal to the rate of soil loss. However, situations may arise naturally where the rate of destructive processes exceed the rate of accumulation and retention of materials from weathering, plant growth and animal deposition. At this point, the soil and its biodiversity become vulnerable to degradation processes, such as wind and water erosion.

How old are soils?

- It is very difficult to accurately assess the age of soils. Since soil-forming factors continue to affect soils during their existence, evidence of earlier cycles may have been destroyed.

- Studies have shown that the rate of soil formation varies from around 100 years for 2–5 cm on volcanic ash in warm humid climates to 1 cm in 5000 years on hard rocks in cool temperate climates.

- Soils in glaciated areas only formed after the ice melted. In North America and Europe, this makes them thousands of years old.

- Human artifacts and buried organic matter can be dated based on the natural radioactivity present in all organic carbon matter.

- There is much debate about the age of soils in the tropical regions of Africa and South America. Many believe that they are millions of years old. Countering this is the view that soil-forming factors only operate at the surface of deeply weathered sediments.

Land cover change over time

Deforestation is the permanent destruction of natural woodlands through the felling of trees in order to make the land available for other uses (apart from forest). All major tropical forests - especially those in the Americas, Africa and Southeast Asia - are under pressure, largely to make way for human food production, including livestock and crops. Additional drivers are logging and the construction of roads or buildings. The loss of trees destroys habitats and biodiversity, and reduces carbon sequestration and soil functions. Deforestation generally increases rates of soil erosion, by increasing the amount of runoff and reducing the protection of the soil from tree canopy and litter. In some situations, it can lead to the onset of desertification. Therefore, tropical deforestation has profound consequences on soil condition and associated biodiversity.

The state of Rondônia in western Brazil is one of the most deforested parts of the Amazon. This pair of satellite images from the MODIS sensor on NASA’s Terra satellite shows the same area in the years 2000 and 2012. On both images, intact forest is deep green, while cleared areas and bare ground are tan (bare ground) or light green (crop, pasture or occasionally, second-growth forest). Over 12 years, roads and clearings have pushed west from the town of Buritis toward the Rio Jacarana River. In this interval, the deforested area along the road to Nova Hannover has expanded northwards all the way to the BR-364 highway. Such time series images show that deforestation follows a fairly predictable pattern. The first clearing that appears in the forest shows a typical fishbone pattern along the edges of roads. Over time, the fishbones collapse into a mixture of forest remnants, cleared areas and settlements. This reflects the establishment of legal and illegal roads into a remnant part of the forest, followed by small farmers who claim (land along the road and clear some of its crops. Within a few years, heavy rains and erosion deplete the soil, causing crops to fail. Farmers then cut down and degrade arable land to pasture and clear more forest for crops. Eventually, these small farmers either sell or abandon their land to large cattle holders, who consolidate the plots into large areas of pasture (NASA) [19].

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Soil-forming processes

Principle processes

The specific properties of an individual soil type are determined by pedological processes that operate during its lifetime. These biological, chemical and physical actions add, transform, move (translocate) and destroy or remove material within the soil. It is important to recognise that soil-forming processes can evolve and change over time in response to factors such as climatic variability and land use. Many soils exhibit several distinct and different phases of soil formation. More detailed information on the processes described in the following pages can be found in (20, 21).

Weathering

Below the soil, solid rock or unconsolidated sediments can be found in (or on) which the soil has developed (see page 12). In reality, all sediments are derived from solid rock by a process known as weathering. Weathering proceeds through a physical destruction of the rock structure which, in turn, facilitates chemical changes to the constituent minerals. In principle, there are two main types of weathering: physical and chemical. Biological activity is also important as it contributes to both types (see below).

Physical weathering

In physical weathering, rocks disintegrate without changing their chemical composition. Typical examples of these processes are the splitting of rocks through daily warming of the sun and cooling during the night (typical of desert environments), or by the repeated freezing and thawing of water (when water freezes, its volume increases by 10 %, causing tremendous pressures if it occurs in confined spaces, such as crevices in rocks).

Physical weathering produces a layer of loose material, which covers the underlying solid rock. This material is known as regolith and can vary from a few millimetres to tens of metres thick. Regolith layers in some parts of west Africa have been found to be more than 150 m thick. There is often a sharp boundary between the bottom of the regolith and the bedrock. This narrow zone is known as the weathering front and is the focus of active weathering.

Chemical weathering

Chemical weathering is a gradual and continuous process. It is driven primarily by the reaction between water or an acid and elements within the parent material, which lead to the creation of secondary minerals from the original minerals present in the rock. Chemical weathering is much stronger if temperature and humidity are high (e.g. in the humid tropics).

Water is the key factor in chemical weathering. Most people are unaware that rainfall is slightly acidic with a pH of around 5.6 in unpolluted environments. Atmospheric carbon dioxide dissolves in rainwater to produce a weak carbonic acid. Some minerals, due to their natural solubility (e.g. evaporites such as highly soluble salts and gypsum) or inherent instability relative to surface conditions (e.g. silicate minerals such as feldspar, mica, augite, hornblende and olivine), slowly dissolve to form secondary products, such as clay minerals (e.g. kaolinite, illite, vermiculite and smectite), iron and aluminium (hydr)oxides, carbonates and essential plant nutrients, such as calcium and potassium.

One of the most well-known solution-based weathering processes is de-carification, which occurs on parent materials that are rich in calcium carbonate, such as limestone and chalk. The weak carbonic acid in rainfall reacts with the calcium carbonate in the limestone to form calcium bicarbonate, which is then removed. This process can be even stronger if gases, such as sulphur dioxide and nitrogen oxides, are present in the atmosphere. These oxides react in the rainwater to produce a weak carbonic acid. Some minerals, due to their natural solubility (e.g. evaporites such as highly soluble salts and gypsum) or inherent instability relative to surface conditions (e.g. silicate minerals such as feldspar, mica, augite, hornblende and olivine), slowly dissolve to form secondary products, such as clay minerals (e.g. kaolinite, illite, vermiculite and smectite), iron and aluminium (hydr)oxides, carbonates and essential plant nutrients, such as calcium and potassium.

Another chemical process involves the simultaneous loss (referred to as oxidation) and gain (referred to as reduction) of electrons in substances. These exchanges are referred to as redox reactions. As materials become oxidised, the unbalanced charge degrades a material’s structural composition.

Biological weathering is caused by the activities of living organisms and has both physical and chemical aspects. Examples of physical biological weathering include the loosening of rock by roots growing into cracks and burrowing creatures, such as termites that mix, or churn, the soil. Chemical biological weathering can be caused by bacterial activity or by strong organic acids from plant roots or litter. A recent study demonstrated a three- to four-fold increase in weathering rate under lichen-covered surfaces compared to recently exposed bare rock surfaces. Biological weathering factors in Africa are highly significant.

Minerals vs. nutrients

- A mineral is a naturally occurring solid substance formed through geochemical processes with a characteristic chemical composition. Rocks are composed of several minerals.
- Nutrients are chemical elements required by organisms to live and grow. Nutrients can be produced by the organism or taken up from its environment.
- Plants absorb nutrients from dissolved minerals in the soil which, in turn, are consumed by herbivores and then by the people who eat the herbivores. People can also obtain nutrients directly from fruits and vegetables. In this way, minerals move up the food chain.

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Common processes in humid conditions

Many parts of the world are characterised by a climate that provides a precipitation surplus during some parts of the year (i.e. when rainfall is greater than evaporation rates). This surplus fills the spaces or voids in the soil, which might have been emptied during the dry season, and then percolates down through the soil body to accumulate as groundwater. In doing so, the water drives three important soil-forming processes:

Leaching

When water passes through the soil, it dissolves soluble salts (such as chlorides, nitrates, sulphates and carbonates) and flushes them, together with organic and chemical solutes, into the deeper parts of the soil. In drier climates, these salts can be re-precipitated, for example, as a calcium carbonate-rich or gypsum horizon in the subsoil. In more humid regions, significant amounts of materials can be completely removed from the soil.

This loss of mineral and organic solutes caused by percolation is known as leaching. The rate and extent of leaching depends on the following two factors:

- the mobility of an element, which is based on its solubility in water and the effect of pH on that solubility - chlorides and sulphates are very mobile, while titanium is insoluble even at a pH of 2.5
- the rate of water percolation, which depends on climate, soil texture and structure, porosity and the slope of the ground - in dry regions, even the most mobile compounds (e.g. sodium chloride) tend to stay in the topsoil and eventually give rise to saline soils

As humidity increases, losses of salts, organic compounds and silica in the topsoil increase and the soil is regarded as being leached.

Leaching is a major controller of soil fertility. As long as calcium carbonate is present, the pH of the soil remains above 7 and the soil is often whitish or light-coloured. When the calcium carbonate is dissolved and leached away, the pH drops and calcium, magnesium and sodium are released from the surfaces of clay minerals and humus, to be replaced by hydrogen and aluminium. Unless there is a change in the soil-forming factors or there is human intervention, the soil pH falls below 7 and, under such conditions, the soil is referred to as acidic.

Highly acidic soils are not very suitable for the cultivation of most plants. Such soils require the addition of calcium carbonate (a practice known as liming) in order to raise the pH to a more acceptable level, depending on the crop. A reduction of pH below 5.5 can cause a release of aluminium cations in the soil solution, which is toxic for some plants and nearby water bodies.

In some instances, immobile elements can be leached when they are combined with organic compounds (e.g. organic and amino acids) derived from the humification of litter or from soil microorganisms. This process, known as cheluviation, is an important mechanism for increasing nutrient availability to plants. Chelates are very important in micronutrient management.

The movement of clay particles

A common soil-forming process is the movement, or translocation, of clay particles from one horizon to another. This involves the mechanical transfer of clay particles from the upper part of the soil by percolating water (eluviation) and their re-deposition deeper in the soil (illuviation) on the surfaces of soil particles or in soil pores and cavities.

Clay movement is dependent on the soil texture, structure and chemistry. If a continuous and coarse pore system exists in the soil, percolating water can then transport the clay particles downwards. Such conditions will develop as the soil shrinks and cracks during dry seasons. The clay accumulates where the cracks end and water movement almost ceases, or where the water penetrates into the dry aggregates and the clay particles are filtered at the ped surfaces forming clay layers or skins called cutans or argillans.

Another process that can lead to low clay content in the topsoil is rainfall distribution. If the rainfall is greater than evaporation rates, the subsurface deposition layer (known as a spodic horizon), overlain by an ash-grey, strongly leached eluvial horizon.

Podzols – very leached soils

A Podzol is a soil type characterised by the presence of a dark subsoil deposition layer (known as a spodic horizon), overlain by an ash-grey, strongly leached eluvial horizon.

Podzols can occur given a specific combination of high precipitation, a coarse-grained and silica-rich parent material (e.g. river sands) and vegetation that releases strong organic acid from its litter as it decomposes. This process is called podzolisation.

These acids mobilise metal oxides in the topsoil. Percolating water redeposits them deeper into the soil, leaving behind a zone of bleached, immobile sand grains.

The redistributed mix of iron and aluminium can form a hardened or cemented horizon which acts as a barrier to the passage of further leached material and roots. Precipitating iron can give a uniform orange-red colouration to this horizon.

Over time, organic matter accumulates on this obstruction where a dark, humus-rich sub-surface horizon develops.

Podzols are found on all continents but predominantly in the temperate and boreal regions of the Northern Hemisphere.
Soil-forming processes

Common processes in a wet tropical climate

A significant part of the world has a humid tropical climate, where constant high temperatures (average annual temperature is around 26°C), copious rainfall (over 2000 mm annually) and high humidity occur throughout the year. In addition, much of tropical Africa and South America is characterised by old, geologically stable landscapes that have been deeply weathered. Under such conditions, chemical weathering, leaching and translocation combine to produce a number of distinctive soils where the geology of the bedrock determines the underlying chemical properties of the soil. The most typical divisions are:

Highly weathered soils with a ferrallic horizon

In deeply weathered sediments, a combination of high soil temperature and intense percolation dissolve and remove all weatherable primary minerals from the soil. Less soluble compounds, such as iron and aluminium oxides, the clay mineral kaolinite and coarse quartz grains, remain behind. This process eventually leads to the formation of a ferrallic horizon. High concentrations of hematite (an iron oxide) give a distinctive red colouration to the soil, while in more temperate conditions, the mineral goethite tends to dominate, giving soils a more yellow colour. To be effective, the process requires low soil pH, geologically stable land surfaces and basic parent material containing abundant levels of iron and aluminium in the form of easily weatherable minerals but little silica. Clay content and texture are relatively constant with depth due to the mixing of the soil by biological activity (primarily termites). Soils matching these characteristics are referred to as Ferralsols. Such soils can support luxuriant natural vegetation (e.g. rain forest), due to a self-sustaining nutrient cycle. If this cycle is broken (e.g. as a result of deforestation), the soil quickly loses its fertility and is prone to degradation processes, such as erosion. Traditional agricultural practices of temporary forest clearance and shifting cultivation recognise this cycle.

Weathered soils with a distinctive nitric horizon

A derivation of the ferralisation process described above can lead to the development of soils containing a characteristic ‘nutty’, polyhedric (i.e. many-sided), blocky structure with shiny red faces. Typically, the soil body is deep, developed in fine textured weathering products of intermediate to basic parent material and contains high levels of kaolinite and iron (hence the red colour). In some respects, these soils could be seen as young examples of the later stages of ferrallisation. Following the intensive weathering and leaching of minerals, alternating micro-swelling and shrinking episodes produce well-defined structural elements with strong, shiny pressure faces. Through biological activity (pedoturbation), the soil can become highly mixed, resulting in a characteristic crumbly or subangular blocky soil structure and diffuse soil horizon boundaries. The spatial distribution of this process is highly dependent on subtle variations in the landscape and parent material. Soils matching these characteristics are known as Nitosols.

Soils with an iron-rich horizon that can harden (plinthic)

On level or gently sloping terrain, a substance known as plinthite (from the Greek plinthos, meaning brick) can develop in iron-rich parent material that is prone to fluctuating groundwater levels. Plinthite is a subsurface accumulation of iron (hydrous) oxides, kaolinitic clay and quartz. Plinthite is generally formed through the segregation of iron in the soil that has been saturated with water throughout the year. The iron has probably been transported by soil water from higher ground as ferrous iron under anaerobic conditions. Alternatively, iron concentrations may increase due to the removal of silica and base cations through the leaching of dissolved weathering products. The resulting ferric iron is precipitated as soft, clayey, red or dark-red ferric iron concretions. Soils with these characteristics are referred to as Plinthosols. If enough iron has precipitated and the soil starts to dry out, the soft clay begins to harden irreversibly on exposure to the open air.

Hardened plinthite occurs in concretionary (skeletal) form or as a continuous layer (petroplinthite), also referred to as ironstone. Soils with petroplinthite are especially abundant in the transition zone from rain forest to savannah. Plinthite concretions can also occur as a dense layer of nodules known as pisoliths, often lying close to the surface due to the removal of the soil between the pisoliths by termites for building their nests.

Soils with an argic horizon and low or high activity clays

As described in the previous pages, clay particles in the soil can be moved from one layer to another, giving rise to a subsurface horizon with a higher clay content than the overlying horizon. Three common soil types occur in the humid tropics displaying clay-rich subsurface horizons:

- strongly acidic soils that develop in the weathering products of aluminium-rich metamorphic rocks, or where the weathering of secondary high-activity clay minerals, such as vermiculite or smectite produce high levels of aluminium, referred to as Alisols. Such soils are most common in old land surfaces with a hilly or undulating topography under humid tropical or monsoon climates. High levels of aluminium in the subsoil give the soil a reddish colour and can hinder biological activity.

- strongly acidic soils that develop on the weathering products of acidic parent material (which give rise to an accumulation of acidic activity clays) in old land surfaces with a hilly or undulating topography under humid tropical climates are referred to as Acrisols. Acrisols generally exhibit a strong yellow- to red-coloured argic horizon overlain by a much lighter yellowish-brown horizon

- where the climate has a pronounced dry season and the soils on old erosional or depositional surfaces are enriched in base cations through different processes (e.g. aeolian dust, biological activity, etc.), the resulting soils are known as Lithosols. Usually, the soil overlying the clay-rich horizon has a notably coarser texture. Many regard these soils as ‘fossilised’, reflecting a more humid climate.

Why are rocks acid or basic?

- The terms ‘acidic’ and ‘basic’ are often used to describe igneous rocks or related parent material of soils.

- However, this does not refer to the pH of the material but rather to the amount of silica in proportion to Mg, Fe and Ca.

- Igneous rocks that contain significant amounts of silica (at least 66% 50%, by mass), which normally occurs as quartz) are referred to as acid. Examples include granite and rhyolite.

- Conversely, the term ‘basic’ is applied to rocks containing dark minerals such as olivine, plagioclase and biotite. Rich in Mg, Fe and Ca but with relatively low amounts of silica. Examples include basalt, dolerite and gabbro.

- Recently, the term ‘mafic’ is used in place of basic while felsic is used for acid. Intermediate rocks (e.g. andesite) contain roughly even mixtures of felsic and mafic minerals.
Common processes in a dry tropical/subtropical climate

Where precipitation is lower than evapotranspiration and high temperatures cause groundwater to rise to the surface, several distinctive soil types can occur. These include:

Soils with accumulations of calcium carbonate

One of the most widespread soil-forming processes in dry climates involves the movement of calcium carbonate ($\text{CaCO}_3$) from surface horizons to an accumulation layer at some depth (a process referred to as secondary accumulation). On wetting (such as after rainfall), lime dissolves allowing calcium and bicarbonate ions ($\text{Ca}^{2+}$ and $\text{HCO}_3^-$, respectively) to move downwards with the percolating soil water. When the water eventually evaporates, calcium carbonate precipitates as calcite where the percolation stopped. Calcite is not evenly distributed throughout the soil matrix. Root channels and wormholes act as channels along which the solution can flow, allowing the calcite to precipitate on the channel walls. When narrow root channels become filled with calcite, the resulting cast-like shape of the root is known as pseudomycelium. Other characteristic forms of calcium carbonate accumulation are soft or hard lime nodules and platy or continuous layers known as calcrete or hardpan. Calcite ‘beards’ can be found as pendants below pebbles. In eroding land, lime concretions may occur near the surface of the soil.

Soils with accumulations of gypsum

Gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) dissolved from gypsumiferous parent materials is moved through the soil by water and, in a similar manner to calcium carbonate, is precipitated in an accumulation layer when the water is removed. Where soil moisture moves predominantly upward (i.e. where a net evaporation surplus exists for an extended period each year), a gypsum-rich horizon forms within the soil body. Gypsum is also leached from the surface soil in wet winter seasons and re-accumulates deeper in the soil as a loose, powdery substance. Over time, gypsum crystals may cluster together as compact layers or surface crusts that can become tens of centimetres thick. Gypsum can precipitate in former root channels (gypsum pseudomycelium), in voids, as coarse crystalline gypsum sand or in strongly cemented horizons (petrogypsic). In places, it forms massive crystalline structures known as desert roses.

Soils with accumulations of silica

In many and regions (although not exclusively), soils known as Durisols contain very hard layers of silica- enriched materials in the subsoil. These materials range from silica-cemented sand and gravel to a nebulous matrix enriched with small silica particles. The conditions under which such features develop are uncertain as nearly all occurrences are ‘fossil’ because such soils do not seem to be forming extensively at present. Theories include the precipitation from silica-rich groundwater in arid/semi-arid climates or by intense weathering in a warm, humid climate. Soils with lower levels of gypsum and calcium carbonate in the upper 30 cm soil layers can support grazing and some drought-tolerant crops when carefully irrigated. The hard duripan material is commonly used for road construction.

Soils with accumulations of salt

A soil is regarded as saline if the salt concentration is around 2500 parts per million (ppm). Soils affected by soluble salts or by their ions are typical of semi-arid and arid regions and are salt pans. Saline soils also occur in ephemeral or closed basin lakebeds, also referred to as salt pans, salt flats, sebkhas, playas or chottas. Strongly saline soils with high concentrations of soluble salts are known as Solonchaks, while soils with dense, clay- and sodium- rich subsoils are known as Solonetz.

Depending on the chemical composition, the reaction between the soil and salts may differ. Salts containing sodium (Na) cause organic compounds to become mobile and are eventually leached out of the topsoil, resulting in the development of a bleached horizon. The pH of such soil types is typically above 9. Salts in soil can also result from irrigation, since almost all water (even natural rainfall) contains some dissolved salts. When crops use the water, these salts are left behind in the soil and accumulate over time. They must be artificially leached or flushed out of the root zone by applying additional water. Salinisation can be increased through poor drainage or use of saline water for irrigation. Saline soils also occur in ephemeral or closed basin lakebeds, also referred to as salt pans, salt flats, sebkhas, playas or chottas.

Soils with accumulations of salt

A soil profile from Namibia which has formed by the evaporation of groundwater out of the root zone by applying additional water. Salinity can also be carried into depressions in the landscape by saline surface water flowing from higher ground. In dry lands, salinity can occur even when the water table is two or three metres from the surface of the soil. The main ions responsible for salinisation are Na$^+$, K$^+$, Ca$^{2+}$, Mg$^{2+}$, SO$_4^{2-}$ and Cl$^-$. Depending on the chemical composition, the reaction between the soil and salts may differ. Salts containing sodium (Na) cause organic compounds to become mobile and are eventually leached out of the topsoil, resulting in the development of a bleached horizon. The pH of such soil types is typically above 9. Salts in soil can also result from irrigation, since almost all water (even natural rainfall) contains some dissolved salts. When crops use the water, these salts are left behind in the soil and accumulate over time. They must be artificially leached or flushed out of the root zone by applying additional water. Salinisation can be increased through poor drainage or use of saline water for irrigation. Saline soils also occur in ephemeral or closed basin lakebeds, also referred to as salt pans, salt flats, sebkhas, playas or chottas.
Soil-forming processes

Common processes in cold climates

In very cold environments, such as those found in high latitudes and elevations, the soil temperature may be below 0°C for much of the year, which means that water in the soil occurs mostly as ice, and permanently frozen ground is common. The upper part of the soil may only thaw during the short summer months. In these conditions, physical weathering through frost shattering and cryoturbation (mixing of the soil as a result of freezing and thawing cycles) is highly evident. The presence and mobility of unfrozen soil water is a key factor as it migrates along the thermal gradient toward the freezing front in the soil. Specific cryogenic processes that affect soil formation are frost heave (where soil material is lifted), churning, sorting and orientation of soil materials, thermal cracking, surface cementing and the build up of ice either as crystals, massive layers or as wedges. These cryogenic processes give rise to very distinctive soils and surface features referred to as patterned ground. In addition, many of the soil processes described in the preceding pages (accumulation of organic matter, leaching, clay movement and destruction) can also be found. Despite the presence of ice, these soils during the summer months still provide the rooting media, nutrients and water for plants and biological life in these extreme ecosystems.

Common processes on volcanic materials

Soils that develop from ejected volcanic materials such as ash, tuff, pumice, cinders and lava often contain high proportions of volcanic glass. Chemical weathering of primary minerals and volcanic glass leads to the formation of secondary aluminium- and silica-rich minerals, such as allophane and imogolite (under high rainfall) or halloysite (where rainfall is lower). The weathering process liberates aluminium (Al³⁺) ions, which become tied up with humus in stable Al-organic compounds as the aluminium protects the organic material against biodegradation. Any free ferric iron (Fe³⁺) usually precipitates as ferrhydrite (a form of iron oxide).

Such poorly crystalline materials have a large surface area and, consequently, can absorb large amounts of water. However, due to their high aeration exchange capacity, such materials have a low ability to retain and supply nutrients, and therefore require very large additions of phosphorus to stimulate higher crop yields.

Soils conditioned by water

When it rains, water percolates through the soil and, in many cases, drains away. However, in some places the soil texture or the presence of an impermeable barrier prevents water from escaping, causing pores and cavities to become full of water (also referred to as groundwater). In some soils, groundwater can be found at relatively shallow depths (~2 m). This situation generally exists due to a slowly permeable substrate, depressions in the landscape, which collect water, or in marshy areas near to the coast.

The presence of a shallow groundwater table strongly decreases the movement of gases in the soil because oxygen and carbon dioxide diffusion in waterlogged pores is very slow compared to air-filled pores. If organic matter is present in the waterlogged soil, the metabolic activity of the microorganisms creates an oxygen deficit and a state known as ‘reduction’ develops. In these conditions, ferric iron is converted to the more soluble, and therefore mobile, ferrous iron (Fe²⁺). While ferric oxides are responsible for giving subsolts their characteristic yellowish- or reddish-brown colours, their disintegration into ferrous oxides gives the soil a distinctive greysish or bluish colour. However, in some of the larger pores where some oxygen may remain, mottles of rust-coloured material indicate the redeposition of ferric oxides. In soil science, two basic types of waterlogged soils are recognised, surface water and groundwater gley.

Soils conditioned by the presence of swelling clays

In areas with distinct dry and wet seasons and where the parent material contains large quantities of swelling clay minerals known as smectites, soils are characterised by the presence of deep cracks in dry periods which close in the wet season. The closure of the cracks is driven by the expansion of the smectite minerals as they absorb water. Such soils are also defined by the presence of characteristic structural aggregates (spheroids). Shrinkage of the clay on drying leads to the formation of cracks. In addition, the surface breaks up into granules or clumps that can fall into the cracks. When the soil is rewetted, part of the space that the soil requires for its increased volume is occupied by the granular material in the cracks, which results in the build up of shear stress within the soil material. Continued pressures through the uptake of more water eventually cause the soil masses to shear and slide against each other.

The shear planes are known as slickensides and display polished surfaces that are grooved in the direction of force causing the movement. Intersecting shear planes produce wedge-shaped angular blocky clods that tend to increase with depth (probably reflecting the moisture gradient). This internal movement of soil, coupled with the deposition of surface crumbs in deep cracks, means that the subsurface soil is pushed towards the surface and mixed. This process is known as churning or pedoturbation. This constant mixing of the soil material results in an extremely deep A horizon. Such soils tend to develop either at the foot of slopes or on plains as a result of the weathering of basalt or redeposition of smectite-rich laustrine sediments.
The effects of living organisms

One of the most important factors affecting soil processes are living organisms. Increasingly, biological activity is being recognised as an important factor in regulating soil processes, such as storage of carbon, and thus soil profile development. The role that living organisms play in soil development cannot be overstressed. The accumulation and decay of organic matter, the development of soil structure, the mixing of soil material (bioturbation), nutrient cycling, the physical breakup of bedrock by roots and the bacterial destruction of clay minerals are all the result of organisms living in the soil, and are critical soil-forming processes.

In a broad sense, the activity of organisms in the soil is closely linked to climate. Nevertheless, biological activity is also present in hot, dry desert regions (see page 87). In low temperatures or in very wet conditions, bacterial decomposition is reduced and organic matter accumulates. In the warm and wet conditions of the tropics, both bacterial and fungal activity are intense. In temperate zones, burrowing mammals, beetles and earthworms can have a strong influence on soil processes by facilitating the transfer of water and air along burrows and channels. In the tropics, termites and ants play a major role in nutrient recycling and the redistribution of soil material – the movement of particles of subsoil to the surface by termites is one of the main factors responsible for the homogenised profiles that are typical of some tropical soils.

Soil organic matter is derived from the remains and exudates of living organisms (predominantly plants). Organic matter is utilised by a variety of soil organisms as both a source of energy (to function) and materials for building their bodies. During this process, water, carbon dioxide (CO₂) and various organic compounds such as sugars, starches, proteins, carbohydrates, lignins, waxes, resins and organic acids, are converted through a process known as mineralisation, into inorganic compounds, such as ammonium (NH₄⁺), phosphate (PO₄³⁻) and sulphate (SO₄²⁻). This process, together with the release of CO₂ from the soil, is vital for plant growth. Some of these compounds are immobilised by being incorporated into the bodies of soil organisms, and are only available after the death of the organism.

The annual return of plant and animal residues to the soil varies with climate, vegetation type and land use. The effect can be easily seen when comparing soils of grasslands and forests. The organic matter content, moisture-retention and nutrient-holding capacity of grassland soils are generally much higher than those of forests. In addition, the type of vegetation can also affect soil characteristics. The litter of coniferous trees tends to be low in calcium, magnesium and potassium, which tends to lead to acidic conditions in the soil. Conversely, soils under natural grasslands favour nitrogen fixers, such as Azo执lutecter (see page 33).

Tropical rainforests generally return about 15 tonnes of litter per hectare each year, compared to around eight tonnes for tropical grasslands, two tonnes for agricultural soils and 0.1 tonnes for alpine forests. Root decay contributes a further 30 - 50 % of the amount produced from leaf fall.

Soil organic matter and carbon

- Carbon is an important constituent of all living matter.
- All soils contain varying amounts of the element carbon (C) in both organic and inorganic forms.
- The term soil organic matter (SOM) is used to describe the organic constituents in the soil (e.g. cells and tissues of soil organisms and plant and animal residues at various stages of decomposition).
- With the exception of calcareous soils, the majority of C in soils is held as organic carbon (OC).
- The term ‘soil organic carbon’ refers to the C occurring in SOM.
- On average, 58 % of SOM is carbon.
- Living organisms play a key role in the C cycle (see page 104).

Peat formation

Peat is a dark, unconsolidated, organic-rich material that has developed when the decay of plant material is slowed as a result of a lack of oxygen in waterlogged (anaerobic) conditions. Such conditions are found in wetlands such as bogs, fens, moors, mires or swamps. Three main types of peat are recognised: sapric (very decomposed, hardly any recognisable plant fibres), hemic (moderately decomposed) and fibric (slightly decomposed).

Peat can also accumulate in tundra and mountain environments where temperatures are low enough to slow down decomposition. In soil classification, organic soils are known as Histosols (from the Greek histos, meaning tissue).

Peat accumulates slowly. Globally, peatlands are distributed very unevenly, with North America accounting for around 44 % of the total area. Most of the remaining peatland is found in Asia (28 %) and Europe (24 %). Approximately 95 % of the world’s peatlands are found in the Northern Hemisphere. Peat is the initial stage of coal formation.

Soil formation driven by human activity

Some people argue that all cultivated soils have been affected or altered by human activity through the mixing of topsoil and subsoil by ploughing, changing the chemical balance through liming, or depleting nutrients through intensive farming. However, there are numerous examples throughout the world where the entire soil body was either totally formed, or at least profoundly modified, through human activities, such as the addition of organic materials or household wastes, irrigation or cultivation. Collectively known as Anthrosols, examples include:

- very deep tillage that is below the depth of normal ploughing – often through the use of terraces
- intensive fertilisation with organic fertilisers such as manure, kitchen refuse, compost, human excrement
- continuous application of earth (e.g. sods, beach sand and shells) or sediment through irrigation
- wet cultivation that involves puddling the surface of the soil or human-induced wetness (e.g. paddy fields for rice cultivation)

Another major human management factor is drainage which affects the frequency and duration of periods when the soil is saturated by water. In waterlogged soils, drainage can allow crops to be grown by allowing oxygen to move within the soil. The drainage of peatlands for cultivation can eventually result in total soil loss from shrinkage and wind erosion if the peat is allowed to dry out completely.

Organic vs. mineral soils

- Soil material is referred to as organic if it contains more than 20 % organic matter.
- Mineral soils, by contrast, contain less than 20 % organic matter but can possess organic surface horizons.

Peat land

- Bogs – water only by precipitation (known as ombrotrophic). Less acidic, higher nutrient levels and more diverse plant community than bogs;
- fens – mostly mineral-rich surface or groundwater (known as minerotrophic). Acids, higher nutrient levels and more diverse plant community than bogs;
- marsh – often found at the edges of lakes, streams and estuaries

Water table

- Litter layer on the floor of a rainforest. Rapid decomposition due to high temperatures and humidity levels leads to a dark-coloured surface soil (10YR).
Map of global distribution of soils

Climate plays an important role in soil formation. Hence, soils generally differ from one major climatic zone to another. Equatorial regions, with high temperature and rainfall levels, have deep, strongly weathered and very leached soils with low nutrient levels. More and conditions, with low precipitation and high evaporation, produce soils containing easily soluble components such as calcium carbonate or gypsum. Soils in temperate climates tend to have more organic matter while the effects of parent material and precipitation levels are more evident. In cold climates, soil formation is restricted and strongly influenced by freeze-thaw processes and the presence of ice in the subsoil (permafrost). Past climates also play an important role in determining current soil distribution, especially in the subarctic and northern temperate regions where glaciers have removed all soil material and new soils were formed after the retreat of the ice. Consequently, soils of these regions are relatively young or ‘immature’.

Soil classification schemes generally reflect different concepts of soil formation. The boxes on these two pages are simplified descriptions of the major soil types according to the World Reference Base for Soil Resources (WRB), an internationally used soil classification system. More information on the WRB system can be found at: www.fao.org/soils-portal/soil-survey/soilclassification/world-reference-base/en

Acrisols: from Latin acer, acid

Strongly acid soils with a clay-enriched subsoil and low nutrient-holding capacity. Mainly found in the wetter parts of the tropics and subtropics. Normally associated with acidic bedrock and deficient in nutrients. Thus requiring substantial applications of fertiliser to produce satisfactory crop yields. (OS)

Albeluvisols: from Latin albus, white, and eluere, to wash out

Soils with a subsurface horizon that tANGES into a horizon which has accumulated clay. Formed mostly in unconsolidated deposits on flat to undulating plains under coniferous or mixed forest. Dominated by cold and temperate climates with cold winters and short cool summers. (EM)

Alisols: from Latin alumen, aluminium

Very acid soils with a clay-enriched subsoil and high nutrient-holding capacity. Acidity is caused by the weathering of minerals which release a large amount of aluminium − often at levels that are toxic to most crops. They occur in humid tropical and sub-tropical climates. (ISRIC)

Andosols: from Japanese an, black, and do, soil

Soils developed from materials ejected from volcanoes (e.g. ash, pumice and cinder) which weather to produce specific clay minerals. In humid climates, many Andosols develop a thick dark surface horizon which contains material rich in aluminium that is released from the weathering of the clay minerals. (ISRIC)

Anthrosols: from Greek anthropos, man

Soils that exhibit surface horizons that have been modified profoundly through human activities, such as addition of organic materials or household wastes, irrigation and cultivation. These include ploughed, paddy and oasis soils as well as the Terra Preta do Indio in Brazil. However, they are not evident due to the scale of the accompanying map. (LID)

Arenosols: from Latin arena, sand

Developed as a result of in situ weathering of quartz-rich parent material or in recently deposited sands (e.g. dunes in deserts and beaches). Among the most extensive soil types in the world. Soil formation is often limited by a low weathering rate. Prone to wind erosion. (ISRIC)

Cambisols: from Latin cambiare, to change

Young soils, generally lacking distinct horizons or with only slight evidence of soil-forming processes usually through variations in colour, the formation of structure or presence of clay minerals. Globally extensive − characteristics depend on the nature of the parent material. (ISRIC)

Cambosols: from Latin cambiare, to change

Soils with a subsurface horizon that tANGES into a horizon which has accumulated clay. Formed mostly in unconsolidated deposits on flat to undulating plains under coniferous or mixed forest. Dominated by cold and temperate climates with cold winters and short cool summers. (EM)

Chernozems: from Russian chem, black, and zemlja, earth

Soils with a very dark-brown or blackish surface horizon with a significant accumulation of organic matter and a neutral pH. Secondary calcium carbonate deposits occur within 50 cm of the lower limit of the humus-rich horizon. High biological activity. Typically found in grasslands in temperate climates. (EM)

Cryosols: from Greek krasis, cold or ice

Soils from cold regions where permafrost is found. Water occurs primarily in the form of ice and cryogenic processes, such as freeze-thawing cycles, cryoconcentration, frost heave and cracking, are the dominant soil-forming processes. Often given distorted horizons and a patterned ground. (SB)

Calccisols: from Latin calcarius, lime-rich

Formed through the leaching of carbonates from the upper part of the soil which precipitate when the subsoil becomes oversaturated or by the evaporation of water which leaves behind dissolved carbonates. Found in dry climates. (EM)

Calcisols: from Latin calcarius, lime-rich

Soils developed from materials ejected from volcanoes (e.g. ash, pumice and cinder) which weather to produce specific clay minerals. In humid climates, many Andosols develop a thick dark surface horizon which contains material rich in aluminium that is released from the weathering of the clay minerals. (ISRIC)

Durisols: from Latin durus, hard

Associated with old surfaces in arid and semi-arid environments. They display hardened accumulations of silica (SiO₂) in the soil. Durisols develop over long periods during which the soil reaction is very alkaline (pH > 8) that the silica becomes mobile. Regarded as ‘fossil soils’. (FE)

Ferralsols: from Latin ferrum, iron, and eluere, to wash out

Mostly associated with high rainfall areas and very old land surfaces, they are strongly leached soils that have lost nearly all of their weatherable minerals over time. Dominated by stable products, such as aluminium/iron oxides, which give strong red and yellow colours. Nutrient poor. (SD)

Fluviosols: from Latin fluvis, river

Occurring in all periodically flooded areas, such as flood plains, river fans, valleys, tidal marshes and mangroves. Fluviosols show a layering of sediments with pedogenic horizons as a result of deposition by water. Their characteristics depend on the nature and sequence of the sediments. (JD)

Gleysols: from Russian gley, ‘mucky mass’

Occurring in low-lying areas or depressions where groundwater comes close to the surface and the soil is saturated for long periods of time. Other than characteristic colours depending on whether oxygen is present, they display little soil development. Often found with wetland vegetation. (OS)
**Leptosols:** from Greek *leptos*, thin

Shallow soils over hardrock, very gravelly material or highly calcareous limed. Limited pedogenic development gives a weak soil structure. Globally present, especially in mountainous and desert regions where hardrock is exposed or comes close to the surface and weathering is active. (JD)

**Histosols:** from Latin *Histos*, tissue

Also known as peat, Histosols contain a high amount of organic matter (more than 20%), have a high water content and very low bulk density. When drained, they suffer from irreversible shrinkage and subsidence. Found in wetlands and cold climates, which slow the rate of organic matter decomposition. (SD)

**Gypsisols:** from Greek *gypsos*, gypsum

Similar to Calcisols, these are soils with secondary accumulations of gypsum (CaSO₄·2H₂O). They are found in the driest parts of the arid climate zone and often reflect former lake beds that have dried up through evaporation. Vegetation is sparse xerophytic shrubs and grasses. (JD)

**Lixisols:** from Latin *lixivia*, washed-out substances

Slightly acid soils that show a distinct increase in clay content with depth (predominantly kaolinite with limited capacity to hold nutrients). Found in the dry savannah regions with low biomass production, they have low organic matter content and lack a well-developed soil structure. Prone to erosion. (EMR)

**Nitisols:** from Latin *nittus*, shiny

Developed mainly from basic iron-rich rocks such as basalt in tropical climates. They have a dark red color and a well-developed structure. The iron content is high, which enforces strong binding of clay particles and the formation of the nut-shaped aggregates with shiny surfaces. (OSR)

**Phaeozems:** from Greek *phaios*, dark, and Russian *zemlja*, earth

Soils with a thick, dark-coloured surface layer, rich in organic matter and nutrients. Their development requires a reasonable amount of precipitation and lush vegetation, preferably grasses. Similar to Chernozems and Kastanozems but more intensively leached. (OSR)

**Plinthosols:** from Greek *plinthos*, brick

Identified by the accumulation of iron (and manganese) in the subsoil as large mottles or concretion that develop under fluctuating groundwater. While buried, the layer (called plinthite) is soft and can be cut by a knife. However, once exposed to air and sunlight, it hardens irreversibly and becomes what is known as ironstone. (ISRIC)

**Planosols:** from Latin *planus*, flat

Soils with very low permeability in the subsoil which causes water entering the soil to stagnate above this layer. The transition to the low permeability layer is very abrupt and the clay content increases significantly. Most Planosols have a structureless topsoil due to the removal of iron in waterlogged conditions. (EVR)

**Podzols:** from Russian *pod*, under, and *pola*, ash

Soils with a distinctive ash-grey horizon which has been bleached by the loss of organic matter and iron oxides. This sits on top of a dark accumulation horizon of redeposited humus and/or reddish iron compounds. Typically occurring in humid temperate climates in coarse sand deposits. (AR)

**Regosols:** from Greek *rhegos*, blanket

Soils in unconsolidated medium and fine-textured material showing only slight signs of soil development (e.g. some accumulation of organic matter producing a somewhat darker horizon). Similar to Arenosols (sand) or Leptosols (gravel). Soil development limited by low temperatures or aridity. (OSR)

**Solonchaks:** from Russian *sol*, salt

Strongly saline soils with high concentrations of soluble salts. Mostly associated with arid regions and areas where saline groundwater comes close to the surface. Their characteristics and limitations to plant growth depend on the amount, depth and composition of the salts. (AR)

**Solonetzs:** from Russian *sol*, salt, and etz, strongly expressed

Strongly alkaline soils with a dense, columnar-clay-rich subsoil containing a high amount of exchangeable sodium, which has the ability to disperse clay particles and organic matter from the topsoil to the subsoil. Normally found in flat lands in climates with hot, dry summers or former salty coastal deposits. (EVR)

**Stagnosols:** from Latin *stagnare*, to flood

Soils with a perched water table, often caused by the presence of an impermeable barrier deep in the soil, leading to temporary water logging and the mobilisation of iron and/or manganese. This process gives rise to a characteristic colour pattern. Commonly referred to as pseudogley (RS) – not visible due to the scale of the map.

**Technosols:** from Greek *technikos*, skilfully made

Soils containing man-made artefacts (e.g. household or industrial waste), material that has been brought to the surface (e.g. mine dumps, oil spills) or soils sealed by an artificial surface (e.g. roads, hard-standing areas). Often contain toxic material. (OSR) – not visible due to the scale of the map.

**Umbrisols:** from Latin *umbra*, shade

Soils with a deep, dark-coloured surface layer that is rich in organic matter but has a low nutrient content. They are mainly associated with acid parent materials and areas with high rainfall. Umbrisols are the counterpart of nutrient-rich soils with a dark surface horizon (e.g. Chernozems and Phaeozems). (EMR)

**Vertisols:** from Latin *vertere*, to turn

Clayey soils that exhibit cracks which open and close upon drying and wetting due to the presence of the clay mineral, montmorillonite. This process brings moisture from the surface into the subsoil, giving rise to a ‘churned’ soil. Typically found in lowland areas that are periodically wet. (EVR)

| Global distribution of the main soil types according to the WRB system. Colours on the map correspond to the colours on the soil name boxes around the map. | (JRC) (2.1) |
Soil is by far the most biologically diverse part of the Earth. Soil biodiversity reflects the mix of living organisms in the soil. These organisms interact with one another and with plants and small animals, forming a web of biological activity. The soil food web includes earthworms, spiders, ants, beetles, collembolans, mites, nematodes, fungi, bacteria and other organisms. (VG, SA, EDM, HN, MPMH, MBE, CAK, LT)
Soil is one of the most diverse habitats on Earth. Nowhere in nature are species so densely packed as in soil communities. For example, a single gramme of soil may contain millions of individuals and several thousand species of bacteria. The complex physical and chemical nature of the soil, with a porous structure, immense surface area and extremely variable supply of organic materials, food, water and chemicals, provides a range of habitats for a multitude of organisms. These range from macro- to micro- levels depending on climate, vegetation and physical and chemical characteristics of a given soil. The species numbers, composition and diversity in a particular ecosystem depend on many factors including temperature, moisture, acidity, nutrient content and the nature of the organic substrates.

Soil biota includes archaea, bacteria, protists, tardigrades, rotifers, nematodes, acari (mites), collembolans (springtails), worms (enchytraeids and earthworms), macroarthropods (e.g. ants, termites, centipedes, millipedes, woodlice, etc.) and burrowing mammals. It also includes plant roots, fungi and lichens. Root exudates attract a variety of organisms that either feed directly on these secretions or graze on the microorganisms concentrated near the roots, giving this busy environment the name ‘rhizosphere’. There are also animals, such as beetle larvae, flies and butterflies, that use the soil as a temporary habitat to reproduce or to spend their early life stages feeding on different live and dead plant materials until they reach their maturity. Soil communities are so diverse in both size and numbers of species, yet they are still extremely poorly understood and in dire need of further assessment. Research has been limited by their immense diversity, their small size and the technical challenge of identifying them.

Organisms can be classified in different ways. Taxonomy (from Ancient Greek τάξις, ‘arrangement’ and -νοµία -nomia, ‘method’) is the science of defining groups of biological organisms on the basis of shared characteristics and giving names to those groups. The rank-based method of classifying living organisms we use today was originally popularised by Swedish botanist Carl Linnaeus (1707-1778). In his landmark publication ‘Systema Naturae’ (first edition published in 1735), Linnaeus used seven taxonomic ranks to classify 10 000 species of organisms: kingdom, phylum, class, order, family, genus and species. Other ranks and sub-ranks have been added over the years, with frequent discussions among taxonomists. The greatest innovation of his system is the general use of binomial nomenclature (i.e. the combination of a genus name and a second term), which together uniquely identify each species of organism within a kingdom. Both names use Latin grammatical forms and they must be written in italics, or underlined when handwritten. Furthermore, in modern usage, the first letter of the first part of the name, i.e. the genus, is always capitalised in writing, while the specific epithet is not. For example, the human species is identified by the name Homo sapiens. When the specific name cannot be identified, the abbreviation ‘sp.’ is used to accompany the genus name (e.g. Lumbricus sp.). The abbreviation ‘spp.’ (plural) indicates ‘several species’ in that particular genus (e.g. Agaricus spp.). These abbreviations are not italicised (or underlined).
Introduction

When Linnaeus developed his classification system, there were only two kingdoms, Vegetabilia (plants) and Animaria (animals). The advances in microscopy and staining techniques led to the identification of new organisms and a better understanding of cellular structure and function. Although a general consensus has not yet been reached on how many kingdoms there are, all proposed classification schemes are based on three main criteria: cell type (prokaryote without a membrane-bound nucleus or eukaryote with a nucleus and other organelles enclosed within membranes); the number of cells in the body (single cell or multicellular); and the ability to obtain food (autotroph or heterotroph).

From around the mid-1970s onwards, there was an increasing emphasis on comparisons of genes on the molecular level (initially ribosomal RNA genes – see box below) as the primary factor in classification (i.e. genetic similarities among organisms). Accordingly, taxonomic ranks, including kingdoms, were to be based on DNA comparisons (see box below). To classify organisms has gained strength. However, the real evolutionary relationship among eukaryotes, in particular protists (see page 31), is still debated and future changes in the classification might be needed.

### Prokaryotic cell

- All the intracellular water-soluble components (proteins, DNA and metabolites) are located together in the cytoplasm enclosed by the cell membrane, rather than in separate cellular compartments.

### Eukaryotic cell

- The cytoplasm accommodates membrane-bound organelles, especially the nucleus, which contains the genetic material, and is enclosed by the nuclear envelope.

<table>
<thead>
<tr>
<th>Prokaryotic cell</th>
<th>Eukaryotic cell</th>
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### Unicellular

- Also known as a single-celled organism, is an organism that consists of only one cell.

### Multicellular

- Organisms that consist of more than one cell.

### Autotroph

- “Self-feeding” organisms that produce complex organic compounds (such as carbohydrates, fats and proteins) from simple substances present in its surroundings, generally using energy from light (photosynthesis) or inorganic chemical reactions (chemosynthesis).

### Heterotroph

- Organism that cannot fix carbon and uses complex organic substances produced by, or available in, other organisms.

#### DNA and RNA

- Deoxyribonucleic acid (DNA) is a molecule that encodes the genetic instructions used in the development and functioning of all living organisms. Most DNA molecules consist of two long polymer strands coiled around each other to form a double helix.
- The two DNA strands are composed of simpler units called nucleotides. Each nucleotide is composed of a nitrogen-containing base known as guanine (G), adenine (A), thymine (T), or cytosine (C) and a sugar called deoxyribose and a phosphate group. According to fixed rules for pairing the bases, A always goes with T and C with G.
- Like DNA, RNA (ribonucleic acid) is a chain of nucleotides, but unlike DNA it is more often found in nature as a single-strand. Furthermore, the nucleotide thymine is replaced by uracil (U) in RNA. Organisms use RNA to convert genetic information into specific proteins.
- Each of the three domains of life recognised by biologists today contain portions of DNA (e.g. DNA, ribosomal RNA) which is unique to them, and this fact in itself forms the basis of the three-domain system and allows for the classification of organisms based on their DNA (phylogenetic approach).

#### DNA and RNA

- Structures of DNA and RNA. RNA presents a single strand, while DNA has the typical double-stranded helix. RNA and DNA are formed by four different nucleobases (nucleotides), three are present in both the molecules, namely cytosine, guanine and adenine. Thymine in DNA is replaced by uracil in RNA. (See box)
However, taxonomic classifications (i.e. using hierarchical ranks) provide little understanding of their lifestyles and functional roles. For this reason, this chapter explores the overwhelming diversity of soil biota using another common approach to classify soil organisms that involves using their body width to identify four broad groupings: microfauna (less than 0.1 mm), mesofauna (0.1 to 2 mm), macrofauna (2 to 20 mm) and megafauna (bigger than 20 mm). Body width appears to be a more consistent classifying criterion than body length, which shows greater variability even among representatives of the same group. However, even these ranges do not provide distinct limits and, on some occasions, there is some confusion as to whether a particular organism should be considered macro, meso or micro.

The size distribution of soil animals, together with some of their anatomical features (such as the presence/absence of legs) and some behavioural responses (reactions to light and heat), determine the best collecting method for a particular group of organisms. For example, the soft bodies of the microfauna and some of the mesofauna living in the water film surrounding soil particles can be extracted using a wet extraction method (Bearmann funnels; see pages 64-65) or by centrifugation. By contrast, the legged microarthropods with hard exoskeletons can be collected using dry extraction (Tullgren funnel; see pages 64-65) because these animals actively move away from light and heat. Finally, hand-sorting and pitfall trapping are often used to collect the macrofauna, while bait trapping has been used to catch mammals such as moles. All of these organisms are involved in creating and maintaining the soil structure and providing essential ecosystem services for humans (such as regulating greenhouse gas emissions or preserving water quality). Most of them cannot survive outside of soil, so it is necessary to preserve healthy and diverse soil systems if we want to preserve their beneficial influence. One of the main challenges that soil conservation faces today is the lack of awareness of the ecological importance of soil biodiversity. So, open your eyes and discover what lives under your feet!
Prokaryota – Archaea

Morphology

Archaea are unicellular microscopic organisms with a striking variety of cell shapes (pleomorphism) and unique geometric forms [25]. Many are rod-like (referred to as bacilli – e.g. Methanococcus and Methanobrevibacter) or spherical (referred to as cocci – e.g. Methanococcus) while the heat-loving (thermophiles) Sulfolobus are highly irregular cocci. By contrast, Methanosaeta and Methanospirillum have both a long rod shape (filamentous) with sheaths that surround adjoining cells. Additionally, some archaea (e.g. Methanosarcina) form clusters, while the cells of Haloterrigena form many irregular shapes. Some species belonging to Halobacteriales can be square-shaped, triangles or flat discs.

Taxonomy

Archaia, the third domain of life (see page 31), were originally split into two phyla, the Euryarchaeota and the Crenarchaeota. The Crenarchaeota have now been divided to make a new phylum, the Thaumarchaeota. There may be other phyla, such as the Korarchaeota, Nanarchaeota and Aigarchaeota, but whether these represent true distinct phyla is disputed. The Euryarchaeota are physiologically the most diverse, with a number of methane-producing orders (methanogens); the aerobic, salt-loving (halophile) Halobacteriales; the thermophilic Thermoplasmatales, sometimes lacking a cell wall, and several orders with members that are not yet described. The Crenarchaeota are almost all extremophiles, living at high temperatures or extremes of pH (see boxes below) and are primarily involved in sulphur or iron metabolism. The Thaumarchaeota contain most of the isolated mesophilic archaea, which are associated with aerobic ammonia oxidation (nitrification). All three major phyla also contain many undescribed groups and we know little about their ecology and physiology.

Microorganisms and the environment

- Some microorganisms, including the archaea, are able to modify their shape or size in response to environmental conditions – this is also known as pleomorphism.
- Organisms that exist only in moderate temperatures, typically between 20°C and 45°C, are referred to as mesophiles.
- By contrast, extremophiles are organisms that thrive in extreme environmental conditions. It is possible to have different classes of extremophiles, depending on the environmental factors:
  - thermophile: an organism that loves high temperature,
  - psychophile: an organism that loves low temperature,
  - alkaliophile: an organism that loves high pH values,
  - acidophile: an organism that loves low pH values,
  - halophile: an organism that loves high salt concentration.

The versatile archaea

- The discovery of archaea altered our understanding of evolution, but recent research suggests that eukaryotes evolved from archaea. So humans may actually be derived from archaea.
- Archaia live in the widest range of environmental conditions of any organisms, from pH 0 to pH 12, 0°C to 120°C, and up to 35% salinity.
- Hyperthermophilic archaea survive at temperatures greater than 90°C by having a thin membrane, made up of double-headed lipids, that insulates the cell interior from the heat. In acid or salty environments, this sort of membrane acts as a barrier to water molecules and other ions.
- The halophilic archaean, now called Haloquadratum walsbyi, was for a long time known as Walsby’s square bacterium as it is box shaped and forms large fragile flat sheets in the environment.
- Archaia do not have a nucleus.

Diversity, abundance and biomass

Over 300 archaeal species have been described, primarily found in extreme environments. However, many more species have been detected in the environment but it is not possible to isolate and describe them. Soils contain between 10^7 and 10^8 microbial cells in each gramme (0.04 ounces), and all contain archaea. Generally, up to 10% of microbial cells in temperate soils may be archaea (mesophilic species), while in conditions of high temperature, high salinity or at high or low pH, archaea (extremophilic species) can be the dominant members of the microbial community.
Prokaryota – Bacteria

Morphology

Bacteria are one of the two domains, along with Archaea, that include prokaryotic organisms [26]. The domain Bacteria comprises microscopic organisms, single-celled or with the cells forming simple associations. Most bacteria are 0.2 micrometres (µm) in diameter and 2 - 8 µm in length. Bacteria have a variety of shapes: round or spherical (commonly known as cocci), rod shaped (bacilli) and spiral (spirocha). However, many bacteria can assume several shapes (pleomorphic). Depending on how the newly formed cells adhere to each other, bacterial arrangements include singles, pairs, chains and clusters. When bacteria are tilted (capable of moving) they have a specific structure (flagellum) for locomotion. The flagellum is a whip-like structure that can occur at one end, both ends, or all over the bacterial cell. Bacteria can live without oxygen (anaerobes) or depend on it to grow (aerobes). They can also be adapted to live either in the presence or absence of oxygen (facultative anaerobes). Some species of bacteria contain endospores or exospores (see box next page). If you break down the term endospore, ‘endo’ means ‘inside’ and ‘spore’ refers to the ‘dormant structure’, so the endospore is a structure of resistance formed inside the cell. By contrast, the exospores develop externally. Spores are a bacterial cell’s way of protecting itself against harsh changes in the environment or nutrient depletion. A spore protects the bacterial genetic material so that, when optimal conditions return, the bacterial cell can reform (germinate) and thrive again.

Taxonomy

Currently, there are 30 known and recognised phyla of bacteria. Highly diverse and abundant phyla in soil are Proteobacteria, Firmicutes, Actinobacteria and Cyanobacteria (see pages 34-35). However, some other phyla, such as Acidobacteria, can also be found in soil.

Diversity, abundance and biomass

Most microbial species (more than 90 % according to the current estimates), including bacteria, still remain unculturable (i.e. they cannot be grown in any culture medium in the laboratory). This means that we do not yet know what they look like or what functions they carry out. Advances in molecular techniques (see pages 64-65) in the past 30 years have enabled us to understand more about these species by sequencing parts of their DNA. These advances have also allowed for the identification of new cultivable species. Today there are approximately 2 800 genera comprising approximately 15 000 species of known bacteria. Soil microbial biomass is made up of bacteria, fungi and other microorganisms. This biomass represents 1 to 4 % of total soil carbon (up to three tonnes of carbon per hectare). The ratio of the size of bacterial to fungal biomass depends on soil properties and other environmental factors (e.g. soil pH, temperature and nutrient availability); for example, a 50-fold decrease in bacterial biomass was found when comparing high to low pH soils.

Microhabitats

Unlike eukaryotes, bacteria can be found in a wide range of environmental, chemical and physical conditions including extremes of pH, temperature and salinity. Many soil bacteria are beneficial to human economic activities and are necessary for environmental sustainability. Bacteria are part of chemical cycles during which they release essential elements for recycling. They also decompose dead organic matter and are the only microbes capable of biological nitrogen N₂ fixation (see page 105). This is the ability to transform nitrogen (N₂) from the atmosphere (about 80 % of the atmosphere is N₂) into ammonia (NH₃) which is assimilated by eukaryotes, plants in particular. Bacteria can exist either as independent (free-living) organisms or as symbionts that depend on other organisms to live, subsisting either as mutualists, parasites or commensalists (see box below).

What is symbiosis?

- Symbiosis is a close and often long-term interaction between two different biological species;
- There are three main types of symbiosis:
  - mutualism is the way two organisms of different species exist in a relationship in which each individual benefits from the activity of the other;
  - commensalism is a class of relationship between two organisms where one organism benefits from the other without affecting it;
  - parasitism is a relationship between species, where one species, the parasite, benefits at the expense of the other, the host;
- Some symbiotic relationships are obligate, meaning that both symbionts entirely depend on each other for survival.
- Other relationships are facultative, meaning that they are not essential for the survival of either species. Individuals of each species engage in symbiosis when the other species is present.
Prokaryota – Bacteria

Proteobacteria

Proteobacteria is the largest and most diverse bacterial phylum [26]. It contains about 30 % of the total number of bacterial species. Proteobacteria comes from the name of the Greek god Proteus, which could take various forms, thus reflecting the enormous diversity of morphological and physiological characteristics observed in this bacterial phylum. Proteobacteria comprises the majority of Gram-negative (see box below) bacteria of medical (e.g. Helicobacter), veterinary (e.g. Acinetobacter), industrial (e.g. Campylobacter) and agricultural interest (e.g. Bradyrhizobium). It also comprises bacteria involved in carbon, sulphur and nitrogen cycles (including N₂ fixers – see pages 99, 105), phototrophic (i.e. organisms that obtain energy from light) and non-phototrophic, aerobic and anaerobic bacteria.

Gram-positive and Gram-negative

• Gram staining, also called Gram’s method, is a method of differentiating bacterial species into two large groups: Gram-positive and Gram-negative, respectively. The name comes from the Danish bacteriologist Hans Christian Gram, who developed the technique. The technique is based on the use of a chemical compound, the crystal violet. The name refers to its colour, similar to that of the petals of a gentian flower. The Gram stain is almost always the first step in the identification of bacterial organisms.

• Gram-positive bacteria are bacteria that give a positive result in the Gram stain test. Gram-positive bacteria take up the crystal violet stain used in the test, and then appear to be purple–coloured when seen through a microscope. This is because in the cell wall of the Gram-positive bacteria there is a layer that retains the stain after it is washed away from the rest of the sample, in the decolourisation stage of the test.

• Gram-negative bacteria are a group of bacteria that do not retain the crystal violet stain. After staining with crystal violet, the excess is washed off with alcohol, which decolourises the bacteria since the crystal violet stain is soluble in alcohol. The Gram-positive bacteria then appear to be red or pink.

Firmicutes

The most representative genera in Firmicutes are Bacillus and Clostridium, which are obligate and facultative anaerobic bacteria, respectively [26]. These genera include important species of human and animal pathogens that produce resistant cell structures called endospores. Spores tolerate different types of stresses. For example, they are more resistant to heat than normal cells by a factor greater or equal to 10⁵. Furthermore, they are 100 times or more resistant to ultraviolet radiation, and more tolerant to drought, antibiotics and disinfectants. Most Bacillus species, such as B. cereus, which causes contamination of food, are soil inhabitants. Due to their pathogenicity on some soil insects, some Bacillus species, including B. popilliae, B. lentiformis and B. thuringiensis, have been successfully used in agriculture to control pests. Bacillus may also be dangerous: Bacillus anthracis is considered the most lethal biological weapon for human beings because it is the origin of anthrax (see box on page 108). Another Firmicute genus, Paenibacillus, includes important soil-living nitrogen fixers (see page 99). Nitrogen-fixing bacteria are also present in both Bacillus and Clostridium genera.

Endospores, what are they?

• Endospores can survive environmental assaults that would normally kill the bacterium. These stresses include high temperatures, high UV irradiation, desiccation and chemical damages. The extraordinary resistance properties of endospores make them of particular importance because they are not readily killed by many antimicrobial treatments.

• When favoured nutrients are exhausted, some Gram-positive bacteria may develop an extreme survival strategy: the formation of endospores.

• This complex development allows the bacterium to produce a highly resistant cell to preserve the cell’s genetic material in times of extreme stress.

• The resilience of an endospore can be explained in part by its unique cellular structure. The outer coat surrounding the spore provides much of the chemical resistance. Beneath the coat there is a thick layer called the cortex. Proper cortex formation is needed for dehydration of the spore core, which aids in resistance to high temperature. A germ cell wall is found under the cortex. This layer will become the cell wall of the bacterium after the endospore germinates. The inner membrane, under the germ cell wall, is a major permeability barrier against several potentially damaging chemicals. The centre of the endospore, the core, exists in a very dehydrated state and houses the cell’s DNA.

• The process of forming an endospore is complex and requires several hours to complete.

Bacteria as workers

• Many compounds are produced in large amounts by bacteria to be used for various purposes in industry and medicine. They can be a part of silk, cotton and rubber manufacturing. Bacteria also synthesise certain antibiotics, such as bacitracin and polymyxin.

• Bacteria are able to degrade complex compounds. For example, they break down the woody and tough tissues of jute, coconut, hemp and flax. They can also degrade hydrocarbons and clean up oil spills.
Actinobacteria

Actinobacteria is a phylum of Gram-positive bacteria that have a highly diverse morphology, ranging from micrococci (spherical) and rods to branched filaments that resemble fungal hyphae (see box on page 39) [26]. The bacterial filaments are narrow (diameter from 0.5 to 2 µm) and can be short and rudimentary or extensively branched. Throughout their life cycles, Actinobacteria may combine these different forms. Their reproduction is by fragmentation of hyphae or through the production of spores. The spores may be of several types (e.g. arthrospores, very primitive spore type, formed through the breaking up of hyphal filaments in Streptomyces and zoospores, motile and flagellate spores, in Spirillospora and Actinoplanes). Spores are produced (from one to several in chains) on hyphae, in spore-producing structures (sporangia) or vesicles. The ecological niche of most Actinobacteria is the aerobic zone in soil. A striking feature of Actinobacteria is the production of extracellular enzymes that degrade complex macromolecules commonly found in soils (e.g. casein, starch, chitin, cellulose and lignocellulose). Furthermore, they synthesise and excrete thousands of metabolites, such as antibiotics. For example, Selman Waksman, one of the most important soil microbiologists, won the Nobel Prize for Medicine in 1952 for his discovery of streptomycin produced by bacteria of the genus Streptomyces. In addition to streptomycin, Streptomyces are capable of producing a wide variety of antibiotics with numerous properties: antibacterial, antifungal, antiviral, antitumor, antiparasitic, insecticide and weed controlling. Actinobacteria also includes the nitrogen-fixing bacteria of the genus Frankia, which form root symbioses with plants of eight botanical families (e.g. Betulaceae – see page 43). Other species belonging to the genera Streptomyces and Corynebacterium are plant pathogens. Animal pathogens are found among the genera Corynebacterium, Actinomyces, Nocardia, Thermoactinomyces and Mycobacterium. Among them, the Mycobacterium avium-interspecies-scrofulaceum stands out as being lethal for people who have contracted the human immunodeficiency virus (HIV).

Cyanobacteria

Cyanobacteria is a group of bacteria that are able to obtain their energy through photosynthesis. This is possible due to the presence of chlorophyll, which is also found in other photosynthetic organisms, such as algae and plants. Being photosynthetic, they manufacture their own food. This has caused them to be dubbed ‘blue-green algae’, though they have no relationship to any of the various eukaryotic algae. They are considered one of the most diverse groups of prokaryotes as they vary from unicellular to complex filamentous or branched forms. In some cases they have highly differentiated cells that carry out different functions, so they may be considered as truly multicellular organisms. Cyanobacteria have the distinction of being the oldest known fossils, more than 3.5 thousand million years old. In fact, the cyanobacteria have been tremendously important in shaping the course of evolution and ecological change throughout Earth’s history. Indeed, the atmospheric oxygen that we depend on was generated by numerous cyanobacteria through photosynthesis. Furthermore, the photosynthetic structure of plant cells, the chloroplast, evolved from cyanobacterial ancestors. Cyanobacteria also contribute to the health and growth of many plants in another way: they have the ability to convert inorganic atmospheric nitrogen into ammonia (nitrogen fixation) that plants can use (see page 106). This process cannot occur in the presence of oxygen, so nitrogen is fixed in specialised cells called heterocysts. These cells have an especially thickened wall that contains an anaerobic environment. Cyanobacteria also form symbiotic relationships with many fungi, forming complex symbiotic organisms known as lichens (see page 42).

Photosynthesis

Photosynthesis is a process used by plants, algae and cyanobacteria to convert sunlight energy into chemical energy. This chemical energy is stored in carbohydrate molecules, such as sugars, which are produced from carbon dioxide and water. Oxygen is released as a waste product. Photosynthesis maintains atmospheric oxygen levels and supplies most of the energy necessary for life on Earth.
Protists

Protists are defined as unicellular eukaryotes (see page 30). Many form filaments (such as some fungi), are colonial or aggregate into larger clusters of cells. They are divided into the Archaeplastida (green algae, red algae and ancestors of higher plants), the Amoebozoa (many amoeboeid species), the Opisthokonta (collar cells, fungi and ancestors of animals), the Rhizaria, Alveolata, and Excavata. Typically, they have one nucleus and soil species have a contractile vacuole for regulating water and ion concentrations. Many species have a swimming dispersal stage with one or more cilia. Cysts form in sub-optimum living conditions or when prey are scarce. Although many protists can be identified under the microscope to family or genus level, species identification is made through DNA sequence analysis (see pages 64–65). [27]

Rhizaria

Morphology

Cells typically produce very thin hair-like extensions called filopodia that can branch and merge together again, forming a complex network in some species. They tend to grow flat on surfaces and their filopodia can extend into small crevices in the soil searching for bacteria. When detached from surfaces, they swim with two cilia. They can also move by amoeboid locomotion or gliding on surfaces. Soil species form resting cysts that enable them to survive adverse environmental conditions. There are many variations of this basic morphology as it is a diverse group.

Taxonomy

This supergroup has one major soil lineage: the Cercozoa [28]. The Cercozoa (common name cercomonads) consist of a diverse variety of species of small bacterial-feeding unicells less than 10 µm in size. One subgroup common in soils is the Silicofilosea that secrete silica scales on their surface. The Silicofilosea also include the Euglypha that form vase-shaped protective layers (known as tests) outside the cell. Other Cercozoa include Vampyrellida that feed on fungal hyphae (see box on page 39), the Dictyostelia, but aggregative species occur in other protists as well. In Arcellinea the cell is inside a vase- or helmet-shaped structure made of protein, sometimes amended with soil particles bound together by proteins.

Amoebozoa

Morphology

The Amoebozoa is another group of unicellular organisms whose cells are covered by a very thin protein layer with or without microscales. [29, 30]

Taxonomy

The Amoebozoa is a supergroup that contains bacterial-feeding amoeboeid species. Several lineages contain mostly aggregative species referred to as ‘social amoebae’, such as the Myxogastria and the Dictyostelia, but aggregative species occur in other protists as well. In Arcellinea the cell is inside a vase- or helmet-shaped structure made of protein, sometimes amended with soil particles bound together by proteins.

Social amoebae

- Social amoebae occur among protists and not just in Amoebozoa.
- They are found in a wide variety of colours; more than 90% species of slime mould occur all over the world.
- Some species may reach sizes of several square metres and masses of up to 50 grammes.
- They live in any type of dead plant material and contribute to the decomposition process.

Microhabitat

Amoebozoa species occur on moist surfaces and live in water microfilms where they forage for palatable bacteria or other prey. Some species prefer wet conditions, others occur in drier conditions, some have depth and litter preferences, and some are known colourers and occur in disturbed soils in which other species are absent. Amoeba are very effective at scavenging surfaces for bacteria. A small number feed on fungal hyphae or prey on protists or microinvertebrates.

Alveolata

Morphology

The Alveolata is a group of protists characterised by folded membranes underneath their cell membranes (called alveoli) [31]. Ciliophora (the only soil-inhabiting Alveolata) have two types of nuclei: a small inactive nucleus with condensed chromosomes, which becomes active only during reproduction, and a large nucleus that is always active and holds many copies of the chromosomes. Most species have rows of cilia that beat in a coordinated manner, and a specialised funnel structure for capturing and ingesting prey. They also often have specific defensive or aggressive structures, called ectosomas. These are made of mucus that is ejected from the cell. A complex network of vacuoles inside the cell regulates the digestion of food and the water balance.

Taxonomy

There are three main supergroups in the Alveolata (Apicomplexa, Dinoflagellata and Ciliophora), but only Ciliophora (ciliates) are found free-living in the soil. Most ciliates ingest bacteria, but some ingest other protists or are specialised symbionts or parasites (see box on page 33). Colpodeidda prey on other protists and can reach higher numbers by feeding on soil invertebrate corpses. The Colpodeida includes most of the ciliates found in high abundance when soil samples are kept in the laboratory. Many genera emerge from cysts when sufficient moisture and bacteria are present and then reproduce. Colpodeids are very diverse and can be identified to the genus or family level (see page 29) through microscopy. The other genera that occur in some abundance in soils belong to the order Hypotricha. These are also diverse but rarely dominant in terms of abundance. The Colpodeida to Stichotrich ratio (also called the Colpodid to Stichotrich ratio) is used as an indicator of environmental quality.

Microhabitat

As soil dries, the ciliates’ habitat becomes restricted to water films on surfaces. They detect prey by chemical-sensing and swim toward the signal, or away from toxic molecules. Their dispersal is by water infiltration through soil pores, or in the air if dry soil is disturbed.

Diversity, abundance and biomass

More than 1500 species of soil ciliates have been described, but many more remain undescribed so far. One study from Namibia revealed 365 species, of which 128 were new species, from 73 soil samples. Temperate soils typically host 20–30 species per gramme of soil, but most are inactive. In moist soils with plenty of bacteria or prey, there can be 10,000 active cells per gramme declining to none in very dry soils. Although the biomass of ciliates per gramme of soil is very low, when active they can ingest several hundred bacterial cells per minute.
**Stramenopiles**

**Morphology**

Stramenopiles are unicellular organisms with two cilia that beat in different directions: a front one that includes tiny hairs (visible on electron microscope images) that pulls the cell, and a trailing one that pushes the cell. In some groups, however, the trailing cilium is missing. Other groups are usually filamentous and only the dispersal cell is ciliated. Terrestrial species form resting cysts in the soil, and in some sexual species dispersal spores are produced after sexual reproduction. [32, 33]

**Taxonomy**

This supergroup includes the brown algae and several groups previously thought to be fungi, such as Hyphochytriales and Peronosporomycetes, which are commonly found in soils. Some species of true brown algae occur in alpine soils (for example, Vauxchena), but they are typically rare or absent. Most terrestrial species have lost the ability to photosynthesise (see box on page 35) and appear colourless. They absorb nutrients from the living or decomposing tissues into which they grow.

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**The Irish Potato Famine**

- The Irish Potato Famine, a period of mass starvation, disease and emigration in Ireland between 1845 and 1852, was caused by *Phytophthora infestans*, a Peronosporomycetes.
- Originally from the Toluca Valley in Mexico, once introduced through infected potatoes, it spread rapidly to much of northern and central Europe.
- Because prior to 1840 they were considered to be fungi, we still lack an effective chemical compound to treat stramenopile parasites sincefungicides (aiming to disrupt fungi) do not work.

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**Microhabitat**

Hyphochytriales are found in moist soil environments. They absorb dissolved nutrients with a network of filaments that extend from the cell. Terrestrial species of Peronosporomycetes are decomposers of organic matter or live as plant parasites. They feed by extending filaments into plant tissues. They are economically important because they include species that cause some of the most damaging plant diseases, such as *Pythium* (which causes the damping-off disease in greenhouses), downy mildews and white blister rusts. *Diatomea* are typically aquatic species that can be found in riparian or regularly flooded soils, and sometimes inside rotting tree logs. Their role and presence in soils is poorly documented. The motile stage is usually a small amoeboid species with two or four cilia that are used to move in search of food, but some have lost either the ciliated stage or the amoeboid stage. The Euglenids are typically spindle-shaped cells covered by a flexible pellicle, and they can be photosynthetic or not, with the non-photosynthetic species feeding on bacteria or other protists. [34]

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**Excavata**

**Morphology**

The general body-type in this very diverse group is a small cell with a cilium directed backwards that generates locomotion and directs food (mostly bacteria) toward a feeding groove on the ventral surface, as observed in *Fornicata*. Many groups have reduced mitochondrial function and prefer micro-aerophilic (low oxygen) or anaerobic (no oxygen) environments. In contrast to many Excavata groups, the Kinetoplastida (commonly called kinetoplastids) have a characteristic mitochondrion with a large amount of DNA. Many kinetoplastid species rely on dissolved nutrients for food (they are osmotrophic). In *Parabasalia*, the single body-type is replicated hundreds of times to form large multiciliated cells. Both *Parabasalia* and *Preaxostyla* have elaborate supporting cytoskeletal elements that provide shape and assist in locomotion. The Heterolobosea are generally amoeboid species with two or four cilia that are used to move in search of food, but some have lost either the ciliated stage or the amoeboid stage. The Euglenids are typically spindle-shaped cells covered by a flexible pellicle, and they can be photosynthetic or not, with the non-photosynthetic species feeding on bacteria or other protists. [34]

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**Other protists**

**Excavata**

**Nuclearia, Ancyromonas and others**

There are several genera that belong to the base of the *Opisthokonta*, the group that includes animals and fungi. These genera are common in soil, though rarely abundant, and contribute to the ingestion of bacteria. These include *Nuclearia*, *Fonticula*, and the *Razelli*. Several genera found in soils cannot yet be placed into our classification system. They are placed as *incerta sedis* in the euksarates. These include *Ancyromonas*, *Breviata* and *Apusomonadida*.
Morphology

Within the fungus kingdom, macrofungi are a group that form visible, often coloured, cup- or cap-like structures (scientifically known as ‘fruiting bodies’ or ‘sporophores’) that emerge from the soil. These fruiting bodies are where the spores are formed. The spores are small (1 - 100 µm), usually single-celled, reproductive structures able to tolerate unfavourable growing conditions (e.g. drought). Below the fruiting bodies, each fungus has a mass of hyphae, the typical branching thread-like filaments produced by most fungi. The mycelium is made up of the mass of these hyphae and is responsible for its growth. In the case of soil macrofungi, a large portion of the mycelium is hidden since it grows belowground. When environmental conditions become favourable, the fungus develops the fruiting body and spores that, once released, disperse through the air, or are carried by insects or water. [35, 36]

Taxonomy

Macrofungi, taxonomically belonging to the subkingdom Dikarya, are classified into two main phyla: Ascomycota and Basidiomycota. The Ascomycota, the largest group of macrofungi with more than 64,000 described species, are usually characterised by a cup-like or disc-like fruiting body (technically known as ascoma), where spores are formed within a typical structure, named the ‘ascus’. The Basidiomycota (more than 31,000 described species) mostly have a fruiting body (called basidioma) with an umbrella-shaped cap (known as pileus) borne on a stalk (known as a stipe) where the spores are produced. Other phyla that include soil fungi are Glomeromycota, Zygomycota, Chytridiomycota and Blastocladiomycota (see pages 40-41).

Microhabitat

Macrofungi are found in most terrestrial habitats, from woodlands to grasslands, but they are probably most diverse in forests. They need the right climatic conditions to form fruiting bodies; in particular, moisture to allow their spores to develop. Depending on their functions, they can be defined as saprotrophic, parasitic or mycorrhizal. The saprotrophic species play a key role in the degradation of decaying organic matter (i.e. soil, leaf litter and dead wood). The parasitic (see box on page 33) fungi are responsible for several diseases in plants (see box, next page), animals (mostly invertebrates) and other fungi. The mycorrhizal fungi form symbioses with plant roots, a mutualistic association that is beneficial to both partners (see box, page 33).

Fungi – Macrofungi

Fungi: edible, poisonous, bioluminescent and giant

• There are several edible Basidiomycota and Ascomycota. Mushrooms, such as Boletus edulis and truffles (Tuber spp., see box on page 40), are consumed in many countries.
• Some Basidiomycota produce deadly toxins, such as amatoxin produced by Amanita phalloides. Thirty grammes of this fungus may kill a person; others, such as Ganoderma lucidum, are considered medicinal fungi.
• Some Basidiomycota (e.g. species belonging to the genus Mycena) are bioluminescent.
• In Hainan Island (southern China) a giant specimen of Fomitiporia ellipsoidea (belonging to the group of bracket fungi, also included in Basidiomycota) was found to be 20 years old with an estimated volume of 409,000 - 525,000 cm³ and a weight of 400 - 500 kg. This represents the largest fungal fruiting body (both in volume and in weight) ever found.

Morphology

The Basidiomycota is a group of fungi that comprises the well known common mushrooms. Their visible part usually has an umbrella-like shape. (a) Hygrocybe sp.; (b) Hygrocybe graminicolor; (c) Cyrtotrama asprata; (d) Gymnopilus juniperinus. (SA)

The Ascomycota is a group of fungi that usually have a visible part, scientifically defined as the fruiting body, with a cup-like shape. (a) Donadinia nigrella; (b) Sarcoscypha coccinea; (c) Phillipsia subpurpurea; (d) Rhodoscypha ovilla. (SDA, FF, SA, AV)
Diversity, abundance and biomass

Fungi are extremely abundant. Millions of species have been estimated, but only about 150,000 have been described. Macrofungi have about 90,000 known species. Together with bacteria, fungal hyphae constitute the largest portion of the microbial biomass of soil. Generally, fungal biomass is found to be greater than bacterial biomass in forest soils.

**Soil-borne plant pathogenic fungi**

- Soil-borne plant pathogenic fungi (SPPF) comprise organisms that are included in the Fungi kingdom and in the group of fungal-like organisms currently assigned to the Stramenopiles (see page 37). As pathogens, they are responsible for several plant diseases [37]
- Among fungi, both Ascomycota and Basidiomycota are represented. The major species belong to the genera Fusarium, Phomopsis, Sclerotinia and Verticillium within Ascomycota, and to Armillaria and Rhzoctonia within Basidiomycota.
- SPPF produce survival structures that may be as simple as cells, called chlamydospores, with a thick wall, or may be more complex like the sclerotia, typical of some fungi (e.g. Sclerotium, Scieretina and Botrytis).
- In addition to the survival function, aggregation of hyphae, called rhizomorphs since they resemble plant roots, are typical of species belonging to the fungal genus Armillaria and may play a crucial role in fungal spread through the soil, host infection and disease transmission.
- Soil type, pH, water content and temperature of the soil are among the major factors affecting the presence of the soil-borne plant pathogenic fungi.
- Fusarium species and Rhzoctonia solani, although commonly present in moist soils, tolerate lower water content levels. They also prefer warmer soils (25–35 °C).
- SPPF are grouped into two functional categories: soil inhabitants and soil invaders. The first category generally includes unspecialised microbes that infect seedlings and young roots, while the second are disease agents that show a degree of host specificity. Seed decay, damping-off and root rot caused by soil-borne plant pathogenic fungi are among the most common diseases caused by soil-borne fungi.
- Soil-borne plant pathogenic fungi are reported worldwide in agricultural and forest soils.
- The number of plant pathogenic fungal species on Earth has been estimated to be as high as 270,000; however, the number of SPPF is largely unknown.
- The abundance of SPPF is generally measured as ‘inoculum density’, which is expressed as the mass, or the number, of spores per gramme of soil. Inoculum density has been reported as ranging from 100 to 100,000 spores per gramme of soil, depending on the species.

How a fungus is made

- A hypha is a long, branching filamentous structure. In most fungi, hyphae are the main mode of growth, and collectively form the mycelium.
- Hyphae grow at their tips. They can branch through the bifurcation of a growing tip, or through the emergence of a new tip from an established hypha.
- There are different types of hyphae:
  - septate, which have cross walls (called septa) at fairly regular intervals;
  - asceptate or acyclospic, which do not have septa.
- Hyphae can fuse to one another. This process is known as anastomosis.
- Yeasts are fungi that do not have hyphal structures. They are the only unicellular fungi.

Spores allow fungi to reproduce. Due to their microscopic dimensions, they can easily disperse through air or water. They grow into new individuals under suitable conditions of moisture, temperature and food availability.

- Spores of Ascomycota (blue coloured) develop inside structures called ascii; Spores of Basidiomycota develop inside structures (red coloured) called basidia.
- Spores of Phytophthora (red coloured) develop inside structures called oospores.
- Spores of Botryotrichum (black coloured) develop inside structures called conidia.
- Spore of Emericella are ellipsoidal, while those of Penicillium are cylindrical.
- Spore of Phoma species are brown, while those of Fusarium species are yellow.
- Spores of Aspergillus species are brown or black, while those of Penicillium species are grey.

**Structures that allow soil-borne plant pathogenic fungi to survive adverse environmental conditions**

- (a) hyphae, as it resembles plant roots, of the fungus *Armillaria*; (b) the black dots are sclerotia of the fungus *Botrytis*; (c) structures that allow soil-borne plant pathogenic fungi to survive adverse environmental conditions (d) asci; (e) spores of fungus *Botrytis*; (f) spores of fungus *Botrytis*.
Fungi – Mycorrhizal fungi

Morphology

Mycorrhizas are literally ‘fungus-roots’ created by symbiotic associations (see box, page 33) between plant roots and fungi. Mycorrhizal fungi help their host plants acquire mineral nutrients from the soil in return for plant sugars. Mycorrhizal fungi form structures outside and inside plant roots. All types form extensive networks of microscopic hyphae that extend outwards from plant roots into the surrounding soil or leaf litter. Arbuscular mycorrhizas (AM), ericaceous mycorrhizas and orchid mycorrhizas are sometimes called ‘endomycorrhizas’ because the fungi form distinctive structures between and inside the cortical cells of plant roots, but do not generally cause obvious changes in root morphology. By contrast, ectomycorrhizas (EcM) often cause distinct changes to roots that can be observed without a microscope. Reproductive structures also differ among mycorrhizal types. Arbuscular mycorrhizal fungi reproduce through spores that can have various dimensions and colours. (a) Broken spore of Gigaspora rosea, (b) vesicles with storage function, and (c) arbuscules, the typical brush-like structure which gives the name to this group of fungi. (SLR, MBR)

Diamonds of cuisine

• Mycorrhizas are among the most widespread symbionts in the world. They are found in more than 80% of all plant species and 92% of all plant families.
• Mycorrhizas can be managed as biofertilisers as they increase plant nutrient uptake (see pages 88-95).

• Many species of ectomycorrhizal fungi are important edible mushrooms and truffles.

They look like potatoes but are mycorrhizal fungi. The white truffle (Tuber magnatum), known as the diamond of cuisine, is a prized ingredient for cooking. (AD)

Glomeromycota

Fungi in the phylum Glomeromycota form arbuscular mycorrhizal symbioses with the majority of plant species, by colonising the root cortex (see box, page 43) and forming an extensive mycelium, vesicles and arbuscules. This phylum contains 17 genera and 240 species distributed in nine families and four orders. Common genera include Glomus, Rhizophagus, Scutellospora, Gigaspora, Cetraspora and Acaulospora. Glomeromycota produce abundant hyphae and spores in soils. In grasslands and agricultural lands, these fungi comprise an estimated 20-30% of soil microbial biomass, making arbuscular mycorrhizal fungi among the most abundant organisms in many soils.

The significant mutual benefit of mycorrhizal symbioses is evident from their tremendous abundance and diversity. Mycorrhizal fungi are found in all terrestrial biomes and in association with most plant families. They are found with trees, shrubs, forbs, grasses and agricultural crops. Arbuscular mycorrhizas are abundant in tropical forests, grasslands, savannahs, deserts and arable lands, and ectomycorrhizas dominate temperate and boreal forests. Ericaceous mycorrhizas are common in boreal forests and heathlands. Orchid mycorrhizas are essential to the survival of orchids throughout the world.

Ectomycorrhizas

Approximately 6000 fungal species establish ectomycorrhizal associations with many species of trees and woody plants. At least 20 families of Basidiomycota (e.g. Amaranthaceae, Rosaceae, Boletaceae) and seven families of Ascomycota (e.g. Pezizaceae, Tuberales) are known to establish ectomycorrhizas. The biomass of ectomycorrhizal fungi mycelia has been estimated to range from 700 to 900 kg per hectare, and 20-40% of an ectomycorrhizal root weight is due to the fungus.

Ericaceous and orchid mycorrhizas

Most plant species belonging to Ericaceae, including the genera Rhododendron, Calluna and Vaccinium, form ericoid mycorrhizas. These plants form delicate roots lacking root hairs and their outermost radial cells become heavily colonised by Ascomycota from the genera Rhizoscyphus and Hymenoscyphus. Orchid mycorrhizas are established between plant species of the family Orchidaceae (20 000 to 35 000 species) and several groups of fungi in the phylum Basidiomycota, as well as some rare Ascomycota.
Fungi – Other fungi

Zygomycota

A unique feature of the Zygomycota is the zygospore, which is formed within a structure called the zygosporangium after the fusion of specialised hyphae called gametangia during sexual reproduction [35, 36]. The mature zygospore is often thick-walled and undergoes a dormant period before germination. Nevertheless, asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae grow over the surface of the material on which the fungus feeds and produce clumps of erect stalks, called sporangiophores. The tips of the sporangiophores form spore-producing structures, the sporangia. Thin-walled spores are produced within the sporangia and are thus shed above the substrate, in a position where they may be dispersed by wind or water, allowing the fungus to spread and colonise new substrates quickly and efficiently. The Zygomycota include two main classes: Zygomycetes (that comprise Mucorales, the most studied order) and Trichomycetes. More than 1 000 species have been described so far. Zygomycetes are commonly decomposers, symbionts or parasites (see box, page 33) in terrestrial habitats. For example, members of the Mucorales are easily isolated from soil, humus and dung. Furthermore, some Mucorales are used to ferment foods and produce important industrial products, such as lactic acid and rennin (used to make cheese). Conversely, some species have a negative economic impact by causing storage rot in fruits. Trichomycetes are obligate associates of arthropods, including insects and millipedes. The host may be an adult or larva, in terrestrial or aquatic habitats. The fungi are usually found attached to the gut lining of the host. The precise relationship is difficult to determine in most cases; however, they often seem to be commensals, doing little or no harm to their hosts, with the fungus gaining nutrients from the gut of the host. Some zygomycota can also be pathogens of animals, plants, amoebae and, especially, other fungi. Of the more than 1 000 species of described Zygomycota, the majority are found in soil, with some genera (Mucor, Mortierella and Phialocephala) that are extremely common and reported in almost all surveys of soil fungi.

Chytridiomycota

Chytridiomycota (chytrids) are characterised by their asexual state, a motile (capable of moving) zoospore with a single whiplash flagellum oriented and located posteriorly [35, 36]. Zoospores are released through an opening in the wall, and their release usually indicates the death of the ‘body’ of fungus, called thallus. They are the only fungi that form flagellate spores. Chytridiomycota are typically unicellular, with limited hyphal growth in some cases. Chytrids require a water film in which zoospores can swim until a desirable substrate is found. For this reason, chytrids are usually regarded as aquatic fungi, although those that thrive in the capillary network around soil particles are typically considered terrestrial. Approximately 700 species of chytrids have been described, including species living in temperate forest and rainforest soils. Soil chytrids include plant pathogens and vectors of plant viruses such as Synchytrium endobioticum, which causes the potato wart disease (black scab) and serious commercial damage. Some chytrids are nematode (see pages 46–47) and algae parasites. As Chytridiomycota often feed on decaying organisms, they are also important decomposers. These organisms are responsible for the decomposition of resistant materials, such as pollen and cellulose. This colonisation of pollen usually occurs during the spring when bodies of water accumulate pollen falling from trees and plants. Estimates of the number of chytrid species occurring in soil are currently unavailable.

Blastocladiomycota

The Blastocladiomycota (blastoclads) are one of the currently recognised phyla within the Fungi kingdom. Blastoclads were originally the order Blastocladiales within the phylum Chytridiomycota, until molecular and zoospore structural characters were used to demonstrate that it was a group separated from chytrids. Similar to Chytridiomycota, Blastocladiomycota produce zoospores to colonise new substrates. Furthermore, members of Blastocladiomycota are capable of decomposing complex materials, such as cellulose and chitin. Of economic importance is Physoderma maydis, a parasite of maize and the causal agent of brown spot disease. There is a blastoclad, Sorochytrium milnesiophthora, that is a tardigrade parasite (see page 44). However, the best known species, belonging to the genus Colostrum, are nematode parasites. As they are mainly known to be aquatic fungi, a reliable evaluation of their abundance in soil is not available.
Photosynthesisers – Lichens

Morphology

Lichens originate from symbiosis, involving a fungus ‘mycobiont’ (the dominant partner) and one or several photosynthetic ‘photobionts’ (the energy producers), either unicellular green algae, cyanobacteria (see page 35) or both. The symbiosis is mutalistic since the fungus benefits from the food (carbohydrates) produced by algae or cyanobacteria, and the algae or cyanobacteria benefit by being protected from the environment by the fungus. This symbiosis is also cyclical as the two partners must activate the association with every new generation. Also, specific bacterial communities are obligate lichen symbionts and, therefore, considered to be an integral part of lichen structure. The thallus is the vegetative and assimilative body that relies on the interactions among the symbionts. The thallus (growth forms) can vary from discrete granules of 0.5–50 mm to pendent lichens of 2 m in length, and have an extraordinary range of growth types, each of which show particular adaptations to different environments. [39]

Taxonomy

Lichens are derived from the fusion of two unrelated groups of organisms, where the taxonomy of the resulting hybrid organism is based on the fungus. Ninety-eight percent of lichenised fungi are Ascomycota in 18 of the 45 recognised orders (only five contain exclusively lichenised taxa), and two percent are Basidiomycota (see pages 38–39). The lichenised green algae are placed in Trebouxiophyceae (Chlorophyta), while cyanobacteria comprise several orders.

Microhabitat

Lichens growing on the ground are ‘terricolous’ or ‘epigeous’ and colonise a wide range of soils. The habitats include: mineral or organic soils, thin layers of strongly weathered rocks, rock crevices, sand dunes, grasslands, bryophytes (i.e. mosses, hornworts and liverworts), damp trunks or rocks, peatlands and rotting wood. In tundras, cushions of ‘reindeer lichens’, mostly Cladonia species, are basic food for these herbivores. Continental steppes harbour specialised types of erratic vagrant thalli that allow them to disperse easily. Lichens are a major component of biological soil crusts (see page 73) in desert and dryland regions, growing in patches that increase soil stability and permeability, as well as resist erosion.

Diversity, abundance and biomass

There are about 28 000 species living in all types of habitats. Only 5–12 species thrive in tundra or desert soils, while in tropical areas, rocks and bark surfaces may support more than 50 species in less than 0.5 m².

Uniqueness of lichens

• Lichens are complex and unique entities with characteristics not found in either the original fungi or algae. These include slow growth, long life, ability to revive from severe desiccation, high habitat specificity, tolerance to extreme temperatures and the ability to survive on all types of substrata and habitats.
• Some rock-inhabiting species are among the oldest living organisms on Earth.
• Lichens are extremely vulnerable to habitat alteration and are effective ‘early warning indicators’ of environmental changes.

Diversity of the lichen genus

Cladonia: (a) C. rangiferina; (b) C. convoluta; (c) C. cervicornis; (d) C. mediterranea; (e) C. pulvinata

Squamarina lentigera

Circinaria fruticuloso-foliacea
Photosynthesisers – Plants

Morphology

Plants are organisms that have a visible part above ground (the shoot system) and a hidden part below ground (the root system). The extreme variety in the shapes of the visible portion of the plants is also present in the roots below the surface of the soil. The two main types of root systems are fibrous and taproot. Fibrous roots are the traditional structures formed by primary and secondary roots branching in all directions in the soil. By contrast, taproots are characterised by a single firm root growing straight down, with minor roots developing either side of it. Other specialised roots do exist, for example, the tuberous roots of sweet potato are modified for the storage of nutrients and water, while the stilt roots of mangroves allow the plant to be stable in wet and muddy soils by cropping up from the trunk and growing downwards. Roots are usually covered by root hairs that are invisible to the naked eye and form a large surface area allowing plants to take up water and mineral nutrients from the soil. [40, 41]

Microhabitat

Plants are found everywhere, from tundra to desert. The aboveground parts of plants are responsible for the photosynthesis (see box on page 35) that provides energy for the plants and replenishes oxygen in the atmosphere. By contrast, the root system has three main functions: 1) absorption of nutrients and water; 2) anchorage to soil; 3) storage of nutrients. Plant roots generally grow anywhere with suitable environmental conditions and readily explore soil macropores (see page 72). The part of the soil that is directly influenced by roots is called the rhizosphere, and is very rich in soil microorganisms (e.g. in bacteria and fungi).

Diversity, abundance and biomass

The number of known plant species has been estimated to be around 400 000. The majority (i.e. 260 000–290 000 species) belong to seed plants with around 1 000 Gymnosperms. Nearly all the others are classified as flowering plants (Angiosperms). It is difficult to estimate plant root biomass because: 1) the fine roots are difficult to sample and 2) the separation of living from dead roots is very tedious. Nevertheless, as a general rule, plants allocate relatively more biomass to roots if the limiting factor for growth is belowground (e.g. water), while they allocate relatively more biomass to shoots if the limiting factor is aboveground (e.g. light). For this reason, a low root biomass is usually typical of plants living in forests and woodlands, while a higher root biomass can be found in desert plants.

Incredible numbers of plant roots

- The maximum rooting depth, 68 metres, was found in a plant in the Kalahari Desert.
- A single winter rye plant (Secale cereale) can grow roots measuring 620 kilometres in only 0.5 cubic metres of soil.
- A grove of over 40 000 cloned quaking aspens (Populus tremuloides), located in south-central Utah (USA), has the largest root system in the world: it is estimated to weigh 6 600 tonnes.

Root structure

Observing a cross section of a plant root, the main visible structures are:

- root hair: they have fundamental importance in absorbing water and nutrients and in attaching the plant to the soil or other growing surface. They are lateral extensions of a single cell,
- epidermis: a single-layer group of cells that forms a boundary between the plant and the external environment. Its functions are protection against water loss, regulation of gas exchanges, and absorption of water and mineral nutrients;
- cortex: formed by unspecialised cells lying between the epidermis and the vascular or conducting tissue (xylem and phloem). These cells can be colonised by symbiotic fungi (see page 40). In some plants, such as carrots, the cortex becomes a storage organ;
- phloem: conducts products of photosynthesis (i.e. sugars – see box on page 35) from leaves to roots.
- xylem: conducts water and minerals from the roots up through the plant.

Typical roots contain monosomatic, elongation, and differentiation zones. In the monosomatic zone, cells undergo rapid division, creating new cells for root growth. These cells begin to elongate (elongation zone), giving the root added length. The zone of differentiation contains mature, specialised cells, such as phloem, xylem, and root hairs.

Taxonomy

Green plants (Viridiplantae), are a kingdom of organisms including from 300 000 to 315 000 different species. The majority, 260 000 to 290 000 species, produce seeds. The two main groups of seed plants are the flowering plants (Angiosperms) and the naked-seed plants (Gymnosperms). Angiosperms produce fruits used as food by humans. Angiosperms comprise naked-seed plants (Gymnosperms). Angiosperms produce fruits and include the most common vegetables and fruits used as food by humans. Angiosperms comprise naked-seed plants (Gymnosperms). Angiosperms produce fruits and include the most common vegetables

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**Microfauna – Tardigrada**

**Morphology**

Tardigrades are microscopic animals (0.1 - 1.7 mm) that are strongly dependent on the availability of water to permit gas exchange and avoid desiccation. This led to their original name 'little water bear', which was given to them by the German pastor J.A.E. Goeze, who first described them in 1773. Their bodies are short, slightly segmented and equipped with eight poorly articulated legs ending in four to eight claws. They move very slowly, in a manner similar to that of a bear. All tardigrades possess an eversible buccal tube and two stylets to pierce animal or plant cells, and a pumping pharynx to suck out their internal fluids, although some species are carnivorous and consume rotifers and nematodes (see pages 45-47). The morphology of the claws, cuticle (outer covering) and the buccal apparatus (mouth) is used to identify the different species. [43, 44]

**Tardigrades in space!**

- Their resistance to cosmic radiation and vacuum has led tardigrades to be part of several space expeditions: the TARDIS project in 2007, as part of the Russian FOTON-M3 mission, which was sponsored by the European Space Agency (ESA), and the Tardkiss experiment in 2011, which included the BIOMIS Project, sponsored by the Italian Space Agency.
- The revelation that these tiny animals survived exposure to the harsh space environment has given further support to the 'panspermia theory'. This old idea holds that 'seeds of life' could have spread between planets and, for some, represents a possible origin of life on Earth. So could these eight-legged creatures have travelled through space to eventually colonise other planets, such as our Blue Planet?
- They are the toughest animals on the planet, able to withstand a dose of 5,000 grays of gamma radiation (a human withstands 4 - 10 grays), temperatures ranging from 151 °C to near absolute zero (-273 °C), and can live for 200 years.
- Recent studies have shown that only 82.5 % of the tardigrade's DNA is pure (see box on page 30), the remainder originating in plants, bacteria and fungi. These fragments of foreign DNA are incorporated during repairing processes of DNA damaged during exposure to hostile environments.

**Taxonomy**

Their scientific name Tardigrada was suggested by the Italian biologist Lazzaro Spallanzani in 1776 meaning 'slow walker'. A number of morphological and molecular studies have tried to resolve their systematic status, and recent analyses indicate that they are probably basal arthropods. The phylum Tardigrada includes three classes and over 110 genera, and is continuously updated with newly discovered species. For example, a new genus, Pilatobius, was proposed in 2014. The class Mesotardigrada includes only one species: Thermozodium esaki. This species was recorded in 1957 from a hot spring near Nagasaki, Japan. Unfortunately, this place was destroyed by an earthquake and subsequent searches for specimens have been unsuccessful.

**Microhabitat**

Tardigrades are common in both marine and freshwater systems but also in the water films surrounding soil particles. They are also found in mosses, which are the plants that have the most developed capacity to absorb and retain water, thus giving them their second common name 'moss piglets'.

**Diversity, abundance and biomass**

Approximately 1,150 species of tardigrades have been described and can be found in almost every type of habitat around the world, from above 6,000 m in the Himalayas to the deep sea (below 4,000 m) and from the polar regions to the Equator. Many of these environments experience dramatic environmental changes throughout the year, and tardigrades survive thanks to their extraordinary ability to enter into a cryptobiosis, a suspended animation (deathlike) state in which their metabolism drops to 0.01 % of normal (or is entirely undetectable) and the water content of the body decreases to less than 1 %. In this cryptobiotic state, known as a ‘furn’, they can live for a long time (up to 200 years!) and can survive extremes of temperature, toxicity, dehydration, salinity and oxygen tension. Revival typically takes a few hours but depends on how long the tardigrade has been in the cryobiotic state. Although their ecological role has not yet been fully evaluated, recent studies suggest they could have a regulatory function for plant-parasitic nematode populations when predatory nematodes have disappeared, due to predation pressure and/or unfavourable environmental conditions.

- **Light microscopy images of tardigrades**
  - (a) Ventral and (b) lateral view of their legs with claws. (c) Tardigrade mousse (remains of the exoskeleton after the individual has moulted) containing eggs (dark circles). In many cases, the eggs are left inside the shed cuticle to develop. (DR, DL)
- **Scanning electron microphotograph of**
  - (a) a tardigrade showing its typical plump shape (b) a tardigrade’s retractile tubular mouth armed with stylets, with the head pointing to the right, where mouth parts and eye spots can be seen. On the left, back claws aid in identification. (c) Tardigrade as it emerges from its cuticle (outer covering) in preparation for moulting. In order to grow they must moult. (d) Female adult specimen and juvenile. (MS)
Microfauna – Rotifera

Morphology

Rotifers are minute multicellular organisms (0.05 to 3 mm long). Their mostly transparent body is subdivided into a head, trunk, and a foot. They have three easily visible unique features: 1) their anterior ciliary organ called the corona (or crown); 2) a specialised food processing apparatus made of strong muscles and a set of hard jaws (the mastax with trophi), 3) a unique and well developed cuticle (the lorica), giving the animals a pseudo-segmented appearance, that can be exquisitely ornamented. The head and foot can be retracted inside the trunk if the animal is disturbed or if the environment dries out. [45, 46]

Taxonomy

Rotifers (phylum Rotifera) are related to other worm-like organisms belonging to Gnathostomulida and Micrognathozoa. Recent studies in DNA evolution (molecular phylogeny) have revealed that the parasitic worms of the phylum Acanthocephala are their closest relatives, if not themselves a group of specialised rotifers. Scientists recognise three groups of Rotifera, but only one, the Bdelloidea, is an important soil inhabitant.

Microhabitat

Like many other minute organisms, rotifers have an absolute requirement for a water matrix during their active phase. They inhabit the capillary water retained between soil particles, litter or masses, where they feed on bacteria or small algal cells. They are filter-feeders (i.e. feed by filtering food particles from water) or browse the bacterium film for particles. A few are predators of ciliates or of other rotifers, or suck out the content of cells after piercing the cell wall using specialised trophi. Although they need water to live actively, the bdelloids, which are the most successful soil rotifers, have an extraordinary ability to survive prolonged periods of desiccation through a process called anhydrobiosis (a type of cryptobiosis – see page 44). In this state (known as a ‘tun’), they not only survive adverse conditions but can also be easily transported to other habitats. Because of this and their reproductive features (see box, below) they are very effective at colonising and recolonising areas. Most rotifers, in particular bdelloids, can only be identified while alive. This has hampered their study significantly, to the extent that little is known of their role in the functioning of soil systems.

Bdelloid rotifers, a female affair

- Rotifers are usually dioecious (have distinct male and female organisms) and sexually dimorphic (have distinct male and female forms), with the females always being larger than the males. They reproduce sexually or parthenogenetically.
- Among rotifers, there is a particular group, the bdelloid rotifers, that originated around 80 million years ago, and there are now about 460 morphologically distinct species.
- Bdelloid rotifers have evolved entirely without sexual reproduction and are assumed to have reproduced without sex for many millions of years. Males are absent and females reproduce only by parthenogenesis.
- No male sex organs have ever been observed in these microscopic animals. Asexual reproduction is generally thought to be an evolutionary dead end as it leads to reduced diversity and the build-up of deleterious mutations.
- The ability to acquire new functions (i.e. of evolving) has been achieved by incorporating DNA fragments of other organisms, such as bacteria, algae and fungi into their genome. This process is known as horizontal gene transfer.
- These findings overturn current thinking that reproduction without sex is less likely to endure evolutionary changes than sexual reproduction.

Diversity, abundance and biomass

There are about 2,030 described species. They can be extremely abundant in moist soils and mosses but can occur in dry soils as well. They live in virtually every terrestrial habitat, from the Poles to the Equator, mostly near the soil surface.
Microfauna – Nematoda

Morphology

Nematodes are aquatic transparent roundworms (0.1 - 5 mm in length in soil species) and are dependent on water films surrounding soil particles for their activity and gas exchange. The ability of nematodes to have many food sources and to live in numerous habitats (marine and freshwater sediments, as parasites of plants, invertebrates and vertebrates) is due largely to their morphological adaptations and survival strategies. Nematodes survive the harshest conditions (desiccation, heat, freezing, osmotic and oxygen stress), by shutting down their metabolism, altering their biochemical pathways and body shape and entering a dormancy stage (cryptobiosis – see pages 44 and 86), which is reversible when favourable environmental conditions return. While in cryptobiosis, they can be dispersed by wind. Nematodes generally have an elongated body shape tapering at both ends, but they also can be spherical or pear shaped. They have a non-segmented flexible cuticle and their body organs (excretory, nervous, digestive and reproductive systems) are in a fluid-filled cavity, called coelom, and present in many other animals (e.g. earthworms – see page 58). Their movement is undulatory, contracting certain muscles against internal pressure. Most soil nematodes have separate sexes but some can be parthenogenic or hermaphroditic. Nematodes generally lay eggs that develop through four moulting juvenile stages to adults. [47, 48]

Nematodes, everywhere!

- Soil nematodes feeding on bacteria occur more than 3.6 km below the surface of the Earth – deeper than any known animal, and at a temperature of 48 °C.
- The smallest nematode, belonging to the genus Micronema, is 0.3 mm in size and lives between sediment particles.
- Nematodes were the first animal genome ever sequenced, and are the smallest nematode, belonging to the genus Micronema, is 0.3 mm in size and lives between sediment particles. (OB, JGB)
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- Nematodes are among the most diverse and abundant animals on Earth: one in five animals on Earth is estimated to be a nematode. Terrestrial nematodes make up a substantial portion of the more than 25,000 described species of the group. Nematodes are found in soils, marine and freshwater sediments, and as parasites of plants and animals, such as insects, humans and birds. Many nematode infections cause serious human diseases in the developing world (e.g. Guinea worm and elephantiasis).

Taxonomy

The phylum Nematoda contains multicellular animals that are related to other molting animals (the Ecdysozoa) such as Nematophora. Terrestrial nematodes predominate in the large orders of Panagrolaimida, Rhabditida, Mononchida and Dorylaimida.

Microhabitat

Global studies of the distribution of soil nematode species show that most are endemic to a site or region, and only a small fraction are cosmopolitan. Climate, vegetation, as well as soil physical and chemical characteristics all contribute to determining the habitat suitability of each community of nematode species. Nematodes are a key group for regulating biochemical cycling and ecosystem processes. These processes include mineralisation and decomposition in the soil system. Nematodes are also indicators of environmental quality. For these studies, nematodes can be differentiated into feeding groups based on their morphology and, in particular, the shape and size of their mouthparts. There are five main feeding types: bacterivores, fungivores, omnivores, plant parasites and predators. Ecological characteristics or life history traits of nematodes can also be indicators of environmental quality. For example, species that reproduce quickly in response to a nutrient-rich addition to the soil, are ‘colonisers’, while species with long life cycles and low reproduction rates are ‘persisters’. Soil nematodes carry bacteria on their cuticle and can excrete viable bacteria, thus serving as a vehicle for translocation of bacteria throughout the soil, and as a potential food source.

Diversity, abundance and biomass

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Plant-feeding nematodes

Nematodes puncture the cell walls of plant roots with large hollow needle-like spears in their mouths and suck out plant nutrients. Their spears are called stylets and vary in shape. Enzymes, (e.g. cellulase and chitinase) are injected through the stylets of some plant parasitic species to help break down cell walls. Other species, such as Xiphinema sp., can carry plant viruses in their stylets and vector the viruses from plant to plant. Plant-feeding nematode species can be migratory or sedentary, feeding either inside the host plant root (endoparasites) or outside the plant root (ectoparasites) and can cause serious economic damage to agricultural crops, including citrus, rice, maize, soybean and numerous vegetable crops. The plant parasitic nematodes Meloidogyne and Pratylenchus spp. infect wide ranges of host plants, while Globodera and Heterodera spp. have more restricted plant host ranges. Crop rotations help avoid damage by the latter two nematode species.

Omnivorous nematodes

These are large free-living soil nematodes (up to 5 mm in length), and are omnivorous, using a variety of food sources. They have a hollow tooth that can pierce other organisms and suck out nutrients. Depending on environmental conditions and food availability, they can feed on algae, filamentous, protists, other nematodes and then, when their primary food sources are unavailable, switch to feeding on fungal hyphae and bacteria. They often have low reproduction rates and generally occur in stable habitats, rather than in newly established or disturbed habitats.
Bacterial-feeding nematodes

Bacterial-feeding nematodes have tubular mouths and graze on bacteria by swallowing them or scraping them from soil substrates using structures on top of their head. Grazing of bacteria increases the rate of decomposition of the chemical compounds in organic matter (carbon and nitrogen mineralisation) in soil. There is also evidence that grazing on bacteria can positively affect the plant root growth. These animals have germination times ranging from a few days to a week, which is advantageous for colonising new habitats.

Fungal-feeding nematodes

Fungal-feeding nematodes have small, fine stylets optimally adapted for feeding on fungal hyphae (see box, page 39). Fungivorous nematodes can affect plant growth indirectly via the destruction of arbuscular mycorrhizal fungi (see page 40) or other beneficial fungi, leading to reduced nutrient availability for the plant. Other species are beneficial for pest control through the destruction of plant fungal pathogens (see box, page 39). Fungal-feeding nematodes are generally less abundant in highly disturbed soils (e.g. agriculture) than bacterial-feeding nematodes.

Predaceous nematodes

Predaceous nematodes have one or more large teeth or a pointed spear that are used to attack and ingest nematodes and other small animals, such as enchytraeids, tardigrades, rotifers and protists (see pages 36-37, 44-45, 48). Predatory nematodes make up approximately 5% of the overall soil nematode community, and decline in abundance when soils are disturbed. Mononchoides spp. can also feed on bacterial cells and can be cultured in the laboratory as biocontrol agents against plant parasitic and other nematodes.
Mesofauna – Enchytraeidae

Morphology

Enchytraeidae are also known as ‘potworms’ and owe their name to first being discovered in flower pots (from the Greek enchytraeon meaning ‘in the pot’). Each body segment bears four bundles of bristles (setae), two located on the ventral side and two occupying lateral or dorsolateral positions. Numbers of setae per bundle vary between 1 and 16. However, two, three, or four are most common, although in some species they are totally absent. Setae are resistant structures, made of chitin, that allow the animal to anchor itself to substrate. Like earthworms (see page 58) and leeches, they are hermaphrodites, as they have reproductive organs normally associated with both male and female sexes. They develop a ‘cibarium’, a glandular modification of the epidermis (the sheet of cells that covers the body of all animals) which secretes a cocoon where the eggs are deposited; however, some species can reproduce through parthenogenesis or asexually by fragmentation (see the box on the right). [49, 50]

Nothing amazing, apparently...

- The most amazing fact about enchytraeids is that there is nothing amazing about them. However, it seems that cold, wet and organic rich ecosystems cannot function without them.
- The largest species (Mesenchytraeus antaeus) can be up to 6 cm long with more than 100 segments; the smallest species (Marionina eleonorae) is only 1 mm long and has no more than 15 segments.
- Enchytraeids have a variety of ways to reproduce: by ordinary cross-breeding, with both partners exchanging sperm and laying eggs; by self-fertilisation; and by parthenogenesis (i.e. without fertilisation), and also completely asexually by breaking up of a worm into several pieces and regeneration of full-grown worms out of each piece.

Taxonomy

The Enchytraeidae are a family of Annelida (class Oligochaeta), resembling small white earthworms (1 - 30 mm in length) that are the dominant soil fauna (in terms of live biomass). Seasonal climatic fluctuations have a strong influence on their population dynamics, and extreme weather conditions, such as summer droughts and severely cold winters, can lead to high mortality rates. Although some species can migrate to deeper soil layers to avoid these adverse environmental conditions, this seems to be a short-term survival strategy due to a lack of food in these more humidified horizons. Feeding and burrowing activities influence soil structure and turnover of soil organic matter, thus making them ‘ecosystem engineers’, like termites, ants and earthworms (see pages 54-55, 58).

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Microhabitat

Enchytraeids are concentrated in the uppermost soil layers (0 - 5 cm), where organic matter accumulates. Most studies regard them as microbivore-feeders, frequently grazing on bacteria and fungal mycelia (see box, page 39), although they are also saprovores, consuming dead organic matter.

Diversity, abundance and biomass

About 700 valid species of enchytraeids have been described. Although they are distributed globally, they are more abundant in non-wooded habitats. In particular, cold and wet organic-rich environments, such as moorlands, contain high numbers (ranging from 12 000 to 311 000 individuals per m²), and here enchytraeids are the dominant soil fauna (in terms of live biomass). Seasonal climatic fluctuations have a strong influence on their population densities. Although some species can move to deeper soil layers to avoid these adverse environmental conditions, this seems to be a short-term survival strategy due to a lack of food in these more humidified horizons. Feeding and burrowing activities influence soil structure and turnover of soil organic matter, thus making them ‘ecosystem engineers’, like termites, ants and earthworms (see pages 54-55, 58).

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Global Soil Biodiversity Atlas | CHAPTER II – DIVERSITY OF SOIL ORGANISMS
Morphology

Soil mites are relatively small (from 60 µm to 2 - 5 mm), have rounded or elongated bodies and, like other Arthropoda, are covered in a rigid structure, called exoskeleton or cuticle. Adult mites and nymphs have usually four pairs of legs, while larval stages have three pairs. They lack jaws and use the chelicerae and pedipalps (cophalic appendages) to grasp their food. Chelicerae are diverse in form, which reflects mites’ varied feeding habits. Most are ground-dwelling (i.e. subterranean) and some have one or two pairs of simple eyes (ocelli) in their outer covering. Being blind, they generally rely on physical and chemical sensing during navigation through the small soil pores. [51, 52]

Taxonomy

Mites (Acari) are an ancient lineage that have been known since the Devonian period, at least. Traditionally, they belong to the class Arachnida, together with spiders. There are roughly 40,000 described soil-living species and more than half of them live on or in the ground. Representatives of both mite superorders (Acariformes and Parasitiformes) are found in soils. Moreover, they comprise up to 40 % of all soil microarthropod species.

Microhabitat

Soil mites occupy practically all natural soil substrates and have a world-wide distribution. They spread across all soil horizons starting from the surface of the litter down to 2 - 3 m in mineral soil. Their normal abundance in undisturbed ecosystems varies from a few hundred individuals in the arctic and tropical deserts up to one million per square metre in temperate mixed forests. Mites are among the first animals to colonise emerging mineral and organic substrates. They disperse in various ways, allowing them to cover large distances. These methods include: transport on mammals, birds and insects (phoresy), as well as passive distribution by wind or flowing water. Most mite species are characterised by clearly defined feeding habits, and their contribution to the cycles of carbon and nitrogen (see pages 104-105) in soil is fairly well quantified. Acariform mites have a variety of feeding preferences, from microbes (microbivory) and the remains of plants and animals (detritophagy) through omnivory to predation. Parasitiform mites are predominantly predaceous as they survive by preying on other organisms.

Distribution, abundance and biomass

In undisturbed systems, hundreds of mite species can be found in one square metre of soil. However, little is still known about general distribution patterns of mite species globally. Despite numerous reviews at both regional and global geographic coverage levels, the drivers of most general trends in mite species richness are not completely understood. However, they seem to be related to climate, availability and quality of organic matter, intensity of disturbance and the geological history of individual regions. Latioatlantal climatic gradients are expected to be the major factor explaining regional oribatid family and species richness across large areas.

An exceptional persistence in nature

- Mites can withstand doses of radioactivity 100 times higher than those that would kill a human being.
- In heavily disturbed ecosystems, such as cities or industrial areas, soil mites can be the last indicator of primary habitats (i.e. habitats present before the development of cities/factories).
- This means that it is still possible to reconstruct the vegetation type and landscape conditions based on the mite communities remaining in the degraded areas.
- Orbital mites (belonging to the superorder Acariformes) have hard exoskeletons that often fossilise.
- That is why fossil mite assemblages, together with pollen analyses, are used by scientists as an additional tool for palaeogeographic (the study of past geography) reconstructions.

Examples of oribatid mites (belonging to superorder Acariformes). (a) The mite Scutoribates perornatus excavated in Baltic amber. This amber dates back 44 million years. (b) The mite Dissoloncha superbus (belonging to the superorder Parasitiformes) is a group of predation mites inhabiting coastal areas of northern countries. (c) An exceptionall persistence in nature: Orbital mites (belonging to the superorder Acariformes) can survive under unfavourable conditions can curl into a very rigid sphere protecting soft tissues and extremities from predators. These minute soil ‘armadillos’ may feed directly on plant debris while other oribatids are predominantly bacterial- and fungal-feeders. (d) a scanning electron microphotograph of Steganacarus sp. (AZA, SMNG)
Morphology

Collembola are small (0.12 - 17 mm) wingless hexapods (with six legs - see page 31) commonly known as ‘springtails’. The scientific name, Collembola, derives from the Greek words kolla (meaning ‘glue’) and embolon (meaning ‘piston’) and was initially proposed in reference to the ventral tube (collophore), which plays an important role in their fluid and electrolyte balance and may also serve as a ‘glue piston’ for adhering to smooth surfaces or for grooming. Another characteristic, albeit not always present, gives them their common name: the forked springing organ or ‘furca’. This is held by a special catch mechanism on the ventral side of their abdomen which, when released, acts as a spring that can propel them, within seconds, several times the length of their body.\[53, 54\]

Taxonomy

Collembola belong to the phylum Arthropoda. They are part of the class Entognatha that, together with the class Insecta, form the subphylum Hexapoda (see page 31). They are classified into four orders: the Entomobryomorpha and Poduromorpha, with a more or less elongated body shape, and Symphypleona and Neelipleona, which are spherical in shape.

The frozen and colourful collembola

- Collembola can withstand freezing conditions by using anti-freeze compounds in their body tissues.
- Cryptopygus antarcticus, native to Antarctica and Australia, is the only Collembola species to have appeared on a postage stamp.
- Collembola can have multi-coloured stripes: Paralobella orousetii from the Philippines has a yellow head and first two thoracic segments, the third thorax segment and the first three abdominal segments are red and the remaining abdominal segments are white.

Diversity, abundance and biomass

There are around 8500 described species, which are found in a great variety of habitats, from Antarctica and the Subantarctic Islands to rainforests, warm beaches and deserts. As well as being widespread, they are the most abundant hexapods in the world, and an average square metre of soil in a temperate grassland or a woodland can yield as many as 40000 individuals.

Generally, habitats may support anything from two to 30 different collembolan species. However, in the tropics, up to 150 species can be found, if species present in epiphytes (plants living in trees) are taken into account.
Mesofauna – Protura

Morphology

Proturans are small soil-inhabiting primitive hexapods (ranging in size from 0.5 and 2.5 mm – see page 31) with no antennae and no eyes. The forelegs are used as sensory organs; they have many sensory organs (‘sensilla’) covering their posterior segments (tarsi). On the dorsal side of the head there are a pair of other important sensory organs (pseudoculi) whose functions are not well understood. Their bodies are cylindrical, pointed at both ends and generally unpigmented, pale or yellowish. Similar to the Collembola, they are wingless arthropods and their mouthparts are entognathous, meaning that they are retracted within the head capsule; the mandibles and maxillae are slender and their maxillary palps (mouthparts) are long, with setae and sensilla. They are born with nine abdominal segments and grow by successive moultings during which they add new distal segments. The adult has 12 abdominal segments. They have small pairs of lateral-ventral appendages on the first three abdominal segments. They lack cerci, the paired appendages on the rear-most segment of the body present in many other hexapods. Reproduction occurs with indirect fertilisation: the males deposit packets of sperm (spermatophores) and the females collect the spermatophores. [55, 56]

Taxonomy

The class Protura (phylum Arthropoda, subphylum Hexapoda) includes three orders: Acerentomata (families Hesperentomidae, Protentomidae and Acerentomidae), Sinentomata (families Fujientomidae and Sinentomidae) and Eosentomata (families Eosentomidae and Antelientomidae).

Microhabitat

Protura are found in moist soils, leaf litter, humus, moss and decaying wood in woodland, grassland and agricultural soils. They do not thrive in very acid soils (e.g. coniferous woodlands). Usually, they are part of the decomposer community and help break down organic matter in soil and litter. In particular, proturans feed mainly on fungal hyphae (see box, page 39), but they are also important prey for small predators, such as spiders, mites (see page 49) and pseudoscorpions (see page 53).

Diversity, abundance and biomass

Proturans are found all over the world, with the exception of the polar regions. There are more than 700 described species. Their density is variable in relation to the characteristics of the soil and the content of organic matter. In disturbed and degraded soils they can be completely absent, while in undisturbed habitats, such as natural grasslands, there can be as many as 85 000 individuals per square metre.

The ‘young’ proturans

- Among hexapods (see page 31), Protura was the last class to be described. The first description of these minute soil arthropods was given in 1907.
- Filippo Silvestri and Antonio Berlese, two Italian entomologists, discovered proturans independently.
- The first species to be described was Acerentomon doderoi, found in soil near Syracuse, New York, USA.
- When disturbed, proturans seem to raise the end of the abdomen in a defensive posture similar to that adopted by scorpions.

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Proturans are small soil-inhabiting primitive hexapods (ranging in size from 0.5 and 2.5 mm – see page 31) with no antennae and no eyes. The forelegs are used as sensory organs; they have many sensory organs (‘sensilla’) covering their posterior segments (tarsi). On the dorsal side of the head there are a pair of other important sensory organs (pseudoculi) whose functions are not well understood. Their bodies are cylindrical, pointed at both ends and generally unpigmented, pale or yellowish. Similar to the Collembola, they are wingless arthropods and their mouthparts are entognathous, meaning that they are retracted within the head capsule; the mandibles and maxillae are slender and their maxillary palps (mouthparts) are long, with setae and sensilla. They are born with nine abdominal segments and grow by successive moultings during which they add new distal segments. The adult has 12 abdominal segments. They have small pairs of lateral-ventral appendages on the first three abdominal segments. They lack cerci, the paired appendages on the rear-most segment of the body present in many other hexapods. Reproduction occurs with indirect fertilisation: the males deposit packets of sperm (spermatophores) and the females collect the spermatophores. [55, 56]
Morphology

Diplura are small wingless hexapods (see page 31), with body lengths ranging from 0.3 to 1 cm, although the largest species can be longer than 2 cm. Diplurans have a narrow and elongated body, and are generally white or colourless. The head has a pair of long and moniliform (a string formed of bead-like segments) antennae and no eyes. The abdomen ends with a pair of cerci, i.e. prominent abdominal appendages, which can contain silk glands. The cerci can have either a pair of pincers (Japygidae) or can be filamentous (Campodeidae). Some species of japygid Diplura are robust and darker in colour, and are often confused with earwigs (Dermaptera – see box to the right). However, Diplura have neither eyes nor wings. Fertilisation is similar to that found in proturans and collembolans (see pages 50-51): the males produce and deposit a large number of spermatophores, capsules containing spermatozoa, on the substrate that are then picked up by a female. The females lay eggs in clumps in the soil cavities or decomposing vegetation. Some species check the eggs and the larvae. Diplura are known to be able to regenerate lost body parts, such as legs, antennae and cerci (57, 58).

Taxonomy

The class Diplura (phylum Arthropoda, superclass Hexapoda) comprises nine extant families, the main ones being Japygidae and Campodeidae (each with more than 400 species).

Microhabitat

Diplura live in wood, leaf litter, under stones, rocks or logs, on the surface of, or in deeper layers of soil, in mosses or in termite and ant nests. Many species are herbivores and detritivores (Feed on decomposing plant and animal parts) and feed on a wide range of plant material. However, some species have well-developed mandibles and eat nematodes (see pages 46-47), small arthropods, enchytraeids (see page 48), etc. They can also consume fungal mycelia (see box on page 39) and plant detritus. They are often part of the decomposer community, helping recycle dead plant material.

Diversity, abundance and biomass

There are approximately 1,000 described species that are common inhabitants of most natural and human modified soils. They are distributed worldwide, from the tropics to temperate zones. They do not have specific habitat preferences and, generally, their population densities are not high (< 50 individuals per square metre).

Maternal care of diplura

- Male diplurans produce large numbers of spermatophores (up to 200 per week), probably because sperm only remain viable in the spermatophore for about two days.
- The eggs of campodeid and japygid diplurans are normally laid in a mass of up to 40, in clumps or on small stalks in little cracks or cavities in the ground.
- Female campodeid diplurans abandon their eggs, but japygid species are known to remain in the brood chamber with the egg cluster, protecting the eggs and the newborn larvae.

Diplurans are not earwigs

- Some diplurans in the Japygidae family may be occasionally confused with earwigs. This confusion is due to the presence in both groups of pincer-like abdominal appendages, scientifically known as cerci.
- Diplurans are not insects. Earwigs are insects of the order Dermaptera and live in similar habitats: moist places beneath stones, boards, sidewalks, debris or in the soil.
- The forcip-like appendages, i.e. cerci, of some diplurans are designed to break off near the base if they are mishandled. This behaviour is probably an anti-predatory adaptation. It is known as autotomy and is typical also of reptiles, such as lizards, and amphibians, such as salamanders. Diplurans are among the few terrestrial arthropods known to be able to regenerate lost body parts (legs, antennae and cerci) over the course of several molts.
Mesofauna – Pseudoscorpionida

Morphology

Pseudoscorpions are tiny arachnids known as ‘false scorpions’ because they look similar to scorpions but do not have an elongated postabdomen with a venomous sting at the end. Usually less than 5 mm in length, they are brownish arachnids with large pincer-like chela (pedipalps). The body is divided into two regions: the cephalothorax (or prosoma, a fused head and thorax) and the abdomen (or opisthosoma) clearly divided into 11–12 segments. The cephalothorax is covered dorsally by a shield (carapace) and bears the appendages. One to two pairs of simple eyes (ocelli) are sometimes present on the head, but many species are blind. The first pair of cephalic appendages, the chelicerae, are two-segmented, chelate (clawed) and used for feeding. Chelicerae have silk glands. Behind the chelicerae are the pedipalps, which are used to capture prey and for defence. Pseudoscorpions, like all arachnids, have four pairs of thoracic legs. The abdomen has no appendages. These animals have a long lifecycle (the course of developmental changes through which an organism passes from its birth to the mature state in which it may give birth to another organism), depending on the environment and the temperature. The males produce a spermatophore, and pull the female over it. The female carries a silken egg bag of about 12–40 eggs in a brood sac that is attached to the ventral surface of the opisthosoma. She can produce several broods each year. The young pseudoscorpions moult, passing from several larval instars (protonymph, deutonymph and tritonymph) before becoming adults that can live three to four years. [59]

Taxonomy

The Pseudoscorpionida or Pseudoscorpiones is a large group comprising 27 different families. They are found everywhere, but their highest diversity is found in the tropics.

A beetle for a house

- The dispersion of the tropical American pseudoscorpion Cordylochernes scorpioides from one tree to another is mediated by the Harlequin beetle Acrocinus longimanus. The males show territorial behaviour on the back of the beetles and even mate with females there.
- Nesticus birsteini (today Carpathonesticus birsteini) distributed in Russia and Georgia, is the only pseudoscorpion to have appeared on a postage stamp.

Diversity, abundance and biomass

Approximately 3,400 species of Pseudoscorpions have been described. Their density, in general, is not high (< 300 individuals per square metre). In some cases they are considered beneficial to humans as they prey on various pest species; for example, carpet beetle larvae, ants, mites and booklice. Occasionally Pseudoscorpions may disperse attached to flying insects, birds and mammals (phoresy).
Macrofauna – Formicidae

Morphology
Ants are social insects, among the most abundant in the world. Many ants have a sting but some groups have lost theirs and instead spray formic acid. They are distinguished from other closely related groups by the petiole (a constriction between the abdomen and thorax with either one- or two-nodes or scales) and their elbowed antennae. Ants live in large complex colonies with a division of labour, involving reproductive and non-reproductive individuals, cooperative care of the young and overlapping generations. This defines them as eusocial insects. This division of labour leads to different castes (groups of individuals with the same function). The reproductive caste is the queen, while the sterile caste are workers (and in a few species also soldiers). Reproductively active males are produced only during the breeding season and die soon after mating. The workers perform all the other functions of the colony, including protection, foraging, cleaning, building nests and care of the larvae. [60, 61]

Taxonomy
Ants have been around for over 120 million years. They belong to the family Formicidae of the order Hymenoptera (the group containing also bees and wasps).

Microhabitat
Ant colonies form nests in which the colony lives. In most cases the colony centre is fixed, but some army ants have no fixed colony centre. Ants can have nests that are arboreal (in tree canopies), epigeic (on the soil surface) or hypogeic (underground). Ants that nest underground dig tunnels that are interconnected by larger chambers, some of which give access to the outside world. The chambers can have specific functions, such as nurseries, larders and rubbish dumps. Among the ants that nest in the ground some of the most impressive are the leaf-cutter ants, especially in the genus *Atta*, that build very large nests up to 300 m² in surface area, and excavate a great deal of soil. *Atta laevigata* nests may resemble that of domestic cattle to humans; hence the name 'ant cow'.

Many ants are predators or herbivores, but others are omnivorous (with a diet consisting of a variety of food sources) or specialist predators (e.g. on termites). Leaf-cutting ants use leaves as a substrate for their symbiotic fungus (fungus-growers), which they use as food source. Ants interact closely with many other organisms and are fundamental for some functions of ecosystems; for example, protection of certain plant species (‘ant plants’) from herbivory and facilitation of seed germination in appropriate locations by carrying them to their nests. Ants also play an important role in the maintenance and functioning of soils, as they dig tunnels and chambers, thus promoting nutrient cycling through soil bioturbation (the reworking of soil) and water infiltration. They produce soil organic debris, thus enabling the processes of decomposition performed by fungi (see pages 33-35) and bacteria (see pages 35-36) and increasing the heterogeneity of the soil resource.

Diversity, abundance and biomass
The family Formicidae is subdivided into 22 extant subfamilies, 300 genera and 14,000 described species. The diversity of species varies among world regions, with peaks in South America, Central and South Africa and Australia. They are dominant invertebrates in many ecosystems, particularly tropical ones, and occur on all continents except Antarctica. The biomass of ants in tropical rainforests is often thought to be greater than that of all vertebrates in the rainforest combined.
Macrofauna – Termites

Morphology
Termites are medium to small sized fully social insects (2 mm to 20 mm long). They are soft bodied and of colours ranging from very pale white to deep brown or black. They live inside colonies with two reproductive individuals (i.e. the king and the queen) and a very large number of sterile castes (i.e. workers and soldiers). The soldiers and workers look very different from the reproductive castes. The workers do most of the various tasks required by the colony (e.g. rearing young, foraging for food, nest building), while the soldiers defend the colony and have no other roles. [62]

Taxonomy
Termites are hexapods (see page 31) that form the order Isoptera, including 12 families. Termites are a special kind of social cockroach and, despite some similarities in shape and size, they are not closely related to ants. However, similar to ants, they are fully eusocial insects.

Microhabitat
They feed on dead plant material at different stages of decay; for example, dead wood, dry grass, leaf litter and soil. Some form a mutualistic relationship with a fungus called Termitomyces that breaks down dead plant material for the termites, who then eat parts of the fungus. They perform many of the same functions as earthworms, but the two groups are generally not found in large numbers together. They are often known as ecosystem engineers (see box on page 95) as they profoundly affect the structure of habitats for other organisms, both inside and outside their nests.

Diversity, abundance and biomass
There are about 2,700 described species. They are found in very large numbers throughout the warmer parts of the world, particularly in tropical rain forests, tropical savannahs and hot arid areas; they are not found, however, in many temperate regions and never in polar ones. They have their highest densities and diversities in tropical rain forests in Africa where they can reach up to 10,000 individuals per square metre (m²) and biomasses of up to 100 grammes per m².

Extraordinary architects
- Termites move around in tunnels in the soil or live entirely in tunnels in dead wood.
- They are nature’s most accomplished non-human architects and build nests and mounds of extraordinary complexity, such as those in savannahs in Africa, South America and Australia.
- Some termite mounds may have been continuously occupied for 50,000 years.
Macrofauna – Isopoda

Morphology

Most species of isopods belong to the soil macrofauna, and adult sizes range from 5 to 15 mm, with some species reaching only 1 to 2 mm. Terrestrial isopods, commonly known as woodlice or pill bugs, have bodies divided into a cephalon (head), pereion (thorax) and pleon (abdomen). The cephalon bears the compound eyes, two pairs of antennae (one pair is vestigial, meaning functionless) and four pairs of mouthparts for food processing. The pereion has seven pairs of walking legs (pereiopods). The abdomen comprises five pairs of modified appendages (pleopods). The pleopods have become modified and adapted for respiration through the course of isopod evolution. In males, the first two pleopods are modified to participate in sperm transfer. The sperm is transferred to the female through the modified second pleopod which, after receiving the sperm from the penis, is then inserted into a female gonopore (genital pore). After successful copulation, the female moults and produces a structure on the ventral side of her thorax that resembles a pouch and is called marsupium. Inside the marsupium the eggs stay protected while they develop into young independent isopods. [63]

Taxonomy

Isopoda is an order of crustaceans (see page 31). The semi-terrestrial and ‘truly’ terrestrial isopods form a monophyletic (developed from a single common ancestral form) group (the suborder Oniscidea), with 3 637 described species.

Microhabitat

Numerous morphological, anatomical and physiological adaptations to the soil environment make isopods the most successful land inhabitants. Terrestrial isopods occupy essentially all terrestrial habitats, ranging from the supralittoral (shore of a lake, sea, or ocean) to the high alpine regions, from the tropics to the cold-temperate zones, from wetlands to deserts. They are crepuscular or nocturnal animals and spend the day mostly hidden underneath stones, coarse woody or loose bark, or in crevices, where they can easily be captured. In deserts, species of the genus *Hemilepistus* form monogamous (having a single partner during their lives) relationships and live inside self-dug burrows essential for their survival. As macro-detritivores, terrestrial isopods significantly contribute to decomposition processes through feeding on and digesting leaf litter, dispersing microbial spores and mediating microbial activity and nutrient cycles (see pages 102-106). Digestion is supported by microbes that are ingested together with food. In their gut, isopods can also develop symbiotic relationships with bacteria, but at least some part of the cellulose digestion seems to be facilitated by endogenous enzymes (cellulases). Gut bacterial symbionts live protected inside the digestive glands, which enables them to survive on nutrient-poor diets that are difficult to digest.

Diversity, abundance and biomass

The Mediterranean region is a hotspot of isopod diversity, and Europe is the most studied region. Relatively little is known about terrestrial isopods in many tropical countries. Regional species richness increases from the cold-temperate to the warm-temperate and the tropical zones. Local abundances are quite variable and are particularly high in temperate forests and grasslands, reaching about 100 to 600 individuals per square metre.

Isopod manipulators

- Bacterial symbionts, such as *Wolbachia*, can induce sex changes and force males to develop into functional females.
- Parasitic acanthocephalan worms can manipulate the pigmentation and behaviour of the infected individuals.

Diversity of terrestrial isopods. (a) The desert isopod (*Hemilepistus reaumuri*) in Tunisia. One individual guards the entrance of its burrow against intruders. (b) *Armadillidium vulgare*, a species distributed worldwide. (c) *Hendyrella hoffmannseggi* (the smallest individual on the picture), the smallest terrestrial isopod endemic to Europe. (d) *Balloniscus glaber* is a common European woodlouse. (e) *Polyarthrus hoffmannseggi* usually lives inside ant nests. (f) *Platyarthrus sp.*, (g) *Porcellio scaber*.
**Macrofauna – Myriapoda**

**Morphology**

Myriapods (centipedes, millipedes, pauropods and symphylans) are small- to large-sized arthropods (0.5–585 mm) with elongated segmented bodies and many legs (from eight pairs up to 750 pairs). Myriapods’ bodies have a head and a more or less uniformly segmented trunk. Millipedes have fused pairs of segments (diplosegments) and, consequently, they have two pairs of legs per segment. Centipedes have forcipules, the first pair of modified walking legs on their trunk segment that contain venom glands to catch and immobilise prey. Pauropods are very small and have branched antennae with segmented stalks. By contrast, Symphyla have a pair of conical cerci with spinning glands on the posterior part of their body. [64, 65]

**Taxonomy**

Myriapods (phylum Arthropoda, subphylum Myriapoda) are categorised into four classes: Diplopoda (millipedes, 16 orders, approximately 12,000 species), Chilopoda (centipedes, five orders, approximately 5,000 species), Pauropoda (two orders, approximately 800 species) and Symphyla (one order, approximately 200 species). The most diverse orders are: Polyzdesmida (flat-backed millipedes, 3,500 species) and Geophilomorpha (soil centipedes, 1,300 species).

**Microhabitat**

Generally, myriapods are soil dwellers. Larger species burrow, while smaller and thinner species use crevices and spaces in the soil. They can be found in both deep and shallow soil layers. They thrive at high humidity, stable temperatures and low ultraviolet radiation levels; therefore, they are typically found under stones, logs and barks, and in litter, in tree hollows, stumps and caves. Some species of millipedes and centipedes can climb trees.

**Diversity, abundance and biomass**

Myriapods are found in almost all terrestrial habitats from deep soil layers and caves to above the timberline in mountains. Antarctica is the only continent with no myriapods. Myriapods are not exceptionally abundant in any habitats, with the exception of some millipede species. In temperate regions, the abundance of millipedes can reach up to tens to several hundred individuals per square metre (m²). In some temperate forest soils, millipedes can reach densities of over 1,000 m⁻². Symphylans and pauropods are distributed more unevenly, and in lower abundance since they are very responsive to changes in soil properties (chemical as well as physical) and food availability. Different myriapod groups have different feeding preferences. Centipedes are generally predators and often regulate populations of smaller animals, although some feeds on decaying plant matter. Symphylans are root-feeders, or saprophagous. Pauropods are fungal-feeders, although some species prey on small animals or suck liquids from rotting plant material. Millipedes are important decomposers of leaf litter. They are estimated to break down 10–15% of the annual leaf fall, and their significance for litter processing is higher than that of earthworms in boreal forests.

**Poisonous, luminous and singers**

- Although centipedes are venomous and sting frequently, the United States National Center for Health Statistics reports only five ‘possible’ deaths attributable to centipede stings in the US between 1991 and 2001.
- Almost all millipedes have defensive poisonous liquid secretion or produce prussic acid (hydrogen cyanide) gas.
- Some species of millipedes are bioluminescent, allowing them to be avoided by nocturnal predators. This luminescence may be the equivalent of colours used in other animal species to warn off potential predators (aposematic colours).
- A defense mechanism of some millipedes is to roll into a ball. Consequently, a male may find it hard to persuade a female to copulate.
- Although millipedes are deaf, males of the order Sphaerotheriida ‘sing’ to potential mates using vibrations in order to uncloak them.
- Some centipedes inhabit tidal zones, probably in search of food. In Brazil, there is a documented record of a sea anemone species feeding on a centipede belonging to the family Scolopendridae.
- The largest millipedes in the world are the African giant black millipedes (Archiprostigmata gigan) which reach 30 cm. They have approximately 256 legs and a life expectancy of five to seven years.
Macrofauna – Earthworms

Morphology

Earthworms are segmented animals with coelom (coelomates). The body is divided into two parts: an anterior part with segments containing cephalic ganglia, reproductive organs, foregut, calciferous glands and hearts, and a posterior part with a series of similar segments which contains the intestine. Earthworms range from a few cm to 2–3 m long, with most species falling into the range of 5 to 15 cm. Size varies considerably within single species populations, and the largest adults may be more than 100 times those of newly hatched individuals. [66, 67]

Taxonomy

Earthworms belong to the phylum Annelida (class Clitellata, subclass Oligochaeta). The Oligochaeta contain 10 400 - 11 200 species in approximately 800 genera, and 38 families comprised of approximately 7 000 true earthworms.

Microhabitat

Earthworms have been classified into three main functional groups, each with a preferred habitat:

a. epigeics, which live in the litter layer, a relatively harsh and exposed environment. They are small and uniformly coloured worms, pigmented green, blue or reddish depending on whether they inhabit grassland or forest. They counterbalance a high mortality rate with high quality food (leaf litter), which allows them to grow and reproduce rapidly.

b. anecics feed on surface litter that they mix with soil. They live in vertical subterranean tunnels created within the soil. They are large worms with a dark pigmentation and strong anterior digging muscles. They are long lived, with low growth and mortality rates.

c. endogeics are unpigmented soil-feeding worms that live entirely within the soil, which is a more buffered and predictable environment than the leaf litter, but where the quality of the food is much lower. They have also developed different ways of exploiting it. They include small filiform earthworms that selectively ingest fine organic rich soil (polyhumics), medium-sized ones that ingest soil with no selection (mesohumics) and the very large ones that live down to a 30–60 cm depth where the extremely low quality of their food is compensated for by steady environmental conditions (oligohumics).

Diversity, abundance and biomass

Although 7 000 ‘true’ earthworms (in 20 families) have been described to date, the total is probably around 30,000 species globally. They live everywhere except in dry and cold deserts. They are, however, mostly found in soil and leaf litter, although they occasionally climb trees and can live in suspended soils of epiphytic plants (that grow on other plants). Local species richness is often as low as 10 or fewer, although it may reach 15 species in well conserved soils of temperate regions and a maximum of 40–50 in some tropical regions. Density is often in the range of 100 to 500 individuals per square metre and may reach 2 000 in temperate pastures of New Zealand or irrigated orchards in Australia. Live biomass commonly ranges between 30 and 100 grammes (g) per square metre, with maximum values of 200 g to 400 g.

Rescuers, hermaphrodites and carnivores

- Earthworms are able to produce plant growth hormones and to modify the expression of plant genes. They may, for example, render a plant tolerant to plant parasitic nematodes (see pages 45-46) by inhibiting the gene responsible for the repair of damaged roots, preventing plant death after all leaves have wilted.

- While several cosmopolitan species are parthenogenetic (virgin births), the majority are hermaphrodites as they can produce progeny after the mating of two sexually mature specimens. Sperm stored in specific structures (spermathecae) fertilise eggs produced by the same individual when the female reproductive system matures.

- Earthworms may ingest up to 20 - 30 times their own weight of soil every day, and more than 1000 tonnes of dry soil a year.

- In West Africa, the genus Astoscolus has been shown to be carnivorous, feeding on smaller worms.

- The title for the largest earthworm in the world, with a length of 2.9 m, is claimed by Amyntas mikonigianus, about the same as Megascodexia australis, the ‘Giant Gippsland Earthworm’.

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CHAPTER II – DIVERSITY OF SOIL ORGANISMS

Macrofauna – Coleoptera

Morphology

The defining feature of beetles (Coleoptera) is the hardened forewings (elytra) that cover their body. The largest known beetles are more than 160 mm long (e.g., Dynastes hercules), but most beetles are less than 5 mm long. Their colours are variable, although most soil-dwelling beetle species are brown or black. Their body shape is also variable: some have long horns or sharp tusk-like appendages, some can curl up like myriapods (see page 57), some are flat and some are slim. A number of soil beetles, such as the genus Carabus, are wingless. [68, 69]

Taxonomy

Beetles are hexapods belonging to the order Coleoptera. This includes four suborders: Archostemata, Adephaga, Myxophaga and Polyphaga. Of these, Adephaga and Polyphaga have more species than other suborders, including most soil species.

Microhabitat

In terrestrial environments, many beetles can be found in soil, humus and leaf litter, under logs or in decomposing wood, under stones, in dung, carrion and in the fruiting bodies of many types of fungi (see pages 38-41). Numerous beetles (families Carabidae, Leiodidae, Staphylinidae and Scarabaeidae) are well adapted to the soil environment. Some carrion beetles (family Silphidae) and some dung beetles (family Scarabaeidae) build nests in the soil, in which they take care of their brood. Some species, such as some members of the family Staphylinidae, live solely in caves while others are myrmecophiles (ant lovers) or termaphiles (termite lovers) as they strikingly resemble ants or termites (see pages 54-55) and live in their hives.

Diversity, abundance and biomass

There are more than 370,000 described species of Coleoptera – it is the largest and most diverse order of organisms on the planet, making up about 40% of all described insect species, and about 30% of all described animal species. The abundance and biomass of beetles on ephemeral and nutrient-rich resources, such as carrion and dung, are very high. Beetles significantly contribute to decomposition processes. Besides being abundant and varied, soil beetles are able to exploit the wide diversity of food sources that are available in their habitat. Many species are predators of small soil animals such as earthworms, collembolans and nematodes (see pages 46-47, 50, 58). Others feed on fungi or dead wood.

The caring gravediggers

A recent study has shown that the dung beetle Scarabaeus saceratus uses the Milky Way to navigate during night time. This is the first known species to do so in the animal kingdom. (KKE)

The carcass of a mouse which was rolled into a ball by a burying beetle in Japan. Burying beetles belong to the genus Nicrophorus and are the best-known members of the family Silphidae. (MN)

Diversity of Coleoptera: (a) a male of the dung beetle Lathrus minutus has a long horn used for defense; (b) the tiger beetle Cicindela japonica with its sharp tusks; (c) the rove beetle Ectophyes sp. from Peru resembles its host hosts (neotropical army ants) in overall body shape and coloration; (d) the beetle Megasoma sp. from Ecuador can curl up when in danger; (e) the ground beetle Panchnes sexalcostatus has degenerated eyes and hindwings to adapt to cave and underground life; (f) a rove beetle Allocnemus sp. (the upper one) living in a termite (lower one) nest; (g) the stag beetle Ananas asianticus from Japan feeds on decaying wood and fungi; (h) the beetle Apsisphyrus sp. covered by spores of a slime mould feeding on it; (i) the burying beetle Nicrophorus concolor feeding their larvae. (YA, TK, MN)
Macrofauna – Soil insect larvae

The vast majority of insects, up to 95% in fact, are linked to the soil during their life cycle. Some lay eggs in the soil or use it as a substrate for overwintering. Due to very specific features of the soil as a habitat, insect larvae have made numerous adaptations to live in this particular environment. According to their life cycle, insects can be classified as holometabolous, hemimetabolous or ametabolous, depending on whether they undergo complete, incomplete or no metamorphosis, respectively (see box below). Larvae of holometabolous insects do not undergo substantial changes in their body form; they are often called nymphs and look very similar to adult insects lacking well-developed wings and the ability to reproduce. The holometabolous larvae differ greatly from the adult and often occupy different ecological niches. The change to adulthood occurs during pupation. Morphologically, holometabolous insects are very diverse and cover a wide range of trophic levels, from detritivores to herbivores and predators. Among different species, they may vary from less than 1 mm to 12 cm. [70, 71]

Hemiptera larvae

Cicada nymphs (Hemiptera) may be among the most well-known, most likely due to their long life in the soil and huge biomass. They feed by sucking sap from roots and can live in the soil for up to 17 years. Emergence of over 500 nymphs of periodical cicadas per square metre represents the highest recorded biomass (up to 4000 kilos per hectare) for any terrestrial animal.

Lepidoptera larvae

Lepidoptera larvae show diverse feeding strategies. The majority feed on green plants. Ghost-moth larvae in Tibet dig soil and feed on live roots. They are often infected by a caterpillar fungus (Ophiocordyceps sinensis, Ascomycota) valued in herbal medicine. Some others live in ant colonies, and are fed mouth-to-mouth by ants, or feed on residuals of ant food.

Diptera larvae

Diptera larvae in general look like small worms as they are all legless. However, their ecological functions are very diverse. Some of them mine taproots (see page 43) and feed on the internal cortex. Others live in litter or dung, which they decompose.

Coleoptera larvae

Coleoptera larvae are represented by hundreds of families with different feeding habits. Some longhorn beetle larvae (Cerambycidae) bore into roots or rhizomes. Click beetles and scarabaeid larvae chew fine roots or decaying plants. Some scarabaeid larvae are parasitised by Hymenoptera. Tiger beetle larvae (Cicindelidae) live in cylindrical burrows, and wait for their prey to pass by on the soil surface.

Metamorphosis

- The word ‘metamorphosis’ derives from Greek meta (change) and morphe (form).
- Metamorphosis refers to a major change in form or structure, usually associated with the development of the wings. One of the most dramatic forms of metamorphosis is the change from the immature insect into the adult form.
- Metamorphosis is sometimes accompanied by a change of habitat or behaviour.
- In insects there are different types of metamorphosis. The principle is that metamorphosis is closely linked to wing development. Therefore:
  - ametabolous are wingless insects (apterygota), so they do not develop wings (no metamorphosis);
  - hemimetabolous insects have wings that develop gradually (incomplete metamorphosis);
  - holometabolous insects have wings that develop during the pupation period (inactive) where the insect undergoes dramatic physiological and morphological changes to acquire the wings and to feed on different things (complete metamorphosis);
- In hemimetabolous insects, immature stages are called nymphs. Development proceeds in repeated stages of growth and moulting (ecdysis), and different stages are called instars. The juvenile forms closely resemble adults but are smaller and lack adult features, such as well-developed wings and genitals. The differences between nymphs in different instars are small, often just differences in body proportions. Examples of the hemimetabolous insects are aphids, cicadas and leafhoppers.
- In holometabolous insects, immature stages are called larvae, and differ markedly from adults. Insects that undergo holometabolism pass through a larval stage, then enter an inactive stage called pupa, or chrysalis, and finally emerge as adults. Examples of the holometabolous insects are: beetles, flies, ants and bees.

One works, the others feast

- Some parasitic species undergo hypermetamorphosis, which refers to a class of variants of holometabolism. In hypermetamorphosis some larval instars (usually the first one) are functional and morphologically distinct from each other.
- In the beetle family Melolonthidae, the first instar is called triangulin (as it has three claws on each foot) and actively seeks out prey on which subsequent instars feed.
- Triangulin is elongated and flattened and in this form it does not feed. When it finds its prey it moults, transforming into a scarabaeiform or verminform larva that does not hunt, but feeds.

Neuroptera larvae

Most Neuroptera larvae are predators, with elongated mandibles. By using the mandibles, they catch and pierce prey, and inject digestive juices. Ant lions (family Myrmeleontidae) create pitfall traps, and eat small arthropods that fall in.
Macrofauna – Ground- and litter-dwelling macrofauna

Introduction

The soil surface and leaf litter are important components of soil and may represent a perfect habitat. In particular, leaf litter, made up of dead plant material, such as leaves, bark, needles and twigs, that has fallen to the ground, is very rich in nutrients and keeps the soil moist. It also offers the perfect conditions in which to build nests; hiding places and protected spots. Many of the organisms inhabiting the ground, and the litter fall within the group of soil macrofauna (animals that are at least one centimetre long). Macrofauna include myriapods, beetles, insect larvae, slugs, snails, spiders and scorpions (see pages 57, 59-60). Some of these organisms spend their entire lives on the soil surface and in leaf litter, while others are found only there at certain points in their lives. These organisms may have a high ecological importance (e.g. as decomposers of litter). In these pages, we focus on the Arachnida (e.g. spiders and scorpions), Gastropoda (e.g. snails and slugs) and some Hymenoptera (e.g. mining bees). [72, 73]

Arachnida

The class Arachnida are arthropods. Their eight legs that distinguish them from insects, which have six legs. The most well-known groups of arachnids are spiders (order Araneae) and scorpions (order Scorpiones). Spiders come in a large range of sizes, from less than 1 mm up to 30 cm, such as the Goliath birdeater (Theraphosidae). A spider belonging to the tarantula family, Scorpions range in size from 9 mm up to specimens such as the Mexican cave-dwelling Tylodochactas mitchellii that can reach up to 20 cm. Spiders’ bodies consist of two sections (tagmata); the cephalothorax or prosoma at the front, and the abdomen or opisthosoma at the back. Spiders have a pair of cephalic appendages in front of the mouth (chelicerae), which they use to inject venom into prey from venom glands. Scorpions’ bodies are also divided into two regions; the head (cephalothorax), the abdomen (opisthosoma), which is subdivided into mesosoma (seven segments) and the metasoma or tail (five segments plus a sixth, the telson, bearing the sting). The sting consists of the vesicle, which holds a pair of venom glands, and the aculeus, the venom-injecting barb. Spiders make up a very large group of organisms comprising more than 40,000 species. About 1,700 species of scorpion have been recorded to date. Spiders and scorpions are found on all major land masses, except Antarctica. Both groups are predators. They mostly prey on insects, although a few large species can also take lizards, birds and small mammals. An exception is represented by the herbivorous spider species Baghera kiplingi. Soil is often used as their hunting ground, in which they use different methods of capturing prey. One of the most clever strategies is adopted by the ambush ‘trapdoor spiders’ (family Ctenizidae); they burrow holes into the soil, often closed by trapdoors and surrounded by networks of silk threads that alert these spiders to the presence of prey. Scorpions are nocturnal hunters, remaining in underground holes or under rocks during the day. Scorpions can survive long periods of food deprivation thanks to a specific food storage organ and slow digestion process; some are able to survive 6-12 months of starvation.

Snails and slugs are the two most relevant groups of gastropods related to soil. Taxonomically, they are both included in the order Pulmonata. The clear difference between them is the presence of a conspicuous shell in snails, which is very reduced, totally absent or internal in slugs. A snail’s shell is made of calcium carbonate and has the typical spiral shape. Both snails and slugs range greatly in size; the largest species can reach 30 cm. Around 25,000 snail species are present worldwide, whereas only approximately 5,000 slug species exist. Terrestrial snails are usually herbivorous; however, some species are carnivores. Most slugs feed on a broad spectrum of organic materials, including leaves from living plants, lichens (see page 42), fungi (see pages 38-41) and even carrion. Some slugs are predators and eat other slugs and snails or earthworms (see page 58). Some snail and slug species can cause damage to agricultural crops and garden plants and are, therefore, often considered as pests.

Gastropoda

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Burrowing or mining bees

• Not all bees (Arthropoda, Ectognatha, Hymenoptera) live in hives like honey bees do and, in fact, five of the seven recognised families of bees are ground-nesting bees (approximately 70 % of the 20,000 known bee species). Their burrows can reach 60 cm in depth and the entrance is often marked by a small mound of excavated soil. Depending on the species, the female fills the brood cells at the end of the branched burrow with pollen, honey or a mixture of nectar and pollen and, once the clump reaches the right size (sometimes after a good number of trips to flowers), she lays an egg on each one. The larva hatches within a few days, grows quickly and pupates within a few weeks. The adults emerge the following spring after hibernation.

• Unlike social bees and wasps, ground-nesting bees do not live in colonies, although some species could nest in large groups (gregarious nesters) and become so visible, especially in lawns and paths, that gardeners consider them as pests. However, in reasonable numbers they will not harm your garden. They are not aggressive insects even though the females do have stings.

• These solitary bees (specifically Colletes and Andrena, two common widespread genera) are good pollinators of economically important plants. They are often ‘idiogastic’, meaning that they collect pollen from only a select few plant species, and if that plant becomes rare or extinct, so does its pollinator.
Morphology

Although the soil animals considered as megafauna are not actually large on a human scale, and rarely exceed 1 kg in weight, they are exceptionally ‘huge’ (usually more than 10 cm long) compared to other soil organisms. These animals often have a morphology adapted to digging and life underground (fossorial lifestyle): e.g. long claws, short tail and/or hair (sometimes hairless) for mammals and a flat, slender, or limbless body to creep in soil/litter for amphibians and reptiles. They sometimes have very tiny eyes or have even lost them altogether. The latter animals develop special organs, such as sensory hair/tentacles, bioelectric receptors, sensitive noses and even echo-location systems like bats, in order to detect their prey in darkness. [74]

Taxonomy

Almost all mega soil animals are vertebrates; therefore, ‘soil megafauna’ is nearly equal to ‘soil vertebrate’. Vertebrates are animals that are members of the subphylum Vertebrata, meaning that they have backbones. Small mammals (class Mammalia), such as moles (family Talpidae), shrews (family Soricidae) and some rodents (like the naked mole-rat) are regarded as soil megafauna as are adult salamanders, caecilians (class Amphibia), and blind snakes and limbless lizards (reptiles, class Reptilia) that superficially resemble earthworms or snakes. These vertebrates utilise litter and soil as both habitat and feeding site. Some mammals, such as hares, rabbits, hedgehogs and foxes may build their dens in soil, but are not part of the soil megafauna. Vertebrates that can be included in soil megafauna are only those that use underground space as both habitat and feeding site.

The golden moles

- Golden moles are small burrowing mammals native to sub-Saharan Africa.
- Their fur colour varies from black to pale tawny-yellow, hence their nickname.
- There are 21 different species of golden moles, and more than half of them are threatened with extinction.
- They are taxonomically distinct from true moles and are regarded as rather ‘primitive’ creatures.
Microhabitat

Moles are known for denning in soil, where they continuously build under-ground tunnel systems as they burrow in search of food. Moles dig two basic types of tunnel: shallow, surface runways, and deep, more permanent tunnels. In addition, moles construct nest and rest chambers. Surface runways may be used only once; others are used frequently as main travel lanes, called main runways, and may be used for many years. Tunnels occur generally from 15 to 60 centimetres underground – deep enough to be below the winter frost line and to remain cool during summer heat. They are used regularly during the mole’s travels between its nest and rest chambers and surface runways. A molehill is built of dirt excavated from these deep tunnels, deposited on the surface in a volcano-shaped mound through a lateral tunnel. Nest and rest chambers are enlargements of a deep tunnel. Nests are made of coarse grass and/or leaves and are often located in protected areas underneath boulders or trees. Soil is also the perfect source of food for mega-fauna. Both moles and shrews have great appetites for soil invertebrates due to their high metabolic rate. Earthworms, termites, ants, insect larvae, centipedes and isopods (see pages 54-60) are the main prey for soil vertebrates. In addition, they often eat caterpillars and terrestrial snails. An exception is the naked mole-rat that mainly feeds on the tubers of plants [75]. Therefore, predation pressure of moles and shrews on populations of soil invertebrates seems not to be negligible, with an important role in soil food webs (see page 96). Furthermore, the carcasses and feces of soil vertebrates are a high-quality source of nutrients and energy for invertebrates and microorganisms in the soil. Soil mega-fauna potentially affect the community structure of soil invertebrates not only through their predation, carrion and feces, but also through modification of soil structure by digging activity (typical of moles). In the soil food web, soil vertebrates are tertiary consumers, sometimes also known as apex predators, as they are usually at the top of the food chain. In the aboveground food chain, soil vertebrates are preyed upon by predatory vertebrates, such as carnivorous and omnivorous mammals, raptors, owls and larger reptiles.

The pocket gophers

- Pocket gophers are burrowing rodents of the family Geomyidae, including 35 species. They live only in Central and North America.
- They create networks of tunnels that provide protection and a place for food collection.
- They are solitary animals, herbivores (they only eat roots, bulbs and other fleshy portions of plants). Some species are considered agricultural pests.

The star 'nose'

- The key to making sense of the star-nosed mole is the habitat where it lives. In this environment, they compete with other animals, especially shrews, for food, so having a prey category to themselves would be especially useful. The star likely evolved as a means to better find and handle small prey quickly.
Methods to study soil biodiversity

The enormous diversity of soil biota, in terms of size, number and characteristics, means that there is a correspondingly large range of techniques required in order to collect and, subsequently, identify the constituent organisms. Collection necessarily involves the separation of the organism from the soil matrix, which can be challenging due to the nature of soil minerals and organic constituents, and the physical nature of the soil matrix. Many prokaryotes (see pages 32–35) are strongly adhered to soil particles, and their release can be achieved by physical disruption (e.g. grinding and sonication) or the addition of specific chemical agents (e.g. surfactants and chelants). Such disruption can lead to damage of the organisms and, therefore, there is always a compromise between disturbance and eventual detection. The substantial differences in density between soil mineral constituents and organisms offers a means of separation by elutriation, centrifugation or density gradients. Mobile and motile organisms can be collected by encouraging movement away from the soil matrix, to entrapment and collection vessels, by a combination of gravity and differential application of heat or light. For example, the fulgurite funnel is an apparatus used to extract living organisms, particularly arthropods, from samples of soil, while the Baermann funnel is used for extraction of nematodes from soil. The active surface-dwelling mobile mesofauna, such as collembolans and mites (see pages 49–50), can be collected by possibly the simplest of all devices, the pitfall trap, which consists of a pot buried in the soil such that the lip is contiguous to the soil surface and fauna fall into it during their passages. The physical form of any organism, whether a single microbial cell or a large animal, is termed the ‘phenotype’, which is formally defined as the interaction between the genetic makeup (‘genotype’) of an organism and the environment in which it has developed and now lives. Historically, identification of soil organisms was predominantly reliant on visual observation, and thus based on the way they appeared (i.e. their morphology). Now biochemical approaches are being increasingly used, primarily based on DNA analyses (see box on page 30). (76, 77)

From morphology to biochemistry

Soil prokaryotes (archaea and bacteria) (although notably a tiny proportion of the total) and many fungi (see pages 38–41) form characteristic colonies when grown in laboratory conditions (in vitro) on enrichment media, which can be used as diagnostic for identification. More visually anonymous forms were often identified on the basis of their distinct enzyme profiles or ability to utilise particular combinations of substrates, but these techniques are now generally archaic, superseded by nucleic acid analysis. There is a long heritage of identification of soil micro-, meso- and macrofauna based on morphological features, but these can be remarkably subtle and require considerable experience and expertise to carry out. The traditional taxonomic tools of microscopes and systematic keys (written, structured identification protocols) are gradually being supplanted by genetic analysis of DNA derived from the organisms, notwithstanding that such approaches currently require advanced laboratory equipment.

Soil DNA and RNA

DNA and RNA can either be extracted directly from soil or from organisms previously separated from soil. Extracted DNA must be purified to avoid interference of organic compounds, particularly humic acids, which are prevalent in many soils. Resultant DNA mixtures should be representative of the entire basal community structure, known as the ‘metagenome’, while RNA is associated with normally active organisms, since this is related to particular forms of DNA being transcribed and, therefore, is known as the ‘metatranscriptome’. There are a number of ways to analyse resultant nucleic acids, from a very broad taxonomic scale to extremely precise determinations of particular species. Rapid advances in technology are revolutionising the scale of such analyses and the throughput that can be attained. It is now feasible to obtain several million sequences in a metagenome analysis of a single soil community sample, and these can then be attributed to their taxonomic origins and allow remarkably detailed descriptions of community structures. Emerging next-generation systems (see box on page 157) will enable thousand millions of sequences to be determined with relative ease, leading to what are likely to be entirely new perspectives on how soil microbial communities are structured and how they function. The incisive analysis and interpretation of such huge datasets is very challenging and also drives new developments in informatics relating to such ‘Big Data’.

Sampling design

- If the identification and/or quantification of target groups of soil organisms is necessary, appropriately organised sampling designs are required.
- The aim is to acquire a collection of samples of the target group that are sufficiently representative of the area or ecosystem under consideration.
- Statistically robust sampling is necessary, since it allows an estimation of the likely variation in any metrics and, consequently, how accurate they are. A wide range of statistical sampling strategies can be prescribed, depending on specific aims. These include designs that can target broad general estimations, or those that focus principally on characterising the spatial patterning or temporal variation of the target groups.
- Where techniques are labourious, sample sizes can be restricted. High-throughput molecular-based techniques are significantly reducing such restrictions, and offering new opportunities in understanding how soil communities are organised in time and space across a wide range of soil scales.
- Sampling of the soil biota is typically based on ex situ and in situ techniques. The former involve removing prescribed volumes of soil, by coring or excavation, and generally transporting them back to the laboratory for assay. In situ techniques involve procedures applied in the field, and generally rely on the movement of the organism(s) to a collecting device.
### Summary of collection and identification approaches of the main groups of soil organisms

<table>
<thead>
<tr>
<th>Main division</th>
<th>Group</th>
<th>Extraction/collection techniques</th>
<th>Identification</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entire community</td>
<td>Whole community phenotype</td>
<td>Extraction of indicator biomolecules from entire soil samples, usually involving organic solvents, such as methanol or hexane</td>
<td>Chemical structure of constituent molecules</td>
<td>The most pervasive approaches are based on membrane lipids such as phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs). The caveat is that relationships between fatty acid composition and taxonomic status is somewhat diffuse. Respiratory quinones can also be characteristic. Generic structural molecules such as ergosterol and hexane are not useful in terms of identification. Extent of community is essentially defined operationally by serve size through which the soil sample is passed prior to extraction.</td>
</tr>
<tr>
<td>Prokaryotes</td>
<td>Bacteria and archaea</td>
<td>Enrichment cultivation in liquid or on semi-solid media</td>
<td>Morphology of colonies and constituent cells, physiological profiling (new archaic), nucleic acid analysis</td>
<td>Colonies – strictly; colony forming units (CFUs) – assumed to develop from individual cells. This underestimation can occur where aggregations of cells are not completely deaggregated. Only 0.1 - 1 % of prokaryotes confirmed as being extant in soil (via analysis of community DNA) are apparently expressed in enrichment culture systems. Representivity for community-scale profiling is therefore questionable, but the technique can be applicable in appropriate circumstances.</td>
</tr>
<tr>
<td>Protists</td>
<td>Ciliates, flagellates, amoebae, etc.</td>
<td>Direct extraction from soil matrices via density-gradient centrifugation</td>
<td>Nucleic acid analysis</td>
<td>Cells must be released from any attachment to soil particles, otherwise density-based discrimination will not operate. Extraction efficiency is accordingly variable, and always less than complete.</td>
</tr>
<tr>
<td>Fungi</td>
<td>Fungi, generic soil</td>
<td>Enrichment cultivation in liquid or on semi-solid media</td>
<td>Morphology of spores (especially), mycelia and hyphae. Can be supplemented by DNA analysis</td>
<td>CFUs can arise from spores or mycelial fragments – hence number apparent will be a function of intrinsic spore numbers and mycelial mass but modulated by the extent of spore cluster dispersal, degree of (and propensity to) mycelial fragmentation, disruption of such hyphal fragments, and complex interactions in the media between emergent structures. Hence 'enumeration' of fungal extensity in the soil system via CFUs should be treated with due caution.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>In situ trapping of active mycelia via their incursion into buried 'growth' meshes/ tubes</td>
<td>Trapped specimens grown-on via media, identified as above</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Extraction of nucleic acids directly from soil samples</td>
<td>Nucleic acid analysis</td>
<td>Whole community DNA. See 'Soil DNA and RNA'</td>
</tr>
<tr>
<td>Fungi</td>
<td>Mycorrhizal</td>
<td>Based on sampling of host roots, via extraction by washing from soil cores, or direct excavation from the field. Spores can also be extracted from dispersed soil by washing and filtration, elutriation or microscope-aided hand-picking.</td>
<td>Morphology of mutualistic structures, morphology of spores (especially arbuscular forms), nucleic acid analysis</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fruiting body collection</td>
<td>Morphology of fruit body and associated spores</td>
<td>Typically more relevant to aboveground manifestation of such structures from Basidiomycetes and Ascomycetes, where they are sufficiently large to be visible to the unaided eye. Relationship to belowground fungal flora and any associated mycelial extent can be tenuous.</td>
</tr>
<tr>
<td>Microfauna</td>
<td>Nematodes</td>
<td>Wet extraction by migration-based filtration through coarse tissue to collection vessels ('Baermann funnels')</td>
<td>Morphology, especially of mouthparts, nucleic acid analysis</td>
<td>Cysts not detected, relies on movement by active individuals, so can be selective</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Direct wet extraction by elutriation and capture on sieves</td>
<td></td>
<td>Cysts and inactive forms may be detected</td>
</tr>
<tr>
<td>Tardigrades</td>
<td>Wet extraction by migration-based filtration through fine mesh to collection vessels, or direct observation via dissecting microscope and physical removal.</td>
<td>Density gradient cushions or centrifugation</td>
<td></td>
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</tr>
<tr>
<td>Rotifers</td>
<td>Wet extraction by migration-based filtration through fine mesh to collection vessels, using differential temperature gradient</td>
<td></td>
<td></td>
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<tr>
<td>Macrofauna</td>
<td>Legged forms</td>
<td>Dry extraction by light and heat-induced migration to collection vessel (Tullgren funnel)</td>
<td>Morphology, nucleic acid analysis (emergent)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>In situ collection of active (foraging) forms via pitfall traps</td>
<td>Morphology</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Enchytraeid worms and Diptera larvae</td>
<td>Wet extraction by migration-based filtration through fine mesh to collection vessels (akin to Baermann funnels – see nematodes above)</td>
<td>Morphology</td>
<td>Only active forms extracted due to reliance on movement to separate them</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Illustration</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macrofauna</td>
<td>Earthworms</td>
<td>Excavation of defined volumes of soil and hand-sorting</td>
<td>Morphology</td>
<td>Laboursome technique, can involve substantial masses of soil.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>In situ extraction from soil matrix via addition of expellants such as mustard solution or formaldehyde</td>
<td></td>
<td>Efficiency relies on pervasive penetration of the soil matrix by expellant solution, once contact with worm is needed to encourage upward migration. Not all worms affected, so take path Fomaldehyde is now discouraged due to potential environmental side effects and health and safety issues.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Electromigration to surface via application of pulsed high voltage, delivered to soil via inserted electrodes in an annular pattern</td>
<td></td>
<td>Affected by soil type and prevailing moisture. There could be health and safety issues.</td>
</tr>
<tr>
<td>Other macrofauna</td>
<td>Hand-picking, pitfall trapping, direct observation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megafauna</td>
<td>General</td>
<td>Hand-picking, trapping, direct observation, including remotely by videography</td>
<td>Morphology</td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER III – GEOGRAPHICAL AND TEMPORAL DISTRIBUTION

From tropical forests and grasslands to cold and hot deserts, agricultural fields and also city parks, soil organisms can be found in every ecosystem on our planet. Soil biodiversity is distributed not only through space, but also over time (i.e. days, seasons and years). (MRI, LTA, BRL, LJR, GA, TTJ)
Introduction

Soils are among the most diverse habitats on Earth, and determination of the forces that operate at different scales that drive this diversity is one of the greatest challenges in soil ecology. Environmental factors work at the local scale of organic particles and plant roots, but also at the level of plant communities and, at more regional scales, related to topography and vegetation systems. Disturbance operates at all these scales and is an important factor for maintaining a high degree of habitat diversity in soil. Limitations in the dispersal of organisms through the soil matrix, and heterogeneous distribution of resources, make the majority of soil particle surfaces devoid of organisms when observed under a microscope. This restricts population processes, such as competition, to local hotspots with high resource availability. Therefore, organisms that normally compete, can coexist by being spatially separated. Many soil organisms utilise similar resources in the soil and there is an apparent contradiction between the high species richness and the low degree of resource specialisation. This high level of coexistence among species in the soil (33 000 bacterial and archaeal taxa can be detected in less than 10 grammes of soil) can only be understood when realising the exceptionally large degree of spatial heterogeneity and microhabitat diversity in the soil. Soil may appear rather homogeneous when viewed on a large scale, but becomes more and more heterogeneous when approaching the scale of individual organisms.

Many soil organisms operate at the level of aggregated particles, and the stability of these aggregates is important when three-dimensional networks of water and air-filled pores are formed in the soil. Recent work using scanners has demonstrated a spatial distribution of potential microbial resources (e.g. polysaccharides, proteins, etc.) at the nanometre scale in microaggregates (10–100 µm in size), demonstrating an enormous spatial complexity which helps explain the high microbial diversity of soils. Soil microbes contribute to this complexity by producing fungal hyphae and sticky substances (e.g. exopolysaccharides, glomalin) that bind organic and mineral particles together into aggregates. Certain properties (e.g. soil structure) influence plant distribution, and the activity of plants is important in shaping soil communities. For instance, substances exuded by roots result in high microbial activity at the root surface (the rhizosphere effect) and such gradients of resources (nutrients, aeriation, redox potential) in soils can be steep and change rapidly over time. Other environmental factors work on much longer time scales (e.g. plant successions). Variation in litter quality and exudation patterns among plants also influence soil organisms, and spatial patterns of soil communities are often reflected in spatial plant distribution patterns. The activity of soil communities can also shape plant communities. For instance, macrofauna, such as termites or ants, redistribute resources, such as organic matter, in the landscape, which has profound effects on vegetation patterns.

Abiotic drivers, such as climate, pH and soil moisture, are often important factors in shaping soil communities on larger scales, but plant functional traits may also be important. For instance, fast-growing plant communities are usually associated with soil microbial communities that are dominated by bacteria, while fungi dominate in soils of slow-growing plant communities. On continental scales, pH is one of the most important factors shaping soil microbial communities, and this factor alone explains most of the variation in microbial soil communities, ranging from tropical forests and grasslands to temperate and boreal forests.

The aim of this chapter is to present the biotic and abiotic factors that influence the spatial and temporal patterns of soil communities, and to give an overview of the global distribution of soil biodiversity on the basis of current scientific knowledge.

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Distribution patterns – Biogeography

Historical and scientific context

Biogeography is the study of the large-scale distribution of biodiversity through space and time. This science aims to reveal biodiversity regulation and its link with ecosystem biological functioning, goods and services, such as maintenance of productivity, of soil and atmospheric quality and of soil health. Although the initial concept dates back to the early 20th century, only recently an increasing number of studies have investigated the biogeographical patterns of soil organisms. This delay is due to the lack of relevant molecular and bioinformatics tools (see pages 64–65) to assess the scale and inseasibility of soil biodiversity through the non-availability of an adequate sampling strategy.[79, 80]

Ecologists studying plants and animals have long recognised that an examination of the modifications in diversity throughout a landscape is pivotal to understanding the environmental factors that drive the magnitude and variability of that diversity. However, this conceptual vision is also relevant to soil life since it can offer valuable insights into the relative influence of dispersal limitations, environmental heterogeneity, and environmental and evolutionary changes in shaping the structure of communities. Soil biodiversity is extremely complex, ranging from microorganisms (e.g. bacterial) to macrofauna (e.g. earthworms). As a consequence, the question to address is whether the same laws govern the distribution of soil micro- and macroorganisms or whether some peculiarities (e.g. small size, short generation time, huge diversity and high dispersal and adaptation of microbial communities) lead to specific patterns of distribution on large spatial scales. To date, the studies dealing with the biogeography of the soil community allow us to answer some of the questions that arise when considering large scales:

- are soil communities a ‘black box’ with no spatial structure or do they exhibit a particular distribution with predictable, aggregated patterns on local to regional scales?
- are spatial variations brought about by contemporary environmental factors or historical land use and contingencies?
- which environmental factors (e.g. soil properties, climate, land-use and human disturbance) contribute most to the structure and diversity of the soil community on large geographic scales?

Drivers of soil biodiversity distribution

The factors that regulate the diversity and distribution of belowground communities are less understood than those acting on aboveground organisms. The activity and diversity of soil organisms are regulated by both abiotic and biotic factors. The main abiotic factors are climate (temperature and moisture), soil texture and structure, salinity and pH. Overall, activity and growth of soil organisms increase at higher temperatures and soil moisture levels. For instance, for collomembrains (see page 50), the optimum average temperature is 20–50 °C, while some bacteria (see pages 33–35) can survive temperatures up to 100 °C.

Soil texture and structure also strongly influence the activity of soil biota. For example, clay soils favour microbial and earthworms (see page 58) activities; whereas sandy soils, with lower water retention potential, are less favourable. Soil salinity can also cause severe stress to soil organisms, leading to rapid desiccation. However, increased salinity may sometimes have positive effects, by making more organic matter available. Similarly, changes in soil pH can affect the activity of species and nutrient availability. The main biotic factors are vegetation composition and diversity, and aboveground trophic interactions. In addition, within soil food webs (see page 96), each group can be controlled by bottom-up or top-down interactions. Top-down effects are mainly driven by predation, grazing and symbiotic relationships (see box on page 53). Bottom-up effects depend largely on competition for access to resources.
Distribution of soil microbial communities

Microbial ecologists describing the distribution of soil microorganisms (e.g. bacteria and fungi — see pages 33-35, 36-41) on a large spatial scale generally invoke one of the oldest fundamental paradigms in microbial ecology: ‘everything is everywhere’. The first part of this paradigm, ‘everything is everywhere’, is supported by several particularities of the microbial model: microorganisms 1) are small and easily transported, 2) have the ability to form a resistant physiological stage that allows them to survive in hostile environments, and 3) form extremely large populations with a high probability of local extinction ([83, 84]).

Bacteria are by far the most abundant organisms in soils, with several thousand million cells present in a single gramme of most soils. Bacteria play important roles in the plant-soil system; firstly, they serve as the primary decomposers of organic matter, recycling nutrients back into the soil and intensifying the relationship with contrasted environmental conditions. Furthermore, they can adapt rapidly to environmental change. This ability causes bacteria to be extremely diverse (i.e. belong to different species) despite only exhibiting a limited number of visible morphological differences. The complex physico-chemical structure of soils allows many different spatial niches for this diversity to flourish, and for this reason soils are known to be one of the most biodiverse habitats of bacterial communities.

New data, new knowledge

In the past, our knowledge of the different types of bacteria found in soil, and the factors affecting their distributions, has been limited to findings from the analyses of cultivable bacteria that can grow on nutrient-rich media in the laboratory (see pages 64-65). These findings are now being complemented by data from large-scale soil surveys using molecular techniques to assess biodiversity.

The molecular approaches typically rely on the determination of bacterial biodiversity by examining sequence differences in DNA that has been extracted from the soil. These new approaches are vastly increasing our knowledge of the different types of bacteria found in different biomes around the world, revealing entire lineages of bacterial life for which no living cultured representative species have been isolated. Molecular surveys of soil have typically been performed to understand how natural factors influence the distribution of biodiversity, but also to reveal how sensitive these bacterial communities and their functions are to environmental change resulting from, for example, human land usage and climatic variations.

Drivers of soil bacterial diversity

A striking consistency in the many large-scale studies that have been performed is the overriding influence of soil properties on soil bacterial communities. Across landscape gradients, from upland bogs and woodlands through grasslands to intensive arable systems, factors such as soil type, climatic conditions, land cover, etc. However, in certain cases the reduced soil sampling methodology (less than 100 sites) can lead to contradictory results given, for example, the influence of climatic conditions on soil bacterial diversity. To date, it is impossible to come to sound conclusions about the rank of environmental filters driving the soil microbial assembly to a large extent.

This biodiversity is made up of many previously undiscovered taxa, such as the acido-bacteria, which are specialised for living in such physiologically harsh environments. In more neutral habitats, like those favoured for agriculture, there are more diverse assemblages of bacteria, that are better-known due to culture-based studies (e.g. actinobacteria — see page 35). Certain bacterial groups, such as the alphaproteobacteria, are ubiquitous (occurring everywhere). Their ubiquity most likely points to a potentially large role that these organisms play in maintaining soil processes.

Soil bacterial communities are also driven by other factors. These are the same forces that affect soil formation itself: climate, parent material, topography and interactions with other organisms (see Chapter I). For instance, plant diversity is of course a key driver in the long term, as it provides the important raw detrital materials on which the microbial communities build the soil. In the short term, plants provide labile exudates from their roots (see page 43), which feed the bacterial activities and the local diversity of communities. It is difficult, perhaps even impossible, to determine the relative importance of each of the different factors in driving soil biodiversity, because of their inherent interdependencies. However, because of the increasing demand for food production, one factor that is heavily altered by human populations is the plant communities. For this reason, there is a heightened interest in plant and agronomic effects on soil bacterial biodiversity. More modern advances in molecular sciences are now used to address these issues.

The recognition and understanding of how and why different soils possess different bacterial communities will allow the development of a better ecological framework for future testing of how global changes will affect bacterial communities.
Distribution patterns – Distribution of soil organisms

Soil fungal distribution

The kingdom Fungi is one of the most diverse groups of organisms on Earth, which are important actors for the regulation of carbon cycling, plant nutrition and pathology (see Chapter IV). Fungi are widely distributed in all terrestrial ecosystems. A study published in 2014 determined the main drivers of fungal diversity and community composition globally. To investigate soil fungal diversity, researchers used DNA (see page 64-65) extracted from hundreds of globally distributed soil samples. The strongest drivers on the richness (or diversity) of fungi are proximity to the Equator and mean annual precipitation. Higher levels of diversity were found in tropical ecosystems. However, ectomycorrhizal fungi (see page 46) were most diverse in temperate or boreal ecosystems. Precipitation and temperature (climatic factors), followed by pH, calcium or phosphorus availability (edaphic factors), are the most significant drivers of soil fungal richness and community composition at the global scale. Strong links found among distant continents reflect their relatively efficient long-distance dispersal (through wind and water) compared with that of large animals.

Another recent study investigated the intensity at a global scale of the colonisation of plant roots by the two main types of mycorrhizal fungi: arbuscular and ectomycorrhizal fungi. The intensity of plant root colonisation by arbuscular mycorrhizal fungi strongly relates to warm-season temperatures, frost periods and the soil carbon-to-nitrogen ratio, and is highest at sites featuring continental climates with mild summers and a high availability of soil nitrogen. By contrast, the intensity of ectomycorrhizal infection in plant roots is related to soil acidity, the soil carbon-to-nitrogen ratio and the seasonality of precipitation, and is highest in sites with acidic soils and relatively constant precipitation levels. Both studies prove the good level of knowledge of the factors determining the distribution of soil fungi at the global scale. Information about the forces driving the spatial patterns are available not only for soil microorganisms (e.g. bacteria and fungi), but also for soil microfauna, namely nematodes.

Nematode distribution

Nematodes (see pages 46-47) have successfully established themselves in all ecosystem types, including soil, marine and freshwater, as well as in harsh environments such as the hottest and coldest deserts on Earth. Soil nematodes are not evenly distributed across the landscape but vary in abundance, species numbers, size and feeding habits. Among the most abundant multicellular animals on Earth (estimated at more than 10¹⁹ individuals globally and up to millions of individuals per square metre of soil), the diversity and abundance of nematode species can vary at local and global spatial scales. [86]

On a global scale, nematode diversity does not seem to follow patterns of aboveground diversity, which increases in the tropics and declines with increasing latitudes toward the geographic poles. Instead, nematode diversity appears to be high across most latitudes, decreasing only in the polar regions. Even at small scales (millimetres to centimetres), nematode species diversity can be high. For example, a single soil core (approx. 100 cubic centimetres) from a Cameroon forest contained 89 nematode species, while molecular tools are discovering increasingly high numbers of undescribed species.

Globally, nematode species distributions show distinct biogeographies, with many species endemic to particular regions or ecosystems. Although soil nematodes readily disperse in water (e.g., through water and snowflakes) or air and horizontally, changes in continental patterns of nematode diversity are largely determined by climate, soil chemistry and plant community structure. Plant parasitic nematodes (PPNs) are cadistributed globally with their hosts and are thus more widespread in the tropics, while the most agriculturally damaging species tend to be more virulent and have broader host ranges.

Insect-associated nematodes are also cadistributed with their hosts and are found on every continent, except Antarctica. Similar to the PPNs, entomophilic nematodes follow patterns of virulence, host-specificity and biogeography.

Nematodes that are not parasitic or pathogens are the most diverse, and typically the most abundant, forms. This group includes the microbivorous nematodes. These nematodes have the broadest geographic distribution (globally) and occupy the most environmentally extreme habitats. Other members of this group include those that feed on cyanobacteria, algae and protists. These nematodes do not appear to be dispersal-limited, and can be found wherever there is suitable habitat. At small spatial scales, nematode distributions are often highly heterogeneous. Even at larger spatial scales (hectares), nematode feeding groups, such as fungal-feeding nematodes, may not cluster together in a single hot-spot location. Instead they distribute as a function of soil moisture, plant species or other soil characteristics. Information on the factors determining the distribution of nematodes is critical for economic reasons. For example, plant parasitic nematodes can cause tremendous crop damage, entomopathogenic nematodes can provide effective control of insect pests, and non-parasitic species play crucial roles in nutrient cycling support for higher trophic levels. How climate change will alter soils, plant communities and nematode biogeography forms the basis of critical research currently underway. Additional studies aim to understand the linkage between host plant and nematode parasites, and the varied and complex contributions of nematodes to soil system structure and functioning.
Earthworm distribution

Earthworms (see page 58) represent one of the main taxonomic groups of soil biota. Earthworms are present in almost all terrestrial ecosystems at varying biomass, density or species richness levels. The distribution of earthworms and the structure of their communities is linked to evolutionary and ecological factors operating at different scales, from global to local. The present global distribution of earthworms is determined by different biotic and abiotic processes. [86]

During the past five centuries, human activities deeply impacted this global distribution by displacing earthworm species generally by accident. For example, many lumbricid species were introduced in New Zealand where communities were dominated by members of the families Acanthoderidae and Megadendridae, and a species (Pontoscolex corethrurus) originating in South America is now found in all tropical lands. After introduction, these exotic species compete with native species, which deeply modify earthworm community structure and soil functioning. Earthworms originate from aquatic organisms, so they still need a minimum amount of liquid water to live. Consequently, they are absent from the coldest (polars and high mountains) and drier regions (deserts) on Earth. Earthworms can, therefore, be found in almost all climates and all latitudes. Only boreal forests lack earthworms, for historical reasons (glaciations). Actually about 7 000 earthworm species have been described for an estimated number of 50 000 existing species on Earth. Many species remain to be discovered and described, especially from tropical regions where earthworm species seem to be highly diversified. 

At a more local scale, earthworms have to adapt to the environment including both abiotic (e.g. climate, soil type, soil texture and pH) and biotic factors (e.g. food resource, litter quality and predators). They have also to face recent anthropogenic changes (i.e. habitat alteration, invasive species and climate change – see Chapter V). Earthworms are relatively fragile organisms, and disturbances generally result in a loss of species. In the Western Ghats in South India, in a small area (10 km²), 10 species were collected from altitude natural grassland, 7-8 species from forests, and 4 species from degraded pastures resulting from deforestation. It is interesting to note that all over the world there seems to be a systematic limitation of community richness to 10–12 species in undisturbed ecosystems.

Competition seems not to be an important factor in structuring earthworm communities, because different niches are available and earthworm species have developed special functional traits (feeding on rich soil, poor soil, humified organic matter, freshly decomposed litter; living in litter, at the soil surface or deep in the ground). Nevertheless, competition pressure occurs in productive ecosystems where resources are scarce. At the ecosystem scale, earthworm density varies from zero to some hundreds of worms per square metre (about 1 000 individuals per m² in some temperate sites), and biomass ranges from zero to a few tonnes per hectare (more than four tonnes in Normandy pastures in France). At a microscale, earthworm assemblages are usually spatially structured in patches ranging from a few tens of centimetres to a few tens of metres. This may be related to soil properties, vegetation and biotic factors (e.g. competition).

Termite distribution

Termites (see page 55) are generally tropical animals, but their spatial distribution reaches into cooler and drier environments. Indeed, they occur in five major biomes: tropical rain forests, tropical savannah woodlands, semi-deserts, temperate woodland and temperate rain forests (see pages 78, 82). Termite distribution is not uniform; in temperate regions their presence is nearly negligible, while in tropical areas they can be the dominant insects in the soil. [91]

Nevertheless, patterns of termite distribution are very asymmetrical within the tropical regions. For example, species of the genus Macrotermes can be easily found in savannahs and forests of Africa and Asia, but not in South America and Australia. Local species richness is influenced by environmental factors. Rainfall, vegetation type, temperature and altitude have all been shown to influence termite diversity. In general, the highest species richness is found in tropical forests (62 genera retrieved in the African Congolese rain forest). Temperate woodlands and rain forests have the lowest richness, with an average of three genera or fewer. The semi-deserts have more genera than the temperate ecosystems. The distribution of termites has also been studied in relation to their feeding preferences. Soil- and humus-feeding termites have their highest generic richness in the African, Neotropical (South and Central America) and Asian tropical rain forests. By contrast, wood-feeding termites are more evenly distributed across all biomes.

Ant distribution

- The Global Ant Biodiversity Informatics (GABI) project is an ongoing effort to consolidate and manage a comprehensive global database of ant species distributional records, including literature records, museum databases, and online specimen databases. [92]

- In 2015, GABI presented a website (antmaps.org) to visualise the known distribution of ant species or higher taxa across the world. Researchers at the University of Hong Kong in China and Japan’s Okinawa Institute of Science and Technology developed the tool.

- The website features a series of interactive maps showing where each of the world’s ca 15 000 known ant species can be found.

- For example, the maps show that Greenland and Iceland have no native ant species, whereas Queensland (Australia) has the highest diversity, with 1458 species.

- The database used to develop the maps, includes records from over 8400 scientific publications, most major digitised museum collections, and online databases such as AntWeb. In total, the database contains over 1.6 million records.
Distribution patterns – Soil biodiversity at aggregate scale

Soil aggregates

Soil is an incredibly complex and diverse organisation of pores and particles, which influence the organisms that live within. These particles, known as ‘soil aggregates’, consist of mineral and organic materials bound together, and are generally defined by their size and their stability in water. These aggregates are typically classified into three main size fractions: macroaggregates (>250 µm), microaggregates (50–250 µm) and clay- and silt-sized aggregates (<50 µm). Different soil organisms live in the network of pores between and within aggregates. (93)

The vast variation in the size of aggregates, as well as their physical-chemical properties, results in a huge diversity of microhabitats for organisms living within the soil. For example, small pores found in clay- and silt-sized aggregates will protect microorganisms (e.g. bacteria – see pages 33-35) against predation from larger organisms, which are restricted to larger pores in meso- and macroaggregates or between aggregates, and also restrict the flow of water and air and the input of new nutrients. Therefore, clay- and silt-sized aggregates are more stable habitats, with reduced competition and predation, and less variation in water influx (due to the capacity of small pores to better hold water), and are less sensitive to mechanical breakdown and influx of environmental pollutants.

Microaggregates are intermediate habitats, mainly populated by microfauna (e.g. nematodes – see pages 46-47). Macroaggregates are considered to be less stable habitats due to greater fluctuations in water and gas flow, increased competition and predation, and their sensitivity to mechanical breakdown (e.g. due to soil tillage, rain and drought cycles – see pages 15, 122-123). Macroaggregates are mostly populated by ecosystem engineers (see box on page 95), such as earthworms and termites (see pages 55, 58).

Microorganisms and soil aggregates

The abundance of microorganisms varies with the size of soil aggregates, and is directly related to the specific environmental conditions and their microhabitats, in order to deliver valuable ecosystem services (see Chapter IV).

Microorganisms stick small soil particles together with polysaccharides (bacteria) or entangle them with hyphal filaments (fungi). Earthworms and aggregates

In most soils, earthworms (see page 58) play a key role in the formation of aggregates. These biogenic aggregates (earthworm-accumulated casts) may represent more than 50% of the soil volume, and earthworms are considered as fundamental agents of aggregation in soil. Different organisms living within the soil are influenced by soil aggregates, and vice versa. This close interaction between soil biodiversity and soil aggregates is dynamic and can change over a short period of time. Therefore, soil management (e.g. conventional field tillage) can greatly affect the soil aggregates and organisms, meaning that better soil management is required to sustain the organisms and their microhabitats, in order to deliver valuable ecosystem services (see Chapter IV).

Functions at aggregate scale

In addition to microbial diversity and distribution, variation in soil aggregates also affects the functions carried out by microorganisms. For example, the composition of free-living bacteria that fix atmospheric nitrogen into soils (so-called diazotrophs – see page 99), differs with the size of soil aggregates. Macroaggregates have a greater diversity and activity of diazotrophs, yet microaggregates can carry between 30% and 90% of the diazotrophic population. These different diazotroph communities exploit specific anaerobic niches within the different sizes of aggregates, creating the conditions required for the fixation of nitrogen.

Similarly, denitrifiers, which reduce nitrate by releasing it back into the atmosphere (in a process called denitrification), are not present and active in all sizes of soil aggregates, but occur mainly in microaggregates, where nearly 90% of the potential denitrification activity can occur. Furthermore, microbial diversity and functions can differ in relation to the location of microorganisms in the exterior or interior parts of aggregates. The process of nitrification (i.e. conversion of ammonium into nitrate) can be 50% higher on the exterior of the aggregates (first mm) than in the interior, due to the aerobic conditions which are required for this process. Conversely, the interior of soil aggregates can provide anaerobic conditions favourable for processes that require low levels of oxygen, such as nitrogen fixation, denitrification or methane production. The interior of aggregates can also protect bacteria against pollutants, such as heavy metals, whereas the bacteria on the exterior of aggregates generally show more resistance to pollutants.

Macroaggregates (>250 µm): roots and fungi growing at the surface or inside macroaggregates and their main binding agent: Ecosystem engineers, mainly earthworms and termites, aggregate the soil into large biogenic structures (casts and mounds).

Microaggregates (50–250 µm): are located inside macroaggregates and are the habitat of microfauna (e.g. nematodes and protozoa) that feed on microorganisms.

Clay- and silt-sized aggregates (<50 µm): contain high bacterial biomass, while fungi are limited to growing mainly at their surface. Microorganisms stick small soil particles together with polysaccharides (bacteria) or entangle them with hyphal filaments (fungi).

Earthworms and aggregates

Macroaggregates (>250 µm): roots and fungi growing at the surface or inside macroaggregates and their main binding agent: Ecosystem engineers, mainly earthworms and termites, aggregate the soil into large biogenic structures (casts and mounds).

Microaggregates (50–250 µm): are located inside macroaggregates and are the habitat of microfauna (e.g. nematodes and protozoa) that feed on microorganisms.
Distribution patterns – Soil biodiversity at the extremes

The Critical Zone

The concept of ‘critical zone’ is becoming central to ecological thinking, and is defined as the area above and below the soil surface that is critical to life on Earth. Generally, the belowground portion of the critical zone is defined by plant roots; therefore, the critical zone in forests is thought of as being several metres deep. However, in drylands, the situation may be very different. Most precipitation events are less than 5 mm, meaning that most microbial activity, nutrient cycling, and other processes crucial to ecosystem functioning, also occur at soil surfaces which are dominated by biocrusts. Therefore, in dryland regions, the biocrusts may well define the critical zone [94].

Biodiversity at the soil surface

Soil organisms are distributed not only horizontally across different ecosystems on Earth, but also vertically, from the surface to the deeper soil layers, passing through the aggregates (see page 72). The most evident and visible example of soil biodiversity on the superficial layer of soil are biological crusts. Biological soil crusts, or biocrusts, are found in most ecosystems where plant cover is limited. This includes hot, cool, and polar deserts, as well as steppe and sub-humid regions (see pages 86-87) [95].

Biocrusts are communities of microorganisms (bacteria, cyanobacteria, fungi and green algae – see pages 33-35, 38-41) together with macroscopic lichens (see page 42) and mosses that cover most of the soil surfaces between the plants. The biodiversity found in biocrusts often far exceeds that of the plant community in which they are embedded, as they contain hundreds to thousands of species, whereas most plant communities contain fewer than 100 species.

Biocrusts play many essential roles in the ecosystems in which they occur and, as the biomass of the biocrust organisms increases, their influence on ecosystem processes increases as well. All biocrust organisms are integral to the formation and stabilisation of soils, and are believed to have been playing this role since they first appeared on land about one thousand million years ago. They accelerate soil weathering (see page 20), altering soil pH by secreting acids and ions (Ca^2+ and OH^-). They also delay evaporation of soil moisture, thereby increasing rock and soil weathering by increasing the length of time these materials are wet.

Biocrusts are vital in soil stabilisation, especially in regions with low cover of other soil stabilisers, such as plants. Stabilisation is mostly a result of cyanobacterial and fungal filaments moving through the soil, as well as across its surface, leaving behind a trail of the sticky, mucilaginous sheath material that binds soil particles together. Lichens and mosses also protect the soil surface from exposure to wind or water, reducing the detachment of soil particles. Combined, biocrust organisms greatly reduce or even eliminate soil erosion in dryland regions. Biocrusts play other ecosystem roles as well. Cyanobacteria, green algae, lichens and mosses are all photosynthetic and, thus, contribute crucial carbon (C) to dryland soils. Carbon content (see page 104) is often very low in these soils and can limit microbial activity, thus having an important role in the contribution of C by biocrusts can be substantial, often equivalent to the soil being covered by a vascular plant leaf. Nitrogen (see page 105) is also contributed to soils by free-living and lichenised cyanobacteria, and it is often the dominant source of this crucial nutrient in dryland soils. Nitrogen deposition (see page 106) has provided evidence that the biocrust surface can reach deep into the bedrock.

Biodiversity in the subsurface

Most studies of the interactions between life aboveground and life belowground have concentrated primarily on connections between vegetation, soil and the uppermost layer of weathered rocks, rarely investigating more than a metre below the surface. Although the processes taking place in deeper zones may profoundly influence life at the surface, important questions remain about the links between the deep biosphere and surface environments, including the soil, how does land use or disturbance at the surface impact the subsurface? How are signals, if any, transported from the surface to the deep biosphere? How long does this take and how long does it last? [96]

Deep life, defined here as beginning below the rooting zone, often extends far below the pedosphere, down through the subsurface to coves and groundwater contained within shallow and deep aquifers. Of course, prokaryotic (see page 30) population densities decrease with depth from the soil surface to the subsurface (see above), but levels of 10^3 to 10^8 cells per gramme can still be found in unsaturated bedrock or 10^5 to 10^6 cells per ml groundwater in saturated bedrock. The lower boundary of the deep biosphere, marking the limits of the influence of life on the rock environment, is still not defined. Molecular methods (see pages 64-65) have provided evidence that the biosphere can reach deep into the bedrock.

Assuming an upper temperature limit of 130 °C for bacteria, life could exist down to a depth of 5.2 km in continental crusts. Although the constraints of temperature, energy, oxygen and space should preclude life of multicellular organisms at these depths, life has been detected in 3.6 km-deep fractures in the deep gold mines of South Africa. Holophotobius mephisto was the name given to this new species, with mephisto, which means ‘he who loves not the light’, alluding to the Devil and referring to the German demiurge Mephistophiles.

For this reason it is also commonly known as Devil’s worm. According to radiocarbon dating, these worms live in groundwater that is 1,000–1,200 years old. Holophotobius mephisto is resistant to high temperatures and feeds on subterranian bacteria. [97]

Imacts on the soil subsurface

Although less is known about the subsurface, humans are beginning to exert an increasing impact on this zone, both directly through activities like heat and energy exchange, and use for waste disposal or gas storage, but also indirectly through the downward communication of changes in the atmosphere and aboveground biodiversity. Since land use is a main driver of aboveground biodiversity change, land use intensification has frequently been shown to negatively affect biodiversity. But how deep can the ‘fingerprints’ of vegetation or land use be traced? Does the subsurface biodiversity really care about land use intensification, about a decline in aboveground biodiversity?

Plant biodiversity can significantly influence the density and diversity of soil organisms, which in turn are likely to govern essential ecosystem processes. Plant biodiversity effects can be even more important for the structure and functioning of soil food webs (see page 96) than changes in atmospheric CO2 concentrations or nitrogen depositions. Therefore, a loss of biodiversity could have at least as great an impact as other anthropogenic drivers of environmental change. Some investigations of the Earth’s critical zone have been established in the past decade to improve our fundamental understanding of the biogeochemical processes in the subsurface and how they are linked to surface properties. Linear core drillings and groundwater wells grant access to the hidden subsurface compartment of the ‘Critical Zone’ and provide an understanding of how the provision of ecosystem services are ultimately linked with biodiversity and processes within the subsurface.
Distribution patterns – Soil biodiversity over time

**Hours and days**

Soil biodiversity is not static. Populations of soil organisms change constantly over time, with changes in the structure and diversity of soil communities occurring over timescales of days to seasons, and even decades to millennia. A common feature of microbial populations is that their abundance can change very rapidly, even over hours or days. Such rapid changes are caused by several factors, including predator-prey relationships and pulses in resource supply. After periods of drought, for example, sudden increases in soil water availability following rainfall events cause spectacular boosts in microbial growth and associated pulses of nitrogen mineralisation and carbon dioxide release from soil. The release of carbon-rich exudates into soil from roots also causes rapid increases in microbial growth, and the time taken from photosynthesis (see box on page 35) to the transfer of photosynthetically fixed carbon to roots, mycorrhizal fungi (see page 40) and free-living soil microorganisms can take just hours in grassland or days in forests. Also, much of this photosynthetically fixed carbon is lost from soil by heterotrophic respiration within a matter of hours or days, which points to the great importance of root exudation for short-term microbial dynamics in soil. [98]

Pulses in root exudation can also be triggered by defoliation events, or when roots are attacked by root herbivores, which stimulates microbial activity and nitrogen mineralisation in the soil surrounding the root, increasing plant nutrient uptake and growth. The following zones have abundant living communities that may vary over short periods of time (detrivusphere (interface between soil and litter), rhizosphere (interface between soil and plant roots), mycohyphosphere (interface between mycorrhizal hyphae and soil), mycosphere (interface between fungal hyphae and soil) and dirlosphere (interface between earthworm burrows and soil). For example, according to a general rule (the Arrhenius equation), microbial processes increase by a factor of two when temperature increases by about 10 °C. Therefore, soil microorganisms in their natural environment will be less active during the night than during the day.

Besides this direct effect of temperature on soil microorganisms, other indirect effects may also influence the daily rhythms of microbial behaviour. For example, plants assimilate carbon during the day and release some carbohydrates into the soil by root exudation at night.

**Prehistoric soil biodiversity**

- Thanks to new DNA-based techniques (see pages 64-65), it is possible to study palaeobiodiversity (i.e. ancient biodiversity).
- Because of its properties, permafrost (see page 16) is able to preserve ancient DNA.
- Permafrost is a soil that remains at or below the freezing point of water (0 °C) for two or more years.
- The theoretical limit of ancient DNA survival under ideal conditions, such as in permafrost, is about 1 million years.
- In 2012, researchers collected permafrost samples dated 16 000-32 000 years old from two localities in Siberia in order to study ancient soil fungal communities. [99]
- About one-third of the fungi found are presumed to be plant associates (pathogens, saprotrophs and symbionts) typical of grass-rich habitats.
- Pathogens likely associated with ancient insects were also found.
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**Seasons and years**

Soil communities also change in abundance and composition throughout seasons and years, caused by seasonal and inter-annual changes in precipitation and temperature, disturbance events linked to land use, and also the seasonality of plant growth. In some situations, seasonal shifts in soil communities are relatively distinct, for example in alpine soils where microbial communities display a complete turnover between winter and summer, with taxonomically and functionally distinct communities occurring at both times.

In other situations, however, communities can be very complex and apparently chaotic over time. In agricultural soils, for example, seasonal and inter-annual patterns in soil animal and microbial communities vary with land use and agronomic practices, including crop type and fertiliser regimes, as well as with soil type. Furthermore, effects of agronomic practices on soil organisms are likely to vary considerably at different times of the year, meaning that careful thought needs to go into how soil biodiversity is evaluated in field experiments to determine the effects of land management practices on the biology and functioning of soil. Moreover, seasonal and inter-annual patterns of soil biodiversity are complicated by the fact that many soil organisms can undergo long periods of inactivity when conditions are unfavourable, which allows them to tolerate periods of harsh soil conditions.

**The case of microorganisms in grasslands**

Temporal variation in the abundance and function of soil microorganisms is especially high in topsoil (see page 10), because the most important drivers (i.e. food resources, temperature and moisture) vary considerably in topsoil throughout the seasons. In an experiment conducted in 2011, researchers tested whether the temporal distribution of a historically natural grassland in Germany changed throughout the growing season. Microbial community spatial structure was found to be positively correlated with the local environment (i.e. physical and chemical soil properties – see Chapter II), in spring and autumn, while the density and diversity of plants had an additional effect in the summer period. Spatial relationships among plant and microbial communities were detected only in the early summer and autumn periods, when aboveground biomass increase was most rapid and its influence on soil microbial communities was greatest due to increased demand by plants for nutrients. The spatial distribution of Gram-positive (Gram+) – see box on page 34) bacteria and fungi (see pages 38-41) changed during the season. For example, the distribution of bacteria shifted from a cosmopolitan to a patchy distribution from May to October. This result may have been due to competition between bacteria and plants for nutrients. In particular, some of the most abundant Gram+ bacteria may suffer from nutrient limitation late in the season, and their growth could then be restricted to ‘hot spots’ in which nutrients are accessible.

The distribution of fungi was patchy early in the season, but in October it was almost uniform, providing evidence for the development of a wide distribution of fungal hyphae over time. This example clearly shows how soil communities change not only across space, but also across time. The assessment of temporal distribution must go hand in hand with the spatial analysis in order to better understand the dynamics of life in soil.

Frozen soils preserve DNA that can be used to study ancient soil biodiversity from nutrient limitation late in the season, and their growth could then be restricted to ‘hot spots’ in which nutrients are accessible.

As temperature, moisture and plant cover change throughout the seasons, from (a) winter to (b) summer to (c) autumn, the same genes for soil communities (CSS, MIR, TD, MBA).

The case of microorganisms in grasslands

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[Image 558x130 to 810x313]

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**Fungi**

<table>
<thead>
<tr>
<th>Month</th>
<th>PFLA 18:2ω6</th>
<th>PFLA 15:0</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>2.51 - 2.7</td>
<td>3.91 - 4.1</td>
</tr>
<tr>
<td>October</td>
<td>3.11 - 3.3</td>
<td>4.61 - 4.9</td>
</tr>
</tbody>
</table>

**Bacteria**

<table>
<thead>
<tr>
<th>Month</th>
<th>PFLA 18:2ω6</th>
<th>PFLA 15:0</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
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<td>3.11 - 3.3</td>
<td>4.61 - 4.9</td>
</tr>
</tbody>
</table>

[Image 74x1038]
Hundreds and thousands of years

Soil biodiversity also changes over hundreds or thousands of years, through processes of primary succession, which is the gradual and natural development of an ecosystem over a longer period of time. Studies have revealed a number of general patterns that occur in soil communities over these long timescales. Most data come from glacier forelands and lava fields, and sand dune systems, that undergo primary succession. These kinds of landscapes are unique observations of soil formation because they contain soil chronosequences (sets of soils that differ only by age) as they have developed on similar parent materials under the influence of similar abiotic and biotic factors. As succession proceeds from its initial stages toward the ‘maximal biomass’, or climax phase, soil microbial communities become increasingly abundant, active and diverse, and they also become increasingly fungal dominated (over bacteria) in nature. Mycorrhizal communities also change as succession proceeds: during early succession, ruderal plants are generally non-mycorrhizal, whereas in mid-succession, the dominant herbaceous plants tend to have a facultative requirement for arbuscular mycorrhizal fungi. Finally, in climax communities, the trees and shrubs, which dominate the vegetation, often have an obligate need for ectomycorrhizae (see page 40). [101]

Similar changes in microbial community composition appear to occur during secondary succession. This process of succession occurs after land has suffered a major disturbance, such as fires or hurricanes, or following the abandonment of agricultural land. Such events commonly lead, over time, to a shift in the make-up of the microbial community toward fungal dominance over bacteria. These changes can take decades to occur and they are most likely related to a build-up in the amount and complexity of organic matter, and changes in the quality of resource inputs to soil resulting from vegetation change. They may also be related to changes in the physical-chemical nature of soils; for example, a decline in soil pH that commonly occurs during succession.

Soil animal communities also change during succession, but patterns appear to be less clear, at least when considering temporal changes in different trophic groups. For example, during secondary succession in abandoned agricultural land, soil invertebrates of different trophic groups appear to respond differently, and some faunal groups do not recover at all. Also, on glacier forelands, the first colonisers of recently exposed glacial debris can be predators, with herbivores and decomposers coming later.

Similarly, the first colonisers of newly exposed glacial moraine in the Arctic have been shown to be spiders (see page 61), whose densities are related to inputs of potential prey items, predominantly midges. In these harsh environments, large inputs of insects could be an important source of nutrients for the developing ecosystem, even before a cyanobacterial crust (see pages 35, 73) forms. Insects are often the first colonisers of newly exposed soils in extreme environments.

Many factors cause soil communities to change over successional timescales, but of most importance is the build-up in the amount of complexity of soil organic matter, which provides resources for the developing soil food web. This is largely driven by changes in vegetation as succession proceeds, which alter both the amount and quality of organic matter entering the soil, and also soil weathering processes (see page 20), which contribute to the formation of mature soils from early stages. In particular, processes of soil weathering determine the depth of soil, its pH and the availability of key nutrients, such as phosphorus. However, soil organisms themselves can also influence vegetation succession.

Let’s give some numbers

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Active range of individual</th>
<th>Passive dispersal</th>
<th>Dormancy stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basidiospores</td>
<td>100–1000 m (m)</td>
<td>100–1000 m</td>
<td>0.01 m per day</td>
</tr>
<tr>
<td>Saprophytic fungi</td>
<td>0.0005–0.005 m per day</td>
<td>0.01 m</td>
<td>100–1000 m</td>
</tr>
<tr>
<td>AM fungi</td>
<td>0.005 m per day</td>
<td>0.01 m</td>
<td>100–1000 m</td>
</tr>
<tr>
<td>Bacteria</td>
<td>0.00001 m</td>
<td>not determined</td>
<td>inactive cells</td>
</tr>
<tr>
<td>Nematodes</td>
<td>0.00001 m</td>
<td>100–1000 m</td>
<td>100–1000 m</td>
</tr>
<tr>
<td>Protozoa</td>
<td>0.000001 m</td>
<td>100–1000 m</td>
<td>100–1000 m</td>
</tr>
<tr>
<td>Collembolans</td>
<td>0.1–100 m</td>
<td>&gt; 1000 m</td>
<td>eggs</td>
</tr>
<tr>
<td>Mites</td>
<td>0.01–0.1 m per day</td>
<td>&gt; 1000 m</td>
<td>eggs</td>
</tr>
<tr>
<td>Millipedes</td>
<td>1–20 m per day</td>
<td>not determined</td>
<td>adult hibernation and aestivalion</td>
</tr>
<tr>
<td>Isopods</td>
<td>10–1000 m</td>
<td>not determined</td>
<td>no</td>
</tr>
</tbody>
</table>

The spatial scale over which soil organisms actively move is generally over a millimetre centimetre metre. Thoroughly answered dispersal propageule structures of resistance – see box on page 54 of bacteria, fungi, protists and nematodes (see Chapter II) have been found thousands of metres from the source.

In other words, as ecosystems age and become increasingly limited in phosphorus, a negative feedback is set in motion whereby low foliar and litter nutrient status reduces decomposer activity, which further intensifies nutrient limitation, thereby leading to ecosystem decline. The entire soil food web (see page 96) is affected by these dynamics. However, effects on soil organisms other than microorganisms have been poorly studied. In New Zealand, it has been observed that the densities of microbial-feeding nematodes and chytrids (see pages 46–48) decrease when an ecosystem begins to decline, whereas the density of omnivorous nematodes initially increases, before decreasing subsequently. The temporal distribution of microarthropods (e.g. mites, collembolans and myriapods – see pages 49–50, 57) has also been studied, showing contrasting patterns. For instance, in a boreal forest in north-eastern Canada, mites showed a significant decline in density and diversity during the decline phase, while no changes were found among collembolans. In conclusion, the very long-term dynamics of the whole soil biodiversity would need further investigation in order to better understand the role of all soil organisms in ecosystem development.

Over timescales of millennia, ecosystems that have not been subject to catastrophic disturbance enter a ‘decline phase’ characterised by a reduction in tree biomass. This decline has been linked to long-term reductions in the availability of soil phosphorus, caused by thousands or millions of years of soil weathering, and the leaching and exclusion of phosphorus into non-biologically available forms. As a result, soil organic matter also becomes increasingly limited in phosphorus relative to other nutrients, such as nitrogen which is made available by biological nitrogen fixation (see page 105). A consequence of this is reduced substrate quality for decomposers, which contributes to reductions in the biomass of decomposer microbes and shifts in the composition of microbial communities toward increasing fungal dominance, which together act to curtail rates of litter decomposition and mineralisation of nutrients.

Millennia

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Soil biodiversity and ecoregions – Map of distribution across ecoregions

Temperate and Boreal Coniferous Forest

Temperate and boreal coniferous forest soils have fungal-dominated microbial communities, rich in decomposer and ectomycorrhizal fungi. Microarthropods and enchytraeid worms dominate the soil fauna, and ants are also abundant.

Podzols are distinctive soils characterised by the leaching of organic material, iron and aluminium from the A and E horizons, leaving behind a bleached layer. Leached material is redeposited as an organocarbon-rich cemented layer in the B horizon.

Temperate Grassland

This ecoregion supports a high level of microbial and faunal diversity. Soils are characterised by a high abundance and diversity of arbuscular mycorrhizal fungi, earthworms, microarthropods and nematodes.

Chernozems are well-structured soils with a dark, organic-rich topsoil and secondary calcium carbonate in the subsoil. They support abundant natural grasses, typical of prairie or steppe landscapes. They grade to Phaeozems (wetter) or Kastanozems (drier).

Tropical and Subtropical Forest

This ecoregion is characterised by highly diverse soils, with both arbuscular mycorrhizal and ectomycorrhizal fungi, and diverse and abundant communities of fauna, especially of termites, dung beetles, earthworms and nematodes.

Ferralsols are highly weathered coarse-textured soils with low pH, and are red or yellowish in colour due to high concentrations of iron and aluminium oxides. Organic matter levels are low. Horizons are absent due to intensive bioturbation, largely by termites.

Tropical and Subtropical Grassland

Characteristic soil fauna in this ecoregion are termites and dung beetles, along with earthworms, microarthropods and nematodes. These soils contain a rich diversity of microorganisms, including arbuscular mycorrhizal fungi and nitrogen-fixing bacteria.

Lixisols are characteristic of drier conditions and exhibit subsurface accumulation of low activity clays with high base saturation as a result of limited leaching or inputs of airborne dust from adjacent deserts. Low in plant nutrients and prone to erosion.

Antarctica

Soils with low diversity, especially in polar deserts. Besides microorganisms, only a few species, such as nematodes, tardigrades, rotifers and collembolans, are supported. Relatively species-rich communities of microarthropods can occur in some parts, while cyanobacterial communities are widely distributed.

The term ornithogenic means that the soil has been strongly influenced by the activity of birds (e.g. the continuous nesting of penguins) and shows an enrichment of phosphorus, calcium and potassium.
CHAPTER III – GEOGRAPHICAL AND TEMPORAL DISTRIBUTION

Global Soil Biodiversity Atlas

Antarctica

Desert and Dry Shrubland

Mediterranean Forest, Woodland and Shrubland

Montane Grassland and Shrubland

Tundra

Mediterranean soils are usually low in organic matter and, consequently, in soil biodiversity. The profusion of shrubs leads to an abundance of mycorrhizal fungi, and biocrusts are abundant. Soil fauna that withstand high temperatures (e.g. ants) are also widespread.

Calcisols are generally well-drained soils with high pH, fine- to medium-textured with a layer of migrated calcium carbonate in the subsoil which can be soft, powdery, hard or cemented. Their chief use is for animal grazing or grapevine, citrus fruit and olive cultivation.

Leptosols are shallow soils, often with large amounts of gravel, lacking well-defined horizons or strong signs of soil-forming processes. Generally found under natural vegetation, specific characteristics reflect local climatic and topographic conditions.

Tundra soils support a relatively high diversity of fungal (both decomposer and mycorrhizal) and bacterial communities, together with a high diversity of nematodes and microarthropods, although, in terms of biomass, the dominant fauna are enchytraeid worms.

Cryosols are mineral or organic soils characterised by the presence of permafrost and waterlogging during periods of thawing. Cryosols can show distorted horizons, cracks or patterned surface features due to ice formation and melting.

Soils of the ecoregion are very variable, containing a high diversity of bacteria and fungi, and both arbuscular and ericoid mycorrhizal fungi. Nematodes, microarthropods and enchytraeid worms are species rich, but few earthworms are present.

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Soil biodiversity and ecoregions – Tropical and subtropical forest

Wet, moist and woody

Tropical forests can be found in Asia, Australia, Africa, South America, Central America, Mexico and on many of the Pacific, Caribbean and Indian Ocean Islands. Tropical rainforests can be characterised in two words: hot and wet. Mean monthly temperatures exceed 18 °C during all months. Average annual rainfall is not less than 250 mm and can exceed 1 000 mm.

Tropical rainforests exhibit high levels of biodiversity. Between 40 % and 75 % of all biotic species are indigenous to rainforests. Rainforests are home to half of all animal and plant species on the Earth. Two-thirds of all flowering plants can be found in rainforests. A single hectare of rainforest may contain 42 000 different species of insects and up to 1 500 species of higher plants. Rainforests are divided into different layers, with vegetation organised in a vertical pattern from the top of the soil to the canopy. Each layer has a unique biotic community containing animals adapted for life in that particular layer. Four layers are distinguishable:

1. the forest floor, the bottom-most layer, receives only 2 % of sunlight
2. the understory layer lies between the canopy and the forest floor
3. the canopy layer is the primary layer of the forest forming a roof over the two remaining layers
4. the emergent layer is unique to tropical rainforests, while the others are also found in temperate forests. It contains a small number of very large trees, called emergents, which grow above the general canopy, reaching heights of 45–55 m; although, occasionally, a few species will grow to a height of 70–80 m

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Soil biodiversity occupies the litter layer of the forest floor. Like soil itself, soil biodiversity is strongly related to properties of upper layers.

Social insects are the most abundant and diverse components of soil invertebrate communities in tropical forests. Tropical forests of Amazonia, for example, may host more than a hundred species at a single location, with all possible functions observed. The impact of termites is more variable and mainly depends on the relative proportions of different functional groups. While humivores (i.e. feeding on humus) and lignonvores (i.e. feeding on wood) seem to be present everywhere, possibly with greater diversity in tropical America, fungi-growing species are only found in Africa and some parts of Asia. Fungus-growing termites and ants (see pages 54-55) are among the most impressive examples of coevolution in the world. They can build impressive and long-term nests containing millions of workers, and the agricultural symbiosis with fungi has allowed them to occupy previously inaccessible riches that have abundant resources.

The surface of tropical soils are characterised by large amounts of decaying material (i.e. plant and animal waste) that support great numbers of fungal diversity. Through DNA-based analysis (see pages 64-65), about 1 700 different species were identified across three major tropical forests in the western Amazon Basin. Distribution of fungi varies not only at spatial but also at temporal scales because of the disturbances caused by seasonal changes in rainfall. Furthermore, it has been shown that pathogenic fungi (see box on page 39) may have a positive effect on plant biodiversity in tropical forests, by acting as a sort of diversity police. Indeed, these fungi spread quickly between closely packed plants of the same species, preventing them from dominating and enabling a wider range of species to flourish.
Cold, woody and acid

Coniferous forests are made up of cone-bearing trees whose leaves are small, mostly evergreen, needle- or scale-like. They are extensive in the northern hemisphere (they also occur, to a lesser extent, in the southern hemisphere but their distribution is not visible given the scale of the map below). Boreal coniferous forests are found between 50 °N to 70 °N and are conditioned by long dry, cold winters and short, warm summers. Temperate evergreen forests are common in the coastal areas that have mild winters and heavy rainfall, or inland in drier climates or montane areas. Temperate conifer forests sustain the highest levels of biomass of any terrestrial ecosystem and are notable for the massive proportions of trees in temperate rainforests. The dominant tree species of the boreal forests are spruce, pine, fir and larch, while cedar and redwood are characteristic additions in temperate regions.

Soils in coniferous forests are often podzolic (see box on page 21) due to the acidic litter, and characterised by the leaching of nutrients downwards into lower soil horizons. The litter layer is composed of acidic and dry needles and fallen twigs, which decompose very slowly. Forest soils take around 1 000 years to form a 25 mm soil layer. The acidic forest soils also shape the habitats of soil organisms, and the largest organism group (by biomass) in boreal forests is fungus. There can be several thousands of metres of hyphae in one gramme of soil, and fungal hyphae can extend over large distances. Fungi are important in forests as they produce extracellular enzymes that can decompose woody material and degrade both lignin and cellulose. The diversity of fungi and their different enzyme production enables the turnover of carbon and other nutrients in forests soils.

Soil biodiversity

Coniferous forest soils contain a wide range of animals ranging in size from nematodes (see pages 46-47) to enchytraeids and ants (see pages 48, 54). The largest groups are enchytraeids and earthworms, followed by mites, spiders, beetles, nematodes, collembolans, protozoans and dipteran larvae (see Chapter III). Nest-building ants are common and can form large colonies, using the pine and spruce needles for nest building. In the boreal forests of Europe, the enchytraeid species Cognettia sphagnetorum can make up 80–90 % of the enchytraeid numbers and biomass, and can be the dominant soil animal species in terms of overall biomass. Because of the acidic conditions in the uppermost soil, acid-sensitive soil animals, such as burrowing earthworms, are normally scarce or absent. The acid tolerant earthworm Dendrobaena octaedra may contribute significantly to the soil animal biomass, but occur usually in productive forests and at more southern latitudes. [103]

Food webs in coniferous forests are dominated by fungi, and soil fauna has a much smaller biomass in food webs. However, when considering the different parts of the food webs in terms of functions such as decomposition, the soil fauna has a larger impact on carbon and nitrogen cycling than their biomass indicates. The number of organisms and their part in the food web can thus influence the decomposition rate of organic matter. Furthermore, natural or human-caused changes in the forest ecosystem can influence ecosystem functions.

The most abundant mycorrhizae in boreal forests are the symbioses between trees, such as spruce and pine, and ectomycorrhizal fungi (see page 40). Coniferous forest trees are highly dependent on their fungal partners, and symbioses contribute greatly to tree growth. Ectomycorrhizal fungi also protect trees from parasites, predators, nematodes and other soil pathogens. Ectomycorrhizal fungi are important for the storage of carbon in soils, and it has been estimated that 10–50 % of all the carbon assimilated by the trees is translocated into fungal hyphae. More than half of the carbon stored in the soil originates from roots and mycorrhizae and, therefore, on a global scale the boreal forest soils are large carbon sinks, driven by ectomycorrhizal fungi.
Soil biodiversity and ecoregions – Temperate broadleaf and mixed forest

Moderate, woody and rich in litter

Temperate forests occur in areas with distinct warm and cool seasons, which give them a moderate annual average temperature (3 to 16 °C). About 570 million hectares are covered by temperate forests, making it one of the major ecoregions on Earth. This biome plays a crucial role in the global carbon budget. In this ecosystem, carbon (C) enters the soil in the form of plant litter through the belowground allocation of C that has been fixed by plant photosynthesis (see box on page 35), and as dead fungal and animal material. As a consequence of the input of new litter (leaves, dead wood) and its transformation, it is possible to recognise three distinct layers in the soil profile:
• the litter (L horizon – see page 10), composed of organic matter derived, almost exclusively, from dead plant biomass
• the organic (or humic) H horizon: representing a mixture of processed plant-derived organic matter and soil components
• the mineral soil horizon: originating both from the decomposition of organic matter and exudation from the abundant tree roots.

Compared to other ecosystems, forest specificity lies in the presence of dead wood material. Dead wood represents between 10 and 20% of plant biomass in these forests. Moreover, it has been estimated that dead wood material (e.g. fine or coarse woody debris) comprises about 18% of the carbon stock in temperate forests. The great presence of woody material influences the communities of soil organisms.

In temperate forests, many beetles, such as this woodboring beetle (Chrysobothris sp.), have a diet that consists primarily of wood (KS).

Soil biodiversity

Soil biodiversity in temperate forests shows a high abundance of decomposers. The diverse assemblage of arthropods associated with dead wood are known to accelerate decomposition. Various processes could take place during the whole process (e.g. consuming and excavating wood, hastening wood fragmentation through mechanical weakening, and facilitating fungal colonisation through tunnelling). The relative importance of each process varies greatly depending on wood traits, faunal composition and abiotic conditions (e.g. temperature, humidity, resource quality, etc.). By contrast, termites (see page 55) are concentrated in warmer regions, and beetles (see page 59) associated with dead and dying wood are distributed much more widely. During the decomposition process, changes in wood characteristics impact the total abundance of millipedes and isopods (see pages 56–57), with their number increasing as wood density decreases. [104]

In temperate forests, the soil community also includes microorganisms. Fungi, particularly the basidiomycetes (see pages 38–39), are the main microorganisms responsible for wood decomposition because of their ability to degrade recalcitrant ligno-cellulose complexes. Fungi that help wood decay can be broadly categorised into primary, secondary and end-stage colonisers:
• primary colonisers are present as spores in the standing trees. They proliferate through the uncolonised wood, utilising easily accessible nutrient sources and then more recalcitrant compounds
• secondary colonisers are present as spores, but also arrive as mycelium that has grown out of colonised resources looking for new substrates
• end-stage fungi proliferate as they can tolerate certain environmental stresses; they are not able to compete for substrates used by primary and secondary colonisers.

Fungi are the main wood decomposers in temperate forests. (G)

Global distribution of temperate forests. The map was created by including only ecoregions from the World Wildlife Fund (WWF) Global Ecoregions database: temperate broadleaf and mixed forests (derived from Olson et al., BioScience, 2001). (LJ, JRC) [12]
Soil biodiversity and ecoregions – Temperate grassland

Seasonal and grassy

Temperate grasslands are located north of the Tropic of Cancer and south of the Tropic of Capricorn. The main temperate grasslands include the pampas of South America, the steppes of Eurasia and the plains of North America. Due to aridity, they are generally desert in Africa (see page 87). Grasslands cover extensive areas, comprising approximately 40% of the Earth’s terrestrial surface, thus making them one of the most successful vegetation types on the planet.

There are different grassland types usually split into three broad groups: temperate, tropical (also known as savannah – see page 82) and montane (see page 84) grasslands. Perennial grasses are dominant; with their growth buds at or just below the surface, they are well-adapted to drought, fire and cold. The tiller, or narrow upright stem, reduces heat gain in the hot summers; the intricate root systems trap moisture. Temperate grasslands have warm summers and severe winters. Snow often serves as a reservoir of moisture for the beginning of the growing season. Seasonal drought and occasional fires help maintain these grasslands, which have played an important part in human history.

As well as being used for grazing livestock since animals were first domesticated over 7000 years ago, many of our commercial grains, such as wheat and barley, were almost certainly first domesticated from wild grasslands. Further distinctions can be made to include the high-altitude grasslands (i.e. montane grasslands), and even between natural (or native) grasslands and secondary grasslands, that derive from a recolonisation of grasslands), and even between natural (or native) grasslands and secondary grasslands, that derive from a recolonisation of grasslands after human-induced modification. Grasslands and secondary grasslands, that derive from a recolonisation of grasslands, are generally have relatively deep soils that are rich in nutrients due to large amounts of tissue dying off each year, which builds up in the organic matter portion of the soil. Relatively few ‘natural’ grasslands remain as most have been turned into farms or are used for grazing livestock.

Soil biodiversity

The amount of life found below the surface of grasslands dramatically exceeds that found aboveground, in both number and mass, as well as species richness, and is particularly rich even when compared to other belowground environments. [105] Grasslands are unique compared to virtually all other biomes in that they have a relatively simple structure but very high levels of species richness. It has been estimated that there are approximately 100 tonnes per hectare of living biomass below the surface of temperate grasslands, consisting of bacteria, fungi, earthworms, microarthropods and insect larvae. The majority of grasslands are managed to some extent, whether through grazing, mowing or by planting specific species of grass for a particular purpose, such as for forage or improved pasture.

A common feature of less managed, species-rich grasslands is that they have fungal-based food webs, contrary to more intensively managed grasslands that have bacterial-based food webs. Arbuscular mycorrhizal fungi (AMF – see page 40) are a common component of grassland ecosystems, where they can influence plant productivity, plant diversity, and plant defense to herbivory and soil stability. Researchers report that the number of AMF species in temperate grasslands ranges from 10 to 24, thus representing one of the most diverse ecosystems in terms of this group of soil organisms. It is well known that plant diversity increases significantly with increasing AMF species richness. Furthermore, it has been demonstrated that grazing (see pages 124-125) decreases AMF spore abundance but increases AMF species richness.

The presence of grazers may also influence other soil communities: 144 species of arthropods from cow dung were recorded in a temperate grassland. Earthworms (see page 58) are also very abundant in grasslands. Soil fauna data show that they form the greatest biomass (70-80% of the total) of temperate grassland animals. Such an abundance has clear effects; it was found that 30% of grass seedlings germinate from earthworm casts. This indicates that earthworm casts increase the spatial heterogeneity of grassland plant communities. Grasslands are also often home to moles (see pages 62-63). The number of mole hills is not a measure of the number of moles in a given area. In order to estimate the number of moles, the total surface of the dug area must be taken into account. It has been calculated that the territory of a mole is about 3000 square metres for males (up to 7000 square metres in the breeding season) and about 2000 square metres for females.
Soil biodiversity and ecoregions – Tropical and subtropical grassland

Grassy, dry and burnt

Tropical and subtropical grasslands, also known as savannahs, are distinguished by a warm and dry climate compared to temperate grasslands, as well as the occurrence of seasonal droughts. Savannahs are amongst the most complex and variable biomes on Earth and are difficult to define precisely. Nevertheless, a number of characteristics define savannahs throughout the world: 1) a continuous or near-complete cover of a mostly grassy herbaceous stratum, with tree and shrub strata varying from a total canopy cover (savannah woodland) to open grassland; 2) marked seasonal contrasts with periodic or annual fires typical of dry seasons, lasting anything from two to nine months; 3) underlain by mostly nutrient-poor soils, prone to desiccation in the dry season and inundated in the rainy season.

The vegetation consists of mixtures of trees, shrubs, grasses and ground plants, but the proportion of these components can change rapidly from place to place and over time. Animal life above- and belowground may show equal diversity. Savannahs are globally distributed almost entirely within the Tropical Belt. There are significant continental differences, with the Australian savannahs generally having the drier and the South American the wettest climatic environments. The African savannah is the most well-known, characterised by grassy landscapes and mixed communities of trees, shrubs and grasses with large grazing mammals.

Soil biodiversity of African savannahs

About 40 % of the arable lands south of the Sahara desert are savannahs, characterised by two very contrasting seasons: dry and wet, with a variable average annual rainfall. The African savannah is a thornbush savannah, which has many different kinds of plants, such as Acacia trees, Umbrella Thorn Acacias, Whistling Thorns, Bermuda grass, Baobab trees and Elephant grass. The soils (Cambisols, Ferralsols and Luvisols – see pages 26–27) are usually well drained and contain little organic matter. In West Africa, soil is managed by alternating crops, such as millet, sorghum and groundnuts, and fallow. This practice affects the activity and diversity of soil organisms. [106]

A large variation in the total density of macrofauna (ants, termites and earthworms) is possible, the most abundant groups being ants and termites (see pages 54–55). The density of termites increases with the age of the fallow. The abundance of functional groups within the various taxonomic groups is even more variable. For example, endogeic earthworms (see page 58) appear to be most abundant in 10-year-old fallow, although they tend to be less abundant in fallows older than 30 years. However, epigeic earthworms that live in and feed mainly on litter are more abundant in older than in the younger fallows. Fungus-growing termites, such as the species Microtermes hollandi, are most abundant in short-term fallows, whereas humivorous (feeding on humus) species, such as Ancistrotermes crucifer, are found more frequently in long-term fallows. Regarding microfauna, various studies carried out in Senegal have shown that there is no significant difference between the total number of nematodes (see pages 46–47) in cultivated and fallow land. However, the diversity of species increases with the age of the fallow.

About 20 % of Brazil’s land surface. (PMO, CJM, ON)

Scutellonema

Diversity of fires and termites

- One of the factors characteristic of all savannah environments is wildfires in the dry season.
- Fire is an important disturbance in African savannahs.
- It has been hypothesised (pyrodiversity-biodiversity hypothesis) that high levels of pyrodiversity (season and frequency of fires) are necessary to maintain high levels of biodiversity.
- Research has shown very little species density and occurrence of termites across the different fire regimes.
- Therefore, for termite control there is only limited support for the pyrodiversity-biodiversity hypothesis.

For example, plant pathogenic species, such as Scutellonema cavendishii, dominant in cultivated fields, persist in long-term fallows, but are significantly reduced. The total microbial biomass (bacteria and fungi – see pages 33–35, 38–41) is low and not significantly different in cultivated fields and in fallows. However, the characterisation of the functional diversity showed that the microbial functional profiles were more diversified in fallows than in cultivated fields. In fallows, mycorrhizal fungi (see page 40) of the genus Glomus are the most abundant.
Mediterranean environments include forest, shrubland, grassland and badland (including and and semi-arid) habitats, with some exceptions. In fact, the combination of many adjacent habitats gives Mediterranean landscapes a distinctive transitional as well as patchy structure, which results in a characteristic diversity of plant and animal populations. Five regions in the world are considered Mediterranean-type ecosystems: the Mediterranean Basin, central Chile, southern and central California, the Cape Province of South Africa and two parts of southern Australia in the centre and the west. Similar climate patterns, with dry and hot summers and rainy winters and the common proximity of marine and arid biomes, provoke clear cases of species convergence. However, a different biogeography and history of disturbances (principally fire and land exploitation) generate differences at the community level among these areas.

Soil types vary among regions due principally to differences in the underlying parent material, in the Mediterranean Basin this is basically limestone, which is reduced to strips in South Africa and Australia, and does not exist in Chile and California. In any case, due to the strong seasonal contrast, Mediterranean soils share a modest profile development, which tends to decrease with increasing elevation. All regions present a mosaic of old and newer soils, showing a general scarcity of nutrients and low water content. This mosaic is accentuated due to the formation of ‘fertility islands’, created by trees, shrubs or even faunal structures, such as ant mounds, in a matrix of almost bare soil. In these islands, plant structure and resources and the biology of the associated soil fauna create very different soil microhabitat conditions between the islands and the matrix and among different types of islands. In general, litter and soil compartments are much more differentiated than in other ecosystems, and the tenuous intermediate phase between them gets thinner from mesic to arid environments.

Although there is a common resemblance among aboveground plant parts such as evergreen plants, root systems are more variable depending on soil and rock conditions. Some widespread adaptations of roots to desiccation and the lack of nutrients in Mediterranean-type ecosystems are: the persistence of the primary root, deep penetrating roots in woody plants while the roots of some succulent plants extend horizontally over wide areas, seasonal variations in the vertical root structure by root contraction or fine-root turnover, and associations with actinobacteria (that form root nodules – see box on page 59) and mycorrhizal fungi (see page 40). In fact, mycorrhizal plants have been mentioned in numerous studies as being crucial components of the root system in Mediterranean ecosystems, especially in semi-arid and arid environments. Another important structural component of some Mediterranean soils is the existence of biological soil crusts (see page 73), which seem to play a fundamental role in soil resistance to erosion.

In relation to microarthropods, the five Mediterranean regions share a generally greater abundance of mites than collembolans (see pages 49-50), due to their high dependence on soil moisture. Among mites, Ornibatida are mainly detritivores, and Protostigmata are predators in Mediterranean environments and, therefore, their diversity has important impacts on ecosystem functioning.

Among soil macroinvertebrates, there are different ecosystem engineers (participating in decomposition processes and soil aeration, drainage and bioturbation) for different habitats. Earthworms (see page 58) are the soil burrowers of more humid forests, while beetle larvae dig through bad land soils. Other detritivores of Mediterranean-type ecosystems are isopods and millipedes (see pages 56-57). Ants (see page 54) and dung beetles (see page 59) also participate in the cycling of organic matter by distributing it among patches and from the surface to deeper soil layers, thus playing the role of termites in tropical ecosystems. An interesting adaptation to belowground patchiness is that of the insects known as ground pears (genus Margarodes), which can develop as root-feeding pests in almost all Mediterranean regions. Active burrowing by herbivores is represented by Curculionidae and scarabaeid larvae (see page 60). Ground beetles, which perform an important role as soil predators, are also typical of the Mediterranean region. They are accompanied by beetles, centipedes, arachnids (see page 61) and pseudoscorpions (see page 53). This last group of arthropods has been subjected to a biogeographical comparison due to their representativeness, wide distribution and available information. Results show that affinities are greater among Mediterranean areas in the same hemisphere than between North and South. In this sense, similarities are greater in America than between the Mediterranean Basin and South Africa.

Different Mediterranean vertebrates, principally mammals but also some sea birds, affect soil fauna by fertilising, digging, burrowing and compacting the soil, but only a few species can be considered truly subterranean.Among them, the Middle East blind mole-rat, a voracious herbivore, and worm lizards (see page 63), small predators, are exclusively from the Mediterranean Basin.

**Soil biodiversity**

Microbial communities are principally associated with the rhizosphere (see page 43) and are subjected to seasonal variations in density. Microbiological activity, including carbon emissions (see page 102), is overall low. Both bacterial and fungal communities (see pages 33-35, 38-41) show great differences among litter and soil levels, while seasonal variations in community structure are higher in the litter layer than in the mineral soil. The bacterial-to-fungal proportion decreases with increasing aridity, indicating the important role of fungi in the decomposition process of Mediterranean-type ecosystems. Belowground fungal communities are very diverse, characterised by a few common types and a large number of rare types, and are very different from aboveground communities. (107)

Protozoa (see pages 36-37), nematodes (see pages 46-47) and other microfauna are also common in Mediterranean soils. However, microfauna is commonly associated with the soil water fraction. Therefore, Mediterranean ecosystems are not the most suitable environments for this category of organisms. Nevertheless, most microfauna have the ability to develop structures that are resistant to drought (e.g. cysts of nematodes). In this context, general statements are not possible because of the considerable lack of studies on this faunal category in Mediterranean-type ecosystems. An exception could be made for nematodes in the Mediterranean Basin, where they are considered as valuable bioindicators (see page 101) of soil quality.

Meso- and macrofauna are well studied soil animal groups, and data are available, also at a global scale, on their abundance, diversity. Again seasonality, patch distribution and a deep vertical stratification are common features, although vertical migration is a strategy against drought only shared by this group. Insect (e.g. Coleoptera – see page 59) and centipede (see page 57) larvae have been described as very important interconnectors between litter and soil compartments. Among them, the darkling beetle (Tenebrionidae) larvae show significant seasonal migrations, which can change the soil food web structure.

**Oak woodlands are characteristic of the Mediterranean Basin and California (SMA)**

**A species belonging to the genus Margarodes (Hemiptera), commonly known as ground pears. Ground pears excavate a sandy covering that completely surrounds their body, apart from their piercing-tucking mouthparts. The wavy upper covering of the insect in the structure most likely to be encountered. The sphere is pink to yellowish-brown and resembles a pearl. The exposed mouthparts are used to feed on and attach to plant roots. (MBE)**
Soil biodiversity and ecoregions – Montane grassland and shrubland

High altitude and unique species

Montane grasslands and shrublands located above the tree line are commonly known as alpine tundra, and occur in mountainous regions around the world. This major habitat type includes the Puna and Páramo in South America, subalpine heath in New Guinea and East Africa, and the steps of the Tibetan Plateau. Montane grasslands and shrublands, particularly in subtropical and tropical regions, often evolved as virtual islands, separated from other montane regions by warmer, lower elevation regions, and are frequently home to many distinctive and endemic plants (i.e. characteristic of a specific place) which evolved in response to the cool, wet climate and abundant tropical sunlight.

The páramos of the northern Andes are the most extensive examples of this habitat type. The heathlands and moorlands of East Africa (e.g. Mount Kilimanjaro, Mount Kenya, Rwenzori Mountains), Mount Kinabalu of Borneo and the Central Range of New Guinea are all limited in extent, extremely isolated, and support highly endemic biodiversity. Drier, yet distinctive, subtropical montane grasslands are found in the Ethiopian Highlands, Zambia and southeastern Africa. A unique feature of many alpine grasslands is the presence of distinctive plant species, such as Lobelia spp. (Africa) and Puya spp. (South America). Montane grasslands form where sediments from the weathering of rocks (see page 20) have produced soils that are sufficiently well-developed to support grasses and sedges. Because of the elevation, in some areas, such as the highest zones of the Tibetan Plateau, plants are not able to grow and the soil is covered by a biological soil crust (see page 73). Of course, such peculiarities may have an influence on soil-living organisms.

Soil biodiversity

Montane grasslands are fragile habitats, exposed to several pressures due to their challenging climatic and soil conditions. Excessive ploughing, overgrazing, burning (see Chapter VI) and growing populations are especially evident. In particular, the activity that has the greatest negative impact on montane habitats is overgrazing. This leads to modifications of the vegetation structure and alteration of soil biodiversity associated with those plant species. In extreme cases, very heavy grazing and trampling can lead to exposure of bare soil and erosion (see pages 128-129), with a possible further reduction of soil life. Because of their distribution and relatively limited accessibility, soil biodiversity in alpine grasslands has not been extensively investigated. However, it is possible to find some interesting case studies.

A good example of an endemic species is the Ethiopian African mole-rat (Tachyoryctes macrocephalus), also known as the giant root-rat or Ethiopian African mole-rat, in a soil-living rodent species present only in the grasslands of the Bale Mountains in Ethiopia (AT). Tachyoryctes macrocephalus prefers soil depths below 50 cm, and its burrowing activity aids in the aeration and mixing of soil and enhances infiltration of water, thus curtailing erosion. There are also other burrowing rodents endemic of alpine grasslands, such as the Chinese Zorok (Eospalax fontanierii) in the Tibetan Plateau. Despite all the presented examples, the spatial and temporal distribution of soil biodiversity in montane grasslands requires further evaluation.

Soil biodiversity in montane grasslands has been conducted in the Tibetan Plateau. For instance, about 30 arbiculular mycophagous fungal species (see page 40) were isolated in two different analyses. Soil biocrust from the Tibetan Plateau was also analysed, and an increase of the cyanobacterial (see page 35) biomass was observed with increasing elevation. The soil microfauna of Tibetan grasslands was also studied. A study of nematode communities along a grazing gradient, from low to high intensity, retrieved a total of 37 genera with, interestingly, the highest richness in the areas subjected to high levels of disturbance. In particular, nematode feeding on plants and bacteria (see pages 46-47) were the most well adapted to those conditions [108]. Lastly, a comparison of mite and collembolan communities (see pages 49-50) showed the dominance of mites in the Tibetan meadows.

Global distribution of montane grasslands. The map was created including only recognised ecoregions from the World Wildlife Fund’s WWF Global Ecoregions database: montane grasslands and shrublands (derived from Olson et al., Biocliance, 2001; L.M., J.R.)
Soil biodiversity and ecoregions – Tundra

Cold, flat and treeless

The word ‘tundra’ originates from the Saami word tūndar, meaning treeless plain. The tundra is a vast, flat, treeless landscape found in the high latitudes surrounding the polar regions, primarily in Alaska, Canada, Russia, Greenland and Fennoscandia (Finland, Norway, Sweden and parts of Russia). The region’s long, dry winters feature months of total darkness and extremely low temperatures. Most precipitation falls in the form of snow during the winter, and soils tend to be acidic and saturated with water when not frozen. Soils are affected by freezing and often have a permanently frozen subsoil, known as permafrost (see page 16).

During the summer, the permafrost thaws, but because of the permanently frozen subsoil, the water cannot drain away and soils become waterlogged, forming a distinctive wetland habitat. The tundra can also be found at high altitudes (see page 84) where the soil temperature is below freezing for large parts of the year (and usually at night in the summer).

Vegetation cover is very similar to high-latitude tundra, but soils tend to be well drained. The landscape is generally devoid of trees, because plant growth and survival are limited by short, cold growing seasons, and the lack of suitable substrates and nutrients. Therefore, the vegetation is composed of dwarf shrubs, sedges, grasses and mosses. Due to the harsh climate, tundra has seen little human activity. Nevertheless, some signs of human presence can be found, reindeer herding is one of the most extensive forms of human interactions with tundra ecosystem. Herding and grazing have significant impacts on tundra vegetation and, consequently, on soil-living organisms. Furthermore, these regions are continuously being developed for their natural resources, such as oil and uranium. Therefore, in the past years new settlements have been developing in many parts of Alaska and Russia. Tourism in these remote areas is also expanding. If not carefully managed, this development can lead to the alteration of the environment. Despite all the adverse environmental and human factors, varied communities of organisms are active in tundra soils.

Soil biodiversity

Tundran soil biodiversity is strongly influenced by physical characteristics, such as the extreme seasonality (short cool summers and long cold winters) and the presence of permafrost. Nevertheless, all main groups of soil organisms can be found in this environment. The Arctic Biodiversity Assessment 2013 evaluated the current status of above- and belowground biodiversity in the Arctic region, thus also taking into account soil-dwelling organisms. Densities of bacteria in tundran soils are lower than in temperate soils, but can still reach substantial numbers. Interestingly, recent DNA-based analyses (see pages 64-65) revealed that, during the transition from a frozen to a thawed (winter-summer) state of soil permafrost, there are rapid shifts in microbial abundances, with an increase in actinobacterial (see page 35) populations. Unfortunately, data on archaea and protists remain limited. [106]

Much more is known about the presence and abundance of fungal species in tundran soils. Fungi have evolved physiological mechanisms to maintain activity and growth at low temperatures, even when soils are frozen. It has been estimated that more than 11,000 species of fungi live in the Arctic region. Among them, about 2,600 have been described, belonging to all the main fungal phyla (Ascomycota, Basidiomycota, Glomeromycota, etc. – see pages 38-41). Another group of well-established organisms in the tundra are lichens (see page 42). More than 1,700 species of lichens have been found in this environment. Their distribution is also well known, for example, 231 different species have been reported in Greenland. In addition, more than 73 genera of nematodes, 200 species of tardigrades, 85 species of enchytraeids, 400 species of collembolans, 600 species of mites and two species of earthworms have been described in tundra’s soils. In conclusion, despite limited data on soil, there is significant belowground life in the tundra biome.
Soil biodiversity and ecoregions – Antarctica

Cold, dry and extreme

Terrestrial Antarctica is one of the most extreme environments found on Earth. It is a cold and (mostly) dry continent that is effectively isolated from the rest of the world by global weather patterns and the Southern Ocean. Even within Antarctica, patches of habitable soils are highly isolated ranging from small patches (in order of metres) to relatively large extents (several kilometres). Yet, Antarctic soils are anything but uninhabited. It is now known that Antarctica is home to substantial microbial diversity and supports a broad range of common soil fauna, including nematodes, tardigrades, rotifers, mites and collembolans. More than 520 terrestrial invertebrates of which about 170 are endemic, inhabit Antarctic terrestrial ecosystems. Many of the native organisms are well adapted physiologically to survive and perform critical ecosystem functions, such as biogeochemical cycling under harsh conditions.

While Antarctic soil systems are in many ways unique, there is much to learn from the diversity and functioning of this extreme environment. They provide, for example, a resource for scientific research into the role of species in ecosystem function, biogeographical patterns, climate change impacts and evolution of life on Earth and, potentially, on other planets. However, solid knowledge of the organisms and communities of terrestrial Antarctica is still lacking, and there is a great need to acquire information on the current diversity and distribution of species within Antarctica and the response and vulnerability of these species to global changes, particularly climate change and human impacts. Here a brief overview is given of the biodiversity of Antarctic terrestrial soil systems and the adaptations that soil fauna have gone through to proliferate in this harsh environment.

Soil biodiversity

Antarctica can broadly be divided into three climatic zones: sub-Antarctic, maritime and continental Antarctica. This page focuses on the maritime and continental regions as these represent the most extreme conditions. Colonization of terrestrial habitats in Antarctica is limited by the Southern Ocean and predominant weather patterns; colonisation events are rare. Therefore, many of the terrestrial inhabitants of Antarctica are endemic species that have survived several glaciation events. Furthermore, the climate, a considerable constraint to the Antarctic fauna and flora, is generally colder than at comparable latitudes in the Northern Hemisphere. Most of continental Antarctica is covered by ice (~0.3% of the land mass is free of snow and ice) and hosts one of the most extreme soil environments with mean annual air temperatures below 0 °C and very limited precipitation compared to the sub-Antarctic islands or maritime Antarctica ([110]).

Consequently, the landscape of continental Antarctica is dominated by polar desert ecosystems that support only a few species of mosses, lichen and algea, although more developed vegetation is found in favourable areas along the coastline. By contrast, sites with well-developed vegetation are more common in maritime Antarctica where two native vascular plants also occur (hairgrass, Deschampsia antarctica; pearlwort, Colobanthus quitensis). Belowground communities are generally simple and highly heterogeneous, with greater biomass and species richness found at sites with well-developed vegetation. Species that have soil fauna, and soil systems impacted by birds and marine mammals supporting the most complex soil food webs. Geothermally active soils represent very distinct microhabitats. Several active volcanoes create geothermally heated soils in an otherwise cold environment and support distinct communities both aboveground (i.e. mosses) and belowground, with several endemic species of bacteria known only from such sites. Importantly, geothermally active soils may have acted as refugia during the last glacial maxima. The diversity of soil invertebrates is relatively low compared with soils in other biomes. Only two higher insects (restricted to maritime Antarctica) and some 225 species of mites, 85 species of collembolans, 49 species of nematodes, 30 species of rotifers and 41 species of tardigrades have been officially recorded.

The species richness of microbial communities is still not well described although recent studies suggest that there is a considerable diversity of bacteria with a high proportion of novel species. Most of the taxa are indigenous and often display psychrophilic or psychrotrophic growth characteristics (see box on page 32), and several genera are unique to Antarctica. Recent advances in molecular tools have provided evidence of an unexpectedly high diversity of microbes in the polar desert of the McMurdo Dry Valleys that was previously thought to support species-poor microbial communities. More than 14 different phyla of bacteria have now been recorded, with the most dominant phyla representing the Acidobacteria, Actinobacteria and Bacteroidetes (see box on page 33). By contrast, the Proteobacteria tend to dominate the soils in maritime Antarctica. Moreover, there is substantial variation in the composition of microbial communities between different regions and landscape types. Therefore, Antarctic soils harbour a high number of novel microbial and animal taxa that contribute significantly to global soil biodiversity.

Adaptations to local conditions

Not only are Antarctic organisms exposed to low water availability and temperatures, they also experience other extreme conditions, such as high salinity and pH values, and even hot soils in the case of geothermally active areas. Many native Antarctic organisms show significant adaptation of growth and survival strategies to cope with the extreme local conditions. For example, Antarctic soil fauna, including nematodes, tardigrades and rotifers, are able to enter a dormant state known as anhydrobiosis that allows them to survive in an ameboblastic state for many years during unfavourable environmental conditions (i.e. limited water availability) but also gives protection against other environmental stresses. Tardigrades (see page 44), for example, have been ‘revived’ from dried plant material after 120 years, and survived being exposed to temperatures near absolute zero as well as several minutes at 151 °C, high pressure and in a vacuum.

Both nematodes and rotifers show similar enhanced capacity to cope with the environmental stresses and the endobiotic state. Other survival techniques include freeze tolerance, as in the case of the chromonid Ilgapsia antarctica and the nematode Panagrolaimus davisii (the only organism known to be able to survive intracellular freezing), or freeze avoidance as in the case of many microarthropods. Water inside animals generally does not freeze at 0 °C, and significant supercooling can be attained by removing the source of ice nucleation (down to approximately −20 °C). By producing anti-freeze molecules, the freezing point can be lowered even further. Some Antarctic organisms display significant supercooling capabilities. The collembolan Gomphiocephalus hodgson, for example, has been shown to be able to avoid freezing down to −37 °C under laboratory conditions. To achieve significantly lower freezing points, native Antarctic collembolans generally produce sorbitol and mannitol, whereas mites produce glycerol.

Antarctic terrestrial ecosystems represent one of the most extreme soil environments on Earth, and are inhabited by a unique collection of species, many of which are found nowhere else on Earth. As many of the native organisms have evolved and adapted to the local environmental conditions they are genetically and functionally distinct from many of the organisms found in what we consider more ‘normal’ environments. Despite these hostile conditions, the soil-free terrestrial areas soil-living organisms native to Antarctica include many types of bacteria, fungi, plants, protozoa and certain animals, such as nematodes, tardigrades and mites. (DP)
Soil biodiversity and ecoregions – Desert and dry shrubland

Hot, dry and hostile

A desert is any region on Earth that can have a moisture deficit lasting the course of a year. Deserts are present on each continent, from the Gibson Desert in Australia to the Thar Desert in Asia, the Sonoran Desert in Mexico and the USA and the Sechura Desert in Peru. They are often regions of extreme temperatures where living conditions are hostile. Deserts vary greatly in the amount of annual rainfall they receive; generally, however, evaporation exceeds rainfall in these ecoregions, usually less than 250 millimetres annually. Temperature variability is also extremely diverse in these regions. Many deserts, such as the Sahara in Africa, are hot all year-round but others, such as Asia’s Gobi, become quite cold in winter.

Despite the limited vegetation cover (mainly shrubs) plant diversity can be high. All plants have evolved to minimise water loss; cacti are a representative example of this ability. Desert soils are usually poor because plant growth and productivity is low and the litter layer is almost absent. Furthermore, evaporation tends to accumulate salts at the soil surface.

Soil biodiversity

Soil biodiversity in deserts is lower than in more moist regions, such as temperate forests, but surprisingly, can be higher than in some agricultural ecosystems. The soil surface can be dominated by a soil biocrust (see page 73). The soil fauna is dominated by mites and nematodes (see pages 46–47, 49). As nematodes require water films to be active, much of their time in desert soils is spent in an inactive state. Other abundant microarthropods include collembolans (see page 50) and a wide variety of insect larvae (see page 60). [111]

Concerning the microbial communities, protists (see pages 36–37) are even more abundant than fauna in deserts. Of these, naked amoebae tend to be the most abundant, followed by testate amoebae, ciliates and flagellates. Protists also require water films for activity and, thus, can remain inactive. Unlike more moist regions, where soil biota are more homogeneously distributed because organic matter is more evenly spread, the distribution of soil biota in deserts is more heterogeneous, found clumped together in soils under the canopy of perennial plants, where organic matter is highest.

However, if interspace soils are covered by a biocrust, soil biota is often more evenly distributed across the landscape. Desert soil communities are critical in driving ecosystem processes, such as nutrient cycling and decomposition (see Chapter IV). Important decomposers in deserts include microorganisms (e.g. bacteria and fungi) and macroorganisms (e.g. mites, collembolans, nematodes, ants, termites, beetles, scorpions and lizards – see Chapter II). Despite the relatively low numbers of soil biota in deserts, they play a critical role in the structure and function of desert ecosystems. The number and biomass of these organisms determine, to a large degree, the rates and overall availability of nutrients for the primary producers (i.e. plants) of the food web (see page 96), and also provide food resources for higher trophic animals (e.g. reptiles and mammals).

Climate and land-use changes represent the main threats to organisms living in desert soils. Higher predicted temperatures will reduce soil moisture and, thus, reduce the overall activity and diversity of soil organisms. If precipitation is concomitantly decreased, further reductions in activity are expected. In addition, the relative proportion of species is likely to change. Human use of deserts is increasing in most areas of the world, with increasing needs for forage, energy and minerals. Many soil organisms are highly sensitive to soil compaction, disturbance and movement and, therefore, will be reduced or extirpated by these human disturbances.

Termites and ants

Ecosystems often have a certain species or groups of species that play dominant roles in ecosystem structure and function; this is also the case in deserts. In most arid regions, termites (see page 55) are numerous in species and number. These insects eat and provide food for many other animals. They are especially important in accelerating decomposition and nutrient-cycling rates. Their activities create macropores and they actively drag litter down into the soil, while bringing soils and rocks to the surface. African and Australian termites are the most diverse, whereas North American termites are fairly depauperate. Despite there being only a few species, North American termites still consume most of the plant and dung materials in these deserts compared to other organisms. Ants (see page 54) discard seed coatings and insects carcasses at the mound entrance, further increasing soil fertility. Many species play dominant roles in ecosystem structure and function; this is often more evenly distributed across the landscape. Desert soil biodiversity is highly sensitive to soil compaction, disturbance and movement and, therefore, will be reduced or extirpated by these human disturbances.
Anthropogenic ecosystems – Agroecosystem

Productive, managed and transformed

Agroecosystems are natural ecosystems that have been modified by humans to produce food, feed, fibre and fuel. Defined by a combination of plant-growing period (in days), climate and soil types, agroecosystems are extensive and diverse. They make up more than 40% of the Earth’s land area: 1.8 and 3.6 thousand million ha for crops and livestock, respectively, and encompass the ancient and fragile soils of Australia and Africa to the relatively young and fertile soils of Europe, Asia and North America. While they coexist with natural terrestrial ecosystems, agroecosystems have been modified extensively since the inception of agriculture 10,000 years ago. They support non-indigenous, domesticated plant species, including crops such as grains (e.g. wheat, maize and rice), legumes (e.g. peas and beans), oilseeds (e.g. canola, soybean and cotton) and pastures (e.g. ryegrass and clover).

Agroecosystem soils have been modified through intensive management practices, such as cultivation, grazing, plant product and residue removal, the addition of fertilisers and pesticides, irrigation, flooding and the creation of drainage systems. Some have been transformed to such an extent that they require reclassification or are deemed ‘new soils’, and classified as Anthrosols. Over the past 60 years, global increases in crop and livestock production systems have also coincided with substantial erosion problems, loss of carbon and nitrogen, salinisation, acidification and increased pest incursions, to the point that the conservation of soil resources and soil quality is a critical priority globally. Several countries are addressing soil decline issues both through voluntary and regulated soil-conservation strategies, such as satellite-guided controlled field traffic systems, direct drilling, diversified crops, cover cropping, plant-residue retention, rotational grazing, liming and subsoil manuring. The extent and diversity of modifications to soil agroecosystems has given rise to both a diverse and dynamic range of biological habitats and, in turn, to diverse and dynamic biological soil communities.

Soil biodiversity

The soils of the world’s agroecosystems contain biota that are visible to the naked eye (e.g. earthworms, dung beetles, ants and termites – see Chapter II) as well as those that can only be seen with the aid of a microscope. These range from micro- and mesofauna (e.g. mites and collembolans – see pages 49-50) to microorganisms and microfauna (e.g. bacteria, fungi, archaea, protists and nematodes – see Chapter II). The application of genetic tools, involving the direct extraction of soil DNA and RNA (see pages 64-65), has allowed researchers to measure the most abundant, as well as the rarest, biota, particularly those at the microscopic level (112).

Generalisations can be made about the relative influence of various factors in shaping bacterial communities at the phylum level based on a number of surveys in the USA, Europe (mainly France, the UK and the Netherlands), China and Australia. The common taxa or groups that make up agroecosystem biodiversity are now well described. Bacteria are by far the most diverse of the soil biota, with more than 30 groups (phylum levels) routinely identified in even the most disturbed agroecosystems, such as in hydrocarbon-contaminated sites and rice-paddy soils. The agriculturally significant functions associated with the modification of soil structure, the mixing of organic material, the mineralisation of nutrients, the promotion of plant growth, the control of pathogens and the remediation of herbicides attributable to these taxa are also becoming more easily identified.

Research assisted by DNA and informatic technologies is enabling the identification of characteristic soil biological communities for many land uses, which is providing baseline data for long-term global monitoring programmes. All features of the habitats that make up global agroecosystems, including the chemistry, structure, input and disturbance regimes, plant diversity and growth cycles, provide the critical metadata needed to describe the current and future status of soil biodiversity. It enables both the reconstruction of soil biodiversity patterns from pre-agricultural times and the prediction of long-term impacts of agricultural management regimes. These approaches will improve restoration efforts and provide decision support to land managers who wish to manage their soils sustainably (see Chapter VI) into the future.
Anthropogenic ecosystems – Urban ecosystem

Built, populated and growing

There is no general agreement on a definition of what is urban, and considerable differences in the classification of urban areas exist among countries and continents. In Europe and North America, the urban landscape is often defined as an area with human agglomerations and with a built-up surface of >50 %, surrounded by other 30–50 % built-up areas, and overall a population density of more than ten individuals per hectare in other contexts, population size, the density of economic activity or the form of governance structure are used to delineate towns, cities or city regions, but there is significant variation in the criteria for defining what is urban. While everyone struggles to define exactly what is meant by a city, nobody negates the shifting patterns of urbanisation or the overall growth of cities.

Soil biodiversity in Central Park

- Central Park is a recreational area in Manhattan, New York City, USA. It was initially opened in 1857 and is one of the most frequently visited urban parks in the world.
- Aboveground, Central Park harbours approximately 393 plant species, more than 250 species of vertebrates and more than 100 species of invertebrates.
- In 2014, researchers collected 600 soil samples in order to investigate the diversity of soil archaea, bacteria, fungi, protists, invertebrates and other eukaryotes. ([115])
- The soils of Central Park harbour nearly as many distinct soil microorganisms as are found in biomes across the globe.
- Despite high variability across the park, belowground diversity patterns were predictable based on soil parameters, in particular soil pH.

Carabid beetles (see page 59) were collected in a metropolitan area in South Korea. Carabid assemblages changed significantly in response to management practices (i.e. mowing). Isopod assemblages were studied in Budapest, Hungary. The data analyses revealed high species richness compared to the total number of species in the country. This may be due to the ecological process known as homogenisation. Biotic homogenisation entails the replacement of native species with non-natives, a process that plays an important role in shaping urban fauna and flora by increasing the similarity of soil communities among cities worldwide. This phenomenon has been observed not only in isopods but also earthworms and millipedes. Another aspect that is increasingly studied is the impact of urbanisation on soil organisms. For example, nematodes (see pages 46-47) assemblages were studied along an urban-rural gradient of land use in the USA. Results showed that there were functional differences in the nematode communities along the land-use gradient, thus confirming that the functional composition of the soil food web is an important component of soil biodiversity that can be affected by urbanisation.

Uniqueness of urban soils

The ecological uniqueness of cities and their continuous growth due to the increasing population size, probably means that the soils of urban areas should be considered as a particular habitat. Several factors make urban soils unique conditions that promote the spread of invasive species (see page 119), the strong influence of human activities prior to urbanisation (e.g. industrial and waste disposal), and the creation of novel soil types with anthropogenic materials (e.g. cement). Furthermore, urban environments may feature a complex mosaic of habitats for soil organisms, from urban parks and private gardens and lawns to roundabouts and sports and leisure areas. Soil biota have been shown to respond to alterations in soil properties associated with urban environments. The effect of these urban pressures on belowground biodiversity is an alteration of ecosystem functions and processes. Nevertheless, the diversity of urban soils may also represent hot spots for soil biodiversity. For example, soil microbial communities in Central Park in New York City are comparable to those found in natural ecosystems (see box above).

Soil biodiversity

Urban soils are subjected to many pressures. Sealing and compaction by vehicles and humans reduce the soil’s permeability to water and air. Furthermore, urban soils tend to accumulate pollutants, mainly heavy metals, from industrial and transport emissions (see pages 120-121). A study showed that soils in cities are generally 1–2 °C warmer, 50 % drier and 1.5 times more dense and lower in organic carbon than similar soil types in the rural environment. All of these aspects affect abundance, diversity and processes carried out by belowground urban life. The interest in understanding urban ecosystems is recent and is leading to an increasing number of studies that describe the soil organisms of green spaces within large cities. For example, soil macrofauna was investigated in urban parks and domestic gardens in London, UK. Five groups of organisms were identified: earthworms, ants, isopods, millipedes and centipedes (see Chapter III). The species densities of the studied soil organisms were comparable to those found in natural ecosystems. ([114])

SOIL BIODIVERSITY IN CENTRAL PARK

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Mapping soil biodiversity

While scientific knowledge of individual groups of soil fauna, together with their role in providing key ecosystem services, is continuously evolving, data on their abundance, diversity and geographic distribution remain scarce. Although the major ecosystems of the planet are now relatively easily mapped and monitored through the vast quantities of data collected by various satellite-based sensing systems, such tools are unable to provide any direct information relating to soil-based organisms. In fact, any comprehensive or large-scale survey and monitoring programme for soil organisms can only be carried out through direct field observations or sampling. Therefore, knowledge of belowground species distribution is very incomplete and, as a consequence, there is a general lack of maps showing the degree of soil biodiversity, especially at global scales.

In addition to the practical problems associated with mapping soil biodiversity, the issue is further compounded by the lack of a precise definition (e.g. does biodiversity relate to total number of species present, the genetic diversity within species, the distribution of individuals among those species, etc.?). When combined with the practical challenges associated with collecting data, the task becomes even more daunting!

It is interesting to note that recent studies have found that the aboveground biodiversity of a region (i.e. the number of species of vascular plants, amphibians, reptiles, birds and mammals) are strongly correlated, at least on a global scale, to the number of soil types in the same area (a concept referred to as pedodiversity). Additionally, findings show that pedodiversity can in turn be used as a broad indicator of aboveground biodiversity, which itself can often be difficult to quantify. Moreover, there is increasing recognition of the influence of these components on each other and of the critical role played by above- and belowground feedbacks in controlling key ecosystem processes.

Methodology

As seen in this chapter, there are numerous groups of soil organisms distributed in different ways across the globe. Also, there is a significant lack of data for many groups of soil-dwelling organisms at global scale. Furthermore, as numerous factors influence the geographical patterns of soil biodiversity, it is not easy to give a static representation of soil biota distribution on a map. For all these reasons, it is difficult to obtain a reliable global map showing the distribution of all soil biodiversity.

Nevertheless, the available data can be used to develop a simple index describing the potential level of diversity living in soils on our planet. In order to make this preliminary assessment, two sets of data were used:

- distribution of microbial soil carbon developed by Serna-Chavez and colleagues (see page 69). This dataset was used as a proxy for soil microbial diversity
- distribution of the main groups of soil macrofauna developed by Mathieu (see page 71). This dataset was used as a proxy for soil fauna diversity

The two datasets were then harmonised on a 0–1 scale and summed. The total scores were categorised into an index ranging from low (i.e. poor level of soil biodiversity richness) to high (i.e. significant level of soil biodiversity richness).

In comparison with the soil biodiversity index map, the plant diversity map shows that areas near the Equator that receive high precipitation and have constantly high temperatures have the highest plant biodiversity. Outside those areas, the highest biodiversity is found in Mediterranean climates where temperatures are moderated by the proximity to the ocean, seasonal precipitation and varied topography which create micro-ecoregions (derived from Kreft and Jetz, PNAS, 2007).
Results

The resulting map is an initial attempt to denote global soil biodiversity levels. The pattern reflects the discussion on the previous pages, which describes the soil biodiversity associated with various biomes.

The analysis shows that most soil biodiversity is found in both humid-temperate and humid-tropical soils, followed by soils where extremes in temperature and precipitation levels are generally absent. Lower levels are found in cooler and drier soils (such as boreal and Mediterranean climates). The lowest soil biodiversity levels are associated with the presence of extreme heat or very cold soils.

It is important to note that this is a simplistic exercise based on two datasets showing the distribution of only a few groups of soil organisms (see pages 69, 71). Further refinement could be provided by including soil microfauna (e.g. nematodes) and mesofauna (e.g. collembolans and mites).

While designed to stimulate debate, this map also gives a clear message of the need for significantly more research and data collection.
Soil biodiversity underpins several functions that allow for the correct functioning of ecosystems. These functions generate benefits known as ecosystem services, for human beings, including the provision of food and clean water, climate regulation, support of human habitats and contribution to cultural values. (GS/CIAT, NP/CIAT, DNO, GKN, MFE, NASA)
### Introduction

Soils start to exist when organisms organise their habitat. They build and maintain soil structure and influence its chemical properties by weathering bedrock, aggregating mineral and organic constituents and developing the pore network. This affects the movement of water and gases, the transfer of nutrients and energy, and the removal of metabolic products, which contributes to the many functions and ecosystem services soils provide [118].

The terms ecosystem ‘functions’ and ‘services’ are often confused. ‘Functions’ is used to define the biological, geochemical and physical processes and components that take place within an ecosystem. ‘Services’ is used to encompass the tangible and intangible benefits that humans obtain from ecosystems. Considering soil, it is possible to say that ecosystem services are derived from different soil system functions and, in turn, each ecosystem service is associated with specific groups of soil biota.

The Millennium Ecosystem Assessment, compiled by the United Nations in 2005, represents a major overview of the effects of human activity on the environment. According to this document, there are four recognised classes of ecosystem services: 1) Provisioning; 2) Regulating; 3) Supporting; and 4) Cultural. Provisioning services pertain to products, such as food and fresh water. Regulating services include benefits, such as climate control and disease and pest control. Supporting services include soil formation and habitat sustenance that are necessary for the maintenance of all soil functions, and provide a suitable rooting medium for plants. Cultural services are the non-material benefits that people obtain from ecosystems, such as cultural heritage, recreation and tourism.

Soil and its biota provide these ecosystem services by contributing to the provision of food, fuel and fibre, the infiltration, storage and delivery of clean water, the suppression of plant pests, the control of nutrient cycles, and the provision of cultural value. This chapter presents and discusses these functions and services provided by soil-dwelling organisms.

#### ECOSYSTEM SERVICES

<table>
<thead>
<tr>
<th>PROVISIONING</th>
<th>ECOSYSTEM FUNCTIONS</th>
<th>SOIL BIOTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant production (food)</td>
<td>Decomposition and carbon cycling</td>
<td>Macrofauna, Mesofauna, Microfauna, Bacteria, fungi and archaea</td>
</tr>
<tr>
<td>Biotechnology</td>
<td>Nutrient cycling</td>
<td>Microfauna, Bacteria, Mycorrhizal fungi, Other microorganisms</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>REGULATING</th>
<th>ECOSYSTEM FUNCTIONS</th>
<th>SOIL BIOTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate regulation</td>
<td>Soil structure and maintenance</td>
<td>Roots, Earthworms, Macroarthropods, Fungi</td>
</tr>
<tr>
<td>Atmospheric composition</td>
<td>Biological population regulation</td>
<td>Macrofauna, Mesofauna, Microfauna, Bacteria and fungi</td>
</tr>
<tr>
<td>Hydrological services</td>
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Introduction

Factors affecting ecosystem functions and services

In soils, ecosystem functions and services result from the interaction of physical, chemical, biological and human factors. These processes operate at different scales of time and space, integrated into each other, and are organised hierarchically. Climate, which operates at the largest scales of time and space, is always the most important factor influencing the provision of ecosystem functions and services. This is followed by the quality of the substrate (i.e. nutrient availability, determined by the initial mineralogy of the parent material), plant communities and the quality of organic matter that they return to the soil. At the smallest scales, the key factor is biodiversity, ranging from invertebrates to microbial communities (see Chapter II). [2]

Physical factors

Physical processes comprise all climatic factors, such as temperature, moisture and their daily and seasonal fluctuations; they determine the rates of metabolic processes in the soil and interact with the physical properties of soil. For example, the total amount of water that can be retained in soils, and the energy used to retain that water to soil particles, depends on the amount and size of the soil pores. This physical property of soil is known as porosity. There are two different types of pores: textural pores, whose size of the soil pores. This physical property of soil is known as porosity, which is always the most important factor influencing the provision of ecosystem services. It involves the organisation of the mineral and organic elements of soil (see Chapter I) into structures of different scales, called soil aggregates (see page 72). Similar to pores, aggregates can be derived from physical or biological processes. Physical aggregates formed by alternation of wet and dry or freeze and thaw periods have sharp edges and usually do not allow large amounts of interaggregate pores to form. These aggregates are mostly stabilised by purely physical forces (such as Van der Waal forces between particles). However, living organisms often play a key role in creating these aggregates (known as biogenic aggregates) by producing the ‘glues’ (for example, the protein glomalin produced by arbuscular mycorrhizal fungi – see page 40) that stick particles together. Biogenic aggregates may be formed by natural physical forces, such as those of growing roots, or physically generated, such as nests and other constructions made by social insects (termites and ants – see pages 54-55) and the organo-mineral casts of earthworms (see page 58).

Chemical factors

Chemical processes include all the transformations that organic residues undergo during the decomposition process (see page 106). Plants produce residues of different qualities. For example, the presence of polyphenol compounds accumulated in plant leaves limits herbivory and greatly reduces decomposition rates: in dead leaves, more than 80% of nitrogen is locked up in phenol protein complexes that only a few microorganisms, such as the white-rot basidiomycete fungi (see pages 38-39), can decompose. Decomposition processes recycle nutrients, making them available again to plants of storing them as resistant polysaccharides, which glue particles together, or entangling particles into ‘nets’ of fungal filaments. Invertebrates (including micro-, meso- and macrofauna – see page 31) play a unique role in mechanical activities by softening, fragmenting and burying plant residues, which facilitates their natural decomposition, and creating channels and pores in the soil that provide habitats for smaller organisms and reservoirs and routes for air and water to circulate and be stored. In addition, invertebrates produce compounds that stimulate plant growth and protection against pests and diseases (see pages 108-109).

Biological factors

Biological processes involve both microbial and faunal functions, which inevitably interact with other soil components. In fact, microbes are the ultimate operators of all chemical transformations in the soil: they facilitate nutrient release through decomposition processes, conservation of organic matter through synthesis of resistant humic compounds, and nitrate fixation. They also help, to some extent, aggregate of mineral and organic particles into solid structures by producing polysaccharides, which glue particles together, or entangling particles into ‘nets’ of fungal filaments. Invertebrates (including micro-, meso- and macrofauna – see page 31) play a unique role in mechanical activities by softening, fragmenting and burying plant residues, which facilitates their natural decomposition, and creating channels and pores in the soil that provide habitats for smaller organisms and reservoirs and routes for air and water to circulate and be stored. In addition, invertebrates produce compounds that stimulate plant growth and protection against pests and diseases (see pages 108-109).

Human factors

In addition to natural factors, another force is becoming prominent in shaping ecosystem functions and services. Human activities modify soil systems, mostly by manipulating plant communities in managed productive systems, altering the soil structure through tillage and indirectly affecting soil biodiversity by reducing abundance and diversity through the excess use of pesticides and/or mineral fertilisers (see pages 122-123).
Spatial scales of soil biodiversity functions

Soil functions are a consequence of the complex interactions between different groups of microorganisms, as well as between micro-, meso- and macro-fauna. Therefore, a reductionist approach, which involves separating the effects of single species, is of limited help in understanding soil biodiversity functions. We must adopt an integrated approach that takes into consideration interactions between organisms, the physical structures built in the soil, and the spatial and temporal scales at which these entities operate. Soil organisms have coevolved for hundreds of millions of years and interact in positive (mutualistic – see page 33) and negative (e.g. predator versus prey – see page 96) ways. In the soil environment, movements are limited by its compact structure; feeding is often difficult due to the generally low quality of resources available, and metabolism rates have to adapt to the alternation of dry and moist periods. No organism is able to face all of these challenges alone. Soil microbes are generally reliant on the action of ecosystem engineers, namely roots (see page 43) and invertebrates (e.g. earthworms – see page 58) along with percolating water, to obtain food. Invertebrates in turn, use the decomposition capacities of microorganisms in different types of mutualist associations to obtain their nutrition from soil. From the smallest (soil pores and aggregates – see page 72) to the largest scales (ecosystems and landscapes), numerous organisms interact to establish a limited number of associations that drive and regulate ecosystem functions and sustain ecosystem services. At each of the five recognised scales, soil organisms form distinct assemblages that live in specific niches, interact and carry out explicit functions. [121]

Chemical versus ecosystem engineers

- Depending on the main functions carried out, soil organisms can be assigned to one of the following two main functional groups:
  - chemical engineers (transformers and decomposers), i.e. organisms responsible for carbon transformation through the decomposition of plant residues and other organic matter, and for recycling of nutrients (e.g. nitrogen, phosphorus and sulphur);
  - ecosystem engineers, i.e. organisms responsible for maintaining the soil structure through the formation of pore networks, bio-structures (e.g. earthworm casts) and aggregation, or particle transport.

- Microorganisms, such as bacteria and fungi, are by far the most important chemical engineers; over 90 % of the energy flow in the soil system is mediated by microbes.
- Earthworms, termites, ants and plant roots are the most important ecosystem engineers. However, soil engineers also include many other invertebrates, such as millipedes, centipedes, beetles and scorpions, which may be more or less responsible for soil formation.

Scale 1

At Scale 1 (a few micrometres), microbial communities (i.e. archaea, bacteria and fungi) – see Chapter III form colonies living in pores inside aggregates or in the inter-aggregate space. They may create small structures using slime (polysaccharides) known as microbial aggregates. Once they have utilised all the organic substrates or nutrients available, they either die, or can enter into dormant stages (see box on page 34) since they generally have very limited abilities to move to new substrates. Fungi can extend their mycelium over large distances, although the distribution of their spores is largely performed by invertebrates and roots.

Scale 2

Scale 2 refers to the soil micro food webs, a complex community of small invertebrates (e.g. nematodes, mites and collembolans – see pages 46–47, 49–50) that usually feed on microorganisms, thereby regulating their community abundance and composition.

Scale 3

Scale 3 is that of the ecosystem engineers (see box on page 95). At scales of centimetres to metres or more, they mix the soil and can build sophisticated networks of connected pores and channels and may produce huge amounts of biogenic aggregates (e.g. earthworm casts). These structures play a vital role in soil functioning, and can have large effects on the flow of water and nutrients within the soil system.

Scale 4

Scale 4 is the ecosystem represented as a mosaic of functional domains. A functional domain is defined as the sum of structures produced by a given population of ecosystem engineers. It presents strong interactions, such as those between earthworms and roots. Indeed, earthworm casts are rich in readily available nutrients and can play a role in structuring plant communities.

Scale 5

At Scale 5, that of landscapes and the whole biosphere, delivery of ecosystem services (e.g. infiltration and soil water storage – hydrological services, see page 107) or climate regulation (see pages 102–106) through the storage of carbon in soil organic matter, is achieved through a set of rather complex interactions among all soil-living organisms, from microorganisms to megafauna, and the different types of ecosystems (e.g. forest and pasture).
Introduction

Biological and functional diversity

The relationship between soil biodiversity, functions and services has led to the distinction between two different types of diversity: biological diversity and functional diversity (122).

Biological diversity

Biological diversity refers to the different species present in a community, including their genetic and intraspecific diversities. Here, the focus is on the number of species and, therefore, an ecosystem is considered to be biologically diverse when it contains species-rich communities.

Functional diversity

Functional diversity is the diversity of roles that the soil community plays in a particular ecosystem. Soil organisms are commonly classified according to size (e.g. micro-, meso- and macrofauna, see page 31). However, it can be more informative to classify them according to the functional role they play in the soil, for example, as plant comminutors (that fragment litter), bioturbators (that mix soil) or mineralisers (that release nutrients). When organisms with the same functional ability occur together, this is referred to as ‘functional redundancy’ (see page 97).

Interactions

Soil organisms, both as individual species and in groups, can interact with each other in either a positive or negative way. The more diverse the soil community, the more opportunity there is for interactions. Often in soils, these interactions are mutualistic, where the community members support each other’s functions (see box on page 33). Understanding these interactions is important when considering the effect of drivers of global change, such as climate change, nitrogen deposition, pollution and urbanisation. These environmental stressors can significantly affect belowground communities, altering community composition and functioning. The consequence of community changes on soil functions is often difficult to quantify and predict, and there is reason for concern that changes in soil communities may negatively affect soil functions.

Trophic levels and food webs

The trophic level of an organism is the position it occupies in a food web. The trophic level of an organism is the position it occupies in a food web. Basal species, such as plants, form the first trophic level and feed on no other living creature in the food web. Species in this level are also known as primary producers, as they are able to convert solar energy into chemical energy through photosynthesis. The intermediate levels are filled with organisms that feed on more than one trophic level (predator-prey relationships) and transfer energy or chemical energy into organic matter. The uppermost trophic level includes top (or apex) predators that have no other species predating on them.

A simplified soil food web

Soils host a complex food web, including predators, herbivores and decomposers, which scientists are still exploring. The trophic interactions among soil organisms are similar to what is observed aboveground between predators, herbivores, plants and decomposers. However, the compact and fragmented condition of the soil environment reduces the opportunity of organisms to interact with each other (PL, JRC).
CHAPTER IV – ECOSYSTEM FUNCTIONS AND SERVICES

Functional redundancy

The role of soil organisms in supporting soil processes depends on the types of functions they carry out. However, more species do not necessarily equal more functions, or even higher rates of soil processes. This realisation lead to the coining of the term ‘functional redundancy’, a concept that describes a common characteristic of soils. Therefore, overlapping functions are an important component of community dynamics, and an important concept when considering global change effects on community composition and diversity. For example, higher functional redundancy can protect ecosystem services when the community is altered. For example, if an organism is lost or decreases in abundance due to a global change factor, another species carrying out the same functional role can ensure that the function will continue. The interactive nature of soil organisms, whether negative or positive, varies between systems and in response to different environmental stressors (see Chapter VI).

Many studies are now focusing on the influence that global change factors has on the response of soil communities and the potential consequences for soil functions.[123]

Resistance versus resilience

Associated with the concept of functional redundancy are the concepts of resistance and resilience. In fact, functional redundancy is often one of the reasons for high levels of resistance of soil communities to a given stressor.

- resistance = how strongly a community can resist a stress without being negatively affected
- resilience = how quickly a community can recover after being negatively affected

As global change continues to increase pressure on soil biodiversity, it is becoming increasingly important to understand the resistance and resilience associated with different soil communities in order to conserve and optimise the ecosystem services we rely on. In fact, alterations in a group of organisms are likely to alter a function and the resistance and resilience of the soil system to compaction.

Conclusions

As global change continues to increase pressure on soil biodiversity, it is becoming increasingly important to know when to protect, conserve or optimise soil communities in order to conserve and optimise the ecosystem services we rely on. In fact, alterations in a group of organisms are likely to alter a function and resist or recover through the whole system.

Many ecosystem services are supported by soil organisms and their interactions. The next pages of this chapter will highlight the most essential services that demonstrate the interconnectivity of the organisms and the underlying functions. Ecosystem services of each of the four classes (Provisioning, Regulating, Supporting and Cultural) will be presented, from the provision of food by increasing plant production, the regulation of climate, the support of the soil habitat to the cultural value associated with soil biodiversity.

Logging vs. microbial resilience/resistance

- Soil compaction is a major disturbance associated with logging in forests. It leads to oxygen and water limitations.
- A recent study investigated the resistance and resilience of soil microorganisms (bacteria and fungi) to this pressure. Fungi are less resistant and resilient than bacteria.[124]
- This can be explained by the generally higher sensitivity of eukaryotes (e.g. fungi, see page 30) to low oxygen pressures compared to prokaryotes (e.g. bacteria).
- Major changes in the microbial communities occur in the medium-term, around 6-12 months after the disturbance. Four years after compaction, the community structure recovers in lightly compacted but not in heavily compacted soils.
- Soil microbial diversity may represent a powerful tool to measure the resistance and resilience of the soil system to compaction.

Soil contamination is removed

When the fungus is not present

Numerous groups of organisms break down leaf litter into small pieces

The process continues even following the loss of a large number of the species

A fungus grows through the contaminated area and consumes the pollutants

Fertile organic matter results

Fertile organic matter results

Soil contamination is removed

Contaminated soil remains

Fertile organic matter remains

Fertile organic matter remains

When the fungus is not present

Fertile organic matter results

Fertile organic matter results

Fertile organic matter remains

Soil contamination is removed

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Plant production

Climate regulation

Habitat supporting

Cultural value

Logging vs. microbial resilience/resistance

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Provisioning services – Production of food and fibre

Soil biodiversity and plant production

Plants utilise associations with soil microorganisms in the same way that animals utilise gut and skin microorganisms to aid their digestion and resistance to diseases. The combined activities of the diverse array of cryptic soil organisms influence plant production and soil health. Recent advances in molecular genetics (see pages 64–65) have revealed a remarkable diversity of fungi and bacteria associated with plant roots (see Chapter II). Some of these microorganisms promote plant growth through enhancing plant nutrition. Other microorganisms increase plant fitness by protecting them from herbivores and pathogens. Some microorganisms also cause disease (see pages 108–109). [38]

Mycorrhizal fungi

Mycorrhizas are ancient symbioses (see box on page 33) between plants and fungi. Fossils indicate that the earliest land plants hosted fungi in their tissues even before they evolved roots. Mycorrhizal fungi (see page 40) provide plants with necessary mineral nutrients and, in return, they obtain plant-derived sugars. Mycorrhizal symbioses are most beneficial in low-fertility soils because fine fungal hyphae can scavenge more efficiently for essential nutrients than plant roots could alone. The mutual advantages of these symbioses are clear from their tremendous diversity and abundance. Over 90 % of all plant species form mycorrhizas (see page 40), their widespread application, especially in natural systems, is controv…

Soil

<table>
<thead>
<tr>
<th>Biome</th>
<th>Soil Type</th>
<th>Nitrogen Source</th>
<th>Mycorrhizas</th>
<th>Fungal Symbiont Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heathland</td>
<td>Organic-raw humus</td>
<td>Organic-protein</td>
<td>Ericoid</td>
<td>Extensive abilities to degrade structural and nutrient-containing polymers</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>Surface organic</td>
<td>Nitrogen-fixing</td>
<td>Ecto-</td>
<td>Considerable saprotrophic capabilities in both Ericoid and Ecto-fungi</td>
</tr>
<tr>
<td>Temperate forest</td>
<td>Brown earth</td>
<td>Ameliorating</td>
<td>Accessory</td>
<td>Eco-fungi of reduced saprotrophic capabilities</td>
</tr>
<tr>
<td>Grassland</td>
<td>Mineral</td>
<td>None</td>
<td>Arbuscular</td>
<td>AM fungi with little or no saprotrophic abilities</td>
</tr>
</tbody>
</table>

- Mycorrhizal fungi and the roots of a beech tree (Fagus sylvatica). (IRL)
- Scanning electron micrograph showing a colony of bacteria on a humus aggregate (TEI)
- Ectomycorrhizas formed by the fungus Laccaria amethystina and the roots of a beech tree (Fagus sylvatica). (IRL)

In addition to increasing plant nutrition, mycorrhizas influence plant production through their influence on soil formation and nutrient cycling. Some mycorrhizal fungi can enhance the weathering of soil parent materials (see page 20). In addition, mycorrhizal fungal mycelia stabilise soil aggregates and interact with other soil organisms by transporting plant-derived carbon compounds through the soil system. In fact, a large fraction of the organic matter in soil is represented by the mycelium of mycorrhizal fungi and, therefore, mycorrhizas account for much of the microbial carbon stored belowground.

Inoculation with efficient strains of mycorrhizal fungi has been shown to benefit the growth of many types of cultivated plants, especially in tropical systems and degraded soils. Mycorrhizal inoculum collected from the root zone of healthy soils, as well as commercially available mycorrhizal inoculum, have been used to enhance plant growth in forest nurseries, orchards and horticultural operations. Recent studies indicate that inoculation with mycorrhizal fungi together with myriad of other plant supporting organisms, such as nitrogen-fixing and phosphorus solubilising bacteria, may have a synergistic effect on plant growth. Individual plants generally host dozens of fungal species in their root systems. Human activities, such as agriculture, forestry and urbanisation can eliminate many beneficial mycorrhizal fungi from soils (see Chapter VI), whereas earthworms greatly enhance plant infection by mycorrhizas in agroecological production systems.

Although little is known about the functions of the many fungal species associated with plant roots, different species of mycorrhizal fungi are known to vary greatly in their effects on host plants. Furthermore, environmental conditions, such as high inputs of chemical fertiliser, can cause some species of mycorrhizal fungi to lose their beneficial effects, or even decrease the growth of their hosts. Consequently, caution should be taken when artificially inoculating plants with mycorrhizal fungi. Mycorrhizal inoculants are commercially available, however, their widespread application, especially in natural systems, is controver…

Decreasing soil pH

- Decreasing phosphorus availability and P:N ratio

\[ \text{Decreasing pH} \quad \text{Decreasing phosphorus availability and P:N ratio} \]
Bacteria and plant production

Many bacterial species that inhabit the plant root zone (rhizosphere) have had beneficial effects on plant growth and productivity. These bacteria, called plant growth promoting rhizobacteria, help plants through several mechanisms, of which improved nutrition is one of the most important. [126]

Even though nitrogen is the most abundant gas in the air, plants cannot utilise nitrogen gas and their growth is frequently limited by a shortage of nitrogen. An estimated 97% of the natural nitrogen inputs in terrestrial ecosystems are from biological nitrogen fixation performed by ‘nitrogen-fixing’ organisms. These organisms, scientifically known as diazotrophs, can convert nitrogen gas into a form of nitrogen that plants can utilise. Many plants benefit from associations with either symbiotic or free-living diazotrophs. Legumes are well known for their symbiotic associations with the nitrogen-fixing actinobacteria of the genus Frankia. The ability to form symbioses with Frankia appears to have evolved independently in at least three different orders of angiosperms. The majority of diazotrophs are not symbiotic but rather free-living inhabitants of the rhizosphere.

After nitrogen, phosphorus (see page 105) is often the most limiting resource for plants. Plants often associate with particular types of bacteria in their rooting zones to improve their access to phosphorus, which is often tightly bound to soil particles. Phosphorus solubilising bacteria include the Rhizobium, Pseudomonas and Bacillus species, along with many other aerobic and anaerobic bacteria. One of the major mechanisms by which these bacteria solubilise mineral phosphate is through the synthesis of organic acids, which causes phosphorus ions to be released from more complex molecules. The abundance, diversity and metabolic activity of nitrogen-fixing and phosphorus-solubilising bacteria and arbusae are influenced by many factors, including soil chemistry, climate, plant community composition and land management.

Plant protection

Soil organisms also enhance plant production through their interactions with organisms that damage plants. For example, fungi (see pages 36-41) of the genus Trichoderma are known to prevent fungal attacks through a variety of complex mechanisms. A wide range of bacteria have similar effects. Earthworms (see page 58) also have recognised effects as control agents for parasitic nematodes (see pages 46-47). A rather diverse set of mechanisms may be implemented (e.g. accelerated etiolation of eggs in compact casts where nematode larvae will get trapped); destruction of nematode chemoreceptors during transit through earthworm guts by a proteolytic enzyme produced by specific bacteria; direct destruction of nematodes during the digestion process. Furthermore, researchers demonstrated that rice plants attacked by parasitic nematodes may become tolerant after earthworm activities have modified the expression of several genes in a way that allows plants to tolerate root grazing by nematodes.

The strange case of actinorhizal plants

Actinorhizal plants are a group of angiosperms that form symbioses with the nitrogen-fixing actinobacteria of the genus Frankia, meaning that they convert atmospheric nitrogen into ammonia. This association leads to the formation of nitrogen-fixing root nodules.

- Actinorhizal plants belong to 24 genera and 8 families. Many are common plants in temperate regions, such as alder, bayberry and sweetfern.
- Actinorhizal plants are found on all continents, except Antarctica.
- Actinorhizal plants are the main contributors to nitrogen fixation in large areas of the world, and are particularly important in temperate forests.
- The symbiosis leads to root cell divisions and the formation of a new organ consisting of several lobes that are anatomically similar to a lateral root, known as actinorhiza.
- Frankia is a bacterial genus named after the German biologist, Albert Bernhard Frank, in 1886. Frankia alni is the only named species in this genus.
Chapter IV – Ecosystem Functions and Services

Provisioning services – Biotechnology

Various groups of soil organisms have the potential to be manipulated and used for a wide range of environmental, commercial and industrial applications, many of which still remain largely unexploited. The use of soil organisms with the aim of generating a useful product or a desired metabolic process is generally known as ‘biotechnology’. Such applications are possible thanks to three major soil biota traits:

a. their ability to break down substrates and to transform them into new compounds
b. their direct involvement in a multitude of biological processes
c. their high sensitivity to changes in the local environment

Of all soil organisms, microorganisms are particularly easy to cultivate (see pages 64-65) and to manipulate. Available microbial products in our everyday lives can be categorised as follows:

a. microbial cells that can be used as nutrients, immunising factors (e.g. vaccines) or clean-up agents (i.e. bioremediation)
b. enzymes and other macromolecules, synthesised by viable microbial cells
c. primary microbial metabolites, essential for cell growth and maintenance (e.g. amino acids)
d. secondary microbial metabolites, which are not essential for cell growth (e.g. antibiotics and steroids)

Each of these microbial products have important environmental, biomedical or industrial applications. Examples of such contributions are described below (127)

Bioremediation

Remediation is the general term for any physical, chemical or biological process used to recover or restore ecosystem functions in contaminated or polluted soil or water. A particular case of remediation is bioremediation (see page 141), which takes advantage of biological activity (bio) for the environmental clean-up (‘remediation’) of contaminants or polluters, such as pesticides, metals and polycyclic aromatic hydrocarbons (PAHs).

Bioremediation has been increasingly regarded as an alternative to the traditional physical and chemical treatments, as it generally has less undesirable impacts on the environment, and is often more cost-effective.

A broad range of environmental contaminants can be immobilised, metabolised into less toxic compounds, or mineralised via soil microbial metabolism. Such strategies can be used in one or more approaches (intrinsick bioremediation, biostimulation and bioaugmentation), depending on the contaminant type and concentration, the status of native microbial communities and the site-specific environmental and climatic combinations.

Intrinsick bioremediation is carried out by native microflora and occurs naturally in contaminated environments, without the need for human intervention. However, in those cases where the local environmental conditions are not favourable for microbial metabolism, there are options to enhance the cleaning-up functions, such as through biostimulation of the native microbial degrading potential (e.g. addition of limiting nutrients, moisture, oxygen, etc.) or through inoculation of natural or custom-made selected species that exhibit specific metabolic features (bioaugmentation).

Agricultural revolution

The Green Revolution was started in the late 1940s by the American biologist Norman Borlaug. Research coupled with technological development allowed for an increase in agricultural production. The basis of the Green Revolution largely arose from the development of technologies, such as synthetic nitrogen fertiliser, pesticides and modern irrigation techniques, combined with the production of novel cultivars, particularly wheat, maize and rice. Such cultivars were created through conventional breeding methods. While a great success in terms of increased productivity and, therefore, increased global food security, the Green Revolution was, unfortunately, not without its negative impacts. In fact, intensified land use in agriculture and forestry is sometimes considered the main cause of biodiversity loss.

Biodiversity has been reduced because of the reliance on just a few high-yielding varieties of each crop. Extensive use of pesticides is generally required due to this switch to monocropping systems. In recent years, aiding pollination in some agroecosystems has resulted in reduced blossom drop and improved fruit set, leading to enhanced crop yield and quality (e.g. tomato growers). For example, the use of artificial beehives containing functional bumblebees (Bombus terrestris – see box on page 61) colonies or other native pollinators has expanded to a range of crops, particularly in greenhouses, where artificial lighting, often inadequate ventilation, coupled with limited access for pollinators may compromise sufficient pollen transfer.

Genetically modified organisms

A range of genetically modified organisms (GMOs – see box on page 123) used (or proposed for use) in agriculture have been produced through biotechnology. These include both pest- and herbicide-resistant plants, as well as crops with augmented nutrient contents, such as golden rice, each of which are discussed in more detail below. The production and use of GMOs is not without controversy, and they are still heavily regulated in some parts of the world, including in Europe, but much less so in other parts, such as Africa and North and South America.

One of the most widely used forms of genetically modified crops is referred to as ‘Bt crops’. These crops have been engineered to express genes from the soil bacterium Bacillus thuringiensis. The plants produce the Bt toxin, which functions as an insecticide, thus helping to protect the crop from insect pests. Such crops have been widely adopted in some countries, mainly the USA, Brazil, Argentina, India and Canada, where they have been associated with a reduction in pesticide use and, consequently, with environmental and economic costs. However, resistance to the first generation of Bt cotton was reported to have arisen in a pest known as the pink bollworm, in 2009. This led to the production of a second generation of Bt crops which have multiple Bt proteins to overcome the problem of resistance. It has been reported that the pest communities that affect such crops are changing, with an increase in the prevalence of pests with sucking mouth parts, which are not affected by the Bt toxins. Clearly the battle against crop pests is far from won.

Another type of GMO that is often used in agriculture is herbicide-resistant crops. The most commonly used varieties of these are Roundup Ready sorghum and maize. The gene used for the modification was derived from a soil species of the bacterial genus Agrobacterium. Such plants are resistant to glyphosate, allowing its use to reduce weed species in crop fields, thereby increasing yields.

Another genetic modification proposed for use in agriculture is the augmentation of the nutritional value of a given crop. One such example is ‘Golden Rice’. This rice has the genes for the production of beta-carotene (a precursor of vitamin A which is usually absent in rice), with the aim of countering the dietary deficiency of vitamin A (see box on page 155). One of the two inserted genes (carotene desaturase – CRTI) is from the bacterium Pantoea ananatis (previously known as Erwinia uredfioris).

The application of biotechnology to agriculture is largely debated, and further research into both the positive and negative effects is required. The consequent adoption of agricultural production and management practices based on biotechnology may contribute to abating some of the negative consequences of the Green Revolution.
Biopharmaceutical and biomedical applications

Complex interactions between soil organisms, such as avoiding predation and competing for food and space, has led to the evolution of a range of mechanisms that allow organisms to gain advantage, in both attack and defence. One of these is the secretion of chemical substances with antibacterial/antifungal (i.e. kills bacteria or fungi) or bacteriostatic/fungistatic (i.e. inhibits growth of bacteria or fungi) properties. These are known as antibiotics. (128)

Chemicals of microbial origin can be isolated and used as antibiotics; these include the well known penicillin (isolated from the soil fungus Penicillium chrysogenum) and semi-synthetic derivatives, as well as amynoglicosides (e.g. streptomycin, kanamycin), lipopeptides (e.g. daptomycin) and tetracyclines (all isolated from soil actinomycetes (see page 35), such as Streptomyces spp.). Besides antibiotics, other valuable therapeutic agents and supplements may be found in soil organisms. Steroids and other hormones, as well as biologically active forms of amino acids (e.g. lysine, glutamic acid, tryptophan) are also common products of microbial synthesis by either naturally occurring or genetically engineered soil microorganisms. In recent years, some microbial secondary metabolites (e.g. red pigments) have also been discovered that exhibit potential anti-tumour and cholesterol-lowering activity, with potential anti-carcinogenic and cardiovascular benefits, respectively.

A number of soil invertebrate groups can be used as bioindicators, including earthworms, enchytraeids, terrestrial isopods and collembolans (see Chapter II). Plant species, such as the turnip (Brassica rapa), oats (Avena sativa) and lettuce (Lactuca sativa), can also be used for their bioaccumulating capacity to detect pollutants in soil (see page 141). The choice of a bioindicator depends on the specific application or threat and the ecosystem of interest. Acceptance of the involved methodology and measurability and costs are generally additional criteria to be considered. However, even within the same system, different microhabitats (e.g. litter layer, foliage, etc.) may be subject to different environmental or ecological changes. Therefore, litter dwellers (e.g. ants and termites, centipedes and millipedes, snails and other molluscs, ground beetles – see Chapter II) or foliage inhabitants (e.g. ants and some groups of leaf beetles, moths and spiders) may also be selected accordingly.

Future prospects and expectations

Although the term is relatively new, the concept of ‘biotechnology’ has existed for thousands of years in the leavening of bread, brewing and other fermentation processes (e.g. in the making of cheese, beer and wine), as well as in direct interventions in animal and plant breeding in farm and agricultural systems. Industrial biotechnology involves industrial-scale processes, such as food and feed processing, manufacturing a range of products and materials, from flavour enhancers to solvents, biofertilisers, biocatalysts, and sources of bioenergy. Due to its large unknown component, soil biodiversity is likely to be an important source of new products for such industrial purposes.

Currently, the scale at which biotechnological production is required in order to meet societal, commercial and industrial requirements is enormous. In order to ensure such feasibility, the targeted organisms (e.g. bacteria) must be able to grow quickly and cheaply, while producing the desired compound (e.g. drug) in large quantities, in ways that are easy and cost-effective to isolate and, subsequently, to recover and purify. Such organisms are hard to find and, considering the vast diversity of life in soils, we are just beginning to scratch the surface.

Along with global climate change and over-population, new challenging targets and refreshing prospects are expected from industrial and environmental biotechnology, whether in terms of impact, mitigation or adaptation strategies. The impacts of such environmental and societal pressures reflect on agriculture, land- and water-management, which are central to our ability to feed our ever-growing population and provide food, energy and fresh water. Adaptation strategies may rely on new and improved crop varieties, with higher nutritional value and increased resistance to drought, pests and diseases, as well as on the exploitation of alternative food products, biomass and bioenergy sources and effective water purification strategies. Contributions to mitigation of the stressors can arise in the form of new or improved biomass conversion and renewable energy, carbon sequestration, sustainable agriculture and land-use measures, and more effective waste management options.

Due to their great diversity, soil organisms offer a lot of resources that are already available, especially in soils with suitable biological, chemical and physical properties. The wealth of natural capital must be further investigated in order to preserve it and evaluate the range of possible applications. Given the many challenges we must overcome to achieve sustainability in light of global climate change and overpopulation, it is vital that we explore the breadth of the options that soil biodiversity provides. Soil biodiversity will be a vital cog in the machine of many adaption and mitigation strategies.
Regulating services – Atmospheric composition and climate regulation

Climate change

Climate change is most likely the greatest challenge that humans will face this century. The role of microbiota in determining the Earth’s atmospheric composition, and hence climate, started with the origin of life. From the first molecules of oxygen produced by marine cyanobacteria 3.5 thousand million years ago, to the production of methane by archaea (see page 32) in the warm, carbon-rich swamps of the Carboniferous period, microbial processes have long been key drivers of, and responders to, climate change. Throughout the history of our living planet, microbes have been the main modulators in determining atmospheric concentrations of greenhouse gases (GHGs), including carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) [129].

Carbon dioxide

The amount of CO₂ in the atmosphere is determined by the balance between photosynthesis (see box on page 35), which consumes CO₂, and respiration, which produces CO₂. It is estimated that ~120 thousand million tonnes of CO₂ are removed from the atmosphere by photosynthesis each year. This is approximately balanced by ~119 thousand million tonnes emitted into the atmosphere by autotrophic (plant – see page 43) and heterotrophic (microbial) respiration.

Soils can act as either a source or a sink of atmospheric carbon. Globally, soils contain a vast amount of organic carbon (~1 550 thousand million tonnes), which is more than the total carbon contained in vegetation and the atmosphere combined. An additional 750 thousand million tonnes of carbon is contained in inorganic forms in soils. These soil carbon stocks are not static, but dynamic over time, with accumulation occurring through plant and animal inputs, and losses via decomposition of soil organic carbon (SOC) leading to the release of CO₂ into the atmosphere. Agriculture and other land-use changes, such as deforestation, that cause soil disturbance, greatly accelerate the decomposition of SOC and thus increase net emissions of CO₂ to the atmosphere. Since industrial activities began (1760–1840), it has been estimated that 40–90 thousand million tonnes of SOC have been released. This is significant considering that the release of 1 thousand million tonnes of soil carbon can result in a 0.5 ppmv (parts per million by volume) increase in atmospheric CO₂.

Soil biodiversity plays both a direct and an indirect role in the flux of carbon (C) to and from the soil. Through the decomposition of organic matter (see page 106), the soil biota are responsible for the release of 60 thousand million tonnes of C via heterotrophic respiration each year. Indirectly, through the regulation of the supply of nutrients (nitrogen, phosphorus and micronutrients – see pages 104-105) that are essential for plant growth, the soil biota influence plant growth and, thus, affect the removal of CO₂ from the atmosphere. There is sufficient evidence to suggest that increasing soil erosion alone could switch the soil from being a sink for carbon to being a source of carbon. The soil biota play a key role in the prevention of soil erosion and, thus, carbon loss through the production of sticky polysaccharides and fungal hyphae that physically bind the soil particles together and limit the susceptibility of soils to erosion (see box on page 149).

Methane

Methane (CH₄) is the second most important greenhouse gas, with a global warming potential (GWP – see box on page 103) estimated to be 26 times higher than that of CO₂. Terrestrial CH₄ emissions are under even greater microbial control than that of CO₂. Natural emissions (~250 million tonnes a year) that primarily (~95 %) originate from terrestrial ecosystems, including natural wetlands, result from the activity of a group of microbes known as archaea (see page 32) through the process of methanogenesis. Soil arthropods (see Chapter III) contribute ~20 million tonnes of CH₄ every year. These are exceeded by anthropogenic emissions (~320 million tonnes per year) from rice cultivation, livestock farming, landfill and fossil-fuel extraction that (with the exception of fossil-fuel extraction) promote abundance and activity of methane-producing biota.

Most of the atmospheric CH₄ is removed by chemical reaction. Nevertheless, a considerable amount (~30 million tonnes per year) of atmospheric CH₄ is consumed by specific soil bacteria through the process of methanotrophy. Additionally, soil bacteria consume between 50 and 90 % of the CH₄ produced in soils. Ultimately, biological removal of atmospheric CH₄ determines whether the terrestrial ecosystem is a net sink for or source of CH₄. Because of the strong biological control of methanogenesis and methanotrophy, soil microbiota are key regulators in the CH₄ flux to and from the atmosphere.

Soil fungi and carbon storage

• Soil is one of the Earth’s main carbon sinks. Soil organic matter contains approximately three times as much carbon as the atmosphere.
• Mycorrhizal fungi (see page 40) are important regulators of soil organic matter.
• Researchers have demonstrated that ecosystems dominated by trees that form relationships with ectomycorrhizal (EM) fungi store about twice as much carbon as systems in which arbuscular mycorrhizal (AM) fungi dominate. [130]
• Differences in the soil bacterial community can also be an important determinant of soil carbon sequestration. It has been reported that soil profiles dominated by specific phyla (acidobacterial) store more carbon compared to soil dominated by Proteobacteria (see page 34).
• This mechanism could be regulated by nitrogen availability. High levels of N availability can reduce microbial mining of soil organic matter and, thus, promote soil carbon storage.
• Free-living soil microbes influence climate warming by increasing the carbon dioxide released from soils into the atmosphere. This effect is smaller in EM-dominated forests and acidobacterial-dominated soil profiles.
• Another explanation might be that trees in these ecosystems allocate more carbon belowground in order to satisfy the greater demands of soil microbes.
Nitrous oxide

The flux of nitrous oxide (N\textsubscript{2}O) from terrestrial ecosystems is predominately biologically controlled through the processes of nitrification and denitrification. Global emissions of N\textsubscript{2}O, which has a GWP 298 times that of CO\textsubscript{2}, are estimated to be 19 million tonnes per year, 36% of which is attributed to anthropogenic activities, mainly from agriculture.

About 55% of natural emissions, and most of the anthropogenic emissions, are released from terrestrial ecosystems. Most of the N\textsubscript{2}O produced by nitrification results from the activity of ammonia-oxidising bacteria and archaea (AOB and AOA, respectively — see pages 52-55). Denitrification is a multi-step process in which each step is carried out by a distinct group of microbes widely distributed across diverse phylogenetic lineages. It is estimated that for every tonne (1000 kg) of reactive nitrogen deposited on Earth, 10-15 kg are emitted as N\textsubscript{2}O through nitrification and denitrification (see page 105). The substrates for N\textsubscript{2}O production (ammonium and nitrate) enter soils via natural biological nitrogen fixation, chemical fixation (lightning and fertiliser production), rainfall, or from the decomposition of plant and animal waste.

Greenhouse gases and their effects

- The greenhouse effect is a process by which thermal radiation from the Earth’s surface is absorbed by atmospheric gases, and is re-radiated in all directions, resulting in an elevation of the average surface temperature above what it would be in the absence of the gases.
- The most abundant greenhouse gases in the Earth’s atmosphere are:
  - water vapour (\text{H}_2\text{O})
  - carbon dioxide (\text{CO}_2)
  - methane (\text{CH}_4)
  - nitrous oxide (\text{N}_2\text{O})

- The concept of Global Warming Potential (GWP) was developed to allow comparisons of the global warming impacts of different gases. Specifically, it is a measure of how much energy the emissions of one tonne of a gas will absorb over a given period of time, relative to the emissions of one tonne of carbon dioxide. The larger the GWP, the more that a given gas warms the Earth compared to carbon dioxide over that time period, usually 100 years. GWPs provide a common unit of measure.
- Therefore, carbon dioxide has a GWP of 1. The GWP of methane and nitrous oxide over 100 years is 25 and 298, respectively. Calculation of the GWP of water vapour is complex as its concentration in the atmosphere depends on air temperature and water availability.
- Venus’s climate is strongly driven by the most powerful greenhouse effect found in the Solar System. The greenhouse gases sustaining it are water vapour, carbon dioxide and sulphuric acid aerosols.

- On Venus, about 80% of the incoming solar radiation is reflected back into space by the cloud layer, 10% is absorbed by the atmosphere and only 10% gets through to heat the surface. However, the radiation emitted by the surface gets trapped by GHGs and results in an amazing 500°C difference between the surface and cloud-top temperatures.

Climate change and feedback responses

There is limited evidence available as to whether the feedback response of climate change will increase (positive feedback) or decrease (negative feedback) GHG emissions. Current evidence suggests that global warming will positively influence the physiological response of the soil biota, and lead to increased decomposition of SOC, resulting in higher respiration rates and levels of CO\textsubscript{2} released into the atmosphere. Similarly, increased microbial activity could lead to increased CH\textsubscript{4} and N\textsubscript{2}O emissions from the soil. However, the extent of such increases in GHG emissions under future climate conditions is widely debated, and estimates are accompanied by large uncertainties. Indirectly, soil biota can influence photosynthesis (see box on page 35) through regulation of the supply of essential nutrients to plants. Under future climate scenarios, the rate of photosynthesis is predicted to increase through warmer temperatures, longer growing seasons and higher CO\textsubscript{2} concentrations. However, this can only be sustained if other nutrients are cycled at an accelerated rate in order to satisfy increasing plant demands for nitrogen, phosphorus and other micronutrients, which will be largely determined by the activities of soil biota.

While microbiota and plants are the main contributors of natural GHG emissions, feedback responses and mitigations, the role of soil dwellers, such as earthworms (see page 58), insects (e.g. ants and termites — see pages 54-55) and small mammals (e.g. rodents — see pages 62-63) is important for the formation of the soil structure (i.e. large pores and tunnels) that directly influence gas permeability and the activity of the microbiota responsible for the abovementioned functions.

The strong correlation between increased human-mediated soil disturbance and increased GHG emissions is clear, but a better understanding of how soil management affects microbial-mediated processes and biodiversity will serve to design management practices that minimise the impacts of future climate conditions on GHG emissions.

Mitigation

While biota act as a source of GHGs, they can also play a major role in mitigation, through careful manipulation and management of soils. Switching land uses (from arable to forestry) or management practices (from tillage and high input of nitrogen fertilisers to a no-tillage and low input system — see Chapters V and VI), where appropriate, will lead to low energy decomposition pathways, dominated by fungal communities and oligotrophic bacteria (see pages 33-35), favouring slower rates of carbon turnover and less CO\textsubscript{2} being released from soils. Such a conversion would also reduce CH\textsubscript{4} flux. Furthermore, it has been proposed that an annual increase of 0.004% of C stored in soils (4 grammes of carbon for every 1 000 grammes of carbon currently stored in soils) would almost completely neutralise the predicted increase in GHG emissions, thus allowing countries to remain within the +2°C limit in atmospheric warming. Practically, this increase would only be achievable in managed soils, resulting in less mitigation potential because of the emissions associated to the management practices; however, the issues clearly demonstrate the importance of preserving and increasing soil carbon stocks.

In agriculture, reduced-tillage practices (see pages 146-147) support the activities of earthworms and other soil fauna as well as fungal communities, and promote C sequestration and nitrogen (N) cycling. Similarly, the conversion of croplands into permanent pastures and the manipulation of plant diversity could be used to reduce the amounts of carbon released from soils. Improved management of flooding frequency in rice cultivation would increase oxygenation and reduce CH\textsubscript{4} emissions, as may the use of effective inhibitors of methanogenesis. Similarly, using nitrification inhibitors can limit denitrification and N\textsubscript{2}O emissions. In addition, to improve drainage and limit denitrification, changes in land management have a great potential for further reducing N\textsubscript{2}O emissions through the use of slow-release fertilisers and, subsequently, decreasing in the amounts of nitrogen that are likely to result in N\textsubscript{2}O emissions.
Currently, the global carbon budget is unbalanced, meaning that the release of CO₂ into the atmosphere is higher than fluxes into carbon sinks, such as peat and some tropical soils. This unbalance is caused by direct human activities.

It is estimated that ~215 Gt (gigatonne = 10¹² kg) of carbon are removed from the atmosphere annually through photosynthesis (~125 Gt) and absorption by the oceans (~92 Gt). Total annual emissions amount to an estimated ~219 Gt via the auto- (~60 Gt) and heterotrophic (~60 Gt) respiration (see page 30) of terrestrial systems and releases from the oceans into the atmosphere (~90 Gt). In addition, anthropogenic activities, primarily through the use of fossil fuels, account for ~9 Gt C per year.

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Nitrogen cycle

The nitrogen cycle is the process by which nitrogen (N) is converted into its various chemical forms. Nitrogen is necessary for all known forms of life on Earth to produce proteins. As such, the nitrogen cycle is an important part of every ecosystem. A large portion of the nitrogen cycle takes place in the soil. The main nitrogen inputs to the soil are made through:

- biological fixation
- industrial fixation (i.e. commercial fertilisers)
- soil organic matter
- rain (deposition of industrial emissions)
- crop residues and animal manure

Nitrogen, already present in or added to the soil, is subjected to several transformations that dictate its availability to plants. Nitrogen is present in the environment in a variety of chemical forms, including organic nitrogen, ammonium ($\text{NH}_4^+$), nitrite ($\text{NO}_2^-$), nitrate ($\text{NO}_3^-$), nitrous oxide ($\text{N}_2\text{O}$) and inorganic nitrogen gas ($\text{N}_2$). The main processes of the nitrogen cycle that transform nitrogen from one form to another are the following:

- ammonification (fixation) is the process whereby atmospheric nitrogen is converted into ammonium
- ammonification or mineralisation is the conversion of organic nitrogen into ammonium
- nitrification is the conversion of ammonia into nitrates
- assimilation is the uptake of nitrogen from the soil by plants, in the form of either nitrate ions or nitrate ions
- denitrification is the reduction of nitrates back into nitrogen gas

Nitrogen cycle and soil biodiversity

Chemical engineers (see box on page 95) play a key role in the nitrogen cycle. Firstly, bacteria or fungi convert the organic nitrogen from decaying animals or plants into ammonium ($\text{NH}_4^+$). A number of microorganisms (e.g. bacteria and fungi) are able to perform this first ammonification step. In N-limited ecosystems, such as the Arctic and Alpine regions (see pages 84-85), some microbes may directly use organic nitrogen forms, such as amino acids, thereby bypassing this mineralisation step. After ammonification, the chemical processes are carried out by specialist groups of bacteria. The nitrification process is carried out by bacteria called ammonia-oxidising bacteria (AOB), which convert ammonia into nitrates ($\text{NO}_3^-$) that are toxic to plants. Other groups of bacteria oxidise nitrates into harmless nitrates ($\text{NO}_3^-$) that are useful for plant growth. Nitrification processes are also carried out by groups of archaea (see page 32) called ammonia-oxidising archaea (AOA). Ammonium can also be directly produced from atmospheric nitrogen by nitrogen-fixing bacteria. Some of these microorganisms are free-living in the soil (e.g. bacteria of the genus Azotobacter), whereas species of Rhizobium (see page 34) live in a symbiotic association with leguminous plants (see page 99).

Plants can absorb ammonium or nitrates from the soil via their root hairs, or through symbiotic relationships with rhizobium bacteria. For the nitrates that are not absorbed by plants, denitrification can take place. This process, which converts nitrates into atmospheric nitrogen, is performed by certain bacteria in anaerobic conditions. These bacteria do not require air, but rather use nitrogen instead of oxygen.

Soil engineers (see box on page 95), such as earthworms and termites (see pages 55, 58), also influence the N cycle. Due to the increased nutrient availability, their structures (e.g. earthworm casts and burrows) are rich in microbial diversity and become preferred sites for a number of soil processes, such as nitrogen fixation. In conclusion, all the described steps clearly show the role played by soil biodiversity in regulating the nitrogen cycle and, consequently, other ecosystem services related to it, especially plant growth support (see pages 98-99).

Phosphorus cycle and soil biodiversity

The phosphorus (P) cycle describes the movement of phosphorus through the soil, water and living organisms. The atmosphere does not play a significant role in this cycle. Phosphorus is an essential nutrient for all organisms since it is incorporated into many molecules that are essential for life, such as DNA (see box on page 30).

The P cycle

For example, studies have shown that P is the limiting nutrient for plant growth. Phosphorus enters the environment from ancient rocks or deposits and is, similar to soil itself, a non-renewable resource. Phosphorus occurs in both organic and inorganic forms (see box on page 104). Soil P chemistry is very complex, with more than 200 possible forms of P compounds being affected by a variety of physical, chemical and biological factors. The relative amounts of each form of phosphorus vary greatly among soils, with the total amount of P in a clayey soil being up to ten times greater than in a sandy soil (see Chapter I). Soil organic P comprises many different compounds, the majority of which are of microbial origin. Organic P is locked up in the soil and is generally not available for plant uptake until the organic materials are decomposed and the phosphorus released via the mineralisation process. Mineralisation is carried out by soil microorganisms (e.g. bacteria) and, similar to nitrogen, the rate of P release is affected by abiotic factors, such as soil moisture, composition of organic material, oxygen concentration and pH. For example, P availability to plants in most soils is greatest when the soil pH is in the range of 6 to 7. The reverse process to mineralisation, known as immobilisation, refers to the tie-up of P by microbes that use it for their own nutritional needs. Microorganisms may compete with plants for P when concentrations are low. However, the roots of many plant species enter into symbiosis (see box on page 33) with mycorrhizal fungi (see page 40), which promote the acquisition of phosphorus.

Microbial mineralisation allows the slow release of P into the soil and is generally not available for plant uptake until the organic materials are decomposed and the phosphorus released via the mineralisation process. Mineralisation is carried out by soil microorganisms (e.g. bacteria) and, similar to nitrogen, the rate of P release is affected by abiotic factors, such as soil moisture, composition of organic material, oxygen concentration and pH. For example, P availability to plants in most soils is greatest when the soil pH is in the range of 6 to 7. The reverse process to mineralisation, known as immobilisation, refers to the tie-up of P by microbes that use it for their own nutritional needs. Microorganisms may compete with plants for P when concentrations are low. However, the roots of many plant species enter into symbiosis (see box on page 33) with mycorrhizal fungi (see page 40), which promote the acquisition of phosphorus.
Regulating services – Atmospheric composition and climate regulation

Decomposition

In a continuous cycle of life and death, plants, flowers and animals live and die. What remains is either broken down by a huge array of microorganisms (e.g. bacteria and fungi – see pages 33-35, 38-41) already living belowground or carried there by invertebrates, such as isopods, earthworms or beetles (see pages 56, 58-59), where it continues to break down. The reduction of raw organic materials to a compost is known as decomposition and results in the production of soil organic matter (SOM). In fact, SOM can be defined as the organic component of soil, consisting of plant and animal residues at various stages of decomposition. Nutrients that are created from the decomposition processes are dissolved when water is added to the soil, providing plant roots with a constant supply of nourishment over time. Decomposition processes also generate long-term SOM and play an important role in the global nutrient cycles. [134]

Decomposition of organic matter in soils is accomplished largely by microorganisms, often in association with invertebrates. Soil microbes, the chemical engineers (see box on page 95), have the appropriate enzymes to break down complex molecules (e.g. lignin) present in plant debris. Soil invertebrates accelerate decomposition in several ways: 1) arthropods (see Chapter II) carry plant matter below the soil surface, where it is prevented from being removed by wind or water and stays moist longer, resulting in more rapid decomposition; 2) organic matter can be ingested, digested and excreted (e.g. by earthworms); 3) organic matter is shredded into smaller pieces, giving fungi and bacteria more surface area for attack; 4) they create macro pores, or soil cavities, that allow more water to enter the soil, thus extending activity times for the decomposers, as most are only active in moist environments.

**Types of humus**

- There are three main types of humus: Mor, Moder and Mull.
- Mor humus is a thick mat of undecomposed to partially decomposed litter, typical of coniferous forests.
- Moder humus is formed by undecomposed and partially decomposed remains of broad-leaved deciduous forest litter.
- Mull humus is well-decomposed organic matter, produced in very biologically active habitats.

Since the decomposition process is carried out by living organisms, it is affected by several environmental variables, including soil moisture, temperature and pH.

The prime source of SOM is plant debris of all types, such as dead leaves and branches, that fall onto the soil and are then decomposed at varying rates depending on their composition. Organic compound degradation is ranked, in descending order, as follows:

1. sugars and starches
2. proteins
3. hemicelluloses
4. cellulose
5. lignins and fats

Plant residues containing these compounds form the fresh organic matter that is converted into a more stable and resistant form known as ‘humus’, through decomposition processes, also known as ‘humification’.

For example, cold and acidic soils, such as those of peatlands and boreal forests (see page 79), have low microbial activities and low invertebrate diversity, which means that plant material is decomposed slowly. In tropical forests (see page 78), the whole process is much more rapid because moist conditions and high temperatures enhance biological activity. Finally, decomposition processes are affected by the type of residues and, in particular, by their carbon-to-nitrogen (C:N) ratio.

**Carbon-to-nitrogen ratio**

The carbon-to-nitrogen ratio represents the relative proportion of the two elements present in a substance. For example, a material containing 50 times more carbon than nitrogen is said to have a C:N ratio of 30:1. The C:N ratio of the organic material influences its decomposition. Indeed, organisms that decompose organic matter use carbon as a source of energy and nitrogen for building cell structures (e.g. proteins). In the soil, organic matter with excess carbon can create problems. To continue decomposition, the microbial cells use any available soil nitrogen, for which they have to compete with plants. This is known as ‘robbing’ the soil of nitrogen, and reduces the availability of nitrogen as a fertiliser for plant growth. So, if there is too much carbon, decomposition slows and plant growth may be problematic. Conversely, when the energy source (i.e. carbon) is less than that required for converting available nitrogen into proteins, decomposition is faster and organisms make full use of the available carbon and get rid of the excess nitrogen as in the form of ammonia released into the atmosphere (see page 105). This also can also be an issue as it results in losses of nitrogen from the soil.

Since organisms use about 30 parts carbon for each part nitrogen, an initial C:N ratio ranging from 20 to 30 promotes rapid composting. Examples of C:N ratios in organic material are:

- food scraps: 15:1
- grass clippings: 19:1
- oak leaves: 26:1
- leaves: from 35:1 to 85:1
- maize stalks: 60:1
- straw: 80:1
- pine needles: from 60:1 to 110:1
- farm manure: 90:1
- alder sawdust: 134:1
- newspaper: 170:1
- Douglas fir (Pseudotsuga menziesii) bark: 490:1

In conclusion, all soil organisms, from bacteria to the largest of the invertebrates, are part of complex interactions that lead to the decomposition of organic matter. As decomposition is the main process that recycles nutrients (e.g. carbon and nitrogen) back into the soil, soil biota is crucial to nutrient cycles and, consequently, to the regulation of the atmospheric composition and climate.
Regulating services – Water supply and quality

Water supply

The safeguarding of soil hydrological services relies strongly on the activity of soil biota. Their role in maintaining soil structure, has both direct and indirect implications for water supply and water quality regulation. In particular, those organisms contributing to the formation of macropores and tunnels have a direct effect on water, air and nutrient movement through soil profiles. They include all the burrowing soil creatures, such as earthworms, social insects and their larvae (see page 54-55, 58, 60), as well as some vertebrate groups, such as moles, rabbits, foxes and badgers (see page 62-63). (135)

Some numbers may explain the ability of soil organisms to dig soil. For example, some earthworm species in Tasmania dig burrows with diameters that range from < 1 mm to > 10 mm, and depths of up to 15 m. Furthermore, it has been conservatively estimated that earthworms can dig about 17 - 40 tonnes of soil per hectare per year. Just one tropical species, Eudrilus eugeniae (the ‘African Night Crawler’), produces around 157 tonnes per hectare of surface casts per year. With regard to ants, there is a general trend of increasing subterranean tunnel networks with increasing colony size. For example, one of the largest colonies ever found was in Japan, containing over 300 million worker ants and one million queens living in 45 000 nests interconnected by underground passages over an area of 2.7 km².

The European mole (Talpa europaea) continuously searches for food, running through its network of tunnels, which can often reach lengths of over 70 m and can vary in depth from just under the surface to up to 70 cm deep. The Zambian mole-rat (Fukomys damarensis) digs some of the longest tunnels in the natural world. A single underground colony, containing just ten mole-rats, can stretch for 2.8 kilometres. Another great digger is the badger. Its tunnels can have a combined length of several hundred metres, although individual tunnels rarely exceed 15 metres in length. All these numbers clearly show the positive impact of soil-living organisms on water circulation in the soil.

Hydraulic engineers in Malagasy rainforests

- In the southeastern part of Madagascar, very fragile soils are protected from erosion by structures created by soil ecosystem engineers (i.e. arthropods in the litter layer and earthworms in the mineral horizon). (136)
- Rainforests grow on very deep soils that are highly prone to erosion due to their specific composition and structure.
- The soil is protected by a 10 - 15 cm thick humic horizon mainly comprised of arthropod (especially dipteran larvae) faecal pellets that are greatly hydrophilic. This layer can absorb between 20 and 100 mm rainfall, thus preventing surface runoff and subsequent surface erosion.
- Below this humic layer that acts as a sponge, the mineral soil exhibits subhorizontal earthworm galleries that form a network of tubular voids that are regularly spaced and with similar diameters. These galleries connected to the surface by vertical sections likely allow for drainage of water from the surface layer to deeper soil layers and to aquifers.
- Deforestation and the consequent elimination of the ecosystem engineers that maintain these structures trigger soil erosion.

Water quality

Soil detoxification and water ‘filtration’ are essential for maintaining the quality of soil and, consequently, that of our surface and groundwater resources. Soil water purification is carried out abiotically (e.g. interactions with organic and inorganic soil particles) and biotically (through adhesion, binding and adsorption onto microbial cells and soil organisms), with any potential soil contaminants also being subjected to dispersal through bioturbation and burrowing activities. In addition to these physical processes, biotransformation and degradation of xenobiotic compounds and contaminants (e.g. metals, pesticides and solvents) within the soil also take place in natural environments, carried out mainly by native heterotrophic (i.e. carbon-eating) soil bacteria (e.g. genus Pseudomonas, Micrococcus, Streptomyces, Corynebacterium and Theobacillus – see page 33-35) and most wood-degrading fungi (e.g. white-rots, such as Phanerochaete chrysosporium and Trametes versicolor – see page 38-41, 100).
Soils are also home to organisms that can cause disease in animals, humans, and plants. It should be stressed, however, that the vast majority of organisms found in the soil do not cause diseases but rather provide a myriad of ecosystem services that are vital for the maintenance of life on Earth, including the regulation of pathogens and pests. Furthermore, disease-causing organisms are often not efficient competitors in the soil and, as such, increased soil biodiversity is usually correlated with reduced numbers of disease-causing organisms. Here we discuss some of the organisms found in the soil that can cause diseases in humans, livestock, and crops. We also present the ability of the soil biota to regulate the spread and incidence of pathogens and pests [137].

Human and animal diseases

There is considerable overlap between human and animal diseases caused by soil organisms – after all, humans belong to the animal kingdom. There are a few notable exceptions, which are discussed in more detail below. There is no general consensus on what constitutes a soil-borne disease, but in a report published by the European Commission, soil-borne diseases are defined as: ‘...resulting from any pathogen or parasite, transmission of which can occur from the soil, even in the absence of other infectious individuals’.

It is important to note that the disease can be spread even in the absence of infectious individuals. Many diseases could be passed through the soil in quite contined circumstances. For example, many viruses can only survive on the soil surface for a very short period of time. It is unlikely that such diseases would infect a new host if the infectious individual is no longer present – transmission through the air when in close contact with an infected person is much more likely. If all such diseases were included, it could potentially ‘cloud the water’ in terms of identifying soil-borne diseases and potential mechanisms by which their incidence may be reduced.

Euedaphic pathogenic organisms and soil-transmitted pathogens

Human and animal pathogens and parasites can be divided into two groups. Euedaphic pathogenic organisms (EPO), which are true soil organisms (i.e. their usual habitat is the soil and they are able to complete their lifecycles in the soil without infecting a host). These include most of the bacterial pathogens and all of the fungal pathogens, some of which have important implications for human health. For example, Clostridium tetani is an EPO with a worldwide distribution in soil and is the causative agent of tetanus. In 2006, 290,000 people died of tetanus, of which 250,000 were neonatal deaths.

The other group consists of soil-transmitted pathogens (STP). These organisms must infect a host in order to complete their lifecycles. Many viruses can only survive on the soil surface for a very short period of time. It is unlikely that such diseases would infect a new host if the infectious individual is no longer present – transmission through the air when in close contact with an infected person is much more likely. If all such diseases were included, it could potentially ‘cloud the water’ in terms of identifying soil-borne diseases and potential mechanisms by which their incidence may be reduced.

STP will often be in a dormant form within the soil and are likely to contribute much less to the provision of ecosystem services. As such, treatments or land management practices that reduce the numbers of such organisms within the soil are likely to have much more limited impacts on the provision of ecosystem services.

Domestic animal diseases

Soil-borne pathogens may also affect domestic animals, such as livestock, which both economic and health implications. The most direct economic impacts of livestock diseases are loss of production and/or productivity, and the cost of treatments. Estimates of the economic costs to agriculture of the outbreak of foot-and-mouth disease in the United Kingdom suggest a loss of approximately 20% of the total income from farming in 2001. The causative agent of bovine spongiform encephalopathy (BSE, commonly known as mad cow disease), the severe acute respiratory syndrome (SARS) and avian influenza (H5N1) can survive for extended periods of time in the soil. These diseases are estimated to have caused over US$20 thousand million (approx. €19 bn) of direct economic losses over the past decade and much more than US$200 thousand million (approx. €186 bn) in indirect losses.

From a human health perspective, zoonotic diseases (passed from animals to humans) represent the majority of infectious diseases that have the potential to become pandemic. However, it should be noted that the majority of zoonotic diseases are not soil-borne, or at most are STP. Of the 1415 known human pathogens, 62% are of animal origin. On average, a new disease has emerged or re-emerged each year since the Second World War, and 75% of these were zoonotic. The influenza pandemic that killed 50-100 million people between 1918 and 1919 had largely faded from public memory by the late 1990s and early 2000s, when outbreaks of SARS and avian influenza occurred. Other examples of soil-borne zoonotic diseases include: anthrax, giardiasis, leptospirosis, Q fever and tuberculosis.

Plant diseases

Plants are the key primary producers in most terrestrial ecosystems and generally exploit soils for resources, using complex root systems.

The root exudates allow for the maintenance of a dynamic and nutrient-rich niche around the root-soil interface called the rhizosphere. The diversity of nutrients and plant secondary metabolites present in the exudates allows for the enrichment of specific taxonomic or functional groups of microbes in the rhizosphere. Soil microbes interact with plant tissues and cells with different degrees of dependence, and have developed several strategies for adapting to the plant environment.

Plant-microbe interactions include competition, commensalism, mutualism, and parasitism (see box on page 33). However, because of its enormous economic importance, one aspect of plant-microbe interactions that has been extensively studied is the plant-pathogen interaction. Losses caused by soil-borne plant pathogens remain important constraints on efforts to increase plant production and productivity worldwide.

Plant diseases are mainly caused by fungi, viruses, bacteria, nematodes and protozoa. Among fungi, disease-causing organisms mainly belong to the Ascomycota and Basidiomycota groups (see pages 38-39). Fusarium spp., Verticillium spp., Ustilago spp. and Puccinia spp. are well known plant disease causal agents. Among protozoa (see pages 36-37), Phytophthora spp. and Phytophthora spp. are also known for their infectivity. Bacterial disease, by comparison, is less severe and inflicts less economic damage. Most of plant pathogenic bacteria belong to the Actinobacteria and Proteobacteria phyla (see pages 33-35). The most common plant pathogenic bacteria include Agrobacterium spp., Erwinia spp., Xanthomonas spp. and Pseudomonas spp. Similarly, some nematodes (e.g. Globodera spp. and Meloidogyne spp.) – see pages 46-47) parasite crop roots and cause significant crop loss in the tropics and subtropics. The severity of damages and economic costs can be minimised through the use of agrochemicals to control disease-causing organisms, by selecting cultivars that are resistant to particular diseases or using agronomic practices (e.g. crop rotations, seed treatments).

Anthrax and soil

- Bacillus anthracis is the name of the causative bacterium of the disease anthrax.
- Despite perhaps being more infamous for its potential use as a bio-warfare agent, the bacteria is actually a relatively common disease of wild and domestic animals, as well as livestock, causing approximately one death per million animals at risk.
- Cases have been declining since the second half of the 20th century due to control and prevention programmes, including measures, such as vaccination, being introduced.
- It can, very occasionally, infect humans but it seems that birds have a natural resistance to anthrax disease.
- The bacterium itself is highly robust and able to dehydrate itself to form a resistant spore that allows it to survive on, for example, times of drought.
- In this state, the organism is also resistant to high temperatures, freezing cold and many disinfectants. The organism thrives particularly well in alkaline soils and is able to grow when conditions, such as moisture, temperature and access to nutrients, are favourable.

### Anthrax

#### Multiplication of bacteria

1. Germination
2. Spores
3. Multiplication of bacteria
4. Spores

#### Spores

- **Bacillus anthracis**, the cause of the anthrax disease
- **Implies anthrax lifecycle.** The disease affects almost any animal, but those most susceptible are large herbivores, such as cows. The bacterium responsible for this disease can survive as spores in the soil for extended periods of time (CDC, 2012).
Pest and pathogen regulation

Pests and pathogens are regulated or maintained below harmful levels by a specific combination of:

a. **biotic factors**, such as predators, pathogens, competitors and host plants.

b. **abiotic factors**, such as climate and land use (agricultural or urban).

c. **socio-economic factors**, such as disease or pest management.

The relative role of abiotic, biotic, and socioeconomic factors in regulating specific pathogens and pest systems is largely unknown. Considering the biotic factors, different components of biodiversity may be involved in the regulation processes. Analyses have shown that, on average, increasing the diversity of natural enemies (i.e., predators, parasites and pathogens) generally strengthens pest suppression. Therefore, it is possible to use biologically control pests by means of other organisms. Biocontrol can be obtained through three main strategies: conservation, augmentation or importation of natural enemies.

Conservation is based on the preservation of existing natural enemies by choosing cultural, mechanical or selective chemical controls that do not harm beneficial species. For example, the elimination or reduction of the use of broad-spectrum, persistent pesticides can allow soil-living predators (e.g. beetles – see page 59) to survive and reproduce.

When resident natural enemies are insufficient, their populations can sometimes be increased (augmented) through the purchase and release of commercially available beneficial species. There are commercially available suspensions or formulations using living microorganisms, such as bacteria, fungi, viruses or nematodes (see Chapter II) for the biocontrol of slugs, ants, flies (e.g. plant viruses), caterpillars, etc. The type of organism used is dependent on the pest population to be controlled. For example, the entomopathogenic nematode Steinernema scapteriscus (see pages 46-47) can be applied to control some mole crickets (Scapteriscus spp.).

Classical biological control, also called importation, is primarily used against exotic pests that have inadvertently been introduced from elsewhere. Many organisms that are not pests in their native habitat become unusually abundant after colonizing new locations without their natural controls. Researchers go to the pest’s native habitat, study and collect the natural enemies that kill the pest there, then transport promising natural enemies back for testing and possible release. This type of practice needs to kill the pest there, then transport promising natural enemies back to the pest’s native habitat, study and collect the natural enemies that kill the pest there, then transport promising natural enemies back for testing and possible release.

Besides these examples of biocultural strategies realised through human interventions, there are also cases of natural biocontrol, such as predatory and herbivorous mites (see page 49). Phytophagous (plant-eating) mites are a serious threat to their host plants; in the absence of predators they tend to over-exploit their food source. To prevent such a crash and maintain as much leaf area as possible, host plants may defend themselves in various ways, one of which is to increase the effectiveness of a group of natural enemies, the predatory mites, of the phytophagous mites. Predatory mites locate herbivorous mites, their prey, using herbivore-induced plant substances that the plant releases when the herbivorous mite starts feeding on it. In so doing, plants can activate their own bodyguard as soon as any damage is inflicted.

With regard to plant pathogens, it has been shown that the beneficial microbes in soils, also known as plant growth-promoting bacteria (PGPB), can affect plant growth through different direct and indirect mechanisms (see pages 98-99). In particular, some examples of the indirect mechanisms, which can probably be active simultaneously or sequentially at different stages of plant growth, are related to the repression of soil-borne pathogens (through the production of hydrogen cyanide, siderophores, antibiotics and/or competition for nutrients). Although significant control of plant pathogens or direct enhancement of plant development has been demonstrated by PGBP in the laboratory and in the greenhouse, results in the field have been less consistent. Because of these and other challenges in screening, formulation and application, PGBP have yet to live up to their potential as commercial inoculants. Recent progress in our understanding of their diversity, colonisation ability, mechanisms of action, formulation and application should facilitate their future development as reliable components for a more sustainable regulation of plant diseases.

The plant transformer

- *Rhizobium* roehebacter (previously known as Agrobacterium tumefaciens) is a soil bacteria known as the causal agent of crown gall disease (also known as plant tumour) in over 140 species of plants. It is a member of the family Rhizobiaceae which also includes the nitrogen-fixing legume symbionts that are beneficial bacteria for plants.

- The infection process of this bacterium consists of the transfer of a portion of its DNA (see box on page 30) into plant cells. This DNA contains genes that can generate the production of the enzymes necessary for the bacteria. The inserted DNA also contains genes that lead to the production of plant hormones responsible for the formation of the plant tumour.

- The DNA transmission abilities of *Rhizobium* have been vastly explored in biotechnology and molecular biology as a means of inserting foreign genes into plants (genetic transformation). This possibility was first described in 1977 by researchers from Ghent University in Belgium.

### Plant pathogens and pests

- A pest is an organism that has characteristics regarded as injurious or unwanted. Plant pests are herbivores (e.g. insects) that extensively eat plants, thus damaging them.

- A pathogen is a biological agent that causes disease or illness to its host. Plant pathogens are the microorganisms (e.g. bacteria and fungi) that cause plant diseases.

**Suppressive soils**

Although extensively studied, pathogenic interactions represent only a fraction of the overall plant-microbe interactions. The majority of plant-microbe interactions are either commensalistic or mutualistic (see box on page 33). The vast majority of plants usually benefit from these microbial associations in terms of growth enhancement, nutrient uptake, disease reduction and/or stress reduction.

It has also been suggested that plants can specifically attract microbes for their own benefit. This selection process allows for the recruitment of different groups of plant-associated microbes possessing general plant growth-promoting traits. Once recruited, these microbes undergo host-specific adaptations, the outcome of which is a highly specialised mutualism. Such mutualisms may make plants better able to tolerate plant-associated microbes without recognising them as pathogens, while the microbes, in turn, become more responsive to the plant’s metabolism.

The diversity of microorganisms in soil is critical for the maintenance of soil health and quality, as a wide range of specific soil microorganisms play important roles in the suppression of soil-borne plant diseases and in plant growth promotion in agriculture. In fact, all natural soil possesses some ability to suppress the activity of plant pathogens thanks to soil microorganisms (general disease suppression). ‘Specific suppression’ occurs when specific microorganisms lead soils to be suppressive against a disease. Development of disease suppression in soils has been reported for many diseases, including potato scab caused by Streptomyces spp., Fusarium wilt disease of several plant species, Rhizoctonia damping-off disease of sugar beet, and the take-all disease of wheat caused by Gaeumannomyces graminis var. tritici.
Supporting services – Soil formation and maintenance

Soil formation

As soils form, mature and age, they pass through a number of different stages, each of which is associated with specific species composition and structure in soil communities and plants. Soil biodiversity actively contributes to the transition from one stage to another, thus contributing to the formation of soils as one of the main factors that supports habitats (see box to the right) for itself and other living creatures. [66, 118]

Stage 1

In Stage 1, bedrock is exposed and weathering begins. Living communities are essentially comprised of microorganisms that form bacterial and algal crusts (biocrust – see page 73) and other structures, with a progressive development of a food web mainly comprised of invertebrate microfauna: protists, nematodes, rotifers (see pages 36-37, 45-47), plus a few meso-faunal components: collembolans and mites (see pages 49-50). Stage 1 is observed, for example, in the years following volcanic deposition or the recent exposure of rocks after glacial retreat due to melting. Depending on climatic conditions, this stage may only last from a few years to decades (e.g. tropical lava deposits) or persist for undefined periods of time (e.g. polar ecosystems).

Plants then appear, at first in the form of mosses and ferns, plus a number of pioneer plants (such as species of the family Bromeliaceae, e.g. pineapple, in the humid tropics or Ericaceae, e.g. heather, in temperate areas). Accumulation of organic matter from their dead materials allows for the development of a first horizon (the A Horizon – see page 10), which is a mixture of fine-textured mineral elements and organic matter. While organic matter produced in these ecosystems is often of a rather low quality, it tends to accumulate on the soil surface, forming increasingly thick accumulations in which a wide diversity of plant and animal remains. Soil in the A horizon is often acidic, humification (production of humus – see page 106) of all types transformers and play a vital role in the decomposition and humification (production of humus – see page 106) of all types of plant and animal remains. Soil in the A horizon is often acidic, which may limit the activity of ecosystem engineers, especially earthworms (see page 58).

Stage 2

In Stage 2, deeper soils allow for the development of bushes and trees. The weathering of the bedrock is accelerated by the direct effects of roots, or indirectly by the effects of different substances (e.g. organic acids) issuing from the decomposing leaf litter. Lixiviation (see box to bottom left) of organic acids from decomposing litter triggers the migration of clay minerals to the bottom of the profile where they form a B horizon, causing an eluviated E horizon to appear.

Vegetation is often dominated by coniferous trees and litter accumulates that form a very active litter system in which fungi (see pages 38-41), collembolans, mites and enchytraeids (see page 48) are abundant. These soil organisms are litter transformers and play a vital role in the decomposition and humification (production of humus – see page 106) of all types of plant and animal remains. Soil in the A horizon is often acidic, which may limit the activity of ecosystem engineers, especially earthworms (see page 58).

Lixiviation vs. eluviation vs. illuviation

- Lixiviation and eluviation are both processes that influence soil formation.
- Lixiviation, also known as leaching, is the loss of mineral and organic solutes as a result of percolation, which is the movement and filtering of water through soil pores.
- Eluviation is the loss of mineral and organic colloids as a result of percolation. Eluviation differs from leaching in that it affects suspended, not dissolved, material.
- Illuviation, however, is the accumulation of dissolved or suspended soil materials in one area or layer as a result of lixiviation or eluviation from another.

What is a habitat?

- A habitat is a geographical unit that effectively supports the survival and reproduction of a given species or of individuals of a given species.
- The biological composition and the abiotic factors therein describe the geographical unit.
- Other organisms include the plants, animals, fungi, bacteria, viruses and protists that also live in a given habitat.
- Abiotic factors include the soil’s physical and chemical properties, water availability, temperature, sunlight, air quality and landforms that facilitate resting, foraging, nesting, mating and other activities.
- The term habitat is one of the most misused and poorly defined in the field of ecology. This is due to the fact that some authors have emphasised the geographical nature of the term, while others have stressed the organism associations inherent in the definition.
- Actually, geographically associated species and abiotic factors are all inextricably linked to the concept of a habitat.
Stage 3

Stage 3 marks the full maturity of the soil system as vegetation reaches full development and soil communities reach their maximum levels of activity and diversity. Plant communities have become fully established, and deciduous trees produce increasingly high-quality organic materials that stimulate biological activity in the soil [66, 118]. Ecosystem engineers become predominant and accumulate their biogenic structures (mainly earthworms, ant and termite galleries, casts and constructions) in their respective functional domains of influence. These are especially earthworms of the anecic and endogeic groups (see page 58) that exhibit deep burrowing activity and mix the soil (known as ‘bioturbation’). The same activity is also carried out by other organisms, such as ants, termites and beetles (see pages 54–55, 59). The dominant group of organisms performing this function varies among ecosystems. Root systems penetrate into deeper soil horizons using channels created by these invertebrates. This improves the resilience (adaptability – see page 97) of tree communities. Natural soil fertility is at its maximum, as is the provision of other soil ecosystem services, such as:

- a. hydrological functions, including enhanced infiltration and water retention in deep soils, facilitated by numerous connected biopores (see page 107)
- b. climate regulation promoted by carbon accumulation in woody biomass and soil organic matter, since biomass production and sequestration of organic matter in stable bio-aggregates are at their maximum (see pages 102-106)
- c. plant growth support (see pages 98-99) and biological control (see pages 108-109) are maximised due to the dense populations of generalist predator and diversity in pest communities which limits the impact of the most aggressive ones; increased robustness of plants due to optimal development of mutualist organisms, such as mycorrhizal fungi (see page 40) and symbiotic bacteria in their rhizosphere

Stage 4

In Stage 4, soil becomes impoverished due to accelerated migration of critical elements of fertility, such as organic matter and iron oxides, to deeper soil horizons. Plant communities change and shift back toward less exigent forms, such as coniferous forests or heathland shrubs. Earthworms and most other ecosystem engineers are progressively eliminated by increasing acidity and low quality of the remaining organic matter.

Later on, highly weathered soils no longer sustain high levels of biomass production, and soil communities progressively lose their structural complexity, returning to patterns comparable to those observed at initial stages, although with much deeper soils. Ecosystem services are provided at lower rates, although with large differences among the different ecosystem service categories. While support of biomass production, and soil communities progressively lose their structural complexity, returning to patterns comparable to those observed at initial stages, although with much deeper soils. Ecosystem services are provided at lower rates, although with large differences among the different ecosystem service categories. While support of biomass production significantly decreases, hydrological function decreases more slowly and can even stop at early stages when drought or excessively cold temperatures limit the progress of biological activity and other processes. Soil formation, scientifically known as ‘pedogenesis’, may also change its course when natural or human-induced events modify any of the three major drivers (i.e. soil biodiversity, bedrock or climate) involved in the process. As a result of different soil communities, geological histories and climatic conditions, soils of the world show a wide diversity in their stages of development (see map page 110).

Earthworms from space

- The South African giant earthworm (*Microchaetus rappi*) is one of the largest earthworms, with an average length of about 1.5 m.
- They have created a unique habitat in the Eastern Cape Province of South Africa known locally as ‘kommetjies’, a wavy or undulating landscape.
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- The exact mechanism for the creation of this landscape, which is visible on satellite imagery, is still being debated. One theory is that the mounds are located in shallow soils where the presence of an impermeable layer (either bedrock or plinthite – see page 22) restricts the movements of the worms. Such soils tend to be very wet after summer rainfall before entering a relatively long period of drought.
- When active, the feeding end of the worm would be located in the more humid part of the soil, with its casting end in more aerated conditions. Large worms would be able to collect more soil material from the wet parts and deposit it on the drier parts. Over time, this aspect would result in a self-sustaining landscape where the scale of the mounds reflects the size of the worms.

Distribution of soil development stages across the Earth

The evolution of soils is a very slow process. Under temperate conditions it can take about 20,000 years to create one metre of soil. When the climate is less favourable, evolution is even slower and can even stop at early stages when drought or excessively cold temperatures limit the progress of biological activity and other processes. Soil formation, scientifically known as ‘pedogenesis’, may also change its course when natural or human-induced events modify any of the three major drivers (i.e. soil biodiversity, bedrock or climate) involved in the process. As a result of different soil communities, geological histories and climatic conditions, soils of the world show a wide diversity in their stages of development (see map page 110).

Charles Darwin and earthworms

- Charles Darwin (1809-1882) was an English naturalist and geologist, best known for developing the theory of evolution.
- His last scientific book was entitled ‘The Formation of Vegetable Mould through the Action of Worms, with Observations on their Habits’.
- The book represents the first significant work on soil formation through the casting activity of earthworms.
- In the conclusion, Darwin writes that worms ‘have played a more important part in the history of the world than most persons would at first suppose’.

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- They have created a unique habitat in the Eastern Cape Province of South Africa known locally as ‘kommetjies’, a wavy or undulating pattern of hollows and mounds. After heavy rains, the hollows can fill up with water.
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The age of soil

As soils evolve, they get deeper and distinct horizons develop. The first horizon (INCIPIENT) forms where organic matter is mixed with minerals detached from the weathering bedrock. Thereafter, another distinct horizon forms (YOUNG) where clay, base and, ultimately, organic matter accumulate (MATURE). Finally a leached horizon (OLD) forms. During this process, soil becomes progressively impoverished in nutrients.

Soil communities comprise four major groups that have different relative importance and functions as soils mature.

- **Microorganisms** are always present, although their composition may vary greatly, with large proportions of nitrogen-fixing algae and cyanobacteria in the earliest stages. Fungi are abundant when leaf litter is continuous and thick, whereas bacteria are more common in humid grasslands and cropped fields where earthworms are numerous.

- **Micropredators** are comprised of a large diversity of small invertebrates of the micro- (< 0.2 mm) and meso- (0.2 to 2 mm) fauna that feed on microbial communities, thus regulating their composition and overall activity. They are the first group to develop in incipient soils, and may also be the only one left in severely degraded soils.

- **Litter transformers** are invertebrates from the meso- and macro- (> 2 mm) fauna that live in and feed on leaf litter. They comprise a large number of micro- and macroarthropods that fragment and digest the partly decomposing litter left by the microorganisms. They are present whenever soil is covered with dead vegetation. They are most numerous and diverse in deciduous forests in temperate regions and in tropical forests.

- **Ecosystem engineers** mainly comprise macroinvertebrates (ants, termites and earthworms), but also some mesofaunal groups (such as enchytraeids), able to cause intense bioturbation through active burrowing. By tunneling, they alter the soil space and create pores, channels and solid aggregate structures that constitute the habitat of other small organisms: microbial communities, and micro- and mesofauna. In the volume of soil that they control, also called their functional domain, they determine the composition and activity of microorganisms and the micro-predator food web.

While ants may be present in every type of ecosystem, with harsh climatic conditions and/or severe degradation, termites and earthworms are more dependent on stable conditions. Enchytraeids dominate wet and cold systems, such as moorlands. Ecosystem engineers are mainly present in well-developed soils at young and mature stages and tend to disappear in soils subjected to intensive agriculture.
Soil maintenance

Other ecosystem services provided by soils and their biota increase and are maintained as the ecosystem functions that they sustain gain in intensity. As described previously, it is possible to identify four stages in the evolution of soils, corresponding to the vertical arrangement of layers in a soil profile (see page 112). Because of their immaturity, developing soils do not provide significant contributions to soil system services. However, young soils are important for supporting plant growth since roots mainly develop in this layer. Mature soils may allow large amounts of water to infiltrate and to be retained in their pore spaces at different matrix potentials, thus optimising supply to plants and, ultimately, allowing water to feed springs and rivers. Older soils play a key role in the control of the hydrological cycle thanks to their greater depth, where water tends to accumulate.[136]

Forces due to folding and faulting of the Earth’s crust (orogenic processes) and erosion continuously bring new bedrock elements to the surface, and new soils are formed while old, highly impoverished soils are slowly disaggregated by erosion, reincorporated into the deep soil cortex by continental plate movements or buried below fresh volcanic deposits. As soon as they emerge above sea level, sediments and rocks start to be weathered by physical and chemical processes, and colonised by increasingly diverse organisms. Coexisting organisms progressively increase in their interactions as new species appear and biodiversity increases.

Coevolution for several hundred million years has led to the emergence of mutualistic interactions (see box on page 53) between micro- (e.g. fungi) and macroorganisms (e.g. plants) that enabled them adapt to two major constraints in soils: the difficulty to move and to find food in a very compact environment and the relatively low quality of the organic materials that comprise the majority of the available food sources. These relationships are crucial to maintaining the proper functioning of soils.

In conclusion, soil-living organisms have two major effects on functions in soil formation and maintenance:

a. as active agents in soil formation, maintenance, organisation and dynamics through intense mechanical effects (bioturbation, burrowing, chemical transformation, transport and mixing of organic and inorganic elements)

b. as a source of organic matter (see page 106) through excreta, as prey and when dead. Organic matter has three major functions: 1) as an energy source for living organisms; 2) as a reactive building material of soil structure acting as a frame or glue in the formation of stable aggregates; 3) as a sizeable stock of carbon subtracted from the atmosphere (thereby also participating in climate regulation)

These two effects allow soils to be maintained in terms of both structure and fertility, thus resulting in the provision of other ecosystem services.

Soil and pollination

Beetles not only play a role in the formation and maintenance of soil through their shredding and burrowing activities. They also contribute to another ecosystem service: pollination.

Most beetles that visit flowers are not there to sip nectar. Beetles often chew and consume parts of the plant they pollinate, and leave their droppings behind. For this reason, beetles are referred to as ‘mess-and-soil pollinators’.

Beetles were among the earliest prehistoric pollinators, and they continue to provide pollination services to flowers today. Fossil evidence suggests beetles first pollinated cycads. They began visiting flowering plants about 150 million years ago, a good 50 million years earlier than bees.

Living beetles seem to prefer pollinating close descendants of those ancient flowers – primarily magnolias and water lilies. Although not many plants are primarily pollinated by beetles, those that do are called cantharophilous plants. Cantharophilous plants are often fragrant, giving off spicy or fermented scents that attract their beetle pollinators.

The flowers that are visited by beetles are typically:

- bowl-shaped;
- white to dull white or green;
- strongly fruity;
- open during the day;
- moderate nectar producers;
- may be large solitary flowers (i.e. magnolias, pond lilies);
- may be clusters of small flowers (e.g. goldenrods, Spirea spp.).

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CHAPTER IV – ECOSYSTEM FUNCTIONS AND SERVICES

Cultural services – Natural capital

Value of soil biota

Natural capital can be defined as the world’s stocks of natural assets, including geology, soil, air, water and all living things. It is from this natural capital that humans derive a wide range of ecosystem services that make human life possible. Ecosystem services provided by soil organisms have been presented in previous sections. With financial capital, when we spend too much we run up debt, which, if left unchecked, can eventually result in bankruptcy. With natural capital, when we draw down too much stock from our natural environment we also run up debts which need to be paid back. Poorly managed natural capital, therefore, becomes not only an ecological liability, but also a social and economic liability. Ultimately, nature is priceless. However, it is not valueless and there are many studies around the world that have tried to estimate our natural capital in financial terms. Since it is extremely difficult to assign a precise economic value, different kinds of values can be assigned to soil biodiversity. [138]

Many of the ecosystem services identified by the Millennium Ecosystem Assessment are driven by the soil biota, often resulting from the interactions between organisms or groups of organisms within the soil. Efforts have been made to place a monetary value on such services to give an indication of the cost that we would face should we have to perform these services ourselves. However, such efforts tend to overlook the fact that the vast majority of the services do not occur in isolation, but rather are intertwined, with some organism groups performing several different services, and many of the services culminating as the output of the interaction between several different groups of organisms. This means that in many instances it would not be technologically possible for us to perform the services ourselves. Furthermore, it can be argued that any study that tries to place a total value on all soil-based ecosystem services is inherently flawed because of the complexity of the soil environment.

Soil-based ecosystem services are vital for our continued existence on Earth; without them we could not survive. Therefore, the value of such services are, for all intents and purposes, infinite. Here we focus on the value of soil biodiversity, which includes economic value but also covers a much wider scope. Soil biodiversity and its associated ecosystem services can be valued in different ways depending on the perspective from which they are considered, including the following:

- functional value. This relates to the natural services that the soil biota provide, the associated preservation of ecosystem structure and integrity and, ultimately, the functioning of the planetary system through connections with the atmosphere and hydrosphere. For example, less value may be placed on degraded soils due to their reduced functioning in terms of storing carbon, cleaning water, and preventing soil erosion and its associated environmental problems;
- utilitarian value (i.e. ‘direct use’). This covers the commercial and subsistence benefits of soil organisms to humankind. Examples include the provision of food by soil organisms, such as mushrooms, as well as biotechnology, such as the provision of antibiotics;
- intrinsic value (i.e. ‘non-use’). This comprises social, spiritual, aesthetic, cultural, therapeutic and ethical benefits. For example, most people agree that there is a value in having green spaces within cities even if we do not live in these cities or use the green spaces. The same is true of natural parks, even though we may not visit and use such natural parks ourselves. Furthermore, hospitals and nursing homes with green spaces have been shown to facilitate the recovery of patients. Such spaces have an ‘intrinsic value’, and as they are reliant on the functioning of belowground communities (i.e. the soil biota), they too must have an intrinsic value;
- bequest value (i.e. ‘option’ or ‘serendipic’). This relates to planetary functions for future generations. It concerns the unknown. The idea is that there is value in not depleting soil biodiversity so that future generations can benefit from the services it provides. This is true in terms of the ongoing survival of humans on Earth. In addition, many novel compounds, such as antibiotics, have been isolated from soil organisms (e.g. bacteria). The vast majority of soil bacteria remain to be fully described, and so it seems likely that there are still many useful novel compounds yet to be discovered. Therefore, there is value in maintaining soil biodiversity so that such compounds still exist for discovery by future generations.

Economic value: the most expensive soil organism

- The most expensive food in the world is a soil fungus. The white truffle (Tuber magnatum Pico) is a fungus that establishes an ectomycorrhizal symbiosis with trees (see page 40).
- White truffles have a limited distribution in southern and central Europe, occurring in Italy, Switzerland, Croatia, Slovenia and Serbia.
- The life cycle of this fungus is complex. Despite many efforts, attempts to ‘domesticate’ the white truffle have not yet been successful.
- The most refined white truffle is from the Piedmont region (Alba) in northern Italy. It is known as the white truffle.
- White truffle prices can reach into the hundreds (or even thousands) of Euros per kilogram, depending on the harvest.
- Each year the price of the white truffle is established at the annual Worldwide Alba Truffle Auction.
- In 2007, a white truffle believed to weigh around 750 grammes was sold for US$208000 (i.e. 2 173 dollars per gramme – approx. £1000).

• Economic value: the most expensive soil organism.
• The white truffle, a soil fungus, is one of the most expensive foods in the world. (EKI)
• The value of soil biodiversity can be considered from different points of view. (a-b) Provision of clean drinking water is an example of a functional value attributable to soil biota. (c-f) The utilitarian value is represented by food. (g-f) The bequest value is related to the need to preserve soil biodiversity for future generations.

The beauty of a landscape, also thanks to the action of soil organisms, shows the intrinsic value of soil biota. (RKA, DFAT, CGU, DEN, NP/CIAT, MMP, BAR)
Food security

It is widely accepted that the near future will see the development of new microbial strains and soil-dwelling organisms that offer potential solutions to problems relating to food shortage. Already, the application of biotechnology in agriculture has resulted in new crop varieties with increased resistance to pests and diseases (see pages 100-101), as well as with higher nutritional values (e.g. Golden Rice) (see below). Nevertheless, such progress does not come without drawbacks, some of which remain controversial. Strict regulations and protocols have already been implemented to minimise potential hazards associated with genetic manipulation and the spread of transgenic organisms, among which the direct threat to human and animal health and the risk to ‘natural’ biodiversity are perhaps of most concern.

In the current challenge of feeding a continuously growing population (see page 18), soil biota may also represent an important ally from another perspective. Since 2003, the United Nations Food and Agriculture Organization (FAO) has been working on topics related to edible insects in many countries worldwide. For example, 32 Amazonian ethnic groups consume more than 100 soil invertebrate species. Edible insects contain high quality proteins, vitamins and amino acids. Insects have a high feed conversion ratio (FCR), for example, crickets need six times less feed than cattle, four times less than sheep, and half of what pigs and chickens require to produce the same amount of protein. In addition, they emit less greenhouse gases than conventional livestock. Therefore, insects are a potential source of proteins, either for direct human consumption, or indirectly in conventional livestock. Therefore, insects are a potential source of what pigs and chickens require to produce the same amount of meat (see page 60) over the same amount of time.

The development of a beneficial product, depends on the local soil characteristics and conditions. Soils with extreme characteristics (e.g. very acidic, very alkaline or waterlogged with low levels of oxygen) provide an ideal environment for preserving organic remains. Soil organisms play a key role in soil formation processes (see pages 110-113); therefore, they can indirectly influence the preservation of archaeological evidence. However, soil biota can also have negative effects, as intense soil microbial activity can lead to degradation of any type of material, including objects of historical interest. Nevertheless, the terrestrial subsurface is generally characterised by low concentrations of organic carbon and oxygen and, by comparison with surface soils, relatively few microorganisms (see page 75). Another important aspect to consider is the material to be investigated.

Some biological materials (e.g. pollen, leather and wool artefacts) are easily degraded by soil organisms; whereas, under other circumstances, it is possible to take advantage of the decomposing action of soil biota. For example, recalcitrant residues from wood decomposition are important marks of the past presence of the so-called ‘post holes’, which are spaces once filled by poles to sustain buildings or other structures. Archaeologists can use their presence to plot the layout of former structures as the holes may define their corners and sides. Despite everything previously described, there are very few measurements of soil microbial parameters at ancient archaeological sites, and the general applicability of these observations to other archaeological sites remains unknown.

Any soil disturbance, such as by drainage or ploughing, may change the optimal conditions for archaeological conservation and, therefore, lead to the rapid decay and loss of material. Archaeologists use these historical artefacts and the layers in which they are preserved to reconstruct the communities that produced them and the environments in which they lived. But to do this, the soil layers must remain undisturbed.

Educational value

Many studies have shown the importance of playing with soil and the positive effects of soil-living organisms (e.g. our beloved earthworms) on children’s health. Some of the reasons are:

• a. a bacterium naturally found in soil, Mycobacterium vaccae, activates the neurons that produce serotonin – a key chemical in many bodily functions, as well as a natural anti-depressant

• b. the typical behaviour of children is to always put dirty things in their mouths. There may be an evolutionary reason for such a universal behaviour, a finding that science seems to corroborate. Called the ‘hygiene hypothesis’, many researchers have concluded that the millions of bacteria, viruses and other organisms that enter the body with every spoonful of soil ‘eat’ are necessary for the development of a healthy immune system

• c. the term ‘nature-deficit disorder’ describes a common condition of younger generations, due to the lack of physical experiences in the natural world, which have been replaced by more solitary and unstructured activities, like playing video games. Children are not given enough opportunities to play outside, which has now been linked to attention disorders, depression and obesity. By contrast, children who play outside laugh more, which means they are happy. It also means their blood pressure and stress levels are lower. They grow in their character development by becoming more adventurous, more self-motivated and more able to understand and assess risks

Conclusions

Soils that sustain high levels of biodiversity are increasingly endangered, mostly due to anthropogenic intervention (see Chapter VI) despite their demonstrably high value, as shown above. Protection, as well as sustainable management and exploitation of soil biodiversity, must be addressed from a conservation perspective (see Chapter VII). Measures to assess threats to soil biota and, consequently, to preserve soil biodiversity will undoubtedly contribute to sustaining environmental and human health and continue to enrich the human condition and way of living. Soil biodiversity is too valuable not to be protected!
Soil biodiversity is potentially under threat because of several pressures acting on soil, ranging from intensive agriculture, pollution, desertification and land degradation, soil erosion and fire to deforestation. Despite all this, the consequences of the reduction or loss of soil organisms are still poorly studied and, therefore, will need further attention in the future.
Introduction

The extraordinary ability of humans to modify the environment in order to meet their own needs underlies the success of humans as a species on Earth. Since the onset of agriculture, humans have altered the local diversity of plants by clearing land and cultivating selected plant species that were desired for food, feed, clothing and building material. The industrial and green revolutions, with the mechanisation of labour and the discovery of how to produce mineral fertilisers and chemicals to control weeds, pests and diseases, resulted in dramatic increases in crop yields. Unfortunately, these fundamentally different methods of land management have also generated unwanted side effects. [140]

In the 1960s, with the publication of Rachel Carson’s Silent Spring, scientists, the general public and policymakers began to realise how pesticide use could cause unforeseen adverse effects throughout the food chain. The disappearance of plant species also has effects on belowground biodiversity and soil food webs. Furthermore, pollutants that end up in soil as a result of oil spills or mining activities can impact soil organisms and the myriad of ecosystem functions provided by soils. Similarly, the physical disturbance of soils, including sealing, compaction and erosion, has the potential to eliminate many belowground taxa.

Soils harbour tremendous biodiversity. However, proliferation and functioning are dependent on their chemical and physical soil properties. As for all life forms, water availability is of utmost importance for life in the soil. Over the past twelve decades, global climate change has altered precipitation and temperature regimes, which impact soil biodiversity both directly and indirectly through their impact on primary productivity and plant diversity. In many cases, the enormous biodiversity found in soils may serve as a source of organisms which can adapt to the new conditions and may even help to improve adverse conditions for plant growth. Awareness of soil biodiversity and its functional importance will enable the development of more sustainable management practices. By more carefully considering how soil biodiversity may be affected by management practices, and adapting accordingly, we will be able to better preserve belowground diversity and the important functions of these communities in order to enhance and maintain soil health.
Loss of aboveground biodiversity

Plant-soil interactions

Aboveground biodiversity refers to all the organisms that live above the soil. The starting point of all terrestrial food webs (see page 96), both above- and belowground, are primary producers, mostly plants and algae. Through photosynthesis (see box on page 35), these organisms transform inorganic compounds of carbon dioxide (CO₂) from the atmosphere and water (H₂O), together with mineral nutrients from the soil, into organic compounds in the form of their own plant tissues. All heterotrophic organisms (see page 30) depend on these primary producers to obtain their energy and nutrients. The question remains, however, how above- and belowground biodiversity are related and whether loss of aboveground biodiversity also implies loss of belowground biodiversity. [141]

When looking at the plants in woods, grasslands or parks, it becomes clear that aboveground plant species are different in their shape, colour and smell (i.e. they are physically and chemically different). Similarly, albeit less well known, plant species also differ belowground in the morphology and chemistry of their roots (see page 43). As a result, the composition of soil organisms also differs between plant species such that a higher diversity in soil biota is positively correlated to a higher diversity in plants. Conversely, there is a risk of losing species of belowground organisms with decreasing plant species richness. It is important to note that some plant species are much more diverse than others, meaning that losing certain plant species from an ecosystem can have much greater impacts on belowground biodiversity than you would expect from the change in plant species number. This, for example, happens when a plant species with unique associations with soil fungi (see pages 38-41) disappears.

Given the vast diversity of soil organisms and, in comparison, the lesser number of plant species, it has been argued that many of the species that live in the soil most likely behave as generalists rather than as specialists with regard to the food they consume. Biodiversity studies do provide some support for this idea especially when the level of dependence on a very narrow or broad range of aboveground species, even very few plant genotypes, are being grown leads to lower declines in biodiversity is land-use change. Conversion of natural land into agricultural systems in which very few plant species, even very few plant genotypes, are being grown leads to lower soil biodiversity. Awareness of the potential negative effect of this process on ecosystem functions, such as natural pest control, has led to the implementation of alternative cropping systems in which plant diversity is increased through the creation of species-rich field borders, diversified rotations and intercropping.

Deforestation in numbers

- A recent study estimated that the total number of trees on our planet is approximately three billion (3 x 10^9) [142].
- This means that there are 422 trees for every person on Earth.
- This more accurate estimate of the number of trees on the planet was based on scientific data gathered from all continents except Antarctica.
- The study also reported that 15 thousand million trees are cut down each year.
- In the 12,000 years since farming began spreading across the globe, the number of trees on our planet has fallen by almost half.

Drivers of loss

Throughout the past centuries, and especially since the industrial revolution and the production of mineral fertilisers, human impacts on biodiversity have been tremendous and are projected to keep increasing in the coming decades. The main cause of declines in biodiversity is land-use change. Conversion of natural land into agricultural systems in which very few plant species, even very few plant genotypes, are being grown leads to lower soil biodiversity. Awareness of the potential negative effect of this process on ecosystem functions, such as natural pest control, has led to the implementation of alternative cropping systems in which plant diversity is increased through the creation of species-rich field borders, diversified rotations and intercropping.

Specialists vs. generalists

The differences between the various species of soil organisms in their response to the decline of aboveground diversity can be explained by the level of dependence on a very narrow or broad range of aboveground species. Specialist species have a narrow range of species on which they can prey, while generalists have a broad range and can easily switch food sources depending on what is available. High levels of specialistism are most notable in organisms that coevolved with each other; meaning that they are adapted to specific characteristics. Two notable examples are orchids and their specialist orchid mycorrhizal fungi (see page 40) and blue butterfly species, whose caterpillars are hosted by ants (see page 54) in their nests in the soil; there, the caterpillars are provided with food and protection until the butterfly’s pupae. [ATA, WPP]

Map showing the arthropodic plant species loss as a percentage of the native plant species richness, including the area of native habitat lost to agriculture and settlements (derived from Díaz et al. (2011) PLoS ONE, 2011, (L.J. BJC) [144])

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Introduction of invasive species

Invasive species: a global issue

In natural ecosystems, species have evolved together in such a way that generally no single group completely dominates the system and, therefore, they can coexist. When an exotic species arrives or is introduced into an ecosystem, it is possible that it establishes and spreads so profusely that the native species completely disappear because they are being outcompeted. This rapid spread of exotic species is known as an invasion. The organisms that become invasive can belong to any trophic group, such as plants, mammals, invertebrates or fungal species. The impacts of these invasive species are not only notable aboveground, they also directly impact belowground diversity and processes (e.g. when the invasive species lives belowground) or indirectly through changes in plant species inputs into the soil. Over time, an ecosystem that has been overrun with invasive species becomes more and more difficult to restore, as the actual habitat may be altered in such a way as to favour the invasive species. [144]

Invasion risk

The risk of invasion increases with the introduction of novel traits. Throughout the last century these potential introduction events have increased tremendously because of greater human trade and mobility. At a global scale it is well recognised that invasive species pose a threat to global species diversity and that invasive species can create substantial economic losses. The Global Invasive Species Database, which is managed by the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) Species Survival Commission, keeps track of which species are invasive, and which are becoming invasive, at a global scale.

Impacts of invasive plant species

Of all types of invasive organisms, the invasion of plant species might be best well known by the general public especially when the invasive species cause direct nuisance to human health, such as by causing allergies (e.g. Ragweed pollen, Giant Hogweed skin irritations). For example, the Latin American tree Prosopis juliflora has become invasive in semi-arid locations of Africa thanks to its tolerance of high temperatures, drought and salinity stress, its production of specific organic substances that are toxic to native plants (i.e. allelopathic effect), and its hosting of soil-borne native nitrogen-fixing bacteria (see page 105) in root nodules that can resume nitrogen fixation once conditions improve.

Less well known is the fact that invasive plant species can also have far reaching impacts on the species composition and functioning of whole ecosystems through plant-soil feedbacks that modify soil biology, chemistry and structure. The increase in soil organic carbon, nutrients and root biomass (of the invasive plant species) creates an environment that can support a large number of soil organisms, which, in turn, further promote the establishment of the invasive species. The biodiversity of these soils often increases significantly; however, the variety of organisms present also differs significantly from those found in the natural stands, once again limiting the growth of indigenous species.

In a recent study carried out in the Amazon Basin, it was shown that conversion of natural rainforest to pastures (with a relatively homogeneous plant cover) also results in more homogeneous biotic communities, meaning that communities become more similar. Similarly, it has been shown that plant invasions also promote the homogenisation of ecosystems as a whole, with a decline in the diversity of plants.

Among the 100 worst invasive species globally there are not only plant species but also several ant species (see page 54), soil-borne fungal pathogens (see box on page 39), and soil-dwelling flatworm species. The ecosystems most prone to severe impacts of invasive species are those that have been isolated for a very long time, such as islands, because their native species can be very different from the exotic species.

A striking example is the invasion of the yellow crazy ants (Anoplolepis gracilipes) on Christmas Island in Southeast Asia, which led to dramatic ecosystem changes. The indigenous red crab (Gecarcoidea natalis) is a key ecosystem engineer on Christmas Island whose feeding and burrowing activities determine the vegetation composition through its impact on the litter layer and plant regeneration.
Effects on soil biodiversity

The impact of pollution on soil biodiversity depends on the type of pollutant and the way it acts on the soil organisms. Oil spills that create a film on the soil block gas exchanges such that it creates a lack of air and suffocates the soil biota in a non-selective way. Pesticides, by contrast, are more selective, killing specific groups of soil organisms as a side effect of their main targets of plant pathogens and pests. For example, insecticides kill insects (see pages 54-55), nematocides kill nematodes (see pages 46-47), fungicides kill fungi (see pages 38-41), bactericides kill bacteria (see pages 33-35) and acaricides kill mites (see page 49). The level of direct toxicity is often dose dependent. It is important to note that soil organisms can develop resistance to pesticides, especially if their starting populations are large, their rate of reproduction is high and their method of overcoming pesticide activity requires few adaptations (e.g. production of proteins that can detoxify a simple chemical compound).

Heavy metals (e.g. zinc, lead, mercury and cadmium) interfere with the normal metabolism of plants and soil organisms, resulting in lethal physiological and neurological disorders. The very specific impact depends on the heavy metal in question and its availability (i.e. mobility in the soil system). Apart from mining, landfills and industrial areas, there are also potential hotspots for heavy metal pollution in the soil. Regulations on the type of waste that ends up in landfills and the recycling of waste to the soil of both natural and modified ecosystems through various routes (direct application, atmospheric fall out, waste disposal, etc.) influence the functioning of soils on a wide spatio-temporal scale, from individual organisms to landscapes.

Earthworms and pollutants

- Earthworms, contrary to ants and termites which tend to be more resistant to several pollutants, are often highly sensitive to soil pollution. Their sensitivity is due both to:
  - close contact with pore water and their highly water-permeable epidermis: water soluble pollutants can easily penetrate into their bodies;
  - the fact that they ingest large quantities of soil.
- Earthworms are able to eliminate excess heavy metals from their bodies, thanks to a physiological control mechanism. Depending on the pollutant, this elimination pathway can be more or less efficient.
- Copper and zinc are easily eliminated by physiological pathways based on carrier systems, which earthworms naturally have for the control of these elements.
- The mechanism of metal detoxification is much slower for cadmium and lead. It involves complex metabolic pathways, including the formation of waste nodules (known as brown bodies). These are aggregated dark-coloured masses usually found in the coelomic cavity at the posterior end of the body and represent the immune system of earthworms.
Acid rain and nutrient overloading

Acid rain

‘Acid rain’ is a broad term that refers to a mixture of wet and dry deposition (deposited material) from the atmosphere containing higher than normal amounts of nitric and sulphuric acids. The precursors of acid rain formation result from natural sources, such as volcanoes and decaying vegetation, and human-made sources, primarily emissions of sulphur dioxide and nitrogen oxides that result from fossil fuel combustion. Acid rain occurs when these gases react in the atmosphere with water, oxygen and other chemicals to form various acidic compounds. The result is a mild solution of sulphuric and nitric acid. When sulphur dioxide and nitrogen oxides are released from power plants and other sources, prevailing winds carry these compounds across state and national borders, sometimes hundreds of kilometres. [146]

The damage that results from acidic deposition has been investigated in all groups of soil organisms. Increasing soil acidity can affect microorganisms (e.g. bacteria and fungi – see pages 29-35) that break down organic matter into nutrient forms that are then available to plants. In general, a reduction of species diversity is observed in the presence of acid rains; however, common patterns cannot be identified as the effects, in particular, under such circumstances there has been a shift in the amounts of nutrients that are available. Considering microfauna, the ability of protozoa to form resistant structures (see pages 36-37) may be an important feature providing shelter from acid stress.

Among the mesofauna, sensitivity to acidity is higher in collembolans and mites (see pages 49-50), whereas many species of enchytraeids (see page 48) are tolerant of acidity. Soil acidification also impacts earthworm communities and their activity (see page 58). In fact, they tend to escape from acidic soils and may eventually die when pH values become too low (pH 2). Furthermore, an inverse relationship between the acidity of the soil and the burrowing rate has been shown; as the environment becomes more acidic (pH 4), earthworms failed to burrow quickly (i.e. under 20 minutes). By contrast, macroarthropods (e.g. coleopterans – see page 59) have a limited susceptibility to low pH values thanks to their hard outer covering (cuticula). However, the high demand for nutrients caused by the development of the cuticula does not allow most of the macroarthropods to survive in an acidic environment.

Acid rain can also have negative effects on plants. Increasing soil acidity allows aluminium (a common constituent of soil minerals) to be solubilised. In its free organic form, aluminium is toxic to plant roots (see page 43) and can lock up phosphate, thereby reducing the concentrations of this important plant nutrient. Nevertheless, the mechanisms associated with these plant effects have not been well studied. Ectomycorrhizal fungi (see page 40) on the roots of some trees help supply much-needed calcium in forest soils subjected to acid rain.

Nutrient overloading

Soils across the globe are receiving nutrient inputs from human activities at rates that exceed those from natural processes. For example, nitrogen (N) inputs to ecosystems are 30-50% greater now than they were 100 years ago. Similarly, phosphorus (P) inputs via fertiliser applications to agricultural lands are now estimated to be approximately 25 thousand million kg per year, rates that far exceed pre-industrial inputs. These excess amounts of N and P typically enter ecosystems via the direct application of chemical fertilisers or manure to soils in agricultural and pasture soils (see page 88). Alternatively, N and P can enter ecosystems (see page 105), even though they are not affected by human activities. Via atmospheric deposition of phosphorus-containing dust or reactive N oxides. The rates at which N and P have been added to soils has increased dramatically over the past 50 years, with important implications for the structure and function of ecosystems worldwide.

In non-agricultural soils, excess nutrient additions can, over time, lead to significant shifts in plant community composition. Nutrient additions can also lead to changes in soil pH and, in some cases, nutrient toxicity if addition rates are sufficiently high. Moreover, nutrient additions can lead to significant shifts in belowground carbon dynamics, due to changes in the amounts and types of plant-derived organic carbon entering the soil and changes in the rates at which litter and soil organic matter pools are mineralised to carbon dioxide (CO₂) via microbial activities (see pages 102-106).
Agricultural practices

Low vs. high inputs

Agricultural activities represent one of the most intensive forms of land use, and their impacts on soil biota can be highly variable as a function of the management options adopted. For example, observations on the impact of agricultural management on soil microarthropod communities (e.g. collembolans – see page 50) show that the high input of intensively managed systems tends to promote a reduction in diversity, while lower input systems conserve diversity. High-input systems favour bacterial pathways of decomposition, dominated by labile substrates and opportunistic bacterial-feeding fauna (e.g. nematodes – see pages 46-47). By contrast, low-input systems favour fungal pathways with a more heterogeneous habitat and resource dominated by persistent fungal-feeding fauna (e.g. termites – see pages 55). [148]

Soil tillage

Soil tillage causes significant modifications in the soil, especially with regard to soil structure, porosity and water-holding capacity, but also organic carbon content. The impact of tillage on soil organisms is highly variable, depending on the tillage system and soil characteristics.

Three main tillage systems are recognised: conventional, minimum and no-till. Conventional (intensive) tillage (i.e. ploughing) inverts and breaks up the soil, destroys the soil structure and buries crop residues, causing the most significant impact on soil organisms. Minimum tillage systems can be characterised by a reduced tillage area (i.e. strip tillage) and/or reduced tillage depth (i.e. by using a rotary tiller, harrow and hoe); crop residues are generally incorporated into the soil instead of being burried. Under no-till conditions (see pages 146-147), the soil remains relatively undisturbed and plant litter remains on the soil surface, similar to natural soil systems, providing a more stable habitat.

As conventional tillage tends to favour bacteria (see pages 33-35), it would also be expected to favour protists (see pages 36-37), since bacteria are their main food source. Total nematode numbers have been found to either increase or decrease with tillage. Their wide range of responses probably reflects the wide range of functional groups and trophic levels (i.e. fungivores, bacterivores, omnivores, predators and plant parasites – see pages 46-47). Considering soil meso- and macrofauna, tilled systems generally host organisms with a short generation time, small body size, rapid dispersal and omnivorous feeding habits. Collembolans (see page 50) are usually inhibited by tillage disturbances, although some studies have shown the opposite effect. Mites (see page 49) exhibit a wider range and more extreme responses. Tillage is also one of the most detrimental factors for earthworm communities in agricultural soils. It disturbs and destroys their habitat, and physically damages them through the plough blades and inversion tillage. The earthworms are moved to the surface where they are exposed to bird predation. The specific effect of tillage on earthworms depends on the type of tillage, and on the earthworm species or functional group (see page 58).

Soil tillage also influences the sensitivity to compaction, which in turn impacts soil biota. Conventionally tilled soils have lower bearing capacity and, consequently, are more sensitive to compaction caused by agricultural machinery. Considering soil organisms, lower earthworm populations are found in fields with more tractor traffic. The abundance of microarthropods generally decreases with increasing soil compaction, with collembolans being more sensitive than mites to this kind of pressure.

Map showing global cropland cover for the baseline year 2005. It has been developed using a bottom-up approach: integration of existing maps shared by the community, and the development and validation of products driven by crowdsourcing through the availability of very high-resolution satellite imagery. For crowdsourcing, the Geo-Wiki Platform (www.geo-wiki.org) was used. Geo-Wiki is a platform that provides citizens with the means to engage in environmental monitoring. In this case, land cover information was gathered for the validation of the map. The map has a resolution of 1 km² derived from Fritz et al., Global Change Biology, 20(25), 65, 861(149)
Fertiliser applications

Fertilisers are often applied in agriculture to maintain high yields. Two main types of fertilisers can be used: organic and inorganic. Organic fertilisers consist of materials that come from different types of organisms. Organic fertilisers, such as crop residues or animal manure, serve as an extra food source for the soil decomposer community (see page 106) and often increase their population density and biomass. Inorganic (mineral) fertilisers are sometimes completely, or at least partially, comprised of man-made materials. Inorganic fertilisers do not directly serve as a food source for soil organisms. However, by increasing crop growth, they make more organic matter (roots or plant residues) available after the harvest and, therefore, may have indirect effects on soil biota.

Several studies demonstrate that the total soil microbial biomass and the biomass of many specific groups of soil organisms reflects the level of organic matter inputs. Therefore, organic or traditional farming practices that include regular inputs of organic matter in their rotation, generally have larger soil communities than conventional farming practices. For example, solid manure has a positive effect on soil organisms, especially on earthworms (see page 58).

Inorganic fertilisers were reported to have variable impacts on soil organisms. For example, several studies show that high levels of nitrogen inputs are associated with a decrease in species richness and abundance of microarthropods. Mineral fertilisers can also impact earthworms by reducing their abundance; the mechanism can be associated with the soil acidification effect of nitrogen from the mineral fertilisers.

Pesticide applications

A pesticide is any substance or mixture of substances aimed at preventing, destroying or mitigating pests. It goes without saying that pesticides are detrimental to their target organisms, but non-target organisms can also be unintentionally negatively affected. Pesticide application to the soil can affect soil communities by influencing the individuals’ performance and modifying ecological interactions among species. When one or more soil-living species are impacted by a pesticide, this can affect the whole soil food web in terms of abundance and composition.

Pesticide toxicity mainly damages soil fauna. The impact is determined by different factors, such as chemical and physical characteristics, species sensitivity and soil type. For example, among soil microarthropods, different taxa have a variety of responses depending on the substance applied. A laboratory study comparing the responses of soil microarthropods to five insecticides allowed for the toxicity ranking of these products and identification of the main non-target collembolans and mites (see pages 49-50) affected. Several studies found negative effects of various pesticides on earthworm abundance. Generally, the negative effects increase with increased dosages of a pesticide. Because of this sensitivity to chemical substances, earthworms are widely used as bioindicators of soil quality and level of soil pollution (see page 101).

The physical and chemical characteristics of soil (see Chapter I), such as structure, texture, pH and organic matter content, also determine the toxic effects of pesticides. For example, it has been shown that the smaller the particles a soil is composed of, the longer a pesticide persists in it.

Pesticide application does not always have negative effects on the soil community. For example, for certain types of soil there is evidence that some taxa can obtain a competitive advantage from the application of certain specific pesticides due to the elimination or reduction of their competitors from the environment.

Monoculture

Another agricultural practice relevant to soil biodiversity is the diversity of crops. Monoculture is the agricultural practice of growing only one crop or plant species at a time. Polyculture, by contrast, where more than one crop is grown at the same time, can crop rotation, where different plant species are grown year after year, are the alternatives to monoculture. Monocultural cropping is a very common practice in industrial agriculture and has allowed for increased efficiencies in planting and harvesting. Continuous monoculture, or monocropping, where the same species is grown year after year, can lead to a buildup of pests and diseases and, consequently, their rapid spread where a uniform crop is susceptible to a pathogen. Therefore, monocultures usually require high inputs of pesticides.

Due to the strong links between above- and belowground communities (see page 118), monocultures can impact soil-living organisms. For example, bacterial communities of soils under monocultures in the Argentinean Pampas are less diverse than those in the same soils under crop rotations. Mesofauna, mite and collembolan communities in a natural forest and a spruce monoculture in the Czech Republic were found to be diverse not only in terms of diversity – mites and collembolans are more abundant in the natural forest – but also in terms of structure. In particular, in the spruce monoculture, groups susceptible to disturbance are suppressed.

Genetically modified organisms and soil biodiversity

- A genetically modified organism (GMO) is an organism whose genetic material has been modified (see page 100). GM crops are used in agriculture, the main crops being maize, soybean, cotton and canola. The global cover of GM crops reached 175 million hectares in 2013. Pesticide-resistant GM crops represent approximately 80% of total GM crops. Insect-resistant GM crops, such as Bt maize and Bt cotton, that contain genes from the bacterium Bacillus thuringiensis (Bt), represent 20% [150].
- Besides the benefits offered by GM crops, such as a reduced use of pesticides, there is concern about the potential negative effects of GMOs on the environment. One of the largest uncertainties is the effect of GM crops on non-target organisms, such as several soil-living species.
- Only limited research has been carried out on the effects of GM crops on non-target soil organisms. In a short-term experiment with the earthworm Lumbricus terrestris in soils containing Bt maize residue, or where Bt maize was grown, Bt toxins were found in the gut of earthworms, but there was no reduction of body weight or increased mortality. Other studies showed the persistence of Bt toxins over the whole cropping season (200 days) – and a decrease in body weight of L. terrestris by 18%.
- Contrasting results were found in an assessment of the impact of GM crops on arbuscular mycorrhizal fungi. A study showed no consistent differences between GM fungal communities associated with GM and non-GM plants. Another study observed a reduction in AMF colonisation in Bt maize. These results show the current need to further investigate the impacts of GM crops on soil biota.

The application of fertilisers and pesticides is used to promote plant growth and facilitate harvest, but can have a negative impact on soil biodiversity (SSS).

Monoculture is the practice of producing or growing crops singly over an area of land. This practice has negative effects on the whole soil community, from microorganisms to earthworms. (SSS)
Overgrazing

Large grazers vs. grasslands

Worldwide, grasslands (see page 81) comprise roughly 40% of the terrestrial surface. Only a small part of these grasslands can be considered ‘natural’, meaning that in the absence of grazing these grasslands would turn into shrubland and, subsequently, forest. A large proportion is used by humans for livestock grazing. These are often located on marginal soils, where arable farming is not possible because of nutrient deficiency or lack of or excess water.

Grazing by large mammals can have both positive and negative effects on soil organisms and, because these processes occur simultaneously, the overall outcome for soil biodiversity will depend on the stocking density of the large grazers. With increasing densities, the negative effects (e.g. trampling, soil compaction, denudation, resource competition, reduction of shelter, and in cases anthelmintic residue in faeces), will soon overshadow the positive effects (e.g. increased root exudation, nutrient return through defecation). When exactly this tipping point is reached is difficult to determine, and is likely to vary with ecosystem type, geographic location and land-use history. [151]

Grazing at high stocking densities, and especially overgrazing, is probably the largest threat to soil biodiversity in grassland systems. This threat can be expected to increase, which is likely to happen in areas with human population growth. What is considered high or low stocking densities is, however, highly dependent on ecosystem productivity (in terms of water and nutrient availability), grazing system (year-round, seasonal or rotational grazing) or soil type. For example, on a highly productive floodplain a density of five sheep per hectare is considered low, whereas this is considered extremely high for a productive floodplain. What is considered high or low stocking densities is, however, highly dependent on ecosystem productivity (in terms of water and nutrient availability), grazing system (year-round, seasonal or rotational grazing) or soil type.

In general, three actions performed by large grazers affect soil processes have contrasting effects on soil faunal diversity, depending on the stocking density of the large grazers. With increasing densities, the negative effects (e.g. trampling, soil compaction, denudation, resource competition, reduction of shelter, and in cases anthelmintic residue in faeces), will soon overshadow the positive effects (e.g. increased root exudation, nutrient return through defecation). When exactly this tipping point is reached is difficult to determine, and is likely to vary with ecosystem type, geographic location and land-use history. [151]

Defoliation

Both large grazers and soil animals depend on plant growth for sustenance. All plant material that is not consumed by large grazers or smaller herbivores will become available to soil invertebrates. Therefore, it can be expected that defoliation (as a result of grazing) takes place at the expense of soil organisms, since they are competing for the same food source. In the short term (hours/days) this is indeed the case: plant material that otherwise would become available to soil invertebrates, takes place at the expense of soil organisms, since they are competing for the same food source. In the short term (hours/days) this is indeed the case: plant material that otherwise would become available to soil organisms, takes place at the expense of soil organisms, since they are competing for the same food source. In the short term (hours/days) this is indeed the case: plant material that otherwise would become available to soil invertebrates, takes place at the expense of soil organisms, since they are competing for the same food source. In the short term (hours/days) this is indeed the case: plant material that otherwise would become available to soil invertebrates, takes place at the expense of soil organisms, since they are competing for the same food source.

Defoliation forces plants to regrow. In order to do so, they produce sugar-like substances called root exudates that stimulate the growth of microorganisms. However, the somewhat larger term (days/weeks) grazing can stimulate the activity and abundance of animals in the belowground food web: the network of interactions between soil organisms. Depletions can therefore stimulate plant growth and increase the total amount of available resources for both above- and belowground herbivores.

Moreover, the plant tissue that regrows after defoliation is much higher quality for herbivorous animals as it is richer in proteins and contains fewer amounts of indigestible cell walls. This plant material is also easier for soil organisms to decompose.
Defecation

Patchy deposition of dung and urine (defecation), through which nutrients are returned to the soil, is a second pathway used by large grazers to affect soil organisms. Dung pellets attract a suite of specialised dung-degrading organisms, such as dung beetles, flies and rove beetles (see page 59). These animals are of great importance for the rapid degradation of dung, as well as the redistribution of nutrients through the ecosystem.

Anti-worming agents (anthelmintics), which are routinely administered to most livestock, can have strong negative effects on dung-degrading fauna as well as on the rates of decomposition of the dung pellet. For example, the use of the broad-spectrum antiparasitic Ivermectin results in reduced growth of beetle larvae and strong reduction in the number of fly larvae. A number of studies have indicated that earthworms (see page 58) are not negatively affected, but cite reason for this is largely not understood. The use of this drug not only negatively affects nutrient cycling, but may also result in a lower abundance of prey items for grassland-inhabiting birds.

Trampling

A final major effect that large grazers have on soil organisms is trampling which can directly affect animals living in the litter layer or, just under, the soil surface. Indirect effects may be stronger. One indirect effect that trampling can have on soils is denudation, where all vegetation is stripped away from the soil. This usually only happens under high grazer densities.

A second major effect of trampling is the compaction of the soil. Soil organisms inhabit the soil matrix, which consists of pores of various sizes. The largest animals generally live in the largest pores, smaller animals live in smaller pores and the smallest pores are usually only inhabited by bacteria. Trampling by grazing mammals can cause these pores to collapse, with the larger pores collapsing first. Therefore, the largest animals would be expected to face the strongest consequences of trampling. However, many studies show that grazing at low densities is not necessarily detrimental to earthworms. This is probably because earthworms can create their own burrows, thereby shaping a habitat for themselves and other soil organisms. Other animals, and especially soft-bodied soil animals such as collembolans (see page 50), which do not possess this ability, have often been found to be very vulnerable to trampling.

The effects of soil compaction are strongest on fine-textured clay and silt soils. The collapse of pore spaces not only affects soil animals directly, but also inhibits the transport of water through the soil. On dry soils, such as the steppes (see page 81) of northern China, soil compaction leads to decreased water penetration. This reduces plant growth and soil biodiversity, and increases superficial runoff and soil erosion (see pages 128-129). By contrast, on very wet soils, such as riverine flood plains and coastal salt marshes, overgrazing of clay soils may result in waterlogged conditions as natural drainage in these soils is blocked. This can result in a decrease in soil oxygen, creating suboptimal conditions for soil Fauna and reduced mineralisation rates. In such soils, invertebrate life is often confined to the upper soil layer.

![Map of global cattle density in 2006 based on statistical relationships between survey and census data and various variables relating to climate and the environment, and other spatial demography and land-cover data (derived from Robinson et al., PLoS ONE,2014) (LJ, JRC) (132)](Image 556x398 to 809x631)
Fire

Fire and human activities

Fire is a natural part of most terrestrial ecosystems. Some ecosystems even came into existence because of fire, such as the savannah (see page 82): Fires needed to burn the forests before grasses could establish themselves, only as recent as ~50 million years ago (flowering plants appeared ~200 million years ago). Fire-exclusion experiments on an Australian savannah showed that, in as little as 20 years, trees can re-establish themselves to such an extent that subsequent fires are not able to kill the trees and bring back the savannah ecosystem. The key factor to consider is the mean fire return interval. The savannah may need a short mean fire return interval of less than 20–30 years, but for other ecosystems the balance between burning and recovery periods ranges widely from about 100 to 200 years for temperate forests to >800 years for peatlands. This natural balance is often disturbed by human activity. Most wildfires nowadays are ignited by humans, through accidents or negligence (e.g. camp fires), side effects of human structures (e.g. sparks from railroads) and, surprisingly commonly, through arson (153).

Apart from igniting wildfires directly, human activity can also prime ecosystems for burning, making them vulnerable to fire. For example, plantations of fire-prone species such as eucalyptus and pine have replaced less fire-prone vegetation in many parts of the world. Inadequate regulation often means that these plantations cover large uninterrupted areas, allowing fires to spread further than they would in the more fragmented landscapes that they replaced. Peatland draining is perhaps one of the most extreme examples of human activity priming ecosystems for burning. Natural peatlands (see page 25) have relatively high water tables, at commonly 10–30 cm depth, which causes the accumulation of organic material from decaying sphagnum moss to depths of one to several metres (at 190-metre depth, the Philippi peatland in Greece is the thickest known peat deposit in the world). To utilise peatlands for agriculture or forestry, people started lowering the water table by installing drains. While under natural conditions a fire would only consume the peatland vegetation, under drained conditions fires can also burn the peat itself, often as smouldering combustion. However, peatlands are sensitive ecosystems, and less severe fires can still have important impacts on soil biodiversity. Considering that peatlands have relatively large numbers of endemic species (i.e. native to that particular area), the impacts of peatland fires on biodiversity may be expected to be disproportionately large.

Effects on soil biodiversity

The impact of fire on soil biodiversity in grasslands, shrublands and forests (see Chapter III) is primarily dependent on the heat flux into the soil, which, in turn, depends on the fire severity (temperature and duration), the distance to the soil and the soil conditions themselves. For example, although crown fires may be very intense, their distance from the soil limits the heat flux to the soil. The heat from a grass fire may be very high, but it also moves quickly thereby limiting the heat flux into the soil. Surface fires that burn shrubs and forest debris produce a high fire severity with an increased likelihood of the heat flux reaching (further) into the soil. Soil conditions determine how deep the heat flux reaches: for example, drier soil of lower bulk density facilitates the heat flux.

Wetland fires

The most vulnerable soil organisms are those that reside in the organic soil layers on top of the soil, such as beetles (see page 59), because the heat flux is strongest there and often the organic soil layers are burnt themselves. Lethal temperatures for soil bacteria (see pages 33–35) range from 50 to 210 °C, while soil fungi (see pages 38–41) are generally more temperature-sensitive than bacteria. Apart from direct effects, the indirect effects of fires on soil biodiversity can be as, or more, important.

The direct effects of fire on soil biology can be severe when there is a large fuel load close to the soil, resulting in a strong heat flux, combined with a low soil moisture content which allows the heat to travel deeper into the soil. In many cases, the direct effects are less severe; otherwise, the soil biology would bounce back from the effects of the heat flux if there were no further disturbances. However, further disturbances after the initial fire event are commonplace and their impacts on soil biota can be as great as, or greater than, the heat flux.

Many soil processes change after a fire, but post-fire soil erosion probably has the greatest impact. Wildfire increases the soil’s vulnerability to erosion by removing the vegetative cover that previously protected the soil from the impacts of rainfall, but it can also alter the soil properties themselves, negatively affecting soil structure and thereby increasing the erodibility of the soil.

Wildfire oxidises the organic matter in the soil, leaving behind a structureless soil that will erode very easily. The subsequent loss of soil by erosion (see pages 128–129) can be gradual or dramatic, depending on the intensity and duration of the rainfall, and forms a loss of habitat for soil organisms. In cases where the actual amount of soil lost is relatively small, the loss of soil structure, organic matter and nutrients can still have impacts on soil biology. This means that, apart from the resilience (see page 97) of the pre-fire biological community, colonisation by new species will also occur.
Post-fire land management

Management operations after wildfire can have positive or negative consequences for soil biology. Scientific experiments have shown that forest residue mulching can keep soil erosion within tolerable limits. However, common practices include ploughing and terracing operations. These often increase soil erosion, for example, terracing can sometimes increase soil erodibility by 10 to 100 times tolerable limits. Beyond erosion of the topsoil (see page 10), including soil organisms, the terracing operations completely remove the topsoil, which then gets mixed and diluted into lower soil horizons of the terraces.

Real-time fire monitoring

- Thanks to satellites, it is possible to monitor fire locations in real-time worldwide, and get a clear overview of which parts of the globe are burning. One of the most reliable systems is the Fire Information for Resource Management System (FIRMS) [154].
- FIRMS was developed by the University of Maryland, with funds from NASA’s Applied Sciences Program and the United Nations Food and Agriculture Organization (FAO), to provide near real-time active fire locations to natural resource managers that faced challenges, by obtaining timely satellite-derived fire information.
- Global maps showing fire activities are available within three hours of a satellite overpass. On the map, each active fire location represents the centre of a 1-km pixel that is flagged as containing one or more fires.

![Post-fire land management near Sever do Vouga, Portugal. The picture shows commercial terracing operations. Tree stumps were removed while the slope was bulldozed into terraces (MMR).](image1)

![Quarterly evolution of burnt areas in 2014. The maps of burnt areas are derived from the MODIS (Moderate-Resolution Imaging Spectroradiometer) Burned Area product distributed by the University of Maryland (USA).](image2)
Soil erosion

Numbers of soil erosion

Soil erosion caused by wind and water is a widespread problem impacting ecosystems worldwide, including cultivated land, forested areas and rangelands. Recent estimates suggest that 80% of the Earth’s agricultural lands (see page 88) suffer from moderate to severe erosion, with more than 75 thousand million tonnes of fertile soil lost per year, a rate that is 10-20 times higher than the estimated rate of natural soil formation. Globally, soil erosion is the leading cause of agricultural lands becoming degraded and, ultimately, abandoned; each year, 10 million hectares of croplands have to be abandoned once the soils become so eroded that they can no longer support sufficient agricultural production. [156]

Although soil erosion is a naturally occurring process, it can be greatly accelerated by human activities, including tillage, removal of vegetation cover, soil compaction and overgrazing by livestock (see pages 122-125), particularly when these practices are conducted on steep slopes in areas subjected to intense rainstorms or wind events. Due to management practices, and climate and soil conditions (see Chapter I), rates of soil erosion can be particularly high in croplands of Asia, Africa and Latin America, which on average suffer 30-40 tonnes per hectare of soil loss per year. Soil erosion not only leads to land degradation, it can also reduce water quality and contribute to human health problems associated with elevated inputs of dust into the atmosphere.

Impacts of soil erosion

The effects of soil erosion on the abiotic conditions of the soil environment are well known. Erosion by either wind or water reduces the soil depth (or at least plant rooting depths - see page 43) and the removal of surface horizons leads to declines in the concentrations of available nutrient and soil organic matter pools. Water infiltration rates and water storage capacities are typically reduced in eroded soils, leading to decreases in the overall soil water availability. The interacting effects of soil erosion also degrade soil structure and reduce porosity. This generates a positive feedback loop that contributes to further reductions in soil water availability. Together, these effects of wind or water erosion typically lead to marked declines in plant productivity, with corresponding direct and indirect impacts on soil biodiversity.

Water erosion vulnerability

Water erosion vulnerability map. Most water erosion prediction equations are based on the amount and intensity of rainfall and on four additional factors. These factors are the ability of the soil to hold together, the surface cover (which provides protection from the forces of erosion), the distance for action (slope length) and the slope gradient. Almost all management solutions to erosion address one or more of these factors. Soil survey reports provide information about water erosion, including erosivity (K factor), soil loss tolerance (T factor) and slope gradient (derived from the USDA Natural Resources Conservation Service). [LJ, JRC] [133]

Soil losses may be due to (a) wind erosion and (b) water erosion. Both these types of processes lead to negative effects on soil-living communities. [DEH, JDY, NRCSSD]
Effects of erosion on soil biodiversity

Soil erosion can alter the amounts and types of organisms living in soil through a variety of mechanisms. Perhaps most importantly, soil erosion preferentially removes organic-matter-rich topsoils (see page 10), eliminating or reducing a resource-rich habitat that supports many soil organisms. For example, high rates of water erosion can cause many tropical soils to lose their organic horizons, leaving behind the underlying horizons that are often too acidic, nutrient-poor and depleted in organic carbon stocks to support high levels of microbial or fauna biomass. Similarly, eroded soils that have reduced water availability and lower organic matter concentrations will typically have lower rates of microbial mineralisation of nitrogen and phosphorus pools (see page 105), further reducing plant-available nutrient concentrations. Similar positive feedbacks occur when erosion-induced reductions in faunal biomass, particularly decreases in the numbers of burrowing earthworms, further reduce water infiltration rates, thereby accelerating water erosion and associated soil degradation.

Convicted of soil erosion

- Some soil organisms, such as some earthworm species, may also facilitate soil erosion by water.
- Charles Darwin was the first to observe that earthworms, under natural conditions, are able to cause erosion through the disintegration of the soil surface that then becomes more prone to runoff. In particular, the casting activities of some earthworms contribute to soil erosion.
- The species that produce lath casts favour surface sealing. These species are known as decompacting species as they produce granular casts.
- Decompacting species may also belong to other groups of soil organisms, such as enchytraeids, millipedes, ants and termites (see Chapter II).
- However, there is also a positive effect due to the tunnels burrowed by these species that increase soil porosity and water infiltration, thus delaying soil erosion.

Wind can cause high rates of soil erosion in many arid and semi-arid ecosystems where soil surfaces are often unprotected from vegetation cover. The effects of this erosion on the diversity and function of belowground biota have been particularly well-documented. Biological soil crusts (see page 73) are common in arid and semi-arid ecosystems worldwide where complex communities of cyanobacteria (see page 35), mosses and lichens (see page 42) often cover the unvegetated soil surface. Biological soil crusts are particularly sensitive to the effects of wind erosion, especially in sandy soils, given that they are concentrated in a thin layer on the soil surface and are, therefore, sensitive to removal by wind or burial by wind-deposited sediments. Furthermore, biological soil crusts typically grow and re-establish slowly following disturbance.

The loss of these crusts via wind erosion can lead to prolonged decreases in the ecosystem services they provide, including: reducing water infiltration rates, decreasing seed germination, nitrogen fixation and carbon fixation (see Chapter IV). Most strikingly, when biological soil crusts are damaged or fragmented by vehicles or trampling by humans or livestock (see pages 124-125), wind erosion rates often accelerate due to the loss of polysaccharides produced by cyanobacteria and fungi (see pages 38-41) present in these crusts that bind soil particles together. This generates a positive feedback whereby loss of biological soil crusts accelerates wind erosion, leading to further degradation of the biological soil crusts and the soils in these ecosystem types.
Land degradation and desertification

A matter of climate and human activity

Desertification, according to the United Nations Convention to Combat Desertification (UNCCD), is defined as ‘land degradation in arid, semi-arid, and dry sub-humid areas, resulting from various factors, including climate variations and human activity’. Therefore, desertification is a natural phenomenon exacerbated by human activities. Approximately 40% of the world’s land surface is covered by drylands (i.e. arid, semi-arid and dry sub-humid lands), which are home to approximately two thousand million people. Unfortunately, a large part of these lands are degraded, meaning that they are gradually losing their ecosystem functioning and productivity. This can eventually lead to desertification, which is the most severe form of land degradation. With increasing pressure on the landscape due to a growing population and economic development, this can have devastating impacts on rural livelihoods. [157]

UN Convention to Combat Desertification

- The United Nations Convention to Combat Desertification (UNCCD) is a global treaty to combat desertification and mitigate the effects of drought through national action programmes.
- The UNCCD was adopted in Paris, France on 17 June 1994, and entered into force in December 1996.
- The UNCCD has 195 parties, making it a truly global convention. All member states of the UN are parties to the convention. Canada was the only country in the world to leave the agreement in 2013.
- To help publicise the convention, 2006 was declared ‘International Year of Deserts and Desertification’.
- The UNCCD facilitates cooperation between developed and developing countries, particularly regarding knowledge and technology transfer for sustainable land management, in order to reduce land degradation.

Drivers of land degradation

There are many drivers of land degradation, including overgrazing by animals (see pages 124-125), which leaves the soil bare as well as compacted through trampling of livestock’s hooves, thus making it difficult for water to infiltrate into the ground. Further unsustainable human activities, including agricultural use of steep slopes and excessive irrigation, can lead to salinisation of the soil and erosion (see pages 128-129). Climate change (see pages 132-133), drought, and flooding further accelerate land degradation in these fragile systems. The more exposed the soil surface is covered by drylands (i.e. arid, semi-arid and dry sub-humid lands), which are home to approximately two thousand million people. Unfortunately, a large part of these lands are degraded, meaning that they are gradually losing their ecosystem functioning and productivity. This can eventually lead to desertification, which is the most severe form of land degradation. With increasing pressure on the landscape due to a growing population and economic development, this can have devastating impacts on rural livelihoods. [157]

Through this type of erosion, the nutritionally rich top layers of the soil are lost, the very layers that support soil biota. Increasing fire occurrence (see pages 126-127) changes the cycling of nutrients and biological and physical soil characteristics, including loss of structure and soil organic matter (SOM – see pages 102-106). These changes can also have indirect impacts, such as increased water repellency of the soil, decreased infiltration and increased runoff, which in turn lead to erosion and further desertification. Most feedbacks between dryland plant communities and soil fertility are linked to their mutual interaction.

Two different groups of feedback have been identified. Firstly, a high allocation of carbon and nutrients to a deep, strong and dense root system together with a notable plant cover and investment in soil microbes and enzyme production has a positive effect on soil fertility. Secondly, albeit by contrast, high retention of nutrients in standing biomass and high C:N ratios (see page 106) in litter prevent the rapid release of nutrients from the SOM, thus slowing soil microbial processes and lowering fertility. Increased drought reduces the first group of positive properties for soil fertility and protection, but intensifies the second group of negative properties. In the short-term, drought can increase SOM by increasing the total amount of litter and dead roots. Long-term experiments suggest that SOM decreases through the reduction of plant cover, implying a decrease in litter and an increase in soil erosion. Microbial activity is sensitive to drought. As the thickness of the water film around soil particles is reduced, diffusion and access to nutrients become more limited. Decreases in soil enzyme activity and respiration have been widely observed.

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Effects on soil biodiversity

Soil bacteria and fungi (see pages 33-35, 38-41) have developed strategies to survive desiccation and rewetting, including:

- a. accumulation of osmoregulatory substances that block water losses
- b. slime production that slows down desiccation processes
- c. production of dormant life forms, such as spores (see box on page 34)

Drought tolerance may also result from morphological life forms. With hyphal networks (see box on page 39) that can cross air-filled soil pores to access nutrients and water from different locations, fungi are generally considered to be more resistant to desiccation than bacteria. Some studies reported that fungi became more abundant than bacteria when soils were drier. Both are capable of rapid activation upon rewetting, and play a role in the mineralisation burst that causes the soil carbon dioxide ($\text{CO}_2$) efflux pulse following rewetting.

In Californian grasslands, the present and potentially active soil bacterial and fungal communities were tracked over a season. The potentially active bacterial community changed significantly as summer drying progressed, then returned to pre-drying composition within several hours of rewetting, displaying spectacular resilience (see page 97). By contrast, the fungal community was not detectably different among sites and was largely unaffected by dry-down, showing marked resistance to desiccation.

By reducing primary production (e.g. plant growth), drought limits food resources in the soil food web, influencing soil animals and the services to which they contribute. Soil fauna (see Chapter II) are also directly influenced as they are adapted to a high-humidity interstitial environment. Earthworms and enchytraeids (see pages 48, 58) are not active in dry soil. Protists and nematodes (see pages 36-37, 46-47) are only active in the water films surrounding soil particles. Short-lived and smaller species were found to be better adapted to drought, as they can access smaller pores where water is held and can recover quickly after drought. Microarthropods (mites and collembolans) inhabit the air-filled spaces between soil particles but their life histories are still affected by drought, with shorter-lived opportunistic microarthropods dominating drought-affected areas.

In conclusion, changes in soil moisture availability may alter trophic patterns within soil communities. Drought ultimately reduces root-mediated energy pathways through herbivores and predators. Some studies indicated changes in ratios between fungal and bacterial channels of the food web. This can have important implications on how tightly nutrients, such as nitrogen, are cycled, as bacterial-mediated decomposition pathways are ‘leakier’ than fungal-mediated pathways. Decreases in the role of fungal pathways in decomposition and nutrient-cycling dynamics may also influence soil structure and the storage of organic $\text{C}$ and $\text{N}$ within soils.

Of particular interest is the behaviour of a specific group of soil fungi, the mycorrhizal fungi (see page 40), in degraded areas. Mycorrhiza are symbiotic associations between the roots of most plant species and fungi. In dry and nutrient-poor ecosystems, mycorrhiza are critical for the improvement of drought resistance and prevention of desertification. However, mycorrhizal fungal communities are also sensitive to soil degradation and summer drought. Both reduce mycorrhizal density but usually the communities do not disappear, thus suggesting a certain degree of adaptation to stress. Mycorrhizal fungi may be the keystone microbe in dryland ecosystems. In fact, if plant carbon inputs are the major control of the soil food web (see page 96), then mycorrhiza could indirectly alter bacterial and fungal abundance and functionality by influencing plant growth. This shows the risks associated with the loss of such a group of soil organisms because of the land degradation and desertification.
Climate change

A few numbers on climate change

Climate change refers to a statistically significant variation in either the mean state of the climate or in its variability, persisting for an extended period of time (typically decades or longer). Climate change may be caused by natural processes or persistent anthropogenic processes that cause changes in the composition of the atmosphere. The most evident effect of climate change is a variation in temperature. Warming of the climate system since the 1950s is unequivocal, many of the observed changes are unprecedented over decades or millennia. Furthermore, the number and strength of recorded extreme events (e.g. heat waves, droughts, tornados and hurricanes) have increased. Each of the past three decades has been successively warmer at the Earth’s surface than any preceding decade since 1850. The period from 1983 to 2012 was most likely the warmest 30-year period of the past 1,400 years in the Northern Hemisphere, where such assessment is possible. The globally averaged combined land and ocean surface temperature data show a warming of 0.85 °C over the period 1880 to 2012. All of the above, of course, also has an impact on terrestrial ecosystems, including soil.[158-161]

Effects on soil biodiversity

Climate change is one of the most important factors of environmental change that will influence soil biodiversity and ecosystem functioning in the coming decades. However, predictions of the consequences of climate change for soil biodiversity are highly complicated by the many features that may covary with climate change. For example, climate change is preceded by a gradual increase in global carbon dioxide (CO₂) levels, which have an influence on plant species distribution and geographical position. Climate change may be caused by natural processes or persistent anthropogenic processes that cause changes in the composition of the atmosphere. The most evident effect of climate change is an increase in global carbon dioxide (CO₂) levels, which have an influence on plant species distribution and geographical position.

In a two-year warming study analysing grassland communities, it was shown that a 3.5 °C temperature increase had little effect on soil respiration and plant biomass aboveground, but the increased root growth had clear effects on the soil fauna for example, earthworms (see page 58) and some groups of mites (see page 49) decreased in numbers, whereas enchytraeids (see page 48) migrated to deeper soil layers. Soil fauna responses to warming would not be generalised, as individual groups differed in their responses. However, epigeic earthworm species completely disappeared from the plots exposed to warming, whereas the diversity of fungivorous mites increased. All together, the composition and trophic structure of the faunal community changed substantially as a consequence of warming, and the systems became more fungal-dominated.

However, the studies are still not exhaustive; therefore, a complete overview of all possible consequences of climate change cannot yet be provided. Nonetheless, there are a number of case studies available that may be used to work out several possibilities of climate change effects on soil biodiversity. Here we provide a number of such cases in order to obtain a first overview of the possible effects of climate change on soil biodiversity. In the near future, when more studies have been carried out, we may obtain a more complete understanding of climate warming effects on soil biodiversity, wherever possible classified by ecosystem type and geographical position. Climate change effects on soil biodiversity requires an understanding of the effects of warming on plant distribution, plant functioning and plant community composition, as these may reinforce, or counteract, the effects of climate change on soil biodiversity.
Climate change and migration

Climate warming influences current range shifts (i.e. migration to areas with more suitable climatic conditions) of many plants and animals. However, little is known about climate-warming effects on soil biodiversity through dispersal-mediated range expansion of soil biota.

In a study of the European coastline, root-feeding nematode communities of the dune grass Ammophila arenaria were found to be the most diverse in north-western Europe. In the Netherlands and Wales, there were eight species of root-feeding nematodes, including all major feeding types varying from ecto- to semi-endoparasites, migratory endoparasites, as well as root knot and cyst nematodes (see pages 46–47). Interestingly, towards the Mediterranean the number of root-feeding nematode species declined and included either root knot or cyst nematodes, but both sedentary endoparasites were not present at the same time in the south. Along the European coast, where nematodes and plant materials will be dispersed by sea currents, dispersal of plant genotypes and nematode species may be less constrained than anywhere on the mainland.

Nevertheless, many plant species are increasingly dispersed from lower to higher latitudes and altitudes. It has been demonstrated that, in the new range, some well-established range-shifting plant species have left behind their natural soil-borne enemies. In a phylogenetically controlled study, the rhizosphere community of range-expanding plant species was compared with that of plant species belonging to the same genus and native to the invaded range. It was shown that range-expanding plants had less fungal hyphal biomass (see box on page 99), strongly changes nitrogen (N) availability. The effects on soil biodiversity have not yet been systematically studied, but it is expected that the decomposition process (see page 106) will change from fungal-based to bacterial-based, which has substantial consequences for further ecosystem changes in these boreal ecosystems (see page 79). Such plant invasions (see page 129) may alter the regional C and N cycles substantially (see pages 104–105), increasing water consumption and air pollution, with subsequent impacts on biodiversity.

Climate change and extreme environments

Climate change can make extreme environments more accessible, which may enable species with novel traits to enter with possible cascading effects on soil biodiversity and ecosystem functioning. For example, biomes in cold climate regions currently become increasingly colonised by nitrogen-fixing plant species, such as the genera Lupinus and Alnus. The nitrogen-binding activity of the root symbionts (see box on page 99), strongly changes nitrogen (N) availability. The effects on soil biodiversity have not yet been systematically studied, but it is expected that the decomposition process (see page 106) will change from fungal-based to bacterial-based, which has substantial consequences for further ecosystem changes in these boreal ecosystems (see page 79). Such plant invasions (see page 129) may alter the regional C and N cycles substantially (see pages 104–105), increasing water consumption and air pollution, with subsequent impacts on biodiversity.

Many studies on the effects of climate change on soil biodiversity have been carried out in Antarctica (see page 96), where climate change has had astonishing effects on soil communities. Although most of Antarctica is warming, some areas are cooling, and there are pulses of wet years. This cooling has had a strong impact on the most abundant nematode species (see page 70) species, Scottnema lindsayeae, which has seen population shifts over the past twenty years with important consequences for soil carbon dynamics. However, with pulses of warming, there is some uncertainty as to whether the populations will rebound. In Antarctica, soil biodiversity can be studied in the absence of vegetation changes. In the Antarctic polar desert of the McMurdo Dry Valleys, Taylor Valley is dominated by large expanses of dry, saline soils. During the austral summer, melting glaciers, snow patches and subsurface ice supplies water to ephemeral streams and wetlands. In one year, an ephemeral stream, Wormherder Creek, produced an exceptionally high-flow event that altered soil properties and communities. The flow of water increased soil water availability and decreased salinity within the wetted zone compared to the surrounding dry soils. The leaching of salts through flooding reduced stresses to levels that are more favourable for soil organisms, improving habitat suitability, which had a strong positive effect on soil-animal abundance and diversity. Moreover, the moisture gradient created greater connectivity within the landscape, which may promote soil fauna dispersal.

Climate change and food web

Soil food web interactions (see page 96) complicate the responses of soil biodiversity to climate change. Climate change may influence individual species, which can change the outcome of species interactions when competing for the same resource. However, when the species that benefits most from warming is preferentially grazed, the effects of warming might be re-set.

This is nicely illustrated by a recent study on saprotrophic fungal communities (see pages 38–41). The composition of fungal communities is a consequence of competitive fungal interactions, and is also a major determinant of woodland decomposition and nutrient-cycling rates. An elevation of atmospheric temperature is predicted to drive changes in fungal community development. Fungal growth, however, can also be regulated by fungal grazers, such as collembolans and isopods (see pages 50, 56). Warming has promoted the competitive ability of one fungal species, but this fungal species was preferentially grazed by all invertebrates. As a consequence, a multispecies assemblage of fungi was maintained by grazing, even though one fungal species was competitively superior under warming. Decomposition was, however, enhanced under warming. The conclusion is that the effects of climate warming on complex communities might be buffered by (unpredictable) alterations of species interactions. Therefore, further investigations are needed to better understand these relationship mosaics.

Future trends

- On the basis of several scenarios exploring alternative development pathways and covering a wide range of demographic, economic and technological driving forces, future greenhouse gas emission trends and mean temperatures can be estimated.
- A range of scenarios concur that it is more likely than that the mean global surface temperature for the period 2081–2100 will be more than 1.5 °C above the mean for 1850–1900 (163).
- Such climate modifications could strongly impact soil organisms either directly, through effects on their ecology, or indirectly, through increased floods, droughts, wildfires, land-use changes and fragmentation of natural systems. An increase in soil erosion rate is also expected.
- Climate change is likely to have significant impacts on soils that may affect all of the services provided by soil biodiversity (see Chapter V). Unfortunately, a precise quantification of these impacts is not possible at the moment. In any case, all mitigation and attenuation measures taken to limit global climate change are expected to have a beneficial impact on soil biodiversity conservation, soil functioning and associated services.
Mapping potential threats to soil biodiversity

Although the role of soil organisms in providing key ecosystem services is increasingly recognised, several factors can affect the health and vitality of soil-living communities. While scientific knowledge on the effect of potential threats is advancing all the time, a geographical evaluation of the global distribution of these potential threats to soil biota is still lacking.

The lack of this type of assessment might be due to the complexity of soil biodiversity itself. As seen in Chapter II, soil communities are extremely diverse. Therefore, a risk to one specific group of soil organisms may be irrelevant to another. In addition, apart from the soil surface, the majority of the ‘habitat’ is underground and out of sight. Furthermore, many of the potential pressures are difficult to map as they result from the interactions of several factors (e.g. it is very difficult to map climate change).

Many environmental factors (e.g. temperature, land cover) are now relatively easy to map and monitor through the vast quantities of data collected by various satellite-based sensing systems. However, such tools are unable to provide direct information relating to the state of soil organisms. In addition to these conceptual problems, the issue of mapping risks to soil biota is further complicated by the lack of a clear and recognised list of the risks that can be considered to be real threats to soil organisms and, consequently, the level to which each impacts soil life.

This atlas has collected information from a group of soil biodiversity experts on potential risks to soil life. The list of threats presented in Chapter V includes those that, at the moment, can be considered as the most relevant and represent a good approximation for a preliminary assessment of potential risks to soil biodiversity.

In this context, the map on this spread is a first attempt to map potential threats to soil biodiversity at a global scale. However, the practical use of this type of map depends on the simultaneous development of systems to monitor soil biodiversity distribution. We can only assess what is under threat if we first know what is there.

Methodology

As seen in Chapter V, there are numerous pressures that can potentially alter soil life. However, it is difficult to obtain a reliable distribution assessment for many of them because 1) there are several factors determining individual pressures and 2) global scale data are often lacking.

The intensive use of soil in agriculture, for example, depends not only on the distribution of croplands, but also on the adopted agricultural practices (e.g. tillage system, fertilisers and pesticide load), which are not always easy to map at the global scale. Therefore, simple proxies were needed in order to spatially represent each of the selected potential threats.

In this context, for example, indices such as the Global Aridity Index, expressed as a generalised function of mean annual precipitation and potential evapotranspiration, can be used as proxy to visualise the distribution of soils potentially affected by climate change.
For the development of this map, the following threats and corresponding proxies were chosen:

- loss of aboveground biodiversity: map of plant species loss developed by the University of Maryland, Baltimore County (UMBC) [143]
- pollution and nutrient overloading: map of the nitrogen fertiliser application developed by the NASA Socioeconomic Data and Applications Center (SEDAC) [164]
- agricultural use: map of cropland percentage cover developed by the International Institute for Applied Systems Analysis - International Food Policy Research Institute (IIASA - IFPRI) [149]
- overgrazing: map of cattle density developed by the International Livestock Research Institute (ILRI), the Food and Agriculture Organization of the United Nations (FAO) and the Free University of Brussels (ULB - LUBIES) [152]
- fire risk: map of fire density 1997-2010 developed by the United Nations Environment Programme Division of Early Warning and Assessment (UNEP - DEWA) [165]
- soil erosion: map of Water and Wind Erosion Vulnerability Indices developed by the United States Department of Agriculture Natural Resources Conservation Service (USDA - NRCS) [133]
- land degradation: map of Desertification Vulnerability Index developed by the United States Department of Agriculture Natural Resources Conservation Service (USDA - NRCS) [133]
- climate change: map of Global Aridity Index developed by University of Leuven (UKL), with the support of the International Water Management Institute (IWMI) and the International Centre for Integrated Mountain Development (ICIMOD) [166]

All datasets were then harmonised on a 0 - 1 scale and summed, with total scores categorised as very low, low, moderate, high or very high level of threat to soil biodiversity.

**Results**

The result is an initial attempt to denote levels of potential risk to soil biodiversity at a global scale. The pattern reflects the discussion in this chapter on the main potential threats to soil life. The areas with the lowest level of risk are mainly concentrated in the northern part of the Northern Hemisphere. These regions are generally less subjected to both direct (e.g. agriculture) and indirect (e.g. climate change) anthropogenic effects. At the opposite end of the scale, the areas with highest risk are those with the greatest exposure to human activities. An important point to highlight is the nature of risk shown in the map. As indicated, the potential rather than the actual level of threat has been mapped. This means that in the areas with high or very high levels of risk, soil organisms may not necessarily be in real danger. However, these areas present a combination of factors that lead their soils, and thus the organisms living in them, to be more sensitive to risk. In conclusion, this map will require much more effort to improve both its reliability and resolution. Furthermore, in order to be useful for conservation purposes it will need to be accompanied by a reliable assessment of the global distribution of soil biodiversity. However, despite these limitations, the map represents a preliminary global assessment of the risk to soil life.
Different management practices may help preserve soil biodiversity, from low-input agriculture, crop diversification, use of organic amendments, afforestation, soil erosion control and conservation of aboveground biodiversity hotspots. The application of such practices can allow soil organisms to contribute to the provision of ecosystem services.
CHAPTER VI – INTERVENTIONS

Introduction

A significant and increasing proportion of the Earth’s land area is covered by crop- and rangelands. Agricultural landscapes hold a large proportion of the world’s biodiversity, but knowledge of the relative contribution of each land management type to the conservation of soil biodiversity, the maintenance of ecosystem functions, and the provision of ecosystem services is limited. [167]

Soil is the critical and dynamic regulatory centre of the majority of ecosystem processes. Soil organisms contribute to a wide range of ecosystem services that are essential to the sustainable functioning of natural and managed ecosystems. As mentioned in earlier sections of this atlas, highly diverse soil biological communities are largely linked to the high diversity of niches found in the soil environment, which are fostered by the extremely high physical and chemical heterogeneity at small scales, as well as the different microclimatic characteristics and functions of organisms that promote the development and maintenance of niche diversity.

Conservation of soil biodiversity in agricultural landscapes is thus intrinsically linked to land use and management systems that conserve and promote soil niche diversity. Recent evidence has shown that there are strong links between aboveground biodiversity (vegetation/crops) and belowground biodiversity (soil organisms). This finding supports the concept that modifications in plant communities as a result of changes in land use and agricultural systems can have profound impacts on the niche diversity underpinning soil biodiversity. Furthermore, it highlights the great potential to strategically utilise land management systems to influence the provision of soil-mediated ecosystem services. Limited predictive understanding of plant-soil feedbacks, however, still constrains the ecological management of soil biodiversity.

In this section, we will explore different ways in which soil can be managed to conserve soil biodiversity and sustain soil-mediated ecosystem functions and services. We start with a broad discussion about ‘land sparing’ versus ‘land sharing’ as biodiversity conservation strategies. This is followed by efforts to address ecosystem restoration challenges associated with invasive species and pollution, as well as large impact systemic changes imposed by the diversification and perennialisation of agricultural landscapes. Next follows management practices that have been adopted with significant impacts on soil biodiversity, including no-tillage systems and fire management. We conclude with more specific management practices, such as erosion control measures, the application of biochar and other soil reconstruction methods.

What can we do to protect soil biodiversity?

- Support soil-friendly cultivation that minimises the use of chemical fertilisers or pesticides. Look for organic products in the supermarket.
- Try to provide opportunities to encourage soil biodiversity where you live. Leave parts of your garden unmanaged, allow branches and garden waste to rot naturally.
- Reduce your rubbish! Recycle where possible so that we minimise the chances of soil pollution.
- Think about your ‘carbon footprint’. How are you contributing to global warming and climate change? Look at your energy consumption, try to use a bicycle or public transport instead of a car.
- Support woodland regeneration schemes.
- Encourage your local authorities to target new developments on brownfield sites so as to minimise their environmental impact. Limit, where possible, the sealing of surfaces by concrete or asphalt.
- Limit soil erosion, organic matter decline, compaction, salinisation and landslides, by identifying and communicating risk areas to land owners and local authorities.
- Carefully dispose of old medicines. Several pharmaceuticals can have significant impacts on organisms. Take old drugs to the pharmacy. Never flush them down the toilet.

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There are several actions that can facilitate conservation of soil-living communities, which can be identified when looking at the environment around us. Most of the measures would be possible through a better management of human activities. From diversification of cropland to no-tillage and soil erosion control. (ARD, JRE)
Land sparing versus land sharing

Strategies for biodiversity conservation

Conserving biodiversity within networks of reserves from which intensive human activity is excluded is part of a strategy referred to as ‘land sparing’. Consequently, agricultural land is presumably farmed more intensively for a higher yield, to reduce the area needed for production. [168]

‘Land sharing’ means adopting wildlife-friendly practices to conserve biodiversity within a matrix of land uses, such as different levels of agricultural intensification, forestry, grazing and human settlements. Given that not all land can be taken out of production, systematic conservation planning focuses on ‘sparing’ areas that contain the greatest concentration and broadest representation possible of species, and which can be maintained as conservation reserves over the long term.

Conservation planners often use vascular plants, mammals or birds as indicators of terrestrial biodiversity, as these are the taxa for which most data are available. Despite the fact that soil is likely to harbour the greatest concentration of terrestrial biodiversity, soil microorganisms and fauna have been almost completely ignored in conservation planning. Conservation research is systematically biased toward vertebrates, even though invertebrates represent nearly 80 % of known species.

Biodiversity hotspots

Relatively few studies have been carried out on the biogeography of soil biota (see Chapter III). From the limited evidence available, soil invertebrates, such as termites, ants, collembolans and earthworms (see Chapter II), appear to follow the same biogeographic patterns of species richness as aboveground species, such as an increase in species richness when moving from high latitudes to the Equator. However, soil microbes (e.g., bacteria and fungi – see pages 33-35, 38-41), nematodes (see pages 46-47) and oribatid mites (see page 49) do not seem to follow these patterns.

Soil microbes reach their greatest diversity in soils with neutral pH, which are more common in temperate climates than in the often acidic soils of the tropics. Ectomycorrhizal fungi (see page 40) are most diverse in boreal and temperate forest biomes, with reduced diversity in tropical forests. Nematode diversity is most closely linked to rainfall and temperature variables, and shows a weak latitudinal gradient. Oribatid mites increase in diversity from boreal to temperate regions, but there is no further increase in diversity toward the tropics.

A recent molecular study suggested that there may even be an inverse relationship between aboveground and belowground biodiversity for some organisms. It has been suggested that areas highlighted for conservation attention due to their high vascular plant species richness may also be important for the conservation of soil macroinvertebrates.

Strong linkages between plant biodiversity and soil biodiversity have been increasingly recognised, including plant-soil feedbacks, and evidence of positive relationships between species richness of vegetation and soil-dwelling fauna, such as termites and oribatid mites. Conservation International has identified 35 global ‘biodiversity hotspots’ which contain at least 1 500 endemic vascular plant species, and which for 30 % or less of the original extent of vegetation remains. Plant biodiversity hotspots are concentrated in tropical and subtropical regions. Protecting these areas may be an important means to indirectly conserve soil biodiversity and the benefits provided to society by these organisms.

Soil biodiversity and reserve network

While numerous site-specific surveys and assessments have been completed around the world, it is difficult to draw clear conclusions about which parts of the world harbour the greatest concentrations of soil biodiversity.

One reason is that taxonomic knowledge of soil biota is far from complete, with the great majority of species undescribed. Biodiversity assessments tend to focus on particular taxa or groups of taxa, given the enormous task of systematically describing the complete suite of soil organisms present in any particular location.

Another contributing factor is that the species present in any particular location are often unique to that location; there are few truly cosmopolitan soil-dwelling species. This means that particular soils and vegetation types may have unique communities of microbes and invertebrates, making it difficult to single out specific, high diversity areas for priority conservation. The adequacy of the existing reserve network to conserve soil biodiversity is unknown. The preservation of a representative suite of soil types in reserve networks, together with conservation management of undisturbed, unique and rare soils, are currently low priorities for environmental policy in most nations. Differences in soil type can explain a large proportion of variation in soil fungal and soil invertebrate diversity. There are indications that particular soils can have unique communities of soil biota, and that ‘pedodiversity’ (diversity of soil types in an area) is directly related to soil biodiversity, as well as aboveground biodiversity. Deliberate consideration of soil diversity in systematic conservation planning would assist in the conservation of soil biodiversity within the formal reserve network.

The 35 global plant biodiversity hotspots. Hotspots must contain at least 1,500 endemic vascular plant species. Protection of these plant species-rich areas may have positive impacts on the conservation of soil organisms (different colours aim at separating the hotspots). Data from Conservation International, 2011 (derived from Myers et al., Nature 2000 and Mittermeier et al, 2005). (LJ, JRC) [171]
Agriculture and biodiversity conservation

Due to the importance of soil biota to soil health and agroecosystem function, much of our knowledge about soil biodiversity comes from research conducted within agricultural areas. Many of these studies have concluded that high soil fauna biodiversity is supported by the heterogeneous nature of soils, and can be influenced over small spatial scales by different land-use practices and habitat variables (see Chapter III). While these studies may not be considered as ‘conservation research’ in the traditional sense, it is apparent that agricultural landscapes are actually very important habitats for a wide variety of soil microbes and invertebrates species.

Agriculture is the most significant and widespread form of human-environment interaction, consuming more resources than any other human activity. As the main driver of land conversion, biodiversity loss and changes in global biogeochemical cycles (see pages 104-105), the management of agricultural landscapes is increasingly important for biodiversity conservation. Human population growth and increasing demands for food, fuel and fibre mean that following a ‘land sparing’ approach alone is unlikely to achieve conservation goals.

The general consensus that soil spatial heterogeneity is largely responsible for the enormous biodiversity housed in soils highlights the importance of ‘land sharing’ approaches that foster habitat heterogeneity through diverse agricultural practices, which optimise rather than maximise the use of natural resources. Over time, both agricultural production and biodiversity conservation may take place within more integrated (rather than segregated) landscapes by following an approach that combines both land sparing and land sharing.

Examples of projects to preserve soil biodiversity

The Conservation and Sustainable Management of Bellowground Biodiversity (BGBD) project selected benchmark sites that represent globally significant ecosystems and land uses. Many of the BGBD project sites coincided with Conservation International’s plant biodiversity hotspots, including those in the Veracruz Biosphere Reserve in Mexico (Mesossamericn hotspot), the Monteverde Cloud Forest Reserve (Sundaland hotspot), as well as the Brazilian Amazon. Soil organisms were sampled along gradients of agricultural intensification at each site, in order to determine the extent to which soil biodiversity conservation could be achieved in mosaic landscapes where sustainable agricultural production was an intensification at each site, in order to determine the extent to which soil biodiversity conservation could be achieved in mosaic landscapes where sustainable agricultural production was an important goal. Additionally, the Alternative to Slash and Burn (ASB) Partnerships in the Tropical Forest Margins assessed the relationship between agricultural land use and soil biodiversity in four benchmark sites, including the Brazilian Amazon, Cameroon (Congo Basin Rainforest), Sumatra and the Peruvian Amazon.

Results from the BGBD project showed that more intensive agriculture often leads to a decline in soil biodiversity. Mechanisms for this decline include a reduction in the amount and diversity of organic inputs into the soil food webs in more intensive agriculture (often by substituting with agrochemicals as the main source of nutrient input – see pages 122-123), and by modification of the soil microclimate. Furthermore, hydrological functions are affected after passing certain intensification thresholds, as reduced infiltration promotes increased runoff and soil erosion (see pages 128-129), resulting in a downward spiral of degradation. ASB studies returned mixed results. In some cases, agricultural intensification led to reduced diversity and changes in community structure, particularly for termites (see page 55), while in some sites there were no substantial changes, and some elements of the biota increased in abundance (such as mycorrhizal fungi and sometimes earthworms – see pages 40, 58). Their research also showed that agricultural diversification and proximity to forested zones can promote and sustain belowground biodiversity.

The ‘land sharing’ approach to conservation recognises that biodiversity can be conserved within mosaic landscapes, including agricultural land use. For many of the tropical biodiversity hotspots, the existing network of protected areas may be inadequate for protecting biodiversity, especially where refuges are small, isolated or poorly protected.
**Benefits of soil biodiversity**

Soils associated with indigenous plants tend to have a higher number of specialist organisms, such as host-specific pathogens, or nematodes (see pages 46–47) that feed on certain root types, but also specialist beneficial (micro-)organisms (e.g. mycorrhizal fungi – see page 40). With the introduction of invasive plants, the species composition of these soils shift to contain more generalist species (see page 118). An example of this shift in species composition is noted with the increased levels of mycorrhizal and decomposer fungi beneath stands of invasive species, and a decline in the number of host-specific pathogenic fungi, which ultimately impacts an aboveground diversity. The build-up of dead plant biomass in the soil provides a greater amount of substrate for the decomposers. However, it is not only an increased diversity of decomposer species that have been noted. [174]

It has also been reported that the diversity of nitrogen-fixing soil bacteria species (symbiotic and non-symbiotic – see box on page 33) associated with the roots of invasive species, increased significantly in comparison to soils under native vegetation. The resulting increase in soil nitrogen not only contributes to sustaining the high growth rates of the invasive species, but also of other soil organisms. Studies have shown a strong correlation between increased soil nitrogen beneath stands of invasive tree species and increases in the diversity of earthworm species (see page 58). These changes, however, are often at the expense of the indigenous soil fauna and flora which were better adapted to the soil conditions that existed prior to the introduction of invasive species.

**Early warning**

Despite the partially positive effects reported above, the introduction of alien species is generally considered to be a serious threat. The impact of an invasive species on native species and an ecosystem functioning depends on the new species’ diet, speed of reproduction and spread, and the cascading effects caused. A well-known example of a devastating invasive species from both an ecological and an economic perspective is the pathogenic protist (see pages 36–37) Phytophthora cinnamomi, which caused mortality in at least 900 tree species, including many fruit trees, chestnuts, walnuts and ornamental species. The symptoms of P. cinnamomi infection are wilting, foliage desiccation and root necrosis. The native range of P. cinnamomi is Southeast Asia; however, it was accidentally introduced and has spread in Australasia-Pacific, Europe, North America and South Africa through the international transport of infected soil and/or roots.

**Prevention and restoration of invaded sites**

Prevention is the most effective management strategy to combat invasive species given the high economic costs and logistical efforts required for chemical control, physical removal of invasive species, and restoration through habitat rehabilitation and replanting. Early-warning and rapid-response frameworks have been put forward to control the proliferation of invasive species. These involve surveillance, early detection (DNA-based identification – see pages 64–65) and monitoring approaches, supported by species databases, inventories and expert registries that have led to the definition of ‘black’, ‘watch’ and ‘alert’ lists. In this regard, the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) runs the Global Invasive Species Database which provides information on invasive species, such as year and pathway of introduction, specific impacts in the places of introduction and possible management options.

**Removal of invasive species**

After the removal of invasive species from an ecosystem, the time since the start of the invasion remains one of the key factors in determining if, and how, the ecosystem will return to its original state. The longer the soils were exposed to the invasive species, the greater the changes that would have taken place in terms of soil chemistry and soil communities and, consequently, the longer it will take for these soils to return to resembling their natural state.

Initially, changes will occur within the microbial communities, as organisms, such as bacteria and fungi, can persist in an inactive state in soil for long periods of time, becoming active only when conditions are favourable. However, changes within the communities of soil meso- and macroorganisms will be slower. Furthermore, allelochemicals (toxic chemicals produced by a plant in order to defend itself) that limit the action of specialist organisms (e.g. certain pathogens or specialist root-feeders) are likely to persist for some time after the removal of invasive plant species, although, it can be expected that these chemicals will be degraded or leached from the soils over time.

As the aboveground vegetation changes from invasive to indigenous species, the input of large amounts of biomass to the soil will diminish, providing less substrate to support the large communities of decomposers, and slowing down the nutrient-cycling processes. It can be expected that, to a certain extent, the niche diversity of these ecosystems will be restored upon removal of the invasive plant species, but this process will take time and is dependent on the management of aboveground species and inputs, such as restoration planting or herbicide use. Furthermore, the removal of invasive plant species will leave soils that are well suited for the re-establishment of invasive plants, thus requiring careful management and revegetation with indigenous species.

The monitoring of these areas, and removal of any newly germinated invasive plants, should continue for a number of years after revegetation by the native plants has taken place. This is necessary as, for a number of years after the original stand of invasive species has been removed, the soil environment will continue to favour the establishment of invasive plants and, as a result, they would still have a greater competitive advantage over the indigenous species.
**Bioresmediation**

**Soil biodiversity for bioremediation**

Without doubt, the best way of managing soil pollution is to prevent it from happening and to regulate the management of waste and the use of pesticides. Over the past decades, growing awareness of environmental impacts has led to regulations on the use of old, often dangerous, substances and the development of new pesticides based on thorough testing of their side-effects on soil life (especially earthworms, entomostracans and collembolans – see Chapter III. 1.75).

In the unfortunate cases where soil pollution occurs (see page 120), soil biodiversity can be of great help through the clearing services it provides in the form of bioremediation agents (see page 100). Notably of organic compounds can be degraded through the use of specific species of soil bacteria and fungi. These species can be inculated to the polluted areas or, if they are already present in the soil, their activity can be stimulated. For example, the capacity of the wood decomposer fungus *Pleurotus ostreatus* (also commercially known as the oyster mushroom) to remove polymeric aromatic hydrocarbons (PAHs) from a highly contaminated soil was tested. After a 12-week treatment period, a reduction in PAHs of 50% up to about 90% was observed, demonstrating the PAH-removal potential of the oyster mushroom.

When bioremediation is carried out by plants (phytoremediation), specific groups of soil bacteria and fungi (see pages 33-35, 38-41) can help to increase speed and/or efficiency. For example, the bacterium *Ralstonia metallidurans* (also commercially known as the oyster mushroom) to remove polymeric aromatic hydrocarbons (PAHs) from a highly contaminated soil was tested. After a 12-week treatment period, a reduction in PAHs of 50% up to about 90% was observed, demonstrating the PAH-removal potential of the oyster mushroom.

**What are heavy metals?**

- At first glance, it would appear to be a rather simple matter to define a ‘heavy metal’: it is a metal that is heavy. Unfortunately, a more in-depth consideration reveals a huge amount of problems with this simple definition.
- Regarding their role in biological systems, heavy metals are classified as essential and non-essential. Essential heavy metals are those needed by living organisms in minute quantities for vital physiological functions. Examples of essential heavy metals are iron, manganese, copper, zinc and nickel. Non-essential heavy metals are those not needed by living organisms for any physiological functions. Examples of non-essential heavy metals are cadmium, lead, silver, mercury and chrome.
- The term ‘heavy metal’ is linked in many people’s minds to metals (or their compounds) that are toxic. However, this is a feeling rather than a conclusion based on scientific evidence. A heavy metal is not toxic per se: it is only toxic when its concentration exceeds a certain threshold. With regard to soil, we are generally concerned with toxicity to plants. In this context, the main heavy metals are cadmium, mercury, copper, nickel, zinc, chrome, arsenic and lead.
- Agricultural soils in many parts of the world are subject to long-term use of fertilisers, sewage sludge application, industrial waste and unsuitable irrigation practices in agricultural lands.

The second mechanism is known as ‘phytostabilisation’. Phytostabilisation is the most successful and well acknowledged process of phytoextraction. In this case, plants provide a suitable zone around their roots where the pollutants can be stabilised and immobilised by soil organisms. Consequently, in this process the contribution of soil biota is more evident. In particular, heavy metals are rendered harmless by soil microorganisms through different mechanisms, such as the production of specific substances (e.g. glomalin produced by arbuscular mycorrhizal fungi) that immobilise metals, the direct absorption by microbial cells and the direct reduction of heavy metal.

The process that facilitates identification of species suitable for bioremediation often requires a long time and several experiments to test the efficiency and applicability of the selected organisms at large scale. Nonetheless, current scientific knowledge shows that the use of soil organisms for bioremediation is feasible and recommended.

**Soil biodiversity as a biodicator**

The abundance and diversity of soil organisms in unpolluted healthy soils are high, while in polluted soils a marked decline in abundance and species richness of soil biota occurs. In particular, slow-growing and highly sensitive species (e.g. some fungal species) are the first to disappear from the soil communities. The targeted organisms and effects depend on the type of pollutants. Therefore, the composition of the soil communities can be indicative of the level and type of pollution, and soil organisms can be used as biodicators (see page 101) of soil pollution.

Nematode communities (see pages 46-47) have been used for this purpose as the ecology and sensitivity to disturbance of many species in this widely distributed group of soil organisms is well established. Based on the species composition of nematodes, indices of disturbance can be calculated (e.g. Maturity Index) and used to assess the severity of the pollution not only for the nematodes but also for the structure and functioning of the whole soil food web (see page 96). In fact, each nematode family can be classified into a coloniser-persister (cp) scale. The scale ranges from one (early colonisers of new resources) to five (persisters in undisturbed habitats). The maturity index (MI) of soil is weighted mean cp value of the individuals in a representative soil sample. In general, low MI values indicate a disturbed and/or enriched environment, high MI values indicate a stable environment. By calculating this index, it is possible to carry out a preliminary assessment of the state of health of a given environment.

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*The figure shows the processes of phytoremediation and phytostabilisation.*

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*The white lupin (Lupinus albus) shows phytostabilisation abilities by reducing the soluble cadmium fraction in soil (DSP).*

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*The maturity index (MI) of soil is the weighted mean cp value of the individuals in a representative soil sample. As a result, the community structure is indicative of conditions in the soil that it inhabits (SCP).*
CHAPTER VI – INTERVENTIONS

Diversification of cropland

**Same time, same place, different crops**

Agricultural intensification associated with the ‘Green Revolution’ led to a dramatic simplification of cropping systems throughout the past century. Farmers, once reliant on complex associations of crops and livestock to manage pests and soil fertility across relatively small areas, now more typically manage vast expanses of farmland dominated by a single crop, and are largely dependent on agrochemical inputs to control the growth environment of the crop (see pages 122-123). While the shift to large-scale monoculture cropping systems has served to dramatically increase crop yields, this form of management has been shown to have deleterious impacts on biodiversity at both plot and landscape scales. [177]

Interest in the diversification of agroecosystems is growing and enhanced complexity of the crop species managed is seen as an important strategy for addressing issues of long-term agricultural sustainability, soil biodiversity conservation and resilience in the face of global change and growing demands on agriculture. Polyculture is one way of diversifying agriculture at the plot scale to enhance overall productivity and the provision of key ecosystem services (see Chapter IV) through:

- the intermingling of different crops, such as the row intercropping system (the cultivation of two or more crops simultaneously on the same field in a row arrangement) and relay cropping (two or more crops on the same field with the planting of the second crop after the first one has completed its development);
- the combination of crops with beneficial plants, such as the companion planting system (the planting of different crops close to those of interest for pest control, pollination or providing habitat for beneficial creatures) and trap crops (species that attract agricultural pests, usually insects, away from nearby crops).

**Effects of polyculture on soil biodiversity**

While the management of polycultures can be different from that of monocultures in a number of ways, the most salient feature is the intentional commingling of multiple plant species in space. To date, research examining the impact of plant diversity on soil communities has yielded somewhat mixed results, yet there exists a general trend suggesting that increasing plant community complexity enhances the biodiversity of soils (see page 118). The exact nature of this effect, however, appears to depend on the ecological context and the taxonomic or functional groups in question, thus suggesting that polycultural impacts on belowground biodiversity are likely to vary. For example, the abundance and diversity of organisms that are intimately associated with plant roots (e.g. mycorrhizal fungi – see page 40) typically show more immediate responses to increases in plant diversity. Meanwhile, decomposer biota more often demonstrate legacy effects, whereby alterations to belowground community structures reflect longer-term shifts in soil organic matter quality and quantity following the transition from monoculture to polyculture systems. It has also been shown that plant diversity impacts on soil biodiversity tend to increase over time, regardless of functional group. This implies that the implementation of polycultures that are frequently disturbed (i.e. those based on annual crops and recurrent tillage) may benefit belowground biodiversity less so than in perennial systems that are based on trees or semi-permanent pastures.

The potential impacts of polyculture on belowground biodiversity mentioned above are likely due, in part, to increased resource heterogeneity in the soil. Greater complexity in plant community architecture, rooting patterns (see page 43), litter chemistry (see page 106), and root exudation, among other factors that are associated with increasing plant diversity, allows for greater niche diversification (e.g. available microhabitats and nutritional resources) and can alter belowground species interactions to enhance overall soil biodiversity. For example, it has been clearly shown that diversity in the quality and quantity of root exudates can impact the diversity and abundance of rhizosphere microorganisms. Furthermore, plant species mixtures often exhibit greater productivity than monocultures and, subsequently, enhance the flow of energy to the soil subsystem in the form of greater aboveground residues and rhizosphere inputs. This augmented resource base offers another means by which polycultures can support larger and more diverse soil communities. This is most evident when distinct plant functional groups are combined to enhance overall resources.

While plant diversity in and of itself (e.g. total species richness) has been demonstrated to be an important driver of soil communities, the inclusion of certain plant species can have disproportionate impacts on belowground activity and diversity. Nitrogen-fixing legumes offer a clear example of a plant functional group that can have long-lasting and cascading effects on soil communities. For example, legumes often enhance earthworm populations due to the improved nutritional quality of organic matter inputs. The promotion of these ecosystem engineers (see box on page 95) has, in turn, been shown to dramatically enhance habitat complexity and the diversity of smaller organisms in soils due to macrocopes and biogenic aggregates, and complete restructuring of soil profiles (see pages 110-112). Other plant functional groups, such as grasses or woody species, can have similar impacts on belowground communities and should receive special consideration in the design and evaluation of agroecosystem diversification schemes. Therefore, while maximising plant diversity within polycultures may be a valid goal for some agroecological contexts, the inclusion of just one or a few additional plant functional groups within cropping systems is often sufficient and a much more feasible option for significantly enhancing soil biodiversity and functioning.

In addition to the abovementioned benefits, there are a number of mechanisms by which increasing spatial and temporal diversity can help support biological activity and diversity in soils. However, relatively little research to date has examined the impact of such agroecosystem diversification on belowground biodiversity and functioning. The polyculture systems discussed in this section focus on crop diversification, which differs from agroforestry, and diversification by the inclusion of trees in cropland areas (see pages 144-145).
Cover crops, green manures and catch crops refer to farming practices where plants are not grown to be harvested but rather to help maintain soil productivity and fertility. The integration of these crops into a cropping system by relay cropping, overseeding, interseeding and double cropping represents a time-tested method that farmers have employed primarily to reduce soil erosion, increase soil organic matter content and nitrogen (N) availability to succeeding crops, control pests and to retrieve available nutrients from the system following a cash crop (i.e. grown for sale to return a profit). The terms ‘cover crop’, ‘green manure’ and ‘catch crop’ are often used interchangeably because they are usually grown to achieve more than one of the goals mentioned above. Here, we will use the term cover crop to refer to this practice.

The addition of cover crops, as mixtures or as individual species, to existing cash crops within cropping systems, can have many impacts on soil biota, both directly and indirectly. The inclusion of cover crops typically increases the spatial and/or temporal diversity of a cropping system, which can contribute to a wide variety of residues and diverse root systems to support soil biota. Cover crop rhizosphere processes are a major source of carbon (C) and nitrogen (N) input to the soil, and microorganisms (e.g. bacteria) preferentially colonise the rhizosphere to access these nutrients. The increased contribution of C by the roots of cover crops also improves soil structure and aggregation, thereby creating a mosaic of microhabitats, whose chemical and physical properties may contribute to the heterogeneous distribution of microorganisms and their activities, and interactions among soil aggregates of different sizes. Qualitative differences among nutrient inputs, in the form of exudates (high C:N ratio) associated with cover crops inputs govern microbial abundance, diversity, and activity (e.g. respiration and N mineralisation – see page 105). These differences may subsequently create a uniquely diverse and active microbial community necessary to decompose and process this melange of inputs. The variety of inputs combined with the associated changes in microbial communities is also likely to have impacts on other decomposer organisms and higher trophic groups.

Besides increasing the amount of resources entering a system, increased plant diversity can also enhance the stability of plant-derived resources of belowground communities by ensuring greater continuity of plant residue inputs over time. This is clearly demonstrated in agroforestry systems (see pages 144-145) where perennial plant components are integrated into annual cropping systems, thus offering both food and other resources to soil biota during the ‘off’ season, when crops are absent or inactive due to drought or cold. Similarly, cover crop management can allow for residue cover and living and decomposing roots to be present in the soil potentially throughout the year. Compared to monocultural systems (see page 125), long-term (>10 years) crop rotations that include legume cover crops have shown greater soil faunal and microbial activity that could lead to a differentiation in N cycling and storage. For example, the annual cover cropping and manure amendments characteristic of organic cropping systems have been shown to produce a more abundant, active, compositionally diverse and resilient community of soil microorganisms and its associated soil health benefits.

**Crop value and production**

- A crop is any cultivated plant that is harvested for food, clothing, livestock fodder, biofuel, medicine or other uses.
- The United Nations Food and Agriculture Organization (FAO) calculates the annual values and production of crops cultivated by the countries of the world (178).
- The value and production of individual crops vary substantially from year to year as global prices fluctuate. Country markets, weather and other factors influence production.
- In 2012, the most recent year with available data, the ten most valuable crops globally were:
  1. rice (~US$187 thousand million – approx. €174 G),
  2. wheat (~US$79 thousand million – approx. €74 G),
  3. soybeans (~US$61 thousand million – approx. €57 G),
  4. tomatoes (~US$59 thousand million – approx. €55 G),
  5. sugar cane (~US$58 thousand million – approx. €54 G),
  6. maize (~US$54 thousand million – approx. €50 G),
  7. potatoes (~US$49 thousand million – approx. €46 G),
  8. fresh vegetables (~US$46 thousand million – approx. €43 G),
  9. grapes (~US$38 thousand million – approx. €35 G),
  10. cotton (~US$37 thousand million – approx. €34 G).

**Indirect impacts on soil communities**

Beyond the relatively straightforward mechanisms described above, a number of indirect and inherently more complex phenomena within polycultural systems are likely to influence soil communities. For example, polycultures have demonstrated clear benefits for aboveground diversity and food web structure (see page 96), compared to monocultures with the same crops. In particular, the promotion of predators and biocontrol agents (see page 109) is an often-cited objective of polycultural management. While often overlooked, population increases in aboveground predators have been shown to yield important consequences for belowground, non-target fauna that often serve as supplementary food sources. Plant diversity impacts on other aboveground groups (e.g. herbivores) can have similar effects on soil communities. While such phenomena may represent major drivers of soil biodiversity in some ecosystems, they remain poorly understood and difficult to predict or manage.

**Associated management impacts**

While the above section discusses the direct and indirect impacts of increased plant community complexity on belowground biodiversity, such modifications to agroecosystems are often associated with other management practices that differ markedly from monocultures and can have important impacts on soil communities. For example, polycultures are often designed to reduce dependence on agrochemical inputs and tillage (see pages 122-123), which can represent important disturbances to soils and soil communities. This is perhaps most important in the case of pest management.

Pesticides can have strong impacts on both above- and belowground communities and have been shown to reduce soil biodiversity and food web complexity, via direct and indirect impacts on multiple taxonomic groups. In this regard, there is growing interest in the use of Brassicaceae and mustard cover crops for their biofumigation characteristics, as they have been shown to release bioactive chemicals during decomposition that can reduce disease, weed and nematode pressure on the subsequent crop. While such biofumigation may have mixed effects for belowground biodiversity in the short-term, increased resource heterogeneity and enhanced productivity of the subsequent crop are likely to help promote overall biodiversity in the long run.

The application of inorganic fertilisers is perhaps less noxious than pesticides to many soil organisms, but these inputs can have deleterious impacts on some soil groups, particularly when applied in excess. Although tillage reduction is not commonly associated with polycultures and cover crop management, this feature is important for some forms of agroecosystem diversification (e.g. agroforestry and emerging no-till cover crop systems – see pages 144-147) and can dramatically alter belowground community structure and function. While other aspects of (agro)ecosystem management may be more important for promoting and/or conserving soil biodiversity, enhancing plant species diversity (both spatially and temporally) offers an important means to both directly and indirectly influence belowground soil communities.
Agroforestry, afforestation and reforestation

Planting trees

Agroforestry is a land use practice that combines trees with crops and/or animals, arranged in space or following a temporal sequence, and benefits from ecological interactions between trees and agricultural components. Agroforestry has been increasingly recognised and practiced as a land management option that can simultaneously contribute to income, food security and the conservation of biodiversity and ecosystem services. Furthermore, it is also considered a climate change mitigation and adaptation tool for agriculture.[179]

Afforestation and reforestation both refer to establishment of trees on land without trees. Reforestation refers to establishment of forest on land that had recent tree cover, whereas afforestation refers to land that has been without forest for much longer. These practices are used by landholders who want to plant and maintain a forest on their land, to, for example, minimise erosion, reduce salinity or improve water quality.

Both agroforestry and afforestation/reforestation can be considered as effective measures to counter deforestation and the consequent loss of aboveground biodiversity that negatively impacts soil life (see page 118).

Effects on soil biodiversity

The integration of trees into landscapes has the potential to generate a number of improvements in the soil as a habitat for soil organisms. Trees promote changes in the soil environment in many ways; the tree canopy intercepts rainfall and provides shade to the understory and soil, and dead or pruned leaves and branches provide soil cover, as well as organic matter and nutrient inputs to soils (see page 17).

Periodic pruning of native trees followed by mulching in dry and sub-humid tropical environments allows for the maintenance of an organic layer on the soil, thus minimising soil erosion, helping to lower soil temperatures, and reducing water losses through evapotranspiration. In addition, the organic layer supports higher soil moisture levels required for the survival and activity of soil organisms, particularly during the dry season. Furthermore, mulch biomass is also a source of carbon and nutrients required for soil biological activity.

The key ‘refuge’ role played by trees in fostering favourable conditions for increased abundance of soil biota in their area of influence has encouraged their recognition as ‘hotspots’ of soil biological activity that contribute toward functional resilience (see page 97). Furthermore, recent agroforestry studies have shown that the distribution of soil biological activity was closely related to the spatial arrangement of trees, and that this effect was more pronounced for some tree species than others.

Examples of agroforestry: (a) trees of *Faidherbia albida* in cropping fields in Tanzania; (b) the legume *Gliricidia* with maize in Zambia; (c) seedlings of teak (*Tectona* sp.) and rice in India. (ICRAF)

(a) A tree planting in a burnt forest for a reforestation project in the USA. (b) Trees planted for an afforestation project in China. Reforestation and afforestation are a land-use change from non-forest to forest land through tree planting; the methods differ only in that afforested lands may not have contained forest previously. (USFS, LPU/CIFOR)
Trees as ‘resource islands’

The concept of ‘resource islands’, analogous to that of trees as hotspots of soil biological activity, has emerged in semi-arid regions of Africa as a result of studies of the native shrubs Guiera senegalensis and Piliostigma reticulatum as key components of farmer-managed natural regeneration efforts contributing toward afforestation. These shrubs have tap roots that reach wet subsoils near the water table and are able to transfer water from deeper soil layers to the rhizosphere (see page 43) that is close to the soil surface through a process known as ‘hydraulic lift’. This finding has changed the paradigm of how ecosystems can function under severe water limitations.

Previously, it was thought that biologically driven soil processes would largely stop during the dry season. Because of hydraulic lift, the diversity and activity of microbial communities (e.g. bacteria – see pages 33-35) can be maintained in the shrub rhizosphere during the dry season. By favouring conditions of resource availability (e.g. water), the trees create an island effect. These results obviously have implications for plant-microbial interactions related to biogeochemical processes, such as organic matter decomposition and nutrient mineralisation (see page 106). Research has also shown that the presence of G. senegalensis significantly increases crop yields of intercropped peanut and millet. This is partly due to improved water retention, and shrubs may assist crops through drought periods (a common occurrence during the growing season in the Sahel). Furthermore, such shrubs could also assist adjacent crops by promoting and harbouring beneficial microorganisms and suppressing plant pathogens. The greater nitrogen content found in soils beneath this type of shrub may suggest that free-living microorganisms are more active or that there are greater populations of soil organisms fixing atmospheric nitrogen.

Perennial cropping systems

- Most of our food crops, such as cereal grains, legumes and oilseed crops are annual plants. An annual plant completes its lifecycle, from germination to the production of seed, within one year. There are also biennial plants that take two years to complete their life cycle. Examples of biennial plants are members of the onion family, some members of the cabbage family, fennels and carrots.
- A perennial plant lives for more than two years. Once established, perennial crops have extensive root systems with increased access to nutrients and water deep in the soil. One downside to perennial crops is that their seed yield is generally lower than that of annual crops.
- Tightening of carbon and nutrient cycling in perennial compared to annual crops results in significantly lower nitrate leaching losses, as well as increased labile soil carbon essential for sustaining soil biological activity.
- Current research efforts toward sustainable production of annual grains include rotations with perennial grain crops, such as perennial wheat (obtained through several crosses of annual wheat Triticum aestivum with perennial grasses, such as Thinopyrum intermedium) and other species related to wheat and Kernza wheatgrass (Thinopyrum intermedium).
- Other perennial crops are: sunflowers, rice and sorghum. They have been developed through crossing with wild species by plant geneticists.
- Other perennial crops are sunflowers, rice and sorghum. They have been developed through crossing with wild species by plant geneticists.

Other beneficial microorganisms in the rhizosphere could be important for promoting crop nutrient availability (e.g. phosphorus mineralisation or solubilisation – see page 105), or be direct predators of pathogens.

Furthermore, the greater carbon inputs and year-round water supply in the shrub rhizosphere could create a balanced microbial community that suppresses soil-borne pathogens (see pages 108-109) through competition.

The contribution of trees to increased soil biodiversity can be attributed to their perennial nature which profoundly impacts microclimate and soil properties, including water availability, and influences the abundance, diversity and activity of soil biota required to sustain critical biological functions underpinning soil-mediated ecosystem services (see Chapter IV).
No-till farming

Global trends

The plough has always been a strong symbol of modern agriculture (see pages 122-123). However, the adoption of no-till farming has gradually increased since the 1970s as a way of dealing with problems of soil erosion and fertility. The availability of herbicides as an alternative to ploughing for weed control has played an important role. Stating in South and North America, no-till farming has spread to Australia, parts of Asia and, to a lesser extent, Europe and Africa. The area of no-till arable land is estimated at 116 million hectares globally and covers a wide range of climates, soil types and crops.[181]

No-till systems minimise mechanical soil disturbance by using direct seeders and allow for the maintenance of a permanent soil cover in the form of crop residues or cover crops (see pages 142-143). These practices include suitable crop rotations to prevent the build-up of pests and diseases. Systems that combine these three principles are known as ‘conservation agriculture’. Besides erosion control and water conservation, the reduction of production costs is an important driver of no-till adoption. On the one hand, when combined with crop residue retention and/or cover crops, no-till can have important benefits for soil life. Indeed, soil organisms are considered even more important for soil functioning and crop production in no-till soils, where they take over some of the functions otherwise initiated by mechanical ploughing, such as breaking up compacted soil, incorporation of organic matter and nutrient mineralisation (see Chapter IV).

<table>
<thead>
<tr>
<th>Continent</th>
<th>Area (hectares)</th>
<th>Percentage of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>South America</td>
<td>49,579,000</td>
<td>46.8</td>
</tr>
<tr>
<td>North America</td>
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<tr>
<td>Australia and New Zealand</td>
<td>17,162,000</td>
<td>11.5</td>
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<td>Asia</td>
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</tr>
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<td>Europe</td>
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</tr>
<tr>
<td>Africa</td>
<td>368,000</td>
<td>0.3</td>
</tr>
<tr>
<td>World total</td>
<td>115,863,000</td>
<td>100</td>
</tr>
</tbody>
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* * *

Effects on soil biodiversity

Tillage can have detrimental effects on soil life. However, some organisms are more affected than others, depending on feeding strategies, habitat preferences and reproductive capacity. Harmful impacts can be direct (e.g., body damage or increased predation).

In the longer term, the indirect effect of habitat disturbance is probably more important. Soil tillage, especially when the soil is inverted, results in the incorporation of crop residues and destroys pre-existing burrows or nest structures. This strongly affects epigeic soil organisms (those feeding on plant litter at the soil surface) and soil ecosystem engineers (e.g., earthworms – see box on page 95). A third mechanism is the change in soil moisture and temperature, with bare, ploughed soil being more prone to fluctuations and extremes. As a general pattern it has been shown that soil fauna (see Chapter II) with larger body sizes and slower reproduction/larger generation times are most sensitive to the impact of ploughing.

All soil fauna impacted by ploughing will benefit from no-till management. Considering soil microorganisms, no-till increases the importance of fungi relative to bacteria (see pages 33-35) as primary decomposers (see page 96), while ploughing creates conditions favourable to bacteria that are more disturbance-adapted and have higher metabolic rates. These changes can have important consequences for the structure of the soil food web in no-till versus ploughed soils and, subsequently, for organic matter decomposition and nutrient dynamics (see pages 104-106). Furthermore, no-till systems are characterised by an accumulation of crop residues on the soil surface and concentration of soil organic matter in the upper layers of the soil. Fungi and fungal grazers (e.g., collembolans – see page 50) are comparatively more important and nutrient mineralisation is often delayed due to higher nutrient immobilisation (high C:N ratio – see page 106). This can also impact plant growth as it changes the synchrony between nutrient availability and crop needs and can result in crop nutrient deficiencies or, on the positive side, reduce nutrient emissions from the system. In practice, the outcome in terms of nutrient-use efficiency by plants will depend on the interactions between crop type, activities of soil organisms, organic matter quality, soil type and climatic conditions. Changes in nutrient dynamics should therefore be accounted for when optimising management of a no-till system in order to ensure successful plant growth.
No-till, earthworms and termites

Earthworms and termites are called soil ecosystem engineers (see box on page 95). Their feeding, burrowing and nest-building activities strongly affect the soil structure and they can incorporate large amounts of organic matter into the mineral soil. By modifying the habitat of other organisms, they indirectly affect flows of energy, nutrients and water. Their impact on physical soil conditions can be impressive (see pages 110-113).

Earthworms (see page 51b) contribute to stable soil aggregation, and both earthworms and termites can break soil crusts and greatly improve rainfall infiltration.

No-till and arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF – see page 40) are an integral component of terrestrial ecosystems that form symbioses with most plant families, including agricultural crops. In this symbiosis, plants supply carbon substrates to AMF and receive nutrients in return, such as phosphorus and nitrogen (see page 98). AMF can also increase drought tolerance and suppress diseases, while their extraradical hyphae can bind soil particles mechanically and chemically to form stable aggregates.

AMF are mostly negatively affected by soil tillage through different mechanisms that affect the propagation structure of AMF (i.e. spores), extraradical hyphae and colonised root segments. One of these mechanisms is the dilution of spore numbers as a result of soil mixing. More importantly, tillage destroys the mycelial network and reduces mycorrhizal infectivity, thereby affecting nutrient acquisition, especially during the early stages of crop growth. Tillage reduces both AMF densities and species richness.

Soil ecosystem engineers can, therefore, play a key role in agroecosystem functioning. It has been found that no-till systems generally support larger and/or more diverse earthworm communities. A shift in relative abundance of different ecotypes is also observed. Epigeic and anecic species that feed at the soil surface especially benefit from no-till, whereas endogeic species that live and feed inside the mineral soil do well in ploughed systems in which crop residues are incorporated. Less is known about the impact of tillage on termites (see page 55), although it is generally assumed that soil disturbance negatively affects species that build subterranean nests. Foraging on crop residues by termites, however, can pose a challenge to maintaining an organic soil cover in tropical no-till systems.

No-tillage

Plant residues

- Earthworms (e.g. enchytraeids)
- Microarthropods (e.g. collembolans, feeding on fungi)

Conventional tillage

Plant residues incorporated

- Earthworms
- Microarthropods (e.g. mites)

Organic farming

- Organic farming is a form of agriculture that relies on more natural production techniques, such as crop rotation, reduced tillage or no-till, biological pest control, and manure, green manure or compost application. It excludes, or strictly limits, the use of mineral fertilisers and pesticides.
- Organic farming relies heavily on the natural decomposition of organic matter by soil organisms, especially microorganisms (e.g. bacteria and fungi), to replace nutrients taken from the soil by previous crops.
- This biological process has been referred to as “feeding the soil to feed the plant.”

In 2013, 78 million hectares worldwide were managed organically (CPA). Drastic shifts in community composition indicate that different AMF species vary in their tolerance to tillage. Indirectly, modifications in physical soil properties or soil nutrient contents in response to soil tillage, as well as changes in weed populations that act as host plants, can influence soil microbial numbers, diversity and activity, including AMF communities. However, long-term no-till farming can also result in soil surface hardening which is unfavourable for AMF distribution.

Two simplified models of food webs in no-tillage and conventional tillage agroecosystems. Larger images represent dominant soil-living organisms (derived from Hendrix et al., BiScience, 1986). (USB, LWE, ADO, AM, EDN, CW, SSR, AZA, JRC) [181]

[181] In 2013, 78 million hectares worldwide were managed organically (CPA).
Benefits of fire

Fire can threaten soil biodiversity both directly due to heat and combustion or indirectly through post-fire soil erosion and degradation. Pages 126-127 describe how fire is a natural part of nearly all terrestrial ecosystems, and that fire only threatens soil biodiversity when the balance between burning and recovery is disturbed by human activity. In this section we will take a closer look at how fire management may promote or conserve soil biodiversity. [183]

Over time, some plants have evolved to adapt to fire. One of the best known adaptations is pyriscence, which occurs when a plant releases its seed in response to fire, in an ecosystem with relatively short fire return intervals and where post-fire conditions offer improved seed germination and seedling survival. In addition to the physical opening of the seed pod, the heat from the fire can also stimulate or inhibit the germination of seeds in the soil. For example, thermal cracking of the seed coat of jelly bean tree seeds has been observed after being exposed to 200 °C for one minute and eight minutes. The resulting fracture pattern after one minute is thought to be indicative of having overcome seed coat-enforced dormancy. The deeper fracturing after eight minutes heating exposes internal parts of the seed, thereby killing it. Research has also revealed that the smoke from a fire can promote seed germination, without any thermal effect. Smoke has been observed to produce a chemical scarification on the seed surface and an increase in the permeability of the internal cuticle, both of which significantly increase the rate of germination.

Effects on soil biodiversity

Our understanding of the beneficial interactions between fire and belowground biodiversity is very limited. An increase in soil microbial activity is often seen shortly after a fire when more substrate or nutrients are available. After varying time periods, the microbial activity is generally observed to return to pre-fire levels, or lower. Changes in soil microbial community structure (e.g. species abundance) have also been observed. However, observed patterns are highly variable and there are insufficient data to obtain a clear understanding of the relationship between fire and aspects of soil biodiversity (e.g. abundance, species richness and functional diversity).

As a form of disturbance, fire may be expected to increase species richness at a moderate intensity or frequency, as suggested by the ‘intermediate disturbance hypothesis’. This states that the highest diversity of species in an ecosystem is maintained by a level of disturbance half way between frequent and rare disturbance. Therefore, in principle, an appropriate use of fire might preserve high levels of diversity. However, what this fire intensity or frequency, or combination of the two, would be for all aspects of soil biodiversity, across the range of terrestrial ecosystems, remains largely unknown and requires further research. Therefore, the application of controlled fires to promote soil biodiversity still remains largely unexplored.

Fire management

The ‘Fire Continent’

- Africa is known as the ‘Fire Continent’ because prescribed burning is a widely recognised and essential ecological factor for managing its savannah ecosystems (see page 82).
- Research investigating fire regime effects on biodiversity has led to a general understanding of the effects of the type and intensity of fires, and the frequency of burning on vegetation.
- The use of fire as a range management practice (known as burning system) has been shown to be beneficial, and viable prescribed burning programmes have been developed for the grassland and savannah areas used for both livestock production and wildlife management.
- Prescribed burning has proven to be very cost-effective and has significantly reduced the hazard of large-scale wildfires.
Soil erosion control

Practices for erosion control

Soil erosion control measures are well established and understood but, surprisingly, still not broadly implemented. There are still many farmers around the world that have not put in place erosion controls and continue to lose tonnes of soil every year. The main reasons for this lack of implementation is that most forms of erosion control require an initial economic investment for a longer-term benefit, they can take up some of the land that otherwise could be cultivated and profitable, and more labour is needed. Therefore, a long-term vision of soil maintenance is required and, even if the vision is there, factors such as lack of land tenure (i.e. the relationship, whether legally or customarily defined, among people, as individuals or groups, with respect to land), determines whether erosion control measures will be effectively implemented or not. [184]

The main method used to increase soil cover is by planting cover crops, which different soil biota can survive. Therefore, soil erosion controls indirectly protect many habitats in soil and reduce the risk of increased pollutant, drought and extreme dry-wet cycles (see Chapter V). Soil erosion control allows for an increase of earthworm burrowing activity. This helps create pores that further reduce water erosion effects. [368 (NRCS)]

In more general terms, any erosion control practice that leads to an improved soil structure will enhance the habitats for soil biota by forming a soil structure with numerous pores and aggregates (see page 72). A good pore structure will lead to a balance between oxygen, water and food for soil biota that need oxygen to survive. In contrast to the pores, the inside of the aggregates contain less oxygen, which is ideal for other biota. An improved soil structure can also better protect the soil biota against pollutants, drought and extreme dry-wet cycles (see Chapter V). Therefore, soil erosion controls indirectly protect many habitats in which different soil biota can survive.

Arbuscular mycorrhizal fungi vs. wind

- Arbuscular mycorrhizal fungi (AMF) – see page 40 – form symbiotic associations with the roots of most plant species and can improve both plant growth and soil structure [185]. AMF improve soil structure and stability with their vast underground network of fungal filaments (hyphae).
- Laboratory wind tunnel experiments were carried out to assess whether AMF were able to increase soil resistance to wind erosion.
- Researchers demonstrated that mycorrhizal fungi have the potential to increase the protective effect of newly seeded plants against wind erosion.

In general, any soil-erosion control practice will 1) reduce how much the soil is exposed to running water or wind and 2) hold the soil as much as possible in place. Therefore, the practice reduces soil disturbance, covers the soil, reduces the length of the water-running or wind-flow path and increases the root biomass holding the soil. For example, no-tillage practices have been adopted for erosion control because they strongly reduce the disturbance of the soil, and the resulting residue layer on top of the soil increases the cover (see pages 146-147). In some agricultural systems, tillage is reduced rather than completely stopped, and plant materials are added to the soil surface for mulching.

The most significant change is that the soil structure improves because of increased root biomass (see page 45), less physical disturbance, and increased soil-biotic activity (e.g. earthworms and fungi – see box to the right) all of these improvements increase soil organic matter as a binding agent that holds together soil particles in greater soil structures.

The soil biota plays an especially crucial role in cementing particles together into stable structures. For example, the burrowing of earthworms through the soil leads to the formation of pores and aggregates. The fungi entangle, just like roots, particles together, and they also produce sticky organic materials that bind particles.

The improved soil structure leads to greater soil stability that can better withstand the impact of rainfall, water runoff and wind. It also increases water infiltration into the soil, thereby reducing water running off the soil surface, which causes erosion.

Effects of erosion control on soil biodiversity

The most direct way that erosion control affects soil biota is by reducing the disturbance of the soil (see pages 128-129). For example, it is well known that no-till systems allow earthworms and fungi to thrive because they are no longer physically cut up by the plough.

Practices to reduce soil erosion: (a) inclusion of trees in agricultural fields helps to hold the soil in place, thereby reducing erosion; (b) terraced fields decrease both erosion and surface runoff; (c) planting of trees around fields as windbreaks is an effective approach to reducing wind erosion; (d) establishing a mulch cover on the soil surface reduces the impact of rainfall on the soil, thereby reducing erosion. [368 (NRCS)]
Soil amendments

Organic amendment

Soil organic matter decline and land degradation are major concerns worldwide because they have negative consequences for soil fertility and belowground biodiversity (see pages 130-131). Soil biota contributes to the fertility of soils by decomposing organic detritus and recycling nutrients, and is vital in building up and maintaining soil aggregates, thereby improving soil aeration and water-holding capacity (see Chapter IV). A positive correlation between soil community biomass and soil fertility has been accepted for a long time, and there is growing evidence that maintaining soil biodiversity is essential to ensuring soil functioning. In fact, some soil processes (e.g. soil respiration) may be carried out by a vast array of species, but others (e.g. some reactions of the nitrogen cycle – see page 105) depend on very precise functional groups consisting of a few species; they may be species-specific (e.g. nitrogen-fixing bacteria – see pages 33-34) (186).

Providing adequate levels of organic matter is central to restoring fertility and diversity to soils degraded by overexploitation, prosion or land degradation. Farms and cities produce huge amounts of carbon-rich wastes (e.g. sewage sludge and manure) that are suitable for this purpose.

The impact of organic amendments on soil biota depends on the application rate and frequency and on the physicochemical characteristics of the amendment (mainly carbon and nitrogen content and organic matter stability). As a general rule, organic amendment enhances soil microbial biomass and metabolic activity, with changes in microbial diversity ranging from no effect to modifications of the whole community structure, including shifts in the fungal-to-bacterial ratio.

Single application leads to long-lasting differences in organic carbon content between amended and non-amended soils and also to differences in microbial diversity that tend to disappear within a couple years. Microbial communities of non-amended and repeatedly amended soils differ in microbial structure and composition, but not necessarily in the ability to drive soil functions. Excessive fertilisation, however, may negatively impact key functional groups, as is the case for arbuscular mycorrhizal fungi (see page 40).

Soil invertebrates also benefit from organic amendments that increase the availability of food resources and suitable microhabitats. Composted wastes particularly boost total soil microarthropod abundance and biomass (see Chapter II). Global invertebrate biodiversity is rarely significantly altered by amendments, although significant changes in the trophic community structure may take place. A frequent feature is the relative increase of fungivorous (e.g. collembolans and mites – see pages 49-50) and predaceous (e.g. mites) functional groups when the organic matter added to the soil has been stabilised through the composting of green wastes. Conversely, amending soil with labile organic matter favours bacterial-feeders and opportunistic groups. Orbibated mites are very sensitive to the chemical quality of the amendment, and their abundance and diversity is negatively influenced by the decreasing abundance of fungii and by saline or polluted organic amendments. Nevertheless, applications of organic amendments on poor soils can be used in order to restore degraded ecosystems and allow soil biodiversity to proliferate.

Vermicompost: worms at work

- Vermicompost is the product of the decomposition of vegetable or food waste and vermicast, using various worms, usually earthworms.
- Vermicast, also called worm manure, is the end product of the breakdown of organic matter by an earthworm. Vermicompost is an excellent and nutrient-rich organic fertiliser.
- Vermicompost is rich in microbial life and can be applied to poor soils.
- Large-scale vermicomposting is practiced in Canada, Italy, Japan, Malaysia, the Philippines and the USA.
- For vermicomposting at home, a large variety of bins are commercially available.
Biochar

Biochar is the solid matter that remains after the pyrolysis (heating in low or no oxygen environments) of organic materials, such as agricultural wastes and animal manures, wastewater sludge, paper mill wastes, as well as trees or other plants. Wood charcoal, as used on barbecues, is produced through a similar process. Many people believe that biochar has beneficial value as a soil amendment and can help mitigate climate change.[187] The idea behind biochar as a soil amendment comes from Terra Preta, a type of carbon rich soil found in the Amazon Basin and attributed to early pre-Columbian activities, which is highly fertile compared to the surrounding soils. Furthermore, evidence suggests that the carbon within Terra Preta soils has remained there for a long time, from centuries to millennia. It is thought that Terra Preta soils were established over extended periods of time through the addition of charcoal and other waste materials. The idea is that adding biochar to soils, as well as helping mitigate climate change, may also lead to other Terra Preta-like properties, such as increased fertility.

Biochar and soil biodiversity

Relatively little is known about the interactions between biochar and soil biodiversity. The interactions with and effects on some groups of organisms have been studied in more detail than others. For example, microbial biomass has been shown to increase in the presence of biochar. While one possible explanation of this increase is that biochar is highly porous and that this pore space can provide a home for soil microorganisms (e.g. bacteria and fungi), recent research questions this hypothesis given the limited number of microorganisms found inhabiting biochar four years after application to the soil. Interestingly, studies using stable isotopes to investigate the availability of carbon in biochar have shown that some of the biochar carbon is more readily used by microorganisms than was previously thought and, therefore, contributes toward increasing microbial biomass.

Much less is known about the interactions and effects of biochar on soil meso- and macrofauna. Earthworms (see page 58) have been shown to prefer soil and biochar mixtures compared to soil alone, although it is very likely that this is not the case with all biochars. This is because not all biochars are identical and the physical and chemical properties of a biochar are highly dependent on the original feedstock and on the conditions that were used to produce it.

Currently, there is only limited ongoing research into the effects of biochar on collombolans or mites (see pages 49-50). Furthermore, there have not yet been any studies investigating the effects of biochar on pollinators that overwinter in the soil (see box on page 61). Such pollinators provide an important ecosystem service, valued at thousand millions of dollars each year, assessing the effects of biochar application to soil on their populations remains an important but unexplored goal.

Benefits and concerns

Despite the abovementioned unknowns, biochar is regularly reported to have several positive effects, often referred to as ‘wins’. These include increased soil fertility and climate change mitigation. Furthermore, biochar production also involves gases and oils that can be collected and used as biofuels. The fact that just about any carbon-rich compound can be used to make biochar has also led to suggestions that biochar production can be used to help reduce waste.

Experimental evidence suggests that biochar can indeed have beneficial properties, including increasing crop yields and reducing the emissions of other greenhouse gasses, such as nitrous oxide ($\text{N}_2\text{O}$ – see page 103). However, whether the application of biochar to soil creates Terra Preta-like properties in terms of increased soil fertility in all soil types remains far from certain. For instance, contrasting effects in terms of crop yields have been reported following biochar application to soils in Europe.

Finally, there are some concerns about the potential negative effects of biochar in some instances. Firstly, if biochar is to be used on a large scale, large areas of land will be required to grow the plants for its production, and land used to grow plants for biochar production cannot be used to grow other crops, or for nature conservation. Secondly, there is a risk of environmental contamination when biochar is applied to soil. Biochars usually contain polyaromatic hydrocarbons (PAHs), which are toxic to animals and plants. However, these have been shown to remain within the biochar and not to be available for interaction with organisms. Nevertheless, this is likely to vary between different types of biochar.

Biochars can also contain other pollutants, such as heavy metals (see box on page 141), if such pollutants are in the original source material. This may be the case for biochars produced from sewage sludge.

Biochar has the potential to be beneficial in terms of soil fertility and climate change mitigation. However, it is also associated with certain risks, and its interactions with the vast array of different soil organisms are still far from well understood. Biochar research is gaining momentum, in the hope of explaining the effects and interactions when it is applied to soil in order to maximise the benefits and minimise the risks to soil biodiversity and the functions and processes driven by soil biota.
Soil biodiversity is often overlooked by policy makers and educators. However, interest in soil life dates back to a thousand years ago, and the number of studies that aim to describe the role of soil biota in a changing world is continuously increasing. There is a strong need to put soil biodiversity in the spotlight and give it the attention it deserves. (JRB, DVD, BML, MPH, TGA, JKL)
Introduction

Changes in the way human societies interact with nature to encourage more sustainable pathways also require changes in perception. Modifying the way people perceive nature is not simple. It requires a better understanding of the current status of nature, of the benefits provided to society and of ways to sustainably manage and conserve natural capital to benefit future generations.

In this chapter, the focus is on the role of environmental policies in the protection of soil as a resource. We also look at the concept of soil as a critical component of natural capital and how knowledge can shape the perceptions of society. Such understanding can guide people in making more informed decisions, ultimately leading to the sustainable management of natural resources.

Firstly, we take a look at policies that have been developed to conserve and manage soil biodiversity. Secondly, we present an overview of historical knowledge about the living soil and its management, showing how perceptions have changed through time. This is followed by examples of research projects from around the world that aim to improve our scientific knowledge of soil biodiversity. We then examine the various ways in which knowledge acquired by land managers is currently shared through participatory approaches and experiential learning that aim to conserve and manage soil biodiversity. The chapter also highlights the important role of education. Especially effective are simplified approaches, particularly for children, that help change negative perceptions about soil organisms, often resulting from an increasingly urban culture that limits both a direct interaction with nature and a balanced perception of reality. Finally, we conclude with a number of resources available to help different sectors of society become aware of the wealth of life belowground and its fundamental role in our lives on Earth.
Policies for soil biodiversity

Biodiversity and policy

Society in general, and policy makers in particular, have neglected soil biodiversity. Initially, no attention was given to the large biodiversity pool stored below ground and only at a later stage, during the implementation of the Convention for Biological Diversity (CBD), was attention given to this important aspect of global biodiversity.

At its 6th meeting in Nairobi, April 2002, the Conference of the Parties (COP) of the CBD decided (COP decision VI/15, paragraph 15) to establish an International Initiative for the Conservation and Sustainable Use of Soil Biodiversity as a cross-cutting initiative within the programme of work on agricultural biodiversity, and invite(s) the Food and Agriculture Organization (FAO) of the United Nations, and other relevant organisations, to facilitate and coordinate this initiative. Following that decision, an International Technical Workshop on the Biological Management of Soil Systems for Sustainable Agriculture was organised by the Brazilian Agricultural Research Corporation (EMBRAPA) and the FAO in Brazil in June 2002, to provide further elements for a coherent global framework to protecting the biological diversity of soils.

• The Convention on Biological Diversity (CBD) is a multilateral treaty brokered by the United Nations. The Convention has three main goals:
  - conservation of biological diversity (or biodiversity),
  - sustainable use of its components,
  - fair and equitable sharing of benefits arising from genetic resources.
• The Convention was opened for signature at the Earth Summit in Rio de Janeiro (Brazil) on 5 June 1992 and entered into force on 29 December 1993.
• One hundred and ninety-five states and the European Union are parties to the convention. All United Nations Member States, with the exception of the United States of America, have ratified the treaty.
• At the 10th Conference of the Parties (COP) to the Convention on Biological Diversity in October 2010 in Nagoya (Japan), the Strategic Plan for Biodiversity 2011-2020 was adopted as the basis for halting and eventually reversing the loss of biodiversity on Earth.
• The Strategic Plan for Biodiversity 2011-2020 includes five strategic goals and 20 ambitious, yet achievable, targets to be reached by 2020. These are known as the Aichi Biodiversity Targets.
  - Goal A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society,
  - Goal B: Reduce the direct pressures on biodiversity and promote sustainable use,
  - Goal C: Improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity,
  - Goal D: Enhance the benefits to all from biodiversity and ecosystem services,
  - Goal E: Enhance implementation through participatory planning, knowledge management and capacity building.
• In 2010, governments agreed to the Strategic Plan for Biodiversity 2011-2020 and the Aichi Targets.
• On 22 December 2010, the United Nations declared 2011 to 2020 as the UN Decade on Biodiversity.
• The United Nations proclaimed May 22nd the International Day for Biodiversity, and 2010 the International Year of Biodiversity.

Progress made by the FAO in coordinating this initiative was reviewed at the 8th CBD COP in Curitiba, Brazil, in March 2006. The conference adopted a framework of action for the International Initiative for the Conservation and Sustainable Use of Soil Biodiversity. This framework was intended to facilitate the implementation at national, regional and global scales of the proposed main activities and actions. Unfortunately, only a few national governments and international organisations adopted the initiative and developed national or international soil biodiversity activities.

Avoided loss of mean species abundance

Expanding protected areas by 20%"}

Reducing deforestation

Closing the yield gap

Reducing post-harvest losses

Changing to healthy diets

Improving forest management

Mitigating climate change without bio-energy

% of mean species abundance

14.2 - 17
2.9 - 5.6
5.7 - 8.5

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Awareness of the value of life in the soil should be complemented by education, training and heightened responsibility of national governments to develop national policies and strategies for measuring, conserving, protecting and restoring their biodiversity resources. At the heart of these measures is legislation that prohibits the taking of species that are endangered (threatened with extinction throughout all or a significant portion of their ranges) or threatened (likely to become endangered throughout all or a significant portion of their range) within the foreseeable future. An additional protection route is to limit habitat alterations that could affect an organism (for example, destroying breeding grounds). Many people may be aware of specific acts to protect aboveground biodiversity (e.g. nature reserves, Red List, ivory export ban, greenbelts, etc.). However, it may be surprising to learn that there is virtually no explicit protection of the organisms that live in the soil.

Part of the problem is that biodiversity is a significantly complex scientific concept compared to other environmental issues, such as air or water quality. Soil biodiversity cannot be measured by simple universal indicators, such as temperature or the concentration of a pollutant. It is clear that soil biota can be offered some security where countries or regions have strong soil protection or nature conservation policies or strategies. Most soil-related legislation aims to secure or restore soil functions by limiting negative effects, such as the physical loss of soil (i.e., by reducing erosion by wind or water, land use change and the sealing of soil by urban development) or by controlling the introduction of potential toxins, such as endocrine disrupters or pesticides.

To be effective, legislation affecting soil biodiversity must be viewed within a broader context of land use planning which must reflect the multiple demands on soil but at the same time ensure that these uses are undertaken in a rational manner under the umbrella of sustainable development. However, it is worth noting that legislation by itself may not solve all issues connected with the conservation of soil biodiversity. Laws and regulations should be complemented by education, training and heightened awareness of the value of life in the soil.

Global Soil Partnership

In 2011, the Food and Agriculture Organization (FAO) took the initiative to propose a new Global Soil Partnership (GSP) as a voluntary platform that would allow for the implementation of sustainable soil management practices. More than 30 years after the adoption of the World Soil Charter, all FAO members, as well as relevant stakeholders from the private sector, NGOs and academia, joined in a common voluntary effort to take action against the rapidly increasing degradation and depletion of our limited soil resources [190]. After the establishment of the GSP, five plans of action were developed:

1. promote the sustainable management of soil resources for soil protection, conservation and sustainable productivity,
2. encourage investments, technical cooperation, policy, education, awareness and extension
3. promote targeted soil research and development, focusing on identified gaps, priorities and synergies with related productive, environmental and social development actions
4. enhance the quantity and quality of soil data and information: data collection (generation), analysis, validation, reporting, and monitoring and integration with other disciplines
5. harmonise methods, measurements and indicators for the sustainable management and protection of soil resources.

Of crucial importance to the development of these plans of action was the establishment, in 2013, of a functioning science-policy interface within the GSP: the Intergovernmental Technical Panel on Soils (ITPS). The ITPS is composed of 27 high-level soil experts representing the seven FAO regions of the world (Europe, Asia, Pacific, Africa, Near East and North Africa, South America and Mexico, and Central America and The Caribbean). Similar to the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), it provides high-level policy advice on soil-related technical and scientific issues. For soil biodiversity, it has developed a close cooperation with the Global Soil Biodiversity Initiative and the IPBES in order to assure a full assessment of global soil biodiversity and the necessary information for implementing adequate policies to protect this important biodiversity pool.

Policies for protecting soil biodiversity

While the main international agreement to protect biodiversity is the Convention on Biological Diversity (CBD), it is the responsibility of national governments to develop national policies and strategies for measuring, conserving, protecting and restoring their biodiversity resources. The CBD is a mandatory instrument, and the first step towards the protection of soil biodiversity should be the adoption of the World Soil Charter. However, it is important to note that the CBD is not designed to address soil biodiversity per se. The convention does not provide for the conservation and sustainable use of soil biodiversity resources and, more specifically, to soil biodiversity.

SDG 1: End poverty

SDG 2: Achieve food security

SDG 3: Healthy lives for all

SDG 5: Gender equality

SDG 6: Water for all

SDG 7: Energy for all

SDG 11: Cities safe and sustainable

SDG 12: Combat climate change

SDG 15: Protect terrestrial ecosystems

Access and secure rights to productive land

Actions to be taken

Changes in land use and cover, resulting in sustainable use

Promoting sustainable agriculture and food systems

Halting deforestation, land and soil degradation, and biodiversity loss

Increased production and consumption of biomass for food, feed, fibre, and fuel

Basic soil-biodiversity-related ecosystem services that must be protected

Carbon cycle regulation and contribution to climate change mitigation

Regulation of water supply and quality

Biological population control and habitat support

Nutrient provision and cycling for crop/forest growth and other ecosystems

Sustainable Development Goals

Following the Rio+20 Conference in 2012, a process was initiated to define the post-2015 global agenda leading to sustainable development. A series of Sustainable Development Goals (SDGs) have been defined that, if implemented, could allow all of us to live on this planet in a sustainable way. The goals have a timeframe of 15 years, starting in 2015, and include a series of goals relevant to soil resources and, more specifically, to soil biodiversity.

Soils are well recognised as one of the major elements of sustainable development. Being a limited, non-renewable, natural resource, they must be managed in a sustainable way for future generations. Soils are relevant to food security (SDG 2 ‘End hunger, achieve food security and improved nutrition and promote sustainable agriculture’), food safety and human health (SDG 3 ‘Ensure healthy lives and promote well-being for all at all ages’) and nature protection (SDG 15 ‘Protect, restore and promote sustainable use of terrestrial ecosystems, manage forests, combat desertification, halt and reverse land degradation and halt biodiversity loss’). Each of the SDGs includes detailed targets to be achieved by 2030.

Soil biodiversity is a key element of the proposed sustainability agenda, especially within SDG 15 which addresses terrestrial ecosystems and land degradation. Very important will be the definition of clear indicators that will allow us to measure progress towards those ambitious goals and targets. Certainly an indicator on soil biodiversity would be very helpful, not only for assessing progress towards protection and restoration of terrestrial ecosystems, but also linked to other related goals of food security and food safety.

Sustainable Development Goals

1. The 68th United Nations General Assembly declared 2015 the International Year of Soils (IYS). The Food and Agriculture Organization (FAO) was nominated to implement the IYS 2015, in collaboration with governments and the secretariat of the United Nations Convention to Combat Desertification (UNCCD).

2. The IYS 2015 aimed to increase awareness and understanding of the importance of soil, including its biodiversity, for food security and essential ecosystem functions.

3. The specific objectives of the IYS 2015 were to:
   - raise full awareness among civil society and decision makers about the profound importance of soil for human life.
   - educate the public about the crucial role soil plays in food security, climate change adaptation and mitigation, essential ecosystem services, poverty alleviation and sustainable development.
   - support effective policies and actions for the sustainable management and protection of soil resources.
   - promote investment in sustainable soil management activities to develop and maintain healthy soils for different land users and population groups.
   - strengthen initiatives in connection with the SDGs (Sustainable Development Goals) process and post-2015 agenda.
   - advocate for rapid capacity enhancement for soil information collection and monitoring at all levels (global, regional and national).

4. In 2002, the International Union of Soil Sciences (IUSS) made a resolution proposing the 5th of December as World Soil Day to celebrate the importance of soil. In 2013, the 5th of December was declared World Soil Day.
Historical knowledge

Nature is essential for humankind

Humans have always depended on nature for their food and shelter. Early humans, by necessity making a living as hunters and gatherers, learned to read the landscape and (by trial and error) discovered which food and water sources could be found above- as well as belowground. Soil-based resources entail plant roots, mushrooms, grubs, seeds, nuts, soil-dwelling mammals, reptiles and insects. In industrialised countries, such knowledge of nature as a natural provider of food, building tools and medicine is no longer present among the majority of people.

In the few ancient cultures that still exist today (i.e. the aboriginals in Australia or Bushmen in Africa), we can still find understanding of above- and belowground biodiversity and its uses; knowledge that was passed on for many generations over thousands of years. This skill was established through storytelling, songs and paintings. It is important to realise that belowground resources are not only very important as food but also for the provisioning of scarcely available water which, for example, Bushmen can obtain from plant roots.

Indigenous people created these soils by adding charcoal, animal bones and organic residues of plants and animals to the soil. This soil management promoted soil structure and enriched the soil with mineral nutrients, such as nitrogen, phosphorus, calcium, manganese and zinc, as well as organic matter and soil organisms. These properties have only been revealed in recent decades, but the creators and users of these soils were clearly aware of the importance of good soil management practices for increasing their crop yields.

Another classic example of the use of inherent soil biodiversity is the practice of mixed cropping of legume species, such as beans or peas, with non-legume species, such as maize or other grass species, as practiced by many ancient civilisations in China, the Middle East and Mesoamerica. This farming system makes use of biological nitrogen fixation (BNF) by legume crop roots in symbiosis with nitrogen-fixing bacteria (see pages 33-34), and benefits plant species that require a lot of nitrogen but cannot support the BNF. Legume species are good hosts for specific species of soil-dwelling nitrogen-fixing bacteria, while grass species are not because they lack the recognition system (via chemical signals) and cannot develop the root nodules that host the bacteria. The whole process of biological nitrogen fixation and the role played by specific soil bacteria was only discovered at the very end of the 19th century by the German agronomist Hermann Hellriegel and Dutch microbiologist Martinus Beijerinck.

Agriculture, soil fertility and biodiversity

Ever since the onset of agriculture approximately 10,000 years ago, mankind has modified the land and the soil. In order to clear natural land to make space for desired plant species (i.e. early crops not resembling those we know today), land was burnt. Not only did the fires create space, they also left minerals in the form of ash to the benefit of plant growth. When production declined after such slash-and-burn practices, another piece of land would be burnt and the old land left to regenerate.

This practice demonstrates knowledge of the interactions between soil properties and plants, our ability to manage it and the need for a recovery period without understanding all the specific underlying mechanisms. In fact, our understanding of the mechanisms of plant growth and the visualisation of soil organisms would only be realised in the 17th - 19th centuries. A good example of well-developed soil management is found in soils of the Neotropics. In these regions, man-made soils created 9,000 to 2,500 years ago by the activity of humans are found to be more fertile than the surrounding non-managed soil. These soils are known as Amazon Dark Earths or Terra Preta (see page 151).

Early descriptions of soil biota

The ecology of some soil biota achieved high worship value in ancient cultures. In ancient Egypt, the cyclic nature of days and seasons was recognised and was of central importance in mythology and daily life. In this context, the dung beetle Scarabaeus sacer of the family Scarabaeidae played an important role as the symbol for the sun god Ra. This god was believed to roll across the sky each day with the power to transform bodies and souls. The behaviour of the dung beetle was seen to match this cycle as the beetle rolls balls from dung and deposits its eggs inside this ball so that the larvae that hatch from the eggs have plenty of food.

The ancient Greek philosopher, Aristotle (384-322 BC), studied and wrote about many scientific disciplines, including biology. He studied plants and animals, their morphology and behaviour. Among his writings on animals, soil-dwelling insects and worms did not go unnoticed. For example, in the History of Animals he noted 'some creatures provide themselves with a dwelling, others go without one: of the former kind are the mole, the mouse, the ant, the bee; of the latter kind are many insects and quadrupeds.' […] Further, in respect to locality of dwelling place, some creatures dwell underground, as the lizard and the snake; others live on the surface of the ground' (translated by D’Arcy Wentworth Thompson).

Worms are the intestines of the earth

Aristotle, Historia animalium, 350 BC.
17th century

Given the very small size of most soil organisms, it is no surprise that it required the invention of the microscope before soil biodiversity could really be explored. The first microscopes and the descriptions of the observations of the very small organisms were initially only of academic interest. The first publication with drawings of microscopic observations was Micrographia by Robert Hooke, published by the Royal Society in England in 1665. The publication of Micrographia and its drawings greatly inspired Antonie van Leeuwenhoek (1632-1723) to further develop his own microscopes with higher resolution and to further explore microbial life.

18th century

The descriptions of new species, including those of microorganisms, continued to expand in the 18th century. With respect to the discovery and descriptions of fungi, the work Nova plantarum genera (1729) by the Italian botanist Pier Antonio Micheli is noteworthy. Not only did it contain descriptions of 1,400 plant species that were new to science, it also comprised 900 species of fungi and lichens and recognised that the lifecycle of fungi occurs through spores (rather than from spontaneous generation).

While the 18th-century Swedish botanist, physician and zoologist Carl Linnaeus (see page 29) described many species of plants and animals, he also developed a simple system of naming (with genus and species names) and ordering or classifying organisms based on their (mostly morphological) characteristics and level of complexity.

19th century

The foundations of the systematic ordering of life on Earth from unicellular organisms to humans by Linnaeus were further developed in the 19th century by the German scientist Ernst Haeckel (1834-1919) and the English scientist Charles Darwin (1809-1882). In his publication Generelle Morphologie der Organismen in 1866, Ernst Haeckel not only found, described and named several new species, he also related all life forms and their evolutionary development in the form of a tree (first example of an evolutionary tree). Furthermore, he is considered to be the father of ecology since the word and concept of ‘Ecology’ (‘Ökologie’) was used for the first time in that same book.

Charles Darwin is best known for his major insights into the process of the evolution of life on Earth. Less well known, but no less important, is that he can be regarded as a founding father of soil ecology. Shortly after his return from his voyage on the Beagle, Darwin showed a keen interest in earthworms and reported on an experiment with earthworms, the first ecological experiment, in The Origin of Species.

In recent years our understanding of the composition and activities of soil biota, and its evolutionary history and future potential has developed significantly due to advances in molecular biology and bioinformatics (see pages 64-65). Furthermore, this knowledge has become more accessible through dedicated websites.

High-throughput DNA sequencing

- In recent years, the high demand for DNA (see box on page 30) sequencing has driven the development of high-throughput (or next-generation sequencing) technologies that accelerate the DNA reading process, producing thousands or millions of sequences concurrently.
- For example, nowadays there are instruments that provide more than 25 million sequences in only two days with 99.9% accuracy.
- To illustrate the nature of the reductions in DNA sequencing costs, and the power of high-throughput techniques, it is sufficient to consider that the cost of sequencing a genome the size of human dropped from 100 million dollars in 2001 to approximately 1000 dollars in 2015. In addition, the first sequencing of the human genome required 15 years, while in 2014 it was possible to sequence over 45 human genomes in a single day.
- Of course, these techniques can also be applied to the study of soil biodiversity to discover an unprecedented diversity of organisms living in soils.
- The future of research into soil biodiversity and, in particular, the possibility to undertake a large-scale assessment and monitoring will be strongly influenced by the use of high-throughput technologies.
Research into soil biodiversity

The Tropical Soil Biology and Fertility Programme

Several international projects remain focused on the study of soil biodiversity and its role in ecosystem functioning.

For more than thirty years since its foundation in 1984, the Tropical Soil Biology and Fertility Programme (TSBF) has promoted and facilitated research into the biological management of soil fertility throughout the tropical regions of Africa, India, Southeast Asia and Latin America. The main target of this programme has been to utilise knowledge of soil biodiversity to enhance the productivity and sustainability of agriculture practiced by resource-poor smallholder farmers, particularly those farming on degraded soils (192). The research follows three main interlinked aims:

1. improve methods for the management of organic inputs, such as crop residues or manure, with or without mineral fertilisers
2. contribute to environmental change research by studying the impact of land-use change on the carbon cycle, particularly with respect to the role of soil organic matter in agricultural productivity
3. manipulate soil organisms and soil biodiversity for improved soil health

One of the most significant and influential outputs from this research was the development of a management tool to facilitate the choice of the most appropriate use of organic inputs for nutrient supply to crops and soil erosion control: the TSBF Organic Resource Database and Decision Support System

All TSBF research projects have been carried out through networks involving collaboration between large numbers of national and international research institutions and universities. An essential feature of such collaboration is the use of standard methods.

Two TSBF Handbooks of methods for soil research have been produced and widely used throughout the tropics. The TSBF was a pioneer in the application of participatory research on soils.

TSBF legacy

To understand the effects of different disturbances on soil biota and to compare sites and treatments, there is a need for standard methods and practical instructions for the inventory of belowground biodiversity. One of the main achievements of the TSBF is the production of texts proposing standard methods for the study of biodiversity. Handbooks for sampling soil organisms have appeared at regular intervals over the past 50 years, but more recently there has been a set of protocols focused on tropical systems, assembled and drafted by scientists affiliated with or associated to the TSBF, such as those of the Macrowauna Network, the Terrestrial Initiative in Global Environmental Research (TIGER) and the Alternatives to Slash-and-Burn project (ASB).

Methods for the analysis of some components of soil biota were included in the pioneering text in 1993 ‘Tropical Soil Biology and Fertility: A Handbook of Methods’. This is a manual largely devoted to physical and chemical analyses, including the study of processes, such as litter inputs and decomposition rates. However, it also recognises the importance of investigating a number of functional groups of soil organisms, including three types of earthworms and both mycorrhizal fungi and root-nodulating bacteria (see Chapter II). In 1996 another book, entitled ‘Methods for the Examination of Organismal Diversity in Soils and Sediments’, also developed as part of UNESCO’s contribution to the DIVERSITAS Programme, presented some instructions for the analysis of soil life.

A great improvement in the standardisation of soil biodiversity investigations is proposed in the 2001 report ‘Standard Methods for the Assessment of Soil Biodiversity and Land-use Practice’. This publication extends the number of functional groups of soil organisms to be considered for a reliable analysis. It adds detailed methods for the evaluation of nitrogen-fixing Leguminosae-nodulating bacteria (see pages 33-34) as well as of members of microfauna, and introduces the concept of extended (100 m) transects for sampling termites and ants.

The Red List of Threatened Species

• The International Union for Conservation of Nature (IUCN) Global Species Programme working with the IUCN Species Survival Commission (SSC) has been assessing the conservation status of species on a global scale for the past 50 years in order to highlight taxa threatened with extinction, and, thereby, promote their conservation.
• Although today the political, economic, social and ecological world is very different from when the first IUCN Red Data Book was produced, the IUCN Global Species Programme, working with many partners, remains firmly committed to providing the world with the most objective, scientifically based information on the current status of globally threatened biodiversity.
• The plants, fungi and animals assessed for the IUCN Red List are the building blocks of ecosystems, and information on their conservation status and distribution provides the foundation for making informed decisions about conserving biodiversity from local to global levels. The IUCN Red List of Threatened Species provides taxonomic, conservation status and distribution information on plants, fungi and animals that have been globally evaluated using the IUCN Red List Categories and Criteria. This system is designed to determine the relative risk of extinction, and the main purpose of the IUCN Red List is to catalogue and highlight those plants and animals that are facing a higher risk of global extinction (i.e. those listed as critically endangered, endangered and vulnerable).
• The IUCN Red List also includes information on plants, fungi and animals that are categorised as ‘extinct’ or ‘extinct in the wild’, on taxa that cannot be evaluated because of insufficient information (i.e. are data deficient), and on plants, fungi and animals that are either close to the threatened thresholds or that would be threatened were it not for an ongoing taxon-specific conservation programme (i.e. are near threatened).

The latest guide presented in the context of TSBF is the ‘Handbook of Tropical Soil Biology, Sampling and Characterization of Below-Ground Biodiversity’. It was released in 2008 as an outcome of the Global Environment Facility (GEF)/United Nations Environment Programme (UNEP)-funded project ‘Conservation and Sustainable Management of Below-Ground Biodiversity (CSM-RGBD)’. It further enlarges the number of functional groups of soil organisms to be analysed in a soil biodiversity survey. In more than 200 pages, sampling methods are described and identification routes recommended for ants, termites, beetles, fruit flies, earthworms, collembolans, mites, nematodes, fungi and bacteria. In addition, it includes the first extensive discussion on the issues related to soil biodiversity sampling in land-use mosaics, with practical advice on what, when and where to sample, as well as detailed schemes for land-use description and classification. Finally, a scientific paper from 2009 summarises progress towards a universal protocol for sampling soil biota in the humid tropics, including a discussion of spatial scaling and replication issues.

All these valuable publications on methods necessarily set the agenda for future belowground biodiversity projects in relation to land-use change and agricultural intensification, by specifying the groups of organisms that must be sampled or assessed. Furthermore, they raise questions on the relationships existing among species diversity, functional diversity, trait diversity, functional composition and the occurrence and intensity of ecological processes (see Chapter IV). Summarising all these aspects, one of the main achievements related to soil biodiversity of the TSBF Programme is the central role of the concept of functional group. It highlights the poor state of taxonomical knowledge for some groups of soil organisms and the lack of agreed or adequate methods to extract and enumerate others. Also, it states the need to examine all components of soil biota to obtain a reliable assessment of soil functioning and quality.
Ecological Function and Biodiversity Indicators in European Soils

The European Union (EU) acknowledges the importance of soil biodiversity in the role of ecosystem functioning. The European Commission’s biodiversity (see box below) and soil strategies are designed to protect soils and their biodiversity while enhancing soil-based ecosystem services, with a view to promoting sustainable soil management. However, while we are gaining knowledge of the role of soil organisms in several processes that take place in soils, we have very little information about the geographical distribution and variation in soil biodiversity or the functional capacity of these belowground communities. [153]

In 2011, the EU Ecological Function and Biodiversity Indicators in European Soils (EcoFINDERS) project was launched to address this lack of spatial information on soils and to generate European datasets of soil biodiversity and ecosystem function. Soil biodiversity (microorganisms and fauna) were assessed at 81 sites across Europe: a sampling campaign of unprecedented scale for soil biodiversity. The sites cover a range of biogeographical zones, that include Atlantic, continental, boreal, alpine and Mediterranean regions. Encompassed in these zones are a range of land uses: tillage, grass and forestry and a large spectrum of soil properties (represented by pH, organic carbon, total nitrogen and texture).

Standardised biological methods were applied to assess the abundance, diversity and functional capacity of organisms found in soils across Europe. These methods were selected for:

- their ability to provide relevant information, their cost-effectiveness
- their applicability in the field (at time of sampling) and laboratory (during analysis)

The diversity of archaea, bacteria, fungi, arbuscular mycorrhizal fungi, nematodes, enchytraeids, mites and collembolans were analysed (see Chapter III).

The data collected provide information to policy makers and land managers for establishing diagnoses of soil quality and designing practices for sustainable land management in order to preserve and value soil biodiversity. Furthermore, all samples being georeferenced will allow for the assessment of temporal variations of soil biodiversity across Europe resulting from global changes and human activities.

More details about EcoFINDERS can be found at the following link: http://ecofinders.dmu.dk/

Biomes of Australian Soil Environments

The Biomes of Australian Soil Environments (BASE) programme is a collaborative effort initiated by the scientific community to develop a publicly accessible database that encourages the discovery and observation of soil microbial communities across Australia’s diverse natural and agricultural ecosystems. The programme delivers a ‘National Framework Dataset’ that provides baseline information on microbial communities from Australian soils, and allows for the exploration of the determinants of these microbial properties at a continental and, ultimately, global scale.

The BASE database comprises microbial and environmental data collected in a systematic and controlled way to ensure reproducibility and inter-sample comparability. Information on the workflow including sampling strategy, DNA extraction, sequencing and physical and chemical analyses can be found on the BASE project portal (see https://ecogapps.com.auflpa-metadata/base/ information for details). All data collected by the project are publicly available via this portal, enabling identification of samples of interest and exploration of associated environmental data.

In 2011, the BASE project could be a model for similar assessments of other continents, to eventually derive a global overview of soil biodiversity.

The repository contains microbial genome data comprised of bacterial and archaean DNA sequences and fungal and other eukaryotic sequences (see pages 64-65). Each sample has associated epifluorescent variables (soil particle size, ammonium and nitrate content, total nitrogen, phosphorus, potassium, sulphur, total carbon, organic carbon, conductivity, pH, copper, iron, manganese, zinc and exchangeable cations and soil particle size) as well as non-epifluorescent site variables (elevation, slope, aspect), regional climate variables, overlying plant community composition and detailed land-use history.

Visualisation of soil biodiversity data is also being developed in collaboration with the Atlas of Living Australia (www.ala.org.au) which provides a useful set of tools to visually describe the spatial distribution of soil biodiversity and the association between below- and aboveground terrestrial diversity. This framework database of soil microbial diversity is a valuable and enduring resource for scientists and the wider community. Insights into the current status of soil microbial diversity across a diverse range of Australian biomes relative to global soil biomes and the potential for future exploration of features presently unknown represent powerful drivers for ongoing participation in the BASE programme. More details about the BASE project, including the list of the 23 collaborating partner organisations, can be found at the following link: www.bioplatforms.com/sound-biodiversity/

The BASE project could be a model for similar assessments of other continents, to eventually derive a global overview of soil biodiversity.

The European Union’s Biodiversity Strategy to 2020

- In May 2011, the European Union adopted a new strategy to halt biodiversity loss in the EU, restore ecosystems where possible, and set up efforts to avert global biodiversity loss. The strategy is in line with the commitments made by EU leaders in March 2010 and the international commitments adopted by 193 countries, including the EU and all its Member States, at the Conference of the Parties to the Convention on Biological Diversity in Nagoya (Japan) in 2010.
- The biodiversity strategy is built around six measurable targets that focus on the main drivers of biodiversity loss. The six targets cover:
  - full implementation of EU nature legislation to protect biodiversity,
  - better protection for ecosystems, and more use of green infrastructure,
  - more sustainable agriculture and forestry,
  - better management of fish stocks,
  - tighter controls on invasive alien species,
  - larger EU contribution towards averting global biodiversity loss.
- Each target is accompanied by a corresponding set of actions. The main challenges ahead include the full and efficient implementation of nature protection legislation - especially the effective management and restoration of areas of high biodiversity value in Natura2000, tackling invasive alien species and protecting ecosystem services.

The European Union project EcoFINDERS analysed soil biodiversity in 81 sites (50 sample sites) across Europe. The project involved 25 different research institutes from 12 European countries (RCR, JRC).
Smallholder farmers around the world have developed a number of detailed local soil classification systems based on years of observations and a variety of soil health indicators. Dominant plant species and earthworms are important indicators commonly used by farmers across different continents for visual characterisation of soil health during selection of areas for agriculture. Above- and belowground biodiversity are closely tied to aspects of soil health, making it possible to use the presence, absence and abundance of species as biological indicators. Increasing efforts in participatory research are currently being promoted in order to foster the integration of local knowledge into soil health monitoring systems and thus support decision-making processes aimed at the sustainable management of natural resources in agricultural landscapes.

While local and technical knowledge share a number of common ‘core’ concepts, each knowledge system has gaps that in many cases can be complemented by each other. Blending local and technical knowledge arms to generate an expanded ‘shared’ knowledge that is more sound and credible, thus facilitating the adoption of agricultural management practices that conserve soil biodiversity.

Knowledge sharing

Participatory research

The increasing global awareness of the impacts of biodiversity loss on human well-being has created great concern and demands for rapid action. Agriculture is the most widespread form of human-environment interaction. Farmers, therefore, constitute the largest group of natural resource managers on Earth. [194]

The increasing attention paid to farmers’ knowledge recognises that experience gained during years of direct interaction with nature can offer many insights into the sustainable management of natural resources. Soil health is an important indicator of the state of natural capital. It reflects the capacity of soil to function as a vital living system and respond to agricultural management by sustaining the biological productivity that underpins the provision of food and fibre, as well as other ecosystem services. Soil health is of great concern to farmers, particularly resource-poor smallholder farmers who rely to a large extent on the biological productivity of soil to sustain their livelihoods. The increasing global awareness of the impacts of biodiversity and its importance to agricultural productivity has generated an increased interest in local knowledge and in the systematic evaluation of soil biodiversity awareness in Honduras.

Soil biodiversity awareness in Honduras

- A participatory research scheme was carried out in an agroforestry system of western Honduras in order to assess the extent to which farmers have incorporated their local knowledge into farm management practices. (195)
- The local knowledge of twenty small scale farmers was identified, classified and prioritised through a number of participatory research tools. Farmers named 16 commonly recognised, distinct groups of soil macrofauna. In addition, they distinguished several local soil types on the basis of soil texture, colour and structure.
- The most detailed knowledge of the relationship between soil fauna and soil quality was on organisms considered to have either beneficial or harmful effects on farming activities, such as earthworms and beetle larvae (see pages 58-60).
- Farmers had a clear understanding of the influence of fire on soils, soil bota, native vegetation and crop yield over various lengths of time, which may have been obtained through a combination of first-hand experience, interaction with technical experts and information gained from other farmers.
- Researchers concluded that local knowledge of the effect of different soil organisms on soil quality, the interactions among them and the role of native vegetation in maintaining agricultural productivity, is an important driver of the success of the agroforestry system.

Illustration showing that farmers’ knowledge and scientific knowledge share a number of common ‘core’ concepts, but each knowledge system has gaps that in many cases can be complemented by each other. An integration of the two knowledge systems is needed to obtain a shared knowledge (derived from Barrios et al., 2012). [194]

Illustration of farmers’ perceptions of the effect of soil invertebrates on components of the farming system (derived from Pauli et al., Geoderma, 2012) [195]

Illustration showing farmers’ shared knowledge and expanded ‘shared’ knowledge

Illustration showing farmers’ perceptions of the effect of soil invertebrates on components of the farming system (derived from Pauli et al., Geoderma, 2012) [195]
Citizen science
Other forms of knowledge sharing through participatory research, which extend beyond agricultural landscapes into natural ecosystems, include citizen-science efforts that have become increasingly common in the past decade. Citizen science can be defined as the participation of volunteers from the public in scientific research. It is considered an effective ecological research tool to increase our understanding of processes occurring at broad geographical scales.

For example, the Great Lakes Worm Watch is a US citizen-science effort to assess the impact of exotic earthworms on forest ecosystem processes [196]. Interested citizens are provided with tools and resources to actively contribute to the development of a database that documents the geographic and spatial distribution and abundance of exotic earthworms, as well as their environmental impact. The Open Air Laboratory (OPAL) network (www.opalexplornature.org) is a broader citizen science initiative in the UK aimed at increasing public awareness of the state of the environment through direct experience.

Changes in public perceptions about the importance of the conservation and management of natural resources achieved through experiential learning aims to guide civil society toward more sustainable development pathways and also influence environmental policy.

Make your earthworm survey
The Open Air Laboratory (OPAL) network provides a kit and all the instructions needed to survey earthworms [197]. The results will help scientists to see whether each species is found in a particular habitat or soil type. For example, there are 26 different species of earthworms in England. Some are common and found in many places, whereas others are rare. Earthworms are sensitive to many environmental factors, which influence where they live. If you find many earthworms in your soil it can be a sign of good soil quality.

Steps and materials needed to sample are very simple and can be found on the OPAL website. Essential items to take outside are:
- magnifier
- mustard
- vinegar
- 2 pH strips
- 5 two 750 ml bottles of water (re-use old plastic bottles filled with tap water)
- a small shovel, spade or trowel
- gloves
- a map and GPS device, if available
- waterproof pen
- 10 a mobile phone
- 11 a camera
- 12 a watch
- 11. a camera
- 10. a mobile phone
- 9. waterproof pen
- 8. a map and GPS device, if available
- 7. gloves
- 6. a small shovel, spade or trowel
- 5. two 750 ml bottles of water (re-use old plastic bottles filled with tap water)
- 4. 2 pH strips
- 3. vinegar
- 2. mustard
- 1. magnifier

When the material is ready:
a. choose a location and record the site characteristics (e.g. weather and vegetation cover)
b. measure a 20 x 20 cm square, dig the soil pit to a depth of 10 cm and apply a mixture of water and mustard to extract deep worms
c. test the properties of the soil (e.g. pH and moisture). Simple instructions to describe these aspects are provided; for example, to test soil moisture it is sufficient to take a handful of soil in the palm of your hand and squeeze it, if water is visible the soil can be considered as wet
d. identify the earthworms. Also in this case keys and hints to identify earthworm species are provided. For example, 12 of the most common earthworm species in England are illustrated in the key. The key should identify approximately 90% of adult specimens. Immature worms cannot be identified but people should still record the total number found in the topsoil and deeper in the pit using the mustard water. The use of a magnifier can help you see key earthworm features (this will help with species identification). Furthermore, a digital camera can be used for identification by taking a picture and zooming in to see the details
e. enter all results on the OPAL website

This example clearly shows the feasibility of participatory research initiatives. These activities can have a double positive effect. Firstly, to enhance awareness of the importance of soil biodiversity and, secondly, to actively contribute toward scientific research.

An amazing story to share!
- There are several anecdotes related to organisms living in the soil or associated with soil, which should be shared in order to increase awareness of the importance and beauty of soil biodiversity
- Osmia avosetta is a rare and solitary species of bee from Iran and Turkey, that makes flower-mud ‘sandwiches’ to construct nests for its larvae [198]
- The female Osmia avosetta digs shallow tunnels in the ground consisting of one or two chambers, each of which is then lined with flower petals glued together with mud
- It then places larval food in each chamber and seals it with soil by folding the petals over. The cell hardens to form protection for the larva against predation and weather
- The reason for the effectiveness of these elaborate nests is the texture, water content and water repellency of the soil used by the bee and the humidity-retaining nature of the petals
- The colourful nesting behaviour of Osmia avosetta bees was discovered simultaneously in 2009 in Turkey and Iran
- Similar to this bee, several species of bumble bees (Bombus spp.) are regarded as soil-dwelling insects since they build their nests in soil and are important pollinators (see box on page 61)
**Education and awareness**

**Need for awareness**

The main scope of this atlas is to educate and raise awareness about the importance of soil biodiversity. Scientific knowledge has been largely restricted to textbooks and scientific journals, which are often inaccessible and incomprehensible to the general public. Recently, there has been increased realisation of the need to engage society with scientific results in a manner that can be more easily understood. Interestingly, providing knowledge about soil biology is a very powerful way to introduce soil issues to the public.

The need to raise awareness and understanding of the importance of soil and soil biodiversity has been highlighted on a global scale. The more we can learn about the role that soil biota plays in sustaining the environment, the more we understand how important it is and, hopefully, the more likely we are to care for it.

**Targets of awareness raising**

It is important that we teach the importance of soil biodiversity to society at large, from young children, school teachers, farmers and gardeners to planners and politicians. Children love playing with soil and have the capacity to learn through simple hands-on activities, such as making mud pies, building wormeries and looking under the microscope at what lives in the soil.

Drawings made by children show their perception of soil and, perhaps surprisingly, such sketches or paintings often convey complex messages about issues such as the food chain or the importance of earthworms in increasing the pore network underground. These are lessons that scientists constantly strive to communicate. The ability to recognise ecological interactions, however, seems to be inherent to many children who are fascinated by life in the soil.

The following sectors also benefit from education and awareness:

- **a. higher education:** the knowledge of soil in general, and soil biology and ecology in particular, is often neglected and should be integrated across disciplines
- **b. scientific community:** should be made more aware of the importance of soil biodiversity. This can be achieved through a multidisciplinary approach where people specialised in different subjects cooperate and understand each other
- **c. farmers and land managers:** farmers generally have a good relationship with the soil because it is the basis of their livelihood. The functions of the living soil system should be clearly communicated. Farmers should be part of the development of management options that are beneficial for soil biodiversity, which in turn can increase yields and reduce costs
- **d. policy makers and NGOs:** should influence public opinion. Soil and related biodiversity usually has a low political priority. Increasing this awareness would contribute to informed decision-making processes that would bring enormous benefits through increased quality of life
- **e. public:** public opinion is a powerful tool for changing societal attitudes toward the importance of soil. Increased education and awareness-raising campaigns must stress the value of soil biodiversity to people’s daily lives

A coordinated approach is required in order to target each sector and to encourage interactions among them.

**Soil biodiversity playing cards**

- A card game was designed and published in French under the GESSOL (GÈSion du patrimoine SOL) research programme, funded by the French Ministry of Ecology, and in English by the European Commission’s Joint Research Centre.
- This card game, ‘The hidden life of soils’, comprises 42 playing cards, each with a large photo and description of a group of soil organisms. This allows for discovery of the hidden organisms that inhabit the soil, how they live and how to study them.
- The cards can be downloaded at the following links:

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**Children love**

(a) drawing soil biodiversity and (b-d) playing with soil. Hands-on activities allow both children and adults to see soil biodiversity from different perspectives (JRC, ACS, DMU, JPA)

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**Molly the Mole**

(a) Molly the Mole is the mascot of all soil awareness events organised by the European Commission’s Joint Research Centre (GBA, LCH/USDA)

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**Sammy Soil**

(b) Sammy Soil is the mascot of the United States Department of Agriculture’s Natural Resources Conservation Service (GBA, LCH/USDA)

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Two of the seven happy families of soil organisms included in the card game (GESSOL)
The good, the bad and the ugly!

Some soil organisms can either bite or sting and may become pests or promote diseases. However, unpleasant soil organisms represent a very small proportion compared to the huge amount of remaining soil organisms. Furthermore, pests and diseases are largely the result of a natural disequilibrium and/or environmental changes, often man-made, resulting in a population explosion of a given species, due to the disappearance of their natural enemies.

Many people have developed phobias to microbes and insects in general, considering them all bad and ugly. Therefore, education is required to show how they can be good and beautiful. Besides, our own lives would not be possible without them!

Curumin and Cunhantã helping soil biodiversity

In the context of the Global Collaborative Project entitled ‘Conservation and Sustainable Management of Belowground Biodiversity’, the Brazilian Federal University of Lavras (UFLA) developed an educative booklet to explain the importance of soil biodiversity. Entitled ‘Curumin and Cunhantã helping soil biodiversity’, the booklet is available in Portuguese, Spanish and English.

Curumin and Cunhantã means boy and girl in a Brazilian native language. Regardless of gender, scientists and children share a common trait: curiosity, which is the stimulus and motivation for science. The booklet tells a story about the importance of soil biodiversity. This story is told by characters based on the Brazilian scientists that worked in the area of a research project in Amazonia, and illustrated with results found there, such as soil type, soil limiting factors, number of plants, and a few key macrofauna (e.g. earthworms) and microbial (e.g. bacteria) species.

Soil biodiversity is presented in an holistic way considering its physical and chemical attributes (soil fertility) and its effects on plant productivity. The value of soil organisms is highlighted by considering them as true super heroes because in nature their activities are real and they help plants, ecosystems and human beings live on planet Earth. This is the reason why we need to help preserve them. The booklet is not only about soil biodiversity, but also about human diversity and how these diversities can help each other.

The booklet can be downloaded at this link:
http://repositorio.ufla.br/handle/1/1476

Curumin and Cunhantã: Helping soil biodiversity

Soil biologist for one day

Soil biodiversity can be easily studied with simple equipment. While bacteria, fungi, microfauna (<0.1 mm, e.g. nematodes) and mesofauna (0.1 to 2 mm, e.g. mites) require special techniques to be isolated and extracted from soil, macrofauna (>2 mm, e.g. earthworms) can be extracted from soil samples using methods accessible even to children.

A simple method to show visible soil organisms and compare the effect of diverse soil conditions (e.g. forest versus prairie, clay soil versus sandy soil) is described below:

1. delineate a square on the soil surface (e.g. 25 × 25 cm)
2. dig around this area to a given depth (e.g. 10 cm) in order to have an isolated block of soil
3. carefully lift this block of soil (25 × 25 × 10 cm) and place it on a tray
4. put on gloves, take out all the small animals that you can see moving and place them in a vial with alcohol. You can use tweezers; however, take care to avoid crushing them. Smaller animals can be collected with a wet paint brush
5. when you are sure that all animals have been removed, they can be counted and viewed under a simple microscope or magnifying glass. Beautiful forms of life invisible to the naked eye will be revealed and children will discover new creatures
6. if needed, the procedure can be repeated for deeper layers (e.g. 10 to 20 cm) and the results compared

The diversity of soil organisms can be evaluated by simply separating them by shape and size. Numbers and types of individuals will differ according to soil types and habitats. Children can also draw the ones they like most.

The presented activities are just a small sample of the myriad activities (see pages 164-165) that can be proposed not only to children but also students and adults in order to raise awareness of the diversity of soil life and the importance and fascination of studying soil-living organisms.

A homemade centrifuge to explore soil biodiversity

- For a simple outreach activity, a working low-speed (around 900 revolutions per minute) centrifuge can be easily made using a household salad spinner
- Styrofoam bases from 50 ml centrifuge tube packs are secured to the bottom of a salad spinner using zip-ties. Putty/modelling clay is used to stabilise the centrifuge tubes. Wrapping a rubber band around the tops of the tubes provides additional stability during spinning
- Use hand trowels to collect approximately 100 ml of soil, mix with tap water in a bucket, and let the sediment settle for 1 minute before pouring the solution through large (1 mm) and fine (<1 mm) mesh soil sieves
- Use squirt bottles to gently wash the material caught on the fine mesh sieve into a 50-ml centrifuge tube, and hand-spin tubes in the salad-spinner centrifuge for 5 minutes. Up to four tubes could be spun at once
- Remove the tubes and empty the liquid, while retaining the loose soil pellet at the bottom of the tube containing soil organisms, such as mycorrhizal spores and nematodes
- Refill the tubes with 60 % sucrose (table sugar) solution, cap and invert the tubes a few times to mix, and put back in the salad-spinner centrifuge for another 3-4 minutes. Soil organisms will float in the sugar water while mineral components sink
- Pour the sugar water solution through the fine-mesh sieve while leaving the mineral pellet in the tube, and gently wash the sieve with tap water to remove sugar residues from organisms
- The material left in the sieve could then be gently washed into small dishes for observation under microscopes. While the samples remain drier and less quantitative than what is possible using higher-speed electric centrifuges, small living soil organisms are clearly visible

*•••* Being a soil biologist for a clay is easy! (a) Dig a hole, take out the small animals that you can see and (b) place them under the microscope (c) an astonishing world will appear before your eyes (FMSM, DSE, MN)
Learning about soils and soil organisms

Often the best place to teach people about soils is to go into a field, a woodland or just a garden. In these environments, students can investigate for themselves the soil biodiversity and the role it plays in keeping our environment alive. Simply digging a small hole, lifting stones to see what lies underneath, sifting through plant litter or just setting a few pitfall traps made from yogurt containers will quickly bring you into contact with soil biota. The use of magnifying lenses or microscopes to show the variety of soil organisms found in a few grammes of soil is a simple lesson, guaranteed to leave a long-lasting impression. A huge amount of educational material is becoming available for both students and teachers. This includes computer programmes, lesson plans, supporting materials and activities for both the classroom and outdoors. The great thing about teaching soil biology is that it is applicable across all ages from young children who make wormeries, to school and university students who discover the importance of soil biology in the global nutrient cycles and ecosystem functions. A number of promising educational initiatives have been developed for the general public and, in particular, for children to learn outside of the school environment. Examples include interactive museums or informative nature walks that tell the story of soil and its role within a particular landscape. Another interesting method is to use images of creatures that live in the soil to help raise public awareness of the importance of life in soil. These examples show very clearly that soil organisms can compete with other, perhaps more well-known and charismatic, animals such as elephants and lions, in raising awareness of soil biodiversity. Here below you will find a list of resources on soil and its biodiversity.

Web links
- Biodiversity International: www.bioversityinternational.org
- Centre for Soil Ecology: www.soilecology.eu
- Earth Microbiome Project: www.earthmicrobiome.org
- European Land and Soil Alliance: www.bodenbuendnis.org
- European Network on Soil Awareness: www.bodenbuendnis.org/en/
- Global Soil Biodiversity Initiative: www.globalsoilbiodiversity.org
- GESion du patrimoine SOL: www.gessol.fr
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services: www.ipbes.net
- Life Under Your Feet: http://lifeunderyourfeet.org
- Soil is Life: www.soil-is-life.info/content_en/index.htm
- Soil Science Teacher Resources. www.soils4teachers.org
- SoilGrids 1km visualisation: www.soilgrids.org
- SoilInfo App: http://soilinfo-app.org
- SoilNet: www.soil-net.com/
- Soils 4 Kids: www.soils4kids.org
- TerraGenome: www.terragenome.org
- The British Society of Soil Science: www.soils.org.uk/
- The Convention on Biological Diversity: www.cbd.int
- The Dirt on Soil – Learning Adventures: http://school.discoveryeducation.com/schooladventures/soil
- Tool for Research Engaged Education: www.tree.leeds.ac.uk/tree_home.php
- Virtual Soil Science: http://soilweb.landfood.ubc.ca/promo/raising-awareness
- World Soil Museum: www.wsc.org/services/world-soil-museum
- Soil protists: https://soilprotists.wordpress.com

Facebook and Twitter
- Bundesverband Boden e.V.: www.facebook.com/BundesverbandBoden
- Che Terra Pestis: www.facebook.com/cheterrapesti
- Global Soil Biodiversity Initiative: @theGSBI
- Plants, Soils, Ecosystems Group: @BESPlantSoilEco
- Soil Science Society of America: www.facebook.com/SSSA.soils

Blogs
- Beneath Our Feet: http://blog.globalsoilbiodiversity.org
- Observerland: http://observer.land/

Summer schools
- Plan-it Earth: www.plan-itearth.org.uk
- Summer of Soil: www.summerofsoil.se
- Summer Soil Institute at Colorado State University: http://soilinstitute.nel.colorado.edu/

E-learning
- Allversity – Understanding Soil: http://www.allversity.org/courses/understanding-soil

Facebook and Twitter
- Bundesverband Boden e.V.: www.facebook.com/BundesverbandBoden
- Che Terra Pestis: www.facebook.com/cheterrapesti
- Global Soil Biodiversity Initiative: @theGSBI
- Plants, Soils, Ecosystems Group: @BESPlantSoilEco
- Soil Science Society of America: www.facebook.com/SSSA.soils

Blogs
- Beneath Our Feet: http://blog.globalsoilbiodiversity.org
- Observerland: http://observer.land/

Summer schools
- Plan-it Earth: www.plan-itearth.org.uk
- Summer of Soil: www.summerofsoil.se
- Summer Soil Institute at Colorado State University: http://soilinstitute.nel.colorado.edu/

E-learning
- Allversity – Understanding Soil: http://www.allversity.org/courses/understanding-soil

Resources

In these pages you will find links and much more to learn about soil. (LRI)

A page from the ‘I Love Soil Coloring and Activity Book’ by the Soil Science Society of America. Go ahead and colour this page! (SSSA)
Movies, arts and more

- A story with heart and soil: www.dirtthemovie.org
- Common Ground: www.commonground191.com
- New film festival strives to raise awareness of soil sustainability: www.iowastatedaily.com/news/article_dff5c4a-315a-11e4-a411-01oa4bfcf87a.html
- Painting With Soil: http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/edu/7bnu1227/cd/nrcs142p2_054304
- Soil Arts: http://soilarts.wordpress.com/
- Soil Biodiversity: www.youtube.com/watch?v=lxQ3rW-bk_s
- Tea Bag Index: www.decolab.org/tbi
- Symphony of the Soil: www.symphonyofthesoil.com
- The Secret’s in the Soil – Modern Farmer interviews the world’s pioneer of ‘soil cuisine’ Toshio Tanabe: http://modernfarmer.com/2013/10/secrets-soil/
- The Youth & United Nations Global Alliance (YUNGA) booklet on soils. (YUNGA)
- Soil Fauna Playing Cards: www.gessol.fr/game-hidden-life-soils
- Soil biodiversity: www.youtube.com/watch?v=oXddZCciIa8
- Soil Arts: http://soilarts.wordpress.com/
- Soil Biodiversity: www.youtube.com/watch?v=lxQ3rW-bk_s
- Tea Bag Index: www.decolab.org/tbi
- The Secret’s in the Soil – Modern Farmer interviews the world’s pioneer of ‘soil cuisine’ Toshio Tanabe: http://modernfarmer.com/2013/10/secrets-soil/
- The Youth & United Nations Global Alliance (YUNGA) booklet on soils. (YUNGA)
- Soil Fauna Playing Cards: www.gessol.fr/game-hidden-life-soils

Scientific articles


Journal articles

- Our Good Earth – The future rests on the soil beneath our feet: http://ngm.nationalgeographic.com/2010/05/soil/mann-text
- Sex & Bugs & Rock ’n Roll: http://planetearth.nerc.ac.uk/features/story.aspx?id=1671&cookieConsent=A
- The importance of the soil: http://ruhlman.com/2014/05/the-importance-of-the-soil/

Videos and radio

- BBC Inside Science: www.bbc.co.uk/programmes/b04krxwhc
- Flight through the pore network of a mm soil fragment: youtube.com/watch?v=7fhufJHzGsM&feature=play erEmbedded
- Forces of Change: http://forces.si.edu/solvis/video/secret_ingred.htm
- Plant soil feedbacks after severe tornado damage: http://vimeo.com/107412178
- Worms at Work: http://vimeo.com/110880643

Books


Calendar


Games

- Soil Fauna Playing Cards: www.gessol.fr/game-hidden-life-soils
- Soil Horizon Game: http://forces.si.edu/solvis/wherethehorizons.html
- Where in the World? http://forces.si.edu/solvis/wheretheintheworld.html

Photos

- “I Love Soil” campaign by the Soil Science Society of America. (SSSA)
Global Soil Biodiversity Initiative

The Global Soil Biodiversity Initiative (GSBI) was launched in Wageningen in 2011 to make better use of our understanding of soil biodiversity. The GSBI is developing a coherent platform in order to promote the translation of expert knowledge into environmental policy and sustainable land management practices, ultimately resulting in better protection and enhancement of ecosystem services. Soils are home to a vast diversity of life that is essential for a variety of ecosystem functions – from the tiniest microbes to larger soil animals and plant roots. Yet soil biodiversity has been largely ignored in global and regional policies addressing land management, food security, climate change, loss of biodiversity and desertification.

Scientific priorities for the GSBI include identifying key knowledge gaps linking soil biodiversity and ecosystem function, developing a platform for the synthesis of soil biodiversity data, methods harmonisation, establishing a forum for global research networks and supporting international soil biodiversity research initiatives and soil-related policy agendas.

The GSBI aims to integrate soil biodiversity science with ongoing global scientific efforts, such as the Global Soil Partnership (GSP), the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) and the Convention on Biological Diversity (CBD). It will enhance soil biodiversity options and identify ways to restore, conserve and promote it, and is open to all scientists, land managers, policy makers and the general public. The GSBI is working to:

- inform policy-making and research by providing clear, transparent and scientifically credible information
- collaborate with existing and new initiatives on biodiversity that relate to soil
- encourage capacity building in all aspects of soil biodiversity and ecosystem services

Leadership

The GSBI is led by an international scientific steering committee, with the Secretariat office hosted at the School of Global Environmental Sustainability, Colorado State University, United States of America. Members of the committee are:

- Dana H. Wall – Scientific Chair, Colorado State University, USA
- Executive Director – Person covering this position changes every three years, Colorado State University, USA
- Ciro Gardi – Scientific Program Coordinator, European Food Safety Authority, Italy
- Fred Auye – University of Nairobi, Kenya
- Richard D. Bardgett – University of Manchester, UK
- Nobuhiro Kaneko – Yokohama National University, Japan
- Luca Montanarella – European Commission’s Joint Research Centre, Italy
- Patama M. S. Moreira – Federal University of Lavras, Brazil
- Johan Six – ETH Zurich, Switzerland
- Wim H. van der Putten – Netherlands Institute of Ecology, the Netherlands

GSBI Activities

The GSBI engages the public and policy sectors through its numerous activities and provides a forum to enhance global sustainability efforts. Existing initiatives by GSBI participants include the early-career scientists creating a network of emerging scientists from around the world, an urban working group to highlight the importance of soil organisms in populated areas, a group interested in the social and cultural values of soil biodiversity and an education section to establish creative methods to deliver this information to a wider audience of all ages. In addition, networking among different groups specifically interested in protists, soil fauna and functional groups across all soil taxa are being established.

Since soil biodiversity data can be used to address questions ranging from ecosystem function to global biodiversity to global change, a Soil Biodiversity Curation Working Group was established to bring together all soil biodiversity data on taxonomy, phylengy and function. This group hopes to:

- provide access to soil biodiversity databases, data sources and related information (discoverability)
- promote the use of standards – provide guidelines, best practice policies, promotion of use
- establish a framework to bring together past, present and future soil biodiversity data and related information (for minimum and optimal uses)

The First Global Soil Biodiversity Conference

On 2 December 2014, more than 700 scientists and interested parties from 57 countries gathered in Dijon, France for the first ‘Global Soil Biodiversity Conference – Assessing soil biodiversity and its role for ecosystem services’.

Organised by the GSBI, the EcoFINDERS project, the European Commission and the French National Institute of Agricultural Research (INRA) Dijon, the conference was designed as a platform to discuss current research in soil biodiversity and its links to Earth processes, and to promote interdisciplinary collaboration. The conference included 13 keynote speakers, 46 oral presentations and 666 poster presentations. On the final day of the conference, a panel discussion brought together government officials, senior scientists and early-career scientists in celebration of World Soil Day (5 December) and the launch of the 2015 International Year of Soils.

Travel funds were awarded to nine early-career scientists from eight different countries, supported by the European Commission’s Joint Research Centre, the International Union of Soil Sciences, TerraGenome, and the United Nations Environment Programme’s Global Environment Facility.

From a survey of conference delegates (264 responses):

- 54 % female, 66 % male
- 56 % early-career scientist (< 5 years post PhD)
- priorities for GSBI: soil biodiversity assessment, platform for synthesis of soil biodiversity data, method harmonisation, a forum for developing global research networks

The 2nd Global Soil Biodiversity Conference will take place in Nanjing, China, in 2017.
Global Soil Biodiversity Assessment

When you scoop up a double handful of earth... you will find thousands of invertebrate animals, ranging in size from clearly visible to microscopic, from ants and springtails to tardigrades and rotifers. The biology of most of the species you hold is unknown... We have little concept of how important any of them are to our existence.


Soil, the thin layer on the surface of the Earth, is vital for the survival of the biosphere. It is alive, with soil biodiversity providing the living basis for functioning of ecosystems. It acts as the Earth's lungs and filtering system; it is our most precious natural capital. It is of vital importance to agriculture, agroforestry, manicature, fishing, pollution control, carbon capture and water purification, nutrient retention and cycling. In the broadest sense, soil organisms are at the core of biogeochemical cycling at both local and global scales. Our living soil is one of the keys to the maintenance of ecosystem processes and life on Earth, both on land and in the sea.

Have we made any progress in our knowledge of this diversity? Yes we have! Based on international reports, such as ‘Life in the Soil – Soil Biodiversity: Its Importance to Ecosystem Processes’ in 1994, the global soil biodiversity community has made enormous progress in the knowledge of taxonomy of soil biota and their role in decomposition, nutrient cycling and other ecosystem services, their intimate interactions with marine and freshwater ecosystems and their contributions to human health.

In addition to regional assessments, such as the EMEND Project in the Boreal Forest (www.emendproject.org), EcoINDIES in Europe and BASE in Australia (see pages 158-159), the SCOPE publication ‘Sustaining Biodiversity and Ecosystem Services in Soils and Sediments’ and the Oxford University Press publications ‘Aboveground-Belowground Linkages, Biotic Interactions, Ecosystem Processes and Global Change’ and ‘Soil Ecology and Ecosystem Services’, have synthesised a lot of global knowledge. With the publication of the Global Soil Biodiversity Atlas, the soil biodiversity research community presents the world, from children to educators, with a portal to the wonders of life in the soil.

Yes, the global soil biodiversity community has made strides, but we recognise that a Global Soil Biodiversity Assessment is even more pressing now for the following reasons.

Why a global soil biodiversity assessment?

Since Darwin’s study of earthworm activity in England, soil biodiversity and its components, their interactions with other biota and with the environment have been studied at various levels throughout the world. These data, some extensive (e.g. for Antarctica and Western Europe), some rudimentary (e.g. Southeast Asian peatlands and mangrove forests), transcend the ‘black box’ view of soil inhabited by an unknown and undefined set of functional groups, but these data need consolidation. Consolidation will showcase gaps in knowledge: the range of archaea, prokaryotic and eukaryotic taxa for which we lack names, classification, DNA data and trait data, the diverse linkages of soil biota to tangible functions underpinning soil-based ecosystem services, and the range in impact of climate change in different soil landscapes.

A Global Soil Biodiversity Assessment would ensure consolidation of data that are presently available on a regional or national basis, and would ensure a long-term home and available portal for this information. Most importantly though, it would highlight gaps in knowledge about soil biodiversity, and where missing data undermine the evaluation of risks and predictions of resilience that are important to society.

Commonalities

Knowledge on soil biodiversity and ongoing research tends to be regionally or nationally based; this is almost always because of availability of funding. Examples of research networks that provide global overviews and integration between countries are rare. The International Long Term Ecological Research (ILTER – wwwILTERneteduresearch) is a good example of how to share research and data globally, with subgroups dealing with biodiversity, such as the Group of Earth Observations Biodiversity Observation Network (GEO BON – wwwgeobonorg). Only a few of these global research efforts consider soil biodiversity; therefore, we lack knowledge of commonalities (and differences) between the diversity in different ecosystems.

For example, temperate grasslands are the foundation of agriculture, they are where much of our food is grown. Thousands of species of microbes and invertebrates inhabit just a square metre of these temperate grassland soils, organisms whose identities and contributions to sustaining our biota are still largely undiscovered. Scientists know a lot about this diversity in Europe and the USA as a result of focussed research and funding in the past 25 years. For example, they can predict the impact of wildfires and overgrazing on food webs, and levels of carbon capture. However, data equivalent to those from temperate grasslands do not exist in other parts of the world or cannot be integrated. Knowledge of commonalities and differences in the components of soil biodiversity and how soil systems function globally could markedly improve predictions of soil system response to global change.

Barcoding soil life

We have only begun to understand a small slice of the grand diversity that is life on earth and that is fast slipping through our fingers as a result of human-induced climate change, habitat destruction and exploitation.

M. A. Goldman. 2015. Digitising the biosphere. Science 348: p. 979 (201)

International efforts to barcode life (wwwbarcodedlifeorg) on Earth through DNA sequencing focus to date on easily accessible aboveground biota. However, many of the antibiotics we use, types of plants that can grow, as well as decomposition, water filtration and soil development rely on soil biodiversity. We need to assess the structure and function of the global soil microbiome in a similar way as is being done in oceans with planetary scale studies on marine plankton and the Global Ocean Sampling Expedition (wwwjoolslaborgresearchprojects/gosoverview).

A Global Soil Biodiversity Assessment would provide a focus for such an endeavour; consolidating data from GenBank, TerraGenome and again, providing a portal for soil DNA research. As the two scientists Dawn Field and Neil Davies noted ‘answers to questions in the life sciences do not end with DNA – they start there’.
Conclusions

The Global Soil Biodiversity Atlas presents the first overview of soil biodiversity for both managed and natural soils on a global scale. This atlas is a remarkable international scientific effort with contributions from about 121 experts from 26 countries. The Global Soil Biodiversity Atlas was made possible through rapid advancements in scientific research on soil biodiversity that are largely due to a plethora of new technologies, including molecular tools, Internet communications, data and image sharing and storage, GPS, and perhaps most importantly, global collaborations that have developed new syntheses and understanding of the importance of soil organisms across the globe.

The designation of 2015 as the International Year of Soils ‘healthy soils for a healthy life’ by the United Nations emphasised soils as the foundation for all life. With unprecedented rates of global change occurring, our soils are under threat with consequences for the dynamic communities of microbes and animal species that live there. Soils, and their inhabitants, are a finite resource that must be respected and conserved. Reduction of soil biodiversity can negatively affect the quality of water, control of pests and both decomposition and nutrient cycling, with significant impacts on plant, animal and human health.

Since the establishment of the Global Soil Biodiversity Initiative (GSBI) in 2011, great progress has been made in bringing together interested parties from across the world and promoting the importance of soil biodiversity to a wider audience. The success of the First Global Soil Biodiversity Conference and the production of this atlas with the European Commission’s Joint Research Centre are real examples of the power of collaboration across regions and disciplines. The Second Global Soil Biodiversity Conference will be held in Nanjing, China, in 2017, hosted by the Soil Science Society of China and the Chinese Academy of Sciences. These meetings have the potential to encourage enthusiasm about soil biodiversity research and facilitate future collaboration and research projects.

Increased education and awareness are key strategies in ensuring that soil organisms are no longer out of sight, out of mind. Through the key messages in this atlas, and efforts by the GSBI and other organisations, we aim to convince the global public of the importance of soil biodiversity to our life and economy. Because soils are under threat, we must promote interactions between scientists, policy makers and the general public in order to transfer and implement findings about the benefits of soil biodiversity and ways to restore and conserve it. Soil biodiversity is critical for soil functioning and plant production but has been largely ignored in global and regional policies that address land management, food security, climate change, loss of biodiversity and desertification.

The gaps in our knowledge of soil biodiversity in many regions around the world must be acknowledged. A global assessment is one possible method to obtain a more comprehensive understanding of the distribution of soil organisms and their functions. This information can be enhanced in the future with continued collection and synthesis of soil biodiversity data, which is urgently needed on a global scale and is required in order to develop predictive models, assess changes over time and better understand the effects of global change. Information about soil biodiversity distribution and function can be combined with other global datasets and maps, such as global carbon models, temperature and precipitation maps, desertification, land use change and climate change occurring in regions of the world.

Global Soil Biodiversity Atlas in numbers

- You are holding the 1st ever Global Soil Biodiversity Atlas (GSBA).
- The Editorial Board started working on the GSBA in 2013, and took 3 years to complete it.
- The GSBA Editorial Board consists of 27 scientists from all over the world.
- More than 100 people from 26 countries have contributed to writing the GSBA.
- There were three workshops to prepare the GSBA and thousands of e-mails sent.
- The GSBA has 8 chapters and 176 pages.
- In the GSBA you can see approximately 900 images and more than 50 maps.
- The GSBA is the 6th soil atlas of the series produced by the European Commission’s Joint Research Centre.
This atlas presents how quickly our knowledge has developed about the living organisms that help form the Earth’s soils and the benefits they provide for all humans. Below we highlight some of the main findings.

**Key findings**

The planet’s terrestrial ecosystems have a diversity of soil life, largely due to the variety of their soil habitats, which reflects the soil-forming factors of climate, parent material, topography, time and biota.

- Soil is home to thousand millions of microbes and animals that vary in shape, colour, size and function
- Scientists can now use molecular techniques to identify life (animals, fungi, protists, archaean and bacteria) in a soil sample
- Scientists are discovering new species, their distribution in soils around the world, and what they do for us
- There are many endemic species of soil microbes and animals in regions and ecosystems around the world
- Soil biodiversity is globally distributed, from pole to pole and through grasslands, forests, urban and agricultural areas
- Many types of organisms (for example, nematodes) do not follow a latitudinal gradient of greater species diversity in the tropics
- Soil properties, such as pH, largely determine soil bacterial distribution

Soil biodiversity is critical for human health: for plant growth and support, water and climate regulation, and erosion and disease control.

- Soil biodiversity consists of communities of organisms. Each soil community is unique and provides benefits for us
- Soil biodiversity is vitally important for the biogeochemical processes and ecological functioning of terrestrial ecosystems
- Soil organisms decay organic matter with relevance for soil fertility, soil structure and carbon storage
- Soil biodiversity is tightly linked to aboveground biodiversity
- Soil biodiversity provides multiple controls on above- and belowground pests and pathogens and, therefore, promotes the health of humans, plants and other animals
- Soil biodiversity enhances plant production in both managed and natural ecosystems

Soil biodiversity is increasingly under threat, which results in changes in the composition of soil communities and loss of species, as well as the benefits they provide to all life.

- Threats to soil biodiversity include climate change, land use change, salinisation, compaction, pollution and invasive species. These threats affect both the soil habitat and soil organisms
- Land-use change, such as intensive agriculture and sealing of fertile lands due to urbanisation, can cause declines in abundance and species diversity of many animals, including termites, earthworms, nematodes and microarthropods
- Loss of soil and its biodiversity represents a loss that is costly to nations

There is a need to celebrate these new discoveries about the life under our feet, as well as to integrate knowledge about soil biodiversity into international policies.

- The biodiversity in soils sustains the life that we see
- Reduction of soil biodiversity is a loss to society
- Measures to preserve soil biota are needed and possible
- Policies to protect and value soil biodiversity are urgently needed

Soil biodiversity is a common ground for achieving sustainability goals. Management and conservation of life in the soil is integral to governmental actions to provide healthy food, reduce greenhouse gases, lessen desertification and soil erosion, and prevent disease.

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(a-d) Chapter IV of the Global Soil Biodiversity Atlas is about services provided by soil organisms. (e) Chapters V and VI describe threats to soil life and interventions to preserve it. (f) Chapter VII presents the importance of research and outreach in raising awareness about soil biodiversity. (HCO, DSA, BB, IUC/USA, NASA, GS/CIAT)
Interstital living in the spaces between soil particles Ion an atom which has an electric charge through having either gained or lost an electron Land tenure the relationship, whether legally or customarily defined, among people, as individuals or groups, with respect to land Leaching process by which soluble materials (including nutrients and salts) in the soil are moved deeper into the soil profile by water Litter fallen leaves and other decaying organic matter that make up the top layer of a soil Maxillary of or relating to a jaw or jawbone Mesic characterised by a moderate amount of moisture Mesophile an organism that grows best in moderate temperatures, typically between 20 and 40 °C Metabolism the chemical processes that occur within a living cell or organism which are necessary for life Metagenome the sum of genomes from all organisms within a given sample (e.g. of soil or water) Metamorphosis a profound change in form from one stage to the next in the life history of an organism. Also geological term for altered rocks Methane microorganism that produces methane Micro-, meso-, macro-, megafauna groupings of animals by size, increasing from micro- through meso- and macro- and up to megafauna Mineral an inorganic component derived from rocks Mineralisation the process of forming a mineral by combination with another element, such as metals or oxygen Monoculture agricultural system that grows a single crop over a wide area, often over many years Mycorrhiza a symbiotic association between a fungus and plant roots Niche the optimal place or function of an organism within an ecosystem Nitrate ion with the formula NO\(^{-}\), base of nitric acid. Combines to form highly soluble nitrates (e.g. sodium nitrate, NaNO\(_3\)). Occurs in urine and also produced by certain bacteria. Key constituent of fertilisers Nitrification the oxidation of amonium compounds in dead organic material into nitrates and nitrites by nitrifying bacteria Nitrite ion with the formula NO\(_2\)\(^{-}\), formed when nitrous acid (HNO\(_2\)) is decomposed. Colourless, odourless inert gas at standard conditions. Occurs in all living organisms Nitrogen chemical element with symbol N and atomic number 7. Essential for life and occurs in high concentrations in plants and fruits Nitrogen fixation a process in which nitrogen (N\(_2\)) in the atmosphere is converted into the soil as ammonium (NH\(_4\)\(^+\)) Nitrogen fertilizer a process in which nitrogen (N\(_2\)) in the atmosphere is converted into the soil as ammonium (NH\(_4\)\(^+\)) No-till a procedure whereby a crop is planted directly into the soil without ploughing after the harvest of the previous crop Nutrient essential element needed by plants and animals to build biomass. Classified as macronutrients if needed in large quantities (primarily nitrogen, phosphorus, potassium, calcium, magnesium and sulphur) or micronutrients if needed in very low quantities (primarily boron, chlorine, copper, iron, manganese, molybdenum and zinc) Nymph the immature form of some invertebrates, particularly insects, which undergoes gradual metamorphosis Occellus (plural ocelli) a simple eye or ocellus of an invertebrate Oligotrophic a type of soil that has a low level of nutrients and is typically found in areas with limited rainfall Parent material geological or organic material from which soils are formed Parthenogenesis a form of reproduction in which an unfertilised egg develops into a new individual Pathogen any disease-producing agent, especially a bacterium or a fungus Ped a natural soil aggregate Pedogenesis process of soil formation and development Pellicle a thin layer supporting the cell membrane in various protists Permafrost ground (soil or rock and included ice and organic material) that remains at or below 0 °C for at least two consecutive years Permeability the measure of a ease with which fluids, gases or plant roots can travel through a soil pH a measure of acidity, measured from 1 (acidic) through 7 (neutral) to 14 (alkaline). Most soils fall in a range between pH 4 and 8 Phenotype characteristics of an organism that are the result of the interactions of that organism’s genes with environmental influences Phoresy association between two species in which one transports the other Phosphorus a highly reactive, non-metallic element with symbol P and a grey metallic colour. Occurs in earth’s crust as phosphates, such as inorganic fertilisers or herbicides are used Photosynthesis process by which plant cells use the sun’s energy to join carbon release and water to make up the food of green plants Physiogenetics the study of evolutionary relationships among groups of organisms Pleomorphism in microbiology, the ability of some unicellular organisms to alter their shape or size in response to environmental conditions Ploughing mechanical cultivation of soils to different depths, creating arable land Pollution introduction of contaminants into the natural environment that cause undesirable changes, causes stress to organisms and can result in death of organisms depending on susceptibility or dose Polymer a large molecule, or macromolecule, composed of many repeated subunits Pore the space between soil aggregates or soil particles. Also referred to as pore space Potassium chemical element with symbol K and atomic number 19. Essential for life and occurs in high concentrations in plants and fruits Precipitation water reaching the ground as rainfall, snow or hail Predator organism which hunts other organisms for food Predatory organism which are hunted by predators for food Prey animals or plants that do not contain a distinct membrane-bound nucleus Propagule a portion of an organism that aids the dispersal of that organism and is capable of growing into a new organism Prototypem, deutonymph and tritonymph juvenile stages of the life cycle of mites Pseudosaprobion a temporary projection of a unicellular organism to create an appendage like protoplasm for and for taking in food Psychrophilic microorganism that thrives in a cold environment Pyriscence seed release by plants in response to fire Reduction the addition of hydrogen, removal of oxygen or the addition of electrons to an element or compound. The opposite of oxidation Rhizosphere zone immediately adjacent to plant roots in which levels of microorganisms can be significantly higher than that of the soil body Rootability the extent to which plant roots can penetrate a soil Root exudates carbohydrates, organic acids, vitamins and other substances released from roots Ruderal a plant species that is first to colonise disturbed lands Sand soil particles between 0.05 mm and 2 mm Saprophytic feeding on dead or decaying organic matter Sclerotium (plural sclerotia) fungal mycelium that has hardened into a compact mass, with a store of reserve food material that in some higher fungi becomes detached and remains dormant until favourable environmental conditions for growth occur Sediment mineral or organic material that has been transported by wind or deposited in water (such as lakes, rivers or the sea). Basis for soil formation and development of soil texture and structure Sedimentary rocks such as sandstone, chalk and shale Splitting cultivation an agricultural system in which land is cultivated temporarily, then abandoned and allowed to revert to its natural cover while the land user moves on to another location Silt soil particles between 0.003 mm and 0.05 mm Sodium chemical element with symbol Na and atomic number 11. A soft, silvery-white, highly reactive alkali metal. Sodium is an essential element in the Earth’s crust and a component of many minerals (e.g. feldspars, rock salt). Produces highly soluble salts that are easily leached in soil Soil compaction a decrease in the volume of pore space between soil particles or aggregates. Severely compacted soil can become impermeable and affect plant growth Soil depth depth of soil body from the surface to parent material, bedrock or to the layer of obstacles to roots Soil fertility measure of the ability of soil to provide sufficient amount of nutrients, water and a suitable medium for healthy plant growth Soil function any service, role or task that soil performs, especially sustaining biological activity (agriculture), regulating and partitioning water and solute flow; filtering, buffering, degrading and detoxifying pollutants, storing and cycling of nutrients, providing support for buildings and other structures; protecting cultural heritage Soil organic matter (SOM) carbon-containing compounds of the soil exclusive of dead plant and animal residues. See humus Soil productivity the capacity of a soil to produce a certain yield of a given economic crop. Soil profile vertical section through soil, often from surface to parent material, showing the arrangement of horizons Soil quality the capacity of a soil, within natural or managed ecosystem boundaries, to provide specific functions such as plant growth, maintain or enhance water quality, structural support for habitation, habitat, etc. Soil sealing covering or destruction of soil by urban fabric or artificial material which may be impermeable to water (e.g. asphalt or concrete) Soil structure aggregation of soil particles into units separated by pores Soil texture numerical proportion of sand, silt and clay in a soil - can be coarse (sand particles dominate), medium (silt particles dominate) or fine (clay particles dominate) Soil/land degradation process that leads to a deterioration of soil/land properties and functions, often caused by human activities Sonication disruption (as bacterial cells) by exposure to high-frequency sound waves Species abundance number of individuals per species in a community Species richness the number of species within a biological community Spore a small, usually single-celled asexual reproductive organism, produced by many bacteria and fungi that are capable of developing into a new individual without sexual fusion Supercooling the ability of organisms to lower the freezing point of liquids through the production of antifreeze molecules such as glucose and mannitol, and reducing the presence of ice-nucleating agents Symbiosis a close and prolonged association between organisms of two different species which may result in benefits to either or both organisms Temperate climatic zone that lies between the tropics and the polar regions; characterised by moderate temperatures and precipitation. Can also refer to extreme weather due to the ocean. Terricolous living on or in the ground Test a protective shell secreted by some protists Thermophile an organism that thrives in warm conditions (c. 41 - 122 °C) Topsoil generally dark-coloured uppermost layer of soil containing decomposing organic matter, usually high in nutrients Trophic relating to nutrition or involving the feeding habits of different organism within an ecosystem Tropics area of land around the Equator bounded by the Tropics of Cancer and Capricorn Undulatory moving in or resembling waves Vascular a membrane-bound cavity within a cell, often containing a watery liquid or secretion Ventral situated on or toward the lower, abdominal plane of the body Waterlogged soil that is very wet, most pore spaces are filled with water (saturated). The opposite is a aerated soil Weathering the breakdown of rocks and sediments through chemical or physical (or biological) agents Weed vague term to define unwanted plants in human-controlled settings where they may be in competition with other plants (i.e. crops) for water, nutrients, sunlight and space with harvests Yield the amount of a specified crop (e.g. maize and coffee beans) produced per unit area. Usually expressed in kg or tonnes per hectare Zoospore a type of asexual fungal spore
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The JRC is a Directorate-General of the European Commission under the responsibility of Tibor Navracsics, European Commissioner for Education, Culture, Youth & Sport. The JRC provides scientific advice and technical know-how to support a wide range of EU policies. More than 25% of EU legislation has a technical or scientific basis and this trend is likely to grow as policies increasingly cut across several disciplines.

The JRC Activities

The JRC research programmes are decided by the Council of the European Union and funded by the EU Horizon 2020 budget. The JRC multiannual work programme, running from 2014 to 2020, focuses on clearly defined themes, reflecting a coherent approach to the JRC’s proven competencies:

- As the Commissioner’s science service, the Joint Research Centre’s mission is to provide EU policies with independent, evidence-based scientific and technical support throughout the whole policy cycle.
- Working in close cooperation with policy Directors-General, the JRC addresses key societal challenges while stimulating innovation through developing new methods, tools and standards, and sharing its know-how with the EU Member States, the scientific community and international partners.
- Key policy areas include: environment and climate change, energy and transport, agriculture and food security, health and consumer protection, information society and digital agenda, safety and security, including nuclear, all supported through a cross-cutting and multidisciplinary approach.

The main customers of the JRC are the policy-making Directorates General of the European Commission. Depending on the subject matter, the JRC’s scientific-technical support covers the complete policy cycle or parts of it: the JRC anticipates policy needs, assesses policy options and their impacts, and monitors and contributes to the implementation of policies. It also provides operational support in certain cases, for example in anticipating environmental disasters, providing assistance to managing crises and assessing any consequential damage and their impact on human life and/or the environment. The ultimate beneficiaries of these activities are the EU Member States.

In July 2010, the JRC published its strategy for 2010-2020 with the intention to focus its efforts on seven thematic areas, which respond to major EU and global challenges and take into account the JRC’s proven competencies:

- towards an open and competitive economy
- development of a low carbon society
- sustainable management of natural resources
- safety of food and consumer products
- nuclear safety and security
- security and crisis management
- reference materials and measurements

In keeping with its mission, the JRC strives to play a role as a centre of reference in its key competence areas through extensive networks with the relevant organisations in the Member States and, where appropriate, international organisations. In addition to these institutional activities, the JRC cooperates closely with external organisations. In line with a strategic approach to the JRC’s role as a partner, several high-level agreements have been set up with large scientific and industrial communities on new networks and research collaboration.

The Institute for Environment and Sustainability

The mission of the Institute for Environment and Sustainability is to provide scientific and technical support to the EU policies for the protection of the environment and the more efficient and sustainable management of natural resources at global and continental scales.

The Institute for Environment and Sustainability (IES) is one of the seven scientific research institutes of the European Commission’s JRC. Located in Ispra, Italy, the IES carries out research to understand the complex interactions between human activity and the physical environment, and how to manage strategic resources (water, land, forests, food, minerals, etc.) in a more sustainable manner. Together with other JRC institutes, the IES provides the scientific basis for the conception, development, implementation and evaluation of EU policies that promote the greening of Europe and the global sustainable management of natural resources. It also works in partnership with other Directorates General to support the strategic priorities of the European Commission.

The Institute brings together multidisciplinary teams who work with observations and numerical analyses, and develops the ICT infrastructures necessary to share data and models. It combines this in-house expertise with its role as a scientific catalyst in order to provide the knowledge base necessary to assess the social, environmental and economic aspects of policy options. The IES plays an active role in partnerships within the EU and global scientific communities, which are a prerequisite for finding sustainable solutions to today’s global environmental challenges.

Soil at the JRC

- The development of the Global Soil Biodiversity Atlas was undertaken by the Land Resource Management Unit (LRM) of the JRC’s Institute for Environment and Sustainability.
- The LRM Unit investigates the balance of land-use demands and access to natural resources and maintenance of ecosystem services with a focus on understanding the components of the human environment system and trends in land condition and management, along with how these respond to changing environmental, societal and economic conditions.
- A key strength of the LRM Unit is its soil activities, which are a single focal point for soil-related data and information for European Commission services and other EU institutions. The Unit maintains the European Soil Data Centre and provides high-level analysis and assessments on the status and trends of soils in Europe and other parts of the world. The Unit is staffed by a team of soil scientists, agricultural scientists, geographers, geomorphologists, IT specialists and modellers. There is a strong competence in soil science, spatial analysis and geostatistics.
- A key aspect of the work is collaboration with strategic partners through networking. The Soil Team of the LRM Unit supports the initiatives of the Global Soil Partnership and regional developments, the European Soil Bureau Network, EIONET-SOIL, GlobalSoilMap, the European Network for Soil Awareness, the Global Soil Biodiversity Initiative and many more.
- The Global Soil Biodiversity Atlas is a striking example of the type of high-level output generated by the JRC Soil Team. By bringing together scientists from all over the world, the atlas illustrates the benefits of international collaboration and the need for scientifically sound policies for the sustainable management of a key natural resource that is the cornerstone of food security, key environmental services, social cohesion and the economies of many countries.

Website: http://esdac.jrc.ec.europa.eu/
JRC Soil Atlas Series

The European Commission’s Joint Research Centre collaborates with soil scientists and researchers from all over the world to develop a series of soil-related atlases. To obtain a copy or for further information, please consult the Publications Office of the European Union (http://publications.europa.eu/) or the JRC SOIL Action’s website (http://eusoils.jrc.ec.europa.eu).

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You can find publications through simple and advanced search functions (e.g. soil atlas), browsing by thematic area or by author (e.g. European Union institution). Furthermore, you may choose to sign up to ‘My EU Bookshop’ and access personalised functions, for example, save search queries for regular use, or be notified by e-mail about new releases that interest you.

The Publications Office aims to make the EU Bookshop the common entry point for European Union publications. Currently, the website is available in 22 languages. All soil atlases are available in hardcopy (€25) or as a pdf file (free of charge).
Soils are increasingly under pressure and so are the organisms living in them. Intensive agriculture, loss of aboveground biodiversity, soil erosion and land degradation are among the most relevant threats to soil life. We can protect soil creatures by taking specific actions. No-tillage, diversification of crops, increasing reforestation and greater use of natural amendments are examples of interventions that may promote life in soils. People need to know about the fascinating world belowground and understand its value. The Global Soil Biodiversity Atlas presents the often neglected protagonists in the environment that surrounds us all.

Soil biodiversity is the variability among organisms living in soils. The images above, from top left to bottom right, show representatives of the main groups of soil-dwelling organisms. Fungi, together with bacteria and archaea, are microorganisms. (BJ) Nematodes, together with protists, tardigrades and rotifers, are microfauna. (AM) Collembolans, together with mites, enchytraeids, proturans, diplurans and pseudoscorpions, are mesofauna. (AM) Earthworms, together with ants, termites, arachnids, isopods and myriapods, are macrofauna. (MK)

Soil is an extremely complex system resulting from the essential interactions between inert and living components. Soils host a myriad of soil organisms ranging in size from a few micrometres to several centimetres, from the microscopic bacteria and archaea to the “giant” earthworms and moles. All these organisms are distributed over space and time, and each ecosystem and season has its unique soil community. Soil organisms interact to provide essential ecosystem services to human beings and the environment, ranging from supporting plant growth to the regulation of climate. Soils sustain life and are full of life. (MT)

What is soil biodiversity? How does it vary in space and time? What does it provide to society? What are the main threats to soil biodiversity? What can we do to preserve it? The first ever Global Soil Biodiversity Atlas uses informative texts, stunning photographs and striking maps to answer and explain these and other questions.

Going through its nine chapters, every reader will learn what soils are and about the amazing creatures living in them. You will discover the factors influencing the distribution of soil organisms, how soil biodiversity supports food production, the pressures affecting soil life and the possible interventions to preserve it. The Global Soil Biodiversity Atlas is an essential reference to understand and appreciate the incredible world living under our feet.