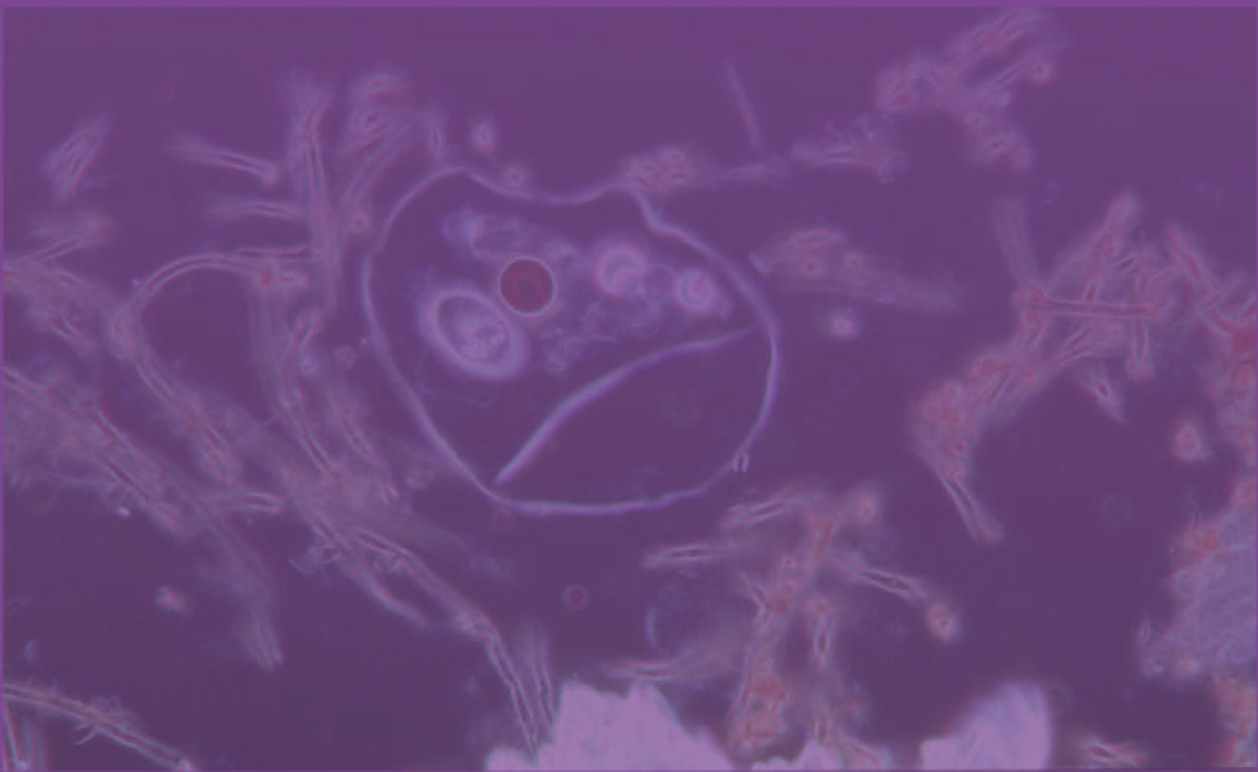
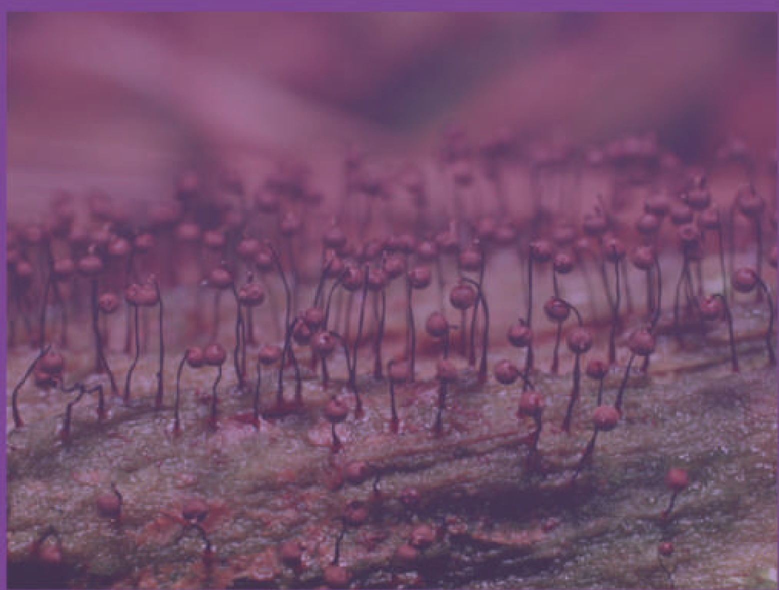


EUROPEAN ATLAS OF SOIL BIODIVERSITY











JRC
EUROPEAN COMMISSION

EUROPEAN ATLAS OF
SOIL BIODIVERSITY

EUROPEAN COMMISSION JRC

Institute for Environment and Sustainability

PUBLISHING DETAILS

The citation for this document is:

S. Jeffery, C. Gardi, A. Jones, L. Montanarella, L. Marmo, L. Miko, K. Ritz, G. Peres, J. Römbke and W. H. van der Putten (eds.), 2010, European Atlas of Soil Biodiversity. European Commission, Publications Office of the European Union, Luxembourg.

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Published by the Publications Office of the European Union, L-2995 Luxembourg.

EUR 24375 EN — European Atlas of Soil Biodiversity

Catalogue number LB-NA-24375-EN-C

ISBN 978-92-79-15806-3

ISSN 1018-5593

doi 10.2788/94222

2010 – 128 pp. – 30.1 x 42.4 cm

Cataloguing data can be found at the end of this publication.

Printed in Luxembourg by Imprimerie Centrale SA

Publications Office of the European Union

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Front Cover

A healthy soil depends on a vibrant range of life forms living below the ground, from bacteria and fungi to insects, earthworms and moles. Together, this rich assemblage of life brings immeasurable benefits to the planet we live on. The images on front cover provide a sample of life in the soil. They include from left to right:

- **(top row):** a terrestrial isopod, also known as a woodlouse; the roots of plants (such as this Pitcher Plant *Sarracenia purpurea*) are a key component of soil biodiversity; a surface-dwelling collembolan;
- **(second row):** map of potential threats to soil biodiversity;
- **(third row):** two images of protozoa;
- **(fourth row):** an Acerentomid proturan of the genus *Parajapygidae*; fruiting bodies of a myxomycete; fruiting bodies of the fungus *Amarillaria ostoyae*;
- (**fifth row: small images):** *Aporrectodea giardi*, an earthworm found in topsoil; soil profile under a temperate grassland; a mole (AJ);
- **(bottom row):** soil-dwelling collembola: also known as springtails; a millipede (*Strongylosoma stigmatosum*); plasmodium of a myxomycete. (RD)

Picture sources (in the same order as above): S. Taiti, R. Artz, U. Tartes; JRC; O. Ehrmann, W. Foissner; D. Walter, K. Fleming, A. Rockefeller; D. Cluzeau, E. Micheli, A. Jones; P. Henning Krog, F. Trnka/I. H. Tuf, R. Darrah.

Back Cover

(clockwise from top-right): a mole, one of only a very few vertebrates that lives permanently in the soil; a carnivorous fungi, *Drechslerella anchonia*, capturing a nematode in rings which grow along its hyphae; a tardigrade of the species *Paramacrobiotus kenianus* sitting on a moss leaf; *Protaphorura fimata*, a white-coloured and blind collembola, an adaptation to life below ground (eu-daphic).

Picture sources (in the same order as above): A. Jones; G. Badon/N. Allin; Eye of Science; P. Henning Krog.

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http://en.wikipedia.org/wiki/Digital_Chart_of_the_World

Soil Data

The maps in this atlas relating to soil characteristics are derived from the Soil Geographical Database of Eurasia, a constituent of the European Soil Database Version 2.0 (Van Liedekerke, M., Panagos, P., Daroussin, J., Jones, R., Jones, A. & Montanarella, L., 2004).

The database is distributed by the European Commission Joint Research Centre, http://eusoils.jrc.ec.europa.eu/

Soil maps are produced by the Soil Action of the Land Management and Natural Hazards Unit, Institute for Environment and Sustainability, Joint Research Centre, European Commission, Ispra, Italy and Lovell Johns Ltd, UK.

Final design and graphical support by Lovell Johns Limited, 10 Hanborough Buisiness Park, Long Hanborough, Witney, Oxfordshire, OX29 8RU, United Kingdom. www.lovelljohns.com

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Acknowledgements

This atlas is the result of a collaboration between the European Commission's Joint Research Centre in Ispra, Italy and world leading experts in soil biodiversity from Europe and beyond. The authors gratefully acknowledge the assistance of the following individuals and organisations. We also thank and offer our apologies if we have inadvertently and unintentionally omitted anybody.

For meetings and discussions before the drafting phase we would like to acknowledge the effort of Ljibert Brussard, Carlo Jacomini, Olaf Schmidt and Siliva Pieper, as well as the other members of the Soil Biodiversity Working Group, most of whom have made important contributions to this atlas and so are listed by name under the authors and contributors. Vit Penziek has provided support with regard to ArcGIS, cartography and advice concerning soil taxonomy.

Nicholas Frost provided assistance with Photoshop and undertook the post production colour addition for many of the scanning electron micrographs.

Linda and Malcolm Jeffery for their help with proof reading of this atlas. Katarzyna Turnau for the provision of several pictures, as well as for the introduction of further contributors that have helped to strengthen this atlas.

Franz Horak helped in the area of the history of soil biodiversity.

The editors are grateful for all invaluable advice and guidance provided by Monika Walter and Mare Maxwell at the Publications Office of the European Union in Luxembourg. In addition, thanks are due to colleagues in DG Communication and the EURESIN consortium for their willingness to collaborate and support the project. Lastly, without the flexibility, understanding and professionalism of Ian Dewsbery and Jon Gammage at Lovell Johns Ltd (UK), the quality of this publication would be shadow of what was finally produced.

Huge thanks also to all the members of the JRC Soil Action an Grainne Mulhern for their eagle-eyed pre-production checks of the final manuscript.

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Soil – the factory of life. Scientists estimate that one-quarter of the species on the planet Earth live in the soil.
This diverse ecosystem performs a variety of functions. It processes waste organic matter to sustain life above the ground, from plants to animals to people; it regulates the carbon flux and the water cycle, it keeps pests at bay and decontaminates polluted land; and it provides raw materials for new pharmaceuticals to tackle infectious diseases.
The workers in this factory are microorganisms, small and large invertebrates, small mammals, even plant roots – their workplace is the dark or dim layers of topsoil beneath grasslands, forests and green spaces in towns.
In the following pages, the atlas describes what takes place in this fascinating environment, presents the workers of this critical factory, outlines the threats to their habitat and the research and legislation that are being undertaken to protect them.
The above photograph shows a soil with an organic-rich topsoil. Both the rhizosphere, the zone in the soil which is influenced by the physical, chemical and biological processes of plant roots, and small burrows made by earthworms and other soil organisms are clearly visible. (EM)

The mole (Talpidae) is one of only a very few vertebrates that live permanently in the soil. A mole's diet consists primarily of earthworms and other small invertebrates found in the soil. Because their saliva contains a toxin that can paralyse earthworms, moles are able to store their still living prey for later consumption in special underground store rooms. Moles excavate extensive burrows with the waste material being ejected as characteristic molehills. Despite their often negative perception amongst gardeners for the damage they cause to lawns, moles are a valuable indicator of a healthy soil. Being a high-order predator, moles require a functioning soil ecosystem and supporting biodiversity in order to survive. Molehills can therefore be regarded as an indicator of healthy soil biomes. While moles can be found in most parts of North America, Asia and Europe, there are no moles in Ireland. (AJ)

PREFACE

Fertile soil is vital for human survival. An estimated 99% of the world's food comes from the terrestrial environment - crops are grown in soil and livestock maintained on it. Soils have a real role in shaping our planet. They can absorb rainwater and act as a buffer against both floods and droughts. Soils also hold more than twice the amount of carbon than is currently contained in the atmosphere. However, most people are unaware that the key drivers of soil ecosystems that control fertility and terrestrial global nutrient cycles are the quantity and quality of living organisms within the soil.

Our knowledge of this habitat is limited. Many of the essential bacteria and fungi are minute, and therefore difficult to visualise. Large-scale investigations are also hampered by accessibility and the inherent variability of soil across the landscape. Therefore, understanding the highly complex and dynamic interactions which occur in life below ground remains one of the most formidable challenges facing scientists if we wish to assess environmental and global change processes and explore possible mitigation strategies.

Growing pressures from an ever increasing global population, as well as threats such as climate change and soil erosion, are placing increasing stresses on the ability of soil to sustain its important role in the planet's survival. Evidence suggests that while increased use of mono-cultures and intensive agriculture has led to a decline in soil biodiversity in some areas, the precise consequences of this loss are not always clear.

The United Nations has declared 2010 to be the International Year of Biodiversity and, for the first time, the biodiversity of soil is in the spotlight. For this reason, we are pleased that an international group of experts and scientists from the Joint Research Centre (JRC), in close collaboration with colleagues from DG Environment, have produced the first ever "European Atlas of Soil Biodiversity". This innovative atlas is a step towards raising awareness on the key role of life within the soil in maintaining life on Earth. The atlas represents a major contribution to the new EU target of halting the loss of biodiversity and ecosystem services in the EU by 2020, and insofar as possible, restoring them.

Given that at least a quarter of the Earth's biodiversity can be found in the soil, and in order to achieve our own biodiversity target and substantiate our support for the Convention on Biological Diversity, we must protect soil biodiversity. As an integral part of its Soil Thematic Strategy, the European Commission has proposed a Soil Framework Directive in an attempt to prevent further soil degradation across the European Union, and to repair the damage that has already been done. This is a growing problem, and unless we tackle it soon and in a coordinated manner, it will cost a lot more to put it right.

We believe that this impressive publication will become a widely-used text and it marks a crucial step towards a better understanding of the role of life below ground. We are also convinced that it will highlight the need for improving the protection of soil and the diverse life within it.

Janez Potočnik
EU Commissioner for Environment
2010 - 2014

Máire Geoghegan-Quinn
EU Commissioner for Research, Innovation and Science
2010 - 2014

FOREWORD

One of the strengths of the JRC is the ability to use its scientific expertise to build and develop networks of cooperation with researchers in Member States and the international science community. Initiatives such as this atlas use science to bring people from diverse national and political backgrounds together to address a common goal. In parallel, the JRC is carrying out a crucial, but often underestimated, role of communicating science to the wider society.

The involvement of the JRC in research to support the EU's Thematic Strategy on Soil and the EU Biodiversity Action Plan are well established. The European Soil Data Centre, managed by the JRC's Institute for Environment and Sustainability, provides decision makers with timely and relevant information on issues affecting soil. Increasing our knowledge of life within the soil and the ecosystem services which it provides is particularly important in our attempts to feed the world's population and to understand the processes and responses to climate change. I am pleased to see that through the efforts of the JRC, information on soil biology is now being made available to both policy makers and the general public.

It is in this context that the Joint Research Centre, as the European Commission's in-house research body, is carrying out research and collecting information with the aim of improving our understanding of life below ground in order to evaluate the need for, and effectiveness of, EU policies to protect both soil resources and the astonishing diversity of organisms that make soil their home.

I hope that you will find this atlas both enlightening and useful as a scientific reference.

Roland Schenkel
Director-General of the JRC

Life in our soils is an enigma, which we have yet to fully untangle. The biology found under our feet is the driving force behind many of the global nutrient cycles that allow our societies to thrive.

There are more than a billion organisms in one teaspoon of grassland soil and this can contain more than ten-thousand individual species of bacteria and fungi. In this light, it is quite amazing that we know so little about the forms of life that can be found in our soils. Or does it explain why we know so little?

Understanding the role and requirements of these organisms is essential to the future protection and the sustainable use of soils. To date, very little information has been made available about the biodiversity of our soils at a European scale. Most research is conducted at a local or catchment level with only a few countries monitoring some individual species at national scale. This atlas provides the first comprehensive assessment of biodiversity in soils across Europe and is the result of an ambitious pan-disciplinary collaboration of scientists from across the world.

This Soil Biodiversity Atlas opens up the illustrious world of soil ecosystems to scientists and non-specialists alike, and provides an excellent tutorial about the organisms we find in the ground. This publication will provide a greatly needed guide to help promote awareness of the hidden treasures of our soils and the need to protect this non-renewable resource which is so often taken for granted.

2010 is the Year of Biodiversity and I am confident that this atlas will put the significance of soil biodiversity firmly on the political agenda as the primary engine of the soil functions that are recognised in the EU Thematic Strategy on Soils.

I would like to congratulate the editors and authors of this atlas, in achieving such a valuable resource.

Dr. Rachel Creamer
Chair of the European Soil Bureau Network

The European Union is committed to the sustainable use of soil and protecting soil biodiversity through the development of scientifically sound policies. Being a European centre of scientific and technical reference covering the entire environmental sciences, the Joint Research Centre's Institute for Environment and Sustainability (IES) uses its expertise to overcome the widespread lack of understanding about the biological processes that occur beneath our feet. Acting as a bridge between the scientific and policy making communities, IES staff are working with internationally renowned experts on the research needed to support the development of polices to maintain and enhance soil biodiversity levels across Europe and beyond.

I am pleased to see that the result of this collaboration has resulted in this striking, informative and, in the context of the International Year of Biodiversity, timely document.

Leen Hordijk
IES Director

CONTENTS

SECTION ONE

Chapter 1 Introduction

1.1 Scope of the Atlas

Soil is one of the fundamental components for supporting life on Earth. It is the processes that occur within soil, most of which are driven by the life that is found there, which drives ecosystem and global functions and thus helps maintain life above ground (Fig. 1.1).

Soil performs numerous ecosystem functions and services, ranging from providing the food that we eat to filtering and cleaning the water that we drink. It is used as a platform for building and provides vital products such as antibiotics, as well as containing an archive of our cultural heritage in the form of archeological sites.

Life within the soil is hidden and so often suffers from being 'out of sight and out of mind'. However, this atlas demonstrates that soil is a vital habitat and aims to increase the visibility of soil biodiversity and educate as to the important roles that the soil biota play in driving life on Earth.

A further aim of this atlas is to function as a comprehensive guide, to allow non-specialists to access information about this unseen world. In order to better elucidate the complex interactions that occur between organisms in the soil, this atlas is divided into two sections. The first aims to give a feel of the below ground environment, the soil biota in general, the functions that it performs, the important value it has for human activities, as well as for driving cycles on a global scale. Furthermore the feedbacks which occur between the environment which shapes the habitats in which soil organisms live, and the organisms effects on the environment, whereby they in turn affect their environment and so the living space for the organisms within the vicinity are also discussed.

The second section aims to function as an 'Encyclopedia of soil biodiversity'. While the astonishing levels of heterogeneity of life present in soils is impossible to represent here, indeed just listing all of the known species of bacteria found in soils could take up many hundreds of pages, this section aims to give an overview of what life below ground looks like. Starting with the smallest organisms, the bacteria, and working up through taxonomic groups, through fungi and nematodes, up to the insects such as ants and beetles 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. Only microorganisms and invertebrates are covered in depth by this atlas. Many vertebrates, such as moles and badgers for example, also make their homes in soil to a greater or lesser extent. However, these groups are generally not as important with regard to soil functioning nor the ecosystem services which soil provides.

This atlas has been written as a European Commission contribution towards the International Year of Biodiversity 2010. For this reason, although this atlas is written in English, and from a European viewpoint, it includes soil biodiversity beyond European borders. As well as looking at tropical soil biodiversity and the soil biodiversity which is found in extreme environments such as hot and cold deserts, the atlas also has contributions from the Convention on Biological Diversity which discusses steps which are being taken to increase our understanding of, and help towards protecting, soil biodiversity on a global scale.

How to read this atlas

This atlas can clearly only give an overview of the remarkable biodiversity that is found below ground, the complex interactions occurring, and the many resulting ecosystem functions and services. This atlas is therefore designed to be used as a reference, to give a strong introduction and to provide information on many of the different areas of soil biodiversity, its study and applications. Each section has been written by different experts, sometimes individually and some times as a team. Through close coordination by, and collaboration with, the Directorate General Joint Research Centre of the European Commission, efforts have been made to keep the style of the atlas similar throughout and the language clear and easily understandable. However, some of the topics are more theoretical and abstract than others, and while care has been taken to keep the language easily accessible, some terms may be new to the reader. For this reason a comprehensive glossary can be found at the back of this atlas. Added to this, where the subject is complex and abstract, efforts have been made to include simple analogies or explanations in supplementary boxes.

Furthermore, as this atlas is designed to be a useful reference as well as a guide to life below ground, it is important that each section works independently of all other sections, to make information readily accessible. For this reason it is unavoidable that a certain amount of redundancy exists between sections, with some important data being shown more than once. This means that the appropriate information is found in each section without the need to jump backwards and forwards to find different tables, facts and figures.

The Directorate General for the Environment have also produced a report entitled "Soil biodiversity: functions, threats and tools for policy makers", for anybody interested in reading about soil biodiversity from a more policy-oriented approach. More information and the report can be found at:

http://ec.europa.eu/environment/soil/biodiversity.htm

Fig. 1.1: A selection of images showing soils in different ecosystems ranging from forest through grassland and peatland to agriculture.

1.2 What is Soil Biodiversity?

The Millennium Ecosystem Assessment defines biodiversity as: "...the diversity among living organisms in terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part. It includes diversity within and between species and the diversity of ecosystems." For the purpose of this atlas we will be discussing biodiversity in terms of the diversity of living organisms in the soil.

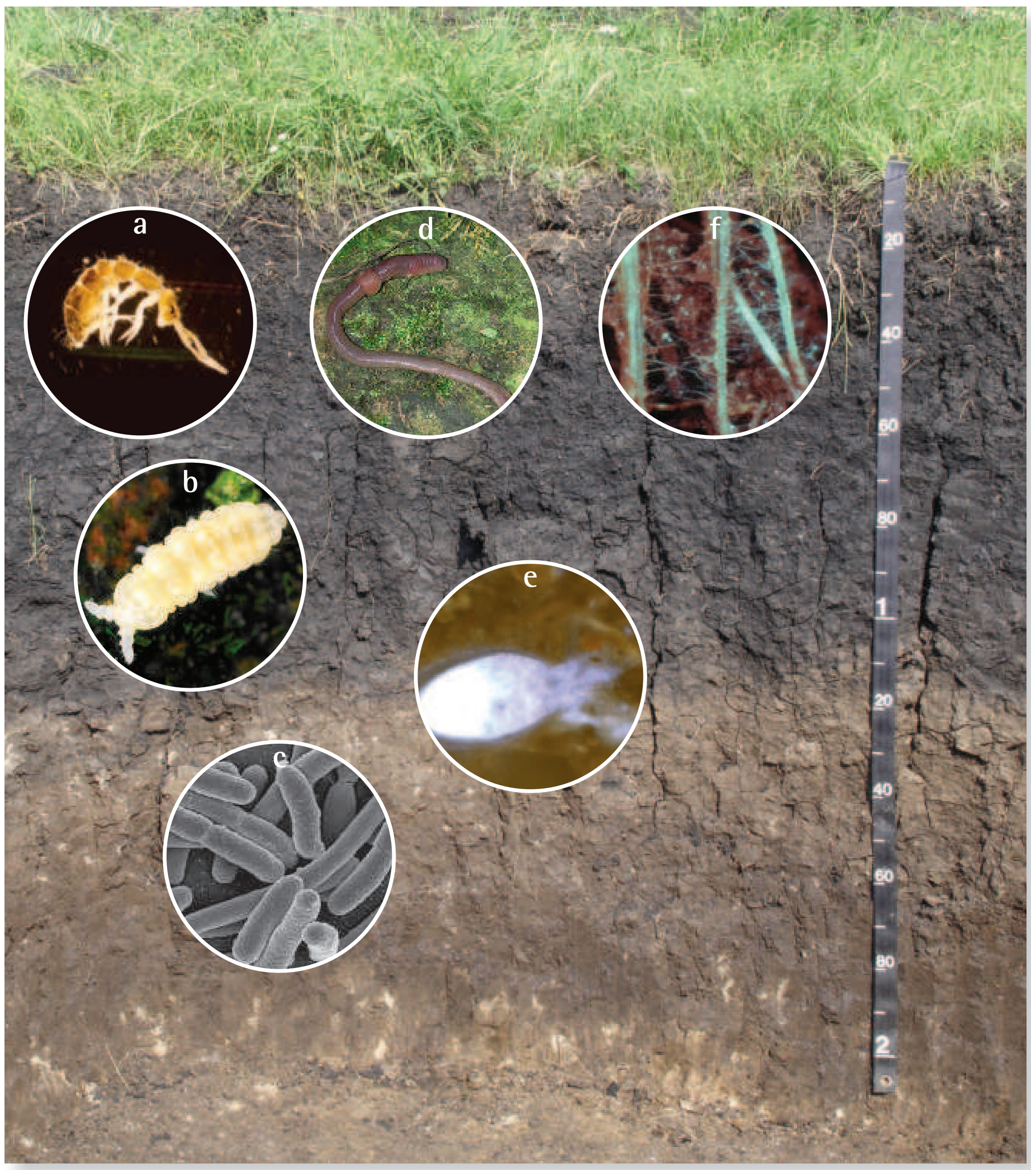
"Soil biota" is a term with a similar meaning to soil biodiversity, but is more specific and refers to the complete community within a given soil system. For example, it is possible to say that the soil biota in a grassland soil is generally more diverse than that in an arable system, or that grassland soils generally have higher levels of soil biodiversity than the soil in arable systems. The meaning is the same in both instances.

The soil system is extremely complex and varies greatly both spatially and over time. Soil itself consists of a "mineral" portion containing mainly silica and a mixture of trace metals, an "organic matter" portion containing a large variety of different organic compounds, and a vast array of different organisms, as well as water in all but the driest soils.

Soil can exist at a variety of textures; meaning they have different proportions of sand, silt and clay. It can contain areas of relative dryness, down to micropores which are almost always water filled apart from in times of extreme drought. The level of organic matter content varies both with depth (generally decreasing with depth), and spatially.

This high level of heterogeneity means that soil contains an extremely large number of ecological niches which have given rise to a staggering array of biodiversity (Fig. 1.2). Using a taxonomic approach to measure biodiversity, it is often said that more than half the world's estimated 10 million species of plant, animal and insects live in the tropical rainforests. However, when this approach is applied to the soil, the level of diversity is often in the range of hundreds of thousands to possibly millions of species living in just one handful of soil!

Fig. 1.2: This highly simplified figure aims to give some idea of the distribution of organisms vertically through the soil profile. It is clearly an oversimplification and in fact microorganisms such as bacteria (c) and protozoa (e) are distributed throughout the soil profile, although with the highest biomass being found near the soil surface which is richer in organic matter. The two collembolans are adapted for living at different soil depths with the species shown in (a) being more adapted for living on or near the soil surface and that shown in (b) being more adapted to living at deeper levels. These differences are discussed in more detail in Section IX. Earthworms are also found in greater numbers closer to the soil surface but can also be found down to depths of 1 metre or more and form three different ecological groups which are discussed in more detail in Section XIII. Fungi are also found throughout the soil profile but are particularly common close to the soil surface where there is higher concentrations of organic matter as well as numerous plant roots with which they can form symbiotic relationships (f). This figure only shows a very few selected organisms. Many more organism groups make the soil their home as this atlas will make clear. (JRC)



Organisms of the Soil

As previously stated, the soil environment is home to an incredible diversity of organisms. Added to that, those organisms which are found in soil are also often found at astonishingly high levels of abundance. The level of abundance and diversity varies from soil to soil, depending on factors such as organic matter content, soil texture, pH and soil management practice. Below is the approximate number and diversity of organisms divided into groupings according to size, typically found in one square metre of temperate grassland soil.

As well as the groups shown below in Table 1.1, some soil biologists make the division between the three groups using effective body width which is more a measure of the ability of different organisms to pass through different soil pore sizes. However, the cut off points are still similar using this technique and there is general agreement as to which organisms fall into which category.

In biology, an organism is any contiguous living system such as animal, plant, fungus, or microorganism. In some basic form, all organisms are capable of response to stimuli, reproduction, growth and development as a stable whole.

An organism may either be unicellular (single-celled) or be composed of many trillions of cells grouped into specialized tissues and organs (as in humans). The term multicellular describes any organism made up of more than one cell.

Table 1.1: The soil biota can be divided into three groups.

Smaller → **Larger**

Microfauna/flora *Size range 1-100 µm*	**Mesofauna** *Size range 100 µm – 2 mm*	**Macro/Megafauna** *Size range > 2 mm*
Bacteria 100 billion cells from 10,000 species	**Tardigrades**	**Earthworms**
Fungi 50 km of hyphae from 100's of species	**Collembola**	**Ants**
Protozoa 100,000 cells from 100's of species	**Mites**	**Woodlice**
Nematodes 10,000 individuals from 100's of species	**Combined** 1,000's individuals from 100's of species	**Centipedes**
		Amphibians and reptiles
		Mammals
		Birds
		Combined 100's individuals from 10's of species

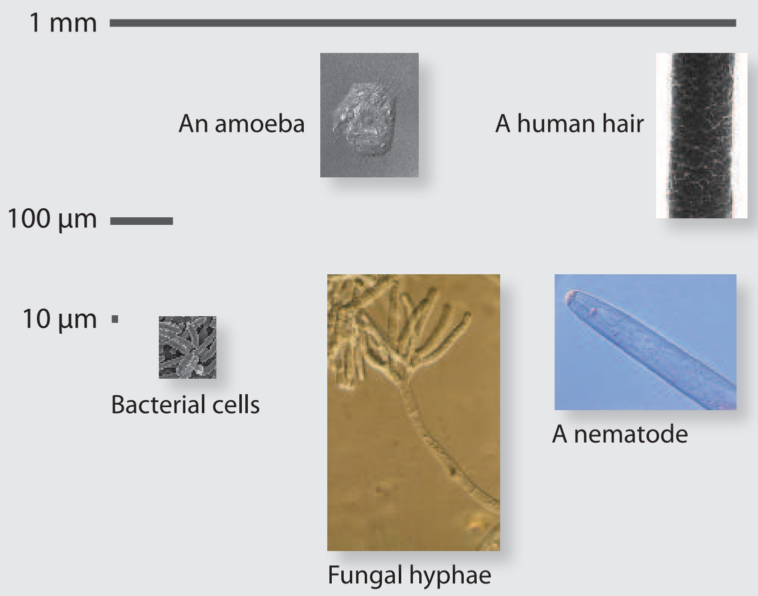
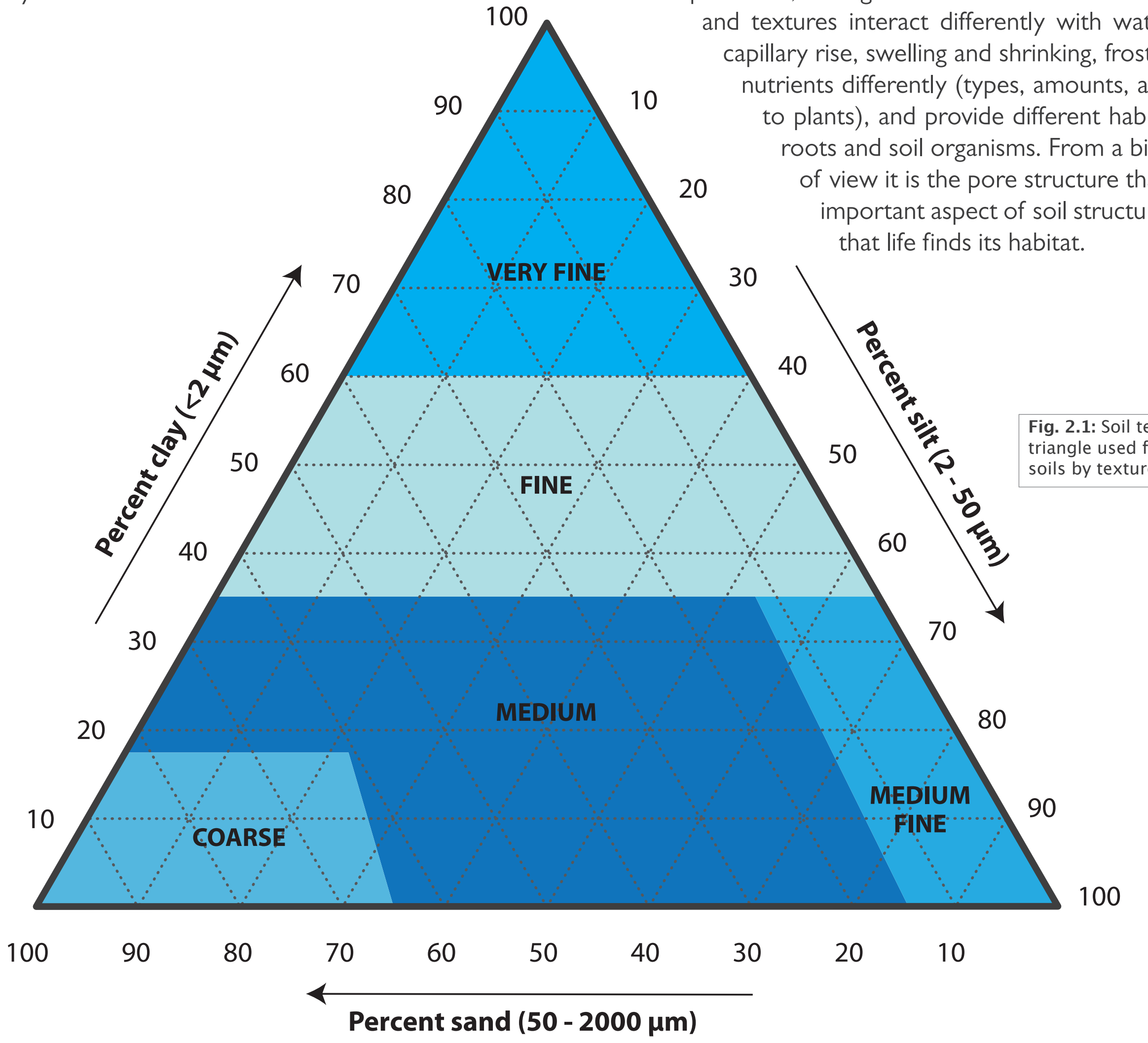


Fig. 1.3: A schematic showing, to scale (approx. 80x magnification), the average relative sizes of different soil microorganisms compared to the thickness of an average human hair. (JRC)

2.1 The Soil as a Habitat

To somebody walking on the soil surface, soil can appear to be an unchanging mass. However, soil is actually an incredibly dynamic and heterogeneous system, full of pore spaces filled with air and water as well as numerous organisms of many shapes, sizes and habitats. The pore network of soils is an immensely complicated structure, full of pathways that can extend metres down into the soil via either relatively direct or incredibly tortuous routes.



Differing proportions of the mineral fraction components - sand, silt and clay - are what give soil its different textures, allowing textural classification (Fig. 2.1), ranging from coarse to very fine. Soil structure is the combination and arrangement of primary soil particles, that is the mineral and organic fractions of soil, into secondary units (aggregates or peds), which have many different sizes and shapes. For example, 'subangular blocky', 'prismatic', or 'granular'. Soils of different structures and textures interact differently with water (drainage, capillary rise, swelling and shrinking, frost heave), bind nutrients differently (types, amounts, and availability to plants), and provide different habitats for plant roots and soil organisms. From a biological point of view it is the pore structure that is the most important aspect of soil structure as it is here that life finds its habitat.

Fig. 2.1: Soil textural triangle used for defining soils by texture. (FAO)

As discussed in the box below, there is a lot of living space in soil for organisms, particularly for microorganisms. The pore space within soils can make up almost 50% of the total volume of the soil, although much of this space is too small for many organisms to enter, with potential consequences which are discussed later. It has been demonstrated that the surface area of the pore space within a clay soil can be over 24,000 m^2 in just 1 g of soil, and that this amount decreases with increasing proportions of silt and sand. While much of this space is confined to micropores which are too small for even bacteria to live in, this demonstrates that, at the scale of microorganisms, there is huge amount of space to function as a habitat for organisms in soil. This is the reason that a relatively small amount of soil can be home to such a vast array and abundance of life.

Soil is considered to be a semi-aquatic habitat with the majority of soil organisms, particularly microorganisms, needing water to live and to move. When a soil is saturated, all of its pores are full of water. Two or three days after wetting, when free draining has stopped, most soil pores still contain water and the soil is said to be at field capacity. This is actually characterised by the amount of suction pressure that is needed to move water from the soil. As the soil dries out, more and more pressure is needed to draw water from the soil. Water drains from the larger pores first as the forces that hold it in the pores are weaker. Medium size pores drain next, with small pores being the last to lose water owing to the fact that at these micro-scales the electrostatic forces between the water and the soil particles are relatively powerful. Water can be bound so tightly in micropores that plants are unable to 'suck' hard enough to be able to remove the water. When the only water remaining in soils is in these micropores, the soil moisture is said to be at (or past) the 'permanent wilting point', with a suction pressure of greater than –15 bar to remove the water from these pores. This is because the moisture is inaccessible to plants and so the plants wilt.

Soil at different scales

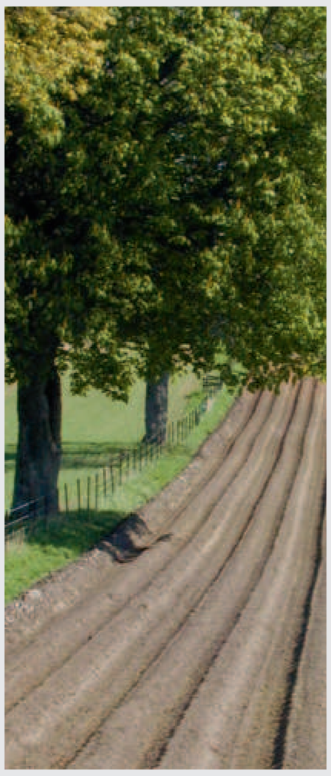
The scales at which most life exists within soil is unfamiliar to most of us. The first two images on the right are at the scale at which we are most used to seeing soil, appearing to exist as a two dimensional planar surface. However, anyone who has ever dug down into the soil for any reason will also be familiar with soil at the increased scale, where soil aggregates and the mixture of organic matter first become clearly visible and it is possible to see the first signs of the pore structure.

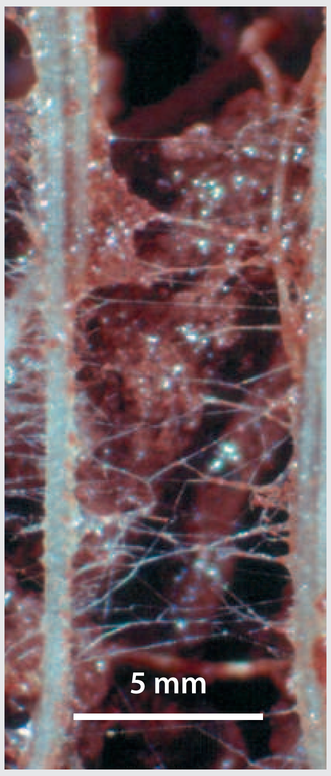
Increasing the magnification further takes us down to the scale shown in the third image to the right. At this scale, the fine roots of plants can be seen, along with the mycorrhizal fungi which form a symbiotic relationship with plant roots, and the amount of space at this scale starts to become apparent.

The fourth image shows a thin section of soil. The soil is imbedded in resin which allows it to be sliced into very thin sections. When a light is shone from below the pore spaces between the aggregates of the soil become clearly apparent (shown in yellow).

At this scale it becomes clear just how high a portion of soil is actually space, containing either air or water depending on the soil moisture content. The proportion of pore space to soil particles in a given soil is dependent on several factors. One of the main factors is the texture of the soil, for example, in a fine textured soil the pore space can be almost half of the total volume of a given soil, whereas a medium textured soil may have a pore space of closer to 40% of the total volume.

Soil structure is also a large factor in the proportion of pore space in soils, with compacted soils having reduced pore space when compared to uncompacted soils, for example.





All photos. (KR)

Soil organisms, especially microorganisms, are not as restricted by water being in small pores as plants are, as they generally move within the water film as opposed to trying to remove it from pores for use elsewhere, as is the case for plants. The fact that water can be so tightly bound within small pores means that water is available for the soil microbiota the majority of the time, except in times of extreme drought.

Different organisms have different methods for coping with the lack of water during times of extreme drought, and all generally involve entering a resistant state of restricted or zero metabolism, where the organisms can appear to be dead, until water becomes available again and the organisms once more 'come to life'. There are important feedback mechanisms between the soil system and the life it hosts. Most of the life within the soil is restricted to the three dimensional pore space that forms its habitat. This means that in order to move about through the pore network, organisms must be able to squeeze through the gaps which are present there. Fig. 2.2 shows testate amoeba located within the pore spaces of a soil and Fig. 2.3 shows an amoeba squeezing through a narrow pore space in search of bacteria on which to graze. Amoeba are in turn predated by other organisms such as nematodes. However, organisms at this scale are unable to move soil particles about much and so must work and live in the pore spaces which are present. Fig. 2.5 shows a nematode curling through the three dimensional pore space. Nematodes are considerably bigger than amoeba, and are also less able to deform their shapes to squeeze through narrow pores. This means that amoeba are able to access areas of the pore system that nematodes are not and so can hide in refugia, small pores inaccessible to nematodes, and so avoid being eaten.

As previously mentioned, the soil system is highly dynamic. This means that the pore network is constantly changing owing to shrinking and swelling upon wetting and drying, as well as freezing and thawing. This means that sections which were once unconnected can become connected as new cracks open up, and areas which were connected can become separated as pores close off. Another effect of the soil biota on the architecture of the soil system is that organisms can function to stabilise aggregates within the pore system. This can be done through the excretion of compounds which function to stick aggregates together, or by physically binding soil aggregates together or linking between them, as is the case with fungal hyphae (Fig. 2.4). These stabilisation effects can have beneficial impacts as they can function to reduce soil erosion.

Fig. 2.2: Testate amoeba located in the pore space of a soil. (KR)

Larger organisms, such as earthworms, are capable of moving soil particles around, and creating their own pore spaces through a process called bioturbation. These pores, which are created by living organisms are called "biopores". These pores are generally relatively large compared to other soil pores and so create zones of preferential flow of water, speeding water infiltration into the soil system and reducing water run-off after rainfall. The large changes that earthworms can cause in the soil system, due to the production of biopores, but also due to them moving soil in the vertical plane, has lead to them being classified as 'ecosystem engineers' as they are capable of 'engineering' their surrounding ecosystem.

Biopores are created by other organisms within the soil as well. Many biopores are made by plant roots which have sufficient penetrating power to force aggregates apart. When the plant dies and the root is decomposed, the biopore which it made remains and functions as an area of preferential flow for water in the soil, as well as for other organisms to move about within the soil.

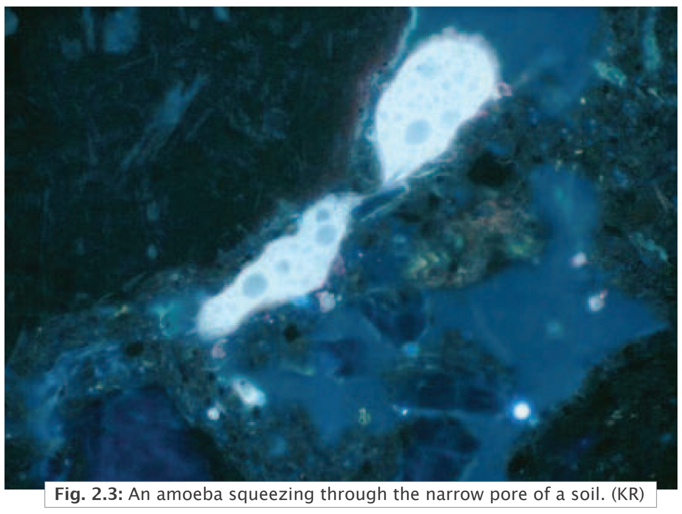


Fig. 2.3: An amoeba squeezing through the narrow pore of a soil. (KR)

Fig. 2.4: Fungal hyphae enmeshing and bridging the gap between two soil aggregates. (KR)

Fig. 2.5: A nematode curling though the pore space of a soil. (KR)

2.2 Soil Structure and the Soil Biota

Soil structure may be defined either as "the shape, size and spatial arrangement of individual soil particles and clusters of particles (aggregates)" or as "the combination of different types of pores with solid particles (aggregates)". Soil structure has generally been defined in the former way and measured in terms of aggregate characteristics. Changes in soil structure have been shown to affect plant growth. In fact, it is the shape, size distribution and arrangement of pores which affect many of the most important processes in soil that influence plant root growth and development. Their properties include storage and movement of water and gases, and solute movements, as well as providing the physical habitat for the soil biota as discussed previously (Section 2.1). For this reason measurements of pore space are increasingly being used to characterise soil structure.

Soil structural quality strongly depends on the organic matter content of the soil. Micromorphological techniques can give useful information concerning the interactions between organic matter and soil structure by means of the microscopic examination of soil thin sections. Fig. 2.6 shows the accumulation of organic matter distributed as coatings along the walls of elongated pores. These coatings on pore walls can effectively seal pores from the adjacent soil matrix, thus stabilizing the pore walls against the destructive forces of water and assuring the functionality of the pores. These favourable conditions, with respect to soil structure, are not permanent. In fact, when the organic matter is totally decomposed and mineralized it loses its effectiveness as a cementing substance leading to the collapse of pore walls and the closing of the pore. This is generally the first step of soil structure degradation.

These observations illustrate the possibility of correlations between soil porosity with some chemical and biochemical soil properties. For example, there has been found to be a correlation between the activity of soil enzymes and pore sizes of 30 to 200 mm equivalent pore diameter, implying that larger pore spaces support increased biochemical reactions, probably as a result of housing greater numbers of organisms. This relationship has also been found to hold in soils treated with compost.

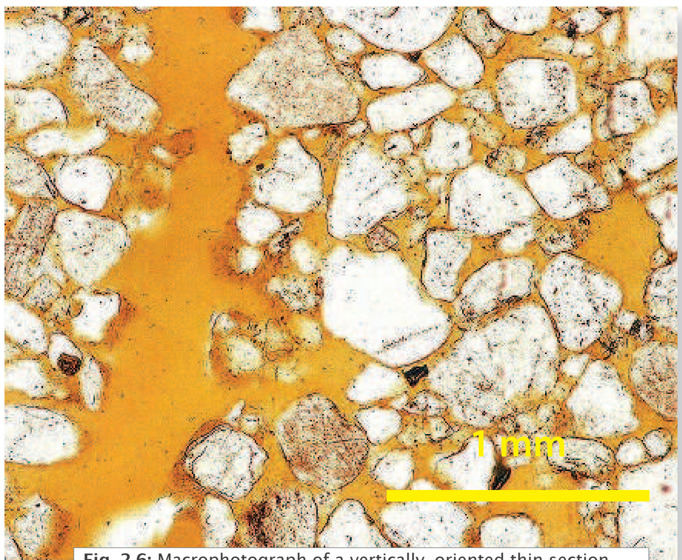


Fig. 2.6: Macrophotograph of a vertically-oriented thin section. Organic materials can be seen clearly as coatings on pore walls. Pores appear yellow. (EAF)

An example of a good pore continuity is shown in Fig. 2.7 which represents a subangular blocky structure. The soil aggregates are separated by elongated continuous pores (planes), are of different sizes and can be rather porous inside. From an agronomic point of view, this is the best type of soil structure because the continuity of elongated pores allows good water movement and easy root growth. Moreover, it is a rather stable soil structure. Therefore, the analysis of pore patterns allows the characterisation and prediction of flow processes in soils. In this picture, besides the continuity of elongated pores, it is possible to notice root remains and accumulation of organic materials (black colour) as a result of biological activity.

The relationships between soil porosity and biological activity are clearly represented in Fig. 2.8 where accumulations of organic materials are visible in the pore spaces. A more detailed examination of this material (Fig. 2.9) reveals the presence of faecal pellets of small insects and mites.

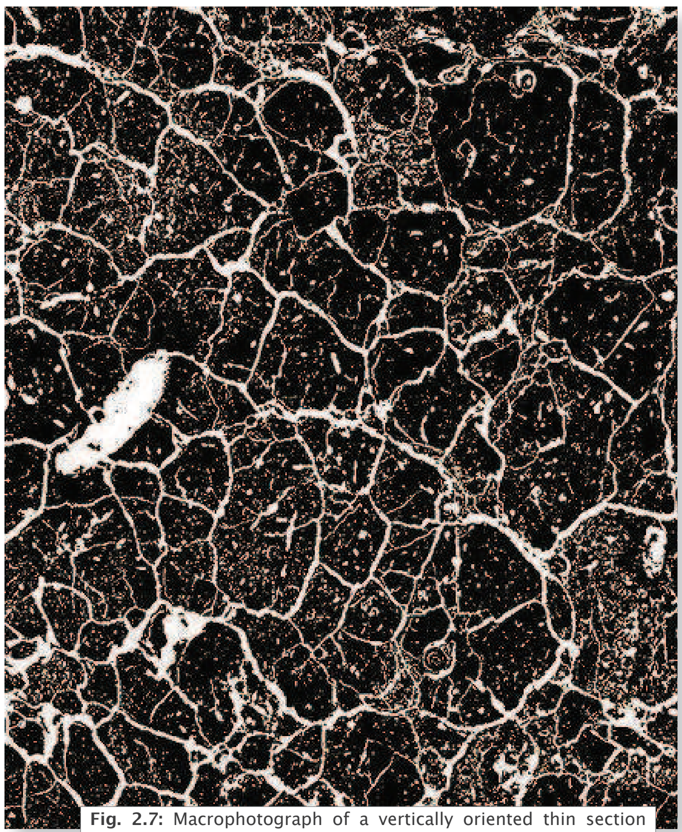


Fig. 2.7: Macrophotograph of a vertically oriented thin section showing an example of subangular blocky structure. The white areas represent the pores. Frame length 35 cm. (EAF)

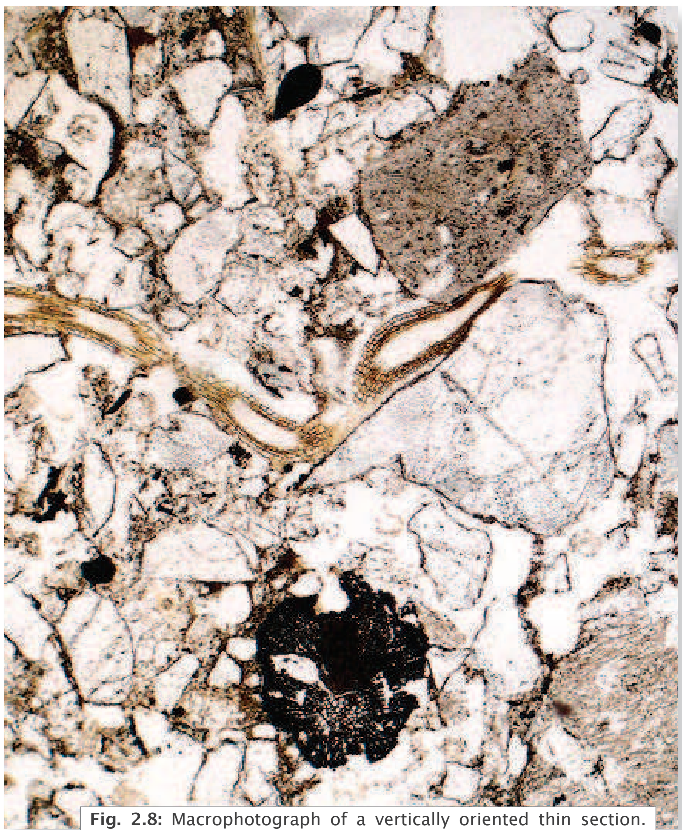


Fig. 2.8: Macrophotograph of a vertically oriented thin section. The white areas represent the pores. In the pore spaces fragments of root remains and small organic materials can be seen. Frame length 32 cm. (EAF)

Fig. 2.10 shows an example of pores formed by the activity of soil fauna. In this case a channel and chamber formed by earthworms can be observed.

Fig. 2.11 (next page) represents the opposite conditions with respect to Fig. 2.7. The soil material is very compact, there are no visible separated aggregates. The porosity is very low and represented by small pores isolated within the soil matrix. This type of structure represents a bad habitat for both plant development and for the soil biota in general and is common in degraded soil with a low content of organic matter.

The impact of soil biota on soil structure can be observed at field scale by the naked eye, especially when assessing the impact of large animals (i.e. macrofauna) such as earthworms. In fact, the potential for earthworms to improve soil aggregation and porosity were observed long ago by Gilbert White in 1777 and Charles Darwin in 1837. They recognised that earthworms promote the growth of vegetation by creating an intimate mixture of organic and mineral matter that aids in water retention and nutrient release and provides a medium suitable for root proliferation.

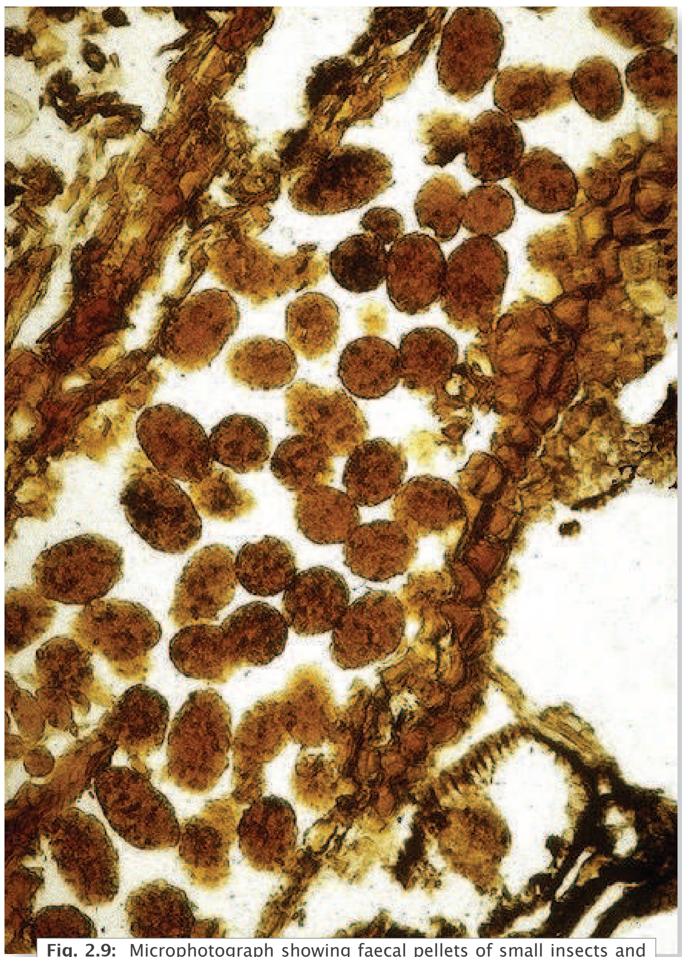


Fig. 2.9: Microphotograph showing faecal pellets of small insects and mites. The white areas represent the pores. Frame length 33 mm. (EAF)

Fig. 2.10: Microphotograph of vertically oriented thin section showing a channel and chamber formed by soil fauna. (EAF)

Soil pores:

A pore is a space within soil resulting from the arrangement of individual soil particles. The space may be totally or partially occupied by either air or water. Generally, three types of pores are recognised. The type and number of pores have a direct affect on soil properties.

- Micropores (<2 µm): Water contained in micropores is usually too strongly bound on to the surfaces of clay mineral for plants to use. However, the water in micropores is important in creating moist anaerobic conditions which are beneficial to certain types of microbes.
- Mesopores (50 µm – 2 µm): When the soil is regarded as being saturated after prolonged rainfall, it means that all the mesopores are full of water. Mesopores are important in an agricultural context as they store water for plants.
- Macropore (>50 µm): Macropores can be caused by soil cracking, gaps between soil aggregates, roots or burrowing creatures. Macropores play an important role in the rapid movement of water within the soil.

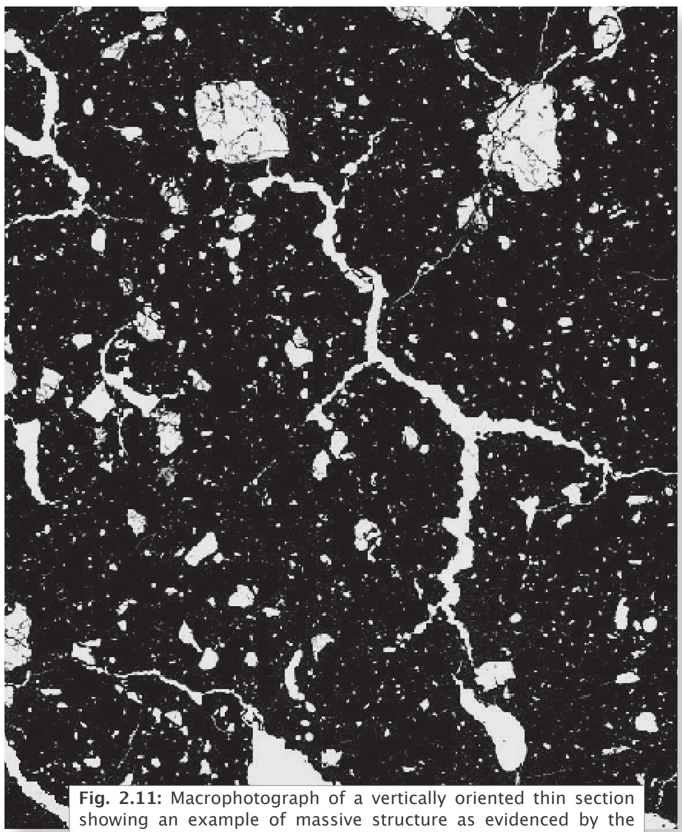


Fig. 2.11: Macrophotograph of a vertically oriented thin section showing an example of massive structure as evidenced by the relative lack of pore space and pore connectivity. The white areas represent the pores. Frame length 35 cm. (EAF)

They also recognised that deep-burrowing earthworms affect water movement in soil and aid in its drainage. Soil fauna, such as earthworms, enhance soil porosity by burrowing through the substrate and creating burrows, or by ingesting soil and excreting it as casts. Earthworms have to ingest and excrete large amounts of soils because of their low assimilation efficiency of nutrients from within the soil. Their actions on soil structure lead to the formation of large pores and casts (Fig. 2.12).

Large pores are usually in the form of tubular burrows (also known as galleries). However, during summer and winter time, some earthworm species decrease their activity (due to soil dryness) and enter a quiescent (inactive) stage in small chambers during these times and this can lead to the development of rounded pores, corresponding to aestivation chambers within the soil (see Section XIII).

Burrow space can represent up to 5% of pore volume in the soil and thus can have strong impacts on water and gas infiltration. The shape and orientation of the burrow networks are strongly dependent on the earthworm's ecological group (see Section XIII). For example, anecic species create and live in permanent and vertical (or close to vertical) burrows which are connected to the soil surface, and can extend up to 2-3 m in depth (depending on soil depth), although between 60 and 90 cm is more common. These burrows can persist long after the inhabitant has died, and can be a major conduit for soil drainage, particularly under heavy rainfall. This means that these burrows help minimise surface water run-off and the associated erosion. These burrows can also provide a preferential path for roots which find carbon and nitrogen in the burrow walls (Fig. 2.14). Endogeic species have a constantly changing temporary burrow system, which is horizontally or subhorizontally oriented, and which are refilled with their casts (as opposed to anecic species which generally excrete their casts at the soil surface). This horizontal burrowing in the top few centimetres of the soil increases overall porosity and drainage. The number of burrows can vary from 100 to 1400 m^{-2} depending on the soil type and the land use (meadow or crop site). However, it has been demonstrated that, perhaps surprisingly, there is no link between the number of earthworms and the number of burrows; for instance, under a cultivated area (e.g. maize crop) where the number of earthworms is low (20 individuals m^{-2}), the number of burrows could be as high as the burrow number observed under meadow despite a higher earthworm number (300 individual m^{-2}). This is due to the high burrowing activity of the few earthworms which are present in cultivated soil.

Concerning earthworm casts, these can be deposited on the soil profile which lead to a granular structure that increases water retention (Fig. 2.13). Casts which are deposited on the soil surface and become associated with organic matter residues and form "middens" (Figs. 2.15). These middens can increase soil surface roughness and may increase resistance to weathering and decrease soil erosion. Cast production may be very important; for instance, in temperate climates the annual production of casts on the soil surface can reach 30 T^{-1} ha^{-1} under meadow, and 240 T^{-1} ha^{-1} when casts within the soil are also included. This action over a time frame of five years can lead to the formation of a topsoil layer of between 5 and 25 cm thickness! In temperate conditions, the positive effects of earthworms on soil structure have been widely demonstrated, but in tropical conditions, where cast production can reach 500 T^{-1} ha^{-1}/year, some studies have demonstrated that earthworms of the species *Millsonia anomila* can actually have a compacting effect on soil structure.

Because earthworms impact on their environment physically, chemically, and microbiologically, they are considered to be "ecosystem engineers", as are ants and termites which can also dig burrow networks and strongly impact soil structure by the creation of ant hills and termites' nests. Furthermore, other fauna groups also act on soil structure, such as insect larva, woodlice (isopoda) and snails (gastropoda) for example, as well as microorganisms, but to a lesser extent. Nevertheless, the impact of soil fauna and plant roots on soil structure is mainly observed in the first 30 cm of the topsoil and leads to rounded aggregate shapes while physical impact (climatic or anthropic, such as tillage) tends to lead to angular shapes.

Agricultural management strongly impacts on soil structure. Therefore, long-term intensive arable cultivations can be associated with damage to soil structure. Conventional agricultural production systems have resulted in excessive erosion and soil degradation, and there is need to control and fight such degradation in order to maintain and increase the sustainability of agriculture. Agricultural management systems can play an important role in preventing soil degradation provided that appropriate management practices are adopted. Long-term field experiments in different types of soils have shown that alternative tillage systems, such as minimum tillage, ripper sub-soiling, etc., improve soil structural quality, whereas continuous conventional tillage leads to a decrease in soil organic matter content and associated decrease in aggregate stability, leading to increased formation of surface crusts, with increases in runoff and erosion risks.

Another consequence of the intensification of the agricultural systems is the increase of soil compaction which is an important factor responsible for environmental degradation. Soil compaction is caused by a combination of natural forces, which generally act internally, and by man-made forces related to the consequences of soil management practices. The latter forces are mainly those related to vehicle wheel traffic and tillage implements. This is because trends in agricultural engineering over the last few decades have resulted in machines of a greater size and weight. Therefore, soil compaction has become one of the most significant aspects of soil degradation, and problems of finding tyres, inflation pressures, etc., able to reduce soil compaction are far from being solved. It is, therefore, fundamental to evaluate and control the impact of agricultural management and fight the degradation caused by compaction in order to maintain and increase the sustainability of agriculture.

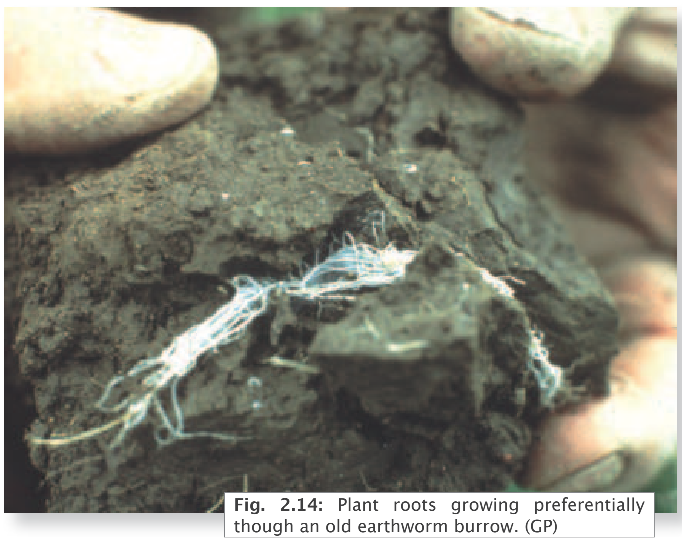


Fig. 2.14: Plant roots growing preferentially though an old earthworm burrow. (GP)

Fig. 2.15: Earthworm middens, showing one close up (**top**) and many distributed over the soil surface (**bottom**). (DC)

Fig. 2.12: Soil structure and porosity created by soil fauna. (BS)

Fig. 2.13: Granular structure caused by earthworm casts on the surface of a sandy soil. (MMK)

The impacts of improving soil structure:

The benefits of improving soil structure for the growth of plants, especially in an agricultural setting include:

- reduced risk of erosion due to greater soil aggregate strength and decreased overland flow;
- improved root penetration and access to soil moisture and nutrients;
- improved emergence of seedlings due to reduced crusting of the surface;
- greater water infiltration, retention and availability due to improved porosity.

2.3 Terrestrial Humus Forms: Ecological Relevance and Classification

Humus consists of partially decomposed organic matter in the soil, generally at or near the soil surface, and has been recognized for a long time as the seat of most biological and physico-chemical processes that are essential to soil development and the functioning of terrestrial ecosystems. This concept applies to every kind of soil where the upper part of which, also known as topsoil, has not been permanently disturbed by human activity (i.e. all non-tilled soils). At the end of 19th century, a scientist by the name of Müller put forward the basis of a multifaceted assessment of humus forms, embracing pedology, sylviculture, biology, geology and climate. More than half a century later this classification was built upon and expanded by Kubiëna who classified European soils based on the interactions between soil animals and vegetation as the driving force of soil development, with local geology and climate providing the context. However, the concept of humus forms as a driver of major processes which shape and stabilise ecosystems has emerged only recently, and has highlighted the need for a better and more universal assessment of the diagnostic characteristics of the various types of humus forms.

Three different humus forms, known as Mull, Moder and Mor (Fig. 2.16) can be viewed as the outcome of three different "strategies" of terrestrial ecosystems.

- Mull is characterised by an intense mixing of organic matter with mineral matter (i.e. as the result of earthworm activity). This results in a crumbly and nutrient-rich organo-mineral horizon.
- Moder is characterised by a less rapid transformation of litter by litter-dwelling animals and fungi, resulting in the accumulation of organic humus at or near the soil surface.
- Mor is characterised by the slow transformation and accumulation of undecayed plant debris, with a sharp, clearly defined transition from the humus to the mineral soil.

Mull, followed by Moder, then Mor, correspond to a scale of decreasing nutrient availability and colder conditions, resulting in decreasing biodiversity and activity moving from Mull to Mor. Animals, microbes and plants are involved in positive (building forces) and negative (stabilising forces) feed-back relationships, most of them taking place in the humus profile. For example, with a forest mull, if the parent rock is rich in easily weathered minerals and the climate is mesic (i.e. is not too cold and not too dry), then plant growth is rapid and so site quality and productivity are said to be high allowing more exacting plants to grow (i.e. annually flowering plants, with nutrient-rich and lignin-poor foliage). In turn, the litter (i.e dead material from trees and forest vegetation) is also nutrient-rich and so favours microbes which are able to rapidly utilise the available nutrients, such as bacteria, as well as animals such as earthworms, the activity of which contributes to favour tree growth and diverse vegetation, which is typical of multi-layered forests.

The same interactions between local geology, climate and biology explain why Mor, on the other hand, is poorer in microbial, faunal and plant species and characterises less productive but more conservative ecosystems. Put in other terms, Mull humus can be considered a "waster" (the cicada from Aesop's fable), while Mor can be considered a "hoarder" (the ant from Aesop's fable), but each of them being the most efficient use of resources as controlled by geology and climate. This shows the indicator value of humus forms whereby recognition of the humus form present can provide information about the local geology and climate of a given ecosystem.

Based on the knowledge accumulated regarding the relationships between morphological, biological and physico-chemical features of humus forms, several attempts have been made to classify humus on the basis of characteristics discernible to the naked eye directly in the field, and to derive from them properties at the ecosystem level (known as site quality assessment).

Benefits of soil organic matter and humus:

The mineralization processes that convert organic matter to the relatively stable substance that is humus, feeds the soil population of microorganisms and other creatures, thus maintaining high and healthy levels of soil biodiversity.

Humus is a colloidal substance that increases the soil's ability to store nutrients and reduce their leaching away by rain or irrigation.

Humus can hold the equivalent of 80–90% of its weight in moisture sustaining the soil's capacity to withstand drought conditions and floods.

During the humification process, bacteria and fungi secrete sticky gums which hold soil particles together. This gives the soil a good structure and allows greater aeration of the soil.

Toxic substances such as heavy metals can be bound to humus and prevented from entering the wider ecosystem.

The dark colour of humus (usually black or dark brown) helps warm up cold soils in the spring.

Fig. 2.16: The five main type of terrestrial humus forms which prevail in temperate ecosystems (bar = 10 cm).

Mull. (JFP)

Moder. (GSa)

Mor. (JFP)

Amphi. (GSa)

Tangel. (GSa)

The concept of humus forms and diagnostic horizons has been explicitly included in the French 'Référentiel Pédologique'. Since that time, the need for a common classification system at the European level, which could be compatible with the World Reference Base for Soil Resources has become increasingly recognised.

A network of European humus researchers was founded in Trento (Italy) in 2003, gathering together 25 specialists from eight different European countries. Since this date, the Humus Group has met each year, in different countries, to exchange knowledge, discover humus forms in new ecological conditions and to progress in harmonising humus form concepts. New terrestrial humus forms have been identified, such as Amphi, others have been re-described, such as Mor and Tangel (Fig. 2.16), and soil organisms have come to be recognised as the main agents of soil structure. The widest possible array of humus forms has been covered, from southern to northern Europe, from seashore to high mountains, and from dry to damp environments.

Figure 2.17 shows a schematic of one concept which has come to be accepted within the humus research community, being the concept of Mull as an attractor for terrestrial humus forms in forest environments, and its deviation under harsher environmental conditions.

On calcareous substrates, Amphi can exist in two states, showing both characters of Mull (crumbly organo-mineral horizon) and Moder (accumulated organic humus), due to a seasonal alternation between phases of high and low biological activity in strongly seasonal Alpine and Mediterranean environments.

Tangel, still poorly understood from a biological point of view, expresses particular characteristics at high elevation and on hard calcareous rocks, where litter is out of reach of soil decomposer activity for most of the year and invertebrates cannot dig through the parent rock.

The main morphological and biological characteristics of Tangel, Amphi, Mull, Moder and Mor are summarised in Fig. 2.18, which shows that the variety of humus forms known in Europe can be ascribed to several possible combinations of annelid oligochetes (earthworms, enchytraeids), the activity of which is of paramount importance for the building of soil structure.

Compost:

Compost is the product that results from the breakdown of organic materials, largely through aerobic decomposition. Commonly used as a way of disposing of garden waste, compost is rich in humus and humic acids and its application to the land is beneficial both as a soil conditioner and as a fertilizer. For a compost heap to work effectively, the correct ratios of carbon, nitrogen, air and water must be present to maintain the decomposition process.

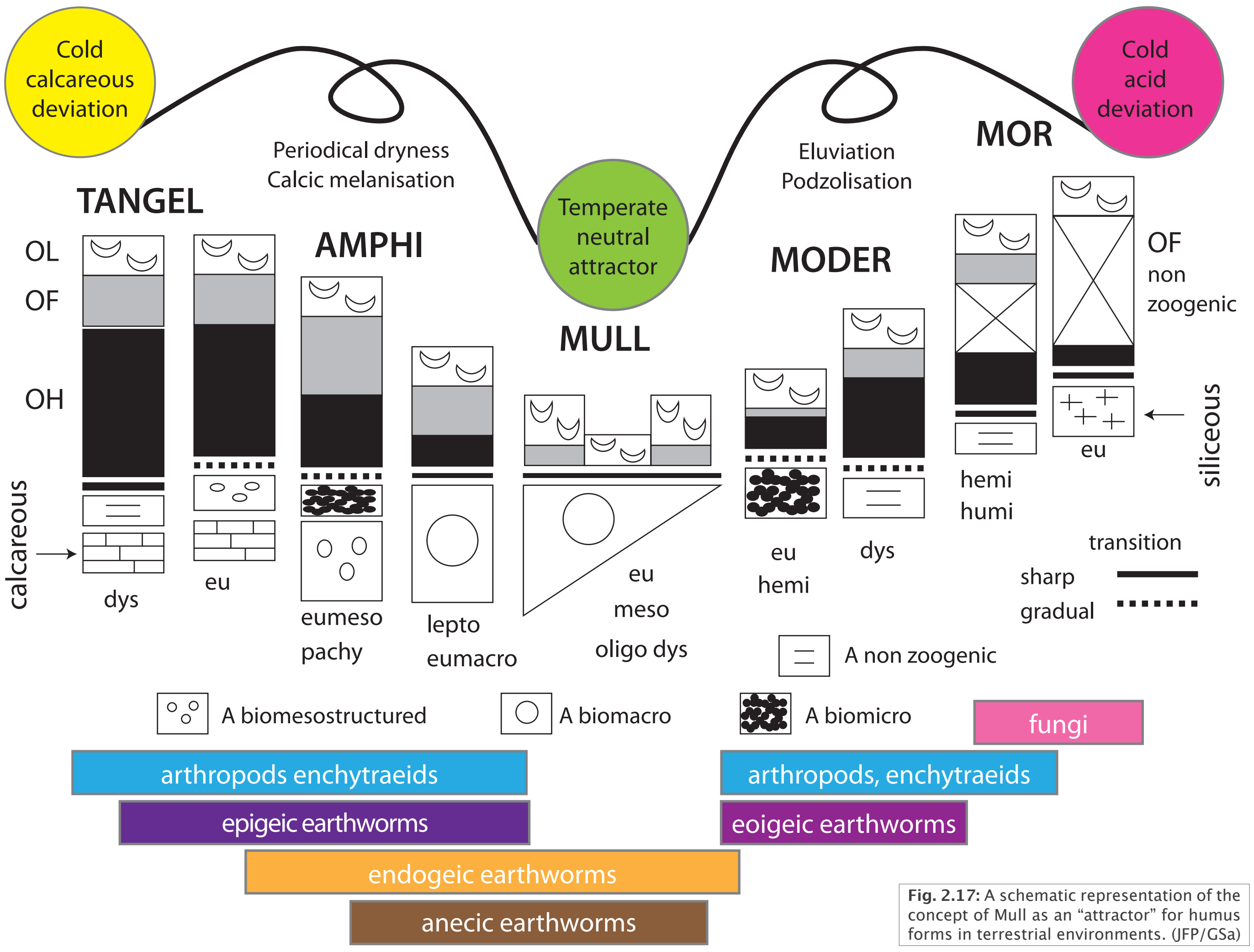


Fig. 2.17: A schematic representation of the concept of Mull as an "attractor" for humus forms in terrestrial environments. (JFP/GSa)

Further taxonomic distinctions can be made in the classification of humus. For example, undecayed litter, fragmented litter, humified litter and the underlying mixture of organic and mineral matter are currently called OL, OF, OH and A horizons respectively. Prefixes such as 'eu' (meaning normal or perfect) or 'dys' (meaning atypical or degraded) are used to characterise humus forms at a subordinate level of classification once characteristics of the main humus forms have been defined. The size of aggregates (invertebrate faeces) is indicated by prefixes 'micro' (<1 mm), 'meso' (1-4 mm) and 'macro' (>4 mm). The presence or absence of traces of faunal activity in horizons is described by suffixes 'zo' and 'noz', respectively. This flexible classification of horizons and profiles allows a wide variety of humus forms to be described and labelled, even when new to science.

As well as being needed by those people who want to describe the topsoil, the classification of humus forms may also help with diagnosis of ecosystems health. The Humus Index, obtained by scaling humus forms of acid soils from Mull to Mor (see upper row of Figure 2.16), has proven to be correlated with soil physico-chemical variables, stand properties and floristic composition of various temperate forest ecosystems. Furthermore, humus forms have been shown to be good indicators of present and past climate conditions and so could be used for predicting future trends of global climate change (Fig. 2.19). This further highlights the need for more expert tools based on a finer characterisation of humus forms. This would enable humus forms to be used as a diagnostic tool, both of ecosystem health and for modelling the possible effects of climate change.

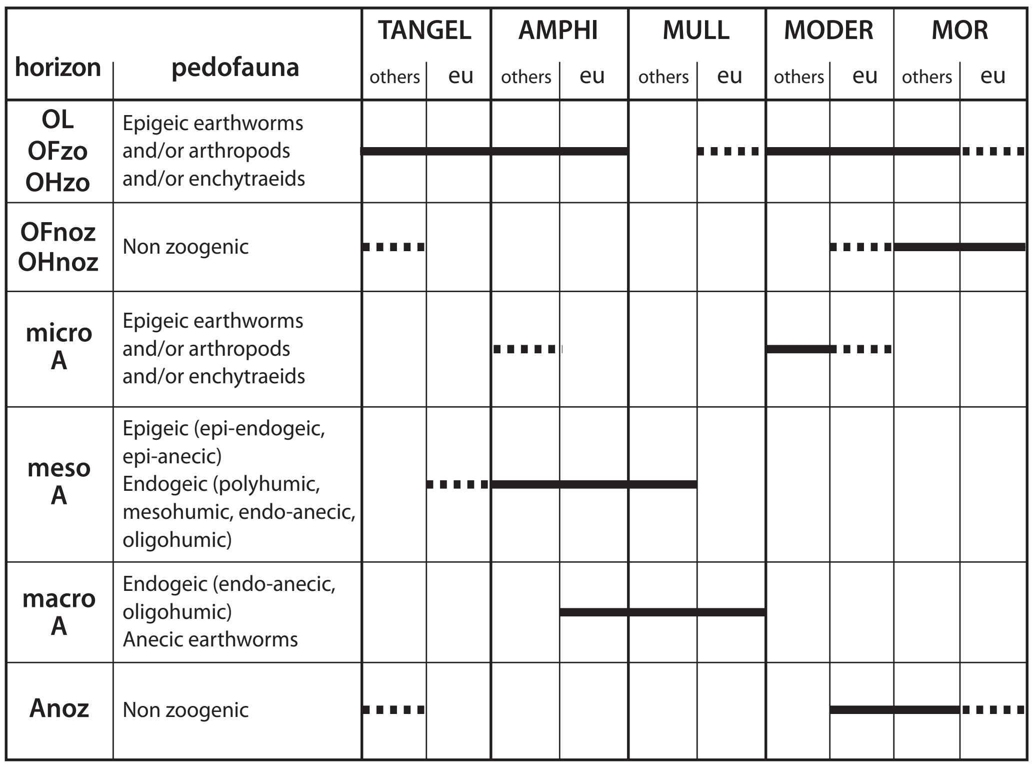


Fig. 2.18. Morphological and biological characters of the five main terrestrial humus forms prevailing in Europe. (JFP/GSa)

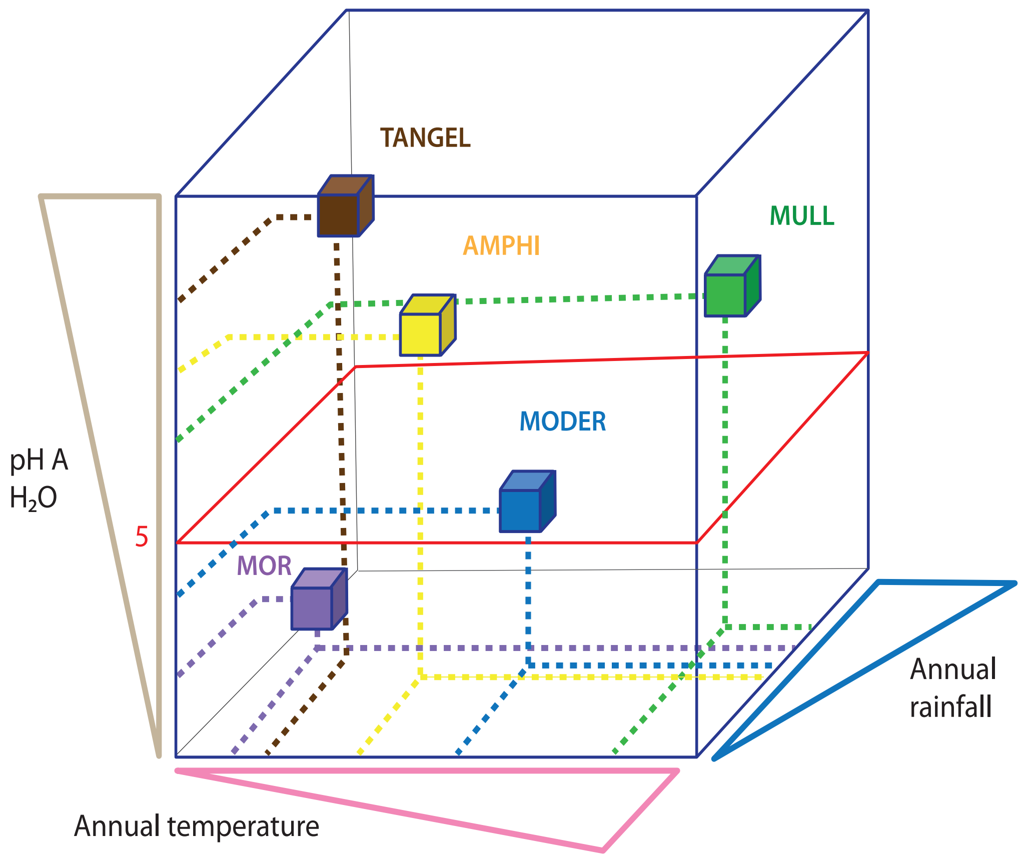


Fig. 2.19: The five main terrestrial humus forms in a 3D frame of environmental conditions prevailing in Europe. Each axis represents the scale of different climatic variables. (JFP/GSa)

2.4 The Rhizosphere

Definition and extension

The term "rhizosphere" was introduced 1904 by the German soil microbiologist Hiltner and defined as "soil influenced by (living) roots". This root influence decreases with increasing distance from the root surface leading to physicochemical and biological gradients between the rhizosphere and the so-called bulk soil. Because of low carbon availability and relatively slow diffusion of nutrients from the plant roots into the surrounding soil, the bulk soil is generally a relatively poor environment with reduced biological activity when compared to the rhizosphere. By contrast, due to the process of rhizodeposition described below, the rhizosphere is often characterised by high biological activity and high nutrient availability.

Depending on soil texture and structure, plant species, and other parameters such as soil moisture content, direct effects of growing roots on most soil properties can be observed at a distance of just a few micrometres up to about 7 mm from the surface of an active root segment. However, rhizosphere effects may also reach beyond this range, up to a scale of several centimetres in some instances, especially when considering highly mobile compounds such as water or CO_2. Moreover, this range can be further increased when it is explored by the fungal hyphae extending from mycorrhizal root segments, known as the "mycorrhizosphere" (Fig. 2.20).

The inner boundary of the rhizosphere is not well defined. Considering the movement of water, nutrients or endophytic microorganisms within the roots, between root cell walls for example, the inner boundary is inadequately represented by the outer surface of the root, as depicted in most rhizosphere models. It has therefore been suggested that it is wiser to include the root as a whole.

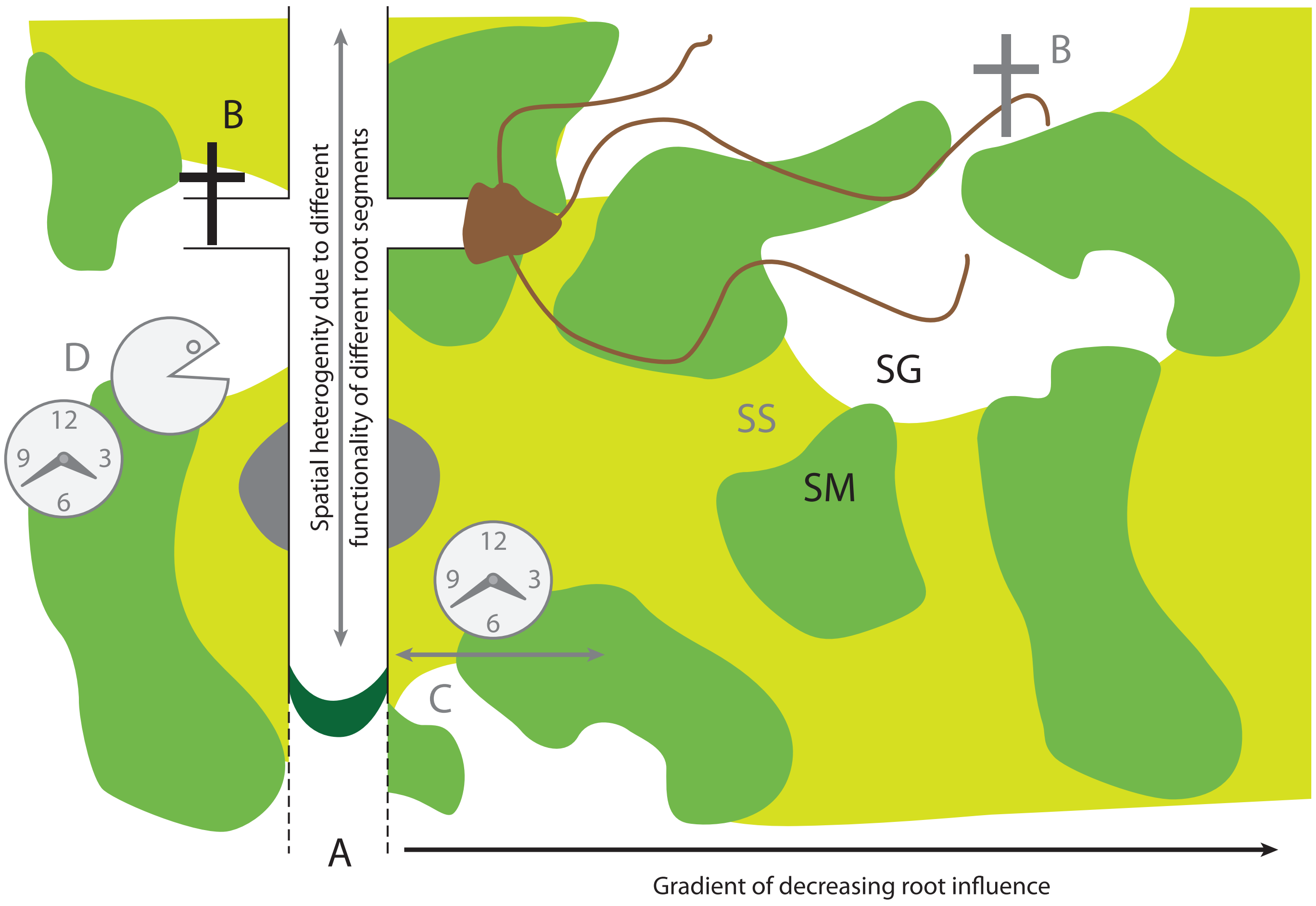


Fig. 2.21: A schematic representation of the rhizosphere as a 3-phase system with soil solid matter phase (SM), soil solution phase (SS), and soil gas phase (SG). Spatial heterogeneity along and perpendicular to root growth added by a developing root system is emphasised and is overlaid by temporal variability: (A) root growth, (B) turnover of roots and fungal hyphae, (C) diurnal or seasonal changes in the activity of roots (i.e. exudation, uptake), or (D) associated organisms. From Luster *et al.* 2009.

Important processes in the rhizosphere

Soil is a complex three-phase system as described in Fig. 2.21, with varying degrees of spatial and temporal heterogeneity of physical and chemical properties. Soil fauna, microorganisms and growing plant roots are the major causes of differences both spatially and over time.

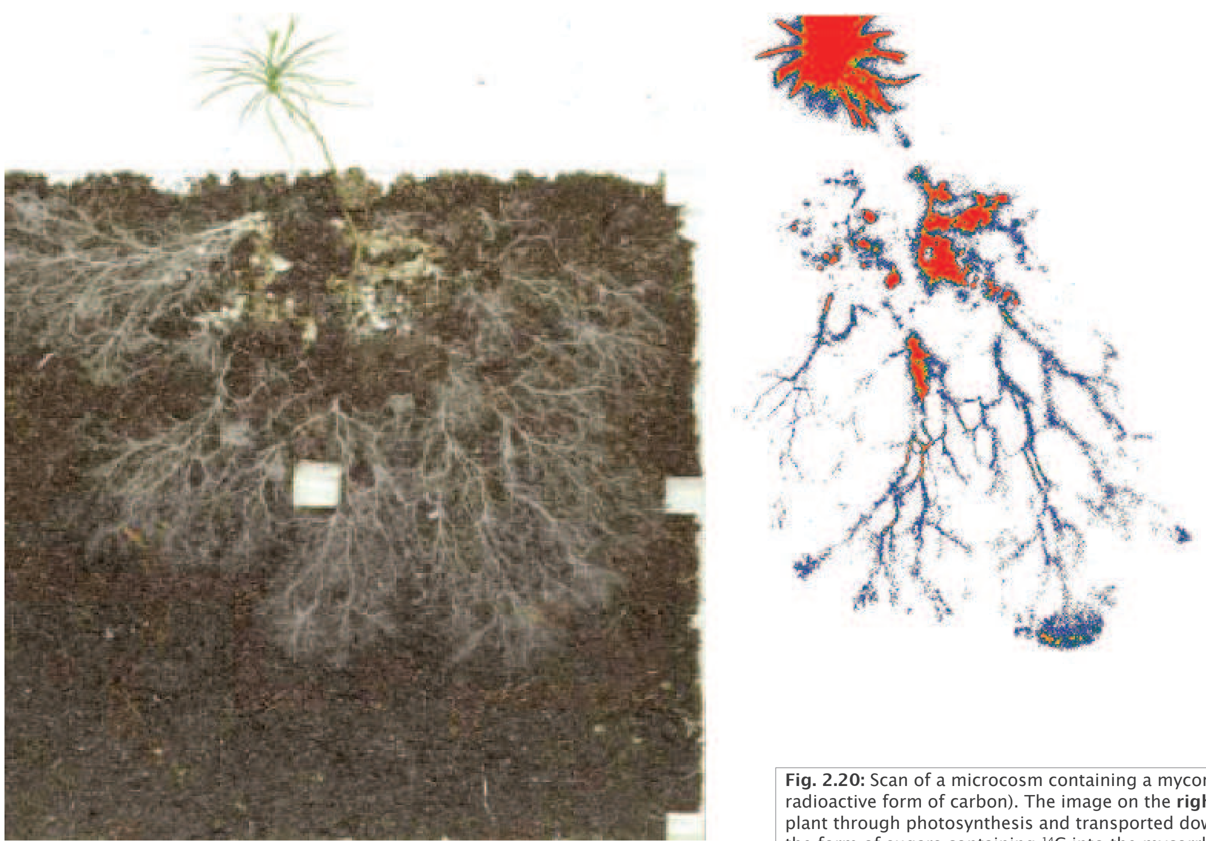
Apart from the physical consequences of root penetration, water and nutrient uptake by roots on the one hand, and the release of organic carbon by roots on the other hand, are the two major processes most affecting soil properties near plant roots.

Plant water uptake leads to gradients in soil moisture. This, combined with nutrient uptake, causes chemical gradients in the soil, both within the solid and the solution phases. Perhaps the most influential process is the root release of photosynthetically fixed carbon into the soil. This process can be induced to increase the availability of nutrients, to reduce the toxicity of soil constituents, to attract and feed beneficial microorganisms or to deter pathogens. For example, plants have been shown to be able to accelerate the exudation of low-molecular weight organic acid anions in order to increase the solubility of phosphorus or to form chemical bonds with aluminium ions in the soil solution and thereby reduce their toxicity (Fig. 2.22).

Root growth is also accompanied by sloughing-off of living cells, senescence, cell wounding and leakage from plant cells whereby a passive release of diverse components from the plant root into the soil occurs. The entire suite of root-released components accumulating in the rhizosphere is termed "rhizodeposition". Furthermore, plant roots and mycorrhizal fungi can release gases such as carbon dioxide or oxygen into the soil. While the former is generally a rather passive mechanism for venting mineralised carbon, the latter can be a means to create a well-aerated environment for wetland plants.

As well as radial gradients extending from roots, there is an additional longitudinal heterogeneity along the root growth direction (Fig. 2.21). Different root segments differ in their functionality in terms of uptake (e.g. water or nutrients) and/or rhizodeposition. For example, hot spots of rhizodeposition occur at root hairs and the apical zone (i.e. the growing root tip). Furthermore, there is a temporal variation in root influence due to daily, seasonal or age related changes in the physiological activity of root segments, however these effects are relatively poorly documented.

After a root's death, the rhizosphere can transform into soil that still is different from bulk soil. Dead parts of the root system first become local sources of organic matter, and after their degradation, macropores, which are left behind after the dead root is decomposed. These can have a strong impact on the soil's transport properties. Together, rhizodeposition and root turnover account for up to 40% of the total carbon input into soil.



Roots:

In vascular plants, the root is the organ of a plant that typically lies below the surface of the soil.

Roots can also grow above the ground (aerial) or extending out of water (aerating).

The first root that comes from a plant is called the radicle.

Roots will generally grow in any direction where the correct balance of air, nutrients and water exists to meet the plant's needs. Roots will not grow in dry soil.

The deepest roots are generally found in deserts and temperate coniferous forests; the shallowest in tundra, boreal forests and temperate grasslands.

The deepest observed living root, at least 60 m below the ground surface, was observed during the excavation of an open-pit mine in Arizona, USA.

The majority of roots are found relatively close to the surface where nutrient availability and aeration are more favourable for growth.

Rooting depth may be physically restricted by rock or compacted soil near to the surface, or by anaerobic soil conditions.

Fig. 2.20: Scan of a microcosm containing a mycorrhizal pine seedling labelled with 14CO_2 (^{14}C is a radioactive form of carbon). The image on the **right** shows where the carbon has been fixed by the plant through photosynthesis and transported down into the roots. The transport of the carbon, in the form of sugars containing ^{14}C into the mycorrhizosphere is clearly visible (from Finlay 2006). Images reproduced with permission from New Phyologist.

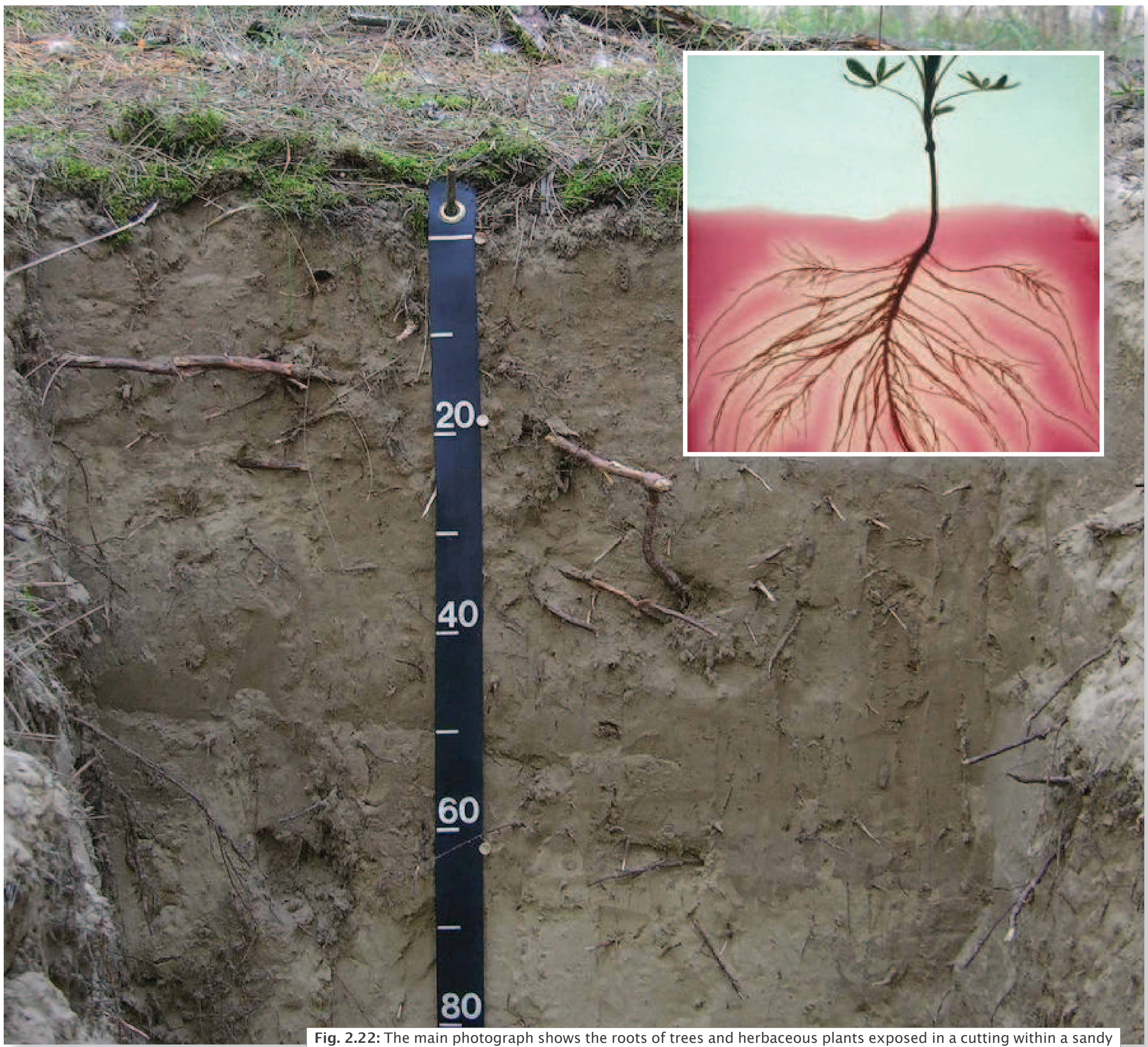


Fig. 2.22: The main photograph shows the roots of trees and herbaceous plants exposed in a cutting within a sandy soil in Hungary. Soil texture and structure are important controls on the development of roots. (EM); The inset shows root exudates binding with aluminium ions in the rhizosphere of *Lupinus luteus*, thereby reducing their toxicity, as visualised as bleaching of the red Al-aluminon complex. (from Neumann 2006)

Biodiversity in the rhizosphere

As a consequence of rhizodeposition, a particularly important characteristic of the rhizosphere is the high availability of easily degradable carbon. This fuels microbial activity, which in the rhizosphere can be up to 50 times higher than in the bulk soil, and forms the basis for a complex food web linking bacteria, fungi, nematodes, protozoa, algae and microarthropods. Many members of this community do not affect the plant, while others exert either deleterious or beneficial effects. Microorganisms that adversely affect plant growth and health include pathogenic fungi or bacterial, as well as nematodes. Beneficial organisms include nitrogen-fixing bacteria, endo- and ectomycorrhizal fungi, and plant growth-promoting rhizobacteria and fungi. The microbial community also actively participates in defining the composition of rhizosphere carbon by degrading and secreting complex organic compounds, and by lysing plant cells.

The number and diversity of organisms depends on complex feedback loops between the quantity and quality of the rhizodeposits, the interactions within the food web and on physico-chemical soil properties such as basic nutrient availability, soil structure and environmental parameters including soil moisture and temperature. An example of such feedback loops is illustrated in Fig. 2.23.

The ecological importance of the rhizosphere

Because of the many and complex interactions between soil, plant root, microbes and soil fauna, the rhizosphere generally is characterised by properties that are essential for plant nutrition and ecosystem functioning. Due to the high biological activity, the rhizosphere is often a hot spot of biogeochemical transformations and related element fluxes. Therefore, this compartment should receive special attention when studying element cycling and related climatic effects. Furthermore, the rhizosphere volume exhibits a greater resistance to external, mechanical stress such as erosion or flooding than soil not associated with roots.

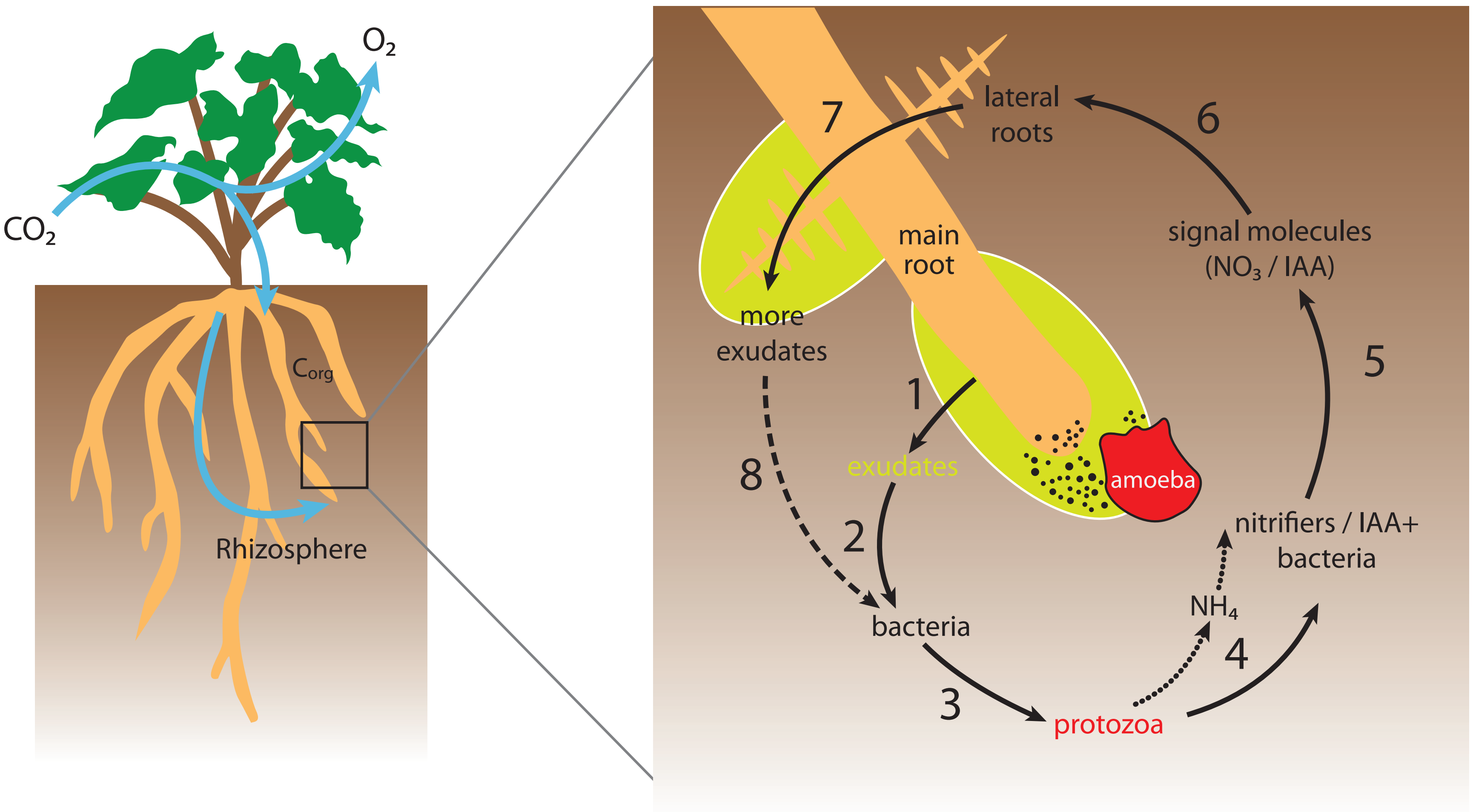


Fig. 2.23: A conceptual model of feedback loops within a rhizosphere involving different members of the soil food web. Root exudation (1) stimulates growth of a diverse bacterial community (2) and subsequently of bacterial-feeders such as protozoa (3). Ammonia is excreted by protozoa and selective grazing favours nitrifiers and indole-3-acetic acid (IAA+) producing bacteria (4). The release of signal molecules (5), such as NO_3^- and IAA, induces lateral root growth (6), leading to release of more exudates (7), subsequent bacterial growth (8), etc. From Bonkowski 2004, reproduced with permission from New Phyologist

3.1 Forest

Forests are species-rich terrestrial ecosystems, and occur in a huge variety of climatic, geographic, ecological and socio-economic conditions (Fig. 3.1). Europe has a total area of forests and other wooded land of around 177 million hectares, accounting for about 42% of its land area (Fig. 3.4). Ecologically, EU forests belong to numerous vegetation zones, ranging from coastal plains to the Alpine zone.

Human well-being is highly dependent on the world's forests, which provide a wide range of benefits and ecosystem services. They provide fuel, building materials, foods and the raw material for many medicines. They play an important role in the global climate and carbon cycle, water balance and provide a range of habitats for life, both above and below ground. They can help mitigate natural disasters such as floods, droughts, landslides and avalanches. Forests are also an important resource for economic welfare and rural development in local communities. In Europe, they provide employment for approximately 4.3 million people in forestry and forest based enterprises. Furthermore, the forests of Europe are a large reserve of carbon with 53 gigatonnes of carbon sequestered in forest biomass and deadwood.

Forest soils

Soil formation is affected by climate, as well as the local geology and vegetation (see Section 4.2). Forest soils vary as widely as the vegetation that covers them; they may be shallow, deep, rich or poor. The tree cover exerts a significant influence on the soil building process. Tree roots grow down and break up the bedrock, and fallen leaves contribute organic matter to the soil. The canopy cover softens heavy rainfalls, and the roots provide a support structure within the soil, two factors that help prevent soil erosion.

The type of forest also has an influence:

In temperate forests, over 70% of the biomass produced (including leaves, needles, twigs, and other organic material) falls to the ground after each growing season (Fig. 3.2). The material is then decomposed, generally by fungi, but also by some bacteria, allowing the nutrients to be returned to the soil where they are re-used by other plants and trees. This is a part of the carbon cycle which is discussed in more depth in Section 5.1.3. For this reason, the soils found in temperate deciduous forests are generally relatively rich owing to the large annual influx of organic matter.

In coniferous forests, the litter layer is made up of tough, dry needles and fallen twigs. This layer does not decompose so easily, and so often remains on the ground for many years. Soils under coniferous forests tend to be poorer and more acidic than those under broadleaves.

The poorest forest soils are found in tropical rainforests because the high level of rainfall leaches the nutrients from the soil.

All forest soils tend to differ from agricultural soil types because the soil formation is greatly influenced by the forest vegetation as well as the type and number of organisms that live in and on the soil. Forest soils are generally more acidic, have well developed organic layers and a much higher organic content. While the organic matter content of soil developed under grassland vegetation is generally incorporated into the rooting zone, forest soils contain a large amount of organic matter that accumulates on the soil surface which is broken down over time to form humus (see Section 2.3). Forest soils also take longer to form than agricultural soils: an average of about 1,000 years to form 25 mm of soil compared with an average of about 500 years for the same amount under agricultural conditions.

Fig. 3.2: Fallen leaves provide a large annual input of organic material into the soil of deciduous forests around the world. (ASM)

Fig. 3.1: A Boreal Forest in Sweden. (TDH)

One of the biggest differences between forest and agricultural soils is that forest soils are relatively undisturbed, having relatively high levels of lignin and other recalcitrant materials in the soils from fallen leaves and branches, and so favouring fungi over bacteria. This is because mechanical disturbance events such as tilling, which often break up fungal hyphae networks in agricultural systems, do not occur in forest environments.

In undisturbed forest floors there may be literally thousands of kilometres of hyphal filaments per gram of leaf litter and several kilometres of fungal hyphae even in the mineral fraction of forest soils. The mycelial component of topsoil within a typical Douglas fir forest in the Pacific Northwest (USA) may approach 10% of the total soil biomass. Even this estimate may be low, not taking into account the mass of the endomycorrhizae and the many other yeast-like fungi that thrive in the topsoil.

The role of fungi

Fungi are particularly important in forest soils because they are capable of breaking down substances such as wood which other microorganisms are not. Although many different types of microbe (including bacteria, fungi and actinomycetes) can break down cellulose and other less recalcitrant molecules, only certain types of fungi are capable of completely degrading lignin, a natural polymer that is found in the cell walls of woody plants that gives wood its strength. Without the brown rot fungi, which break down cellulose (and are so-called because the lignin remains intact so the wood keeps its brown colour), and especially the white rot fungi, which degrade lignin by producing oxidising enzymes that are released from their hyphae, old plant material would not decay and the soil nutrients would be locked into an ever accumulating mass of undegradable biomass.

Another very important role played by fungi in the forest is their role as symbionts with trees (and other plants). Known as mycorrhizal fungi (from "myco"= relating to fungi and "rhizal"= roots), these organisms form a mutually dependent, beneficial relationship with the roots of the host plants. This role is so important that around 80% of all terrestrial plant species are associated with some species of mycorrhizal fungi. In exchange for sharing nutrients produced by the host plant, the fungus increases the absorbing surface of the host's roots, improving its ability to absorb minerals and giving it a higher tolerance to drought and other extreme conditions.

Actinomycetes and symbiotic nitrogen fixation

Several important forest plant species are known to develop nodules when their root hairs are invaded by soil actinomycetes of the genus *Frankia*, and thanks to these symbionts they can then fix nitrogen. Among the genus interested by this process are *Alnus*, *Elaegnus*, *Ceanothus*, *Coriaria*, *Myrica*. It has been estimated that, on a worldwide basis, the amount of nitrogen fixed thanks to this process may even exceed the quantity of nitrogen fixed by legume crops!

Due to their nitrogen-fixing ability, some tree/actinomycetes associations act as pioneer plants, colonising poor, infertile, or recently formed soils.

Fig. 3.3: A magnified image of *streptomyces*, an actinomycete that as well as fixing nitrogen is one of the main organisms responsible for giving soil its earthy smell. (GC)

Mycorrhizal fungi are divided into four main groups, two of which are common in forest soils: – the ectomycorrhizal fungi which form a mat of tissue around the plant root, growing between its cells but not crossing the cell walls, and the endomycorrhizal fungi whose hyphae actually enter the plant's root cells. It is now recognised that a forest's health is directly related to the presence, abundance, and variety of fungi within the soil owing to their ability to break down recalcitrant compounds and also particularly due to the mycorrhizal associations that they form with trees.

Some mycorrhizal fungi are not only useful to trees, but are also sought after and valued by both animals and people as food sources. One of the most famous (and expensive) is the truffle, the fruiting body of a group of ectomycorrhizal fungi mostly from the genus *Tuber*. There are many species, the most well known being the white truffle (*Tuber magnatum*) from Italy and the French black truffle (*Tuber melanosporum*). Varying in size from a few grams to over a kilo, truffles can be found buried between the leaf litter and the soil near a host tree. Traditionally a truffle hog (sow) was used to detect the hidden delicacy, but because of their tendency to eat the truffles once discovered, trained dogs are now generally used instead. Cultivation is possible but difficult. One of the most successful methods is to plant seedlings near a known host tree and then to transplant them when they become infected with the fungus. This takes time so many truffles are still harvested in the wild, which accounts, at least in part, for their expense.

Record-breaking pest

Not all fungi are symbiotic to trees. Some fungi are pathogens or parasites, which live off and harm, or even eventually kill their hosts. One such genus is *Armillaria*, commonly referred to as "honey fungus" because of the honey colour of the fruiting bodies (Fig. 3.5). This well-known garden pest is difficult to eradicate as there are no effective chemical controls for it. The edible, mushroom-like fruit bodies only appear when the host tree is already dead or dying, while the black rhizomorphs (referred to as "bootlaces" because of their appearance) gradually spread out from the site in search of the next victim. Its high destructiveness comes from the fact that, unlike most parasites, it does not need to moderate its growth in order to avoid killing its host, since it will continue to thrive on the dead material. In an undisturbed forest, it can therefore spread a considerable distance. In the 1990s a survey in Oregon revealed a colony of *Armillaria ostoyae* spreading over an area of more than 890 hectares and estimated to be 1,500-2,400 years old. All cells were genetically identical, meaning that all of the fungal hyphae had grown out of one spore, and therefore making this both the oldest and the largest living soil organism in the world!

Fig. 3.5: Fruiting bodies of *Amarillaria ostoyae* (AR)

Deadwood

Deadwood is an important constituent of the forest ecosystem. Perhaps surprisingly, dead and dying trees in a forest are not necessarily signs of a sick environment, but can help contribute to a forest's wellbeing. The evidence suggests that reasonable levels of dead trees are no danger for the forest, and that they may shelter a significant group of parasitoids and predators that can control the populations of pests.

Up to a third of the species living in European forests depend on veteran trees and deadwood for their survival. As the deadwood progresses through various stages of decay until its ultimate incorporation back into the soil, the fallen tree/soil interface offers a relatively cool, moist habitat for animals and a substrate for microbial and root activity. This interface is particularly important for insects and fungi, many of which spend at least part of their life cycle in the soil, as well as lichen, all of which play an important role in recycling nutrients back into the soil. Deadwood also provides germination spots for small seeds, regulates water flow, contributes to the nutrient cycle and helps to build the soil. It plays a key role for sustaining forest productivity and provides ecosystem services such as helping to stabilise forests and storing carbon.

Despite this key role in the forest ecosystem, deadwood levels are critically low in many European forests because many management practices have often focused on removal, either for fuel or because of belief that it is harmful (i.e. a disease or fire risk). Awareness of its importance is gradually increasing, however, and deadwood is now accepted as one of the pan-European indicators for sustainable forest management adopted by the Ministerial Conference on the Protection of Forests in Europe (MCPFE; now known as Forest Europe) in Vienna in 2002, and measures are now being taken to encourage deadwood accumulation owing to its recognised importance in forest ecosystem health.

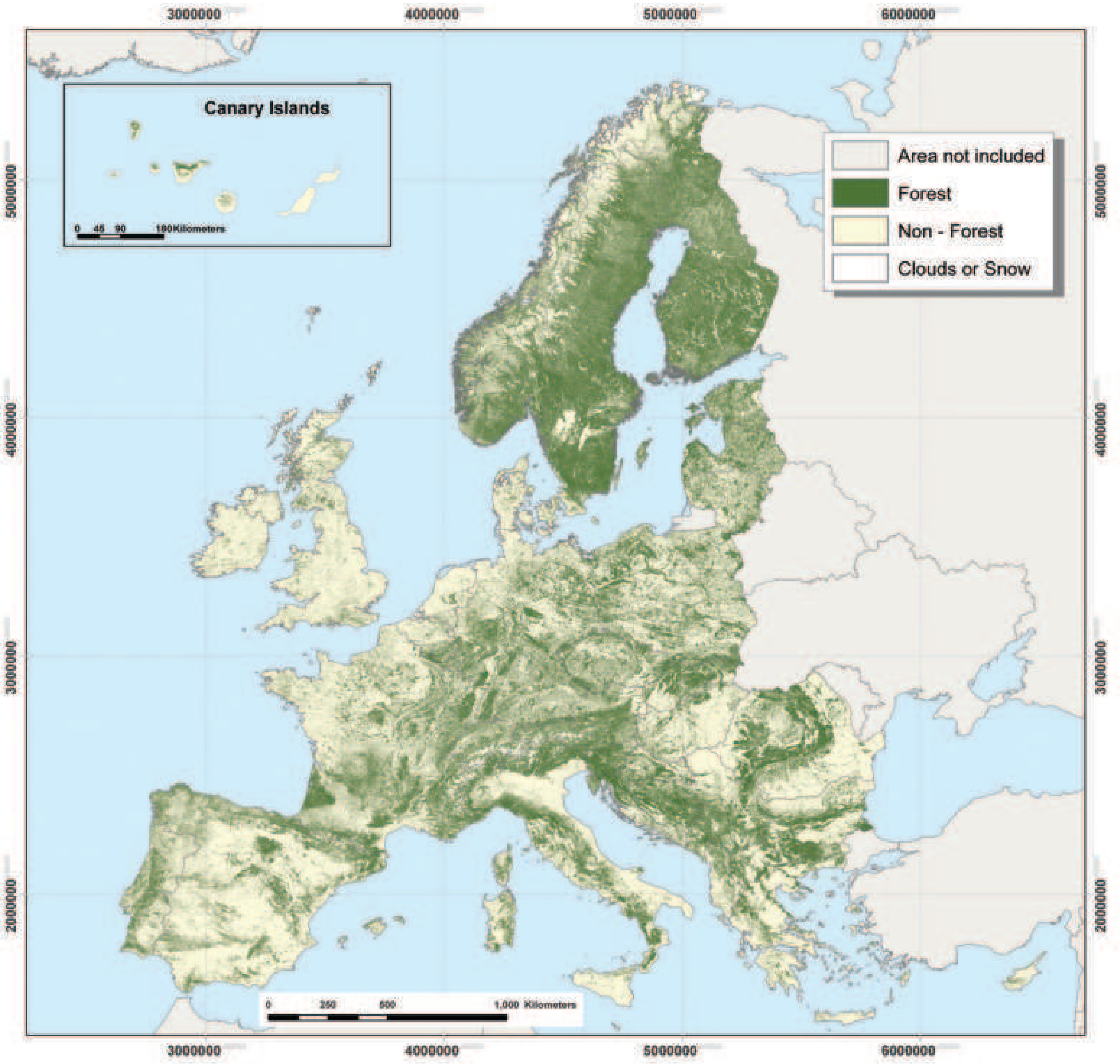


Fig. 3.4: A map showing forest cover in Europe. (JRC)

Forest soil animals

Forest soils contain an enormous range of animal life, ranging in size from microscopic nematodes, mites and springtails through worms, beetles and myriapods and up to mammals such as badgers and foxes which use the soil for their homes. Mites (Acarina) and springtails (Collembola) represent 75 to 80% of the total number of arthropods generally found in forests: in one metre square of forest soil more than 140,000 microarthropods may be found! The proportion of which are collembola and which are mites is highly variable and depends on a series of factors, such as the forest productivity and management and the physico-chemical characteristics of soil.

The number and the composition of soil microarthropod communities can affect the rate and magnitude of ecosystem processes such as decomposition of organic matter and nutrient mineralisation, and any natural or human induced change affecting soil arthropods can, therefore, influence the ecosystem's functioning.

Within the forest environment, most organisms play an important role in helping to recycle the large amounts of organic matter from the forest floor back into the soil. Many soil animals feed on dead plant matter and are known as detritivores. However, within the forest, soil fauna form a very complex food web, and the animals can be classified into different categories according to their feeding habits. As well as detritivores, some organisms are decomposers, that is organisms which break down chemical compounds into simpler organic compounds. Further to this, there are organisms that feed on living roots (plant-feeders), others feed on bacteria (bacterivores) and fungi (fungivores), as well as predators which eat other animals, and some other organisms are parasites.

Larger invertebrates, such as earthworms, ants and myriapods, act as "ecosystem engineers", transforming and incorporating litter into the soil and contributing to build the soil structure. For example, beetles chew through deadwood, opening it up to colonisation by plants and fungi and further aiding the decomposition process. Earthworm burrows increase soil aeration, drainage and porosity. They also mix the subsoil with the topsoil and deposit their nutrient-rich castings on or near the soil surface. A variety of species act as transport for bacteria and fungal spores, which are carried either on the outer body or within the intestine, thus aiding dispersal of less mobile species. All of these are important functions within the complex habitat of forest soils.

3.2 Peatland

Fig. 3.6: A peatland landscape in Lahemaa National Park, Estonia. (CG)

Peatlands are particularly unique soil ecosystems (Fig. 3.6). They differ from most other soils in that plant matter from primary production is not fully utilised along the food chain or decomposed and so accumulates as peat. Another major feature of peatlands is their semi-constant wetness and the lack of direct input from mineral or particulate matter. Some peatlands (fens) may receive mineral input through flushes of groundwater, but other types (bogs/mires) rely on nutrient input entirely through precipitation. It is the combination of these and other constraints that define the biological diversity in these unusual soils. As a consequence, peatlands exhibit high species uniqueness but low species richness, both above and below ground. That is to say that while peatlands may not contain many different species, many of those that are found occur solely in peatlands. This highlights their importance in biodiversity maintenance at a global level.

Peat only accumulates where there is sufficient soil moisture to limit decomposition, and so its presence is usually correlated with increasing latitude, where rainfall exceeds evapotranspiration (Fig. 3.7). However, tropical peatlands also exist in places such as South East Asia, as well as in Africa and Central and South America. The presence of semi-constant waterlogging in peatland soils is related to the unusual growth forms of the plants found there. Many vascular plants in peatlands rely on specialised (aerenchymatous) tissue that enables efficient gas exchange in the waterlogged, oxygen-deprived conditions. The proximity to water and nutrients fosters establishment of Sphagnum mosses and other bryophytes which do not have roots. Similarly, the roots of some species have become adapted to intercept water and nutrients from rainfall. A particularly unusual example is the negatively geotropic roots (i.e. the roots grow up instead of down) of a species of rush called *Empodisma minus*, in the peatlands of the North Island of New Zealand which can form a fine and dense root network on the peat surface.

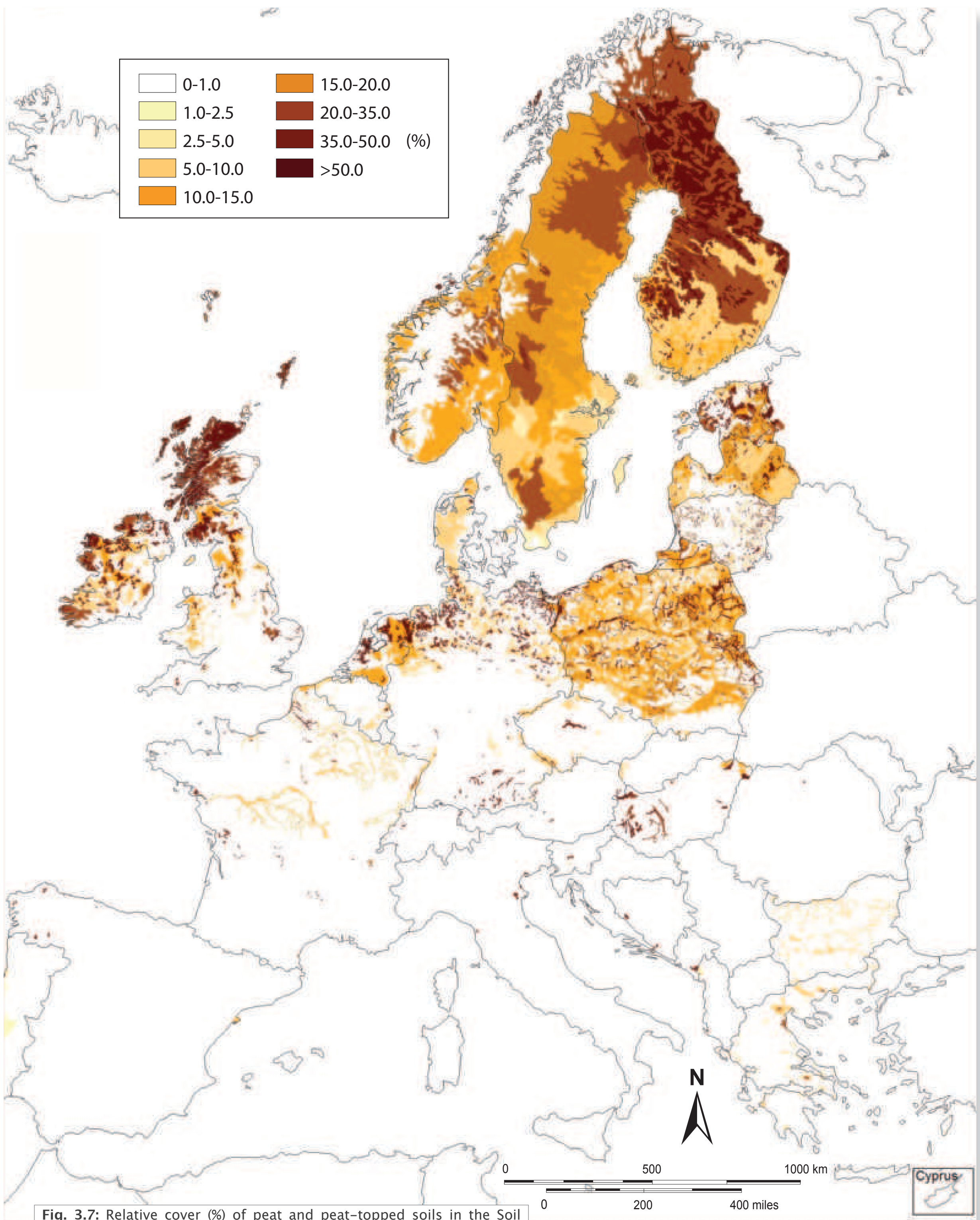


Fig. 3.7: Relative cover (%) of peat and peat-topped soils in the Soil Mapping Units (SMUs) of the European Soil Database. (JRC)

Many peatland plant species show adaptations to nutrient limitations. Nutrient-poor peatlands offer a particular niche to plants that obtain their nitrogen through adaptation to carnivorous activity. Examples of this are the various species of the genus *Drosera*, the sundews, which are characteristic of many Northern peatlands, and *Sarracenia purpurea*, the pitcher plant (Fig. 3.9), indigenous to North American peatlands but now naturalised in several European locations. Similarly, many bryophytes have associations with nitrogen-fixing microbial species.

As mineral nutrient inputs in ombrotrophic peatlands are entirely from precipitation and the majority of potentially available nutrients are locked up in an organic form, many plant species rely on intimate associations or symbioses with fungi in their root tissues to obtain nutrients. Many ericaceous species (e.g. Rhododendron and Calluna) show examples of this. The curious exception, until recently, appeared to be the sedge family, which instead have adaptations to their root tissue in the form of hairy root clusters to enable nutrient uptake (known as dauciform roots). However, there is now also evidence of an association between sedges and a group of fungi, characterised by their dark, septate hyphae, which exist as endophytes within the root tissues of sedges. Their contribution to plant growth and nutrient acquisition is, however, thus far equivocal.

In the case of ericaceous plants, the adaptation to nutrient limitation is in the form of an association with a relatively small group of fungi that form specialised structures within the plant root cells and envelop fine hair roots with a mesh of hyphae. All known ericoid mycorrhizal fungi are ascomycetes which rarely produce fruiting bodies (Fig. 3.8). These fungi are currently thought to have enzymatic capacities for nutrient acquisition from organic matter that places them somewhere in the middle of the continuum between truly saprotrophic, decomposer fungi and truly mutualistic mycorrhizal fungi and it is thought that it is partly this trait that enables niche differentiation for both the ericaceous host and the fungal partner.

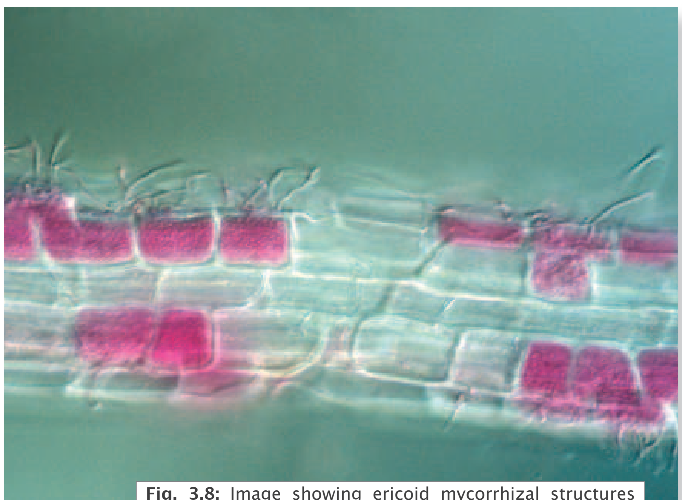


Fig. 3.8: Image showing ericoid mycorrhizal structures (stained red) penetrating inside root cells. (AT)

Fig. 3.9: Photo of the Pitcher Plant, *Sarracenia purpurea*, a carnivorous plant which is native to North America but which can now be found in various peatlands across Europe. (RA)

Other unique, fungal oddities that occur predominantly in peatlands are, for example, the bog beacon (*Mitrula paludosa*), so named because of the curious yellow beacon like shape of their fruiting bodies (Fig. 3.10), and *Sarcoleotia turficola* (Fig. 3.12) which occurs predominantly in association with Sphagnum. Both have also been found in wet areas or freshwater environments outside of peatlands albeit more rarely than within peatlands.

Similarly, *Omphalina ericetorum* (Fig. 3.11) is a lichenous fungus that is commonly, but not exclusively, found in ombrotrophic peatlands. Furthermore, some rare and threatened species of fungi can also be found in peatlands. For example, *Armillaria ectypa*, the marsh honey fungus, is only found in Sphagnum bogs, with only one known site in the UK. It is also on the provisional Red List (an official list of endangered species within the UK) for fungi. *A. ectypa* is a bioluminescent fungus and it is this quality which may produce some of the strange light phenomena observed in peatlands at night. A particularly unusual example is the ghostly light seen hovering over the surface, the so called "will-o'-the-wisp". It is thought that this light probably stems from a chemical reaction whereby methane, the end product of the activity of methanogenic archaea, reacts with volatile phosphorus compounds, which produces light.

Methane production in peatlands is one of the highest of all soil types. One of the natural recycling routes for methane is by oxidation, carried out by methane oxidising bacteria. The highest rates of methane removal by this pathway is usually in the presence of oxygen and within peatlands. Such bacteria tend to cluster around the plant roots where oxygen is more readily available in water-logged environments.

Peatlands are important environments when it comes to climate change owing to the fact that they store vast amounts of carbon. When peat bogs are drained, the previously anoxic peat is exposed to increased levels of oxygen from the air, meaning that microorganisms can utilise the stored carbon as a substrate leading to its decomposition and subsequent devolution as CO_2. Furthermore, owing to the anaerobic fermentation processes by which the majority of the subsurface microorganisms in peatlands derive their energy, approximately 30 megatonnes of methane are emitted from peatlands globally each year. The feedback between climate change and soil biodiversity is discussed in more detail in Section 5.1.3.

As well as numerous specialised fungal species, some examples of which are previously discussed, peatlands can also be home to numerous invertebrates. For example, enchytraeids can reach their highest population densities in some peatland soils, and dipteran larvae (e.g. maggots) can also be very abundant. Protozoan taxa are also well represented in peatlands, specifically the testate amoeba (Rhizopoda; Fig. 3.13). They are a taxonomic group often used in paleoecological studies for reconstruction of past climates due to their strong associations with particular site conditions (e.g. pH and surface wetness).

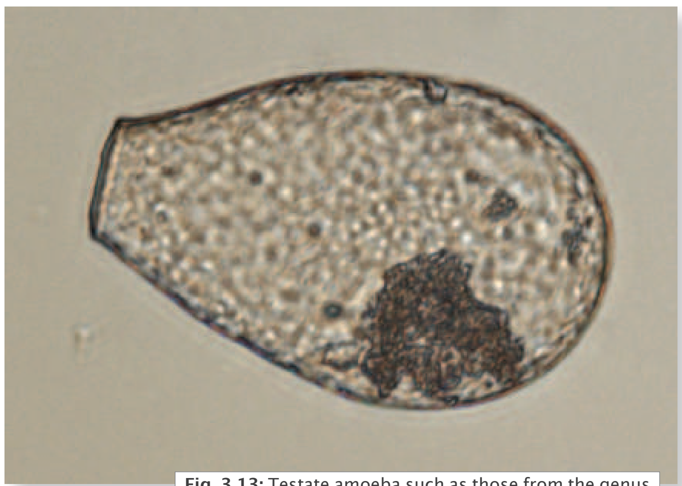


Fig. 3.13: Testate amoeba such as those from the genus *Nebela* are common in peatland environments. (RA)

Peatlands can also offer refuge for other species. Amphibians, for example, may not inhabit peatlands all year round, but often utilise them for survival during harsh summer or winter conditions (Fig. 3.14). Sometimes very intimate associations can form between many of the rather distinct species found in peatlands and, as a consequence, some can be under considerable threat from any change to either of the species' habitat quality. An example of this is the association of a newly described moth species (*Houdinia flexilissima*), nicknamed "Fred the Thread" for its thinness during the caterpillar stage. The caterpillar stage feeds inside cane rush (*Sporadanthus ferrugineus*), a plant species native to Northern New Zealand, which has stems only about a millimetre wide. Due to the limited distribution of the host plant, and threats to the habitat quality, both are now endangered species. Thus, in terms of soil biodiversity, peatlands can be seen as unique biodiversity 'islands' that promote species uniqueness and offer refuge to certain taxa, at the expense of species richness.

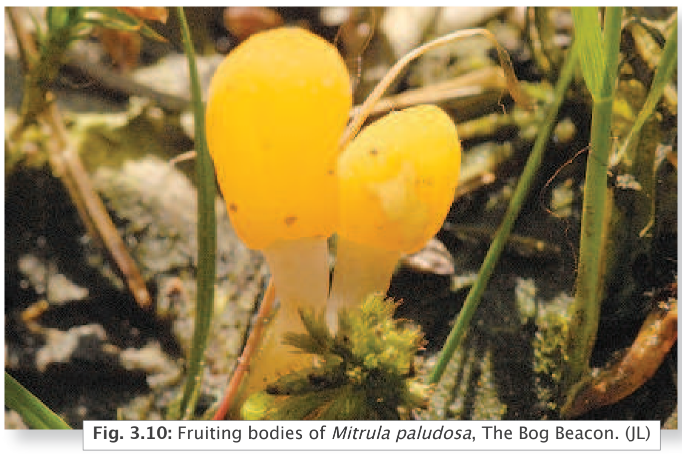


Fig. 3.10: Fruiting bodies of *Mitrula paludosa*, The Bog Beacon. (JL)

Fig. 3.11: Fruiting body of the lichenous fungus *Omphalina ericetorum*. (RA)

Fig. 3.12: Fruiting bodies of the fungus *Sarcoleotia turficola*. (CF)

Fig. 3.14: While amphibians may not generally inhabit peatlands all year around, they can be essential refuges for some species such as frogs and other amphibians at times of harsh summer or winter conditions. (RA)

3.3 Grassland

Grasslands cover extensive areas, comprising approximately 25% of Earth's terrestrial surface, making them one of the most successful vegetation types on the planet (Fig. 3.13). A common attribute of most grasses is that they cannot tolerate shady conditions very well. This means that there has always been competition between grasslands and forests, as grasses are unable to grow under the shady canopies of forests. For this reason, it is generally thought that grasslands probably became established at high altitudes, above the tree line, as grasses first start showing up in the fossil record in the late Cretaceous period, about 100 million years ago. At this time, the majority of the Earth's surface was covered in huge, extensive forests meaning that grasslands could not establish themselves across much of the terrestrial environment.

Grasslands have played an important part in human history. As well as being used for grazing livestock since animals were first domesticated over 7,000 years ago, many of our commercial cereals, such as wheat and barley, were almost certainly first domesticated from wild grassland. Natural grasslands are rather obviously dominated by grasses, although other herbaceous plants may also be present as well as a scattering of woody plants such as small shrubs and occasionally trees.

Different grassland types exist which are usually split into two broad groups; tropical (and sub-tropical) grasslands and temperate grasslands. Tropical grasslands include savannah and shrublands. These are found in semi-arid to semi-humid climatic regions and exist on all continents apart from Antarctica. Savannahs are grasslands which have scattered trees, such as the famous savannahs in Africa, whereas shrublands are dominated by shrubs, such as the Nullarbor plain in Australia and low shrublands in Hawaii. Temperate grasslands include the North American prairies and the steppes of Europe, and can also be sub-divided into temperate savannahs and shrublands depending on the dominant plant types. Further distinctions can be made to include the high altitude grasslands (i.e. Alpine grasslands), and even between natural (or native) grasslands and secondary grasslands, that derive from a recolonisation of herbaceous plants after a human induced modification (Fig. 3.15).

Grasslands generally have relatively deep soils which are rich in nutrients due to large amounts of tissue which dies off each year and 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. Furthermore, North American grasslands are still being converted into arable land at a rate of 2,530,000 ha per year. The amount of life found below the surface of grasslands dramatically exceeds that found above ground, in both numbers and mass, as well as species richness, and is particularly rich even when compared to other below ground environments. For example, research carried out in Northern Italian irrigated grasslands found 35,000 Acari and 30,000 Collembola per square metre, 10 to 20 times higher than the numbers found in neighbouring woodland.

Fig. 3.16: An irrigated grassland area from northern Italy. (CG)

Grasslands are unique from 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. If this biomass could be lifted up above ground it would be the equivalent to having a stocking rate in the region of 2,000 sheep per hectare. In reality above ground stocking rates of >10 sheep per hectare are considered high!

What's more, the species richness of below ground communities in grassland ecosystems can be staggering with tens of thousands of bacterial species, thousands of fungal species and hundreds of insect and worms species in just 1 m^2 of grassland soil!

It has been demonstrated that life below ground is very important for grassland ecosystem health (as is the case for other ecosystems). In controlled grassland experiments it was found that an absence of decomposers such as collembolans and earthworms leads to a strong decrease in total plant and plant shoot biomass. Root biomass in grasslands was also found to decrease in the absence of either collembolans or earthworms, and particularly when neither organism group was present. Conversely, when both organism groups were present it was found that root biomass increased more than when either group was present alone, suggesting that it is not just the organisms themselves which are important to plant health in grasslands, but rather the interactions between these organisms which is important.

The majority of grassland is managed to some extent, whether through grazing, mowing, planting specific species of grass for a purpose such as for forage or as improved pasture (Fig. 3.16). One particularly common species of grass which is grown for a variety of purposes from lawns to forage, is 'tall fescue grass' (*Lolium arundinaceum*). This grass species was originally introduced into the United States from Europe in the early 1800s and is a perennial grass which develops into a uniform, thick turf. It is highly invasive and is a weed species in situations where high plant diversity is desirable. Tall fescue grass generally grows with a below ground symbiont in the form of a fungus called *Neotyphodium coenophialum*. As well as aiding the plant to obtain nutrients, as do most symbiotic fungi (generally known as mycorrhizal fungi), one genetic variety of this fungus is capable of producing alkaloids which are toxic to certain herbivores, however, another genetic variety of the same species of symbiotic fungi does not produce these alkaloids.

Furthermore, it has been demonstrated that by inoculating tall fescue grass with different genetic varieties of mycorrhizal fungi it is possible to change the behaviour of the plant. Inoculation with one strain reduces the 'aggressiveness' and seed production of this grass species with other grasses and herbaceous flowering plants being able to grow in its presence. This shows that by fully understanding the interactions between plant and soil species it can be possible to develop new and novel ways of managing ecosystems such as grasslands, and to reduce the potentially damaging impacts and ecological consequences of human management of grassland ecosystems.

Fig. 3.15: Two semi-natural grasslands. The photo on the **left** shows grassland used for grazing in the Peak District of northern England. The photo on the **right** shows an alpine grassland in Northern Italy which is over 2,000 metres above sea level. (KR)

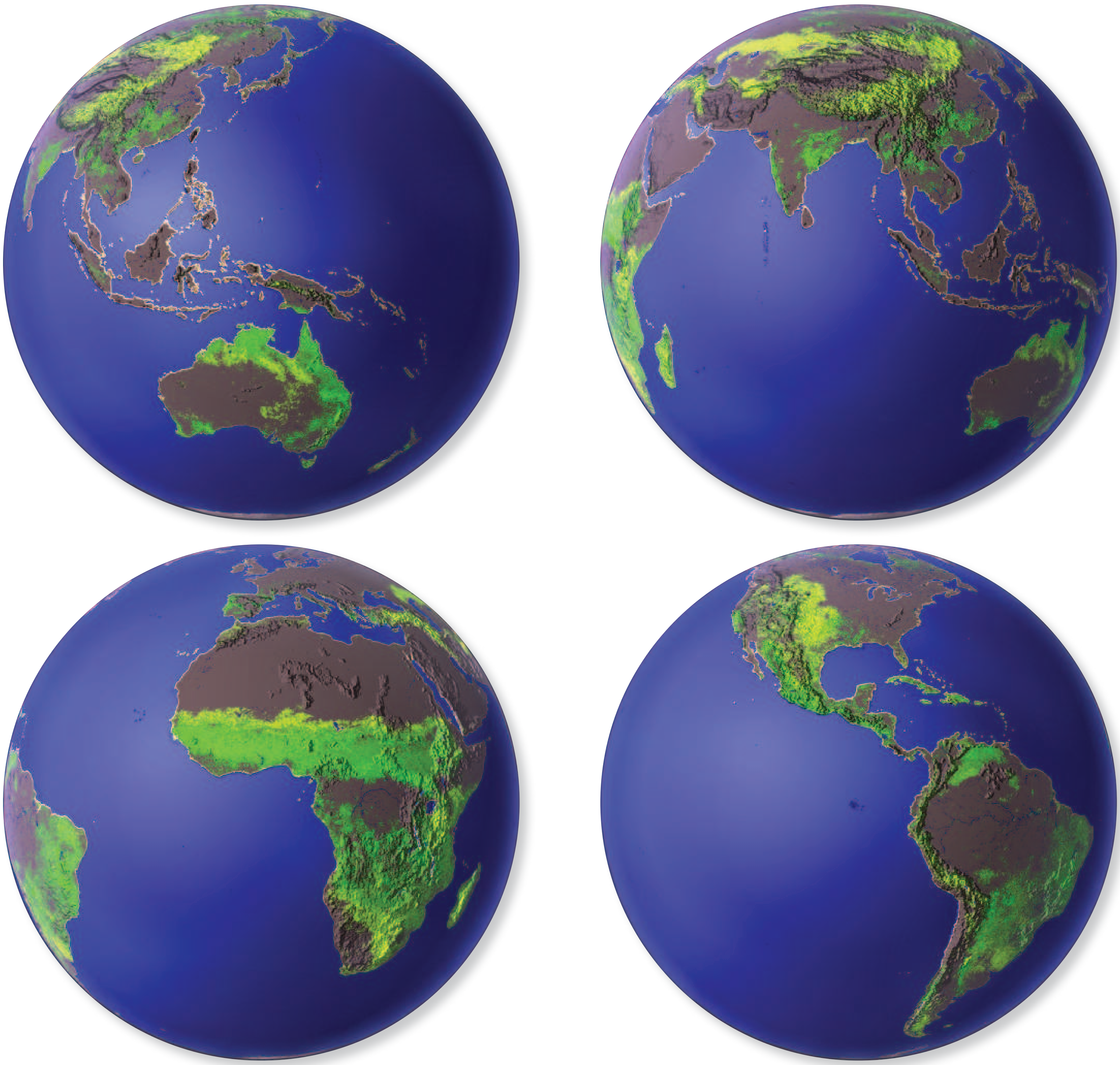


Fig. 3.17: The above four images show the global cover of grasslands shown in green. The images were produced by NASA using data obtained from Terra/MODIS/Land Cover at a 1 km resolution. (Images courtesy of NASA/Goddard Space Flight Center. Scientific Visualization Studio.)

Improved Pasture

Improved pasture is a form of highly managed grassland which normally has species of grass and clover of high grazing value (Fig. 3.18). They are generally established by reseeding, and maintained by grazing control and use of lime and fertilizers. Both establishing and maintaining improved pastures can be expensive. However, the improvements that they deliver in animal productivity compared to native pasture generally outweigh the costs.

Turning native pasture into improved pasture can have dramatic consequences on the soil biota. Just how dramatic the consequences are depends on the similarity of the original ecosystem to the derived ecosystem after management practices have been put into place, as well as the specific management practices used, be it introducing new grass or clover species or adding lime or fertilizer.

Generally improved pasture has been found to increase populations of earthworms, both with regards to the biomass present and the species richness, when compared to native pastures. Collembola have been found to be affected by the management practices of producing improved pasture. For example, in Australia, introduced collembola species are generally found in greater abundances in improved pastures whereas native collembola are found in greater numbers in native pasture. This suggests that increased use of techniques for improving pasture will be detrimental to native collembola species in the long term.

Furthermore, it has been found that improving pasture through introducing non-native species of grass and clover can potentially co-introduce invasive or pest species of soil organisms such as pathogenic fungi. Therefore, while potentially bringing positive effects, such as increased animal productivity and increased earthworm abundance with the associated increase in ecosystem services that earthworms provide, care must be taken to minimise any negative effects.

Fig. 3.18: An area of improved pasture in Ballintium, Perthshire, U.K. (foreground) contrasted against a non-treated grassland area in the background. (KR)

3.4 Tropical

Soils are among the most biologically rich habitats on earth – and this is true for temperate soils (e.g. Europe) as well as tropical soils (i.e. South America, Central Africa or South East Asia). While this section cannot cover in depth the vast levels of biodiversity found in tropical regions, it will highlight some of the similarities and differences between tropical and temperate areas.

It is well known that one single site of the Brazilian Amazonian rain forest can have several thousand species of invertebrates and this total number is probably higher than at similar sized sites in Central European deciduous forests. However, the difference between biodiversity in temperate and tropical soils is smaller than in other ecosystem compartments (e.g. the biodiversity existing between the tree canopy of temperate and tropical regions). The numbers of organisms found in tropical soils are huge, which can partly be explained by the huge size of tropical regions combined with a high degree of endemism (i.e. many species occur only in very restricted small areas). For example, more than 50,000 species of soil and litter inhabiting animals have been described in Brazil (Table 3.1). Only few of these species are of giant size, such as some earthworms (Fig. 3.19); most are microscopic (e.g. nematodes, tiny roundworms) or very small (insects, e.g. beetles and ants). Furthermore, tropical soils also support large amounts of fungal diversity (Fig. 3.20).

Fig. 3.19: Giant earthworm (*Rhinodrilus priolli*) from the Brazilian Amazon. (MVBG)

Fig. 3.20: Fungus of the litter layer in the Brazilian Mata Atlantica, with a small fly inside. (HH)

To an even larger degree than in European soils, tropical soil organisms are mostly not known to science. For instance, it is thought that only between 3 and 5% of the world's estimated diversity of nematodes and mites is currently known. However, the lack of specialists who are able to identify these many different organisms is a problem worldwide, with this aspect being more critical for specialists able to identify specimens from tropical regions (the most important collections of soil invertebrates are located in European and North American museums).

Table 3.1: The number of soil species found in Brazil compared to the rest of the world

Taxonomic/size categories Common (Scientific) names	**Number of species[1]** **Brazil**	 **World**
Microfauna		
Protozoans (Protista)	[3,060-4,140]	36,000
Nematodes (Nematoda)	[1,280-2,880]	15,000
Rotifers (Rotifera)[2]	457	2,000
Tardigrades (Tardigrada)[2]	67	750
Mesofauna		
Diplura	NA	659
Mites (Acari)	1,500	45,000
Potworms (Enchytraeidae)	100	800
Pseudoscorpions (Pseudoscorpionida)	>100	3,235
Sprintails (Collembola)	199	7,500
Macrofauna		
Ants (Formicidae)	2,750	11,826
Beetles (Coleoptera)	30,000	350,000
Earthworms (Megadriles)	306	3,800 [8,000]
Harvestmen (Opiliones)	951 [1,800]	5,500
Centipedes (Chilopoda)	150	2,500
Millipedes (Diplopoda)	NA	10,000
Scorpions (Scorpionida)	119	1,259
Snails (Gastropoda)	670 [2,000]	30,000
Spiders (Aranae)	2587 [10,000]	38,884
Termites (Isoptera)	290 [600]	2,800
Velvet worms (Onychophora)	4	90
Woodlice (Isopoda)[2]	135	4,250

1. Number of classified species.
2. Includes aquatic and soil species.
Numbers in brackets are estimated numbers.

Source (modified): Brown, G.G. *et al.* (2006).

Because soil communities are so diverse yet so poorly known and described, they have been called the "other last biotic frontier". In fact, it is not actually known how many species live in the soil - neither in tropical nor in temperate regions. However, as previously discussed, the incredibly complex tropical soil system, with its high numbers of microbial and animal species interacting, allied to diverse fungi and plant communities provide a range of ecological functions and ecosystem services to mankind. Such services, e.g. food provision or climate regulation, have been estimated to be worth billions of Euro annually (see Section 4.6). However, due to lack of knowledge and economic pressures, tropical soil ecosystems are under growing stress, especially due to land use changes (e.g. forest clearing, biofuel plantations).

Examples of tropical biodiversity

Despite the fact that the major groups of soil organisms are similar in European and tropical regions, there are some major differences. The most obvious and wellknown one is the occurrence of giant earthworms, which can reach a length of 1 – 2 m. However, these usually occur in small numbers and, therefore, seem to have an important, but not as dominant an influence on tropical soil ecosystems when compared to the role of other earthworms that act as "ecosystem engineers" in Europe.

However, even small earthworm species may have huge effects globally. For example, the earthworm species *Pontoscolex corethrurus*, originally coming from the northern part of South America, has within the last six hundred years invaded most of the tropical regions of the world (Fig. 3.21). In some cases, when occurring in high numbers at recently cleared rainforest sites, it has caused a sealing of the soil surface due to its high cast production meaning that water can no longer infiltrate into the soil leading to negative impacts on plant growth.

Fig. 3.21: Juvenile and adult specimen of the species *Pontoscolex corethrurus*. (MVBG)

Impact of Current Land-Use Changes in Tropical Soil Ecosystems

Over a third of the Earth's surface has been directly altered by human land transformation. Tropical soil ecosystems are under major stress, usually caused by human activities. A major factor is forest clearing, which due to lack of food input (organic matter), changes in soil properties (decrease of soil moisture) or climatic influences (erosion caused by rain), causes a drastic decrease in numbers and diversity of soil organisms (Fig. 3.22). Also, land management practices in intensive agriculture, such as monocultures (e.g. palm plantations) often have negative effects on soil organisms, partly due to the same reasons as stated above, partly due to the application of pesticides (Fig. 3.23). The regulation of functions through soil biodiversity has progressively been replaced by regulation through demanding chemical and mechanical inputs, leading to severe problems such as soil compaction.

Fig. 3.22: Soil destruction caused by erosion after clearance of forest (Parana, Brazil). (JR)

Fig. 3.23: Tree plantation in the Brazilian Amazon: left side with and right side without herbicides. (JR)

Another earthworm species (*Enantiodrilus borellii*) has an even bigger influence and really dominates the landscape of East Bolivian savannahs due to its cast "towers" which can be up to 30 cm in height. These towers seem to be necessary due to this region of the Beni-Province being flooded regularly (Fig. 3.24). This production of large surface casts by earthworms has been shown to also have positive effects on plant growth, as well as on the diversity of other soil organisms, such as the anecic earthworm *Martiodrilus sp.* from the Colombian "Llanos". Moreover, the removal of this earthworm from the soil has been shown to lead to problems within the soil system (Fig 3.25).

A bigger difference between European and tropical soils is the dominance of social insects in the tropics, especially termites (generally in savannahs) and ants (more often in forests). Unfortunately, due to the very sporadic distribution of these organisms (i.e. huge numbers at nesting sites, but low and infrequent findings between nests) in both groups, but in particular among termites, some species have been able to adapt to human settlements (i.e. they have become a pest).

Termites live in all parts of terrestrial ecosystems. That is, they can be found in all vegetation layers as well in the various soil layers, starting from the litter layer deep down into the mineral soil. Some of these nests belong to the biggest structures made by invertebrates and can be many metres in diameter and depth into the soil as well as being several metres high above ground. Their nests are often inhabited by millions of individuals, belonging to different casts such as workers or soldiers. However, small colonies can occur too, especially in wood of standing dead trees.

Termites usually feed on wood which they can use due to symbiotic microbes living in their gut. Recently, the role of termites in the production of "greenhouse gases" such as methane and carbon dioxide has become a subject of increasing research as they produce about 4% and 2% of the overall global production of these two gases respectively.

Some exceptions do occur, however. For example, the integrated annual methane flux coming from termite mounds in the "Llanos" of Colombia has been found to be only 0.0004% of the total global emissions of CH_4 attributed to termites. The reason for this is that the methane appears to be mostly oxidised in the soil before escaping to the atmosphere. In rainforests, an average of 100 termite species per hectare have been found. Due to their high activity and biomass, termites can be considered as almost always positive for the soil structure and soil properties. In some cases, especially in the Sahel zone of Africa, termites are artificially introduced in order to degrade fine wood matter to produce compost to use as fertilizer for agriculture.

The diversity of ants in tropical regions, especially rain forests, is also extremely high. For example, more than 500 species can occur within an area of 10 square km. Currently, there are 12,513 species described worldwide, with about 25% being found in just South America alone. Other astonishing facts include that 114 species were found at a soil plot of 10 x 10 m in Peru, while 82 species were caught on a single tree in the Brazilian Amazon rainforest.

Fig. 3.24: Cast towers of one earthworm species after the end of the flooding season (Beni, Bolivia) (WH)

Fig. 3.25: Impermeable layer of earthworm casts (grey zone) at the soil surface of a recently cleared forest site now used as meadow. (JR)

3.5 Agriculture

Humanity has been farming for at least 10,000 years, and until now it has generally been able to obtain all of the food necessary for its growing global population. During the last 50 years or so, farmers in some parts of the world have been able to markedly increase total crop yields. This has been the result of a rapid revolution in the technology of agricultural production, availability of resources and information, and policies favouring high productivity. Farmers in these areas have managed to intensify farming systems using technologies that rely on agricultural chemicals, mechanisation, and plant breeding. Unfortunately, intensification in many cases has come with an environmental price, caused by the overuse of agricultural inputs, the application of practices which lead to the deterioration of soils and the mismanagement of natural resources.

Monocultures

Wheat is one of the most widely grown plants on the planet covering approximately 210,400,000 hectares of the global land surface (about the same size as all of France and Spain combined!) and providing approximately 20% of the world's calorific intake. However, its growth in vast fields of monocultures has been shown to have detrimental impacts on the soil biota leading to overall reductions in soil biodiversity.

(CG)

While intensification has resulted in areas of high productivity, extensive (or low input) agriculture is still practiced in many areas of the world. These farming systems are largely small-scale, labour-intensive and use relatively simple technologies. In addition, often when extensive agriculture systems are practised under growing population pressures, there is less and less opportunity to restore soil fertility during fallow periods. Altogether, improper agricultural practises, in both intensive and extensive systems, can have several undesirable impacts on the environment, ecosystems, human health and economies. These impacts affect soils in the form of increased erosion, depletion of organic matter, reduced soil fertility, salinisation, pollution, damage to soil biota often leading to reductions in soil biodiversity, and consequently land which is less productive.

Examples of impacts of improper agricultural practices include:

- Deterioration of soil quality and reduction of agricultural productivity due to nutrient depletion, organic matter losses, erosion and compaction;
- Pollution of soil and water due to the excessive use of fertilizers, and the improper use and disposal of animal wastes;
- Increased incidence of human and ecosystem health problems due to the indiscriminate use of pesticides and chemical fertilizers;
- Loss of biodiversity due to the reduced number of species being cultivated for commercial purposes;
- Loss of adaptability traits when species that grow under specific local environmental conditions become extinct;
- Loss of beneficial crop-associated biodiversity that provides ecosystem services such as pollination, nutrient cycling and regulation of pest and disease outbreaks;
- Soil salinisation, depletion of freshwater resources and reduction of water quality due to unsustainable irrigation practices throughout the world;
- Disturbance of soil physicochemical and biological processes as a result of intensive tillage and slash and burning.

No-till farming:

Tillage is a general term that describes several processes used in the preparation of soil for planting crops. These activities can lead to unfavorable effects such as soil compaction, loss of organic matter, degradation of soil aggregates and a disruption of soil organisms. No-till farming (also called zero tillage) is a way of growing crops from year to year without disturbing the soil through ploughing the land which can increase the amount of water in the soil, decrease erosion and lead to an increase in the amount and variety of life in and on the soil.

Roles of soil biota on ecosystem health

Scientists now know that the complex processes carried out by the soil biota (including plant roots) have significant effects on the health of ecosystems, the quality of soils, the incidence of soilborne plant and animal pests and diseases and, consequently, on the quality and yields of crops. Over the last few decades scientists have slowly unveiled the roles of some of the soil's organisms in soil fertility regulation and plant production. While there are still many groups and functions that are not well known, and only little information is available on the interactions among above ground and below ground soil biota, there are many examples of both positive and negative effects of some groups of soil organisms in plant production.

The ecosystem services provided by soil organisms that may influence agricultural productivity are described in Table 3.2, with examples of the groups providing such services.

Roles of soil biota in maintaining soil fertility

Decomposition and cycling of organic matter:

Farmers often use organic materials, such as crop residues, manure, food wastes and compost, as a source of nutrients to maintain or improve soil fertility. Once applied to fields, organic materials are utilised by organisms living in soils which transform them into other substances, energy or nutrients.

Decomposers are the organisms responsible for these transformations; they carry out a series of processes which are fundamental to the conservation of soil quality and the transformation of organic matter into a form that provides nutrients to plants.

Decomposers are found in several main soil groups and perform different functions:

- Microflora: certain types of bacteria and fungi are the major or primary decomposers; they are capable of digesting complex organic matter and transforming it into simpler substances that can be utilised by other organisms;
- Microfauna: certain types of protozoa and nematodes feed on or assimilate microbial tissues and excrete mineral nutrients;
- Mesofauna: includes a large number of organisms, ranging from small arthropods like mites (Acari) and springtails (Collembola) to potworms (Enchytraeidae). They break up plant detritus, ingest soil and organic matter or feed on primary decomposers thereby having a large influence on regulating the composition and activity of soil communities;
- Macrofauna: including ants, termites, millipedes and earthworms, contribute to organic matter decomposition by breaking up plant detritus and moving it down into the soil system thereby improving the availability of resources to microflora (through their nest building and foraging activities).

Table 3.2. Essential ecosystem services provided by soil biota (modified from Bunning and Jiménez, 2003)

Ecosystem services	Examples of Soil biota groups providing the service
Decomposition and cycling of organic matter	Bacteria, fungi and actinomycetes (primary decomposers). Meso- and macrofauna such as various saprophytic and litter feeding invertebrates (detritivores) including earthworms (e.g. *Lumbricus rubellus*, *Lumbricus terrestris*, *Eisenia fetida*, *Allolobophoridella andrei*), ants, (*Formicidae* sp.), Collembola (*Folsomia candida*, *Protaphorura fiata*, *Proisotomoa minuta*) and mites (*Acari*)
Regulation of nutrients availability and uptake	Mostly microorganisms like mycorrhizae, actinomycetes, nitrogen fixing bacteria (*Rhizobia sp.*, *Azotobacter* sp., *Frankia*, *Klebsiella cyanobacteria*) and bacteria that mineralize nitrogen (*Nitrosomonas*, *Nitrosospira*, *Nitrosococcus*, *Nitrosolobus*, *Streptomyces*, *Nocardia*, *Nitrobacter*, *Nitrospina*, and *Nitrococcus*), some soil and litter feeding invertebrates such as ants and earthworms
Suppression of pests and diseases	Bacteria (e.g. *Pseudomonas chlororaphis*, *Pseudomonas fluorescens*, *Bacillus thuringiensis*); fungi (e.g. *Beauvaria bassiana*, *Arthrobotrys dactyloides*, *Trichoderma harzianum*), nematodes (e.g. *Steinernema carpocapse*), Collembola, earthworms and decomposers as well as predators (e.g. predatory mites, centipedes or beetles)
Maintenance of soil structure and regulation of soil hydrological processes	Bioturbation by invertebrates such as earthworms (e.g. *Lumbricus* sp.), ants (*Formicidae* sp.), termites (macrostructure) and plant roots, mycorrhizae and some other microorganisms (microstructure)
Gas exchanges and carbon sequestration	Mostly microorganisms and plant roots, some (organic) carbon protected in biogenic aggregates made by earthworms, ants or termites
Soil detoxification	Mostly bacteria (e.g. *Pseudomonas* sp., *Micrococcus* sp.) or fungi (*Coniochaeta ligniaria*)
Plant growth control	Plant roots, rhizobia, mycorrhizae, actinomycetes, pathogens, phytoparasitic nematodes, rhizophagous insects, plant growth promoting rhizosphere microorganisms, biocontrol agents
Pollination of horticultural crops	Soil-nesting insects such as solitary bees (*Peponapis pruinosa*)

From the transformation of the organic matter in the soil, a particular class of organic substances is produced: the humus (see Section 2.3). Humus is a long-term reservoir of soil fertility and also plays an essential role in the creation and stabilisation of soil structure, as well as the regulation of water movement in soils.

Decomposers are fundamental in the biosphere and their processes are crucial for maintaining life. In the case of agriculture, they contribute to improve yields by making organic matter and reservoirs of nutrients available.

Regulation of nutrient availability and uptake

There are 16 elements that are essential nutrients for plant growth. Plants can only take those nutrients from soils if they are easily available or in specific chemical forms. Chemical, physical and biological processes contribute to the availability of these nutrients in soils. In this context, processes carried out by soil biota are important for the maintenance of crop production and good crop yields. They also contribute to plant nutrition in areas where chemical fertilizers cannot be applied. Below are some examples of how the soil biota can contribute to the formation of nutrient pools and the availability of nutrients.

Nitrogen availability

Nitrogen is the most important limiting nutrient for plant growth and is responsible for vigorous growth, branching, tillering, leaf production and yield. Plants can only utilise nitrogen in forms such as ammonia and nitrate as well as a few organic nitrogen containing compounds. These forms are normally made available from more complex compounds through transformations carried out by the soil biota.

Soil nitrogen deficiency is common in both the tropics and subtropics. Finding ways to obtain nitrogen and use it efficiently is of utmost importance for crop production in these regions. In addition, concerns regarding the availability of fossil fuel reserves for fertilizer production, as well as the associated increases in fertilizer prices, may lead to requiring alternative plant nutrition methods. For this reason, the soil biota may become even more prominent in agricultural practices to provide nitrogen, either through biological nitrogen fixation or nitrogen mineralisation.

Biological nitrogen fixation

Several groups of soil microorganisms are capable of taking up gaseous nitrogen from the atmosphere, where it makes up almost 80% of the gasses present, and transforming it into ammonia, a form of nitrogen which plants can use. This process is called biological nitrogen fixation (BNF) and it can take place in soils, water, sediments, on or within roots, stems, and leaves of certain plants, and within the digestive tracts of some animals. Estimates of global terrestrial BNF range from 100 to 290 million tonnes of N per year, of which 40-48 million tonnes are estimated to be biologically fixed in agroecosystems. This shows that the contribution of BNF to crop production in agroecosystems is certainly substantial.

In agroecosystems, BNF is carried out by microorganisms that live in association with plants (symbiotic) or by microorganisms living freely in soils (non-symbiotic).

Symbiotic nitrogen fixing microorganisms living in (or on) the tissues or roots of legumes (e.g. peanuts, Fig. 3.22), several grasses and cereals contribute significantly to BNF. The best known example is that of *Rhizobium* which live in association with legumes such as bean, lentil, soybean, clover and peanut. Most soils contain these bacteria but their populations may not be adequate or effective for forming productive associations with the crops sown. In such cases, the organisms must be artificially introduced into the system. This is generally done by coating seeds with bacteria (an 'inoculum') before sowing (Fig. 3.27). In addition, legumes are often used in crop rotations to increase the nitrogen content of soils through BNF. Nitrogen fixation from symbiotic microorganisms can range between 30 to 300 kilograms of nitrogen per hectare per year.

Fig. 3.26: Peanut plant with root nodules hosting BNF bacteria. (PC)

There is a great diversity of non-symbiotic microorganisms found in soil which are capable of BNF. This includes about 20 genera of non-photosynthetic aerobic bacteria, (e.g. *Azotobacter, Beijerinckia*) and anaerobic bacteria, (e.g. *Clostridium*). Furthermore, there are approximately 15 genera of photosynthetic cyanobacteria (bluegreen algae), such as *Anabaena* and *Nostoc*. In general, the amount of nitrogen that non-symbiotic microorganisms fix within the soil is significantly lower than that of symbiotic microorganisms.

Nitrogen mineralisation

Organic matter contains nitrogen in various organic forms, such as proteins and amino acids. These organic forms are transformed by microorganisms into inorganic forms such as ammonium, nitrite and nitrate.

The conversion of proteins and amino acids to ammonium is called ammonification. It can be carried out by most of the microorganisms involved in the decomposition of organic matter. Microorganisms obtain energy from the conversion of organic nitrogen to ammonium, while also using ammonium as a nutrient. Since microorganisms often produce more ammonium than they need, the excess is released into the soil and becomes available as a nutrient for plants, or a substrate for other microbial processes.

Ammonium can be used by many plant species as a nutrient, particularly those that live in acidic soils and water. However, most plants that occur in non-acidic soils cannot utilise ammonium efficiently, and so require nitrate as their source of nitrogen. Ammonium is converted to nitrate through a process called nitrification.

The nitrification process requires the mediation of two distinct groups: bacteria that convert ammonia to nitrite (*Nitrosomonas, Nitrosospira, Nitrosococcus, Nitrosolobus, Streptomyces, Nocardia*) and bacteria that convert nitrite to nitrate (*Nitrobacter, Nitrospina,* and *Nitrococcus*). Recent evidence has come to light which suggest that archea also play an important role in the nitrogen cycle in soils, but the precise details of their interaction with the nitrogen cycle has still not been fully explored.

Macrofauna can also play a major role in soil nutrient dynamics, including that of the nitrogen cycle, by changing soil properties. Earthworms, for example, modify soil porosity and aggregate structure, varying the distribution and rates of decomposition of plant litter, and altering the composition, biomass and activity of soil microbial communities. In fact, casts and burrows of earthworms are a favourable environment for microbial activity. Earthworm excreta, such as ammonia and urea, and body tissues are rapidly mineralised by the soil microbiota. It has been estimated that fluxes of nitrogen from earthworm populations in agroecosystems can range from 10 to 74 kg nitrogen per hectare per year.

Fig. 3.27: Rice fields in Austria having been treated with Azolla bio-fertilizer which has been found to give the same yields as those treated with chemical nitrogen fertilizers. (SP/FAO)

Uptake and availability of phosphorous and other macro and micronutrients

Soil microorganisms also contribute to, and affect, the availability of other macronutrients such as phosphorus (P), potassium (K), magnesium (Mg) and calcium (Ca) and micronutrients including zinc (Zn), iron (Fe), copper (Cu) and sulphur (S). One of the most studied groups in this respect are the arbuscular mycorrhizal fungi (AMF), which are symbiotic soil fungi that colonise the roots of the majority of plants.

Arbuscular mycorrhizal fungi can play a significant role in P nutrition of crops, increasing the total uptake of P and in some cases P use efficiency. This may be associated with increased growth and yield. In situations where colonisation by AMF is disrupted, the uptake of P, plant growth and, in some cases, yield can be significantly reduced.

Although P uptake seems to be the most important outcome of the AMF symbiosis, there is evidence that AMF can play a further role in the uptake of other macronutrients by the host plant, including that of N, P and Mg as well as influencing the uptake of Zn, Cu and Fe. It has been suggested that AMF may also function to enhance plant uptake of N from organic sources. Still, the mechanisms of nutrient uptake and potential competition between different nutrients resulting from AMF associations are not well known.

Mineral weathering

Soil minerals contain inorganic nutrients such as Mg, K, Ca, Fe and P, which are released through weathering. Soil microorganisms such as fungi, as well as earthworms, play an essential role in releasing nutrients from primary minerals. Bacteria and fungi excrete organic acids which act as weathering agents. Fungi can contribute to physical degradation of mineral particles by breaking them with their hyphae (a thread-like structure) (see also Section 4.2).

If the studies on the mechanisms of biological weathering continue to advance, in the future it may be possible to use efficient mineral weathering microorganisms to reduce the current reliance on synthetic fertilizers. This type of biofertilisation could result in a reduction of both the economical costs and environmental impacts of crop production.

The role of soil biota in soil structure formation and regulation of hydrological processes

Good soil structure facilitates the germination and the establishment of crops, has improved water holding capacity which can prevent or delay drought, has a better infiltration capacity which prevents waterlogging, and also improves aeration of the soil. Furthermore, good soil structure offers resistance and resilience against physical degradation such as erosion and compaction and helps the movement of organisms in the soil.

Soil structure is determined by the spatial distribution and composition of soil particles, their aggregates and pores. The formation of soil structure is mediated by physiochemical processes and by the activity of living organisms such as bacteria, fungi, meso and macrofauna and plant roots.

While decomposing organic material, soil microorganisms excrete substances that can act as binding agents between soil particles and facilitate the formation of aggregates. The organic material becomes encrusted with soil particles, which slows down decomposition and improves soil organic matter pools in the soil. Larger organisms such as earthworms, ants and termites move the soil when excavating burrows, forming pores and channels that increase water infiltration or aeration (Fig. 3.28). Earthworms receive a lot of attention from researchers for their soil forming activities: they ingest and excrete the soil, while their casts form aggregates that are generally more stable than non-worm made aggregates and contain more stable microaggregates.

Macropores made by macrofauna in the soil surface direct the flow of rain water through such burrows and nests, facilitating quick water infiltration. This prevents sheet erosion and provides routes for increasing soil moisture in deeper soil layers. For example, in places where crop residues and mulch layers are left on the soil some researchers have observed that the increased activity of termites (tunnelling) has improved soil structure and reduced run-off.

When the soil is disturbed by tillage, macropores are destroyed and the soil becomes more vulnerable to erosion, waterlogging and compaction. Because tillage also disturbs the habitat of soil organisms, their populations often decline, and their positive effect on soil structure is reduced. No till or minimal tillage practices usually promote the activity of soil engineering organisms and can improve the soil physical characteristics.

Fig. 3.28: Harvester ants, *Messor cephalotes*. (DMa)

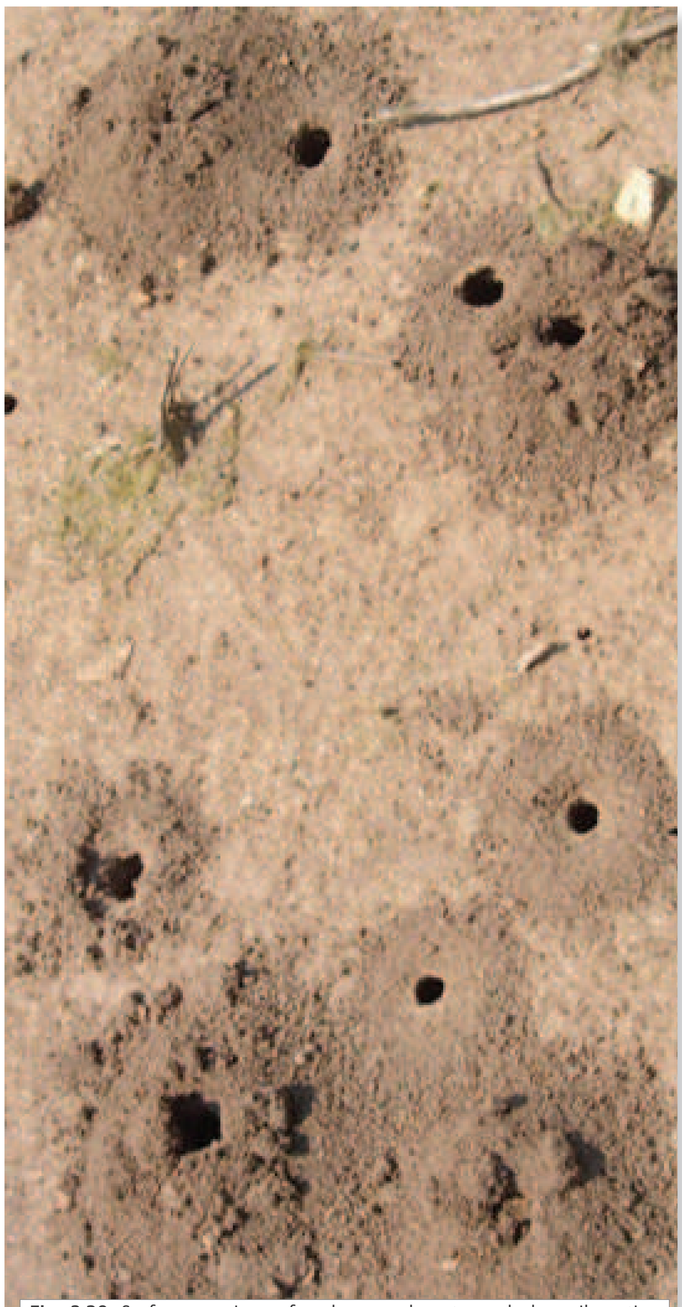


Fig. 3.29: Surface openings of underground nests made by soil nesting bees, showing tumuli formed at the soil surface. (EM/The Xerces Society)

Soils and the soil biota in pest and disease control

In agricultural systems, the reduced plant diversity (due to monoculture) combined with improper agricultural practices, can create favourable conditions for the increase and spread of pests and diseases, potentially causing severe damages to crops, both quantitatively and qualitatively.

A healthy soil, which has a diverse soil community, can control the spreading and increase of pest populations. Soil organisms, including fungi, bacteria, viruses, protozoa, nematodes and other invertebrates, can contribute to control soil-borne pathogens through competition, antibiosis, parasitism and the induction of plant disease resistance (see also Section 4.4).

Some examples of organisms that contribute to the biological control of pest and diseases include:

- *Trichoderma harzianum*: is a common soil fungus that is known for its antagonistic nature to other fungi. Its hyphae surround other (pathogenic) fungal hyphae and release enzymes that degrade the cell walls of the host, thus limiting its growth. *Trichoderma harzianum* is often used as the active ingredient in several commercial biofungicides;
- 'Nematode trapping fungi' such as *Drechslerra anchonia*: These fungi produce special structures on their hyphae with which they trap nematodes. Afterwards they penetrate the host and digest it from the inside out, using the nutrients for their own growth and reproduction;
- Bacterial: *Pseudomonas* sp. are known to effectively colonise the plant roots environment (rhizosphere) and protect the plant against several pathogens. This probably happens through competition for nutrients (particularly iron) as well as the production of antibiotics and by improving plant health and thereby increasing its resistance to pathogens;
- Entomopathogenic nematodes: being nematodes that are pathogenic to insects. A couple of genera are well studied owing to their pathogenic properties to insect pests (e.g. *Steinernema* sp.).

Some soils, called suppressive soils, have particular properties that suppress soil-borne diseases. These soils have attracted the attention of both farmers and researchers alike. Some are known to suppress the activity of pathogens such as *Fusarium oxysporum, Gaeumannomyces graminis* var. *tritici, Pythium* sp., *Rhizoctonia solani, Streptomyces scabies*, all of which are well known pests of various crop plants. Plants growing in such soils do not develop disease or only develop relatively light disease symptoms, even if a pathogen is present or artificially added to the soil. Soil suppressiveness appears to be due to soil physicochemical characteristics, the soil biota, or a combination of the two. The soil biota can play a key role in soil suppressiveness by controlling pathogens through competition, antibiosis, parasitism, or enhancement of plant resistance.

Integrated Pest Management (IPM) promotes the use of biodiversity and natural enemies to reduce pests and diseases. When IPM also considers soil, below ground biological processes can have positive impacts on pests and disease control above ground.

Soils and pollinators

Two-thirds of the world's crop species depend to some degree on insects for pollination, and 35% of the world's global food production comes from these pollinator-dependent crops. The worldwide economic value of the pollination service provided by insect pollinators, mainly bees, was estimated at €153 billion in 2005 for the main crops that feed the world (See Section 3.6). The services provided by pollinators are not limited to agricultural productivity, but are also key to the function of many terrestrial ecosystems, as they enhance native plant reproduction. Many pollinators have critical associations with the soil ecosystem, where they develop through their larval and immature stages.

In the early spring or rainy seasons around the world, small mounds of earth may often begin to appear in lawns and lightly vegetated areas. These mounds are usually 'tumuli', made of soil excavated by ground-nesting bees (Figure 3.29).

Immature stages of several important groups of pollinating insects develop in the soil, including flies, nesting bees and wasps. Soil nesting bees, including both solitary bees and some social colonies (e.g. stingless bees and bumble bees), are among the most important crop pollinators. For example the squash bee *Peponapis pruinosa* (Fig. 3.30) is a specialist bee, only collecting pollen from the genus *Cucurbita* (squash and pumpkin) and nests in the ground, sometimes amid its host crop plants.

Soil-nesting bees often are found amid bare ground, and therefore often colonise agricultural fields. Hard and compacted soils are generally avoided by ground-nesting bees as they are more difficult to excavate. In general, soil-nesting bees commonly prefer to nest in moderately moist sands and loams, with little plant cover and bright illumination and warm soil surface temperatures.

The alkali bee, a commercial pollinator of alfalfa grown for seed, has been introduced into cropping areas through cutting and transporting of soil cores with nesting larvae inside. However, the bee's preference for damp, silty nesting soils makes the preparation of such cores difficult. Thus managing for bee nest sites primarily requires minimal disturbance of sites where they are located, as many ground nesting bees nest in aggregations. One such protected "nesting bed" of 1.5 ha in Washington State (USA) has persisted for over 50 years, and produces an estimated 5.3 million bees annually to pollinate adjacent alfalfa seed production fields.

The small flies which pollinate cacao, upon which 90% of the world production of cacao is dependent, reproduce in the decaying organic matter on the soil surface, such as discarded cacao pods. Equally, nitulid beetles which are responsible for pollination of *Atemoya* or Custard apples (*Annona cherimola* and *Annona squamosa*) lay their eggs on decaying plant material. These soil-associated organisms are only very rarely explicitly managed, even though they may be critical to optimising production of crops where the pollinators breed in the mulch-soil interface including in addition to cocoa and *Atemoya* such crops as pomegranate and jujube.

Agricultural practices which may affect soil-nesting bees include tillage, irrigation and livestock management. Although the nests can be deep, below the plough layer, tillage has been correlated with sparser abundances which is likely due to disruption of the entry tunnels. Initial steps are being taken to overcome these problems and detrimental impacts on soil dwelling pollinators. For example, strip tillage, whereby only the soil that is to contain the seed row is tilled, has been used to minimise nest disturbance in some farms growing alfalfa in Europe.

Irrigation management is only a concern during the nesting period. Flood irrigation during nesting can damage nest cells. Cattle may also directly destroy nests through trampling and compacting soils sufficiently to deter ground-nesting bees, but conversely, alkali bees have been reported to preferentially nest in livestock corrals and lambing pens. The precise reasons for this are currently unclear and remain to be investigated.

Managing soil biodiversity to increase the sustainablity of agriculture

The striking increases in agricultural production during the last century have been wrought through even more massive transfers of inputs into farming systems. It has been estimated that the doubling of world food production since 1950 was accompanied by a seven-fold increase in the annual global rate of nitrogen fertilizer application and a 3.5-fold increase in phosphorus fertilizer application. However, we are rapidly reaching the limits, both in terms of availability of these inputs, and in the capacity of agroecosystems to remain productive under such high input management. Agricultural systems that currently rely on fossil fuel-based pesticides, fertilizers and heavy machinery, will need to adapt to the changing global realities, including increases in fuel prices, increasing soil and water quality deterioration, and the contribution of intensive agriculture to greenhouse gas emissions.

The real challenge is the encouragement of agricultural practices that, while using existing ecosystem services to increase production, also reduce the impact of farming practices on the environment. Use of mixed cropping, particularly using nitrogen fixing crops for example, is one methodology that can foster a thriving soil biota as well as being beneficial to crop production, while at the same time keeping nutrients in the farm's soils without them leaching out and polluting waterways.

Central to virtually all practices that contribute to sustainable agriculture are measures which cultivate and promote a diverse soil biota. The endogenous processes and potentials found within soil systems serve to sustain and enhance production in the long term, while promoting ecosystem health. Farming practices which increase soil biodiversity, through greater organic matter retention, reduced tillage, the use of integrated pest management (IPM), and cultivation of diverse crops through intercropping and/or crop rotation, can create multiple benefits for farmers, farming communities and societies worldwide.

Soils are complex systems in which living organisms are fundamental to the preservation of their quality and capacity of production. Soil organisms contribute to regulate soil characteristics, sustain soil fertility and break down toxic compounds. The next challenge in the evolution of agriculture demands that farmers focus more on working with the soil biota and their functions in soils to allow us to utilise soils sustainably, to the benefit of both agriculture and the environment.

Fig. 3.30: Squash bee, *Peponapis pruinosa.* (JC/USDA)

3.6 Urban

More than the half of the world's population lives in urban areas and in Europe this percentage is above 80%. Included in the definition of urban areas are all of the artificial surfaces such as industrial zones, commercial districts and transport infrastructure. A survey carried out in the year 2000 found that in the EU the urban fabric covered 180,000 km^2 corresponding to 7.6% of the EU25 territory (Fig. 3.31).

The soils of urban areas are strongly influenced by anthropogenic activities and this generally leads to a higher degree of contamination and degradation when compared to the soils of surrounding non-urban non-urban areas (Fig. 3.32). In general, urban soils, when they are not completely sealed by a layer of asphalt or concrete, are more affected by degradation processes, particularly contamination and compaction. Of course this is not always true, and in some cases it is possible to find soils in a better condition in terms of structure and organic matter content when compared to rural soils, for instance within urban parks or other green areas.

The major sources of pollution in urban environments are industrial emissions, traffic, burning of fossil fuels and wastes from industrial and residential activities. Soils are exposed to a continuous accumulation of contaminants that can come from either localised or diffuse sources. Typical pollutants of urban soils are heavy metals, recalcitrant organic compounds (e.g. PAHs, chloro-organic compounds) and also radionuclides. Furthermore, the through-fall of nitrogen is generally higher in urban soils when compared to rural soils.

Sealing and compaction as consequences of building processes and the physical pressure exerted on soil by vehicles and human "stepping" has led to a, more or less, complete inability of soil to be colonised by plants in some areas, or to provide a habitat for life below ground. Furthermore, the permeability to water and air is strongly reduced; this can lead to an increased likelihood of flooding owing to reduced water infiltration into urban soils. Data produced by research carried out in the USA showed that urban soils are generally 1-2 °C warmer, 50% dryer, 1.5 times more dense and lower in organic carbon than similar soil types in the rural environment. They were also found to have double the concentration of copper, lead and zinc than the surrounding rural soils.

Fig. 3.32: Soil in a road side verge. Soil is common throughout the urban environment in situations such as this. (CG)

These characteristics of urban soils have a strong influence on the soil biota that live within these soils as well as on the processes carried out by the soil organisms. In many cases, the abundance of soil organisms, their diversity, and particularly the food web structure are affected. In some cases, the abundance of organisms such as earthworms can be higher in urban environments, and the species diversity can be enhanced by the contribution of invasive species and by the existence of very diverse microhabitats. Concerning diversity one relatively common process in urban soils is "biotic homogenisation", being the occurrence of the same set of common species in separate urban soils. For example, in urban environments from a very diverse range of geographical positions, research has found that the common species of earthworms, isopods and diplopods showed a similar composition in both North American and European towns.

Fig. 3.31: A map showing the artificial areas, including urban areas, highways, railways, airports and industrial and commercial districts. The map was produced using CORINE data; Land cover provided by EEA for the year 2000. (CG)

Fig. 3.33: Some urban soils exist as small isolated patches, such as those supporting trees. These soils can become highly compacted due to pedestrians walking on them repeatedly. (CG)

Ecosystem functioning is also affected, with existing data showing contrasting behavior. In some cases urban soils have higher N-mineralisation, nitrification and respiration rates, whereas in other cases the reverse has been found to be true. The apparent inconsistencies of these results are associated to the huge variety of environmental conditions that are present in urban environments, including soil factors, climate and vegetation cover.

The urban environment is a complex mosaic of land cover/ land use and ecosystems. Within the urban environment the following main categories of land use can be found:

- Small residual soil patches, characterised by very high soil compaction (e.g. the central reservation between roads, the margins of railways, etc.) (Figs. 3.33, 3.37)
- Small, intensively used, urban parks (Fig. 3.34)
- Larger corridors along roads, railways and roundabouts
- Allotments (Fig. 3.35)
- Private gardens and lawns (Fig. 3.36)
- Sports and leisure green areas
- Archeological sites
- Marginal lands
- Wetlands
- Coastal areas
- River corridors, riparian areas
- Large extensive urban parks

Fig. 3.34: An urban park in the Italian city of Bologna. (CG)

Each of the above types of land use, listed in decreasing order of human pressure, presents very different potential habitats for soil organisms. Generally, urban settlements, being composed of such a diverse group of land uses, can act as biodiversity hot spots and reservoirs. For example, a quarter of the rarest forest, mires and aquatic plant species of Finland can be found in Helsinki. In the urban gardens of London, the species density of soil invertebrates is comparable with those found in natural ecosystems. Even brownfield sites, which cover large areas in European industrial towns, can represent a challenging opportunity for ecological restoration and for the creation of new biodiversity hot spots within urban areas.

However, urban areas can also be the spreading point for invasive and aggressive alien species, owing to their often reduced levels of diversity and for this reason special precaution should be adopted in the management of urban green areas.

Soil ecosystem services in urban areas

Many soil ecosystem services are perhaps even more crucial in the urban environment. One example is the water cycle regulation service, which is quite often a critical issue in towns, especially those that are prone to flooding. The fact that a large proportion of urban areas are completely sealed and other areas are severely compacted can lead to increased frequency of urban flooding. In this context, the importance of ensuring that the remaining unsealed soil area maintains the best hydrological properties possible can represent a possible mitigation against these types of hazards. In order to enhance the hydrological functions of urban soils, the role of soil biota, and the relationships between them and the vegetation cover must be taken into account.

Fig. 3.35: An allotment plot in Prague, Czech Republic. (PV)

Fig. 3.36: An urban garden in Bexhill, UK. (LJ)

Fig. 3.37: A series of urban soils found in Milan, Italy. (CG)

3.7 Soil Biodiversity in Extreme Environments

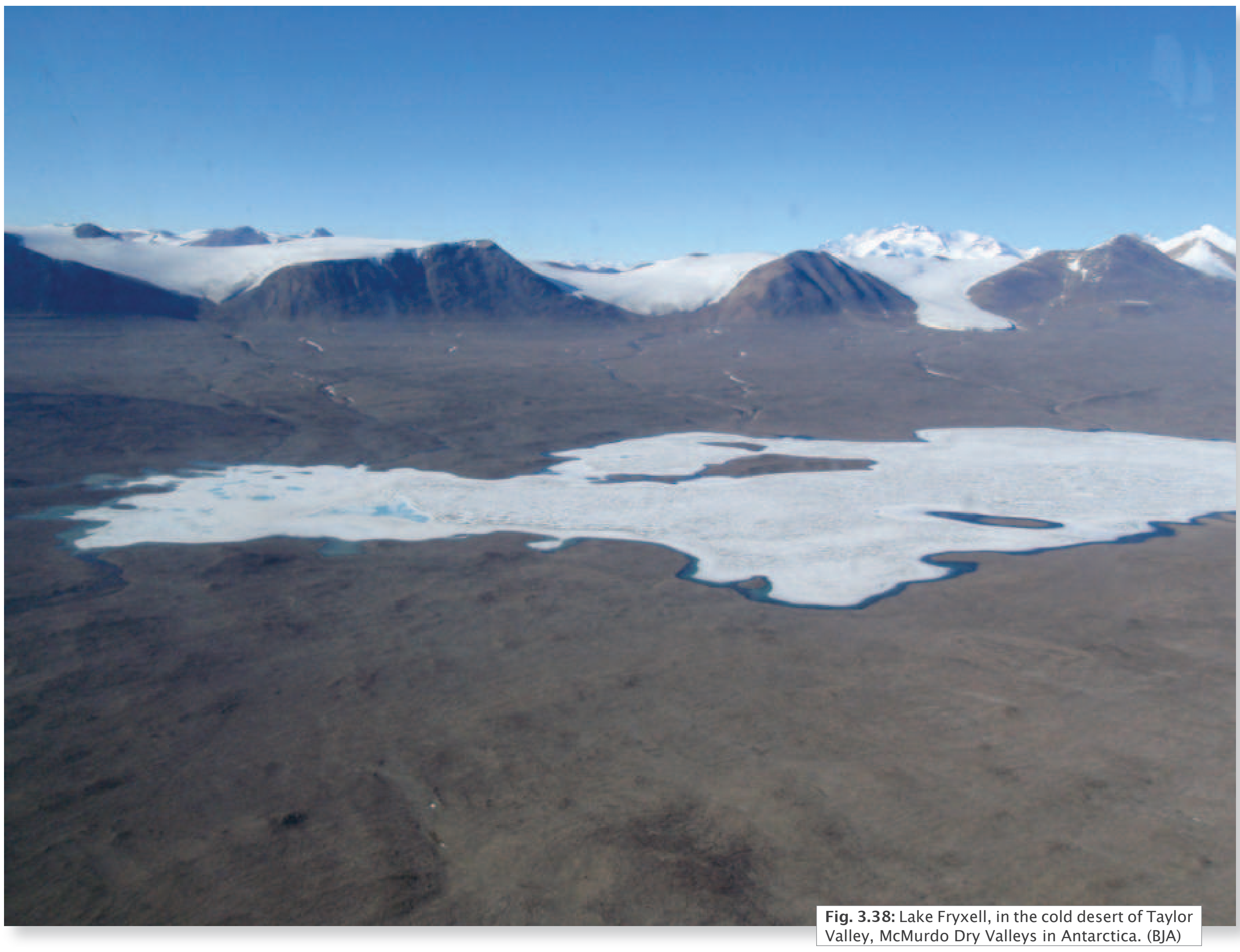


Fig. 3.38: Lake Fryxell, in the cold desert of Taylor Valley, McMurdo Dry Valleys in Antarctica. (BJA)

There are a number of terrestrial soil environments that can be considered extreme, from underground caves that stretch deep into the Earth, to cold or hot deserts (Fig. 3.38 and 3.39), and including the highest mountain tops. Many of these extreme ecosystems, once thought to lack life, are now known to host many organisms that have adapted physiologically to survive and perform critical ecosystem functions, such as biogeochemical cycling. Although extreme soil environments often support food webs that are limited in the number of species present, their diversity provides unique species and an often seperate gene pool for global biodiversity. Therefore, organisms of extreme ecosystems are viewed as valuable by many as a source for bioprospecting for commercial, medical or industrial use. Furthermore, recent evidence has shown that there is much to learn from extreme environments and their soils. They are, for example, proving a resource for scientific purposes, such as studies of the evolution of life on both our, and other planets, and in ecology for elucidating the role of species in ecosystem function. However, our knowledge of organisms and communities of extreme environments is limited and, therefore, a great need exists for acquiring information on the response and vulnerability of these species and extreme ecosystems to global changes (e.g. land use change, climate change). This is confounded by recent evidence which indicates that an effect of loss of species is likely to have a greater influence on processes and function in ecosystems with inherently low diversity, as found in extreme soil environments or highly disturbed soils. Therefore, as species extinctions are occurring at a rapid rate globally, it is important to identify those species that are present, determine whether they perform key roles in a particular extreme soil, and whether these species are common to similar extreme soil habitats. Because of the breadth of what might be considered an extreme environment, it is necessary to first provide a definition of 'extreme', and to give examples of extremes that organisms survive and even prosper under.

Extreme environments and their inhabitants

Life persists in most environments found on Earth, and some organisms survive and prosper in environments that to us appear harsh and unsuitable for life. Extreme environments range from cold habitats, such as cryoconite holes formed in glaciers, and the permanently frozen soils found at high latitudes and/or high altitude, to very hot habitats, such as desert soils which can reach temperatures in excess of 50°C!

Each of these environments presents significant challenges to life forms. Many organisms have adapted their growth and survival strategies to these conditions and for them the severe environment is the norm. Such organisms are collectively referred to as extremophiles, literally meaning 'lovers of the extreme'. Other organisms may only tolerate these extremes i.e. low or high temperature, low or high soil moisture, that may occur on a seasonal or even daily basis, but while they may be able to survive spells at these extremes, they do not grow or reproduce during these times of relatively extreme environmental conditions. Such fluctuations in environmental conditions can be extremely difficult for the biota to cope with, and have forced these biota to evolve specific survival strategies or life stages. Some have suggested that a stable environment could be considered normal and that only highly variable fluctuating environments should be considered extreme. However, for the purpose of this atlas, an extreme environment is defined as "any unmanaged (i.e. not including environments with human caused pollution or toxic waste) environment where conditions exist (e.g. temperature, moisture, hydrostatic pressure) that are beyond the range in which most organisms would grow optimally - whether a continuous or event based condition". While some factors, such as extreme temperatures and low water availability, may be considered the main stress factors for life, many other variables, including but not limited to pH, salt concentration, osmotic pressure, radiation, heavy metals and toxins, may also influence growth rates. However, it is beyond the scope of this chapter to describe all of these.

Fig. 3.39: The Chihuahuan Desert, a hot desert near Orla, Texas. (MC)

Extreme soil environments

There are many types of extreme soil ecosystems, and most of those factors listed in the previous section are commonly encountered by soil organisms (although some factors, such as high pressure and high radiation may be of little influence in most extreme soil environments). The most prominent extreme conditions encountered by organisms in soils include severe temperatures, low water availability, high and low pH values, and high salt concentrations (see Table 3.3). However, in most extreme soil environments there is generally a high spatial and temporal variation of stress factors that may act in concert to influence the organisms' growth. Locally extreme conditions are often reflected in the topography, geology, climate and weather patterns and the vegetation.

Deserts are defined by precipitation, or the lack of it, and are generally classified as either: semi-arid (<600 mm precipitation year^{-1}), arid (<200 mm precipitation year^{-1}) or hyper-arid (<25 mm precipitation year^{-1}). Deserts are found in hot regions, relatively mild areas in rainfall shadows, in coastal areas, at high altitude and in the Polar Regions. The most extreme soils are the hot and cold deserts where the organisms experience not only low water availability but also extreme temperatures. Within deserts the local weather patterns, topography and vegetation (or lack thereof) have a great influence on the below ground communities which, therefore, show a considerable spatial and temporal heterogeneity. However, in general, the biodiversity tends to decrease with the severity of water limitation within and between desert types and in the most extreme hot and cold deserts (or in the most extreme areas within hot and cold deserts), the diversity of soil biota is limited to a few groups of organisms.

Table 3.3: Some examples of extreme conditions experienced by soil organisms, where such conditions occur and the organisms that are common in these extreme soils.

Environmental condition	Examples of soil habitat types	Definition of organisms	Example of type organism(s)
Temperature - Low	Polar and Alpine soils including the permafrost layer	*Psychrophile*: grow optimally at <20°C *Psychrotroph*: grow optimally at>20°C but can grow at lower temperatures	The nematode *Scottnema lindsayae* is the most abundant invertebrate in the McMurdo Dry Valleys, Antarctica and thrives in the dry cold soils found here. The nematode *Panagrolaimus davidi* found in Victoria Land, Antarctica, shows highest growth rates above 20°C but can grow at much lower temperatures and can tolerate intracellular formation of ice crystals. A wide variety of bacteria dominate in very cold soils.
Temperature - High	Hot deserts and geothermally heated soils	*Thermophile*: grow optimally at 60-80°C *Hyperthermophile*: grow optimally >80°C	The only truly thermophilic soil organisms are the microbes, but a wide variety of soil mesofauna can survive exposure to very high temperatures including nematodes, tardigrades and rotifers. Termites and ants are often the dominant invertebrates in hot deserts.
pH – Low	Bogs; Peatlands	*Acidophile*: grow optimally at pH <3	Enchytraeids are often the dominant invertebrates in peaty soils that can be very acidic, and fungi are the dominant microbes under these conditions.
pH – High	Some Antarctic soils	*Alkaliphile*: grow optimally at pH <9	Mostly microbes grow at high pH values
Water - Low	Hot and cold deserts; Exposed surface soils	*Xerophile*	Similar to environments with high or low temperatures. Many species of soil biota have adapted to tolerate desiccation.
Salinity – High	Many hot and cold desert soils	*Halophile*: >0.2% soluble salt	Archaea and bacteria represent most of the halophilic species found in soils, but many species of soil mesofauna including the nematode *S. lindsayae* can tolerate high salt concentrations.

Hot deserts

Hot deserts are distributed widely across the globe (Fig. 3.39 and 3.40). Here, soil organisms not only need to cope with high temperatures, as well as large daily fluctuations in temperature between day and night, but also limited water availability due to high evaporation rates and low rates of precipitation, and in some areas, high salt concentrations. Globally, each desert tends to support different species, but as research on the biodiversity of hot desert soils is limited to some well-explored areas, an estimate of the total number of species found below ground in hot deserts cannot easily be given. Furthermore, species distribution in desert soils is influenced by the soil chemistry and physical factors, vegetation type and rooting depth, local and regional precipitation patterns, and the land area classified as desert, making species diversity highly variable across any given desert region. Generally, however, soil biodiversity is lowest in dry barren soils with high mineral content. Thus, species estimates for soil biodiversity in deserts are likely underestimated.

Termites and ants, which can function by altering the physical structure of soils and as such are often called 'ecosystem engineers', are often the most abundant animals in hot desert soils. However, the species richness of both groups is generally lower than that found in other ecosystem types, as these invertebrate communities are often dominated by a few desert-adapted species. Termites and ants appear to have a similar role to earthworms and enchytraeids in more temperate and tropical organic soils (i.e. ecosystems with high primary production). Therefore, earthworms and enchytraeids, which can be numerically abundant in, and have a great impact on turnover of organic matter of organic soil, are less important in the highly mineral soils of deserts. However, earthworms and enchytraeids can be present in, and influence the decomposition rates of litter layers in hot deserts. As well as termites and ants, the most numerically abundant soil fauna in desert soils are microarthropods and nematodes. Microarthropods are often dominated by the oribatid mites, which in many desert soils account for more than 50% of microarthropods, but other mite groups, springtails and other small arthropods also contribute to the total pool of microarthropods. The species richness of microarthropods and nematodes in desert soils are generally low compared with other soils. For instance, a study investigating the nematode richness in 4 deserts in North America found 9 taxa in the Sonoran Desert, 11 taxa in the Chihuahuan desert and 17 taxa in the Great Basin and the Mojave deserts compared with hundreds which could be expected to be found in temperate grasslands. It appears that areas with greater species richness of plants also support a greater diversity of soil fauna. For example, 26 species of mites (Oribatida, Prostigmata and Mesostigmata) and 4 species of springtails were found under shrubs on the edge of a small arroyo in the Chihuahuan Desert. The Australian deserts also show a limited species richness of soil microarthropods. In a large survey of arid south Australian ecosystems (<252 mm precipitation per year) no more than 23 species of mites and 6 species of collembolans were recorded in the soils sampled. In comparison, hundreds of species of mites and nematodes are often found locally in tropical and temperate grasslands and forests.

In the more extreme hot deserts, vascular plants are absent as these cannot live due to the lack of available water and the soils are often barren and appear lifeless. Yet, even here there is life, although this tends to be limited to microbes. For example, a survey of samples collected from sand dunes in the pre-Saharan desert of Tataouine, Tunisia, which receives approximately 115 mm precipitation every year and virtually no rain at all during summer, revealed a wide variety of microorganisms with more than 90 different taxa representing over 10 different bacterial groups and the archaeal group Crenarchaeota. The Yungay region of the Atacama Desert is recognised as one of the driest ecosystems on Earth. The driest areas of the Yungay support no vascular plants or invertebrates, and the soil biodiversity is very low. Although water is crucial for life, the species here seem well adapted: cyanobacteria grow beneath quartz rocks in the soils of the Atacama Desert. The quartz allows light to penetrate and support photosynthesis and the soils beneath the quartz contain more moisture than the exposed surface soils providing a habitat for cyanobacteria. However, these communities may not occur everywhere across this desert with only 2 cyanobacteria and a μ-Proteobacteria species being found in the driest areas (<2 mm precipitation per year). Most of the quartz rocks investigated were not colonised, indicating the extreme harshness of this desert for life. In short, the overall below ground diversity found in hot desert soils globally is substantial although the small-scale diversity appears to be very limited compared to other wetter, vegetated 'normal' soils. Our knowledge of the biodiversity of hot deserts, and the influence of this diversity on ecosystem function, is however limited. Many people live near and in deserts, and rely on the ecosystem services they provide, such as erosion prevention. As climate change alters desert ecosystems, information on the biodiversity in soils and their influence on ecosystem function will help with management options.

Fig. 3.40: Sand dunes with sparse plant growth in the Tunisian Sahara near Ksar Ghilane. (JS)

Cold soil environments

The coldest environments on Earth are found at high latitudes and/or high altitude (i.e. Polar Regions and alpine areas) and cover a large proportion of the Earth's land surface area. All of these areas are undergoing significant changes in biodiversity due to climate warming (see Section 5.1.3). The landscape in the Polar Regions is dominated by tundra, bare soil and rocks, or covered by snow or ice. Tundra is a vegetation type that is most often associated with the Arctic, but vegetated areas of Antarctica and some alpine areas also fit this classification (Fig. 3.41). This vegetation type is dominated by lichens, mosses, grasses, sedges, herbs and some dwarf shrubs, and is associated with cold annual temperatures, short growing seasons, high frequency of freeze-thaw cycles and the presence of permafrost, i.e. permanently frozen soil.

The plant community in the Arctic tundra is generally specious and fairly productive, compared with other extreme environments, providing a high input of organic matter into the soil food web (Fig. 3.42). Therefore, despite the cold temperatures, with annual average temperature below -10°C at many sites, the Arctic tundra soils support more than 700 mite species, 400 species of collembolans, 500 nematode species and 70 species of enchytraeids and earthworms. However, the species richness and density of invertebrates within a site tend to be low compared with temperate soils. For example, in the high Arctic it has been found that the communities of oribatid mites and collembolans were plant specific and that only 6-7 and 4-6 species of oribatid mites and collembolans, respectively, were present in the soils associated with 6 different plant species. Similar results have been found for plant species on Svalbard. In contrast, nematode communities are generally more diverse than microarthropod communities. For instance, 29 species of nematodes have been found in the top 3 cm soil of a sub-alpine heath in northern Swedish Lapland, although this is well below the diversity of nematodes found in non-extreme ecosystem types. New molecular tools do, however, indicate that the diversity of soil flora may be substantially greater.

The diversity of the microbial communities in the Arctic is less known but molecular methods indicate that Arctic soils also support a high diversity of microbial communities. For example, in one study of Siberian tundra soils, where winter temperatures often fall below -40°C, found 43 unique genetic sequences, related to the Proteobacteria and Fibrobacter groups. Furthermore, it has been demonstrated that bacterial diversity in Arctic tundra soils can have over 2000 phylotypes, a high proportion of which might not be found elsewhere.

In contrast to the Arctic, several factors contribute to a lower terrestrial diversity in Antarctica, and especially in the polar deserts of continental Antarctica. Colonisation of terrestrial habitats in Antarctica is limited by the Southern Ocean combined with predominant weather patterns, and so colonisation events are relatively rare. This means that many of the terrestrial inhabitants of Antarctica are endemic species that have had to survive several glaciation events. Furthermore, the climate is generally more severe than at comparable latitudes in the northern hemisphere, and this harsh climate is a considerable constraint to the Antarctic fauna and flora. Most of continental Antarctica is covered by ice (only about 2% of the land mass is ice-free) and hosts one of the most extreme soil environments, with mean annual air temperatures below 0°C and very limited precipitation (in some areas <100 mm year^{-1}).

All of this contributes to a relatively low biodiversity, which is very evident above ground with only 2 species of vascular plants and 2 higher insects found in maritime Antarctica and none at all in continental Antarctica! Despite this, overall the Antarctic soils support at least 225 species of mites, 85 species of collembolans, 49 species of nematodes, 30 species of rotifers and 41 species of tardigrades, of which about 170 are free-living endemics. This is just the number of species of each group which have currently been found, and so there is a possibility that these numbers will increase further. Microbial communities are also fairly diverse and show a high degree of endemism. For instance, 35 different species representing 22 different genera of microfungi have been found in the Windmill Island region, 28 fungal taxa representing 18 different genera in Victoria Land, and at least 24 species of endoparasitic and nematode trapping fungi occur throughout Antarctica. Cyanobacterial communities are widely distributed throughout soils in Antarctica, even in the barren soils. For example, 15 taxa have so far been isolated from 18 polygon soils with a maximum of 12 taxa from one single soil sample at Cierva Point on the Antarctic Peninsula, and 6 taxa from 124 soil samples in the La Gorce Mountains, one of the most southern ice-free areas of Antarctica. The species richness of bacteria is still not as well described but recent studies suggests that there is a considerable diversity of bacteria with a high proportion of novel species. As in hot deserts, soil organisms tend to be very unevenly distributed across the Antarctic desert landscape with greater biomass and diversity in wetter microhabitats. The biotic hotspots of Antarctic soils include vegetated soils and soils beneath bird nests and moss beds. However, the species richness of soil fauna in the most extreme parts of Antarctica is much lower.

Fig. 3.41: Autumn tundra near Red Dog Mine, Alaska. (JS)

One of the most extreme cold deserts is the McMurdo Dry Valleys of Antarctica (Fig. 3.43), where low precipitation (<100 mm per year) and average annual temperatures of about - 20°C limit water availability to a very short time window during the austral summer (25-75 days with temperatures above 0°C). The Dry Valleys are dominated by soils with very low nutrient availability and high salt concentrations, in addition to high daily fluctuations in temperature, leading to frequent freeze-thaw events. It, therefore, represents one of the most challenging environments for life on Earth. The large expanses of very dry soils (often <5% soil moisture) are dominated by the nematode *Scottnema lindsayae*, a microbial feeder, which often represents the only larger soil animal in these soils. Experimental evidence suggests that a warming climate would decrease the extent of these dry soils, and thereby reduce the range of *S. lindsayae*. *S. lindsayae* is the most abundant invertebrate in the McMurdo Dry Valleys, and it has been estimated to be responsible for 6-7% of soil organic carbon turnover, a significant amount, indicating that climate changes may have critical impacts on ecosystem processes. In areas with greater soil moisture the below ground communities are generally more diverse. Here, the nematode genera *Plectus* and *Eudorylaimus* occur in concert with several species of tardigrades and rotifers and a few species of microarthropods. The microbial communities in the McMurdo Dry Valleys can be relatively diverse, but the diversity of microbes, as with invertebrates, decreases with decreasing soil moisture. In short, Antarctic soils harbour a high number of novel microbial and animal taxa.

Fig. 3.42: Life flourishing on a Hyperskeletic Leptosol in Northern Canada in the form of the Arctic Poppy *(Papaver radicadum)* - one of the hardiest plants on the planet. Even these poor soils are an important component of the Earth's environment. (CT)

One dominant feature of cold environments is the presence of a permafrost layer (i.e. ground that remains frozen for more than 2 years). Permafrost covers a large proportion of the Earth's land surface, and presents some adverse growing conditions for biota including extreme cold, and frequent freeze-thaw cycles. Far from being devoid of life, microbial communities of permafrost are very diverse. For example, more than 30 bacterial genera have been isolated from Arctic permafrost soil collected on Ellesmere Island in Canada, and almost 50 strains of bacteria have been found in a permafrost sample collected on the Qinghai-Tibet plateau. Moreover, some microbes found in the permafrost are active during cold periods and have been shown to be able to grow at temperatures as low as -39°C. These examples demonstrate that polar soil environments show substantial differences in their soil communities and that even in the most extreme cold desert there are more species than might be thought.

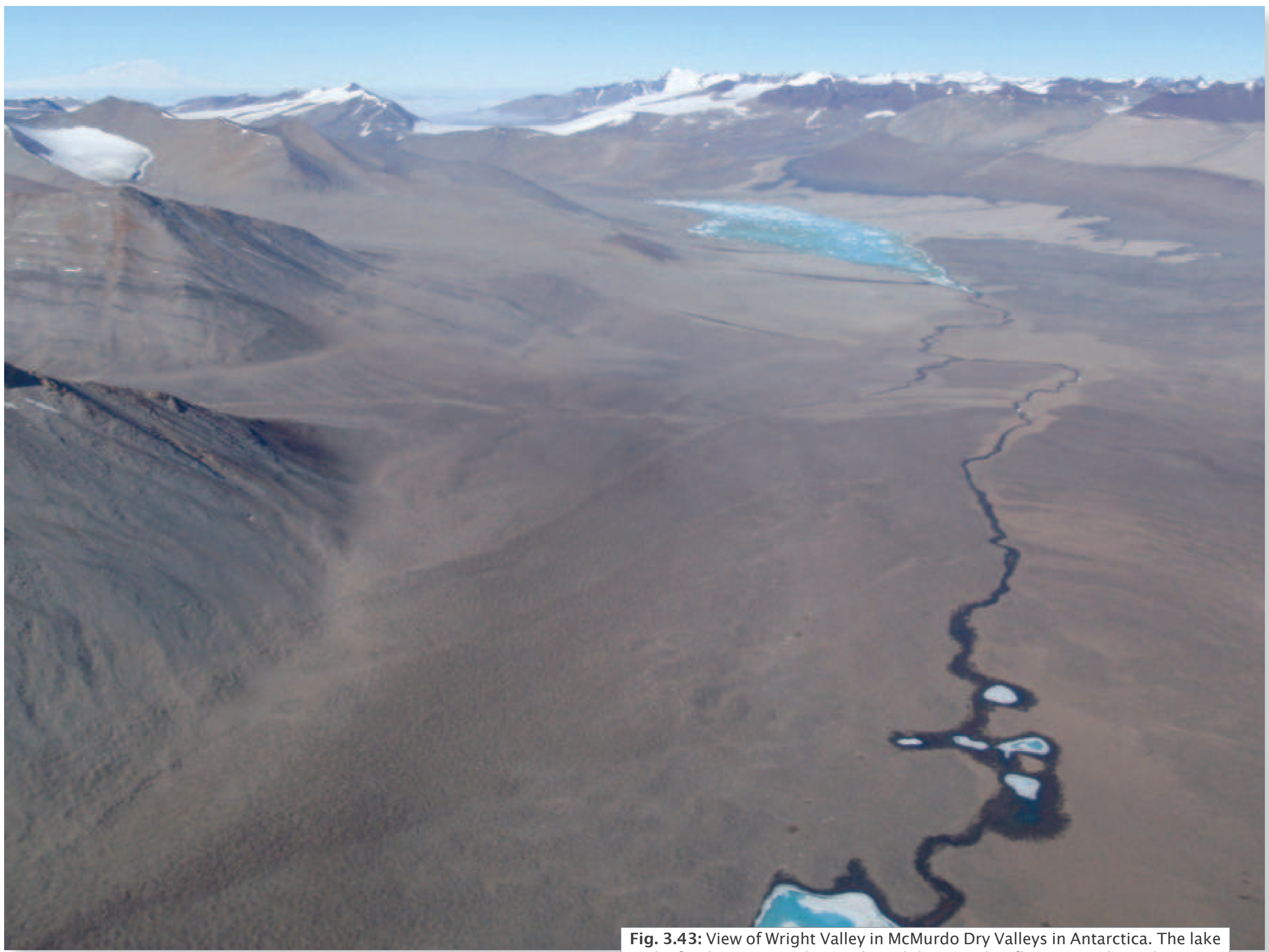


Fig. 3.43: View of Wright Valley in McMurdo Dry Valleys in Antarctica. The lake in the far distance is Lake Vanda and the river that flows toward it is the Onyx, the largest river in Antarctica. The dry soils in this valley are characteristic of the extreme polar desert of the dry valleys of Antarctica. (BJA)

Other extreme soil environments

As well as extremes of hot and cold there are many other types of extreme soil environment. Saline soil environments, for example, occur primarily in dry regions, but are becoming more prevalent in many agricultural soils and results in soil degradation and often reduced yields and even plant death (Fig. 3.44). Saline soil environments are defined as being is any soil with a concentration of > 0.2% (w/v) of soluble salts. Some organisms have adapted well to these environments so well that they grow best at salt concentrations of 15-25% and are even often unable to grow at low salt concentrations. The diversity of archaea in saline soils is particularly impressive. For example, a small scale study of archea diversity in soils with salt concentrations ranging from 7 to 18% found an estimated 104 to 177 unique phylotypes in each soil sample comprising 7 different phylogenetic groups. The archaeal communities changed over the salt gradient and diversity increased with greater salt concentrations indicating the importance of small-scale variation in soil properties on soil biodiversity. At more moderate salt concentrations bacterial diversity increases dramatically.

Although there are many other types of extreme soils, hot soils not associated with deserts and found near geothermal activity, such as hot springs and volcanoes are particularly interesting (Fig. 3.44). These can represent very distinct microhabitats and in some cases are 'hot spots' for extreme soil biodiversity. For example, the environmental conditions in continental Antarctica are considered the coldest, driest and windiest on earth, but not all of continental Antarctica is cold. Several active volcanoes create geothermally heated soils in an otherwise cold environment. These heated soils support distinct communities both above ground (i.e. mosses) and below ground, with several endemic species of bacteria being found at these sites.

Summary

Evidence shows that there are several types of extreme soil environments occupying a range of terrestrial habitats and that these are inhabited by a unique collection of species, many of which are found nowhere else on Earth. As many of the organisms found in extreme environments have evolved and adapted to a particular set of extreme conditions they are genetically very different from many of the organisms found in more 'normal' environments.

Although the biodiversity of these extreme environments can range from many species to only a few, and include many higher taxa or only a few microbes, these extreme soil environments, represent an invaluable pool of novel genes as well as unique functions. For example, many of the organisms found in extreme environments, including extreme soils, have evolved to function under conditions in which most organisms cannot survive. These organisms may provide ecosystem functions or services beneficial for human-well being, or be utilised for biotechnology to produce goods for multiple uses. Currently, some of the most extreme hot and cold deserts appear to be devoid of life, but as with other ecosystems, the refinement of molecular and other techniques may eventually reveal a diversity of species, which may prove useful as noted above. In conclusion, it is clear that extreme soil environments contain an invaluable pool of extraordinary species.

What is salinity?:

Salinity is the degree to which water contains dissolved salts. Normal seawater has a salinity of 33 parts per thousand. This rises to 337 parts per thousand in the Dead Sea.

Fig. 3.44: (Left) Salt affected soils, such as this example from Hungary, often exhibit a white or grey salt crust that covers the surface of the ground. While high concentrations of salt may give the soil a pH of around 8.5 or higher and interfere with the growth of vegetation, several specially adapted plants and soil organisms thrive in such conditions. Salt affected soils often exhibit a temporal or seasonal variability which can affect the type and amount of soil organisms. (ED) **(Right)** Soil organisms can still be found in the areas subjected to active volcanic activity where high ground temperature and high levels of sulpher preclude the existance of vegetation and most living matter. (AJ)

4.1 How does Soil Biodiversity Affect Ecosystem Function?

Soil organisms are vital for soil functioning as they carry out a range of important processes which underpin the delivery of a numerous ecosystem goods and services (See Fig. 4.1) In fact, the functions performed by soil organisms can have impacts at the global scale, such as by locking up carbon in the soil or releasing it, with consequences for global climate. These 'functions', which are often the product of complex interactions between organisms within ecosystems, are called 'ecosystem functions'.

The remarkable variety of life below ground is explored in more detail elsewhere in this Atlas, but it is worth stressing at the outset that effective ecological functioning, and hence the future of our civilisation, crucially depends upon the soil biota. Life in earth drives life on Earth, and soil biodiversity represents a vast biological engine, driving processes upon which our very survival depends.

Why is biodiversity important for soil function?

The relationships between biodiversity and function are complex and somewhat poorly understood, even in above ground situations which are more easily studied and arguably less complex. The exceptional complexity of below ground communities further challenges our understanding of soil systems. Three important mechanisms which underlie the relationships between biodiversity and function are:

Repertoire: for a biologically-mediated process to occur, organisms that carry out that process must be present. A diverse system will inherently carry a wider suite of potential abilities that will underwrite a wider range of functions

Interactions: most soil organisms have the capacity to directly or indirectly influence other organisms, either positively or negatively. A greater diversity of organisms offers a greater potential for interactions, and a more complex network of interactions may be more adaptive to change and resilient to disturbance

Redundancy: It is important to note that redundancy from an ecological view point is not a negative term and has no link to whether something is necessary, as it is more generally used. Within ecology, the more organisms there are that can carry out a function in a particular soil, the more likely it is that if some are incapacitated or removed the process will remain unaffected; those that remain may fill the gap (Figure 4.2 and 4.3).

There is theoretical and experimental evidence that soils with greater levels of biodiversity are more resistant to environmental disturbances, and are in turn more resilient (i.e. show an increased tendency to recover following such stresses) than those with reduced levels of biodiversity. There are also some circumstances where if the level of biodiversity is reduced below a certain level or threshold, the functions can be irreversibly reduced or compromised. These circumstances tend to involve very low levels of biodiversity and are more related to process carried out by relatively few species or groups of organisms (know as "ecologically narrow processes" - see below). This can be of great significance in restoration ecology, whereby efforts are made to restore damaged ecosystems to their pre-damaged states. In some situations 'biotic barriers' to effective restoration of ecosystems can occur. It should be noted, however, that the expected level of diversity of a given group of organisms is site specific and varies greatly between ecosystems and biomes.

Biodiversity and community structure

Some of the reasons why the diversity of the soil biota is in itself important are outlined above. However, effective functioning also requires an appropriate range of properties (or 'traits') to be present within the community. It is therefore considered that functional diversity may be a more appropriate way to consider the biotic status of soils than biodiversity *per se*.

The main argument for measuring functional diversity as opposed to taxonomic diversity (i.e. the number of species of groups or organisms present) is that the main issue concerning ecosystem functioning is whether the community has an appropriate repertoire of functional capabilities. This relates more to the actual functional traits of the organisms rather than how taxonomically diverse they are. This is because for many soil organisms, and particularly microbes such as bacteria, the relationships between their taxonomic status and their functional traits in the soil are often variable.

Communities are often also structured via a hierarchy of tropic levels (often referred to as food chains or food webs), a concept used to describe the patterns of feeding inter-dependencies between different biotic groups which also shows how energy is transferred though the system. This has huge functional implications since many of key nutrients are cycled through ecosystems and are important for ecosystem functioning as well as soil fertility and other ecosystem functions important to humans (often referred to as 'ecosystem services' - see Table 4.1).

Broad and narrow processes and the insurance principle

Ecosystem functions can be split into broad or narrow processes. Broad processes tend to be carried out by a greater number of species or groups of organisms, whereas narrow processes tend to be carried out by fewer species or groups of organisms and so are more easily compromised by ecological disturbances. This has lead to the formulation of a widely accepted theory known as "functional redundancy", whereby functions may not be affected by the loss of a species from an ecosystem if other species are able to perform the same function (Figure 4.2 and 4.3). Again, it is important to note that here redundancy is not a negative term, but relates to the fact that several organisms performing the same task means that there is insurance within the system and if one organism group is lost another can continue to perform the function.

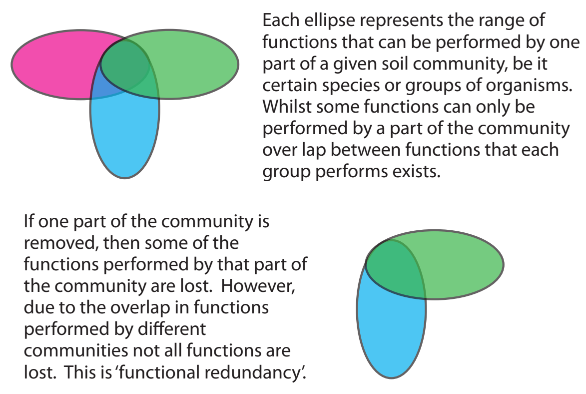


Fig. 4.2: A schematic representation of functional redundancy. (SJ)

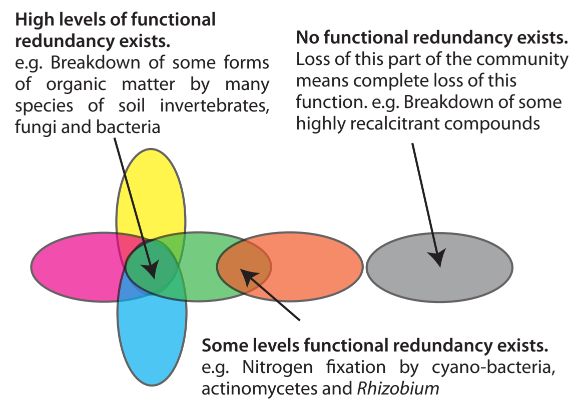


Fig. 4.3: A Schematic representation showing different levels of functional redundancy for different examples of ecosystem functions. (SJ)

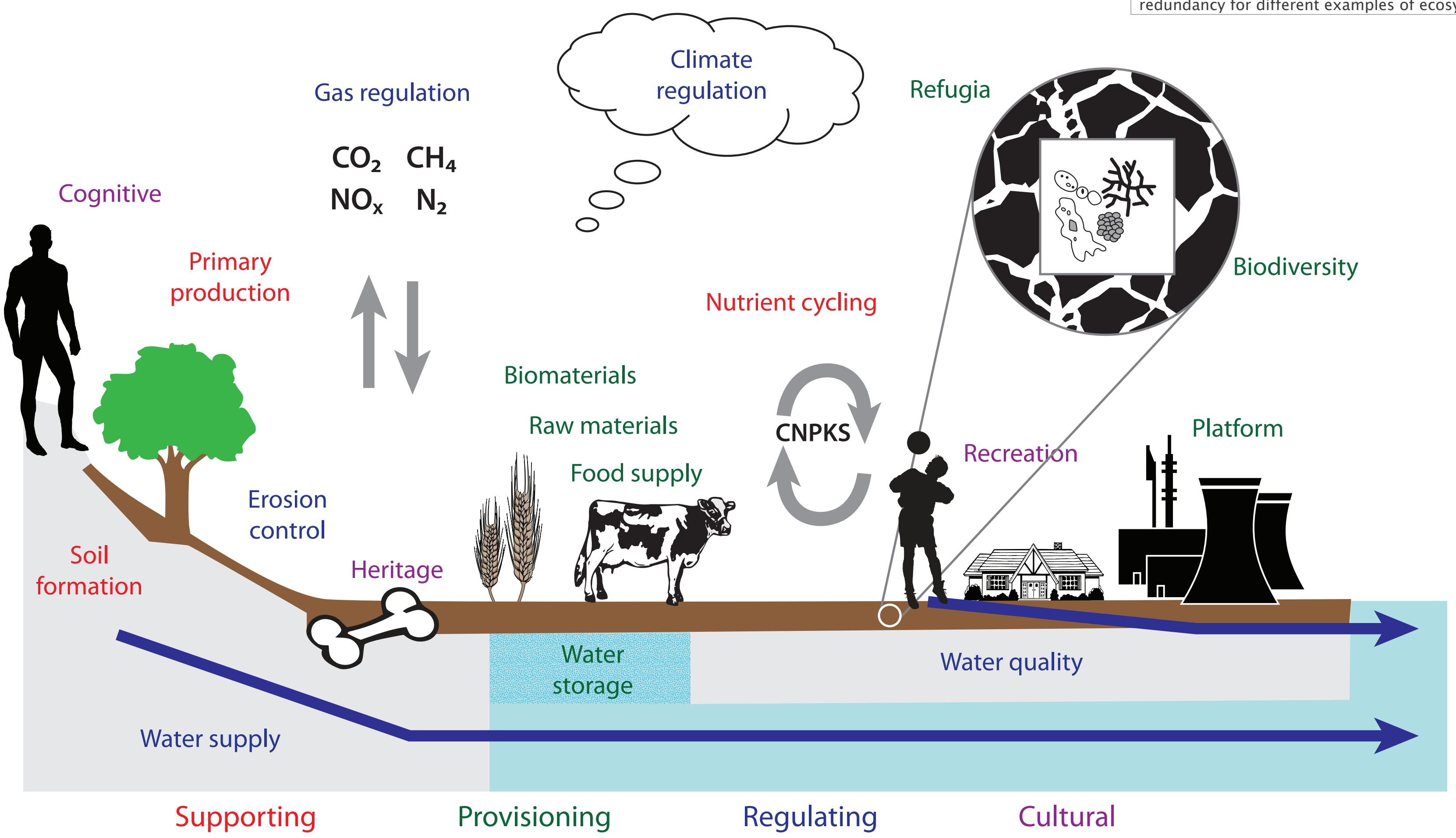


Fig. 4.1: A schematic description of the functions performed by soil. From Haygarth and Ritz, Land Use Policy 2009

Table. 4.1: A list of the ecosystem services along with example organisms which provide the services. From Haygarth and Ritz (2009).

	SOIL-BASED ECOSYSTEM SERVICES	ASSOCIATED GOODS, PROCESSES AND FUNCTIONS	SPECIFIC EXAMPLES OF SOIL BIOTA INVOLVEMENT
SUPPORTING	a. Soil formation	Mineral weathering of parent material and pedogenic processes	Lichens Organic acid production by many bacteria and fungi
	b. Primary production	Direct: fixation of carbon Indirect: interactions with vascular plants (principal autotrophs)	Cyanobacteria, e.g. *Nostoc* sp. Algae, e.g. *Calothrix* sp. Links to many services and functions
	c. Carbon cycling	Organic matter decomposition: Physical: comminution and mixing Biochemical: primary: enzymatic decomposition secondary: faunal ingestion	Macrofauna, mainly earthworms, millipedes, termites, ants and insect larvae Many bacteria, archaea, fungi Many protozoa, nematodes, other fauna
	d. Nutrient cycling	Nitrogen: N-fixation: free-living root-associative symbiotic ammonification nitrification denitrification ericaceous mycorrhizas Phosphorous: P-solubilising bacteria and fungi Mycorrhizal mediated plant uptake Sulphur: Iron: oxidising/reducing Manganese: Other metals and trace elements	e.g. *Azospirillum* sp. *Azotobacter* sp. *Rhizobium* sp. Many bacteria e.g. *Nitrobacter* sp. *Pseudomonas* sp. *Hymenoscyphus* sp. e.g. *Bacillus* spp. / *Aspergillus* sp., *Glomus macrocarpum* e.g. *Gigaspora margarita, Glomus intraradices* e.g. *Beggiatoa* sp./ *Desulfotomaculum* sp. *Acidithiobacillus ferrooxidans* / *Geobacter* sp. *Ascomycota* sp. / *Pseudomonads* sp. e.g. *Microbacterium arborescens*
PROVISIONING	e. Platform	Soil structural stability	Many microbes e.g. via bacterial adhesion, fungal binding; formation of clay-humus particles by earthworms and other macrofauna
	f. Water storage	Soil structural dynamics (porosity)	Much biota, e.g. adhesion, binding, burrowing, restructuring, especially anecic earthworms
	g. Refuge	Soil structural dynamics (porosity)	Much biota, e.g. adhesion, binding, burrowing, restructuring
	h. Biodiversity/genetic resources	Reservoir for adaptive and evolutionary processes Source of new biotech pharmaceutical compounds	All biota Many as yet unknown!
	i. Food supply	Via primary production, edible fungi	Entire biota e.g. *Lentinula edodes* (Shitake)
	j. Biomaterials	Antibiotics single-cell protein	e.g. *Actinomyces* sp. *Fusarium venenatum* (Quorn®)
	k. Raw materials	Industrial crops via primary production	Entire biota
REGULATING	l. Water quality regulation	Purification via: structural dynamics (porosity) xenobiotic and pathogen degradation	Much biota, e.g. adhesion, binding, burrowing, restructuring, plus bacterial/fungal biodegradation
	m. Water supply regulation	Structural dynamics (porosity)	Much biota, e.g. adhesion, binding, burrowing, restructuring
	n. Biotic regulation	Food webs C and nutrient cycling	Entire biota
	o. Atmospheric gas regulation	Carbon dioxide Methane: emission (methanogens) absorption (methanotrophs) N oxides (denitrification)	Entire biota e.g. *Methanococcus* sp. *Methylococcus* sp. *Pseudomonas* sp.
	p. Climate regulation	Via interactions with gas regulation	e.g. Photoautotrophs, Methanotrophs
	q. Erosion control	Structural dynamics Surface stabilisation	Much biota, e.g. adhesion, binding, burrowing, restructuring
CULTURAL	r. Cognitive	Via underpinning soil system Charismatic species	Entire biota e.g. moles, earthworms, mushrooms
	s. Recreation	Underpinning sport and parkland grassland	Entire biota
	t. Education	Learning resources and potential	
	u. Health and wellbeing	Links to entire soil system via all goods & services provision	
	v. Heritage	Interactions with archaeology	

4.2 Bioweathering

One important function of the soil biota, and soil biodiversity, is the weathering of rock. Weathering of rock is the process of the breaking down and changing of rocks and sediments at or near the Earth's surface by biological, chemical, and physical agents or combinations of them. Classical examples are: the disintegration of rocks by water in cracks freezing, thereby expanding, and forcing the rock to break (physical weathering) and rocks dissolving in acidic rainwater (chemical weathering). Biological weathering was classically regarded as 'indirect' by enhancing physical weathering (e.g. in the moist environment underneath mosses and lichens growing on rock surfaces) and chemical weathering (acids released by plants or in the litter layer). However, scientific progress over the last decades has shown remarkable 'direct' microbiological weathering of rocks, while fungi have also been shown to play a role in the neoformation of minerals in soils.

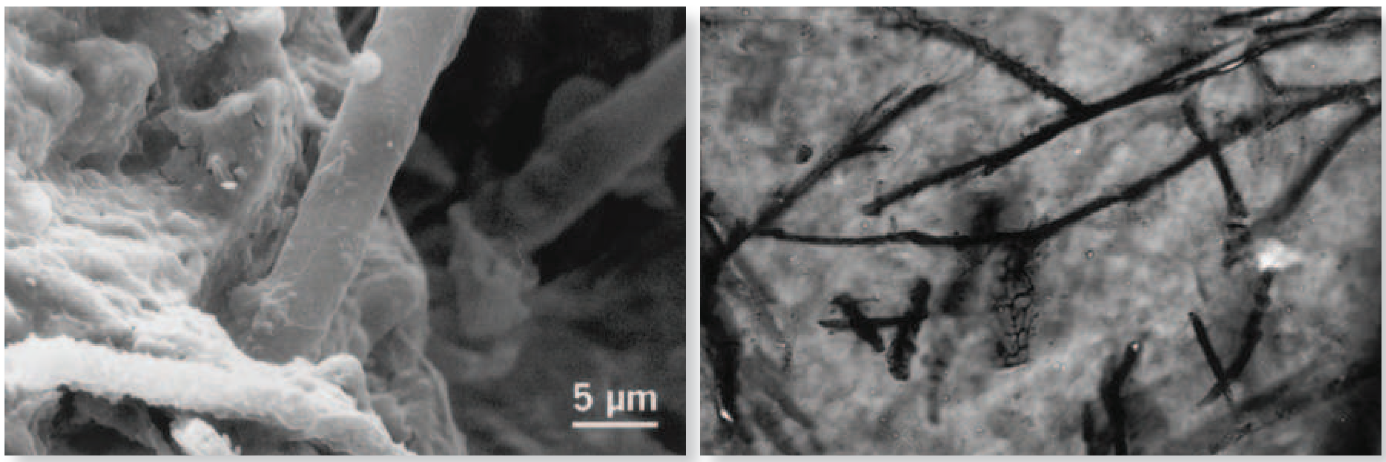


Fig. 4.4: Rock-eating mycorrhiza. **Left**; Scanning electon micrograph showing two fungal hyphae penetrating a feldspar grain: (EHd) **Right**; Thin section micrograph of a feldspar grain from a Podzol E horizon, criss-crossed by tunnels of about 5μm in diameter; The feldspar grain originates from the E horizon of a 5400-year-old sand dune along Lake Michigan. (LvS)

Table 4.2: Selected examples of bacteria solubilising minerals

Bacteria	Solubilised material
Rhizobium	Phosphate
Burkholderia	Biotite, phosphate, iron, granite
Azotobacter	Pyrite, olivine, geothite, hematite
Geobacter	Iron
Acidithiobacillus	Pyrite
Pseudomonas	Biotite, phosphate, iron
Shewanella	Smectite, iron, calcite, dolomite
Paenebacillus	Biotite, bauxite
Streptomyces	Hornblende

Bioweathering Mechanisms

Bacteria, fungi, and lichens have been found to weather rocks via a variety of mechanisms and are regarded important 'producers' or 'liberators' of minerals from rocks (Table 4.2), which then continue their existence as nutrients for plants. The recognised mechanisms mostly involve redox reactions, or the production of organic acids and chelates by bacteria and fungi.

Fungi are more mobile than bacteria and have additional ways of weathering rocks. Fungal hyphae have left striking evidence of their weathering powers. Figure 4.4. shows bioweathering of feldspar, a common mineral component of granitic rocks. 'Mineral tunneling' by fungi has been observed mostly in feldspar particles in E horizons of Podzols which are widely distributed over Europe, particularly in the north (Fig. 4.5). This process causes an influx of calcium (Ca) and potassium (K) into the ecosystem and as such as one of the many important ecosystem services provided by fungi.

These minerals may diffuse through the ecosystem and so aid soil fertility in soil types other than the Podzols where the minerals were initially released. The mechanism involved is believed to be mineral dissolution by anions exuded at the tips of mycorrhizal hyphae. The osmotic pressure produced by fungal appressoria (infection organs) can be up to 10-20 $\mu N/\mu m^2$, which is sufficient pressure to penetrate inert bullet-proof material! Over time, as the hyphae grow they may form tunnels into the solid mineral particle, or grooves on the surface.

Much remains to be discovered regarding the role of soil biota in weathering processes and relative importance compared to physicochemical weathering of many minerals. For example, Figure 4.6 shows fungal hyphae attaching to (and so in the initial stages of weathering) a Galena crystal. Weathering is an important and necessary part of soil formation. In many soils around the world, and particularly agricultural soils, erosion rates are currently greater than soil formation rates and, therefore, the overall quantity of soil is diminishing. In fact, even relatively low levels of soil erosion can be unsustainable due to weathering being such a slow process. Weathering also produces nutrients that are required for plant production in many ecosystems.

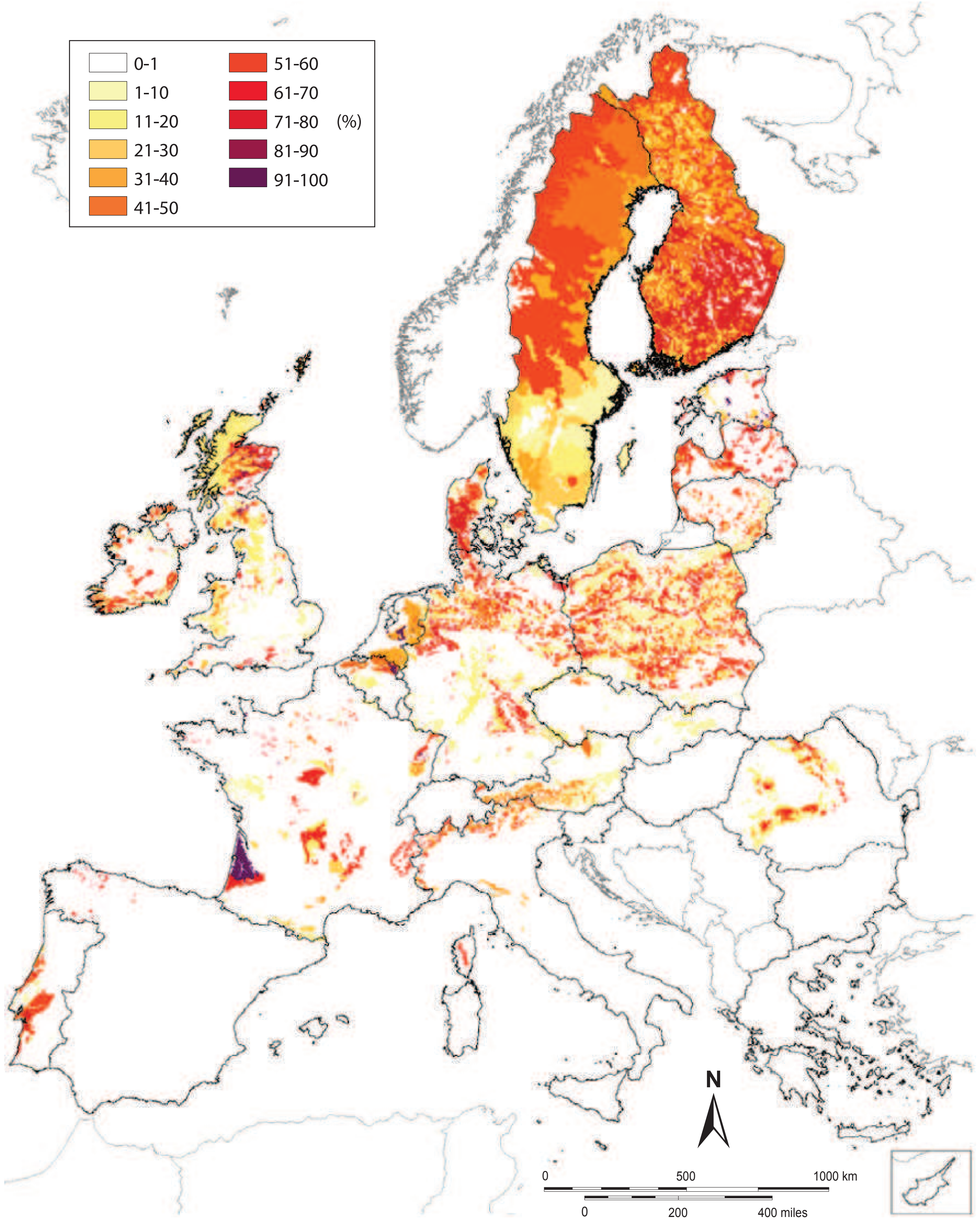


Fig. 4.5: Distribution of Podzols in the European Union. (JRC)

Mineral neoformation

Secondary mineral formation has been observed in freeliving and symbiotic fungi: metal oxalates have been found to be formed by lichens and mycorrhizal fungi; iron (hydr)oxides and clay minerals by have been found to be formed by lichens and ectomycorrhizal fungi, and carbonates have been found to be formed by mycorrhizal fungi and lichens. The crystalline material nucleates and deposits onto and within cell walls (Figure 4.7).

Calcium oxalate (Fig. 4.8) is the most common oxalate in soils and the litter layer and the formation of it by fungi operates a calcium reservoir, and influences phosphate availability. This shows that the feedback between the soil biota and the mineral component of soil plays an important role in governing nutrient availability and so soil fertility.

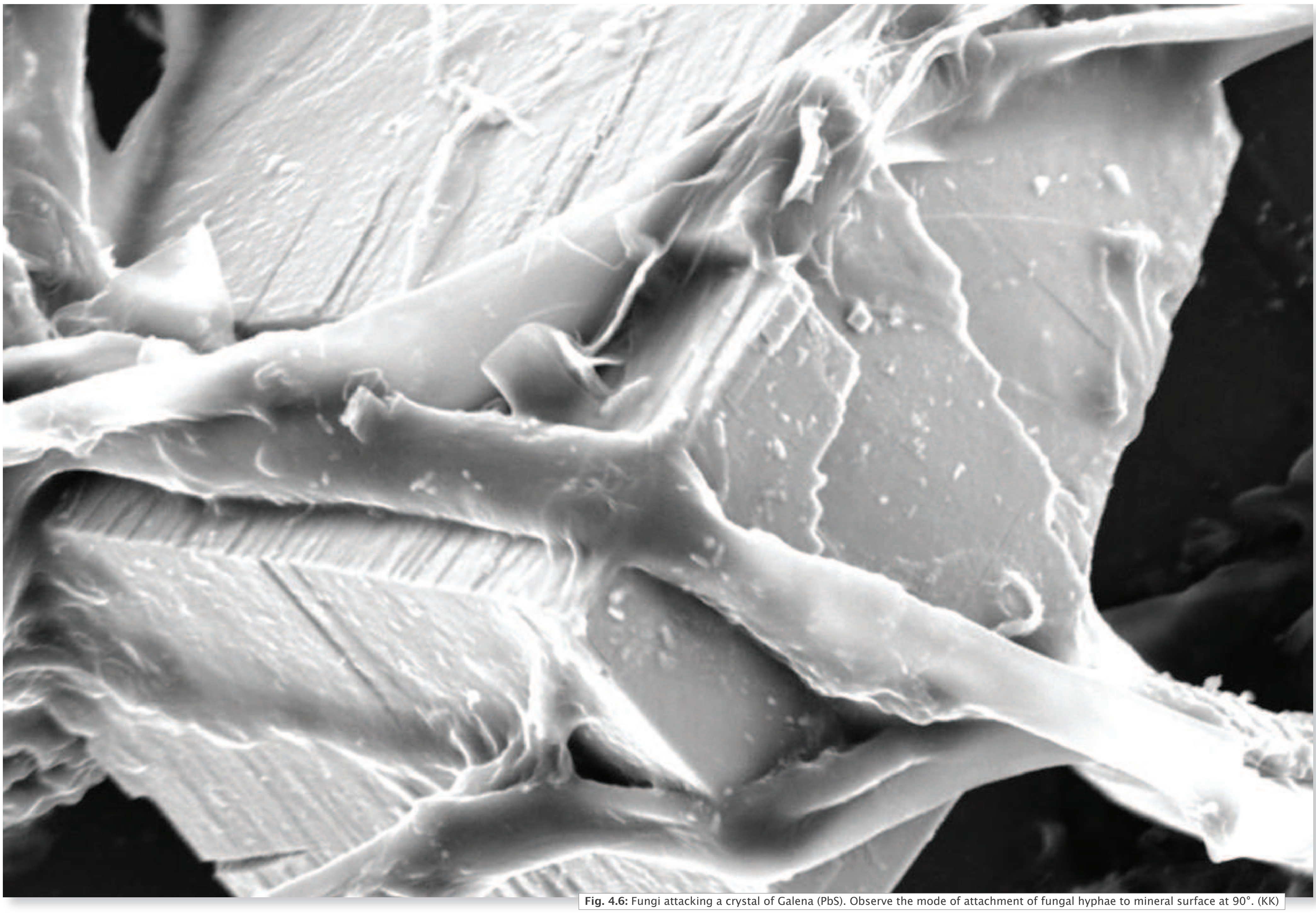


Fig. 4.6: Fungi attacking a crystal of Galena (PbS). Observe the mode of attachment of fungal hyphae to mineral surface at 90°. (KK)

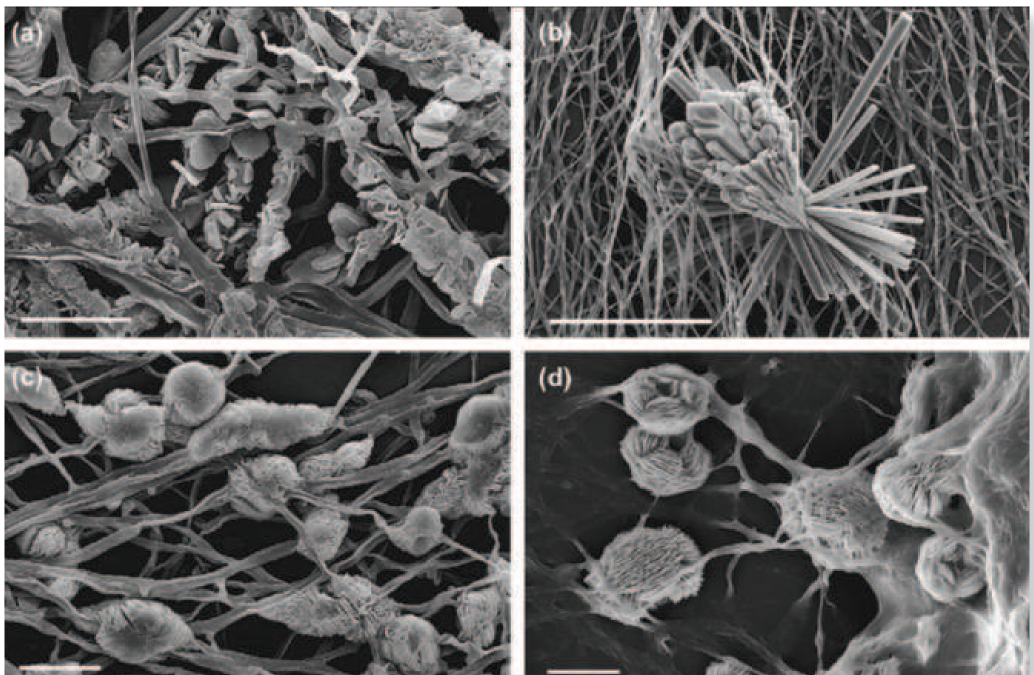


Fig. 4.7: Mycogenic oxalates. (a) Magnesium oxalate and hydromagnesite precipitated on *Penicillium simplicissimum*; (b) strontium oxalate hydrate on *Serpula himantioides*; (c) calcium oxalate monohydrate and calcium oxalate dihydrate on *S. himantioides*; and (d) copper oxalate hydrate precipitation on *Beauveria caledonica*. Bars (a) 20 μm; (b) 100 μm; (c,d) 20 μm. From Gadd 2007.

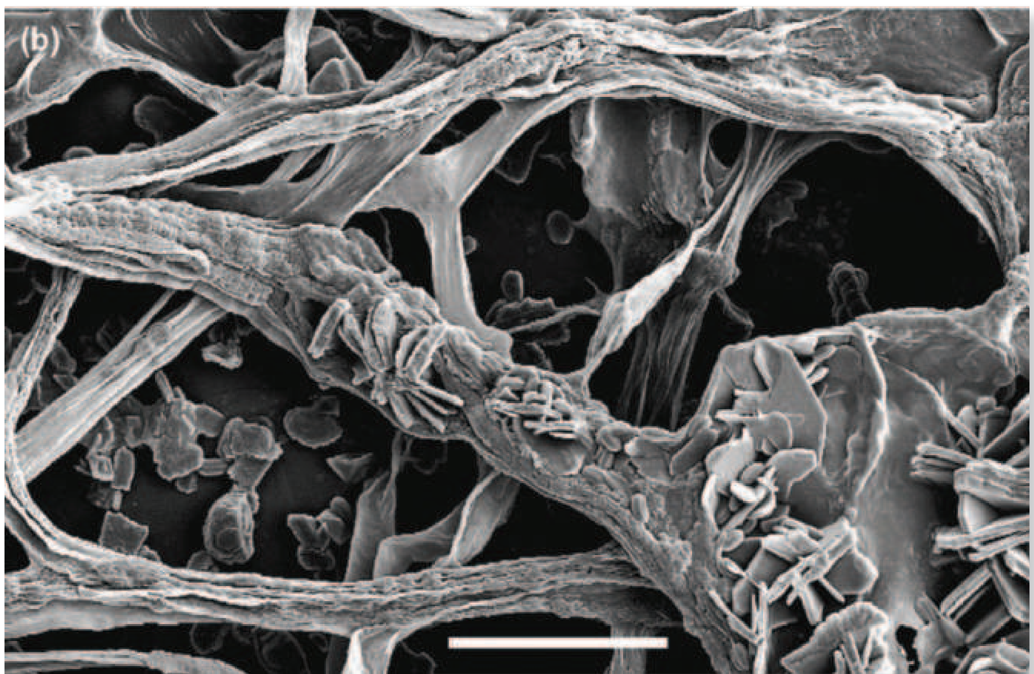


Fig. 4.8: Calcite and calcium oxalate monohydrate precipitated on *Serpula himantioides*. Bars (b) 10 μm; From Gadd 2007.

Soil Biodiversity and Soil Formation

Of course, soil is much more than just the mineral component. Soil formation is the result of complex interactions between the living, mineral and organic parts of the soil. Early colonisers, such as lichens and other photoautotrophic organisms, fix carbon dioxide from the atmosphere as they grow and start to establish small amounts of organic matter which other organisms can utilise as an energy source. Over time, the amount of organic matter builds up as more carbon is put into the system through photosynthesis, allowing other organisms to colonise the system. Once there is sufficient organic matter and other nutrients available, higher plants are able to colonise the soil which can then aid and speed up the soil forming process through their roots growing into cracks in rocks and causing cracks to expand thereby increasing the surface area exposed to weathering. Weathering is the primary source of essential elements for organisms within the soil system, with the exception of nitrogen, which has to be retrieved from the atmosphere, and carbon. Feedback cycles exist between the soil biota and the weathering process whereby, as weathering occurs, essential elements are released, aiding growth within the soil biota. This in turn adds to the weathering process as the soil biota increases weathering rates. Weathering has also been shown to be accelerated by earthworms, including evidence of the transformation of smectite (a clay mineral) to illite (another form of clay mineral). This highlights that the level of biodiversity of a soil will affect the formation rate, as well as the final charecteristics of the soil.

4.3 Applications of Soil Biodiversity

As well as soil organisms being directly involved in, or being facilitators of many biological processes, soil organisms are also highly sensitive to several stressors and are, therefore, widely used as indicators to assess the quality of the soil.

Several soil meso and macrofauna groups (e.g. Collembola, earthworms, acari) have been used as biodiversity indicators for assessing changes in below ground biodiversity in several monitoring programmes. (see Application One).

These groups have also been used as ecological indicators by evaluating structural and/or functional changes in their communities for assessing the effects of stressors such as soil management practices or land-use changes. So far, several bio-indication programmes have been developed and implemented in different European countries, using changes in soil fauna communities as indicators for monitoring soil (see Section 8.3).

All of these programmes have a common principle in that they are based on the "reference condition approach", whereby the community of any impacted site is compared to the community from a reference site of the same region and with similar pedological, land-use and climatic characteristics (see Application Two).

A similar approach is used on Site-specific Ecological Risk Assessment schemes. Changes in soil fauna community composition and species richness observed in contaminated sites are compared to those of non-contaminated reference sites. This is one type of ecological information integrating the Ecological Line of Evidence (ELoE) which together with the Chemical Line of Evidence (ChLoE) and the Ecotoxicological Line of Evidence (EcLoE) composes the "Triad" (see Application Three).

The sensitivity of soil organisms to chemical contamination means that they make good environmental indicators. Species from different soil fauna groups such as springtails, earthworms, enchytraeids, mites and coleopterans (i.e. beetles) are used not only to assess the ecotoxicological potential of contaminated soils, but also to evaluate the risks of chemical substances to the environment (e.g. pesticides, industrial chemicals, wastes etc.). For assessing the effects of these substances, ecotoxicological tests measuring chemical effects on individuals, populations or community parameters of soil organisms can be performed (see Application Four). Some of these tests are legally required to grant the authorisation for the use of chemicals such as the use of pesticides in the European Union.

Soil organisms don't all live at the same soil depth. Some species live in the top 5 cm (i.e. most mesofauna groups), some concentrate their activity in the upper 20 cm of the soil (e.g. endogeic worms), and some species live in galleries up to 2 m depth (e.g. anecic worms). Knowledge of these different "living strata" are important for accurately assessing the risk of particular stressors, such as pesticides, to these species. Therefore, if a precise risk assessment is desired, ecologically relevant exposure scenarios of soil fauna need to be defined. Soil biodiversity may also be used for constructing a new Soil Ecoregion map of Europe (see Box 5), considering soil properties, land-use, climate and the potential soil community existing under these conditions. This potential soil community is defined by its functional composition and not their taxonomical composition. In particular the biological and ecological (characteristics) of soil fauna species that influence their exposure to chemicals, such as the soil layer where they live, their locomotor behaviour, or resistance to desiccation, must be considered for the accurate development of any soil ecoregion maps.

Application One

The observed depletion of soil biodiversity at several spatial scales is recognised as being one of the major threats to soil quality within the EU, mainly because soil biodiversity exerts a key role in soil biological processes and in the delivery of important ecosystem services. Therefore, the development of operational biodiversity indicators and the implementation of biodiversity monitoring programmes has been a priority at EU level in recent times. Recently, the project "ENVASSO" launched a series of indicators of soil biodiversity which are ready for use in extensive and intensive monitoring programmes. Indicators were selected based on the following criteria:

1. availability of standardised sampling and/or measuring methodology;
2. complementarity to other indicators; and
3. ease of interpretation of results, at both scientific and policy levels.

Key issue	Groups of species	Level I (all core points of the monitoring network)	Level II (all core points or selected points relevant for specific issues and availability of resources)	Level III (optional)
Species diversity	Macrofauna	Earthworm species	All macrofauna	
	Mesofauna	Collembola species (Enchytraeidae if no earthworms)	Acari sub-orders	Activity based on litter bags or on bait lamina
	Microfauna		Nematode (functional) diversity based on feeding habits	Protista
	Microflora		Bacterial and fungal diversity based on DNA / PLFA extraction	
	Vascular plants			For grassland and pastures
Biological functions	Macrofauna			Macrofauna activity (e.g. biogenic structures, feeding activity)
	Mesofauna			Mesofauna activity
	Microflora	Soil respiration	Bacterial and fungal activity	

Application Two

In the Netherlands, the "biological indicator for soil quality" (BISQ) indication system is routinely used to monitor soil quality using the monitoring network established by the RIVM (over 200 sites; see Section 8.3). The system was launched by the Dutch National Soil Quality Network to comply with the ratified Rio Convention on Biodiversity in 1992, and therefore aims to protect biodiversity and the sustainable use of soil functions (nutrient cycling, self-purifying capacity, filtering capacity).

BISQ is composed of 25 indicators comprising both biotic parameters (abundance and community composition of nematodes, earthworms, enchytraeids and soil micro-arthropods), functional parameters (microbial biomass and respiration, microbial structural and functional diversity, and C and N-cycling) and abiotic parameters (chemical and land-use parameters). Using different types of parameters is an advantage as it allows a holistic assessment of the sustainability of soil use.

The principle of BISQ is simple: the indicator values measured at one particular site are compared with the reference values taken from corresponding reference site(s). Currently, the scheme comprises of 10 reference conditions including different farm types on different soils, semi-natural grasslands, heathlands and forests, as well as urban green areas. The higher the deviation from the expected community, the higher the disturbance is assumed to be. The values for each indicator are integrated in a radar histogram, i.e. a circular histogram plot representing all indicator values, scaled against the desired reference situation (the reference value for each variable is scaled as 100%; see Fig. 4.9). Negative or positive deviations from the 100% indicate a departure from the reference situation.

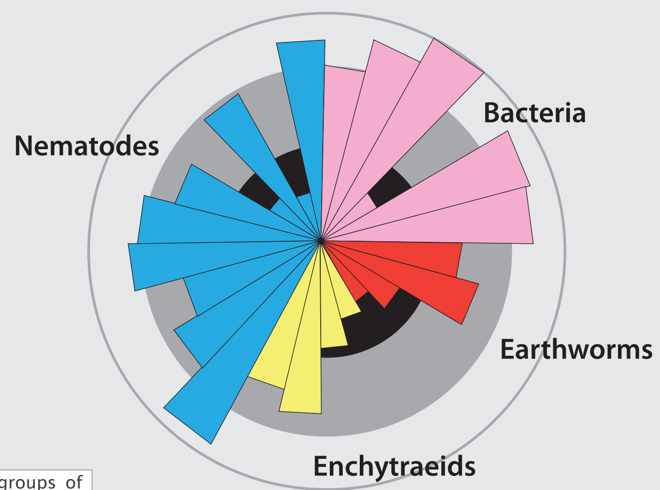


Fig. 4.9: Example of a radar histogram showing four groups of indicators. The outer ring corresponds to 100% (reference situation); the grey circle corresponds to 50%-75% of the reference situation (i.e. a 25% - 50% impairment of the indicator) and the black circle corresponds to 0% - 50% of the reference (i.e. an impairment of 50% to 100% of the indicator).

Application Three

The “Triad” is composed of three complementary lines of evidence (LoE; Fig. 4.10) aiming to provide information to assess the risk that contaminated soils at a specific site can pose to defined ecological receptors that are important to protect (e.g. soil fauna or soil processes):

Chemical Line of Evidence (ChLoE) - includes the measurement of concentrations of chemicals on the site and comparison with limit values;

Ecotoxicological Line of Evidence (EcLoE) – includes performing toxicity tests with soil samples collected at contaminated and reference sites using particular soil fauna species (direct toxicity assessment)

Ecological Line of Evidence (ELoE) – includes the collection of ecological information (e.g. plant and soil fauna species richness and composition, microbial parameters) from both contaminated and reference sites

The Triad can be is applied using a tiered approach, starting with simple measurements from each line of evidence and, if uncertainties exist (i.e. if the different LoEs do not indicate a consistent response in the same direction; either risk or no risk), the process continues by getting further relevant information for each LoE.

On the first tier (the screening tier) survival and avoidance ecotoxicological tests are performed using collembola and earthworms (EcLoE), where a bait-lamina assay is conducted integrating the ELoE. On the tier where a detailed evaluation is made, reproduction tests with both these and other groups of soil fauna (e.g. enchytraeids) are performed (comprising the EcLoE) and soil fauna surveys are conducted collecting data for the ELoE.

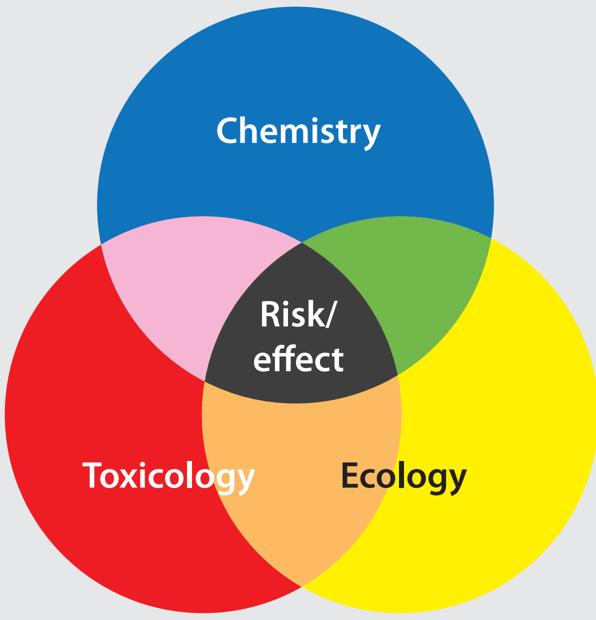


Fig. 4.10: Scheme of the TRIAD. Risk is evaluated joining information from the three lines of evidence. Picture from Jensen and Mesman (2006)

Application Four

Ecotoxicological tests with soil fauna can be performed at different levels of complexity, usually integrated in a battery of tests, starting with simple worst case laboratory tests, and ending in more complex semi-field and field tests. To assess the effects of substances, laboratory tests are usually conducted in artificial soil (the so called “OECD soil” because it was developed under a OECD guideline) composed of quartz sand (70%) kaolinite clay (20%) and peat (10%) (Fig. 4.11). However, nowadays, as a way to increase the ecological relevance of ecotoxicological data, more and more tests are conducted with natural soils. A series of initiatives exist proposing some of these soils as reference materials representing different European regions to be used in ecotoxicity testing.

The basic principle of most ecotoxicological tests is that the organisms are exposed to a series of concentrations of the substance being tested during a defined period of time which depends on the parameter(s) measured and the organisms tested. Laboratory tests exist for evaluating effects at either individual (e.g. survival, growth, behaviour) or population level (e.g. reproduction) (Fig. 4.12). Semi-field tests such as mesocosm tests evaluate effects mainly at the community level (e.g. changes in species composition or functional groups) (Fig. 4.13). Contrary to laboratory tests, these are conducted with natural soils, increasing the ecological realism of the data obtained.

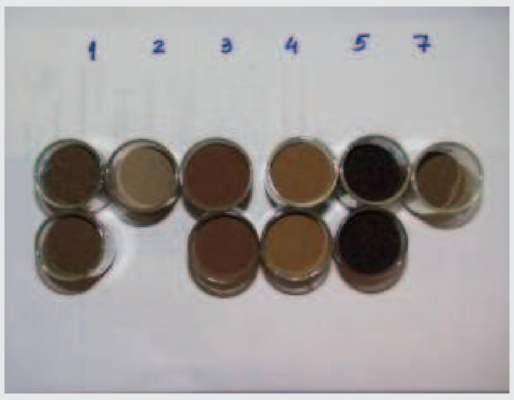


Fig. 4.11: The three components of the OECD artificial soil: quartz sand (70%), kaolin clay (20%) and sphagnum peat (10%). Clear differences can be seen in the appearance of the OECD soil (**left**) when compared to natural soils (**right**). (TB and JR)

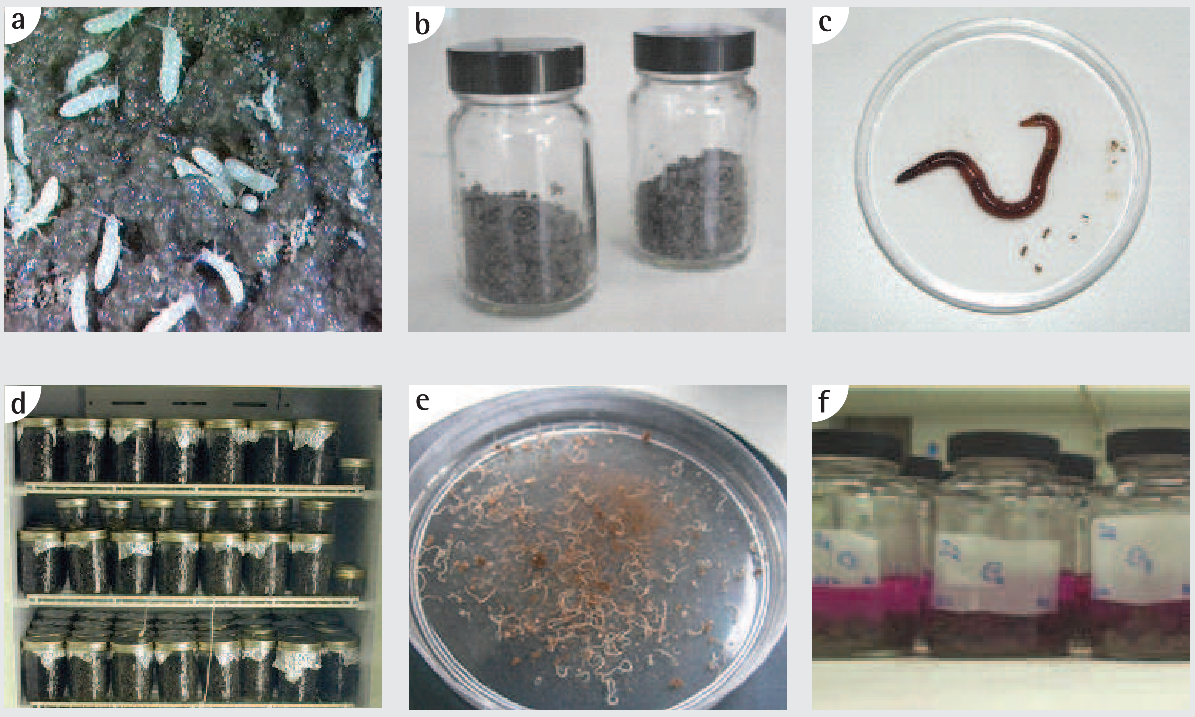


Fig. 4.12: Laboratory tests: (a) *Folsomia candida* (a collembola species widely used in ecotoxicological tests); (b) Test vessels with soil for collembolan tests; (c) *Eisenia andrei*, an earthworm and the most common soil species used in ecotoxicological tests; (d) Climatic chamber with test vessels for an earthworm reproduction test; (e) *Enchytraeus crypticus* (enchytraeid – potworm) on a sieve ready to be selected for a test; (f) enchytraeid reproduction test vessels with rose Bengal to stain the animals; at the end of the test, and before counting, the animals are stained in order to gain a better contrast. (TL (a, c, e–f), PW (b) and GSt (d))

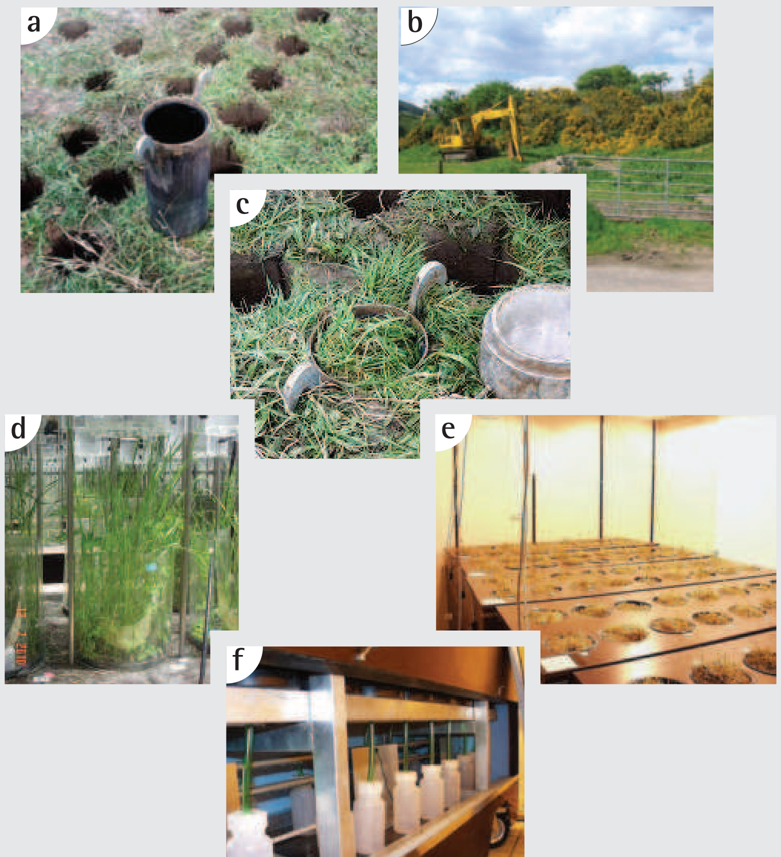


Fig. 4.13: Semi-field tests (Terrestrial Model Ecosystems – TMEs): (a–c) extracting TMEs in the field; (d–e) TMEs in the cart system already in the laboratory; (f) detail of the cart system showing the leachate collectors connected to the bottom of each TME. (BF and JR)

4.4 Soil Biodiversity and Plant Disease

Among the different kinds of microorganisms that live in the topsoil, fungi and bacteria deserve particular attention as they are the most prevalent and can be either beneficial or able to infect plants, depending on the species, host plant and environmental conditions.

Under native, undisturbed circumstances, there is a large variety of soil microorganisms which exist in a form of dynamic equilibrium. Plant diseases are the exception. The majority of fungi and bacteria present in soil are considered to be beneficial to higher plants by:

a. direct association with roots (e.g. mycorrhizae, nodule forming bacteria);

b. breakdown and release of minerals from soil organic matter thereby increasing the availability of essential elements to plants;

c. parasitising disease causing microorganisms or suppressing their growth through other kinds of interactions such as competition for nutrients and production of toxic metabolites.

However, conventional agricultural practices induce changes in the microbial communities of soil, often suppressing biodiversity and reducing the ability of ecosystems to withstand periods of stress. This means that in stressed systems, such as cultivated soil, the resident competitors of plant pathogens may be negatively affected thereby allowing the pathogens and the associated diseases to spread.

Soil-borne phytopathogens

Soil-borne phytopathogens are fungal or bacterial microorganisms present in soil which are able to infect higher plants (here meaning cultivated plants or crops) and can cause a range of diseases. Soil-borne phytopathogens may complete their entire life cycle within the soil, or may spend part of it on the phyllosphere (i.e. above ground surfaces of a plant such as the stem and leaves). During their parasitic phase, these pathogens grow in susceptible hosts. However, they may also spend part of their life cycle surviving in soil between moving from one host crop to the next, as saprophytes on plant residues, or as resting propagules such as chlamidospores, sclerotia or oospores. Their survival in soil may last from several weeks to several years, depending on their biology. A plant disease occurs when three conditions are met. There must be a pathogen and a susceptible host, and the two must meet under favorable environmental conditions. If one of these three conditions is met, no disease occurs.

Soil-borne phytopathogenic fungi and bacteria are responsible for various plant diseases which remain a topical problem in many growing areas, all over the world. The main fungal diseases are caused by the soil-borne fungi *Armillaria mellea*, *Colletotrichum* sp., *Fusarium* sp., *Gaeumannomyces graminis* var. *tritici*, *Macrophomina phaseolina*, *Phoma* sp., *Phytophthora* sp., *Pythium* sp., *Rhizoctonia solani*, *Sclerotinia* sp., *Slerotium rolfsii*, *Thielaviopsis basicola* and *Verticillium dahlia* (Fig. 4.14).

Among bacteria, the most common groups of plant pathogens are *Agrobacterium tumefaciens*, *Erwinia carotovora* and *Plasmodiophora brassicae*. Soil-borne pathogens, depending on the species, are responsible of disease on mainly vegetables, cereals and flowers and sometimes also on trees in orchards. The potential damage caused by plant pathogens may have a considerable effect on crop cultivar and rootstock selection, crop rotations, planting density and timing, seed treatments, and agrochemicals. However, as previously mentioned, as well as the host and pathogen meeting, environmental conditions must also be favourable. One factor which can mean that environmental conditions are not favourable is the presence of other, suppressive microorganisms.

Microorganisms involved in pathogen suppressive soils

A soil is considered suppressive when, in spite of other favorable conditions for disease occurrence, a pathogen does not establish or persist, establishes but causes little or no damage, or establishes and causes disease for a short time and then declines, although the pathogen may continue to persist in the soil.

In contrast, conducive (non-suppressive) soils are soils where the disease readily occurs. Soil suppressiveness is related to both the fertility level and nature of the soil itself, as well as to its microbiological activity. Suppressiveness has been further defined into general suppressiveness and specific supressiveness.

General suppression is the result of total microbial biomass and high biodiversity which creates conditions unfavorable to the development of plant diseases. Specific suppression, on the other hand, is due to the effects of individual or selected groups of microorganisms during particular stages of the pathogen life cycle and is also transferable (with between 0.1% and 10% effectiveness) to a conducive soil.

Because suppressiveness is mainly of biological origins, both general and specific suppression are eliminated by either autoclaving (30 min at 120°C) or exposure of the soil to gamma radiation. Furthermore, general suppression is reduced, but not eliminated by soil fumigation and may withstand 70°C moist heat, while specific suppression is eliminated by pasteurisation (30 min at 60°C).

This is likely the result of greater levels of biodiversity being involved in general suppression, meaning that more functional redundancy exists within the soil community. Conversely, specific suppression is likely the result of far fewer species or groups of organisms and so functional redundancy is likely to be lower, meaning more reduction in its effectiveness after an environmental stress such as pasteurisation. It has been asserted that specific suppression occurs along with general suppression and as such suppressive soils owe their activity to a combination of both general and specific suppression.

a

b

c


Fig. 4.14: (a) Onion plants with symptoms of fusarium wilt by *Fusarium oxysporum* f. sp. *cepae*, on the left, compared with a healthy plant on the right; (b) Symptoms of *Rhizoctonia solani* infection on bean plants; (c) Corgette plants with symptoms caused by *Fusarium solani* f. sp. *cepae* race 1. (RR)

Fig. 4.15: *Trichoderma harzianum* parasitizing *Rhizoctonia solani hypha* with pincers and hooks. (APi)

Beneficial microorganisms, which are present in suppressive soils, are able to act against pathogens by several mechanisms including; nutrient competition, direct parasitism, direct inhibition through production of antibiotic metabolites, and even by inducing plant resistance. Among microorganism populations, a major role has been given to fluorescent pseudomonads. Their implication in soil suppressiveness has been shown to be related to siderophore-mediated iron competition (e.g. in soils suppressive to fusarium wilts) and antibiosis (e.g. in soils suppressive to take-all). Take all decline (TAD) and fusarium wilt-suppressive soils are the most cited examples of suppressive soils.

Take-all, caused by the ascomycete fungus *Gaeumannomyces graminis* var. *tritici*, is a root disease of wheat of worldwide importance. TAD is the spontaneous decrease in incidence and severity of take-all occurring after monoculture, usually lasting approximately four to six years, with a susceptible host crop and one or more severe outbreaks of the disease. TAD is a phenomenon that occurs globally in a broad range of soil types, climates, and agronomic conditions, and can be reduced or eliminated by breaking monoculture with a non-susceptible crop. Different microbial antagonists and mechanisms are responsible for TAD. Among antagonists fluorescent pseudomonads are involved in TAD worldwide.

Pseudomonas sp. are plant growth promoting rhizobacteria (i.e. non-symbiotic, beneficial plant bacteria, living in the rhizosphere) and are able to synthetize a variety of antifungal compounds (including mainly 2,4-diacetylphloroglucinol) which exert inhibitive effects against *G. graminis* var. *tritici*. Populations of these bacteria increase greatly on roots with take-all lesions.

Fusarium wilts, caused by several *formae speciales* of the pathogenic fungus *Fusarium oxysporum*, are significant diseases worldwide, causing yield losses in numerous crops. Extensive studies of fusarium wilt-suppressive soils have been carried out in France (Chateaurenard) and USA (e.g.. Salinas Valley in California). Interestingly, the suppressiveness of these soils is associated with the activity of non-pathogenic *F. oxysporum* and fluorescent *Pseudomonas* species which compete for carbon and iron, respectively and are also able to induce systemic resistance in plants. In contrast to other soil-borne pathogens, the induction of suppressiveness to fusarium wilts has been associated, in several cases, with continuous cropping of partially resistant cultivars.

Examples of soil-borne pathogens such as *Rhizoctonia solani* and *Sclerotium rolfsii*, which have been extensively studied for decades, are not controlled by suppressive soils through the mechanisms of general suppression because they have large propagules which are less susceptible to microbial competition. However, these are sensitive to "specific" beneficial microorganisms, such as *Trichoderma* species able to colonise and parasitise the harmful propagules, thereby reducing the disease potential. The beneficial fungus *Trichoderma* locates *R. solani* through chemical stimuli excreted by the pathogen, then attacks it. *Trichoderma* hyphae entangle the pathogen mycelium and often coil around it, forming hook-like structures which are easily visible at the microscope (Fig. 4.15). During its parasitic action, *Trichoderma* releases lytic enzymes that digest the pathogen cell wall and sometimes penetrates the host mycelium. The final steps of this parasitic action can be the collapse and complete degradation of *Rhizoctonia* cells.

Delivery of beneficial microorganisms to control soil phytopathogens

Over the past hundred years or so, research has repeatedly demonstrated that phylogenetically diverse microorganisms are natural antagonists that are capable of inhibiting or even completely destroying undesirable phytopathogens. The soil represents a large reservoir of antagonistic microorganisms which have been extensively investigated for their exploitation in the agricultural environment for plant disease control. The interactions between microorganisms and pathogens can be complex and include antibiosis, competition and parasitism. It has also been demonstrated that antagonistic microorganisms can interact with plants to induce systemic resistance to phytopathogens. Intensive screening both in the USA and in Europe have provided numerous candidate microorganisms known as biocontrol agents (BCAs) for commercial development. Indeed, public concern for high quality food, without the residues of pesticides, and for sustainable agricultural systems preserving soil fertility, as well as for preventing environmental pollution, has stimulated research dealing with biological control. At present, there is a large number of commercial products containing antagonistic microorganisms, biopesticides (USA) or biofungicides (EU), currently marketed for biological treatments against soil-borne diseases of several crops. They include bacteria belonging to the genera *Streptomyces* and *Pseudomonas* and fungi belonging to the genera *Coniothyrium*, *Gliocladium*, *Pythium* and *Trichoderma* (Table 4.3). These products are applied in various ways, including seed treatments, soil inoculants or soil drenches, depending on the BCA strain and on the formulation.

Fig. 4.16: Colony of *Trichoderma* sp. on potato dextrose agar. (RR)

BCAs offer several benefits compared to other chemical pathogen control options. For example, because they are a natural resource, they can be used both for organic farming and integrated crop protection (ICP) programmes. They may also increase biodiversity because the majority of BCAs are naturally occurring soil microorganisms and generally more target specific than most chemicals used for soil application. In fact, the biological vacuum is one of the worst deleterious effects of pesticide application to soil (soil disinfestation) such as caused by the fumigant methyl bromide (now banned). Furthermore, the risk of recolonisation of the biological vacuum with pathogens is high, leading to further and more serious disease incidences. That said, some genera, such as *Trichoderma* (Fig. 4.16) and *Gliocladium*, are often less sensitive to fumigants and other chemicals used in disinfestation, leading to them recolonising the soil in more dominant numbers post disinfestation. While it is not possible to restore the balance of microorganisms that was present under native, undisturbed conditions, a new balance of soil organisms that will be adapted to the altered soil conditions can be built and soil management should strive towards the desired outcome of disease prevention.

Table 4.3: Antagonistic fungi and bacteria included in Annex 1 of Directive 91/414/EEC and authorised at national level for the biological control of soil-borne diseases in several European countries. (Up to date March 2010)

Microorganism	Target
Coniothyrium minitans CON/M91-08	*Sclerotinia minor, S. sclerotiorum*
Gliocladium catenulatum J1446	Wide range of fungal soil-borne pathogens
Pseudomonas chlororaphis MA 342	Seed and soil-borne pathogens of cereals
Pythium oligandrum M1	Main soil-borne pathogens and some foliar pathogen
Streptomyces K61 (formerly *S. griseoviridis* K61)	Wide range of fungal soil-borne pathogens
Trichoderma asperellum ICC012 (formerly *T. harzianum* ICC012)	Wide range of fungal soil-borne pathogens
T. asperellum T11 (formerly *T. viride* T-25)	Wide range of fungal soil-borne pathogens
T. asperellum TV1 (formerly *T. viride* TV1)	Wide range of fungal soil-borne pathogens
T. atroviride T-11 (formerly *T. harzianum*)	Wide range of fungal soil-borne pathogens
T. gamsii ICC080 (formerly *T. viride* ICC080)	Wide range of fungal soil-borne pathogens
T. harzianum T-22	Wide range of fungal soil-borne pathogens

4.5 Soil Biodiversity and Biotechnology

Virtually, all groups of soil microorganisms (bacteria, fungi, viruses, algae and protozoa) have the potential for a wide range of environmental, commercial and industrial applications, most of which remain largely unexploited. The ability of microorganisms to break down substrates and to transform materials and compounds into new substances is a valuable resource in industries such as pharmaceutical, food and feed processing, chemical and even mining. The exploitation of microorganisms with the intent of generating a useful product or a desired environmental change is generally regarded as biotechnology. In it's broader sense, biotechnology covers wider grounds. For example, it is also a tool for acquiring scientific knowledge in fields, such as genetic information processing, metabolism, cellular and whole organism systems (e.g. environmental adaptation, immune, endocrine, etc.). This section focuses on biotechnology applications of soil organisms.

Microbial biodiversity and biotechnology are strongly interrelated and interdependent. In fact, biodiversity is the foundation and engine of biotechnology. In other words, it is the multitude of microbial characteristics, translated into a swarm of metabolic features that enable all of the applications and make possible for so many products to be available to us (see Table 4.4). Whereas the term is relatively new, biotechnology as a concept has long been around, in the leavening of bread, brewing of beer, fermentation of food products (Fig. 4.17) and direct intervention in animal and plant breeding (such as those in the farm and agricultural systems). The industrial revolution enabled the implementation of large scale fermentation units and so the era of modern biotechnology began (Fig. 4.19).

Fig. 4.17: Cheese making is one form of biotechnology which has existed for thousands of years. (PDI)

Recently, biotechnology has seen a spectacular expansion with the increasing understanding and exploitation of molecular biology (i.e. the study of interactions between the various systems of a cell) and recombinant DNA technology (i.e. the creation of 'new' DNA though combining sequences that would not normally occur together). In fact, microbial cells can be manipulated through the transferring of specific genes from one microorganism to the next, within the same species or to different species. This process occurs naturally in microbial populations in the environment and blurs the line between what individual "species" actually are in the bacterial world. The transferring of genes from such disparate groups as plant or animal cells into bacteria, fungi or yeast is even possible. In this context, the role of microbial genetic engineering is to create 'tailormade' or super-microbial strains with specific biochemical/ metabolic features, in view of new or 'improved' applications, thus further enhancing the range of 'natural' biodiversity.

Undoubtedly, microorganisms are essential for life as we know it. For example, the microbial cells themselves can be used as nutrients, immunising factors or clean-up agents. The enzymes and other macromolecules, as well as compounds synthesized by viable cells are invaluable resources in enhancing our quality of life. Table 4.4 provides an overview of some of the most well established industrial and environmental applications of soil microorganisms in the realm of biotechnology.

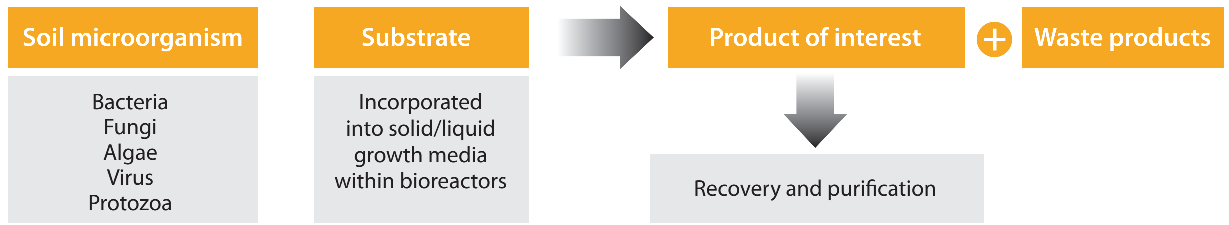


Fig. 4.18: Typical steps in microbial-based industrial production of relevant compounds.

It all starts with an 'intelligent' microbial screening program in order to identify microorganisms with a specific desired feature. These microorganisms can be either isolated from commercial culture collections or environmental samples (e.g. soil and water from a wide range of pristine and disturbed micro- and macro-habitats). The microorganisms are then cultured in bioreactors, often in the form of immobilised cells onto an inorganic support (such as diatomaceous earth). Within the reactor, key parameters such as aeration, pH, nutrients and temperature are automatically controlled to match their nutritional and environmental requirements.

When the application is the production of a specific compound of interest, a series of isolation and purification steps of the final product are then required (Figure 4.18) in order to remove it from the growth medium. It is clear that microbial production needs to take place in a large preferably industrial scale in order to be commercially feasible. Scaling-up microbial production can often be difficult, as it is dependent on many factors, such as the type of microorganism and that of the product of interest, as well as the characteristics of the growth medium required, among others. Ideally, the microorganism should have a high growth rate, a high ability to produce the desired compound in large quantities, be easy to culture in inexpensive and readily available media and should not be pathogenic. In turn, the desired product should be easy to isolate from the culture media, while the recovery and purification steps should be quick and cost-effective.

Bioremediation

The soil biota consists of many different organisms, the majority of which are decomposers. These are heterotrophic organisms which break down organic substances to gain energy, and in doing so recycle carbon and nitrogen back into the environment. This process can also be utilised as a form of biotechnology known as bioremediation, which is the process of using organisms ("bio") to return a contaminated area back to its pristine state ("remediation"). Despite this broad definition, most bioremediation is actually undertaken through the use of microorganisms due to their ability to utilise a vast range of carbon sources as a substrate. Of course, while bioremediation can be used in some instances to remove pollution from soils, it is not always possible, depending on the pollutant, soil and climatic conditions. It is always best to avoid the need for bioremediation by avoiding contamination of soils or the environment in the first place.

Different soil decomposers are capable of degrading different types of organic substances. Readily degradable compounds either naturally occurring or of anthropogenic origin (e.g. carbohydrates, amino acids) are susceptible to decomposition by a wide range of soil microbial groups. In contrast, complex substrates like lignin, cellulose and hemicelluloses, are highly recalcitrant and can only be broken down by a selective group of microorganisms, such as white rot fungi and some bacteria. Interestingly, many man-made organic pollutants such as hydrocarbons (e.g. crude oil), which are composed of long chains of carbon and hydrogen can be structurally similar to lignin. Hydrocarbons generally last much longer in the environment but such similarities mean that fungi can often be used for their bioremediation in contaminated soil or water. Determining the right type of bacteria or fungi for a given bioremediation program is key for ensuring its success, that is, the effective metabolism/removal of the contaminant.

Bioremediation occurs, or is undertaken in, three different forms:

- **Intrinsic bioremediation:** This process occurs naturally in contaminated soil or water and is carried out by microorganisms native to the site of the contamination. No human intervention is required.
- **Biostimulation:** In this process, nutrients and/or oxygen are added to contaminated soil (or water) to encourage the growth and activity of the microorganisms living at the site of the contamination and hence increase the rate of decomposition of the contaminating compound.
- **Bioaugmentation:** This is the process of adding organisms, generally microorganisms, to soil (or water) to aid the intrinsic bioremediation, or to introduce organisms capable of degrading a contaminant which the intrinsic population is unable to.

Bioremediation can be highly effective in removing contaminants from affected sites. In one case an estimated 38,000 m^3 of soil in Canada was contaminated with an oil-tar byproduct containing polycyclic aromatic hydrocarbons, cyanide, xylene, toluene and heavy metals by a gasification plant. After application of a bacteria and nitrogen nutrient mix (a combination of biostimulation and bioaugmentation techniques), the various constituent pollutants of the oil tar were reduced by 40-90% in just 70-90 days (organic pollutants are broken down whereas heavy metals can become locked up within the microbial communities and so not bioavailable to other less tolerant organisms). Further evidence of the effectiveness of bioremediation of hydrocarbons is can be seen in Fig. 4.21 (over page).

Fig. 4.19: An industrial scale fermentation unit. (PDI)

Table 4.4: A selection of biotechnologies which rely on soil organisms, including examples of species used.

Application category	Example of microbial product or application	Representative producing microorganism (B = Bacteria; F = Fungi)	Additional information and description
Pharmaceuticals, therapeutic agents and supplements	Antibiotics (e.g penicillin and related μ-lactams, streptomycin, cephalosporin, etc)	*Penicillium chrysogenum* (F), *Streptomyces griseus* (B) and *Acremonium chrysogenum* (F) (respectively)	Antibiotics are the most popular amongst the pharmaceuticals produced by soil microorganisms. *Streptomyces* and *Penicillium* together produce more than half of the antibiotics used worldwide.
	Steroids and steroid hormones	*Rhyzopus nigricans* and *R. arrhizus* (F)	Cortisone, hydrocortisone and aldosterone, help regulate the levels of serum glucose, as well as sodium and potassium. *Rhyzopus* is used as mediator in the bioconversion of progesterone into cortisone-related compounds.
	Vitamins (e.g. riboflavin - vitamin B2, cobalamin -vitamin B12 and ascorbic acid- vitamin C)	*Streptomyces olivaceous* (B), *Pseudomonas denitrificans* (B) and *Bacillus megatherium* (B), and some species of *Gluconobacter* (B) (respectively)	Generally, vitamins are not synthesised in sufficient amounts by higher organisms, although they are metabolically essential to all. Vitamins have relevant applications in a range of sectors (e.g. food and feed, pharmaceutical, cosmetics, etc).
Food and feed products, preservatives and flavour enhancing agents	Camembert, Brie and Blue cheeses (e.g. Roquefort, Stilton)	*Penicillium camemberti* and *P. roqueforti* (F)	Prepared cultures of these moulds are intentionally introduced during the making or aging of the cheese for providing a unique texture and flavour.
	Mushrooms and mycoprotein	Edible mushrooms (e.g. *Agaricus*, *Pleurotus*, Truffles), *Fusarium venenatum* (F)	Many fungal species have invaluable commercial relevance. Mycoprotein (derived from F. venenatum inexpensively grown in industrial reactors), is widely used in vegetarian diet and can be found in various food products (e.g. Quorn™).
	Organic acids (e.g. citric, glutamic)	*Aspergillus niger* (F) and various species of *Corynebacterium* (B) (respectively)	Citric acid is a preservative and explains the acidic taste of soft drinks, while glutamic acid (in the form of monosodium glutamate) accounts for the savoury (umami) taste, when used as food additive and flavour enhancer.
	Starter cultures for cured and fermented meat	*Penicillium nalgiovense* (F)	P. nalgiovense is added (often in the form of spores) during processing of certain food products for developing specific flavour features while preventing the growth of undesirable microbes.
	Biomass (single-cell protein, SCP)	Some species of *Bacillus* (B) *Pseudomonas*(B), *Trichoderma reesei* (F), *Penicillium* (F)	The process employs inexpensive culture media, supplemented with readily available nutrients for the cells. Although SCP is being produced in large scale as supplements for food and feed, it has yet been accepted as food alternative.
	Amino acids (e.g. lysine, threonine, tryptophan)	Various species of *Corynebacterium* (B) and Bacillus (B)	Amino acids are mostly used in the industries of food and feed, as well as pharmaceutical and cosmetics. For example, it is estimated that *C. glutamicus* industrially produces ca. 600,000 tons of lysine annually.
Enzymes, solvents, detergents and materials	Various proteolytic, hydrolytic and dehydrolytic enzymes	Various species of *Clostridium* (B), *Bacillus* (B), *Aspergillus* (F), *Penicillium* (F),	Such enzymes are used in a wide range of applications, ranging from processing of food and feed products, pharmaceuticals, biological detergents and biofuels (biological conversion of biomass).
	Chemicals (e.g. acetone, acetate, ethanol, propanol, butanol, butyrate)	*Clostridium acetobutylicum* (B)	The bacterium has been producing chemicals by fermentation of carbohydrates (e.g. sugars, starch) since 1916. Acetone, acetate, butanol, butyrate and ethanol all derive from a common precursor (acetyl-CoA).
	Polysaccharides (e.g. bacterial cellulose)	*Acetobacter xylinus* (B)	Bacterial cellulose shows to be promising in industries such as food, paper, cosmetics, lumber and textile, providing that the fermentation process can be effectively scaled up.
Plant hormones, biofertilizers and biocontrol agents	Gibberellic acid and related gibberellins	*Gibberella fujikuroi (syn. Fusarium monoliforme)* (F)	Gibberellins are plant hormones, some of which are growth regulators, controlling seed germination, stem elongation, and flowering.
	Biofertilizers	*Rhizobium* (B), *Azospirillum* (B), mycorrhizal fungi (e.g. *Glomus*)	Biofertilizers increase soil nutrient availability through natural processes (e.g. fixing atmospheric nitrogen, solubilising phosphorus, synthesising plant growth promoters).
	Bioinsecticides	*Bacillus larvae, B. thuringiensis (B), Verticillium lecanii (F), Hirsutella thompsonii (F)*	Commercial sprays (mixtures of toxic protein and/or microbial spores) are available for homes and gardens, greenhouses and crops for control of moths, butterflies, skippers and beetle larvae. They are considered animal- and environmentally-friendly.
	Biofungicides	*Pseudomonas (B), Bacillus (B), Metschnikowia fructicola (F), Trichoderma harzianum (F)*	The bacteria are applied either by direct inoculation (e.g. dipping seeds in culture, aerial spraying) or through solid-phase inoculants. It has seen successful results in biocontrol of diseases in rice (e.g. blast, bakanae).
	Bionematicides	*Pasteuria penetrans (B), Bacillus chitinosporus* and *B. firmus (B), Myrothecium verrucaria (F)*	Bionematocides are used in the control of parasitic nematodes ('roundworms'). Commercial formulations, which are considered environmentally-friendly, are available mainly for greenhouse production of vegetables, flowers and foliage plants.
	Bioherbicides	*Chondrostereum purpureum (F), Phytophthora palmivora (F), Colletotrichum gloeosporioides (F)*	Liquid or solid commercial formulations are available for the biocontrol of broad-leaved "weed" trees (e.g. red alder, aspens), strangle vine (*Morrenia odorata*) and plants of the mallow family (e.g. Malva) respectively.
Mining	Biohydrometallurgy (recovery of metals from low-grade ores)	*Thiobacillus thiooxidans and T. ferrooxidans (B), Ralstonia metallidurans (B)*	The bacteria derive energy from the oxidation of sulphur compounds (e.g. elemental sulfur, sulfides, thiosulfate). Various procedures are in place concerning their use as an environmentally safe and cost-effective approach to metal recovery.
Bioremediation of environmental contaminants	Clean-up of aromatic and halogenated organic compounds (e.g. benzene, PCBs, pesticides and herbicides) in soil, water and industrial effluents	Various species of *Pseudomonas* (B), *Corynebacterium* (B), *Streptomyces* (B) and wood-degrading fungi, such as white rot (e.g. *Phanerochaete chrysosporium, Trametes versicolor*)	Bioremediation uses either naturally occurring or custom-made cultures of microorganisms with specific metabolic features to neutralise/ immobilise/metabolise the contaminant (into a less toxic substance). For example, white-rot fungi degrade xenobiotics by means of co-metabolism, i.e. they require the presence of lignocellulosic substrates (e.g. corncobs, straw, sawdust, etc), as they are unable to use the contaminant as sole source of carbon and energy.
	Clean-up of heavy metal (e.g. zinc, mercury, cadmium) contaminated soil, water and mine tailings	*Thiobacillus thiooxidans* and *T. ferrooxidans* (B), *Ralstonia metallidurans* (B) and *Deinococcus radiodurans* (B)	*T. thiooxidans*, *T. ferrooxidans* and *R. metallidurans* are able to tolerate high levels of toxic metals, while D. radiodurans thrives in radioactive environments. Together they may prove indispensible for treatment of radioactive waste and/or long-term restoration of sites contaminated with radioactive residues.
Bio-treatment of wastewater and sludge	Anaerobic digestion and aerobic oxidation	Anaerobic and aerobic bacteria and fungi (e.g. *Agrobacterium radiobacter*, *Achromobacter* sp.)	Anaerobic digestion and aerobic oxidation are biological processes in the large-scale (e.g. municipal) treatment of wastewater and sludge, in order to reduce/remove the amount of organic material present.
Bio-treatment of solid waste	Bio-treatment of agricultural (e.g. fruit pulp), forestry and paper wastes	Wood-rotting fungi (e.g. white-rot, such as *P. chrysosporium* and *T. versicolor*)	This type of waste is rich in lignin, cellulose and hemicellulose, which are major substrates for wood-rotting fungi and their range of powerful extracellular ligninolytic enzymes.
	Composting	Aerobic bacteria, fungi and yeasts (e.g. *Bacillus* sp., *Serratia* sp., *Pseudomonas* sp., *Streptococcus* sp.)	Long used in (small scale) subsistence farming and home gardening, composting is becoming increasingly important for reducing municipal solid waste and green waste going into landfills. Composting involves different groups of meso- and termophilic microorganisms and counts with the contribution of numerous soil organisms (e.g. springtails, ants, nematodes, isopods).
Renewable energies	Biogas	Facultative and strict anaerobic bacteria (e.g. *Cellulomonas*, *Clostridium*, *Bacillus*, *Ruminococcus*, *Eubacterium*, *Methanobacterium*)	Biogas is industrially produced by anaerobic digestion of organic matter (e.g. biomass, manure, energy crops, sewage) in reactors. One of its key components is methane, which can be used in generators for the production of electricity and/or in boilers for heating purposes.

Antibiotics

The soil contains a complex array of food webs and interactions between the diverse groups of organisms found there, with organisms predating each other and competing for resources. As such, a host of processes for both attack and survival have evolved. One of these is the use of chemical substances as a form of chemical "warfare" between soil organisms. Some of these chemicals, when isolated, can be used for medicinal purposes, such as antibiotics (Fig. 4.20).

Antibiotics isolated from soil organisms include (but are not limited to): penicillin, isolated from *Penicillium chrysogenum* (often referred to as "the penicillin fungus", which is found in soils and which, along with several semi-synthetic derivatives, is still in wide use). Aminoglycosides, such as streptomycin and kanamycin, as well as tetracyclines were isolated from soil dwelling actinomycetes. Lipopeptides such as daptomycin have also been derived from Steptomyces, a type of actinomycete.

Antibiotics are generally classified according to their effect on the competing microorganism: those that kill (i.e. are bactericidal) and those that impair microbial growth (i.e. are bacteriostatic). Furthermore, each class of antibiotics has a different mode of action. Some attack the cell wall (e.g. penicillin) preventing its formation, whereas others attack other cellular constituents such as those involved in protein synthesis (e.g. aminoglycosides). It is for this reason that some organisms are susceptible to some antibiotics but not others, depending on whether they have the specific form of cellular constituent which the antibiotic attacks.

Antibiotic resistance

As well as not being susceptible to some antibiotics, microorganisms are also capable of developing resistance over time. Whilst this is often viewed as a problem for clinical microbiology, precedents for various modes of antibiotic resistance seen in the clinical environment can often be found in the soil environment. This is because soil microorganisms are often exposed to a wide range of compounds in their local environment, some of which, such as antibiotics, may be harmful. This places an evolutionary pressure on the organisms to develop resistance to the harmful compound. On the other hand, antibiotic-producing microorganisms must also contain some form of antibiotic resistance mechanisms to prevent them committing suicide through production of their own antibiotic compounds.

The soil environment, therefore, represents an important pool for research into the underlying mechanisms of antibiotic resistance, including possible mechanisms which are not yet seen in clinical microbiology. Utilisation of this resource to better improve our understanding of the biochemical processes occurring may allow the circumnavigation or reduction of further antibiotic resistance developing. This is an area of research which is just starting to gain prominence. Evolution has even taken antibiotic resistance one step further. It has been shown that some soil microorganisms are capable of growing even when exposed to several different antibiotics, and even use some of the antibiotic compounds as a food source.

Microorganisms are clearly highly adaptable, in ways which we are only recently coming to understand. Antibiotic resistance occurs because antibiotics provide an evolutionary pressure on a given population whereby those organisms with natural resistance can survive and reproduce and those organisms which do not have the resistance factor die. Once a resistance factor has developed it can spread rapidly within a population or even a community though a process known as horizontal gene transfer where DNA is transferred from one bacterium to another of the same generation (as opposed to vertical gene transfer from parent to offspring). This horizontal transfer of DNA containing antibiotic resistance genes (as well as other genes) can occur through three processes:

Transformation. When a bacterium dies and lyses (splits open), other bacteria which are actively-growing in close proximity can pick up its DNA.

Transfection. Phage, which are viruses that infect bacteria and fungi, sometimes pick up extra genes from the microorganisms that they infect which are then passed on to other organisms which they later infect

Conjugation. Bacteria can fuse their cell membranes together and exchange plasmids or fragments of their chromosomes.

These processes can occur between distinct 'species' of bacteria meaning that mechanisms of antibiotic resistance may only have to evolve once and can then spread throughout an entire community.

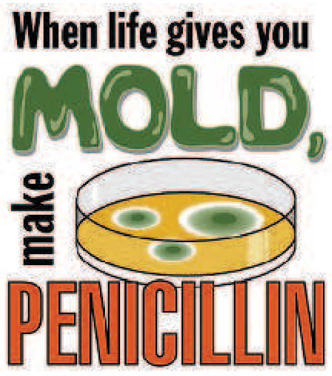


Fig. 4.20: Penicillin antibiotics are historically significant because they were the first drugs that were effective against many previously untreatable diseases and infections. Although still widely used, many types of bacteria are now resistant to penicillin. (PDI)

a

b

c

Fig. 4.21: These three images show an example of bioaugmentation / bioremediation (as described on Page 44) of a crude oil spill by combined strains of the soil fungi *Trametes versicolor* and *Pleurotus ostreatus* (better known as the edible oyster mushroom). (LDe)

(a) shows the oil spill on day 1. Due to the porous nature of soil it would not be possible to remove the oil spill without removing a large amount of soil which would then have to be treated as contaminated waste. Due to the toxic nature of crude oil it is very unlikely that any plants could grow here with the soil in this condition.

(b) shows the oil spill on day 14 after inoculation with the combined strains of *Trametes versicolor* and *Pleurotus ostreatus*. The fungal hyphae are so abundant growing on the oil spill that they are clearly visible as the white on the soil. Already, after just 2 weeks the oil is greatly reduced.

(c) shows the same area of soil after 49 days. The original patch of soil is all but gone, along with the fungi, neither strain of which is now readily apparent. Some small patches of oil are visible at the edges, but further application of the fungi to these areas will remove them.

A Gift from the Soil of Easter Island

One important compound which was isolated from a soil organism, in this case a soil bacteria called *Steptomyces hygroscopicus* is the compound known as Rapamycin (also known as Sirolimus). The bacteria was first found in a soil sample form Easter Island, and was a find of sufficient importance that a plaque now commemorates its discovery on Easter Island (right).

Rapamycin was initially developed as an antifungal agent but many other potentially important properties have since come to light. It is now often used as an immunosuppressant to prevent the rejection of organs in transplant patients.

Rapamycin has also been found to have anti-proliferative effects. These effects have already been shown to aid recovery after heart surgery and appears potentially to have a role in treating cancer. Furthermore, a recent study has shown that Rapamycin has the ability to extend life spans by almost 15%, in mice at least. All of these wonderful properties from just one compound isolated from one bacterial species. With potentially hundreds of thousands of species of microorganism yet to be discovered, who knows what other useful, lifesaving compounds are yet to be found!

Biocontrol of pests

Biocontrol of pests is the use of natural 'enemies' as biological control agents, such as predators, parasites or pathogens, to control or reduce the population of a given pest. It is often used as an alternative to pesticide use. Broad spectrum pesticide use can be highly problematic as they often act on insects which are beneficial to crops as well as harmful insects. There is also a possibility of these chemicals being washed into groundwater or any nearby waterways causing contamination. Biocontrol is one method which can be used to reduce the need for large scale applications of broad spectrum pesticides (Fig. 4.22). When the pest is a pathogen, such as in the case of plant diseases, then the biological control agent is often referred to as an 'antagonist'. Biological control generally falls into three different types of strategy, referred to as:

Conservation, where care is taken so that natural biological control agents are not eradicated by other pest control processes;

Classical biological control, where a biological control agent is introduced into an area to control a pest species;

Augmentation, which involves the supplemental release of a biological control agent.

An example of biocontrol through augmentation is the use of entomopathogenic nematodes, which are often released at rates of millions or even billions per hectare, for the control of certain soil-dwelling insect pests.

It is generally recognised that the ideal biocontrol organisms should include the following characteristics (From Kerr 1982):

1. The organism should survive for an extended period of time in the soil in an inactive or active form.
2. The organism should contact the pathogen either directly or indirectly by diffusion of chemicals.
3. Multiplication in the laboratory should be both simple and inexpensive.
4. It should be amenable to a simple, efficient and inexpensive process of packaging, distribution and application.
5. If possible, it should be specific to the target organism; higher specificity means less (medium- to long term) harm for the environment
6. Its preparation, distribution or application should not be a health hazard.
7. It should be active under the same environmental conditions as the target organism.
8. It should control the target pathogen both efficiently and economically.

Soil biodiversity clearly has many more current and potential uses for biotechnology and this is an area ongoing area of research.

Biodiversity as a resource for biotechnological innovation is invaluable. A large number of important microbial- based products and applications have already been developed and established and hundreds more are currently in various stages of development. Yet, it is the general consensus that microbial biodiversity remains largely unexplored and that advances in microbial isolation methods will reveal a much wider range of undiscovered metabolic pathways and microbial compounds which have potential uses for humans. Furthermore, progress in 'strain improvement' and molecular biology, including how it is possible to influence the development of new products, or the improvement of currently existing products, are likely to have broad implications worldwide. It is widely expected that the near future will see the emerging of new microbial strains that offer potential solutions for problems ranging from food shortages through to pollution, including biofuels and disease control. Already, the application of biotechnology in agriculture has resulted in new crop varieties with increased resistance to pests and diseases, as well as crops with increased nutritional value (e.g. Golden Rice). There is still no firm consensus between scientists, however, regarding the safety of widespread use of genetic manipulation of organisms for biotechnological purposes, particularly genetically modified crops. This is an ongoing area of research and political debate, the specifics of which are beyond the scope of this atlas.

Research involving soil microorganisms has lead to exciting progress taking place in the field of renewable energies. For example, the bacterium *Ralstonia metallidurans* has been focus of increasing attention in fuel cell research, due to its ability of withstanding high levels of heavy metals and of precipitating metals from solution. Furthermore, many consider soil microorganisms and their underlying diversity to be an exciting potential source of biogas and biofuels (e.g. bioethanol, biodiesel), besides that of biomass. For example, bioethanol is being industrially produced by soil microorganisms or their enzymes through the fermentation of sugars, starches or (less commonly) cellulose, although currently this process still largely relies on 'superstrains' of carbohydrate-fermenting yeasts and the enteric bacterium *Escherichia coli*, genetically manipulated for optimising alcohol production.

Nevertheless, advances and applications of molecular biology do not come without drawbacks and some remain controversial. Strict regulations and protocols have already been put in place in order to minimise the potential hazards associated with genetic manipulation and the spread of transgenic organisms, among which the direct threat to human and animal health and the potential danger to 'natural' biodiversity are perhaps of most concern although precise scientific evidence of these threats is limited, where it exists at all. There is therefore strong pressure and incentive to utilise natural biodiversity to meet the ever growing consumer demands for such products in our increasingly environmentally focused society. However, soils, which sustain such microbial diversity are increasingly endangered, mostly due to anthropogenic intervention. For every organism which goes extinct in the soil environment, as with other ecosystems, some as yet undiscovered biotechnology is also potentially lost. It is vital, therefore, that soil biodiversity is conserved as much as is reasonably possible and that the awareness of this need is raised within the scientific community, policy makers and the public in general. The conservation and sensibly-managed exploitation of microbial biodiversity thus arise as urgent issues to be addressed in their own right, not only from the conservationist, but also from the microbiological and biotechnological point of view. Awareness of this fact should raise within the scientific community, policy makers and the public in general. Preserving soil microbial diversity is not only means of sustaining environmental (and therefore human) health, but also of enriching the human condition.

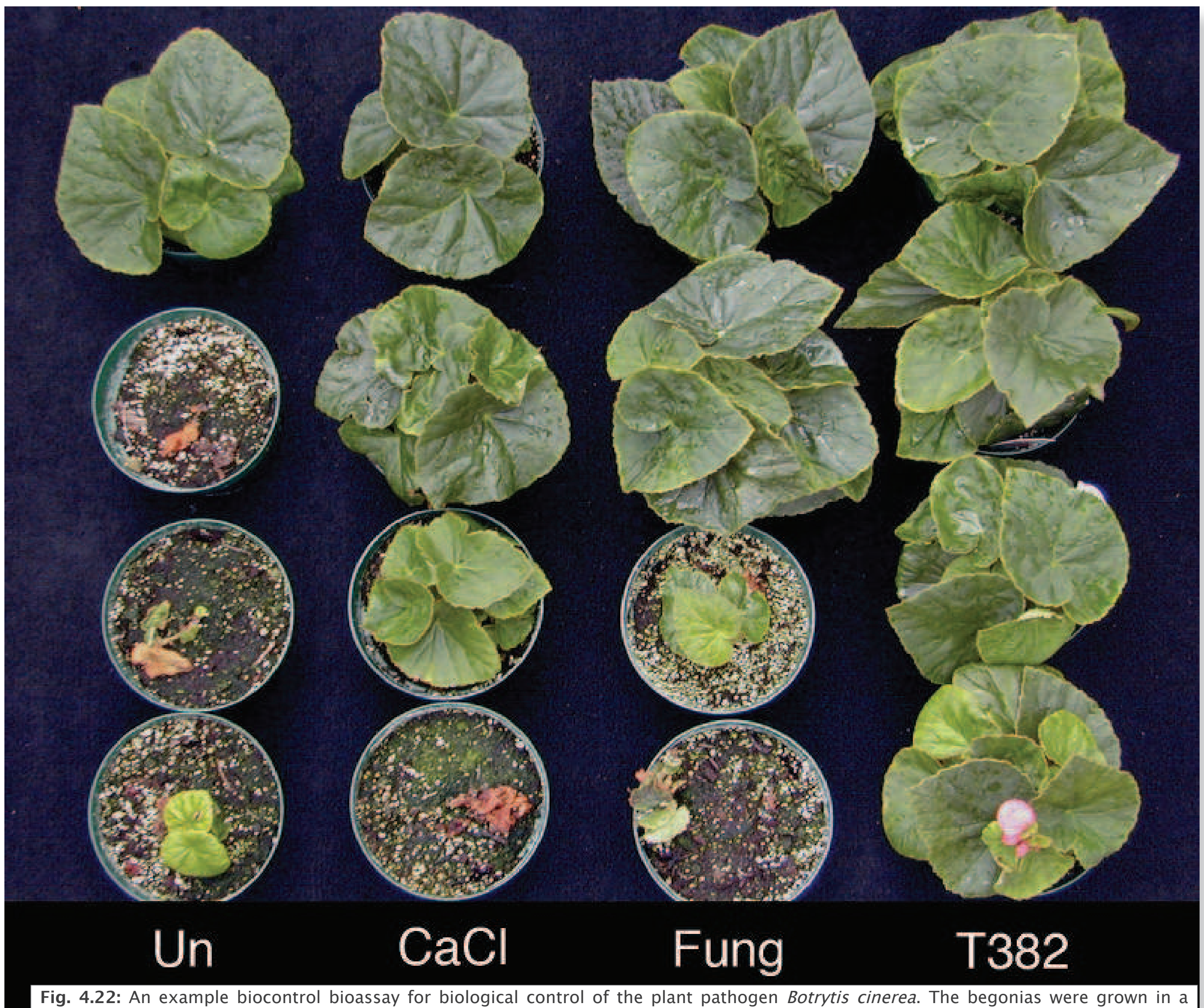


Fig. 4.22: An example biocontrol bioassay for biological control of the plant pathogen *Botrytis cinerea*. The begonias were grown in a greenhouse under optimum conditions for the development of the pathogen. Treatments differing in their efficacy are shown, from left to right: untreated control (Un), $CaCl_2$, a fungicide (Fung), and a fungus as a biocontrol agent *Trichoderma hamatum* (strain T382). Clearly the biocontrol agent shows the best results with the plants protected from the pathogen by this fungus producing the most foliage. (HHo/LH)

4.6 What is Soil Biodiversity worth?

As the preceding pages have made clear, there can be little doubt of the crucial and diverse contributions that soil biodiversity makes to ecosystems health and human welfare in the form of generated ecosystem services. Given the paramount importance of soil biodiversity, the question is why it has not been given the same level of attention as other natural resources and why soil resources have been, and continue to be degraded so extensively throughout the world? Before answering this question, it is important to note that this discussion addresses the value of soil biodiversity and not the economic value of any individual organism. With this in mind, the answer lies partly in the fact that soil biodiversity, owing to its scale and its complex nature and interactions with the production of various ecosystem services, is somewhat poorly understood and hard to measure and quantify. More importantly, however, the reason for the loss of biodiversity as a resource is that it is undervalued due firstly to its full value not being integrated in decision making, and secondly due to the lack of markets for many of the services it provides. For example, very limited or no markets exist for ecosystem services such as waste recycling, carbon cycle regulation, and ecosystem resilience. This is due to the "public-good" characteristics that many biodiversity functions and services exhibit. In economics, a public good is a good whose consumption has two properties: it is non-rival (i.e. consumption of the good by one person does not reduce the availability of the good to others) and non-excludable (i.e. the provider of the good cannot exclude non-payers from consuming it). The "public-good" character is one of the main reasons why valuation of ecosystem services is highly problematic.

A further complication which arises when attempting to value ecosystem services is that there is an inherent mismatch between the private and social costs, and benefits, of biodiversity conservation. For example, conservation of soil biodiversity generally benefits society as a whole through the provision of ecosystem services. Many of these ecosystem services, such as nutrient cycling, function on a much larger scale than that at which efforts of conservation generally occur, such as at farm or natural park scale. As there are currently no, or very few, mechanisms to support the conservation of biodiversity or a given ecosystem service, it is frequently more beneficial for a resource user to overexploit and run down the resource (i.e. to maximize profit through yields even if that leads to a loss of biodiversity). Therefore, private economic choices, in this case maximizing yields, do not necessarily mirror and respond to additional societal values, in this case conserving biodiversity, as the consequences of the choices and their associated costs are not solely met by those demanding the services (i.e. a farmer may make more money by maximizing yields but society as a whole faces the costs of reduced ecosystem services). However, biodiversity loss can also be the result of ill-judged incentives provided to resource users by well-intended but ill-conceived government policies and regulations. Notable examples of policy failures that have led to environmental degradation and associated loss of ecosystem services are those financial incentives, subsidies and pricing schemes that cause deforestation, depletion of water resources and degradation of agricultural lands.

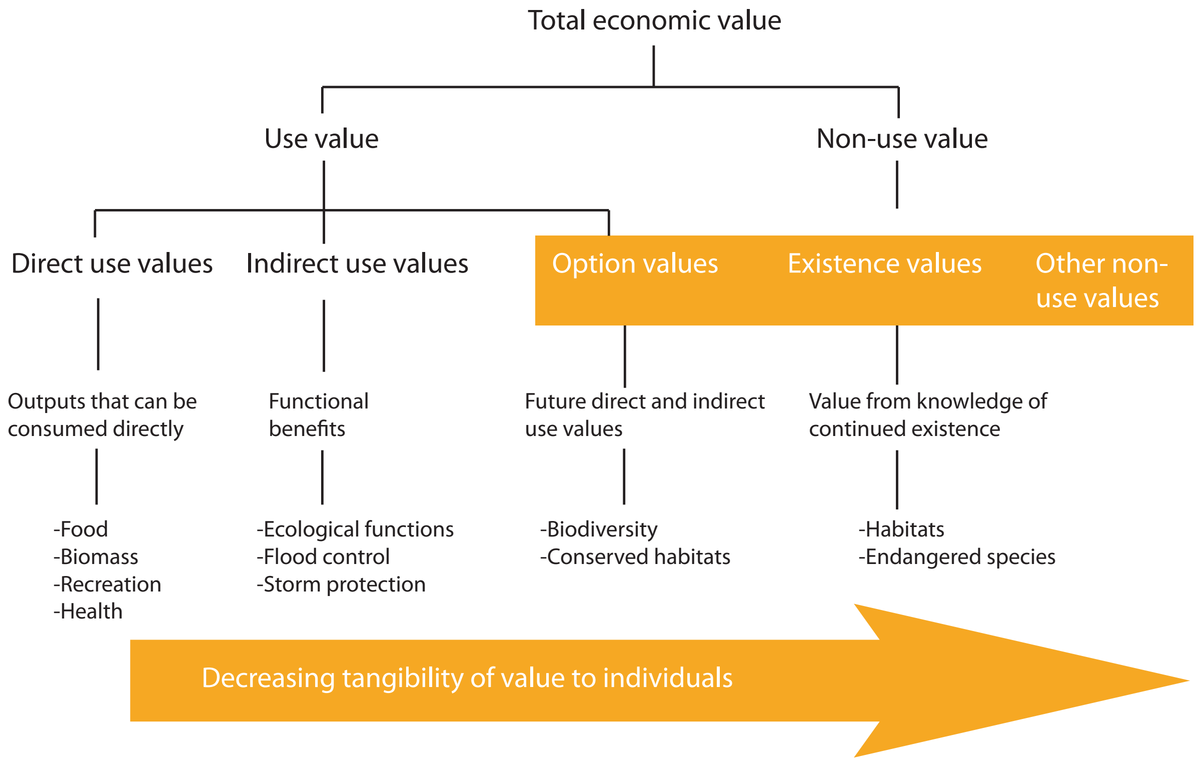


Fig. 4.24: Schematic representation of Total Economic Value Framework. (www.eoearth.org)

Environmental economists have long been trying to measure the economic value of biodiversity and non-marketed ecosystem services such as water regulation and erosion reduction. Such efforts stem from the belief that if it is not possible to demonstrate the value of biodiversity to those who control its fate, people will be unwilling to incur the 'opportunity costs' of its conservation (with the opportunity cost being, in this case, the lost opportunity to use the conserved habitats or soil organisms for any purpose other than conservation i.e. agriculture, industrial development etc.). Therefore, the goal of economic valuation of biodiversity is to impute a value for its many ecosystem services and in doing so to inform and guide decision making into increasing the efficiency of resource allocation among uses with different objectives.

It can be argued, however, that demonstrating the true economic value is a necessary, but not a sufficient, condition of ensuring sustainable use of biodiversity. It is also necessary to devise ways for policy makers to use these values and for resource users to capture this value. Various economic instruments have already been applied in numerous cases, such as income from ecotourism, payments to avoid deforestation for carbon sequestration purposes, conservation easements, debt-for-nature swaps, etc. Regardless of which instruments are used, what matters is that any action taken forms part of a well-informed decision framework such as that proposed in Fig. 4.23. What this figure shows is that measuring economic value is not an end in itself; rather, the aim of valuing natural capital and ecosystem services is to facilitate decision making, thus resulting in better actions relating to the use of land, water, and other natural resources.

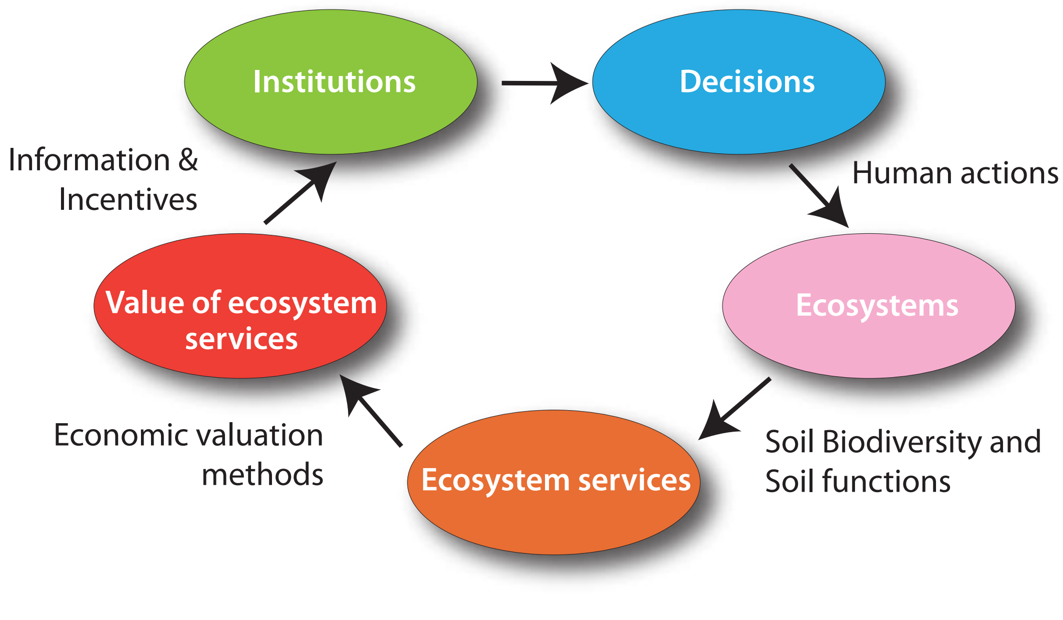


Fig. 4.23: Decision loop to facilitate decision making regarding natural resources. (proposed by Daily *et al.* (2009)

Total Economic Value (TEV)

In valuing environmental goods and services economists often employ the Total Economic Value (TEV) framework (Fig. 4.24). According to this framework, the TEV can be divided into "use value" (UV) and "non-use value" (NUV). Use values arise from an actual use made of a given resource, i.e. the use of a forest for timber, or use of a lake for recreation or fishing. Use values can be further broken down to "direct use values" (DUV), which refer to actual uses such as fishing, timber extraction etc; "indirect use values" (IUV), which refer to the benefits deriving from ecosystem services, such as the soil's nutrient cycling function; and "option values" (OV), which are expressed as individuals' willingness to pay to preserve an asset for the option of using it at a future date i.e. basically an insurance value. Finally, non-use values are those held by individuals who value a resource's mere existence without intending to make use of it either now or in the future i.e. people that live in a city may give value to having a natural park, even if that park is so far away that they will never visit it.

Thus, in total we have:

$$TEV = UV + NUV = (DUV + IUV + OV) + NUV$$

Schematically, this can be represented as seen in Fig. 4.24.

In practice, although measurement of direct and indirect use values have been relatively successful in various contexts, identification and measurement of option and non-use values has been rather problematic, mainly due to their elusive nature. It should be noted here that the TEV of different types of environmental resources consist of different types of economic value and that the more encompassing, large and familiar a resource is, the more components its TEV will have. For instance, in measuring the economic value of conserving a particular stand of tropical forest, it is necessary to be able to identify direct and indirect use values, as well as non-use values. Direct use values would include sustainable logging, non-timber products and ecotourism, whereas as indirect use values would include any water regulation and carbon sequestration potential the forest might hold. The non-use value of this forest would be the willingness to pay of people who derive satisfaction from knowing that this forest will continue to exist and therefore would potentially be willing to pay for its conservation.

The TEV of soil biodiversity, and particularly the ecosystem services that it provides, involves mainly indirect use values, as indirect services such as nutrient cycling and ecosystem resilience are not utilised directly, but the organisms performing these services still bring a clear value to the ecosystem. The soil biota does also provide direct use values, for example in the form of genetic information which has been extracted and used by the biotech and pharmaceutical industries in developing new products such as antibiotics. Non-use value is, however, perhaps more limited with regard to soil biodiversity as it generally lacks any charismatic species that people are familiar with in above ground ecosystems such as elephants and lions etc.

Valuation Tools & Studies

In terms of the various methodologies for economic valuation, it is possible to distinguish between two broad categories, each made up of a number of techniques: Direct (or Stated Preferences) and Indirect (or Revealed Preference) approaches. The direct approach employs methods that attempt to elicit values directly i.e. through the use of surveys and experimental techniques. Essentially, such methods ask respondents to express their willingness to pay (WTP) or willingness to accept compensation (WTA) for changes in the provision of certain environmental assets. The main advantage of this approach is the ability, at least in theory, to estimate non-use values, though it has been regularly used to measure use values as well.

The main drawback is the techniques' hypothetical nature meaning that possible biases can be introduced when relying on subjective thought processes and interpretations.

The indirect approach makes use of the notion of weak complementarity, which allows the inference of the value of a non-market good or service from the influence it exerts on a well-recognised market commodity. For instance, through the knowledge that air and noise pollution affect house prices it is possible to improve knowledge of the housing market. As people spend money to travel to natural parks and reserves, it is possible to look at those expenditures to see if we can infer the recreational value of such sites. Finally, the economic damage of soil degradation in agriculture can be quantified by valuing the loss of income due to reduced yield output.

It should be noted that no valuation technique is without shortcomings and the suitability of each of them depends on issues such as data requirements, policy context, scale and many others. Moreover, different types of values lend themselves to different types of valuation techniques. A comprehensive analysis of the above issues is presented in Chapter 5 of the TEEB D0 report Ecological and Economic Foundations". For more information visit the website at http://www.teebweb.org.

Studies attempting to measure the economic value of environmental resources, services and amenities abound in the literature. The most famous study was undertaken by Costanza and colleagues in 1997, and was reported in Nature. The study purported to estimate the economic value of the world's ecosystem services. The authors suggested that a minimum estimate of such values is US$33 trillion a year which is more than half of the annual global GDP (estimated by the World Bank at US$57 trillion in 2007). Along similar lines, although focusing on terrestrial ecosystem services as opposed to global ecosystem services encompassing the marine environment, the work published by Pimentel and colleagues in 1997, entitled Economic and Environmental Benefits of Biodiversity (Table 4.5), focused on the global economic value of terrestrial biodiversity. According to this study the annual contribution of biodiversity to the world economy is almost US$ 3 trillion. Out of this amount, approximately $1.5 trillion is attributable to services provided by the variety of soil organisms. While the Costanza paper tried to value all ecosystem services as opposed to just terrestrial ecosystems and their services as was the case in the Pimentel paper, a large discrepancy is still visible in the values produced. This highlights the difficulty in attempting to put a precise monetary value on ecosystem services, which of necessity require several assumptions to be made.

Furthermore, these studies have spurred intense debate, with some economists pointing out flaws on several fronts. The most fundamental criticism is that these studies confused marginal and total values. When considering economic value, it is the value of marginal incremental changes in the provision of goods and services that must be estimated. This is because in economics the value of a good is determined by the benefit we derive from consumption of a little more of that good, expressed in terms of other goods (typically money) we would be willing to give up in order to obtain it. It is clear that natural ecosystems and biodiversity are of immense economic value to humans, with the value approaching infinity, because without them life as we know it would not be possible due to the many vital ecosystem services they provide. By putting a price on entire ecosystems, the marginality principle is eschewed, as the implied tradeoffs are far from incremental. Therefore, when estimating the economic value of life-sustaining natural ecosystems and services, these studies actually undervalued systems which have an all but infinite value as without them life as we know it could not exist. That said, by providing ballpark figures, such work has had an important role and positive impact, as it helped raise the profile of biodiversity and ecosystem services and attempted to put them in a context which is easily understandable by policy makers and legislators, being the context of monetary value.

Another shortcoming that several studies have exhibited when attempting to value ecosystem services, especially at the global scale, is the extensive and somewhat arbitrary use of benefits transfer, which is the technique of applying value estimates derived in one setting to valuation of services generated in another setting. This is often done by obtaining data from various earlier studies estimating economic values of services, generated by particular ecosystems in specific locations and extrapolating these estimates on a per hectare basis to superficially similar, but in reality different, settings around the world.

In the case of biodiversity, these criticisms suggest that its TEV is not some index of overall economic performance. It is, rather, a measure of the economy-wide consequences of some incremental change in biodiversity and the services stemming from it. At this point, it should be noted that although the studies that estimate the economic value of various environmental goods and services number, nowadays, in their hundreds or thousands, studies on the economic benefits of biodiversity *per se* are much rarer. In fact, most studies focus on measuring the economic value of biological resources and the habitats that sustain them, rather than their diversity as such.

All this is not to say that there has been no work on estimating the economic value of the diversity of biological resources. Originally, attempts to value biodiversity were approached through using the diversity function, which is defined in terms of pair-wise genetic distances among species. The diversity function approach is based on the implicit assumption that diversity is desirable. However, it does not make clear or establish why it is desirable, nor does it establish a mechanism for linking the size of genetic distances to some well-defined concept of usefulness or desirability. More work in environmental economics is now generally undertaken viewing biodiversity as a commodity.

Biodiversity as a commodity

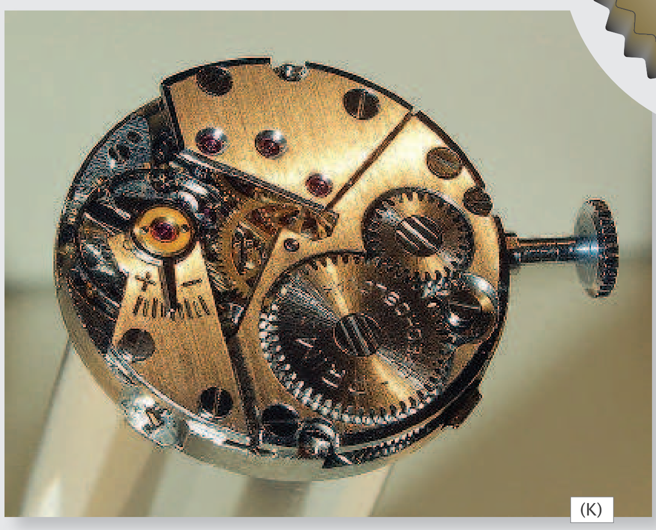
From an economic perspective, a basic guiding principle for valuing biodiversity should be the association of diversity with some useful traits that it possesses or useful services that it provides or enhances.

Table 4.5: Proposed economic value of various ecosystem services provided by the soil biota (Pimentel *et al.* 1997)

Activity	Soil biodiversity involved in such activity	World economy benefits of biodiversity (billion $/year)
Waste recycling	Various saprophytic and litter feeding invertebrates (detritivores), fungi, bacteria, actinomycetes and other microorganisms	760
Soil formation	Diverse soil biota facilitate soil formation, e.g. earthworms, termites, fungi, etc.	25
Nitrogen fixation	Biological nitrogen fixation by diazotrophic organisms	90
Bioremediation of chemicals	Maintaining biodiversity in soils and water is imperative to the continued and improved effectiveness of bioremediation and biotreatment	121
Biotechnology	Nearly half of the current economic benefit of biotechnology related to agriculture involving nitrogen fixing bacteria, pharmaceutical industry, etc.	6
Biocontrol of pests	Soil provide microhabitats for natural enemies of pest, soil biota (e.g. mycorrhiza) contribute to host plant resistance and plant pathogens control	160
Pollination	Many pollinators may have edaphic phase in their life-cycle	200
Other wild food	For example, mushrooms, earthworms, small arthropods, etc.	180
Total		1542

No Species is an island and soil is not a black box – the pocket watch analogy

A useful analogy when thinking about the soil system, which is very complicated, is to think of a pocket watch. This is because many people view the soil in the same way that most people view pocket watches: We know that if we wind up the clock it will keep the time, but most people don't really know how, and view the inside of the watch as a bit of a 'black box'. Soil is often viewed in the same way. If we put seeds in the ground then they grow into plants, if we put compost into the ground it can enhance plant growth, but as with the watch, most people don't really know why this works and so also view the soil as a black box.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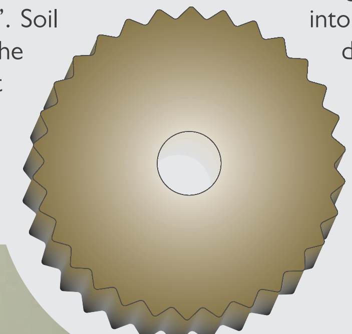

Within a watch there is a very precise arrangement of cogs and springs which, when energy is input by winding, all link together and allow the watch to perform the function of keeping the time. The soil biota is similar in that it consist of different species, all linked together and interacting. When energy is put into the system in the form of sunlight (either directly through exudates of plant roots or indirectly though dead organic matter - which contains energy stored from the sun when from when the organisms was alive), the soil functions to provide a range of different ecosystem services, including nutrient.

Of course, watches are not really 'black boxes' and experts do understand the intricacies of their workings; it is only these people that are capable of fixing watches when they break. The soil system is the same. Only by understanding all of the intricacies and interactions of soil organisms can we hope to be able to protect it, and to fix it if ever it does 'go wrong' including nutrient cycling and aiding plant fertility.

Valuing soil biodiversity

Valuing a watch and its constituent parts can be more problematic than it may seem at first. A good watch can be worth hundreds or thousands of Euros. To buy 1 cog that is used in the watch mechanism may cost only a few tens of Euros, but if that cog is removed from the watch then the watch becomes useless. Therefore, what is the overall value (as opposed to price) of the cog?


(MJ)

The soil biota is similar. It provides some services which can be valued, such the provision of nitrogen to plants by the soil biota through the nitrogen cycle. It is possible to calculate the reduction in nitrogen fertilizer needed on a given field owing to nitrogen fixation by the soil biota.

However, within the nitrogen cycle there are several steps, such as nitrogen fixation, which need to occur for the cycle to continue. Valuing these steps is more problematic in the same way as valuing a cog in a pocket watch. If we remove key organisms, the nitrogen cycle stops. Adding to the complication in nature, some processes may possess functional redundancy (as discussed in Section 4.1). Clearly, valuing ecosystem services and the species responsible for them is a far from trivial task!

Biodiversity is now often thought of by economists as being a commodity that is valuable from an economic perspective. This is because it possesses the following qualities:

Insurance in respect to future services

For example, there is the possibility of finding genes in non-commercially used species that can be used to build resistance against lethal diseases affecting other crop species. Therefore, genetic diversity can be viewed as insurance against catastrophic events or infections. More importantly, however, insurance is provided through the resistance and resilience enhancing properties of systems characterised by high functional diversity as increased diversity is usually associated with increased functional redundancy.

The maintenance of the ecosystems' resilience protects us from incalculable welfare losses that would be incurred due to exogenous or anthropogenic shocks. The economic importance of ecosystem resilience lies mainly in its function to minimise the risks of such shocks. The value of biodiversity therefore includes a significant insurance component. Soil biodiversity's insurance services stem mainly from maintaining ecosystem stability and resilience through functional diversity. Despite the obvious economic importance of this service, quantifying it is very difficult. Recently, there have been a handful of studies attempting to value ecosystem resilience without, however, explicitly linking ecosystem resilience to biodiversity.

To estimate the value of resilience it would be necessary to first relate different levels of biodiversity to varying levels of soil ecosystem services, and to identify critical thresholds in the provision of these services and the functioning of the soil ecosystems. Of course, such thresholds may not assume a strict, absolute value but rather depend on the attitudes and tolerance levels of different stakeholders whose preferences should also be accounted for. Biodiversity levels (as expressed by the use of biodiversity indicators) that are higher than the threshold levels necessary for a particular ecosystem service to be performed can be considered as possessing "resilience stock". The further away an indicator is from a perceived threshold, the higher the resilience stock, meaning a reduced probability of a regime shifting to an undesirable state is lower and therefore the survival probability of the ecosystem service is higher. The value of resilience is the shadow price of a change in the resilience stock. Crudely speaking, this is estimated by calculating the expected economic loss (through e.g. decreased agricultural profits or land prices) due to a system flip and multiplying it by the increased survival probability, owing to improved biodiversity.

Enhanced ecosystem productivity

This pertains to the observation that more diverse systems are more productive than less diverse ones. There are several empirical studies relating the number of plant species in ecosystems to plant productivity which have established that functional diversity is a key factor explaining plant productivity. Moreover, the wider availability of genetic material found in diverse plant systems has been used by the plant breeding community and has contributed significantly to agricultural yield increases of the past few decades. In a similar fashion, economic gains from enhanced plant and crop productivity can be attributed to services, such as soil formation, pathogen repression and nutrient cycling, which are performed by the soil biota. The challenge here is to better understand and quantify the relationship between the level of soil biodiversity and the productivity enhancing services, and subsequently to estimate the economic values of these services.

Enhanced ecosystem services

As well as providing services that directly impact ecosystem productivity, biodiversity is responsible for ecosystem services which have welfare-enhancing effects that are diffused across various stakeholders. For example, soils are known for their capacity to attenuate pollution, thus reducing the risks of water contamination and consequent adverse health impacts. Part of this ability is due to the physical properties and acidity of different types of soil as well as due to microbial activity. Therefore, although soil biodiversity provides services that are clearly beneficial from an economic point of view, the fact that such benefits extend beyond the farm level, makes it hard to isolate the effect of soil biodiversity on, for example, pollution attenuation or any other large scale ecosystem service.

Knowledge

This refers to biodiversity's role as a source of knowledge with which new products in the biotechnology and pharmaceutical industries can be developed. There is little doubt that agricultural and pharmaceutical products of great economic value and significance to our wellbeing have been developed by making use of the genetic diversity found in various plants and other living organisms. Estimates of biodiversity's contribution to the world economy, in the form of new crop strains and medical drugs is in the region of $6 billion with almost 40% of the value of pharmaceuticals sold in the USA being derived directly or indirectly from plants and other living organisms. Such eye-catching figures, however, are not particularly helpful in guiding private or public decision-making with respect to channeling funds in biodiversity protection, as they do not adhere to the marginality principle discussed previously.

Valuing

In the context of genetic diversity, valuation at the margin has been carried out in the form of studying bioprospecting incentives to invest in biodiversity conservation in the tropics. Unfortunately, from the viewpoint of a biotech or pharmaceuticals investor interested in economic returns from genetic information, investing in conservation often loses out to alternative uses of the land. The reason for this is that for the valuation of the marginal value of species diversity, the possible substitutability of species must be accounted for. It is arguable that there are large redundancies concerning the production value within the species pool, which stem from the fact that identical chemical compounds can be produced by different species and even different chemical compounds can have similar functions concerning their use for the development of pharmaceutical products. Considering these substitution possibilities, the value of a species depends not only on the probability that the prospecting of a species will lead to the commercial development of a marketable product, but also on the probability that all other species cannot contribute to the development of this product. As a result, for an assumed number of one million species, it has been estimated that a marginal value of less than 0.1 cents results.

There are millions of organisms which may provide valuable genetic information, and, as it is not possible to determine *a priori* which of them will provide such information as the cost of doing so is still prohibitively expensive, there is a potentially huge supply of genetic leads, which is likely to be greater than pharmaceutical companies can process (see Section 4.5). Under these circumstances, the market price for such leads would be low, much like the price of water that in some cases may be nearly zero, owing to its abundance relative to observed demand. This demonstrates that the marginal value of species diversity to the pharmaceutical industry is low, even though the economic benefits to the whole industry and society are clearly quite substantial. Given the immense diversity of the soil biota and the extent of functional redundancies, it is quite likely that the value of soil biodiversity as an input to the biotechnology and pharmaceutical industries is equally low, even though, as previously stated, the value of services provided by the soil biota to society at large verges on infinite.

Therefore, calls to conserve soil should be based on sources other than the development of new pharmaceuticals and biotech products, such as the need to protect the ecosystem services that the soil provides, which as previously discussed has an all but infinite value. Clearly, the difficulties involved in quantifying the economic value of soil biodiversity must not deter investment in soil conservation. This is because soils (and therefore soil biodiversity) form part of wider ecosystems such as forests, agriculture and pasture land, which also generate many beneficial and well documented ecosystem services. This means that services stemming from soil biodiversity affect, and are affected by, the wider ecosystems that the soils are part of. As a result they impact on the provision of goods and provisional services that people ultimately value (like food, timber, etc). In many cases, the economic value of these ecosystem services (as opposed to biodiversity *per se*), or the cost of losing them, is known or is relatively easy to estimate. It has been demonstrated that consideration of such values is often enough to tip the decision scale and justify conservation. Thus, for those cases that the soil biodiversity-specific economic benefits are hard to quantify, the great value generated by the wider services of the ecosystems that soils are part of, and which would not function well without the input of soil biodiversity, suffice to ensure that the protection of soil and the associated supply of biodiversity services make economic sense (Fig. 4.25).

TEEB

As briefly mentioned, an ongoing economic evaluation of ecosystem services called "The Economics of Ecosystems and Biodiversity" (TEEB) is being undertaken by an international group of experts, being led by the United Nations Environment Programme (UNEP), with financial support from the European Commission, the German Federal Ministry for the Environment, the UK department for Environment, Food and Rural affairs, the Norwegian Ministry for Foreign Affairs and The Netherlands' Ministry of Housing, Spatial Planning and the Environment, in partnership with the Government of Japan and many private and non-governmental organisations. The main aims of the study, which will report its findings in the Nagoya 2010 CBD Conference of the Parties, are:

- The integration of ecological and economic knowledge to structure the evaluation of ecosystem services under different scenarios
- The recommendation of appropriate valuation methodologies for different contexts
- Examination of the economic costs of biodiversity decline and the costs and benefits of actions to reduce these losses
- Development of "toolkits" for policy makers at international, regional and local levels in order to foster sustainable development and better conservation of ecosystems and biodiversity
- The enabling of easy access to leading information and tools for improved biodiversity practice for the business community – from the perspective of managing risks, addressing opportunities, and measuring impacts
- Raising public awareness of the individual's impact on biodiversity and ecosystems, as well as identifying areas where individual action can make a positive difference.

The study is still a work in progress with not all of the reports being publish at the time of this atlas going to print. The progress and available reports can be found on the TEEB website at http://www.teebweb.org.

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Fig 4.25: As this section has made clear, while clearly of vital importance, the valuing of soil biodiversity and its associated ecosystem services is as complicated and difficult as the many and varied uses to which soil is put. Whether it be growing crops (**top left**), the aesthetic value of urban gardens (not to mention the value of urban gardens in conservation of both above and below ground species; **top right**), use for sport and recreation (**middle**), or as a platform on which to build houses, roads and other infrastructure vital to the efficient functioning of our towns and villages (**bottom**).

Chapter 5 Threats to Soil Biodiversity

5.1 What are the Main Threats to Soil Biodiversity

There is increasing concern regarding the possible decline of soil biodiversity, even though there is only limited data available showing this. It is well known, and widely reported, that the planet is currently losing biodiversity, with the actual rate of species extinction being several orders of magnitude higher than it would be in absence of human activities, but little specific data for soil organisms.

That said, it can be assumed that if extinction is accelerated regarding mammals, birds, reptiles, amphibians, etc., it is almost certainly also occurring to the variety of organisms living into the soil.

Soil ecology and soil biology are relatively new disciplines which is the reason why historical records concerning soil organisms are limited. Some evidence exists of the decline of mushrooms species in some European countries. For example, a 65% decrease in mushroom species over a 20 year period has been reported in The Netherlands, and the Swiss Federal Environment Office has published the first-ever "Red List" of mushrooms detailing 937 known species facing possible extinction in the country.

Furthermore, invasive species have been shown to cause a decline in soil biodiversity: garlic mustard, an invasive plant in North America, is responsible for the decline of arbuscular mycorrhizal fungi (AMF) in many native hardwood forests and in the UK a flatworm from New Zealand (*Arthurdendyus triangulatus*), is probably one of the main threats to indigenous earthworms. These, and the specific threats of invasive species on soil organisms are discussed in more depth in Section 5.1.2.

A necessary starting point to achieve the objective of preserving soil biodiversity is to reach an adequate level of knowledge on its current extent, its spatial and temporal distribution as well as a full understanding of the "pressures" that the soil biota faces.

The evaluation of the environmental pressures, can be achieved by applying the DPSIR framework (Driving Forces-Pressures-State-Impacts-Responses; Figure 5.1), which is widely used to assess and manage environmental problems.

- "Driving forces" are the socio-economic and socio-cultural forces driving human activities, which can either increase or mitigate pressures on the environment
- "Pressures" are the stresses that human activities place on the environment
- "State" refers to the state or condition of the environment
- "Impacts" are the effects of environmental degradation and
- "Responses" refers to the responses by society to the environmental situation.

The application of DPSIR framework was originally proposed for the global evaluation of biodiversity pressures but has been applied below in the context of soil biodiversity specifically.

For Europe, the main anthropogenic disturbance factors (pressures), have been identified for the three levels of biodiversity: ecosystem, species and gene.

At the level of ecosystems, the main pressures derive from:

- Land use change
- Overexploitation
- Change of climatic and hydrological regime
- Change of geochemical properties

At the level of species, the main pressures on soil biodiversity derive from:

- Change in environmental conditions
- Change of geochemical properties
- Competition with invasive species
- Effects of ecotoxins

At the level of genes, the main pressures derive from:

- Change of environmental conditions
- Effects of ecotoxins
- "Genetic pollution"

Other pressure factors, which may be important for biodiversity in general, are less important for soil biodiversity in the majority of instances. This is the case for habitat fragmentation, which can theoretically be very detrimental for soil biological diversity, but, owing to the usually small sizes and limited migration ranges of soil organisms, only at spatial scales that rarely occurred in practice. In fact there is some scientific evidence regarding the effects of small scale habitat fragmentation on soil organisms, but the dimension of the habitat fragments used in this research was in the order of few square centimetres, far removed from the scale at which 'real world' habitat fragmentation is likely to occur.

It is important to consider that in addition to the above listed pressures, any physical loss of soil, or other soil degradation processes, can lead to loss of biodiversity. Based on the DPSIR approach, Fig. 5.1 details the main pressures on soil biodiversity, and the related driving forces.

Expert evaluation of threats to soil biodiversity

A soil biodiversity expert working group was invited to the Joint Research Centre (JRC) a Directorate General of the European Commission, to advise the Commission on areas of soil biodiversity research which were particularly pertinent, as well as several other issues. The opportunity was used to conduct experts questionnaires to try and quantify expert opinion regarding the relative weighting of many of the threats listed above. Each of the 20 experts were asked to give each threat a weighting between 1 and 10, with 1 meaning virtually no threat and 10 meaning very severe threat. The weighting given by the experts for each threat were summed and calculated as a percentage out of the maximum score that each threat could have received (200). This allowed the removal of any bias which may have been introduced due to subjectivity of the threat scale. The results can be seen on the page opposite in Figure 5.2. This survey was conducted due to the many difficulties which exist in assessing threats to soil biodiversity. The main difficulty that the survey overcomes is subjectivity which is normally introduced owing to people's individual background and area of expertise. Added to this, soil biodiversity is a relatively new field of research and so relatively little empirical data exists concerning threats to soil biodiversity.

Generally, knowledge is very limited for most species regarding their exact functions, their ability to respond to environmental pressures, their interactions with other organisms and the spatial distributions throughout the soil matrix. Current levels of soil biodiversity in most areas is still unknown and while quantification of current levels of soil biodiversity is difficult, it is vital to allow assessment of future impacts. Functional redundancy also makes the evaluation of a given threat's effects on a soil system difficult to quantify as function may remain, even when species diversity is reduced (See Section 4.1).

The expert evaluation led to the production of a map of Soil Biodiversity Potential Threats (Section 5.2), the description of which can be found in the caption of the map (see page 62).

Agriculture and human intensive exploitation

The abundance and diversity of soil organisms are influenced by a wide range of soil management practices.

Agricultural management practices include, for example, variations in tillage, treatment of pasture and crop residues, crop rotation, applications of pesticides, herbicides and fertilizers, manure, sewage, ameliorants such as clay and lime, drainage and irrigation, and control of vehicle traffic on fields. Furthermore, differences in agricultural production systems, such as integrated, organic or conventional systems, have also been shown to affect the soil biota with respect to overall biomass as well as biodiversity.

Soil tillage operations lead to deep modifications within the soil environment, especially in reference to soil architecture (soil structure, porosity, bulk density, water holding capacity etc.), crop residue distribution and organic carbon content. The soil environment itself directly influences soil communities within the soil with respect to both numbers (biomass) and composition (biodiversity). The impacts of soil tillage on soil organisms are highly variable, depending on the tillage system adopted and on the inherent characteristics of the soil.

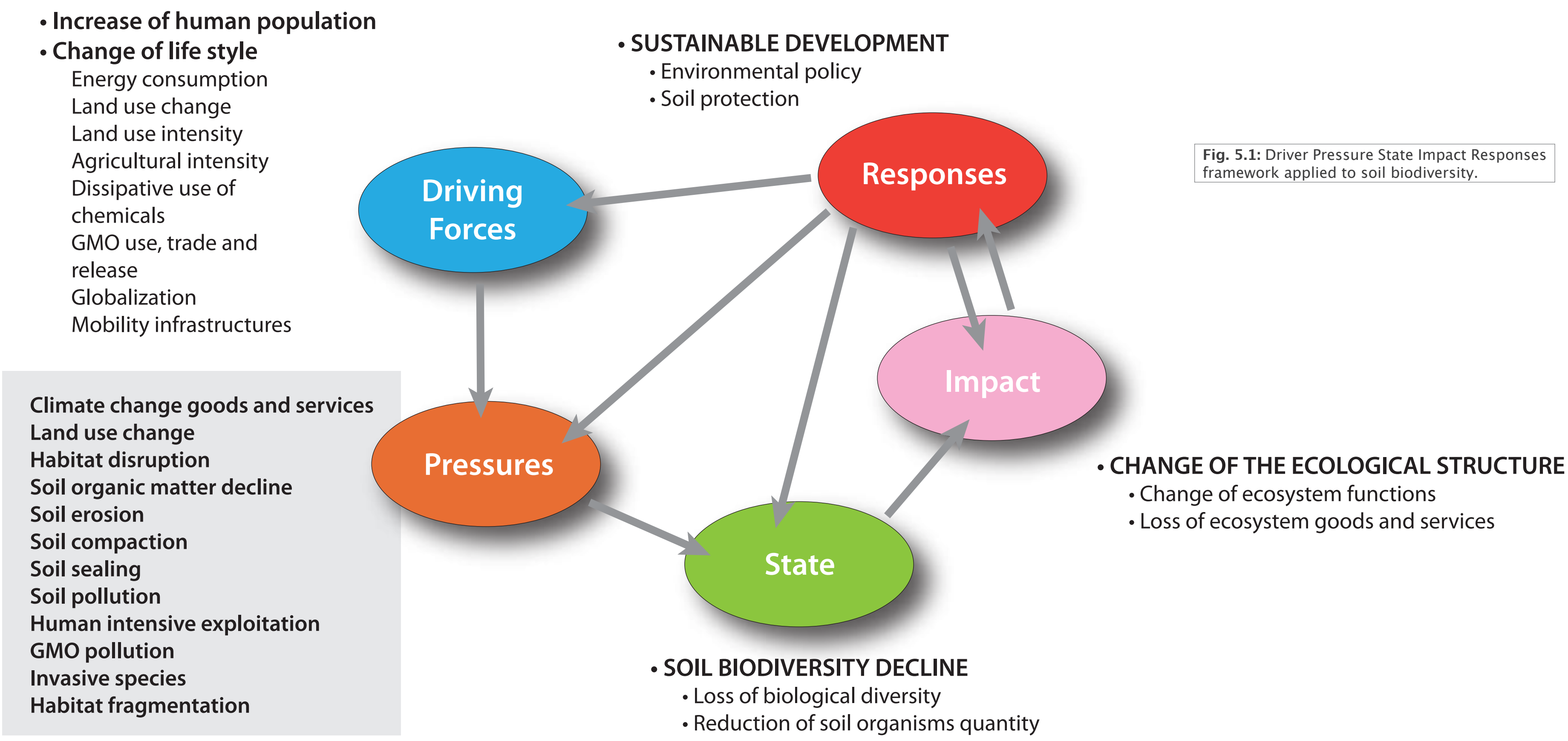


Fig. 5.1: Driver Pressure State Impact Responses framework applied to soil biodiversity.

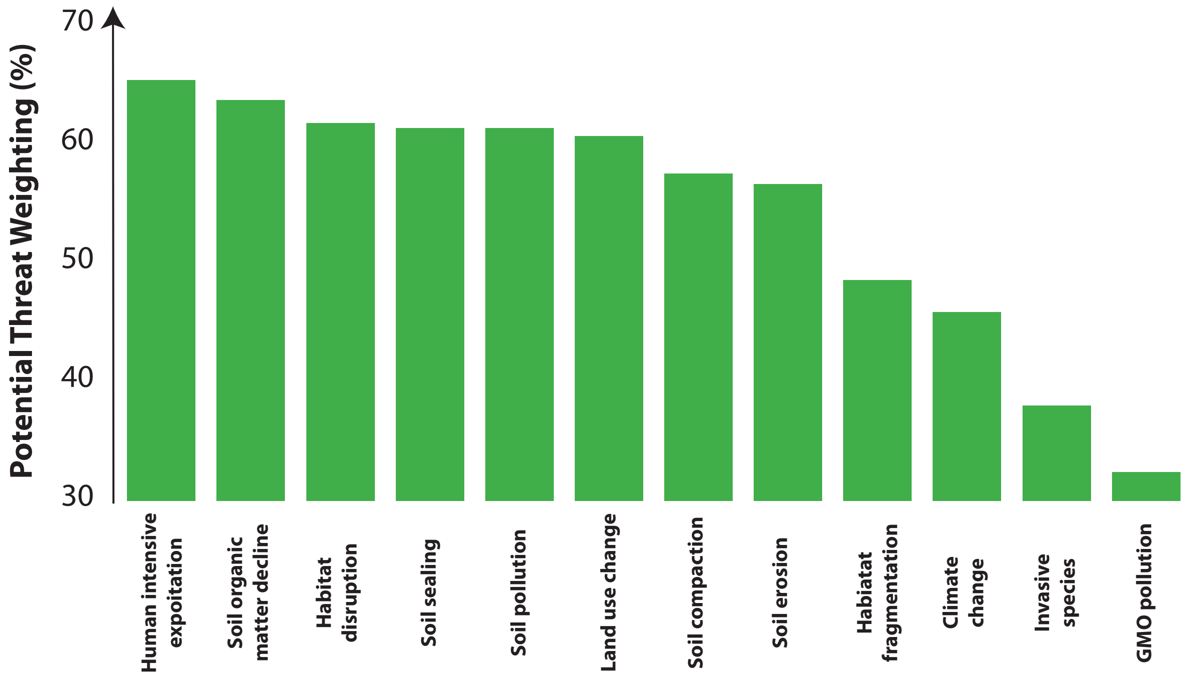


Fig. 5.2: The potential threat weighting given to a selection of possible threats to soil biodiversity by the Expert Working Group at the JRC on 2nd March 2009. (JRC)

Concerning mineral fertilizer application, it has been observed that high inputs tend to lead to lower biodiversity while lower input systems tend to conserve biodiversity. Furthermore, high input systems tend to favour bacterial-pathways of decomposition (as opposed to fungal), dominated by labile substrates (that is, chemicals which are easily used for energy such as sugars, as opposed to those which are harder to break down such as cellulose) and opportunistic, bacterial-feeding fauna. Conversely, application of manure, or other organic matter sources, tends to lead to larger and more diverse soil communities.

Soil organic matter decline

Soil organic matter is both the main 'fuel' driving the 'engine' of the soil food web as well as being the result of soil organism activity. A reduction in soil organic matter is generally associated with a lower soil organism abundance and diversity.

Soil biodiversity is intimately bound to soil organic matter: each type of soil organism occupies a different niche within the food web of life and favours a different substrate and nutrient source. Consequently a large, varied source of organic matter will generally support a wider variety of organisms due to it containing a greater range of substrates and nutrients.

Soil organic matter decline is a common occurrence in many areas of the planet as a result of the intensification/ modification of agricultural practices and climate change. In turn, the reduction of soil organic matter is the large contributor to other soil degradation processes, such as soil erosion and soil compaction.

Land use change and habitat disruption

Land use change is considered likely to be one of the main manifestations of global change in the future and the main cause of change in biodiversity for tropical, Mediterranean and grassland ecosystems. It is unlikely that soil biodiversity will not differ substantially from above ground biodiversity regarding the effects of land use change, even though the soil is generally considered to be a more conservative and resilient environment than above ground ecosystems.

Forests, either tropical or temperate, generally represent the biomes with highest levels of soil biodiversity. Consequently any land use change concerning the removal of perennial tree vegetation is likely to cause a reduction in soil biodiversity. In some cases forests are converted to pasture or perennial grasslands, while in other cases they are converted to arable land. Changes in soil biodiversity will be affected by the land use type following the deforestation. Cultivation, for instance, is known to reduce the number and diversity of microarthropods such as collembola and acari (see Encyclopaedia section) populations from levels observed under natural forest or grassland vegetation. Land use change in the form of urbanisation can lead to even more dramatic reductions in levels of soil biodiversity.

Soil erosion

Soil erosion affects managed and natural ecosystems, and the consequences of this process on soil biodiversity will be both direct and indirect. The direct effect of soil erosion consists in the removal of soil biota and its habitat through the loss of soil from the eroded site. The indirect effects occur through vegetation regulation. This is because above ground vegetation is linked to and affects below ground biodiversity. Above ground vegetation is affected by soil erosion due to loss of nutrients in the form of organic matter which is present at higher concentrations in topsoils which are the zones most prevalent to erosion, and this has knock on effects onto the below ground biodiversity.

Soil sealing

Soil sealing is the process of covering soil in concrete, or asphalt and literally 'sealing' the soil so that it is disconnected from above ground ecosystems as a consequence of urbanisation.

The urbanisation process has led to the conversion of natural ecosystems to various forms of anthropogenic land use, leading to habitat fragmentation and isolation due to increases in local human population density. The urbanisation process has been identified as one of the leading causes of decline in soil biodiversity, particularly affecting soil arthropods and reducing both their diversity and abundance in areas where soils are sealed. The sealing process interrupts the contact between the soil system (pedosphere) and other ecological compartments, including the above ground ecosystems, and the atmosphere, preventing, or dramatically reducing, infiltration of water, diffusion of gases, and input of organic materials. This leads to modified chemical and physical conditions of soil which strongly affects the biological communities within the soil, leading to a reduction in both number and variety of soil organisms.

Soil pollution

Soil pollution can have very detrimental effects on the soil biota, reducing both the abundance and the diversity of organisms. This process is generally caused by the presence of man-made chemicals or other substances, not normally found in soil. The most common chemicals involved are pesticides, fertilizers, petroleum hydrocarbons, solvents, recalcitrant organic compounds and heavy metals. Some of these substances are deliberately applied to soil, such as herbicides and fertilizers whereas others end up in soil as consequence of accidents or mismanagement or deliberate dumping of waste chemicals.

The effects of a given pollutant on the soil biota can be highly variable depending on the pollutant. Some are highly specific, and as such only affect portions of the soil biota, be it invertebrates or some parts of the soil microbiota such as fungi. Some other pollutants have more general biocide effects and negatively affect or kill large portions of the soil biota, affecting all organisms from bacteria up to soil invertebrates such as collembolans and mites and including plants.

Owing to the possible negative impacts on the soil biota, which can persist for extended periods of time in the case of some contaminants, regulations as to what can be put on the soil have existed across Europe for at least two decades.

Soil compaction

The use of heavy load machinery in agriculture, especially when combined with the reduction in soil organic carbon content can lead to soil compaction whereby the pores space of the soil is reduced and the bulk density of the soil is increased. High soil bulk densities affect root penetration, soil pore volume, water infiltration and air diffusion rates, as well as reducing the overall pore space which is available as a habit for soil organisms. The effects of soil compaction are not the same for different groups of soil organism but generally increased compaction leads to a reduction in soil biodiversity as well as a modification of community composition. Compaction generally reduces water infiltration rates (Fig. 5.3) and also leads to soil becoming anaerobic in places which can have very large impacts on the types and distribution of soil organisms present.

Fig. 5.3: Soil compaction reducing water infiltration at a field entrance (FV)

Habitat fragmentation

Habitat fragmentation can have a very large impact on the level of above ground biodiversity, with biodiversity decreasing with increasing habitat fragmentation. However, it is generally considered to be a less important factor affecting soil biodiversity. It is theoretically possible for habitat fragmentation to be very detrimental for soil biodiversity, but only at spatial scales that rarely occur in practice. Scientific investigations have been undertaken on the effects of small scale habitat fragmentation on soil organisms, but the scale of the habitat fragments used was in the order of few square centimetres, far away from the scale of habitat fragmentation which generally occurs in the real world.

Climate change

Climate change, being both the change in mean temperature and precipitation variations in both time and space is likely to play a large role among soil biodiversity threats. However, precise predictions of the effects are problematic as there is a need to predict the alteration of soil biodiversity patterns due to global climate change which is currently beyond our scientific knowledge. That said, research which is currently undertaken in extreme environments such as arctic and desert soils can provide important information on the possible effects of climate change on soil biodiversity and ecosystem function. Experimental results from extreme environments have demonstrated that an increase in mean temperature usually leads to an increase in bacteria, fungi and nematode numbers, but an overall reduction in biodiversity. The possible effects of climate change on soil biodiversity are discussed in more detail in Section 5.1.3

Genetically Modified Organisms

The land area planted under genetically modified (GM) crops reached 117 million hectares in 2007 (equivalent to all of the UK, France and Germany being planted with GM crops). There is a great concern in Europe on the potential effects of genetically modified organisms (GMOs) on both environmental and human health. One of the largest uncertainties is the effect of GM crops on biodiversity and on the fate of modified DNA in the soil. Pesticide resistant GM crops make up approximately 70% of all GM crops grown worldwide, while insect resistant GM Crops, including the *Bacillus turingensis* (Bt) crops, such as Bt corn and Bt cotton, make up approximately 20%. Bt crops continually produce the Bt protein, which is harmful to insects, and release a portion of this into the soil. However, in several reports (e.g. Environmental Protection Agency Report, 2000), there is no mention of the susceptibility of the soil dwelling microbiota to this protein. Most research into the effects of the Bt protein have been carried out using Lepidoptera (i.e. moths and butterflies such as *Helicoverpa virescens*, *Helicoverpa punctigera*), or soil nematodes as test organisms and consequently little information on the effects of the protein on soil microarthropods are available. The few studies dealing with the evaluation of the effects of commercial GM crops on soil microarthropods have generally reported a lack of any significant deleterious effect of GM herbicide resistant soybean on the collembolan community in the soil. However, the scarcity of data on the effect of GM crops on soil microarthropods, and on soil biodiversity in general suggests that further, independent studies are needed.

Salinisation

Salinisation is the accumulation of soluble salts of sodium, calcium, potassium and magnesium in soil causing a deterioration or loss of one or more soil functions. Salinisation of soils occurs either as a result of natural processes or as a consequence of mismanagement of irrigation practices or poor drainage conditions. This process, which in Europe affects an estimated area of several millions of hectares (4 dS m^{-1} is the threshold to define saline soils), has consequences not only for crop productivity, but also for soil organisms. Several studies have been carried in the laboratory and the field, showing effects of salinisation on survival and reproductive activity of soil organisms. In 'normal' soils, an Electrical Conductivity (EC) above 1 - 1.5 dS m^{-1}, can have significant effects on Collembola, Enchytraeids and especially Earthworms. Naturally-occurring saline soils exhibit high degrees of above ground biodiversity and indications are that below ground the microbial populations have evolved to live with salt (halophilic and halotolerant bacteria; see Section 3.7) and these may have useful applications

Fire

Fire can be deliberately apply in managed land (i.e. straw burning), or be related to wild fires in forests and rangeland. The most evident effect of fire is the death of almost all the above ground plants and other living organisms, but also the below ground biota can be affected to a variable degree.

The effects on soil microbial communites is largely related to the fire intensity, and can lead to the total sterilisation of the surface layers of soil in case of very hot wildfires. In any case the structure and the function of soil microbial community can be deeply altered; in some cases there is an increased rate of microbial processes (i.e. denitrification, respiration, methanogenesis) in the months following the fire.

Studies on the effects on litter decomposing microarthropods (i.e. mites, springtails) have generally found that they decreased in abundance, especially with frequent fire, as a consequence of the habitat lost. Other studies suggested that changes in the size of the microarthropod population in soils of burned areas might serve as an indicator of fire intensity. The effects of fire on soil biodiversity as discussed in more depth in Section 5.1.1

Desertification

Sometimes dramatically associated with sand dunes moving into populated areas, desertification actually refers to land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors, including climatic variations and human activities. As a threat to soil biodiversity, desertification is a cross-cutting threat that integrates soil organic matter decline; soil compaction; soil salinisation; soil erosion (by water, wind and tillage) and soil sealing. Habitat fragmentation can be a striking result of desertification with the degradation of land from continuous vegetation cover to a discontinuous, and eventually island, vegetation cover. Wildfires, normally ignited by people, constitute an important driving factor behind desertification, but also impact on soil biodiversity directly (see Section 5.1.1). Because of its worldwide importance, the United Nations has formulated the Convention to Combat Desertification (UNCCD), to which the European Union is a signatory. Each one of these threats has a human-induced component, which is likely to make up a different proportion for the different threats depending on the location. Therefore, mapping 'risk of desertification' is more than just mapping the environmental factors, like for example the aridity index (Fig. 5.5)

The influence of environmental factors and (historic) human management becomes clear when we zoom in to a relatively small area like the Greek Island of Lesvos (Figure 5.4) where large differences are found in the risk to desertification at close proximity.

Soil biodiversity can both be affected by desertification and affect desertification itself by feedback mechanisms, although much remains unknown about critical thresholds. For example, inappropriate pesticide use may reduce the activity of some soil organisms, thereby slowing down the decomposition of organic matter causing a reduction in the availability of a nutrient that is limiting for the vegetation. When this coincides with, for example, an extended period of drought, it may cause the vegetation to die back and not completely reestablish, leaving the bare soil prone to erosion (Fig. 5.4).

Conclusions

The threats discussed so far are by no means an exhaustive list, and only a very brief overview has been given of those threats that are discussed. Intensive exploitation of land, soil degradation processes, soil pollution, soil compaction, soil sealing, habitat disruption, organic matter decline, invasive species and climate change represent some of the main threats to soil biodiversity. New, emerging threats are likely to affect agricultural soil biodiversity, especially the use of GMOs and the biofuel sector, with potential threats that are little known. It is therefore evident that further investigation into the various pressures on soil biodiversity is needed to allow its effective protection. As this atlas makes clear, soil biodiversity is necessary for global function and performs ecosystem services worth trillions of dollars a year and as such its protection is clearly necessary.

An effective policy for conservation of soil biodiversity should be integrated with both soil protection and broader environmental and sustainability strategies. For the European Union this objective could be achieved by broad application of Soil Thematic Strategy discussed later in this atlas, and by the effective application of the revised EU Sustainable Development Strategy (EUSDS II).

The following three sections look more at three specific threats to soil biodiversity in more detail. It should be noted that these three threats have not been chose because they represent the greatest threats to soil biodiversity. Rather, they are threats which are mentioned quite regularly in the popular media, being wildfires which are widely reported in the news during the summer months, invasive species which are a cause of discussion for many gardeners and environmentalists, and climate change which is widely discussed by only vary rarely, if at all from the point of view of soil biodiversity.

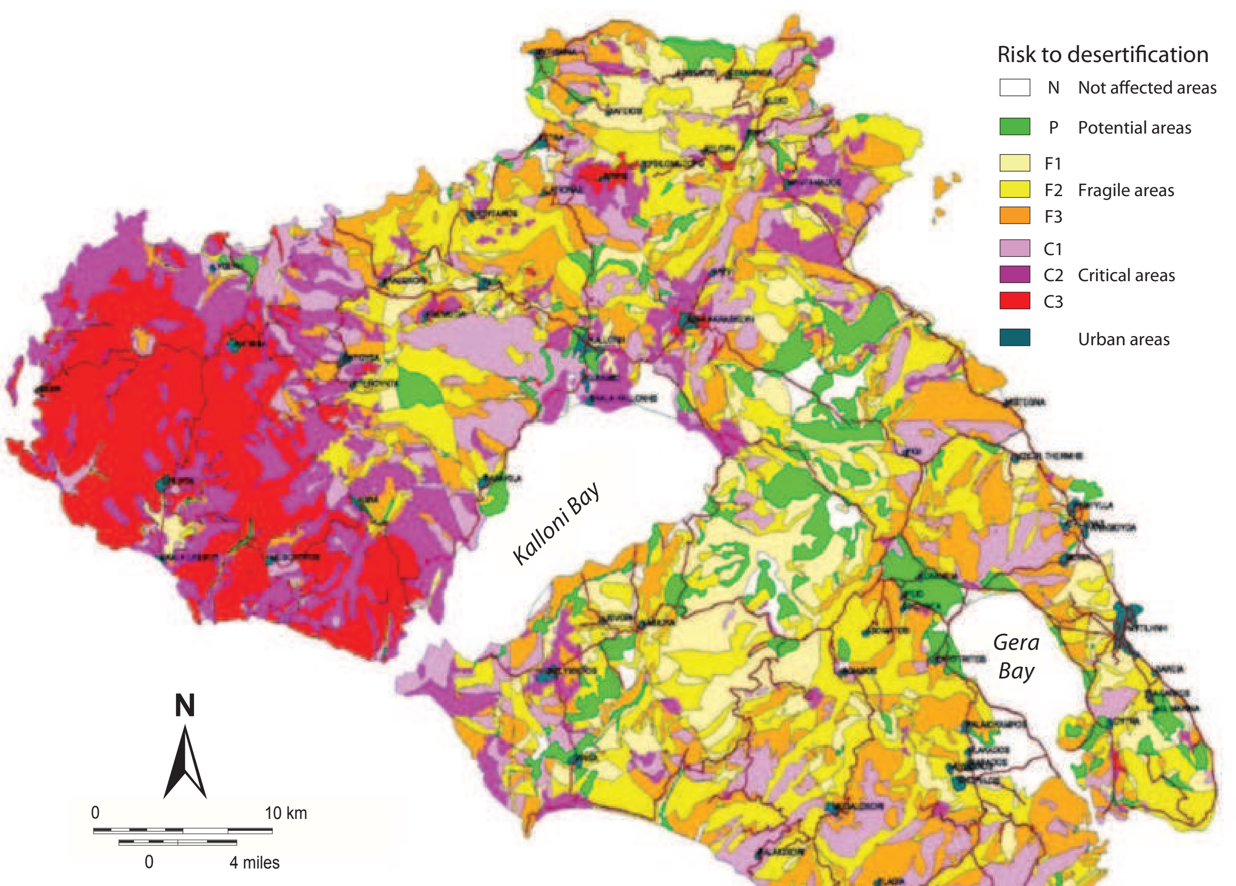
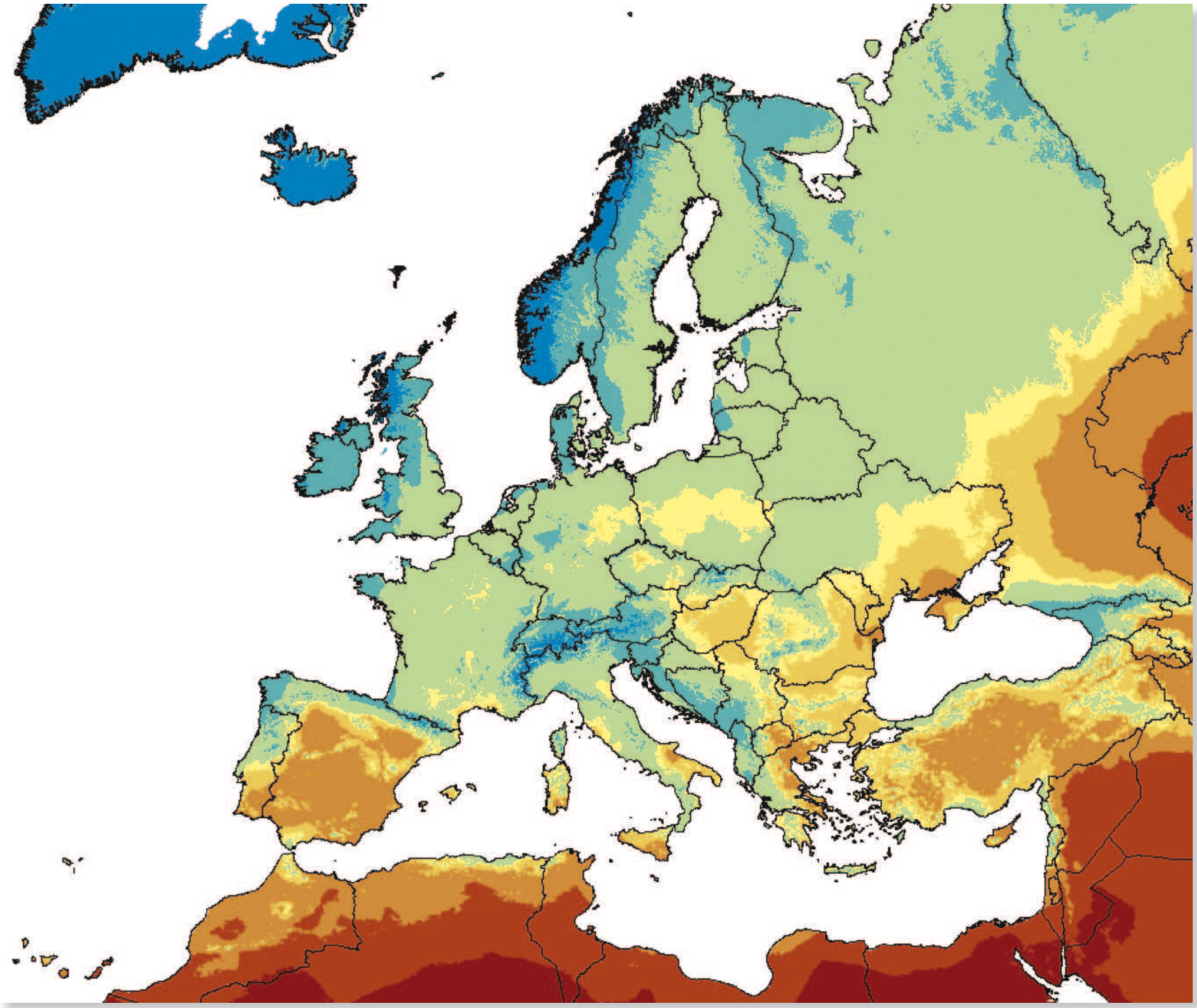


Fig. 5.4. Map of environmentally sensitive areas to desertification for the island of Lesvos, Greece. Note that the colours in the legend correspond to risk from low risk (white) to high risk (red). (After Kosmas *et al.*, 1999a)

Aridity Index (P/ETo) for Desertification



Aridity Index Zones

	No data	
	Hyper arid	(<0.03)
	Arid	(0.03 - 0.2)
	Semi-arid	(0.2 - 0.5)
	Dry sub-humid	(0.5 - 0.65)
	Sub-humid	(0.65 - 0.75)
	Humid	(0.75 - 1.25)
	Very humid	(1.25 - 2.5)
	Wet	(>2.5)

Aridity Index = Precipitation / Potential Evapotranspiration

UNEP (1997 World atlas of desertification (2nd. edition).
United Nations Environmental Programme, Nairobi, Kenya.

Data adapted for figure from:
Trabucco, A., and Zomer, R.J. 2009. Global Aridity Index (Global-Aridity) and Global Potential Evapo-Transpiration (Global-PET) Geospatial Database. CGIAR Consortium for Spatial Information.
Published online, available from the CGIAR-CSI GeoPortal at http://www.csi.cgiar.org/

Fig. 5.5: European Aridity Index map. This has important implications both for risk of desertification and for risk of wildfires. (RH)

Three Examples of Threats to Soil Biodiversity

5.1.1 Wildfire Effects on Soil Biodiversity

As mentioned at the end of the last chapter, the following three sections aim to provide a more detailed overview of three specific threats to soil biodiversity. These threats where chosen as they are thought likely to be of most interest to a non-specialist reader. They were not chosen because they represent the greatest threat to soil biodiversity.

Wildfires can impact on the soil biota directly and indirectly, as well as in the short and over the long term. Direct effects are injury or death of soil organisms by the heat wave of the fire travelling down into the soil or by (partial) combustion by the fire as well as habitat loss. Indirect effects include changes in nutrient availability, pH, soil organic matter and hydrological behaviour of affected soils. Short term effects can include, for example, a flush of nutrients from the ash. Medium term effects can include the formation of hydrophobic layers at a certain depth in the soil, and long term effects can include the destruction of the soil by a sub-surface fire or by soil erosion caused by an intense rainfall event after a surface wildfire has left the soil exposed (Fig. 5.7, bottom left).

To appreciate the impacts of wildfires, an understanding is required of the three types of wildfires: crown fires; surface fires; and sub-surface fires. Sub-surface fires combust the actual soil itself. These occur in organic soils (e.g. peatlands, or litter layers in forests and shrublands; Fig. 5.7, top right) and spread very slowly, but literally consume the soil organisms along with the organic matter, thereby destroying both life within the soil and the habitat in which it lives. Surface fires are the most common type of wildfire and spread relatively quickly depending on the fuel conditions (e.g. moisture content) and meteorological conditions (e.g. wind fanning the flames). Depending on conditions, surface fires can initiate sub-surface fires, or, in forests and shrublands, surface fires may start flaming combustion in the canopy layer of the vegetation, i.e. crown fires, which can spread very rapidly and burn very intensely. However, generally, crown fires do not affect soil organisms directly, but only indirectly and to a relatively minor degree.

Naturally occurring sub-surface fires are relatively rare (e.g. Fig. 5.6). However, prescribed (or managed) burning in forests to prevent large wildfires, or in shrublands to promote fresh shoots (e.g. for grazing), is common and can affect both the litter layer on top of the mineral soil, and the organisms that live therein or depend on it. When sufficiently intense and not too fast-moving, the heat wave of surface fires can travel down into the soil, killing or injuring soil organisms in the top few cm and thermally altering the soil organic matter leading to knock-on effects for the soil organisms that feed on it.

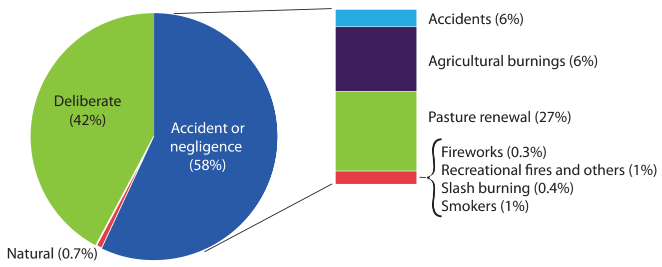


Fig. 5.6: Main causes of forest fires in Portugal in 2008. (JRC)

Soil biology is affected at much lower temperatures than those needed to affect soil physicochemical properties. Even at temperatures below 50°C plant roots and small mammals can be killed. At 60°C fungi in wet soil start dying, at 70°C seeds, at 80°C nitrifying bacteria, and at approximately 95°C vesicular mycorrhizae. The moisture content of the soil plays an important role as well. In drier soils the threshold temperatures are higher: 80°C for fungi, and 90°C for seeds, partly because of the greater thermal conductivity of water over air and partly because dry soils contain a greater proportion of drought resistant spores.

There are three main strategies for soil organisms to cope with wildfire: run, hide, or protect (i.e. forming resistant spores or cysts). Depending on how fast the fire spreads, vertebrates such as amphibians, reptiles and rodents have a good chance of survival because their mobility allows them to escape the lethal temperatures by burrowing into the soil or by fleeing on the surface. However, indirect effects can affect vertebrate numbers after wildfire through loss of habitat and food sources, as well as increased predation in an environment more exposed to predators due to reduced plant cover. Soil invertebrates, such as ants, beetles or collembola, generally have a much lower mobility and, therefore, fire generally has a much more detrimental effect on them. Particularly at risk are those invertebrates that reside primarily in the litter layer or the upper part of the soil. These organisms literally have nowhere to run to or hide during a wildfire. The recovery of beetle populations after wildfire has been found to depend on the size and shape of the burnt area and the proportion of the bordering area housing the same beetles, as re-colonisation occurs from there. Microbial responses to wildfires have been described as being as diverse and complex as the microbial communities in soil themselves (see Section 8.1). Nevertheless, some general observations can be made as seen in Table 5.1.

For soil bacteria, lethal temperatures range from 50- 210°C. Soil fungi are typically more sensitive to heat than bacteria, although some studies have shown an increase in functional diversity of soil fungi after wildfire. Mycorrhizal colonisation of roots has been reported to either decrease and increase after wildfires depending on numerous environmental factors. Soil microbial recolonisation occurs predominantly from viable populations deeper in the soil or from unburnt patches.

Fig. 5.7: Wildfires. **Top left**: Raging wildfire at night, Coimbra, Portugal, 2005 (AF); **Top right**: Ground fire aftermath. Trees are only slightly damaged, but the ground layer vegetation has been destroyed and a small subsurface fire can be seen (JK); **Bottom left**: wildfire has removed the entire vegetation cover. The soil surface is now very vulnerable to erosion by wind and rain (AF); **Bottom right**: wildfire threatening a population centre, Coimbra, Portugal, 2005. (AF)

Land degradation and desertification

The direct and indirect effects of wildfires contribute to the process of land degradation generally, and can contribute to desertification (see Section 5.1), which is a result of soil erosion, soil salinisation, soil compaction, and a decline in soil biodiversity combined. Soil erosion after wildfires can be very intense because the vegetation cover and litter layer that protected the bare soil from the impact of raindrops, has been removed (see Fig. 5.8). In addition, depending on fire severity, soil structure is often reduced along with concurrent reductions in water holding capacity due to the combustion or volatilisation of organic matter possibly combined with the formation of a hydrophobic layer in the soil. Low density soil particles, i.e. organic matter, are removed preferentially by erosion (both wind and water), which leads to a further loss of substrate. Severe erosion can also physically remove the soil organisms that are found deeper in the soil.

Table 5.1: Effects of fire intensity on soil temperatures, organic matter, and root and microbial mortality.

	Fire severity		
Parameter	**Light**	**Moderate**	**High**
Surface temperature	250°C	400°C	675°C
Temperature – 25 mm	100°C	175°C	190°C
Temperature – 50 mm	<50°C	50°C	75°C
Litter layer	Partially scorched	Mostly consumed	Totally consumed
Soil OM – 25 mm	OM distillation start	Partially scorched	Consumed/scorched
Soil OM – 50 mm	Not affected	OM distillation start	OM distillation start
Surface roots	Dead	Dead	Dead
Roots – 25 mm	Dead	Dead	Dead
Roots – 50 mm	Live	Live	Dead
Surface microbes	Dead	Dead	Dead
Microbes – 25 mm	Live	Selective die-off	Dead
Microbes - 50 mm	Live	Selective die-off	Selective die-off

Fig. 5.8: Rainmakers: Wildfires can leave the soil very susceptible to both water and wind erosion processes, one of the main components of land degradation and desertification. Here, scientists are simulating rainfall, after a wildfire in a Eucalyptus plantation, and measuring soil erosion by water. (MM)

Evaporation from the bare soil surface also tends to increase soil salinisation, which can have further detrimental effects on soil organisms.

Peatland wildfires

Although mostly associated with the Mediterranean, wildfires also occur in more northern latitudes (Figure 5.11) and even in peatlands where partially decayed plant matter accumulates (see Section 3.2). In boreal forest on peatlands, wildfire is a natural component of the ecosystem with fire return intervals of between 60 and 475 years, although fire return intervals appear to have increased substantially (up to 10 times) by human activity (i.e. increased ignition as well as drainage). Peatlands only cover 3% of the Earth's land surface, but contain 15-30% of the global soil organic carbon pool and, as the 1997 wildfires of tropical peatlands in Borneo showed, can lead to large greenhouse gas emissions.

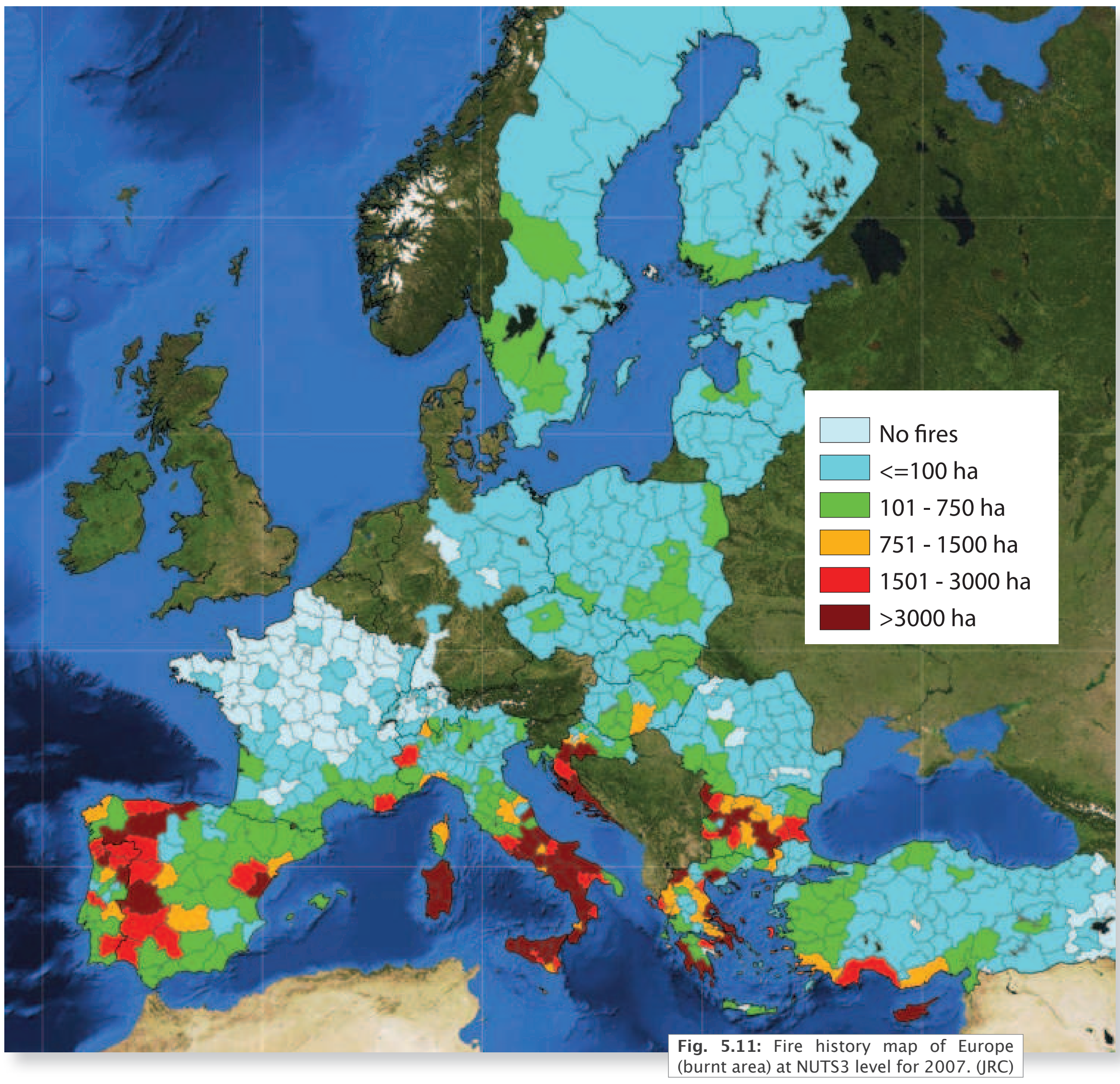


Fig. 5.11: Fire history map of Europe (burnt area) at NUTS3 level for 2007. (JRC)

Fig. 5.9: Peatland surface wildfire in the Silver Flower NP, Scotland, April 2007. (AM)

Peatland soils are, in part, made up of sphagnum, a genus consisting of many species of moss (up to 350) that can hold up to 20 times their dry weight in water. As it grows at the surface, the lower parts of the plant become submerged and eventually compact into peat. When the water tables drop sufficiently, sub-surface wildfires can occur which can burn for years and release large amounts of greenhouse gasses. However, even when water tables do not drop by much, the surface vegetation can dry out enough for surface wildfires to burn (see Fig. 5.9). It has been observed that although sphagnum moss does not always combust during these fires, the heat wave of the fire can cause the sphagnum to 'bleach' thereby creating white fluffy hummocks that some scientists have named 'sphagnum sheep' (Figure 5.10). Depending on the fire severity the sphagnum may, or may not, recover.

For soil vertebrates, invertebrates and microbes, similar effects may be expected as discussed for mineral soils above, although very little data is available on wildfire effects on soil biota in peatlands. Because many peatlands are sensitive ecosystems with low nutrient concentrations and pH, and high endemism, increased wildfires may be expected to have greater effects on soil biodiversity than in other ecosystems. More research is needed to elucidate effects and mechanisms.

Future wildfires in Europe?

Wildfire is a natural component of most ecosystems. However, as Figure 5.6 shows, the vast majority of wildfires are caused by humans. The European Forest Fire Information System (EFFIS) has been established by the Joint Research Centre and the Directorate General of Environment of the European Commission in order to provide comprehensive information on forest fires in Europe, including fire history monitoring (see Figure 5.11). This system will also help in detecting trends in wildfires over time.

Whether wildfire occurrence (frequency, area burnt, etc.) will increase in Europe in the future and with climate change is uncertain and the topic of many ongoing modeling studies. One of the difficulties lies in trying to model human activities and responses. Figure 5.12 shows large regional variation in estimated wildfire distribution as a result of a model that uses a moderate climate change scenario, human influence, lightning occurrence, and net primary production (fuel availability) at coarse spatial and temporal scales. In this case, Europe is estimated to experience a substantial increase in wildfire occurrence over the 21st century.

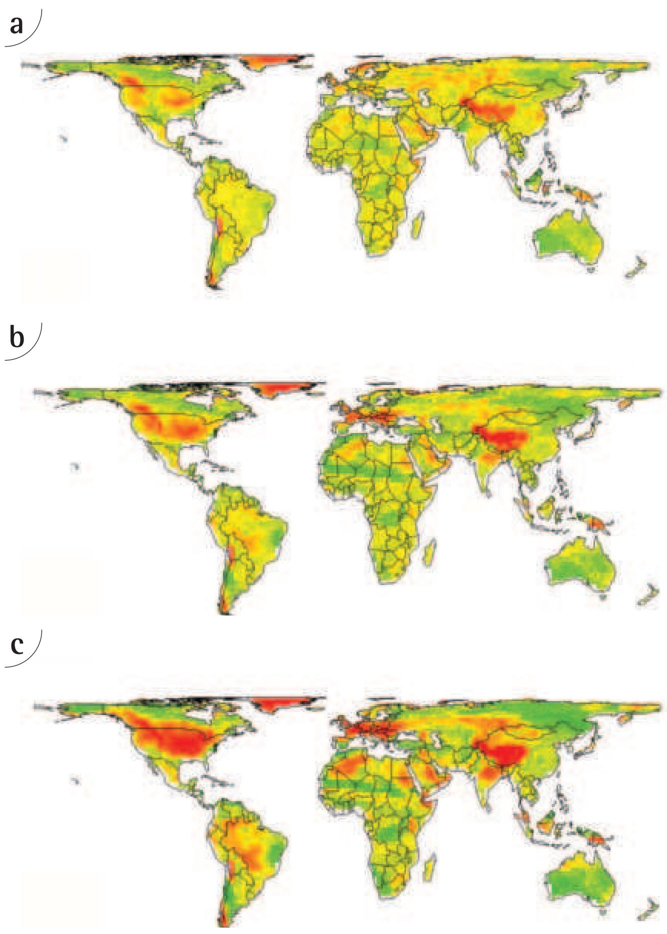


Fig. 5.12: Increased wildfires in Europe? Modelled changes in global distribution of wildfire. Colours indicate relative change in risk. Green indicates a decrease in fire occurrence, yellow no change, and red an increase. A=2010-2039; B=2040-2069; C=2070-2099 (Krawchuk *et al.*, 2009).

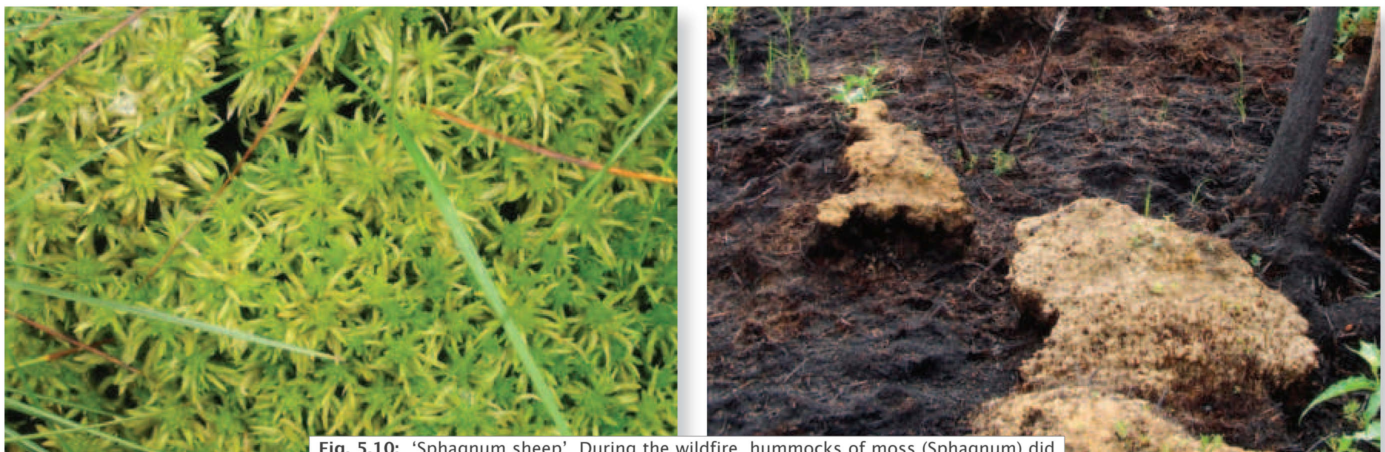


Fig. 5.10: 'Sphagnum sheep'. During the wildfire, hummocks of moss (Sphagnum) did not burn. However the heat of the fire 'caused the normally colourful moss (**left**; RA) to become 'bleached' leaving white fluffy hummocks reminiscent of sheep (**right**; MT).

5.1.2 Biological Invasions and Soil Biodiversity

What are biological invasions?

Biological invasions are introduced exotic species which become a problem in the invaded areas because they develop excessive abundance. An overview of invasive species in Europe can be found on DAISIE European Invasive Alien Species Gateway (http://www.europealiens. org) where the current estimate is that approximately 11,000 species are invasive in Europe.

Classical examples of invasive species are the black rat and Giant Hogweed (Fig. 5.13), a plant species originating from the Caucasus that causes severe blisters when it comes into contact with the skin.

Fig. 5.13: Giant Hogweed (*Heracleum mantegazzianum*). (MBe)

However, there are relatively few known examples of invasive soil organisms. These include the New Zealand Flatworm (Fig. 5.15) which is currently causing a large reduction in earthworm diversity in some areas in the UK, as well as some invasive soil pathogens. It is likely that the number of invasive soil organisms is much greater than assumed, but most of these species, as with all soil dwelling organisms, are difficult to be sampled and identified.

The problems caused by invasive species can be ecological and/ or economic. Examples of economic costs are species that prevent or reduce ongoing economic activities, and that require much effort to be controlled. For example, water hyacinths block ship traffic, tigernut sedge is a problem weed in root stock fields, and Eucalyptus trees in southern Europe enhance the incidence of forest fires, because their leaves decompose slowly and act as fuel for the fires.

Ecological costs become obvious when exotic species replace native species. For example, as with the replacement of native red squirrels in the UK by invasive gray squirrels from the US or exotic plants that suppress symbiotic soil dwelling fungi which are essential for tree seedling establishment. Another ecological cost occurs when exotic species alter ecosystem functioning, for example when invasion occurs by fast growing plants which produce easily decomposed litter, thereby enhancing nutrient cycling between soil and vegetation. This can lead to overall changes in plant community composition in affected areas with concurrent changes in below ground biodiversity.

Human activities are the major causes of biological invasions, as it is usually humans that enable exotic species to cross natural boundaries in the landscape such as oceans or mountain ridges. Colonisation of North America, Australia and New Zealand by European settlers is the main reason why there are so many invasive exotic species in the New World; they were introduced and released by the colonists. While many introductions were not intentional, quite a few have been deliberate. For example, the introduction of Black Cherry (Fig. 5.18) to Europe was aimed at enhancing soil fertility, as this cherry species produces large amounts of leaves. It was thought that the fallen leaves would enhance the fertility of poor sandy soils by increasing the soil organic matter when the leaves were decomposed. However, the Black Cherry became a plague that is now controlled by pulling up of saplings by hand and other expensive and time consuming activities.

Introductions of invasive species are often the result of transport or tourism. For example, the Western Corn rootworm in Europe is frequently found initially around airports and from there the insects spread out across the country. Other such examples of introductions include biological control organisms, being organisms that have been introduced to control another pest species (e.g. Black Ladybird), fungal diseases or vector insects (insects which are capable of transmitting disease) in potting soils of tropical plants (e.g. Asian Tiger mosquito), Chinese mitten crabs were introduced into many areas via ballast water in ships, and many weed seeds that are dispersed by both cars and trains.

Fig. 5.14: Austrian yellowcress (*Rorippa austriaca*). (TE)

Fig. 5.15: New Zealand Flatworm (*Arthurdendyus triangulatus*). (KRB)

Introduction alone is not sufficient for an exotic species to become invasive. In fact, only one out of a couple of hundred of introduced species becomes really invasive. This percentage is so small because there are many prerequisites necessary for a species to become invasive in a new location. For example, the circumstances for establishment have to match the requirements, both from a biotic (relating to living organisms) and an abiotic (not referring to living organisms, so usually physical or chemical) perspective. Invasiveness requires, among other things, that introduced exotic species have to not be in contact with the various factors which controlled their abundance in their native ecosystems, and that the right growth conditions regarding both soil and climate are present.

With the ongoing climate change, new areas are becoming suitable for species that, until now, have been living at the edge of their climate preference. For example, since 1889 narrow-leaved ragwort from South Africa has been introduced at three places in southern and northern Europe (Fig. 5.17). Currently, this species is spreading rapidly towards the north and east, suggesting that it may be making good use of the current relatively milder climate conditions in that part of Europe.

Climate warming is also causing range shifts of plant and animal species (see Section 5.1.3). Recently, it has been shown that some range expanding plants, for example, Austrian yellowcress (Fig. 5.14) have moved northward while their natural enemies have not yet moved, or have failed to become established in the more northern areas meaning reduced control for the expanding plant species.

It is also possible for plague organisms to switch host plants when expanding their range. In these cases, successful range expanding species may show invasive properties, especially when they are released from control by natural enemies. Enemies of plants can be present above ground (insect, pathogens, large grazers), as well as in the soil (insects, nematodes, pathogens). Much of the theory developed for invasive exotic species can also be used to study the possible consequences of climate warming induced range expansions: will these species perform as invasive exotic species, or as normal natives do? Much of this is still a big mystery, but it is already clear that the soil and its biodiversity play a crucial role in these responses of ecosystems to climate change and invasive species.

Effects of biological invasions on soil biodiversity and ecosystem functioning

Considering the immense biodiversity of organisms which are present in one gram of soil, it is irrelevant to simply describe how invasive species influence the total numbers of soil organism species. It is more insightful to consider what sort of species exotic invaders influence and what the functions of those species are. Here, the effects of invasive plants, animals and soil organisms on soil biodiversity are discussed.

European earthworms, for example, while very beneficial for European soils, are often considered to be invasive species in the USA as they have been shown to be capable of changing the structure of plant communities.

One particularly successful invasive soil organisms is the earthworm *Pontoscolex corethrurus*. This organism originally comes from the Guayana plateau, but has now invaded almost all anthropogenically impacted tropical soils world-wide and has even been found in Finnish greenhouses!

Fig. 5.16: Eucalyptus (*Eucalyptus globulus*). (LB)

Plant invasions

Plants influence soil organisms directly by being a host for pathogens, food for herbivores, and partners for symbiotic mutualists (that is two organisms that exist in a relationship where both gain benefits). Other soil organisms, such as microbes and soil fauna which are involved in the decomposition of organic matter, are influenced by plants in a more indirect way, through their feeding on dead organic matter, mainly leaf litter and root exudates. Exotic plants have the highest chance of becoming invasive when they are not attacked by the local soil pathogens and root herbivores and when they can still use, or do not need, mutualistic symbionts in their new range. This provides the exotic species with an advantage in competition when compared to the native flora and contributes to their disproportionate abundance. When the exotic plants are poor hosts for symbiotic soil organisms, the exotic plants can indirectly reduce the growth possibilities of native plant species that depend on symbiotic relationships due to the reduction in the soil biota capable of supporting the growth of the native plants.

Exotic plants that grow fast and produce high quality litter will enhance the abundance and possibly the diversity of decomposer soil organisms, which in turn enhances the nutrient supply to the plants. When the chemicals present in the litter of invasive plants are very different from the native community, this can cause a huge shift in soil community composition and functioning as the soil decomposer communities have not evolved in the presence of the new chemicals and so generally won't have the ability to break them down or may even find them toxic.

Often, exotic plants increase their invasive abundance via the aforementioned acceleration of nutrient cycling. A famous example of an invasive plant that completely changes nutrient availability concerns the invasion of Hawaii by the shrub *Myrica faya*. Because this shrub is capable of converting aerial nitrogen (not available for use to plants) into mineral nitrogen (available for use to plants) via a process called nitrogen fixation, it strongly increased pools and fluxes of nitrogen on Hawaii. Before Myrica started to invade Hawaii, no indigenous plant was capable of fixing nitrogen, and so this invasive species has completely changed the ecosystem in much of Hawaii. However, there are also many examples where exotic plants do not influence nutrient cycling differently to native plant species. In other ecosystems the effect of exotic species seems limited to shifts in specific groups of organisms: the invasive smooth cordgrass has been found to lower diversity of nematodes in marshes, whereas Japanese knotweed has been found to decrease snail and isopod abundance and diversity, but to increase predators.

In conclusion, some invasive exotic plants can reduce, and others increase, the diversity and abundance of soil organisms, as well as the nutrient fluxes processed by the soil community in the new range. Possibly, the reason why so many exotic plant species do not turn into invaders is in part because these plants are controlled by local soil pathogens which are already present in the soils or ecosystems at large in the new range. The usefulness of local soil pathogens for controlling invasive plants therefore has potential, but needs further research to test effectiveness and ensure safety.

Current and future issues

Effects of biological invasions on ecosystem functioning in Europe

Ecological studies over the past two decades have raised awareness regarding the effects of biodiversity loss of biodiversity on ecosystem functioning. In the case of biological invasions, their effects on ecosystem functioning are evident. Besides a potential loss of biodiversity (which has not yet been shown that often), the invasive dominance of ecosystems by few species can have an enormous impact on nutrient cycling, water-holding capacity of soils, fire incidence (for example due to introduced Eucalyptus trees in southern Europe – Fig. 5.16), and also on the resistance of ecosystems to drought, erosion and other large-scale disturbances. Moreover, the invasive species can outcompete highly valuable, from an ecological viewpoint, indigenous species and thereby indirectly reduce the provisioning of ecosystem goods and services. Until relatively recently, the generally accepted view was that the New World was far more susceptible to invasions, but in reality, Europe too has become flooded by exotic species, some of which have developed into notorious invaders.

Fig. 5.17: Narrow-leaved Ragwort (*Senecio inaequidens*). (TE)

Does soil biodiversity offer protection against biological invasions?

Ecological theory predicts that resources will be optimally used in biologically diverse communities. Therefore, in species-rich communities most available niches are expected to be occupied. Consequently, loss of biodiversity is likely to enhance the chance that exotic species can become invasive owing to the availability of niches within a reduced biodiversity ecosystem. Currently, there is little evidence either supporting or rejecting this hypothesis, but it would be worthwhile to consider soil biodiversity as an insurance against biological invasions. This "insurance effect" of soil biodiversity may also function in other ways. For example, soil biodiversity may increase the chance that pathogens and root herbivores are present that can potentially control the abundance of exotic plants. Such control may be immediate, in the case of soil pathogens which are preadapted to break through the resistance of exotic plants at the start of an invasion. It may also be that the soil pathogens can become adapted through natural selection, which may enable the pathogens to circumvent the resistance genes of the invasive plants. As a result, these adapted soil pathogens may suppress the invasion over time. Decline of invasive potential of exotic plants over time has been reported, but the role of adaptation of soil pathogens has not yet been investigated.

Is recovery from invasions possible?

Exotic invaders that change the structure, chemistry, or biodiversity of the soil may cause changes in the invaded ecosystems that are difficult to be reversed. For example, exotic plants that cause loss of symbiotic mycorrhizal fungi (fungi which interact with the roots of plants and increase nutrient uptake from the soil) can have strong negative effects on the re-establishment of native mycorrhizal-dependent plant species such as orchids and tree seedlings. Often, management of exotic invaders is planned with the aim of eradicating the invader. However, this in itself, may not be sufficient in order to restore the original ecosystem and its functioning. Current awareness is growing that soil biodiversity needs to be restored in order to promote the restoration of former vegetation, ecosystem properties and therefore the associated ecosystem services. The ecological interactions in soil can be extremely complicated and as such much more research is needed in order to develop effective management options. For example, in coastal fore dunes of north-western Europe, the native marram grass is protected against root-feeding nematodes by a highly complex, multi-factor interaction web. If this balance were to be disturbed by an exotic invader, the original interaction web might not easily be rebuilt. It is possible that the invaders may change the ecosystem properties so profoundly that recovery of the original state is simply impossible.

Fig. 5.18: Black Cherry (*Prunus serotina*). (SW)

5.1.3 Soil Biodiversity and Climate Change

The Carbon Cycle

Soil processes have a large effect on the global carbon cycle. This is because soils currently contain approximately twice the amount of carbon (C) in the atmosphere. Fluxes totaling in the hundreds of gigatonnes of carbon occur between the soil and the atmosphere on an annual basis (Fig. 5.19). A complete understanding of the carbon cycle is vital for increasing our understanding of the feedback of carbon between the soil and the atmosphere and if, or how, this may be controlled or utilised for climate change mitigation.

Figure 5.19 is clearly a simplified schematic of the carbon cycle but the figures presented in it are all well established and relatively uncontroversial. The figure shows is that if all inputs of carbon into sinks are added together the total amount of carbon going into sinks from the atmosphere is 213.35 Gt per year. Conversely, when all of the carbon emitted into the atmosphere from non-anthropogenic sources are added, they total 211.6 Gt per year. This equates to a net loss of carbon from the atmosphere of 1.75 Gt carbon. It is for this reason that the relatively small flux of CO_2 from anthropogenic sources (5.5 Gt per year) is of such large consequence as it turns the overall carbon flux from the atmosphere from a loss of 1.75 Gt per year, to a net gain of 3.75 Gt carbon per year!

The Impact of Soil Organisms on CO_2

It has been estimated that approximately 13 million tons of Carbon are lost from soils annually in the UK alone. This is the equivalent to 8% of total UK carbon emissions. Evidence suggests that these losses of soil organic carbon (SOC) were found to be independent of soil properties which lead to the formation of the hypothesis that the stability of SOC is dependent on the activity and diversity of soil organisms. While it appears that UK soils have been functioning as a source of CO_2, there is evidence that some other soils function as a sink for CO_2 in some areas. Fig. 5.21 shows the current distribution of carbon in soils over Europe.

Studies at different latitudes have shown that the rate of soil organic matter decomposition doubles for every 8- 9°C increase in mean annual temperature. While this increase in temperature is greater than the predicted increases due to climate change, all other factors being equal, increasing global temperatures will speed up soil organic matter decomposition rates and, therefore, feedback into even greater losses of CO_2 from soil. However, it is important to note that contradictory results have been produced by field and laboratory studies. Under laboratory conditions a long term increase in temperature has been shown to increase microbial respiration from soil. This is significant as microbial respiration is one of the main mechanisms by which organic matter is released from the soil in the form of CO_2. This is counter to studies which have examined the microbial respiration of forest soils at different latitudes, where there are differences in mean temperatures, which found that microbial respiration and hence organic matter decomposition is more or less constant at different latitudes.

Soil biodiversity can also have indirect effects on as to whether soil functions as a carbon sink or source. It has been demonstrated repeatedly that soil biodiversity affects the erodibility of a soil due to a number of mechanisms including the influence of extracellular exudates and physical binding of soil particles by fungal hyphae, for example. It has been demonstrated that soil erosion alone is can be sufficient to turn soil from carbon sink to a carbon source. However, how large an effect this is remains controversial and is an area of ongoing research.

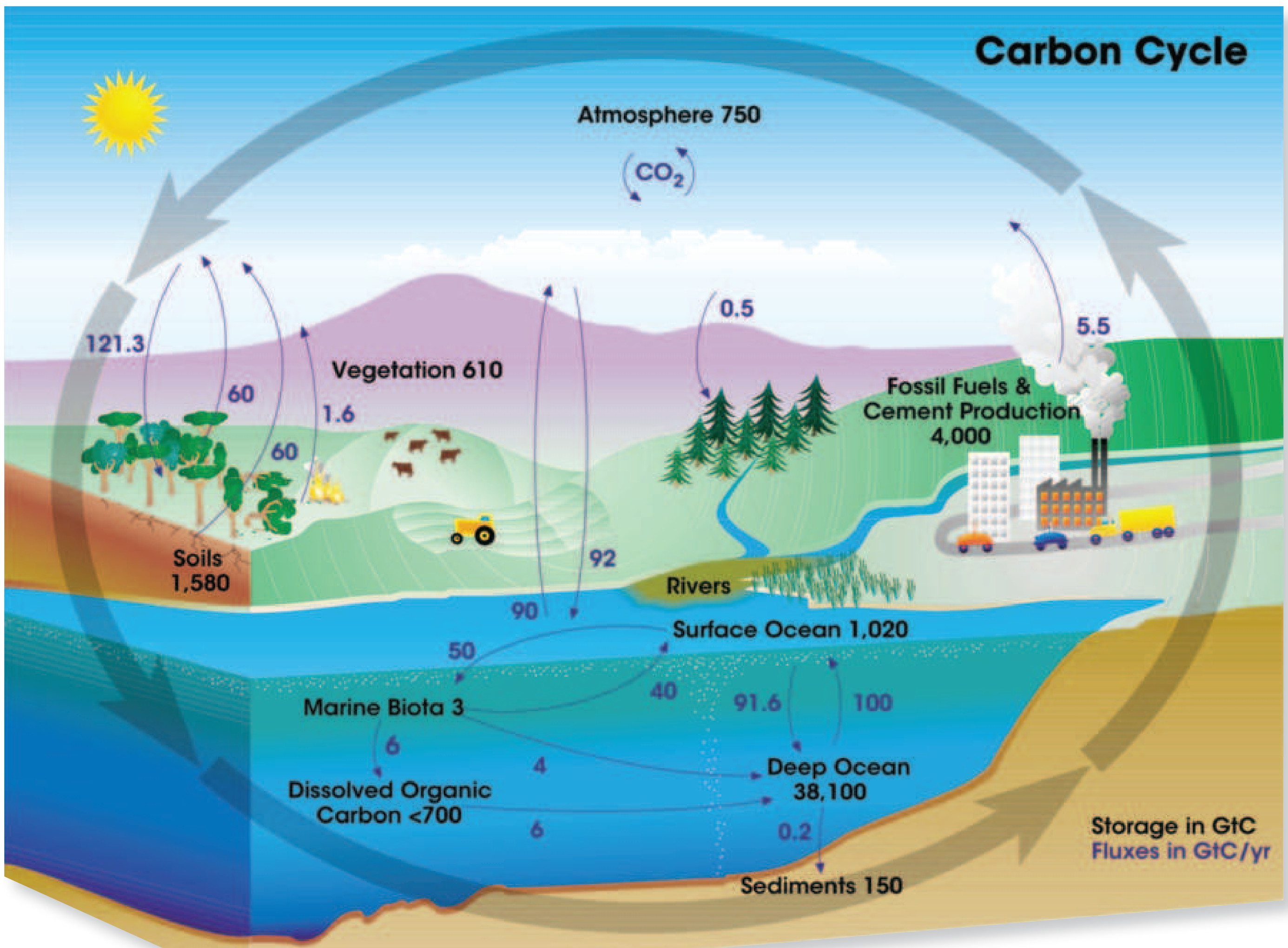


Fig. 5.19: Schematic showing the carbon cycle. The black numbers indicate how much carbon is stored in various reservoirs, in billions of tons ("GtC" stands for Gigatonnes of Carbon and figures are circa 2004). The purple numbers indicate annual carbon flux between reservoirs. The sediments, as defined in this diagram, do not include the ~70 million GtC of carbonate rock and kerogen. (NASA)

Fig. 5.20 There is much evidence from around the world that general climatic patterns are changing. In their 2000-2005 survey, the World Glacier Monitoring Service reported that virtually all glaciers under long-term observation in Switzerland, Austria, Italy and France were in retreat (the few that were not were stationary). The Mer de Glace, the largest glacier in France, has lost 8.3% of its length (1 km) in the last 130 years and thinned by 27% (150 m) in the midsection of the glacier since 1907. (GC)

The Impact of Soil Organisms on other Greenhouse Gases

Processes carried out by the soil biota are responsible for output of several key greenhouse gasses. Methane (CH_4) production also occurs as a part of the carbon cycle. It is produced by the soil microbiota under anaerobic conditions through a process known as methanogensis. Anaerobic conditions generally occur in soils when they become waterlogged for extended periods of time and as such marshland and paddy fields are areas which generally have increased methane emission when compared to areas such as forests or arable fields. Methane is about 21 times more potent as a greenhouse gas than carbon dioxide (Fig. 5.21) and so finding ways to limit its emission from soils through soil management practices is an important area which requires ongoing research. For example, microorganisms are capable of consuming methane and so can function to reduce the emissions of methane from soils.

Nitrous oxide (N_2O) is produced as a part of the nitrogen cycle through processes known as nitrification and denitirification which are carried out by the soil microbiota. Nitrous oxide is about 310 times more potent as a greenhouse gas than carbon dioxide and as such researching soil management techniques to limit its emission is vital.

Of the totals emitted, 80% of N_20 and 50% of CH_4 are produced by soil processes in managed ecosystems. This increase in emission when compared to natural ecosystems highlights the influence of soil management techniques on greenhouse gasses.

While these gases are potentially more potent greenhouse gases than CO_2, only approximately 8% of emitted greenhouse gases are CH_4 and only 5% are N_2O, with CO_2 making up approximately 83% of the total greenhouse gases emitted. When the potency of each gas to function as a greenhouse gas is adjusted to account for the amount of each gas emitted, it is possible to calculate the contribution of each greenhouse gas to climate change. This can be seen in Fig. 5.20b.

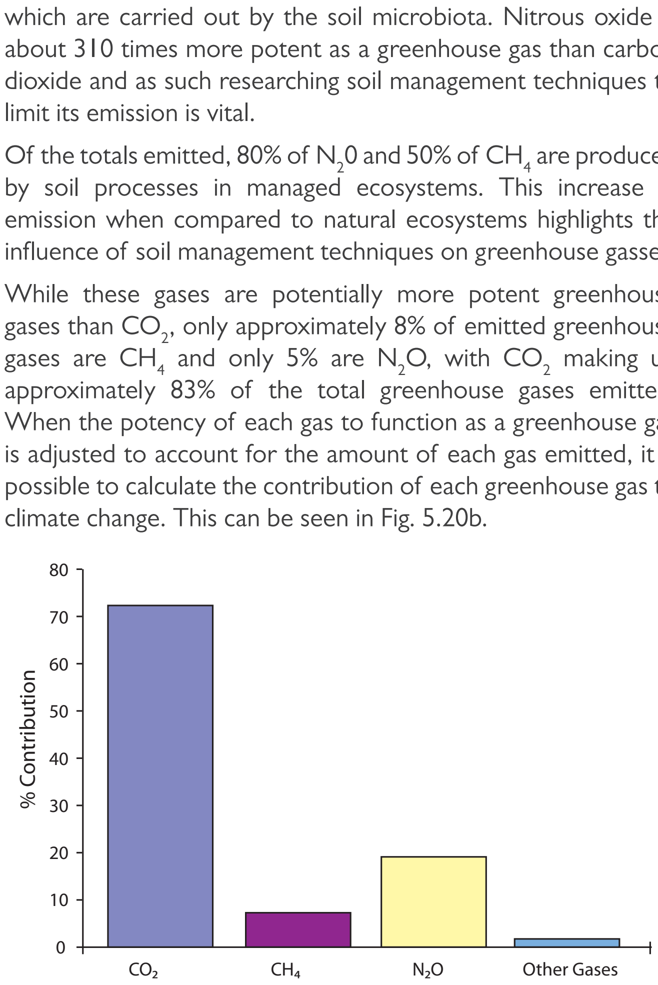


Fig. 5.20b: Contribution of gases to climate change (From natural and anthropogenic sources: excluding water vapour). (JRC)

The Impact of Climate Change on Soil Biodiversity

Quantifying the possible effects of climate change on soil biodiversity is highly problematic. It is likely this which is the reason for the relatively low threat rating given to climate change in Section 5.1. The reason it is so problematic is because current climate change models are not able to predict climatic changes with sufficient accuracy, at sufficiently small scales, for the possible effects on the soil biota to be determined. It seems probable that changes in climate, particularly changes in precipitation patterns and the associated changes in soil moisture regimes, and mean average temperatures are likely to have an impact. For example, there is already some preliminary evidence that species are migrating towards the poles owing to warmer temperatures, and spring starting earlier.

One other area in which warming is allowing the migration of organisms to colder climes, is the altitude shift in mountainous regions. Most people are aware of changing ecoregions with altitude in the mountains, the most obvious being the tree line, the altitude above which climatic conditions no longer favour the growth of trees. Evidence suggests that this tree line is migrating upwards. As there are clear links between above ground and below ground species and diversity, if the above ground ecoregions are migrating upwards then it is safe to assume that the below ground ecoregions will follow and this clearly has the possibility of leading to biodiversity loss as described in Fig. 5.22.

Above the tree lines there is still life; high altitude shrublands and grasslands host a huge variety of plant and animal species. Further up, lichens can be found on the rocks, microorgansisms in the soil and invertebrates such as collembola are still present. All of the organisms found above the tree lines are specially adapted to the environment which is generally cold, often very windy, and with relatively high levels of solar radiation. As the tree line moves up the side of the mountains, the amount of habitat for those species adapted to living above the tree line is necessarily reduced. This is because the mountain peaks provide an upper limit regarding the amount of vertical migration can occur (see Fig. 5.22). Observations and quantifications of this vertical migration have found the migration to be occurring at a rate of between 1 and 4 vertical metres every 10 years.

With all other things being equal, an increase in altitude of 100 m normal equates to a 0.5°C decrease in temperature. This means that the warming that has occurred over the last few decades should have led to a shift in altitudinal ecozones of about 8 to 10 m per decade. The fact that the observed displacement is lower is a concern as it possible means that the biota which make up the ecozones are not able to adapt fast enough to the increasing temperatures, and so this increases the risk of local extinctions.

Such clearly defined ecological zones are not generally easily visible in the latitudinal plane and as such quantification of any migration in species towards the poles is more problematic. However, the fact that vertical migration is occurring, driven by increasing temperatures, means that it is almost certain that the same process must be occurring in the horizontal plane, with soil communities shifting towards the poles where mean annual temperatures are increasing. Some evidence of this is already available. For example, Austrian yellowcress which is discussed in Section 5.1.2 (Fig. 5.14) has been found to have migrated northward. When this type of migration occurs, the migration of natural enemies can sometimes be slower, or can fail to become established in the more northern areas meaning reduced control for the expanding plant species. Furthermore, in the same way that biological communities which migrate vertically up a mountain in response to increased temperatures can 'run out' of mountain in which to migrate too, once the mean temperature regime at the highest point of the mountain is too hot for the endemic community leading to local extinctions, the same is possible for communities shifting towards the poles. Northwards and southward migrations will eventually be stopped by either the Arctic Ocean or the Southern Ocean, again possibly leading to local extinctions.

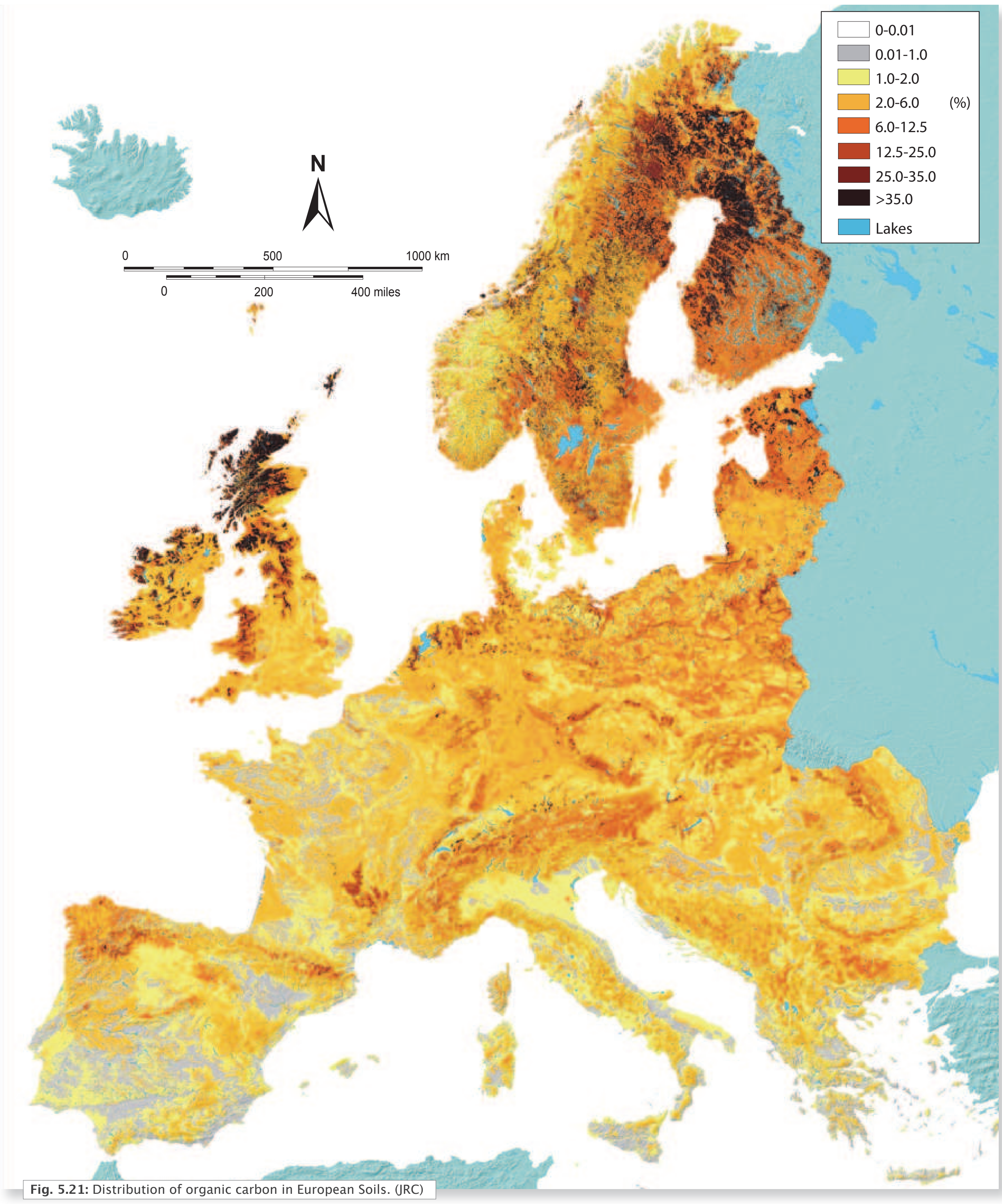


Fig. 5.21: Distribution of organic carbon in European Soils. (JRC)

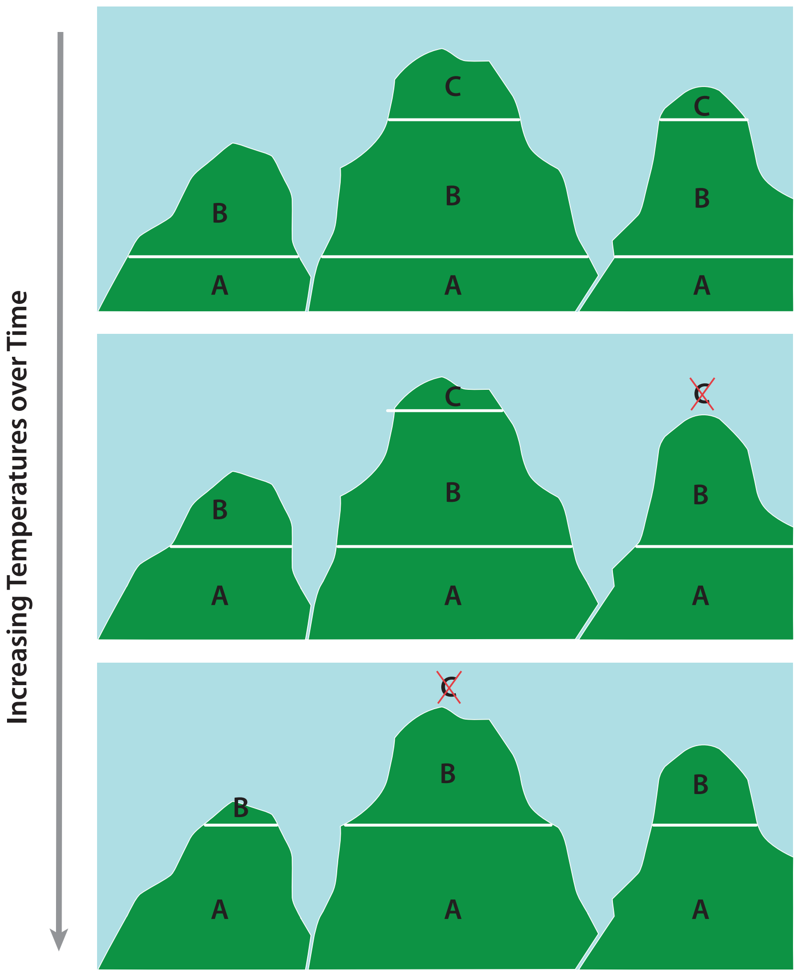


Fig. 5.22: These schematics show the effects of local warming on the vertical distribution of different altitudinal ecological zones. As the temperature increases, there is a vertical migration of the biota. This leads to a reduction of available space for ecological zone type C, eventually leading to local extinction owing to encroachment of ecological zone B and a lack of higher space to migrate to. Continued warming can mean that this local extinction of ecological zone can occur on successively higher and higher peaks and has the potential to lead to global extinction of species. (JRC)

5.2 Map of Soil Biodiversity Potential Threats

Threats to soil biodiversity

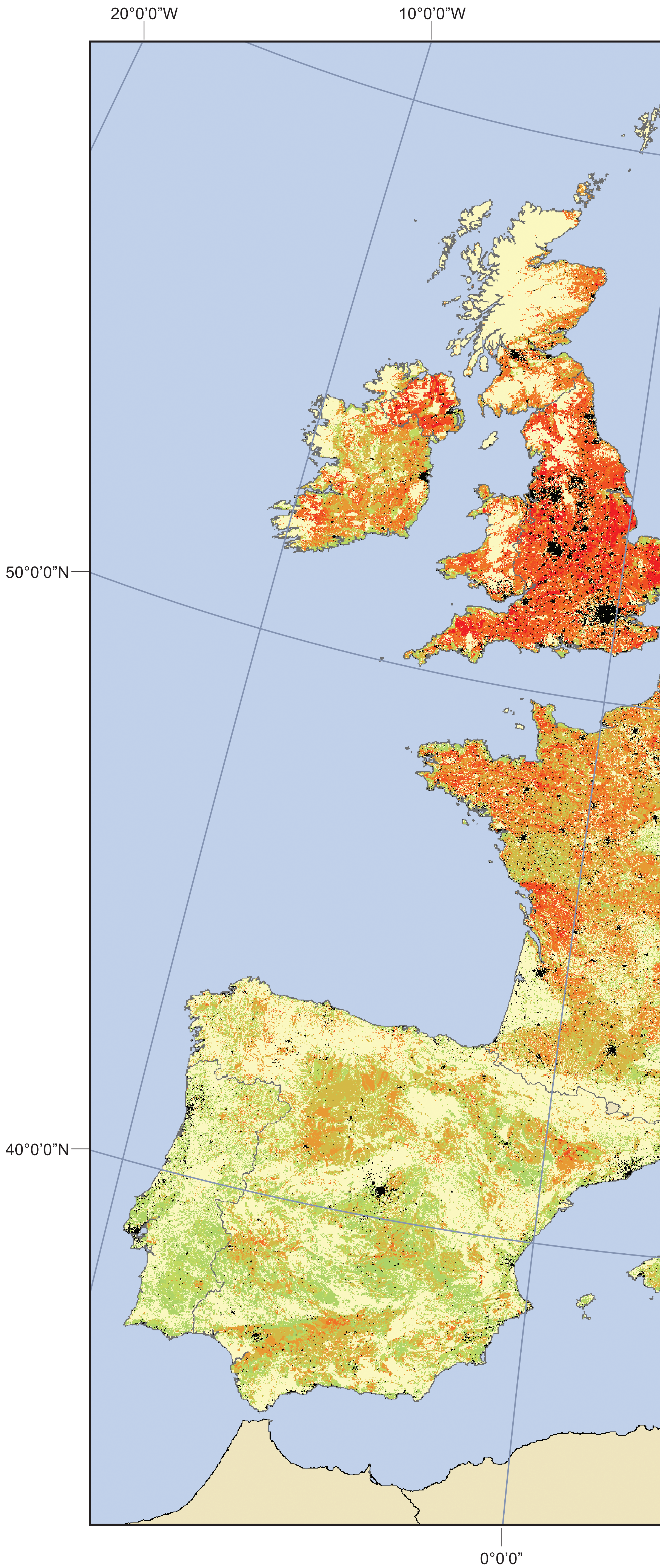
- No Data
- No Threats
- Extremely Low
- Very Low
- Low
- Moderate/Intermediate
- High
- Very High
- Extremely High
- Country borders
- Urban Areas

N

0 500 1000 km

0 200 400 miles

PROJECTION: Lambert Azimuthal



Soil biodiversity potential threats have been selected and ranked on the basis of Expert Evaluation, realised on the basis of the Budget Allocation approach. The following threats have been considered in the calculation of the indicator, where data existed:

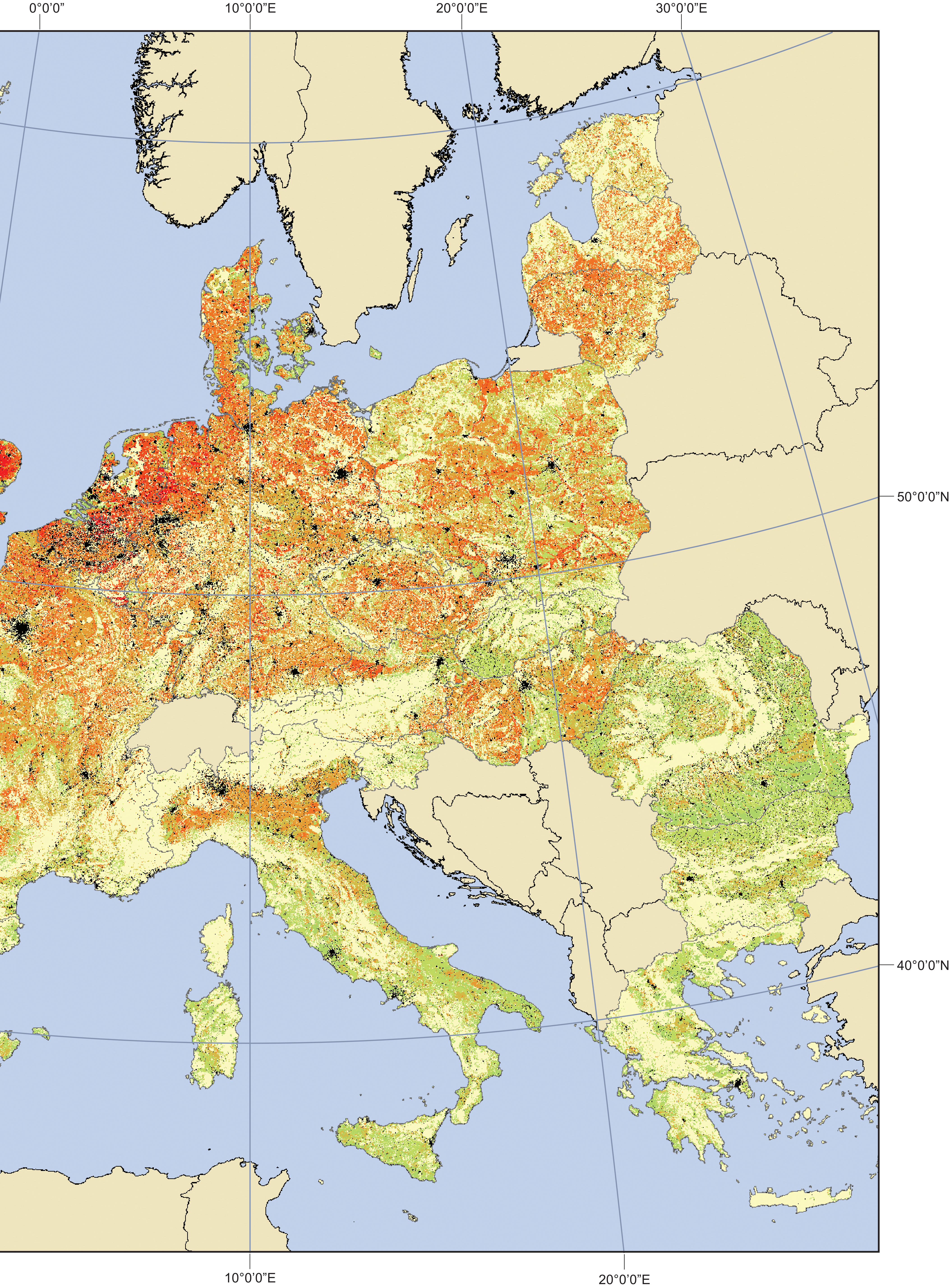
- Land use change/Habitat disruption
- Human intensive exploitation
- Invasive species
- Soil compaction
- Soil erosion
- Soil organic matter decline
- Soil pollution

For each of the above parameters a map, in form of a raster layer (1 x 1 km grid cells) has been realized. The values present in each grid have been classified into 5 classes. These values have been weighted using the coefficients obtained from the expert evaluation (Fig. 5.2).

The final indicator has been calculated, with an operation of map algebra, as the sum of the individual raster values. The values displayed on the map are related to the potential threats on soil biodiversity, for twenty three EU countries and are not representative of the actual level of soil biodiversity. In the following two pages, maps showing the distribution of four of the seven factors considered in the calculation of the index are presented.

The high score (high potential threats) of several parts of the UK and central Europe are determined by the combined effect of a high intensity agriculture, with a high number of invasive species and by the risk for soil to lose organic carbon. Compared to these situations, the intensive agricultural areas of southern Europe are less affected by the risk of losing organic carbon, and by the effect of invasive species.

It should be kept in mind that the map indicates an evaluation of the potential risk of soil biodiversity decline (with respect to the current situation) and is not a representation of the actual level of soil biodiversity.


0°0'0"
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30°0'0"E
50°0'0"N
40°0'0"N
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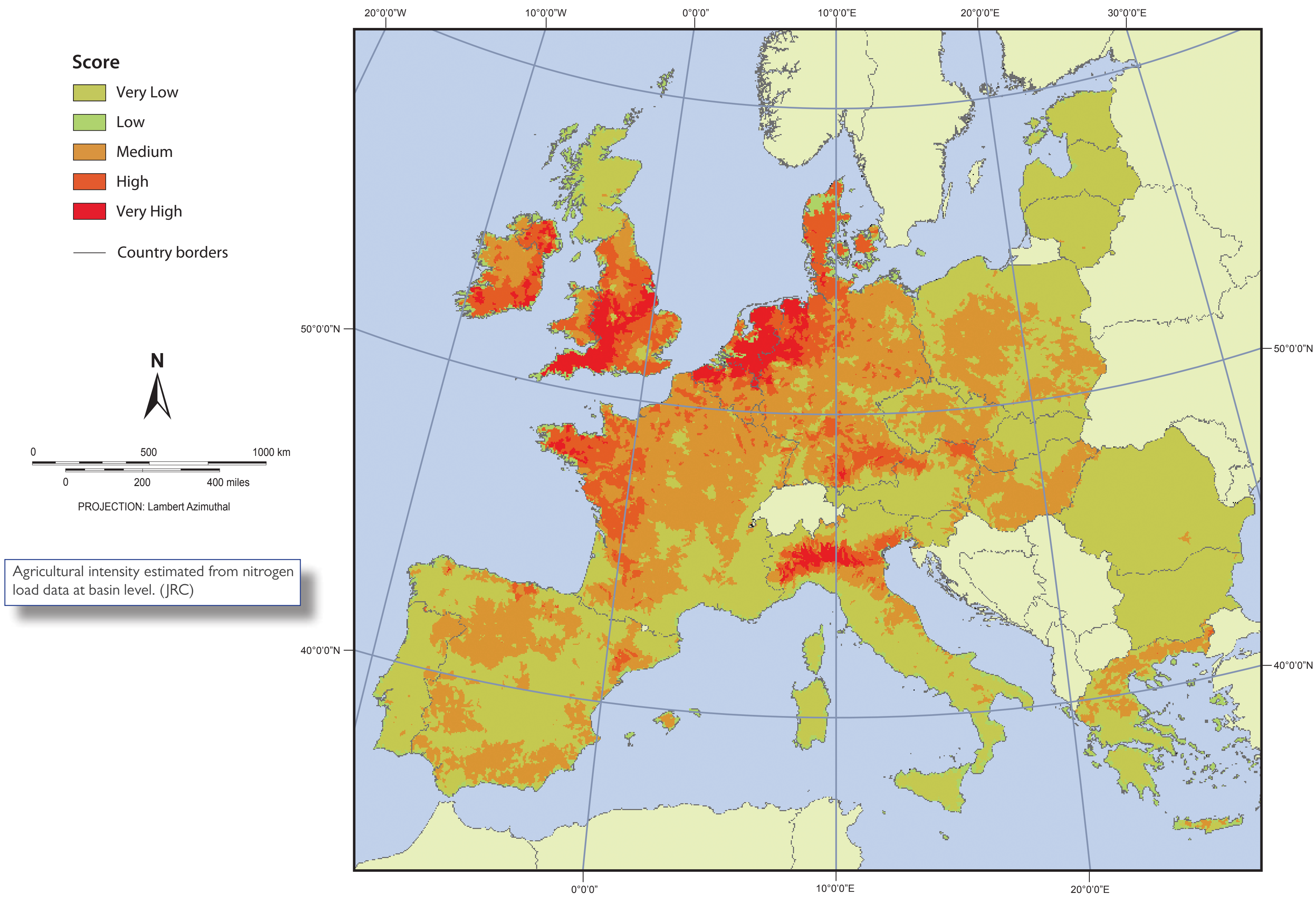
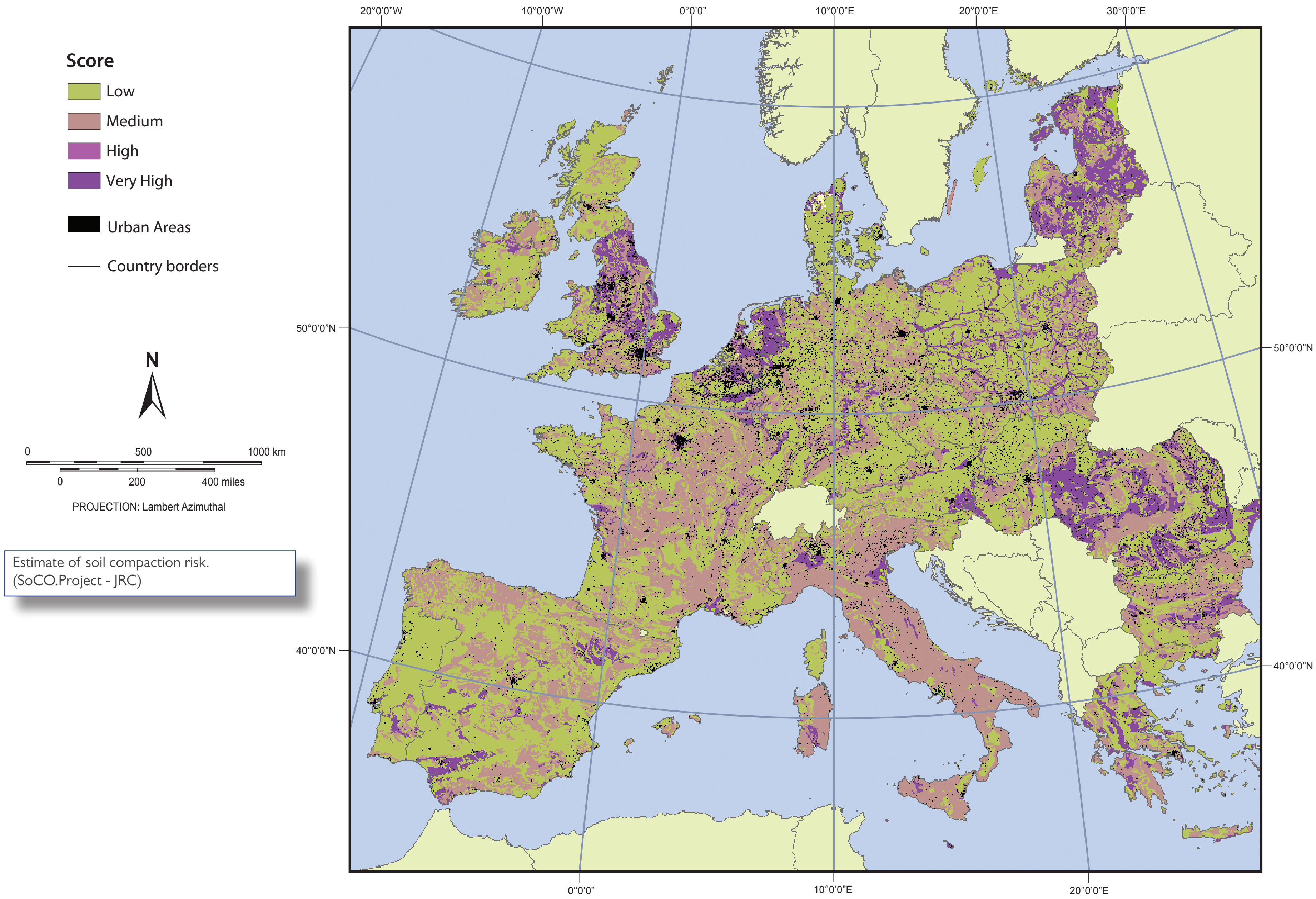
5.3 Maps showing the factors used to create the 'Map of Areas of Soil Biodiversity Under Threat' (Section 5.2)

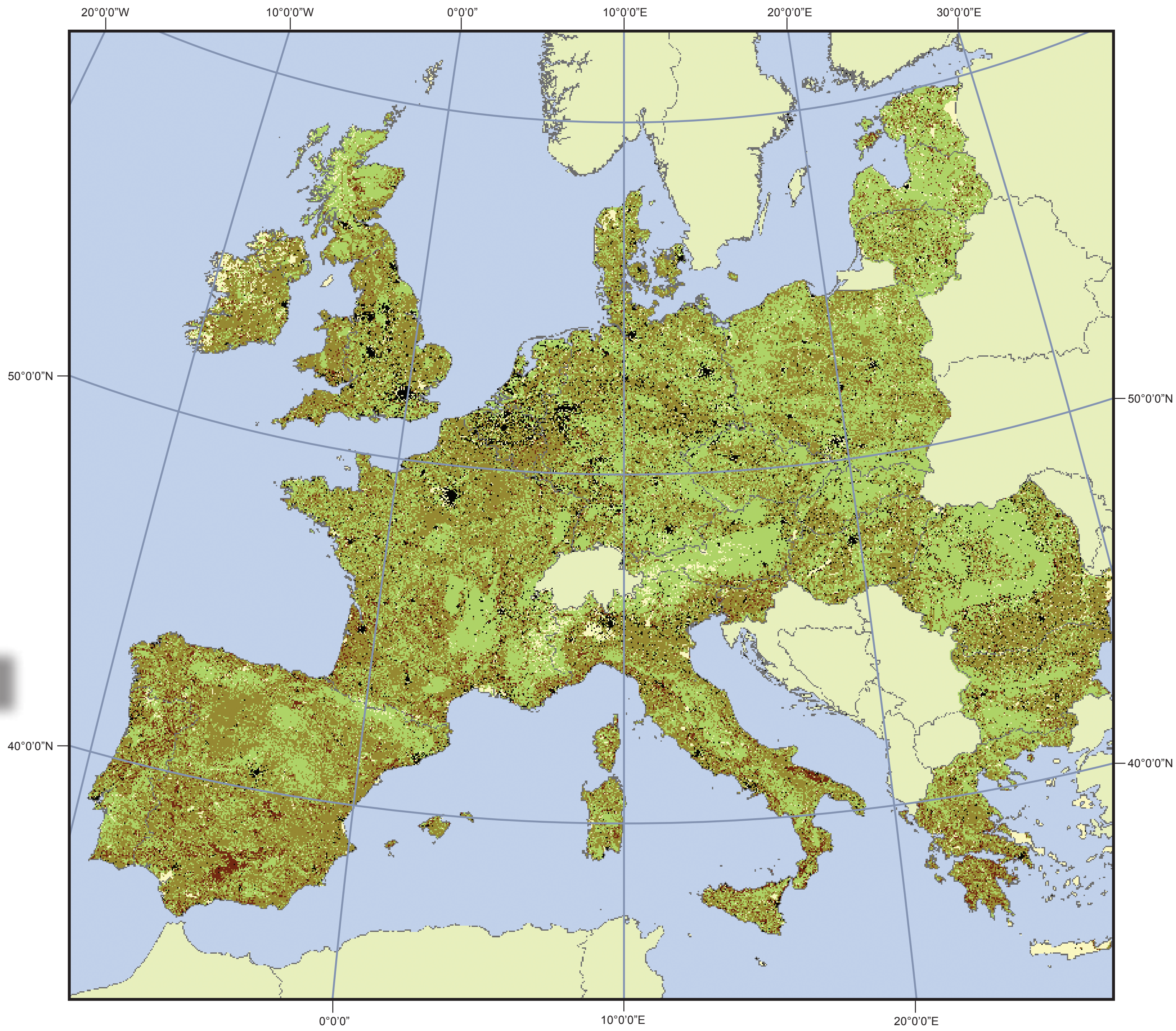
5.3.1 Agricultural Intensity



5.3.2 Soil Compaction Risk

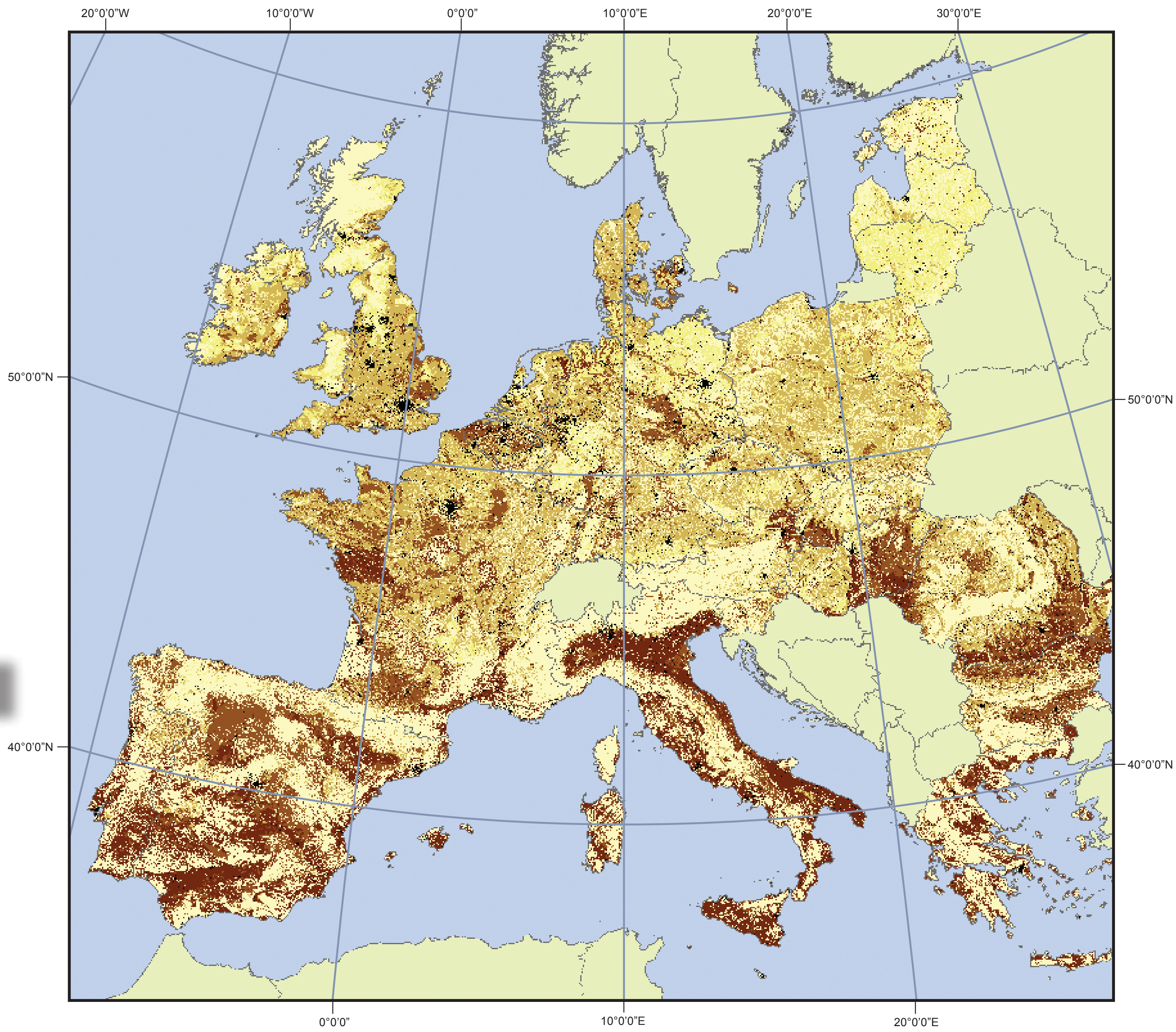


5.3.3 Soil Erosion Risk



Estimate of potential soil erosion by water. (PESERA - JRC)

5.3.4 Potential to lose Soil Organic Carbon



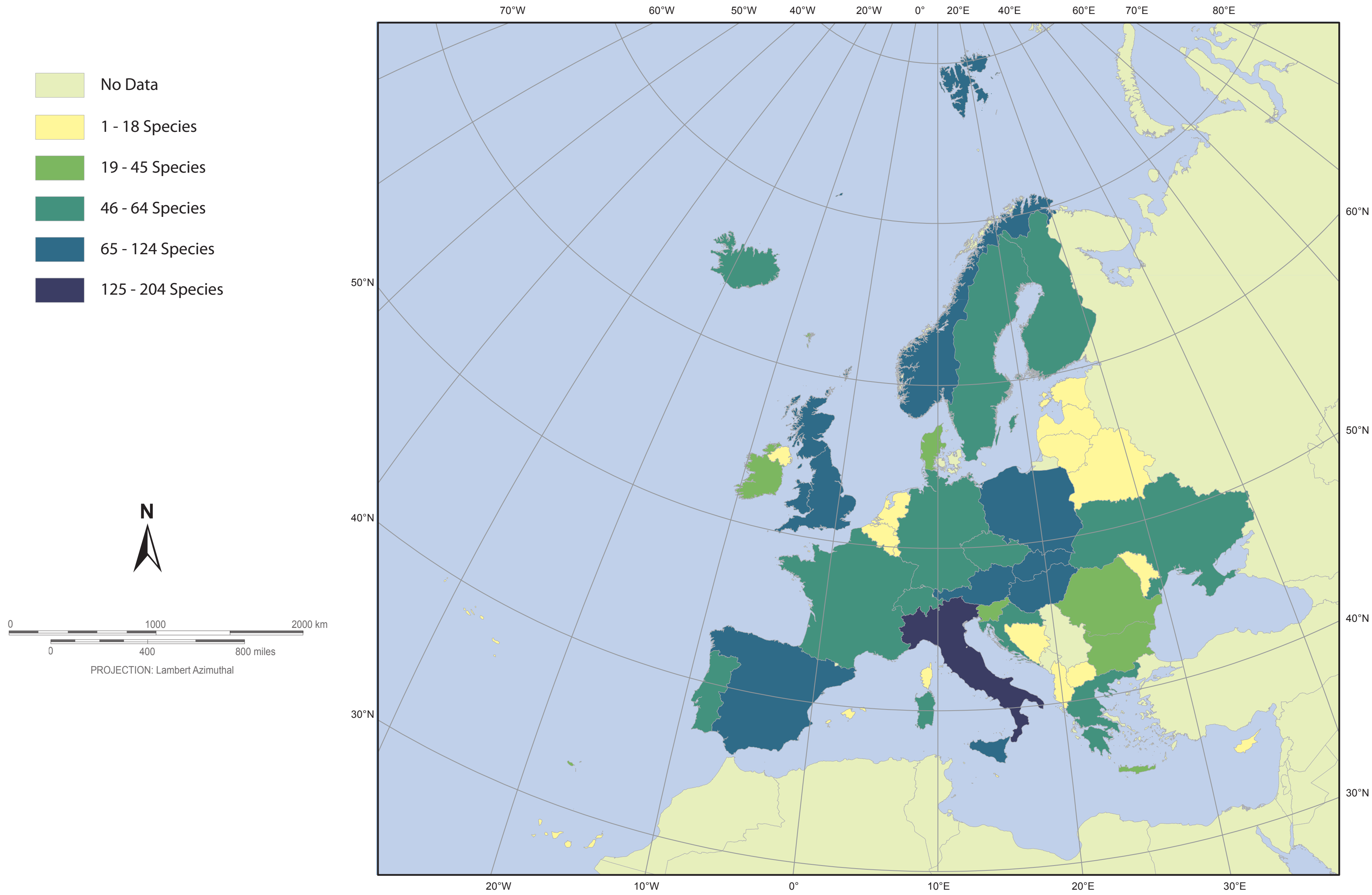
Estimate of the potential of soils to lose organic carbon. (SoCO.Project - JRC)

6.1 Distribution Maps Soil Faunal Groups of Europe

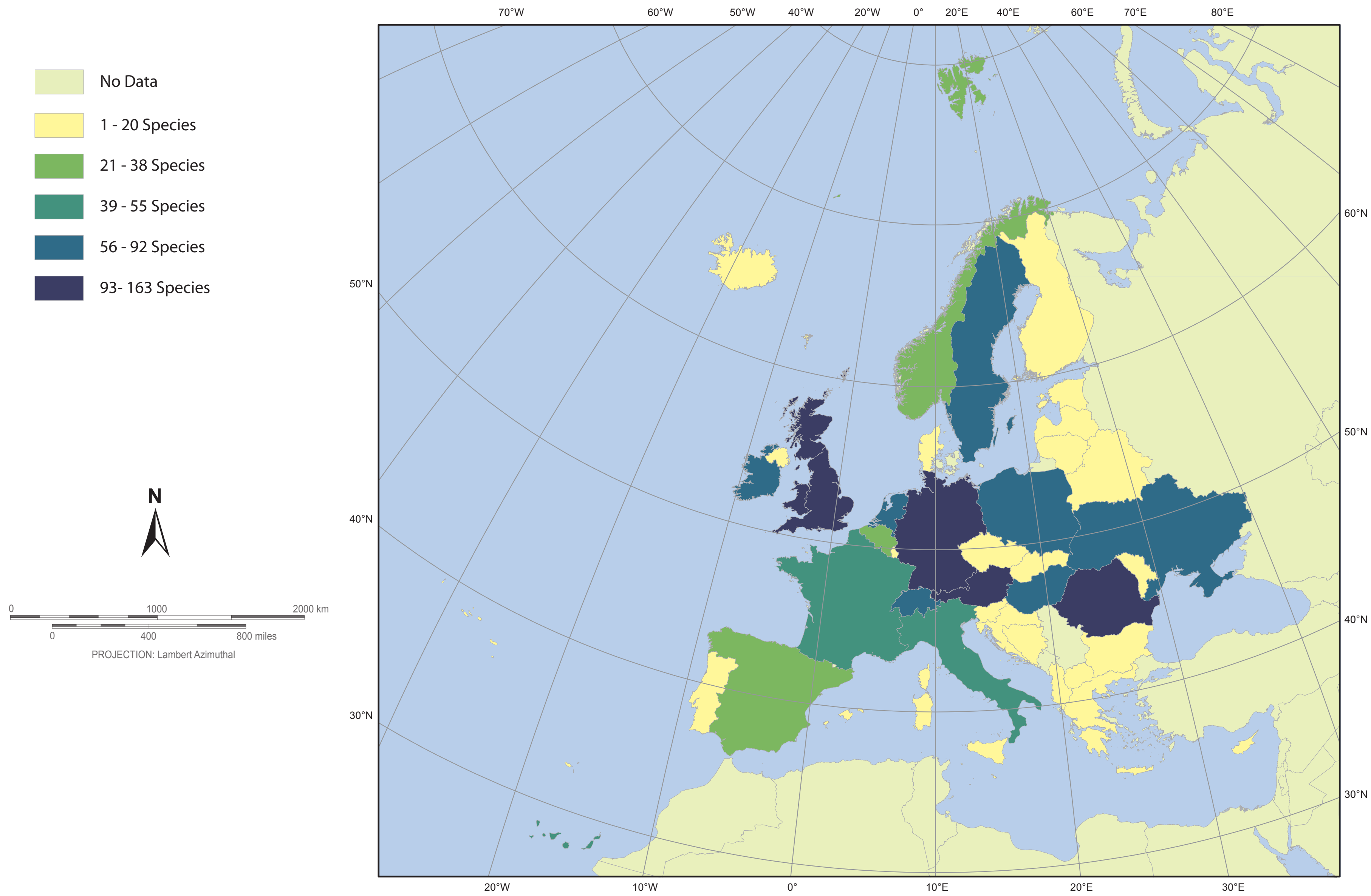
6.1.1 Distribution Map: Tardigrades

Data provided from Fauna Europaea (http://www.faunaeur.org/) – The maps show the estimated number of species in biogeographic areas or countries and are indicative only as low values may also be due to lack of observations or evidence.

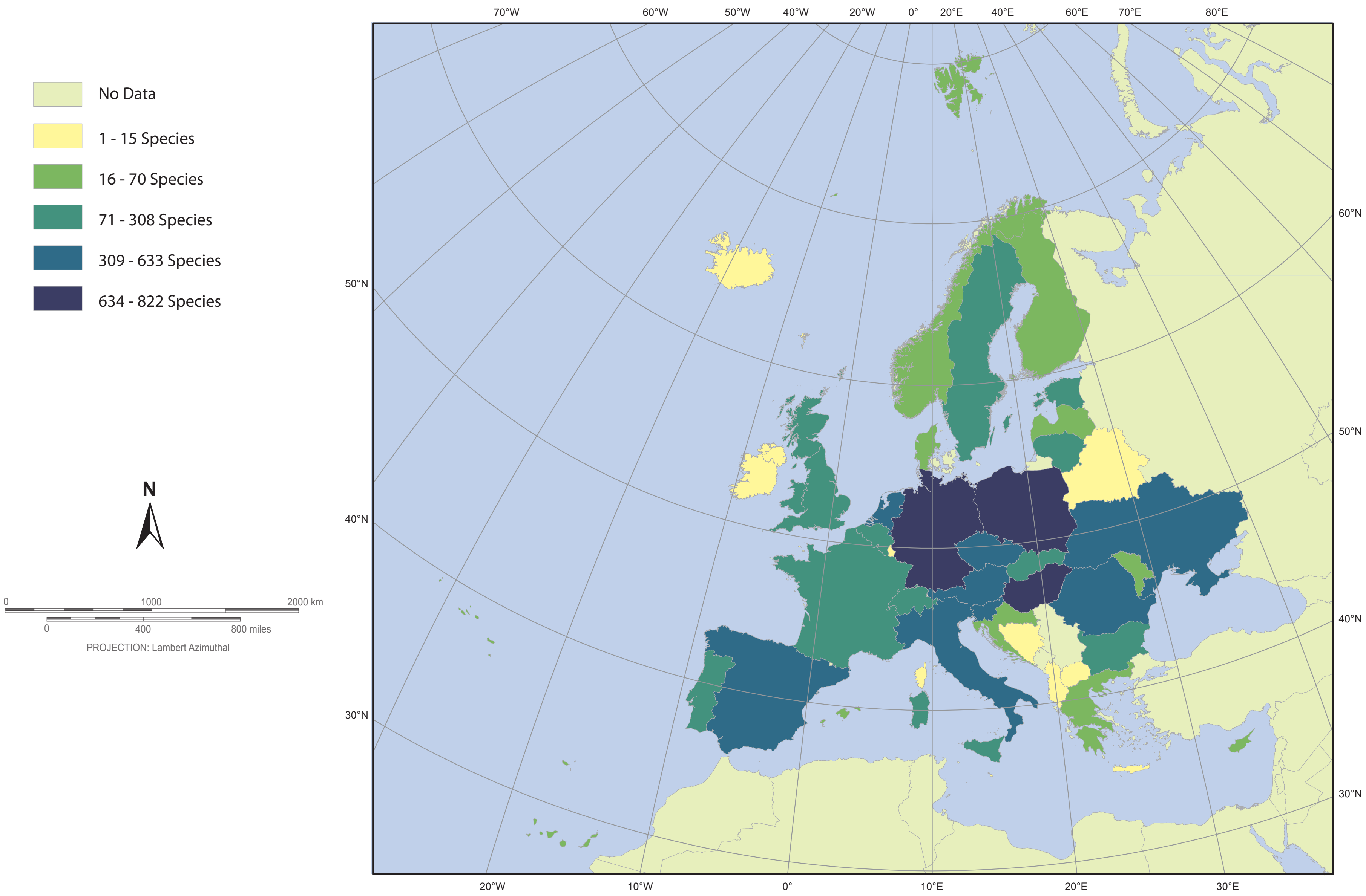
Fauna Europaea was supported by the European Commission under the Fifth Framework Programme and contributed to the Support for Research Infrastructures work programme with Thematic Priority Biodiversity.



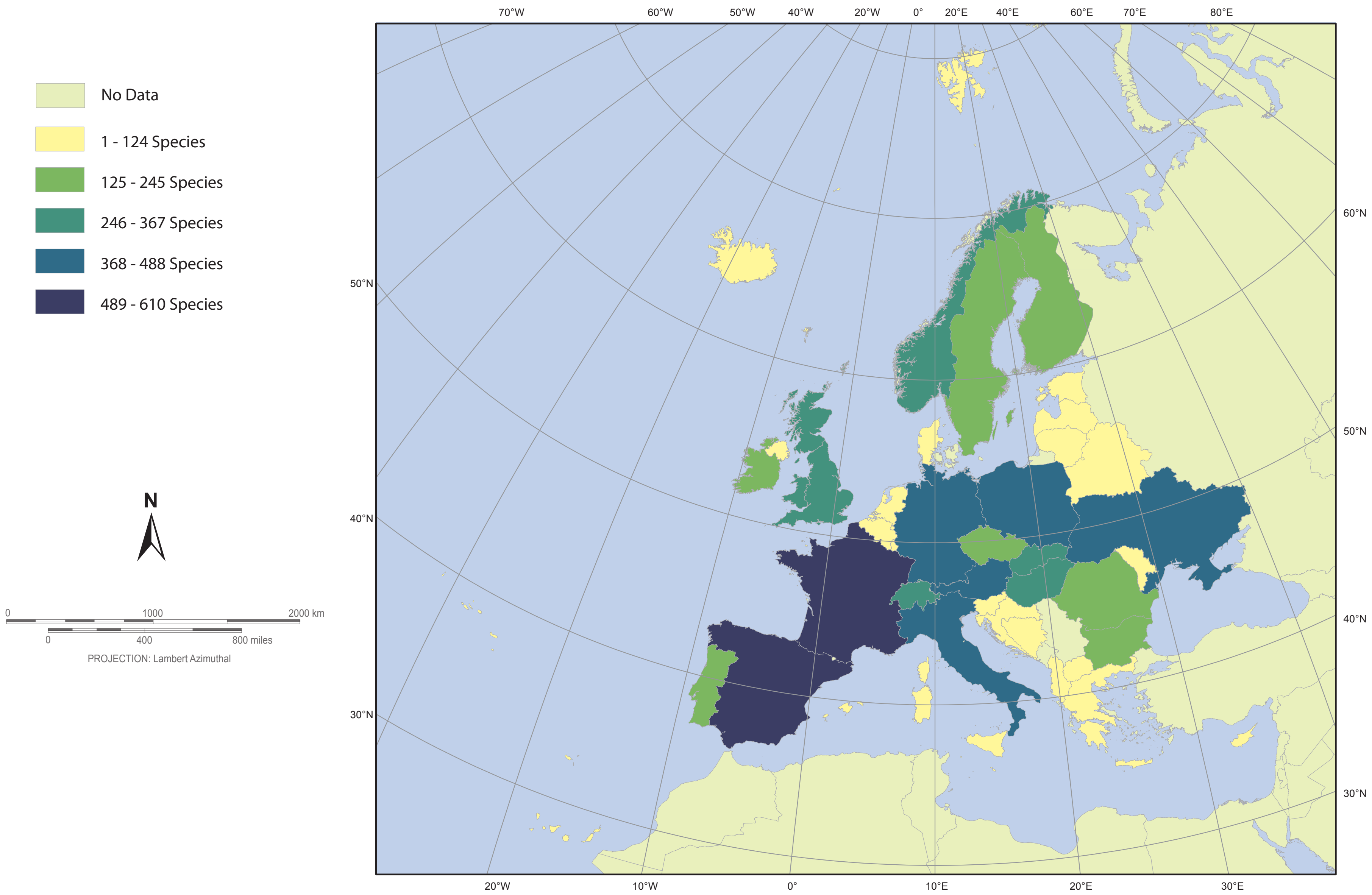
6.1.2 Distribution Map: Rotifers



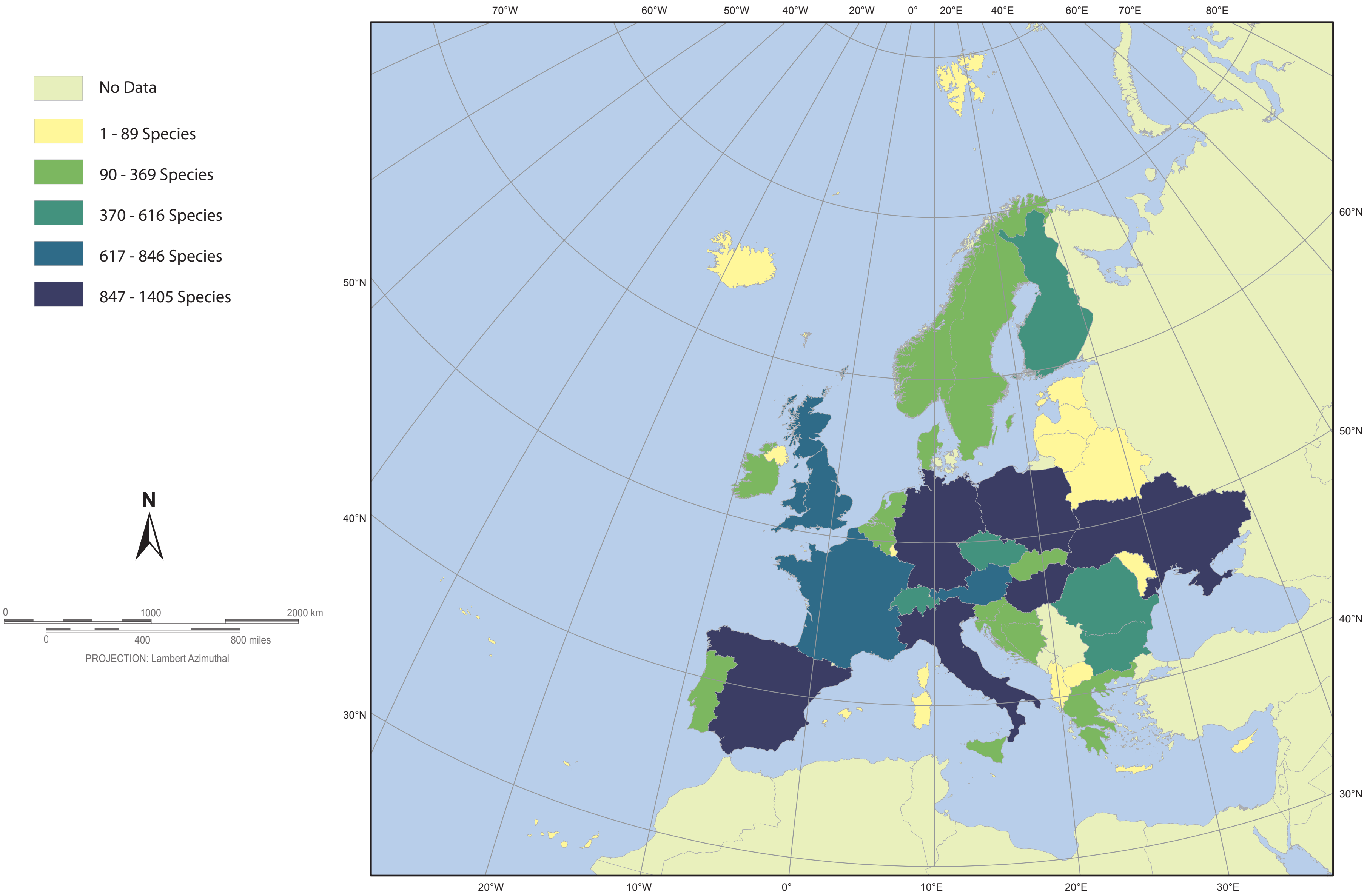
6.1.3 Distribution Map: Nematodes



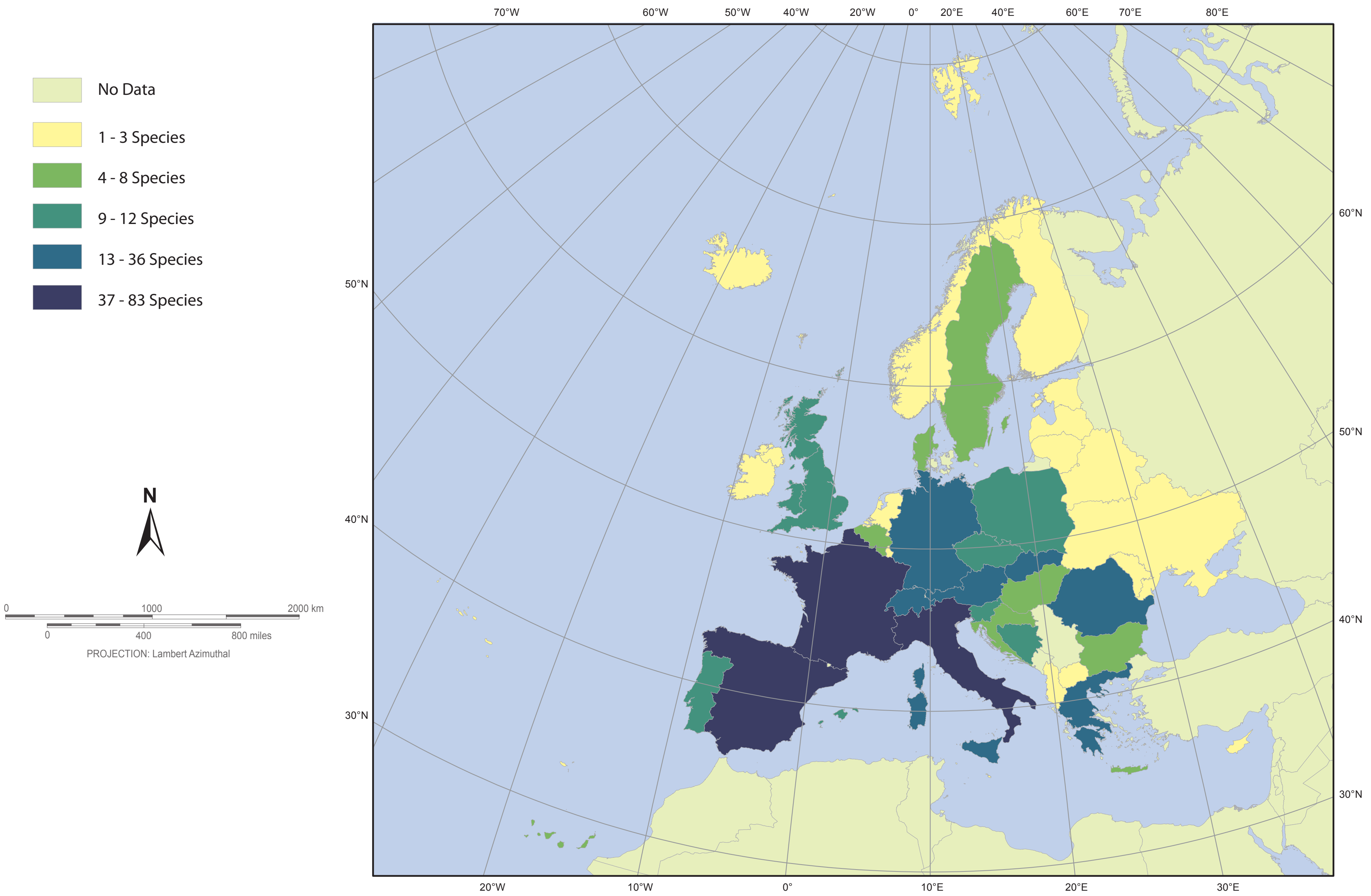
6.1.4 Distribution Map: Collembola



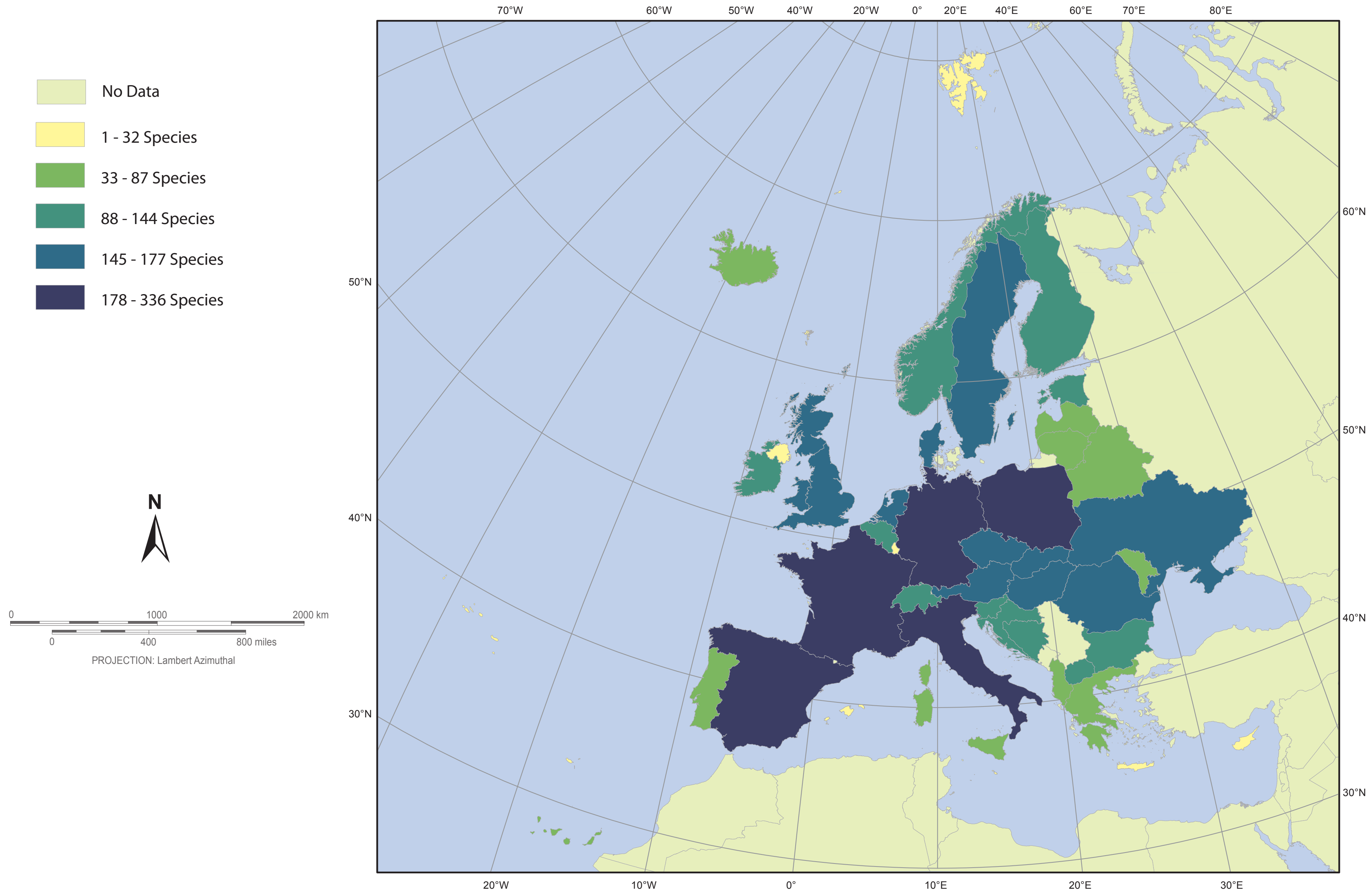
6.1.5 Distribution Map: Acari



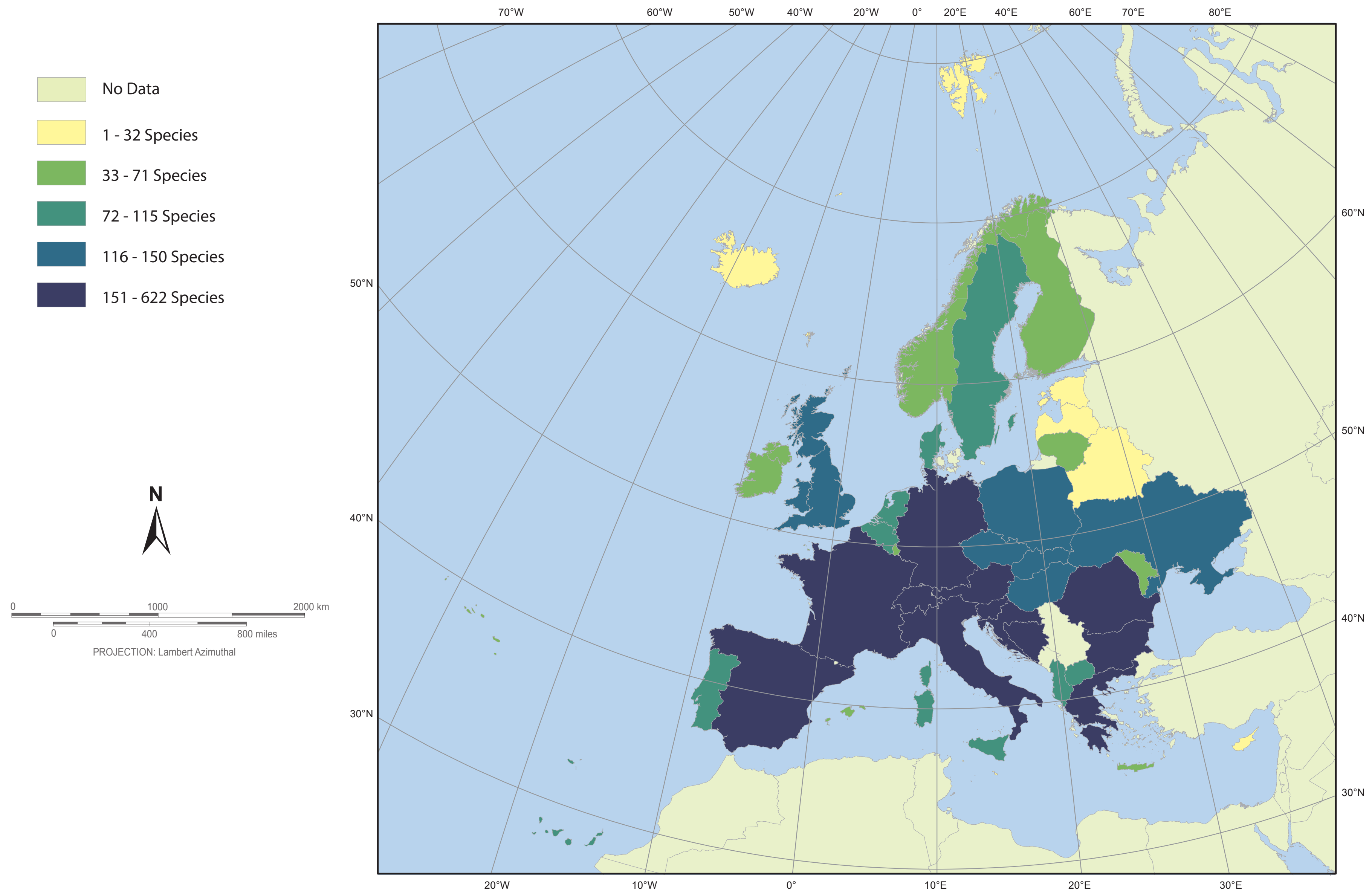
6.1.6 Distribution Map: Diplura



6.1.7 Distribution Map: Annelids



6.1.8 Distribution Map: Myriapods



Chapter 7 Soil Ecology

7.1 Soil Microbiota

Soil microbial ecology is a multi-disciplinary science with strong interconnections between genetics, biochemistry, molecular biology, physiology, modeling, paleobiology, soil science, parasitology, epidemiology and others, with important crop, public health and environmental implications. Microbial ecology is generally considered apart from "classical" ecology due to the technical and conceptual specificities of the microbial world. The small size of microorganisms, the difficulty defining bacterial species and the huge diversity, both genetic and metabolic (being the diversity of food sources that can be utilised), particularly in the soil environments which they colonise, have led to the development of specific concepts and methodological approaches for investigating the role of microbes in ecosystem function.

Microbial ecology is a scientific domain derived originally from medicine and agronomy due to the need to elucidate the relationships and interactions between microbes and their natural habitats (soil, water, sediments, rhizosphere, animal or human gut and circulatory systems etc.). The analysis of historical and recent advances in this scientific field shows a "step-by-step" evolution in both methodologies and concepts which has occurred (Fig. 7.1). In the 1960s, most comprehensive studies focused on cultures of single species which lacked interactions between other microorganisms and their habitat.

In the 1980s, one of the main advances was to take into consideration not only single organisms but also density, diversity and activity of microbial populations isolated from natural environments and in the 1990s, many studies were dedicated to this type of approach and this provided the basis for understanding the microbial world and its role in ecosystem functioning. In parallel, many efforts have been dedicated to the development of molecular methods to enable the characterisation of microbial information contained in the nucleic acids, such as DNA, extracted from environmental samples. These developments enabled the characterisation of variations of the microbial community structure and diversity in multiple situations and allowed the identification of populations preferentially associated with various habitats and different environmental situations. Altogether these methodological developments led to high-throughput screening and sequencing methodologies which enabled access to the 'metagenome' (the collective DNA from all microorganisms present in an ecosystem), and provided the majority of DNA sequences now found in databases such as GenBank.

In spite of these recent advances in molecular biology, which have allowed the development of tools to assess microbial diversity in environmental samples without culturing, most of the studies have focussed on cataloguing the bacterial diversity at particular sites and describing how bacterial communities were affected by environmental disturbances. As a result, data obtained from various studies are difficult to compare and so the trends deduced are often inconsistent, demonstrating the weak genericity of many studies in microbial ecology.

From microbial community to biogeography

Although microorganisms are the most diverse and abundant type of organisms on Earth, the progression of microbial diversification and the distribution of microbial diversity from small scales such as micrometre and millimetre scales, up to large scales such whole landscapes or even continents, has been poorly documented and is little understood. With respect to the diversification of prokaryotes, nearly all studies have focused on variations due to mutations (changes in genetic code) and/or horizontal gene transfer (transfer of genetic material to other individuals of the same generation i.e. not to offspring) and subsequent selection from environmental stresses and from competition for resources. Fewer studies have considered other more neutral mechanisms such as genetic drift due to physical isolation, whereby a microbial community may split into two genetically distinct communities upon becoming physically isolated, due to random mutations occurring within each community leading them to 'drift apart' in genetic terms. To date, there has generally been a crucial lack of integration of the spatial scale in studies of microbial community assembly.

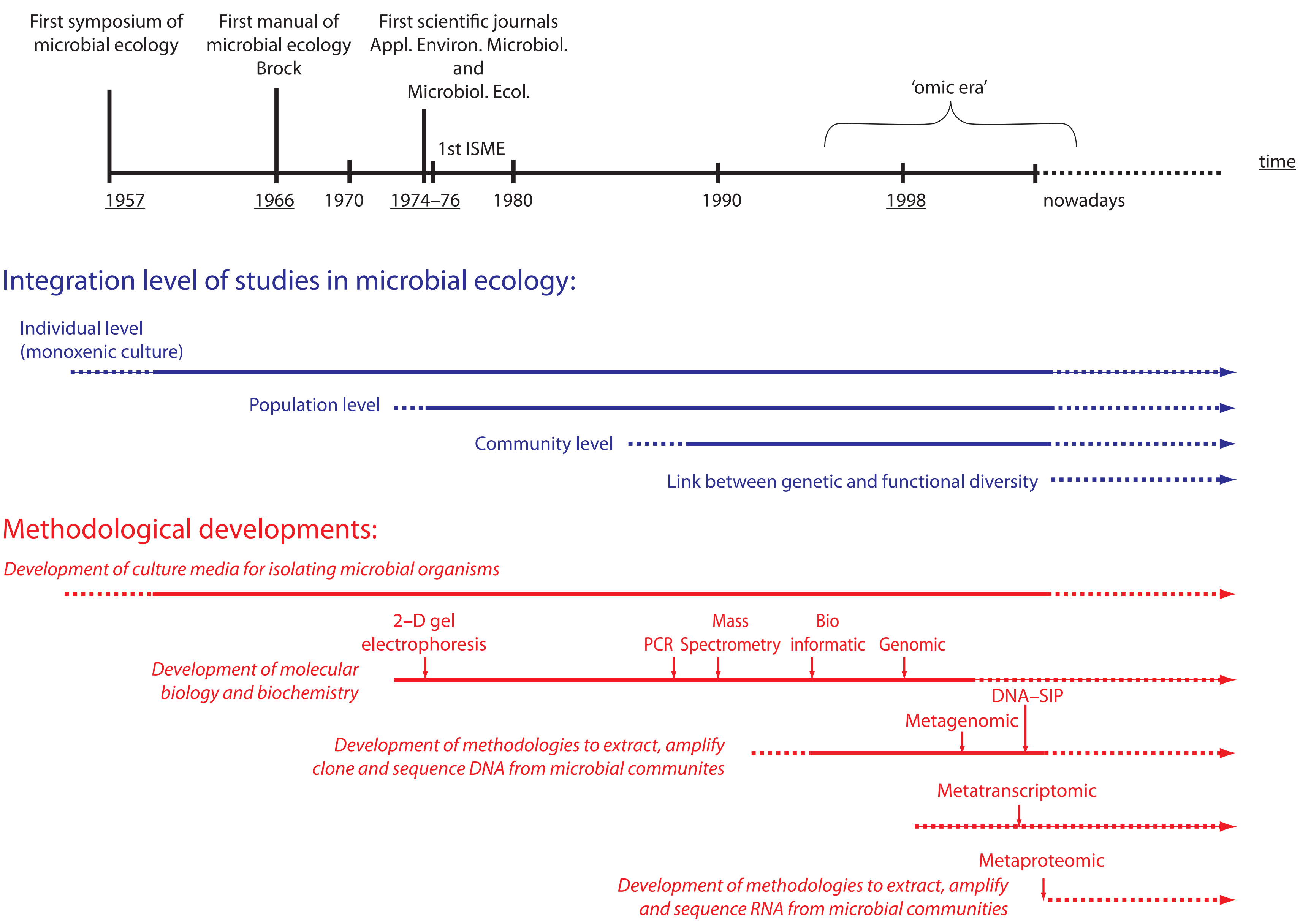
Ecologists studying plant and animals have long recognised that studying the modifications of diversity across a landscape is central for understanding the environmental factors driving the magnitude and the variability of biodiversity. However, this conceptual vision is also relevant for microorganisms since it can offer valuable insights into the relative influence of dispersal limitations, environmental heterogeneity, as well as environmental and evolutionary changes, in shaping the structure of ecological communities.

Despite the statement that spatial patterning of microbial diversity can have important consequences regarding to plant community structure and ecosystem functioning, studies attempting to integrate a wide spatial scale have generally been poorly investigated and the environmental factors which affect biodiversity remain largely unknown. Furthermore, the relationship between the number of species and area sampled (taxa-area relationship) has not been explicitly examined for microorganisms as it has been for plants and animals. Microbial ecologists describing biodiversity on a wide spatial scale (i.e. microbial biogeography) often invoke one of the oldest hypotheses in microbial ecology *"everything is everywhere, but the environment selects"* which was deduced by Baas Becking in 1934, building on from work initially published by Beijerinck in 1913. The hypothesis "everything is everywhere" is supported by several particularities of the microbial model: i.e. that microorganisms

1. are small and easily transported,
2. have the ability to form resistant physiological stage that allow them to survive in hostile environments,
3. have extremely large population sizes with a high probability of dispersal and a low probability of local extinction.

The fact that more than $10^{18} – 10^{20}$ microorganisms are estimated to be transported annually through the atmosphere, between continents, supports the hypothesis of a wide dispersion of microbes. Other evidence is that it is possible to isolate bacteria from places where they might not be anticipated such as thermophilic bacteria from cold sea water. So the hypothesis states that the reason for this is that while bacteria may be found where they might not be anticipated, they are present in very small numbers, often below detection limits and in dormant forms, as the environment has selected for a different, better adapted microbial population to flourish in that particular area. Developing the hypothesis, you would therefore expect the community to change upon changing environmental conditions, such as if cold sea water were collected and added to a hot spring, so that the previously dormant bacteria come to dominate. This has been observed experimentally to some extent.

Fig. 7.1: Historical and salutatory evolution of microbial ecology (from Maron *et al.*, 2007)



The counter hypothesis is that "everything is not everywhere", which suggests that geographic populations can be isolated due to some, or possibly the majority of, microorganisms having a limited dispersal and, therefore, have a limited species range which can lead to a local and particular speciation.

To date, the number of studies dealing with biogeography of soil microbial community remains low and insufficient to answer the different questions which arise when considering the spatial distribution of microbes:

- Do microbial communities have a spatial structure in the same way that macroorganisms do? i.e. do they exhibit a particular distribution with predictable, aggregated patterns from local to regional scales? In other terms, does a taxa-area relationship exist in microbial-biogeography?
- Are spatial variations due to contemporary environmental factors or historical land use and contingencies?
- Which of the environmental factors (edaphic, climatic, land use, anthropogenic) contribute most to the structure and diversity of bacterial communities in soil when considering wide geographic scales?

In an attempt to answer these questions, a global compilation of data from the studies dealing the biogeography of soil microbial communities was analysed which demonstrated that:

- despite a high local diversity, soil microorganisms may have only moderate regional diversity
- soil bacterial diversity appears to be unrelated to site temperature, latitude and other variables that typically strongly influence plant and animal diversity, and that community composition was largely independent of the geographic distance.
- the environmental factor most influencing bacterial diversity appeared to be the soil pH, with a highest diversity in neutral soils and a lower diversity in acidic soils.

Biogeographical patterns of microbial diversity have been drawn at a regional scale in France where it was found that these patterns were more related to local factors, such as soil type and land cover, than to more global factors such as climatic and geomorphological characteristics.

Altogether, these studies have demonstrated the weak taxa-area relationships for soil microorganisms and, therefore, show that microbial biogeography fundamentally differs from the biogeography of "macroorganisms".

The low number of studies available might be explained by the limitations in our current abilities to resolve the huge microbial diversity in natural ecosystems as well as the difficulty in detecting minor populations which can be below current detection limits.

Another explanation is that the high levels of difficulty in building up and managing an adequate sampling strategy, which must integrate large scale of sampling (region, territory…) with a precise squaring representative of the modifications of landscape, implies the need for a very large number of samples (several thousand) to be taken and analysed, and this work has not yet been undertaken to a sufficient degree.

Fungi

The previous part of this section has focused mainly on the ecology and biogeography of bacteria. However, the microbial world is generally considered to include three main groups; bacteria, fungi and archaea.

Traditional approaches to the study of soil fungal ecology were similar to those of studying bacteria in that they were based primarily on the isolation and growth of fungi in culture or on the appearance of fruit bodies (mushrooms) above ground. However, both these approaches give very biased views of the communities of fungi present; as with bacteria, only a very small proportion of fungi are culturable and only a small proportion of fungi produce fruiting bodies. This means that the original investigations focused on culturable species, or those which produced fruiting bodies, and all but neglected the rest.

The time line for advances in our ability to examine the diversity and functions of fungal communities is very similar to that shown for bacteria (Fig. 7.1). However, unlike with bacteria, the traditional view of fungal communities being dominated by a few common species with the rest of the species being rare has not changed so much with our ability to detect and characterise the community. What has changed is the resolution at which we can examine species and the estimates of total species richness.

Fig. 7.2: A fairy ring with fruiting bodies growing at the advancing mycelial front. (KR)

The most recent advances in the molecular analyses of fungal communities have found that there can be more than 1000 species in one gram of forest soil. Fungi have been traditionally classified based on their reproductive structures either sexual or asexual. However, DNA databases have now been populated with sequences from morphologically identified fungal species and now form the basis for comparing fungal DNA sequence data derived from environmental samples, although it is clear that a large number of known species remain to be included within these databases. The greatest obstacle to improving our ability to characterise fungal communities is the huge number of fungal species that remain to be described; it has been estimated that as few as 5% have been described so far.

Soil fungi may be considered as constituents of a number of different functional groups, although they are not always restricted to a single functional group. Most species are saprotrophs, living on dead organic material, but a small but very significant number are parasites of plants and animals, causing a range of economically important diseases. Furthermore, many soil fungi are symbiotic with plants, either forming mycorrhizas involved in the uptake of nutrients (see Section 2.4) or colonising plant tissues without any visible signs of infection known as root endophytes.

Fungi exist in two different forms, either as single celled organisms called yeasts, or in hyphal forms whereby they grown to form extensive branched networks (see Section III). The size of fungi can vary considerably with unicellular yeasts being typically 4-5 µm in diameter, whereas the individual hyphae of filamentous fungi may be 4-5 µm in diameter they can form mycelia that can be very extensive. For example, the fairy rings which can appear in lawns and grasslands in summer and autumn are good examples of extensive fungal individuals, with the rings of darker grass marking the edges of the advancing mycelial front (Fig. 7.2). Some of these can grow at rates of over 1 m a year and can form ring structures over 200 metres across!

The largest known fungal individual, which is a parasite infecting the roots of forest trees, covers an area of 890 ha and has been estimated to weigh an incredible 80 tons. These extensive structures suggest that individuals of some fungal species can live for hundreds if not thousands of years. The amounts of fungal hyphae in soils can be huge with estimates varying from 100-700 m g^{-1}, which can be equivalent to 700-900 kg ha^{-1}, with the highest values being in forest soils (see Sections 3.1 and III).

Biogeography of fungi

For many years it was believed that ecological versatility of fungi and the physical adaptation of their spores for long range dispersal made them unreliable as biogeographical indicators. Furthermore, as it was assumed that they didn't have species ranges their distribution was also thought to fit the hypothesis that everything is everywhere but the environment selects. However, this view is being challenged with molecular makers being used to detect geographic patterns within species at both global and at more localised scales within continents. Recent work as shown that post glacial migrations can be detected in fungi. For example, the migration of the highly prized Perigord truffle (*Tuber melanosporum*) northwards from southern France has been documented from refugia which apparently survived during the last glaciation. Much older distribution patterns have been linked to the break up of Eurasia into N. America and Europe, with the resulting population fragmentation likely leading to genetic isolation and the emergence of new species.

Archaea

The third group of microorganisms are archaea. These are bacteria-like organisms in that they do not have cell nuclei and are microscopic single celled organisms, but there the similarities stop. Archaea actually have several metabolic pathways and genes which are more closely related to eukaryotes than to bacteria, although they are able to utilise a greater variety of energy sources than eukaryotes, being more inline with bacteria. However, the cell membranes of archaea differ considerably from those of bacteria or eukaryotes, implying that archaea actually have an independent evolutionary history from other prokaryotes and eukaryotes. In fact the types of lipids found in the cellular membranes of archaea have been found in ancient sediments in Greenland, which are in the region of 3.5 billion years old and suggests that the archael linage may be the most ancient on Earth.

These differences are so fundamental that they led to an revision of the taxonomic system which used to be focused on the five kingdom approach, to a newer approach where life is, at the lowest resolution, devided into three domains, being bacteria, eukarya (including all organisms that have nuclei in their cells, from protozoa up to plants, fungi and animals, including humans), and archaea.

Archaea were originally thought to be extremophiles, organisms which grow in harsh environments such as hot springs and salt lakes. However, as molecular methods have been employed more and more widely, allowing the overcoming of such problems as the lack of culturablility in laboratories, archea, as with other microbes, have been found just about everywhere including soils. In fact, it is now thought that archaea may make up as much as 20% of the total living biomass on Earth! Furthermore, as research on these organisms has intensified over recent years, archaea have come to be recognised as a major part of life on Earth and play an important role in the carbon and nitrogen cycles as well as the sulphur cycle.

Some archaea appear to have quite restricted species ranges, with differences in community structure having been observed even between adjacent hot springs and so provide some evidence against the 'everything is everywhere' hypothesis at a relatively small spatial and temporal scale.

7.2 Soil Fauna

The interactions between soil organisms and the factors that control them is the main focus of soil community ecology. Information on the actual diversity of groups of below ground soil biota is sparse compared to that of above ground organisms. This lack of knowledge is understandable, because soil organisms are not easily seen, they are difficult to study and they lack the 'sentimental appeal' that many above ground species have. However, soil organisms have been known since the 17th century (Fig. 7.3).

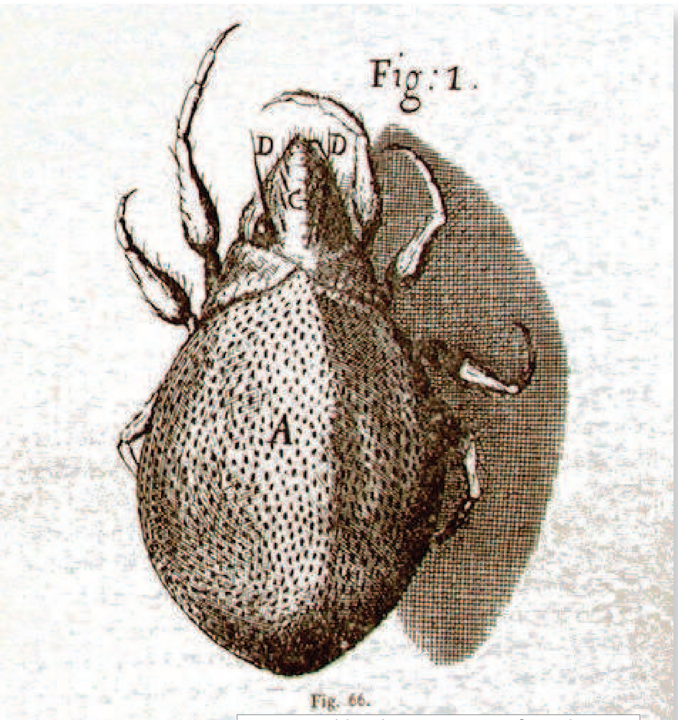


Fig. 7.3: Oldest known picture of a soil mite.

Soil biota are thought to harbour a large part of the world's biodiversity and to govern processes that are regarded as globally important components in the cycling of organic matter, energy and nutrients. Moreover, they are also key players in several supporting and regulating ecosystem services as previously discussed (see Section 4.1). Furthermore, they are key components of soil food webs (Fig. 7.4). Rough estimates of soil biodiversity indicate several thousand invertebrate species per site (for example between 1500 - 1800 invertebrate species were found in one German beech forest), as well as the relatively unknown levels of microbial and protozoan diversity.

By far the most dominant groups of soil organisms, in terms of both numbers and biomass, are the microorganisms, i.e. bacteria and fungi. Estimates on the number of microbial species (genotypes) in the soil, range from 10^4 - 10^5 per gram of soil. As well as these organisms, soil ecosystems generally contain a large variety of animals, such as nematodes, microarthropods such as mites and collembola, enchytraeids and earthworms. In addition, a large number of macrofauna species (mainly arthropods such as beetles, spiders, diplopods and chilopods, as well as snails) live in the uppermost soil layers, the soil surface and the litter layer. In general, soil invertebrates are classified according to their size in three classes, being microfauna, mesofauna and macrofauna.

Despite several decades of soil biological studies it is still very difficult to provide average abundance and biomass values for soil invertebrates. This is partly caused by their high variability in both time and space, as well as by differences in sampling methods used. In addition, most work has been performed in forest soils of temperate regions, while other ecoregions such as the tropics, or other land uses such as agriculture, have been seriously neglected. This is particularly true for crop sites.

In Table 7.1, the range of abundance of several organism groups in forest sites are shown. The maximum numbers are based on optimum conditions (e.g. the high numbers of enchytraeids was found in an acid moor soil where almost no other invertebrates are normally found). In agricultural soils, which are characterised by several threat factors for soil invertebrates (e.g. ploughing, fertilizers, compaction and pesticides), these numbers are clearly lower (Table 7.1). However, in Central Europe an "average" earthworm population is characterised by a density of 80 individuals per m^2, a biomass of 5 g dry weight per m^2 and on average 4 species per m^2. These figures should also be true, more or less, for the soil in your garden!

Soil fauna are highly variable and the majority are also highly adaptable with regard to their feeding strategies, ranging from herbivores through omnivores and including carnivores. Depending on the available food sources many soil fauna are able to change their feeding strategies to a greater or lesser extent with many carnivorous species able to feed on dead organic matter in times of low food availability.

The interactions between soil fauna are numerous, complex and varied. As well as the predator / prey relationships and in some instances parasitism, commensalism also occurs. One example of this is the method of dispersal of several species of pseudoscorpions which are like scorpions in that they have pinchers, but they lack the elongated tail with sting. It has been noted that some species of psuedoscorpion disperse by concealing themselves under the wing covers of large beetles. Through this type of interaction whereby one type of organism benefits and the other is neither harmed nor benefits, known as commensalism, the pseudoscorpions can be dispersed over a wide area while simultaneously being protected from predators. The beetle, apart from having to carry a little extra weight while flying, is otherwise unaffected.

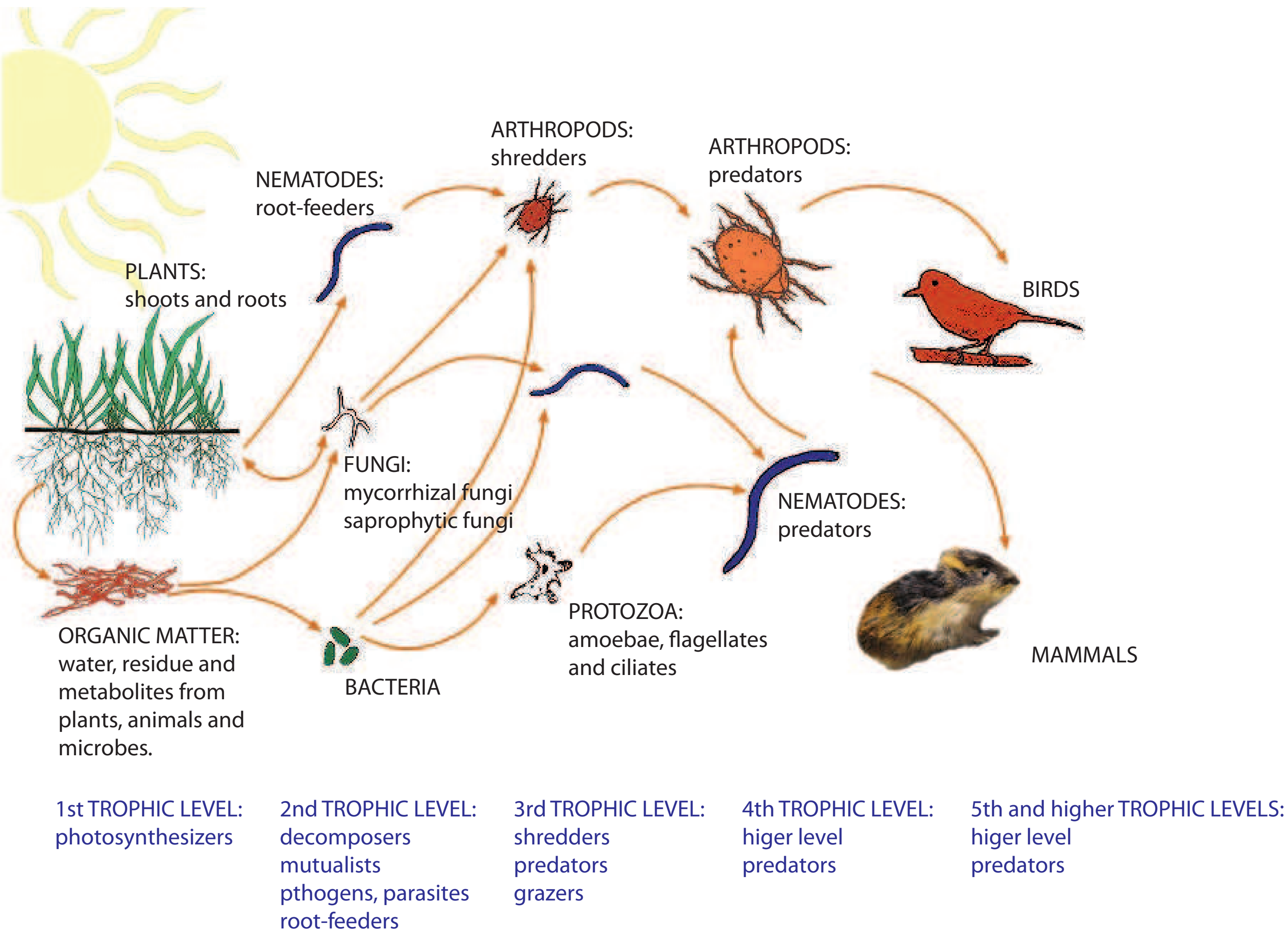


Fig. 7.4: Schematic representation of soil food web.

Table 7.1: Abundance of the most important soil invertebrate groups in temperate regions (mainly forests); mean and maximum values

Size class	Organism group	Mean ind/m²	Maximum ind/m²
Microfauna	Flagellata	100,000,000	10,000,000,000
	Nematoda	1,000,000	100,000,000
Mesofauna	Acari (mites)	70	400
	Collembola	50	500
	Enchytraeidae	30	300
Macrofauna	Lumbricidae	100	500
	Gastropoda	50	1000
	Isopoda	30	200
	Diplopoda	100	500
	Beetles (larvae)	100	600
	Diptera (larve)	100	1000

Table 7.2: Abundance of a selection of soil organism groups in Mediterranean soils.

* numbers given per kg soil DW (dry weight); ** families, not species; ≈ numbers deduced from grassland sites

Organism group	Abundance (ind/m²)	Biomass (mg DW/m²)	Species number
Nematoda*	3000 - 13000	≈ 440	17 - 20**
Acari (mites)	<1000 - 5000	≈ 120	3 - 10
Collembola	1500 - 33000	≈ 120	17 - 38
Enchytraeidae	2000 - 30000	110 – 640	3 – 22
Lumbricidae	0 – 200	100 - 12100	1 - 7

Fig. 7.5: Typical Portuguese cork oak forest. (JPS)

The composition of the soil organism community of a typical Mediterranean oak forest (Portugal – Fig. 7.5) is shown below (Fig. 7.6). In the Mediterranean, soils are often inhabited by macroarthropods such as coleopterans, spiders and ants. Collembola are also both diverse and abundant with the community being dominated by eu-edaphic and hemi-edaphic species (litter species are less abundant (Fig. 7.7).

In the box at the bottom of the page, two typical communities are described.

On the left of the box, a soil organism community of a Scandinavian coniferous forest stocking on an acid soil (mor profile). These sites are characterised by the almost complete absence of earthworms and macroarthropods while enchytraeids, springtails and mites can reach huge densities.

On the right of the box, a soil organism community of a Central European beech forest (mull profile). At such sites earthworms are highly dominant, but other macrofauna such as snails or diplopods are also common. Mesofauna groups are diverse but less abundant than in acid soils.

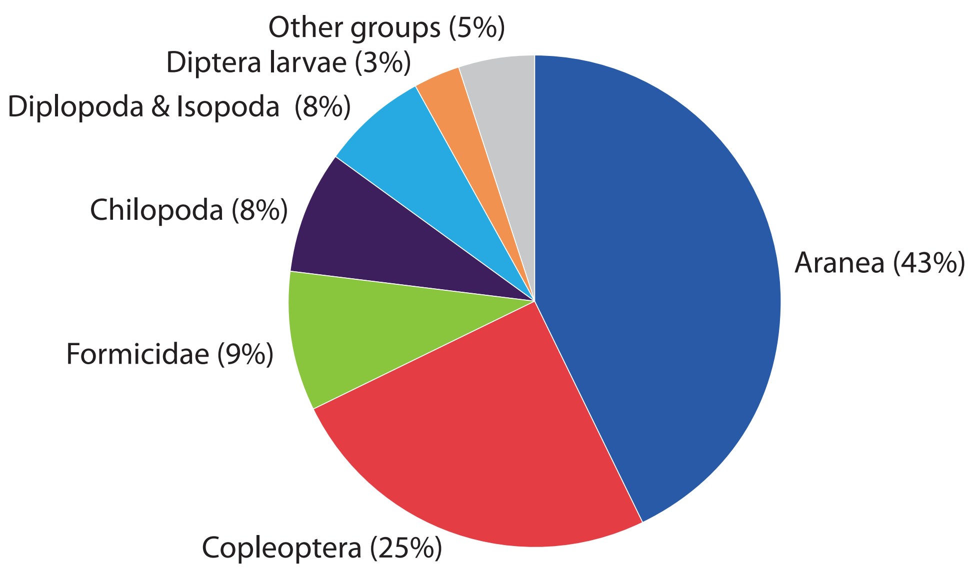


Fig. 7.6: Percentage of species richness of soil macroarthropods in a cork oak forest area in southern Portugal (samples taken using the ISO method). (JPS)

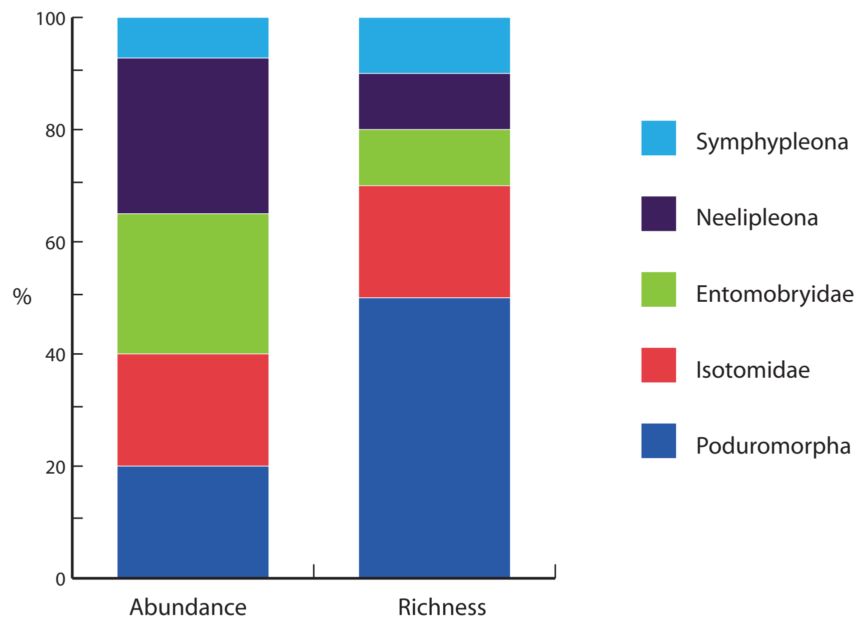


Fig. 7.7: Collembola community profile in terms of abundance and species richness in a cork oak forest area in southern Portugal (samples taken using a split corer according to the ISO method). (JPS)

Mor And Mullfauna

In Central and Northern Europe, soil organism communities differ considerably along a gradient of humus types, pH and other soil characteristics (see scheme below). Extremes are 'mor' sites (left side of the scheme; Fig. 7.8), often occurring in coniferous forests or moors, which are characterised by acidic soils and a thick, well stratified litter layer. Macrofauna is usually missing in these site types but collembola, mites and enchytraeids can be extremely abundant. In contrast, at 'mull' sites (right side of the scheme; Fig. 7.9) the organic matter is not concentrated at the soil surface but incorporated into the soil, due to the activity of earthworms and other macrofauna. Here the soil is not acidic and the litter forms only a relatively thin layer. (Humus is discussed in more detail in Section 2.3)

Fig. 7.8: Typical mor profile: slow decomposition of organic matter, thus thick layers of dead organic material accumulate. (JFP)

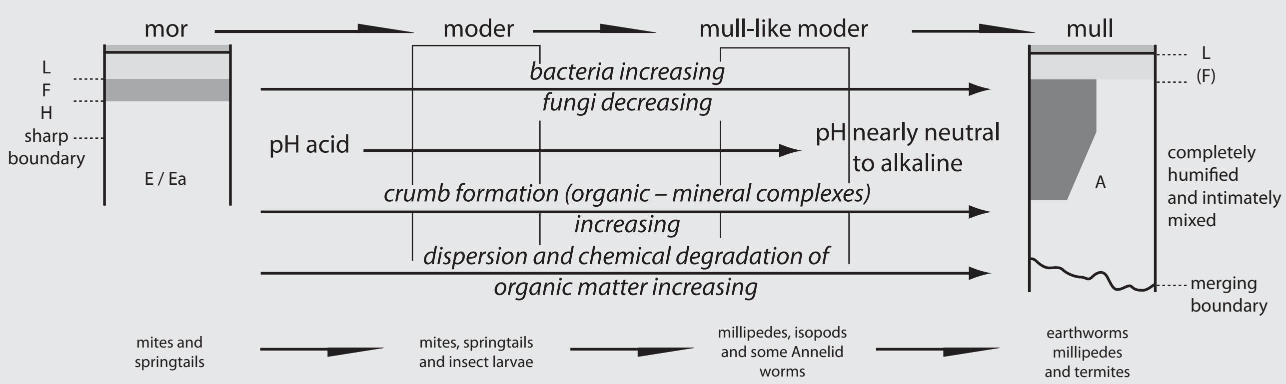


Fig. 7.9: Typical mull profile: high biological activity, thus quick decomposition of organic material; litter layers are missing. (JR)

7.3 Soil Fauna Life Strategies

The degree of interactions between soil organisms and the soil itself can be highly variable among taxa and depending on the part of the life cycle that is spent in the soil. In particular, with regard to this, combined with the morphological adaptations and the ecological functions of organisms, it is possible to classify soil fauna into four main groups: temporary inactive geophiles, temporary active geophiles, periodicals geophiles, and geobionts (Fig. 7.10). It should be noted that these groupings do not have any taxonomical significance but rather are useful when studying the life strategies of soil invertebrates.

Temporary inactive geophiles are organisms that live in the soil only for some phase of their life, such as to overwinter or to undergo metamorphosis, when protection from climatic instability is more necessary. Due to their relative inactivity, the organisms belonging to this group have a weak influence on the ecological function of soil, although they can be important as prey for other organisms.

Temporary active geophiles live in the soil in stabile manner for large part of their life (i.e. for one or more development stage, and emerge from the soil as adults). Most of these organism are insects, such as cicada, Neuroptera, Diptera, Coleoptera and Lepidoptera. Organisms having "pupae" part of their life cycle, play a minor role in soil during these phase, while the "larvae" stage is much more important for the ecology of soil, especially when the population density is high. Most the larvae can act as both detritivores and predators.

The periodical geophiles spend one part of their life cycle in the soil, generally as larva, but throughout their lives they occasionally go back to soil to perform various activities, such as hunting, laying of eggs or to escape dangers. Several Coleoptera groups (e.e. carbides, scarabeids, cicindelids) spend their larval stage in the litter or in the upper layers of mineral soil, and when adults, use soil as food source, refuge and for other purposes.

Geobionts are organisms that are very well adapted to life in soil and can not leave this environment, even temporarily, having characteristics that prevent survival outside of the soil environment due to lacking protection from desiccation and temperature fluctuations, as well as the sensory organs necessary to survive above ground by finding food and avoiding predators. Several species of Myriapods, Isopods, Acari, Molluscs and the majority of Collembola, Diplura and Protura, belong to this group.

These different types of relationships between soil organisms and soil environment determine a differentiated level of vulnerability among various groups, as a consequence of any possible impact on soil environment. For instance, if soil contamination will occur, any impact will be highest on geobyonts (because they can not leave the soil and must spend all their life there) and lowest on temporary inactive geophylus. These principles have been applied for the use of soil mesofauna as an indicator of soil biological quality, such as the case of the QBS index developed by the University of Parma, Italy.

The relationship between soil and vertebrates:

Although some vertebrates spend part of their time in the soil, their importance in the food web of soil ecosystems is often overlooked or deemed minimal. Some vertebrates have a pronounced impact on soil ecosystems.

Several vertebrates create dens or nests in the soil and usually have little or no impact on soil communities. These include birds, rodents; lizards, toads, frogs and mammals such as foxes and badgers. In most cases, such dens or chambers become mini-ecosystems for non-burrowing animals such as beetles and frogs. The build up of organic debris in the dens promotes the growth of fungi, which, in turn, is eaten by insects and mites that become food for vertebrates. However, the overall effects of these chambers on soil communities are probably small.

Vertebrates that create burrows in the soil probably have a substantial impact on soil communities. Burrowing rodents, moles and prairie dogs bring soil material from lower depths to the surface where they are broken down, incorporated with organic matter and carried off by water and wind. Mixing deep and surface materials also may have significant effects on the texture and composition of the topsoil. Vertebrates can also influence the soil by adding additional organic material. Faeces, urine and animal remains are a rich source of important soil chemicals.

However, not all mammal associations are beneficial to the soil. Disturbance caused by burrowing animals can increase erosion, prevent natural revegetation and a decline in the numbers of other soil species. Livestock can cause compaction, leading to waterlogging, increased surface runoff and eventually, erosion.

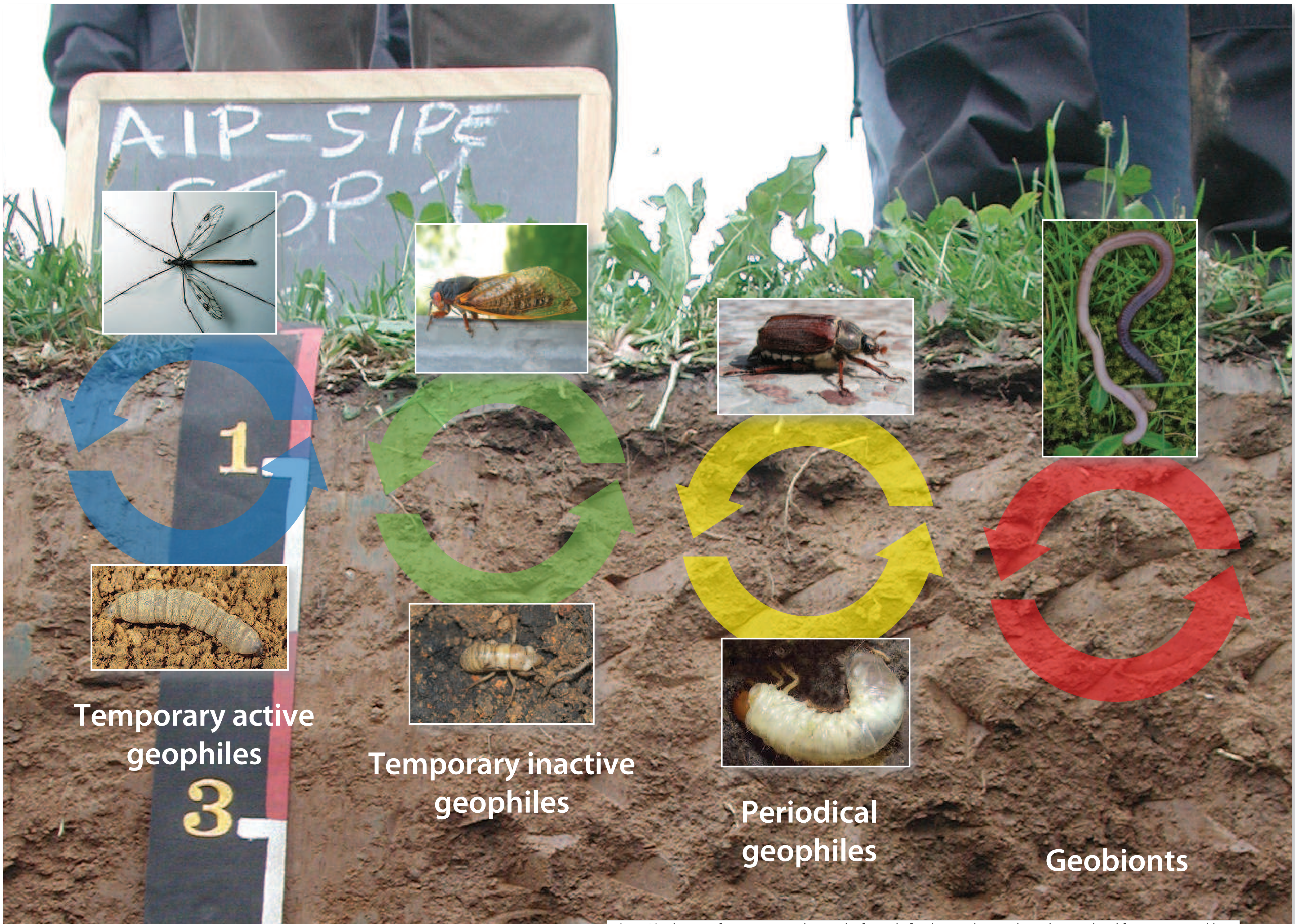


Fig. 7.10: The main four groupings that can be formed of soil invertebrates, depending on their life strategies and how closely they are linked with soil. The image contains examples of organisms from each group, showing both the larval and adult stages of each organism where applicable. Alternative terminology that is also used refers to temporary, transient and permanent edafon. The meanings are synonymous with those listed above. (A, D, LW and GP)

7.4 Soil Microarthropod Diversity and the Evolutionary Convergence Phenomena

In evolutionary biology, a convergence phenomenon is defined as being "the independent evolution of similar phenotypes by distant genealogical species". The relationships between evolution and ecology in regarding convergence phenomena remain a relatively unexplored scientific area. Traditionally, convergence phenomena are explained with the adaptation orthodoxy. In other words, the evolution of convergent phenotypes in unrelated species is driven by the tendency to have similar morphological solutions in similar environmental conditions (Fig. 7.11).

Fig. 7.11: Scorpion (**left**) and pseudoscorpion (**right**) show similar chelate structure on the pedipalpus. (CM)

Differences in morphology appears to be the product of co-evolution of organisms within their respective environments, combined with the processes that have linked these animals with the other ecosystem components for more than 600 million years.

Among the various groups that have colonised the soil, microarthropods are organisms that are proving to be more and more important in understanding how the soil of many of Earth's ecosystems functions. There are many extremely old groups of microarthropods in soils, such as collembola and mites, dating from the Devonian period (more than 350 million years ago). In relation to the origin of soil microarthropods, it is possible to form two hypothetical groups:

1. The first group originated in epigeous (above the soil) habitats and only subsequently adapted to soil. Included in this group are: e.g. Coleoptera (beetles), Chilopoda (centipedes), Diplopoda (millipedes) and Diptera (flies).
2. The second group possibly originated directly in the soil. This group contains organisms such as Protura (Fig. 7.12), Diplura (Fig. 7.13), Symphyla (Fig. 7.14), Pauropoda (Fig. 7.15), and Palpigrada (Fig. 7.16) which do not have forms in epigeous, or aquatic habitats (some exceptions are found in caves, where the environmental conditions are very similar to that of soils).

Over the very long period of adjustment to below ground life, the bodies of euedaphic microarthropods have become adapted with characteristics that allow them to survive within the soil habitat. During this process of adaption, impressive levels of convergence have occurred with many of the adaptation characteristics being morphological, and easily explainable and understood. For example, reduction of the visual apparatus, loss of pigmentation or cryptal coloration (camouflage), reduction

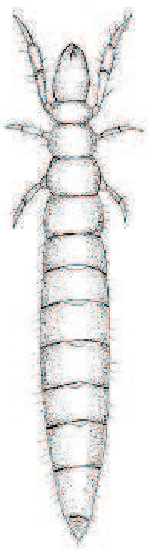


Fig. 7.12: Protura. (CM)

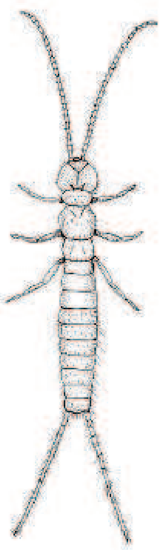


Fig. 7.13: Diplura. (CM)

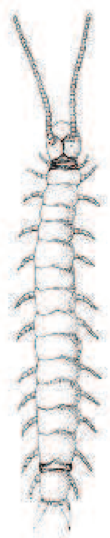


Fig. 7.14: Symphyla. (CM)

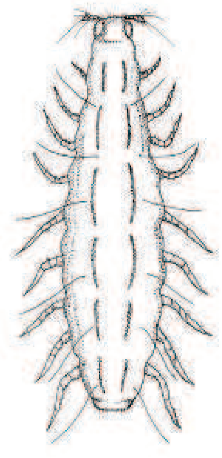


Fig. 7.15: Pauropoda. (CM)

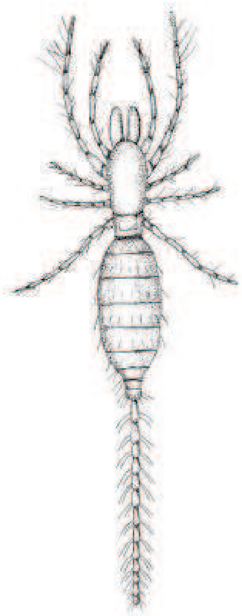


Fig. 7.16: Palpigrada. (CM)

of appendages and the acquiring of special structures essential for life below ground. Some of these characteristics, such as the reduction of body length (miniaturisation), loss of the appendages (legs, antenna, etc.) and the loss of eye functionality, which in some cases leads to the complete disappearance of eyes, are direct consequences of degenerative processes of structures which are very important in above ground habitats but useless in the soil. Conversely, soil microarthropods have developed characteristics that permit them to live in the particular conditions present in the soil, such as chemico- and hydroreceptors, often distributed not only in the oral region, as they are for most above ground organisms, but also on other structures of the body.

The confinement of these groups to soils, i.e. the groups' incapacity to leave them, is due to the relative stability of these habitats. In fact, diverse factors such as water, temperature and organic matter vary only slightly over the short- and medium-term, as compared to large variations in above ground environments. In addition, there is obviously no light in soil at depths greater than a few millimetres. As a result of all of these factors combined, euedaphic microarthropods are sensitive and unable to survive abrupt variations in environmental factors. They are particularly sensitive to soil degradation and to the disturbances caused, for example, by agricultural cultivation and trampling.

Collembola (springtails) represent one of the most important groups of soil microarthropods, both because of the number of species, and the number of individuals, generally present in soils. They have some characteristics that make this taxonomic group very interesting and useful for studying soil evolution convergence phenomena (see box below; Fig. 7.17). Furthermore, they are very useful as indicators of soil quality as their biodiversity and density that are influenced by numerous soil factors (in particular organic matter and water content but also other factors such as contamination.

How old are mites?:

Much older than the dinosaurs! Fossils of soil mites have been discovered in rocks that are around 400 million years old. During this period the first fish evolved legs and started to walk on land, and the first seed-bearing plants appeared. The first dinosaurs did not appear for another 100 million years.

Fig. 7.17: Different adaptation levels to soil in five species of Collembola

Lepidocyrtus paradoxus:
Epigeous surface dwelling form. Has well-developed appendages, well-developed setae (hair like structures) and protective cover of pigmented scales as well as well-developed visual apparatus. (CM)

Isotoma violacea:
Hemi-edaphic form. Still has developed visual apparatus and a cuticle with pigmentation but not elongated appendages. (CM)

Ceratophysella denticulata:
Hemi-edaphic form. Reduced number of ommatidia (light sensing units in the eyes), scarcely developed appendages, short furcula (the 'spring' organ in springtails), pigmentation present. (CM)

Mesaphorura krausbaueri:
Clearly eu-edaphic form, no pigmentation, no furcula, short appendages, presence of typical structures such as pseudo-occuli, apomorphic sensory structures. (CM)

Folsomia candida:
Eu-edaphic form with no pigmentation, furcula present, but reduced. (CM)

8.1 How do we measure Soil Microbial Biodiversity?

Organisms that live in soil include not just the true plants everyone is familiar with, but also animals that use soil as a habitat and breeding ground (e.g. badgers, moles, various small herbivores) as well as lower plants (mosses), invertebrates such as beetles, spiders, mites and worms and also the 'hidden' microscopic life forms of the fungi, bacteria and protozoa. There is therefore a community of organisms in the soils which varies from soil to soil.

The diversity of microorganisms in soil is vast, so how do we measure it? Current estimates suggests that globally soil consists of ten times more microbial cells than the oceans, with more microbial cells being found in just one handful of grassland soil than there are humans on planet Earth. In addition to reservoirs of industrial products worth €100s billions, microbes play vital role in biogeochemical cycling and sustainability (see Section 4.1). The collective organisms that constitute soil biodiversity live together, interacting in a variety of ways including eating each other, engaging in biochemical warfare, sharing nutrients and facilitating each others lives by modifying food and energy sources and living space to the advantage of others. Understanding microbial community structure, diversity and their ecological function is essential to understand life strategies, evolution, the functioning of soil and so the sustainability of life on Earth. Measuring soil biodiversity and the composition of this community is very challenging and is now an important scientific frontier.

There are several ways of looking at soil biodiversity. For higher plants, animals and many invertebrates, taxonomic identification is relatively more complete and straightforward and what can be seen by eye can be described and counted. The conventional taxonomic approach is, however, far more limited for identifying microorganisms in soil and consequently different approaches have been used to describe and quantify diversity in functional and genetic terms.

For many more of the organisms, we have a very incomplete understanding and only estimates of what diversity there might be. This pertains mostly to the microscopic life forms. While we can see them under the microscope and some are very ornate and can be distinguished, identified, described and counted (Fig. 8.1), many more such as bacteria are morphologically difficult to discriminate this way.

Some microbes can be grown in the laboratory and isolated on special growth media and use colony descriptors to identify them (Fig. 8.2). However, using direct observation by microscope and new DNA fingerprinting techniques it is now known that the organisms that are capable of being grown in artificial lab conditions represent a tiny percentage of the total number. This is known because it is possible to extract DNA directly from soil and estimate the number of different species by analysing the complexity of this whole community DNA.

A variety of biochemical techniques also exist which extract compounds from the cells to characterise different groups and classify them. Soil can be extracted to recover biochemical components of organisms that can be measured by conventional chemical analysis techniques to obtain biochemical markers or signatures. The use of signature lipids which vary in cell walls (Fig. 8.3) of different microbial groups is one common method and allows an investigator to determine quantitatively the relative proportions of fungi, bacteria and different phyla within the bacteria domain while avoiding the problems of only detecting a tiny fraction of the community as with culture based techniques.

It is also possible to use functional attributes of the community for example how chemical substrates can be transformed by enzymes or can be metabolised and broken down into carbon dioxide to look for differences in community functioning. Often metabolic attributes are measured using colourimetric indicators for the different reactions (Fig. 8.4). The organisms in soils all produce a variety of enzymes, some held intracellularly and some exuded as extra-cellular enzymes. Such enzymes are one example of the many proteins produced by soil biodiversity, and it is possible to analyse these by extracting the protein directly, and using a technique called 'gel electrophoresis' to separate the proteins and detect them. The proteins can be further analysed to determine their structure and composition and so their function can be identified. This proteomic approach is also starting to be applied to soils even though soils present significant challenges due to the presence of many substances which inhibit or interfere with their extraction.

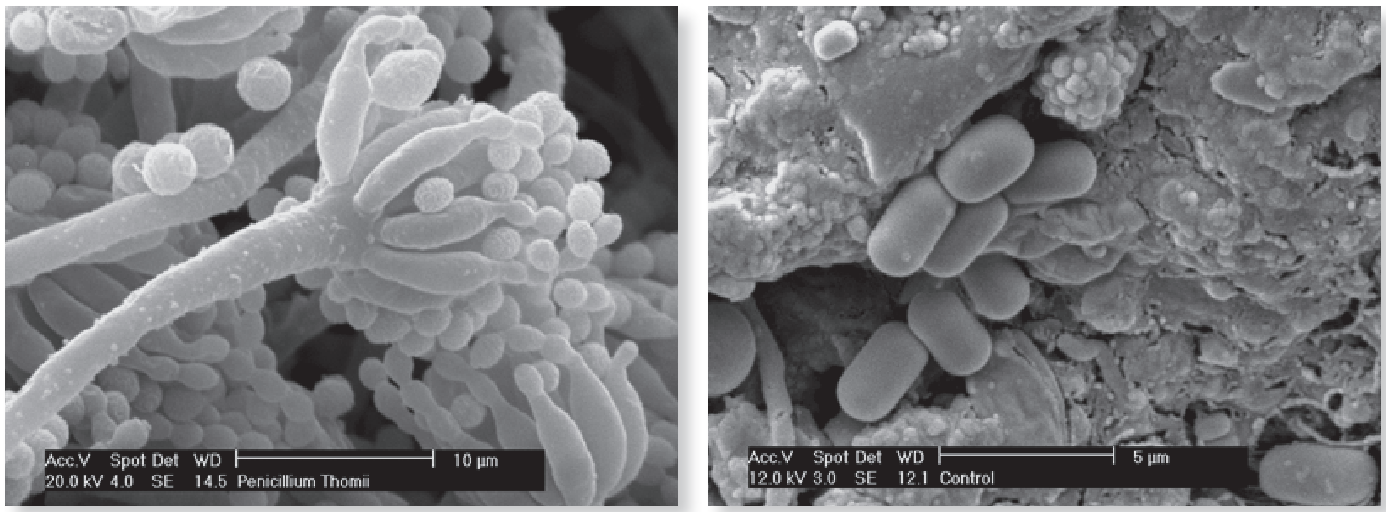


Fig. 8.1: In some instances morphological differences exist between species as shown above with fungal spore bearing structures on the left, but in many cases different bacterial species can look identical morphologically as shown on the right. (PDI)

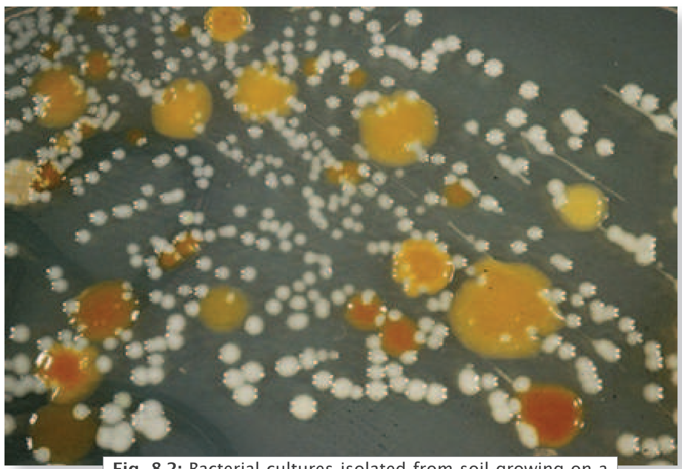


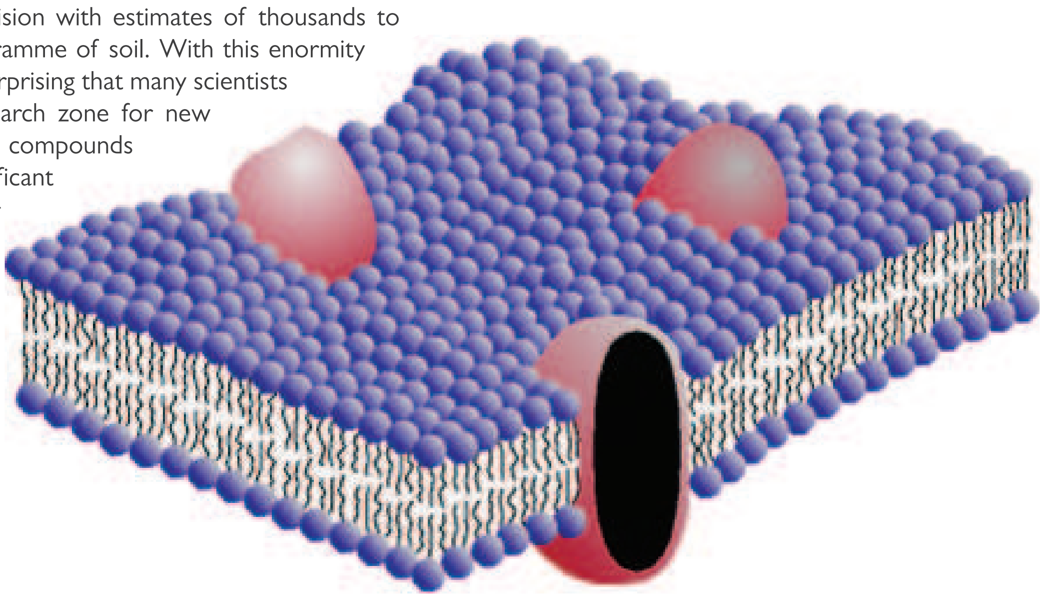
Fig. 8.2: Bacterial cultures isolated from soil growing on a synthetic growth medium. Each dot represents a colony of microorganisms that started as just one cell. (PDI)

Of all of the techniques which analyse directly extracted material from soils, those which fingerprint DNA or RNA have made the largest difference to how we perceive and measure soil biodiversity. The last 20 years has seen an explosion in molecular methods of describing biodiversity and the ability to 'barcode' or fingerprint DNA using new molecular sequencing equipment means there is unprecedented data coming from such studies.

DNA:

Deoxyribonucleic acid, or DNA as it is more popularly known, is a very long molecule that contains the genetic instructions used in the development and functioning of all known living organisms and is often compared to a set of blueprints.

Estimates of the extant diversity of microorganisms in soil are under continued revision with estimates of thousands to millions of species per gramme of soil. With this enormity of biodiversity it is not surprising that many scientists see soil as a primary search zone for new life, enzymes, bioactive compounds and genes, and a significant opportunity to mak new discoveries exists we can fully describe ar understand the Earth soil biodiversity.



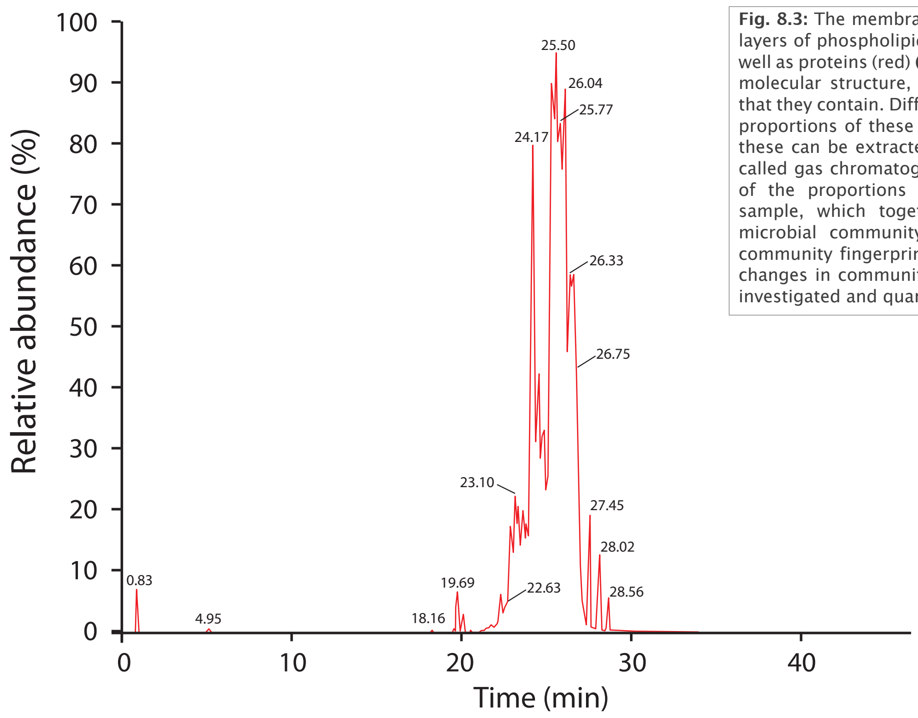
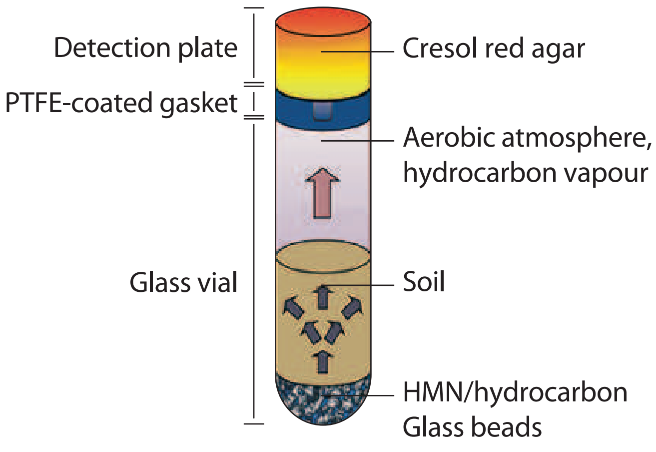


Fig. 8.3: The membranes of all living cells are made up of 2 layers of phospholipids known as the lipid bi-layer (blue) as well as proteins (red) **(above)**. The phospholipids vary in their molecular structure, such as the number of carbon atoms that they contain. Different microorganisms contain different proportions of these lipids in their cellular membranes and these can be extracted and quantified through a technique called gas chromatography **(left)**. This allows quantification of the proportions of each phospholipids within a soil sample, which together produces a 'fingerprint' of the microbial community. Through comparisons of different community fingerprints the effects of different variables or changes in community structure over space or time can be investigated and quantified. (PDI)



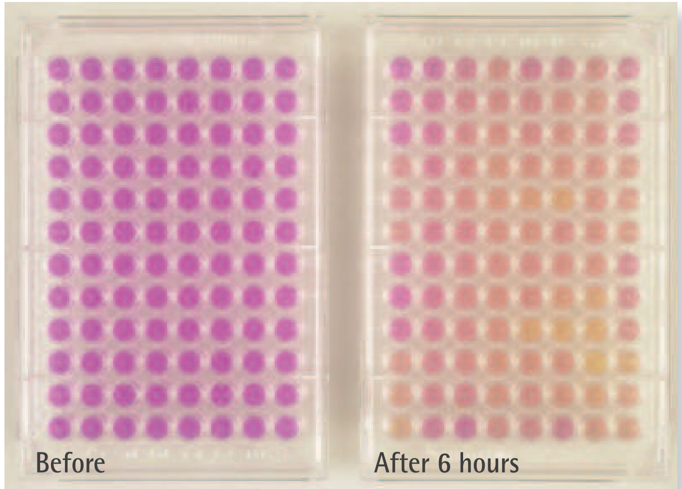


Fig. 8.4: Biochemical tests can be performed on both soil extracts and whole-soil and the rates of reaction measured to give a metabolic profile. For example, in one form of biochemical test, homogenised soil is added to plates containing a range of substrates (**top right**). After incubation for a period of time the CO_2 respired as the microbial community utilises the different substrates reacts with a chemical in the gel leading to a change in colour (**right**). By analysing the amount of colour change it is possible to calculate the amount of CO_2 respired by the community in response to different substrates and so differences in the metabolic abilities of microbial communities from different areas or exposed to different stressors can be quantified. (PDI)

Fig. 8.5: DNA extracted from soil, cleaned and stained with a fluorescent dye. This small amount of DNA contains the sequences of tens of thousands of species. (PDI)

Soil is first extracted using surfactants, buffers and/or solvents and this extract is separated and cleaned and the DNA precipitated (Fig. 8.5). The DNA can then be subjected to various treatments and analysis methods. One common approach is to amplify the DNA selectively using the polymerase chain reaction (PCR) probes, which are synthetic and specific short DNA sequences that match particular taxonomic or functional genes. In the amplification process the polymerase enzymes along with the probes and soil DNA that they match, are put through several temperature cycles which cause the DNA strands to replicate and enrich these DNA sequences to make them more easily detected and analysed. These amplified DNA products can be analysed for their size and composition on a DNA sequencer or by electrophoresis to separate them out on a gel to produce a fingerprint (Fig. 8.6). Individual bands on the gel can be cut out and sequenced to determine their DNA code and identity.

Other methods can avoid the PCR step and so avoid the selective bias involved. As above some molecular probes can be linked to fluorescent chemicals and fluorescence used to detect which sequences match fragments in the soil DNA and so indicate what genes are present. These probes can be 'spotted' in very small spots on large arrays onto glass slides or microchips to allow tens of thousands of tests to be done on a single sample. This approach is very useful to determine which genes are actively switched on and is used commonly in medical studies of disease conditions. Arrays now exist for determining community composition ('phylochips') and a functional array has been developed for soil called the 'GeoChip' which can measure which functional genes are switched on most in a soil sample. These techniques are providing much greater insights into the functional diversity of soil communities.

Sequence analysis on a DNA sequencer determines the DNA code in terms of base pairs (bp) e.g. A-T-G-C and their order in sequence and this can be used to search databases of known sequences to identify genes and organisms. A new generation of sequencers that can sequence much more of the total DNA very quickly (massive parallel sequencers) are now being used to get greater and greater detail of the large amounts of DNA found in whole genomes of organisms and in complex mixed species DNA from environmental samples. It is now feasible to process hundreds of samples at a reasonable cost and to obtain thousands of sequences from each sample to obtain a comprehensive picture of even the most diverse communities.

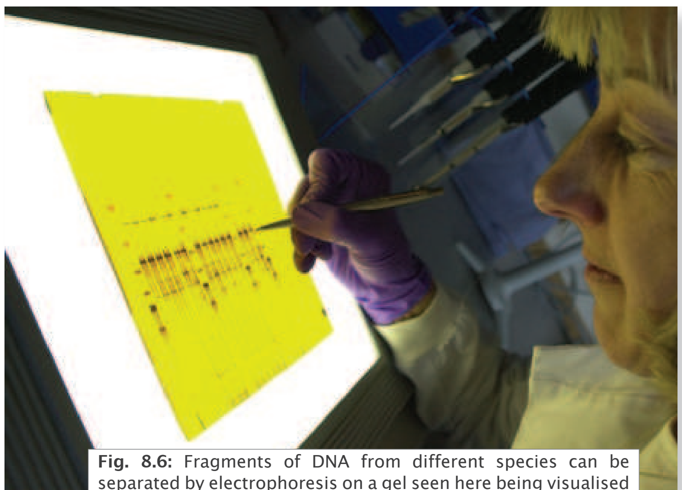


Fig. 8.6: Fragments of DNA from different species can be separated by electrophoresis on a gel seen here being visualised under UV light to show the DNA fluorescencing. (PDI)

The main drawback of these approaches is that the length of the obtained sequences is currently limited to between 200- 500 bp, which can restrict taxonomic resolution but new analysers may read up to 1000 bp so this is likely to revolutionise our knowledge of species diversity and discovery of functional genes in soil.

While it is now becoming conceivable that we can characterise the whole community genome (metagenome) of a soil it will take great efforts to handle the data being generated and understand all the ecological implications and differences between major soil types. There are major challenges for characterising soil microbial community genomes in the way it has been done for the Human genome and Sargasso sea metagenomic projects because of the soil's mega-diversity. However, the scientific community are now starting to tackle this with the formation of the 'TerraGenome' project which is setting out to describe the complete genome of the soil from the long term experimental site at Park Grass in England.

While it is known that there are clear differences in soil microbial communities between soils with different soil properties, vegetation and management, a systematic understanding of variation at field, region or continental scales does not yet exist. To do this many thousands of samples will need to be analysed. Some of the new molecular biology techniques are well suited to this task because they are capable of high throughput at intermediate levels of resolution.

Some of the new techniques that measure the microbial community composition are now being used increasingly in systematic soil surveys in EU member states so that we may also soon have new baseline data to understand how microbial communities vary in the landscape and how soil biodiversity is affected by different soil properties. In addition because DNA is relatively stable there are now also DNA archives being established to aid not just current studies but future studies that might want to look back from the future with even more sophisticated molecular techniques.

Microbes:

A microorganism (from the Greek *mikrós*, meaning small and *organismós* meaning organism) or microbe is an organism that is too small to be seen by the naked human eye and can only be viewed by using a microscope. Microorganisms are very diverse and include bacteria, fungi, archaea, and protists; microscopic plants (green algae) and animals such as protozoa.

Some microorganisms are a vital part of the nitrogen cycle as they can fix nitrogen in soil through nodules in the roots of legumes that contain the bacteria of the genera *Rhizobium, Mesorhizobium, Sinorhizobium, Bradyrhizobium*, and *Azorhizobium*.

Methods to measure soil biodiversity

- Direct observation and counting
  - microscopy
- Functional tests
  - Enzyme analysis
  - C source utilisation profiles
  - Protein analysis
  - Functional gene arrays
- Taxonomic tests
  - Phospholipid fatty acid analysis (PLFA)
  - Nucleic acid finger printing techniques
  - Cloning
  - Gene arrays
  - Massively parallel sequence analysis

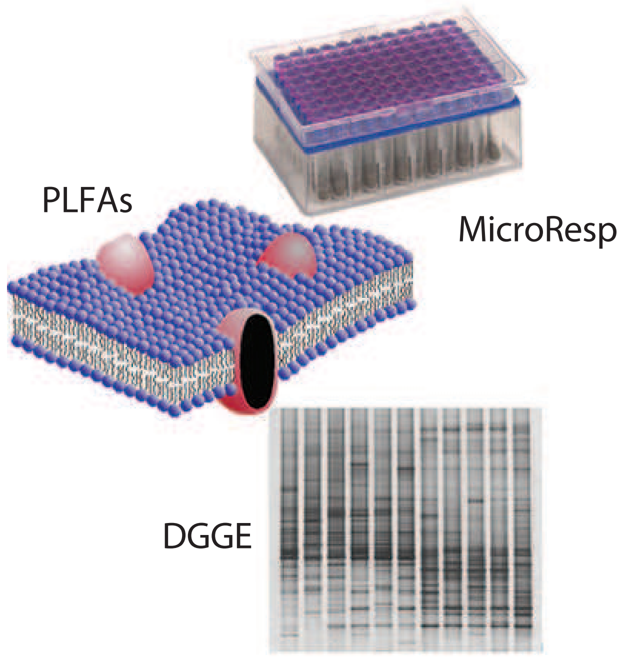


Fig. 8.7: A summary of some of the various methods which can be used to quantify differences between microbial communities, as well as identifying species and functional genes in some instances. (PDI)

8.2 Methods of studying Soil Fauna

Soil organism communities are very diverse, often consisting of thousands of species at one site. Most of them are microorganisms (See Section 8.1), while only very few vertebrates live permanently in the soil. In Europe, the mole is the best known example, but in other regions of the world, as well as mole-like mammals, some amphibian and reptile species also spend the largest part of their life-cycle in the soil.

Existing at somewhere between the levels of population density and diversity of soil microorganisms and soil vertebrates are soil invertebrates such as earthworms and collembola. These are sampled and identified using very different techniques to those previously described for microorganisms.

Below are presented the most important and widely used methods for collecting soil invertebrates. Before sample collection, it is important to consider for which purpose such organisms are sampled as this will influence the methodology used. If aiming at achieving an overview of the species living in the soil, qualitative sampling is appropriate (i.e. individual specimens are collected by whatever method is appropriate. For example, soil and litter can be searched by hand in order to catch larger animals such as earthworms or woodlice using a forceps).

Alternatively, soil invertebrates are often collected for ecological reasons and for monitoring purpose, meaning that in both cases their number, biomass and/or community composition are investigated. In these cases, methods are needed which are able to relate to, for instance, the number of animals caught within a given area (most often a square metre) or weight (often 100 g soil dry weight). In addition, these methods need to be standardised in order to be able to compare the results of one investigation with others conducted in other places or at the same place, but at different times. In addition, as biological information concerning a soil at a given site may be used for site-specific regulations (or possibly to guide remediation of that site), any monitoring method must be standardised in order to be legally valid. Therefore, the methods intended to be applied for these purposes should be based on ecological methods which have been well-established for decades. Following the need for methods which are suitable for such ecological questions, the International Organisation for Standardisation (ISO) is currently harmonising standard guidelines known as "Soil quality – Sampling of soil invertebrates".

As it is impossible to standardise methods of all soil invertebrate groups it was decided to prepare these guidelines only for those groups considered to be the most important: earthworms, enchytraeids, nematodes, microarthropods (e.g. springtails and mites) and macroarthropods (e.g. woodlice, or millipedes). All guidelines cover the technical details of the most appropriate methods but also contain modifications of the methods required in special cases (e.g. when working in different climatic regions such as the tropics).

It is proposed to use these methods in all studies where data collected on soil organism communities will be used for legal purposes, e.g. monitoring or soil quality assessment. The five methods are described briefly below.

Sampling of earthworms

Earthworms are the considered to be the most important group of soil organisms in many, mainly temperate, regions of the world. Additionally they are the only group for which an ecotoxicological field testing method exists.

Standard approach: Combination of two methods

1. Hand-sorting; 2. Formalin extraction

Characterisation of hand-sorting: Size of sampling plot: 50 x 50 cm (= 0.25 m^2); Depth of sampling plot: 10 – 20 cm; Number of samples depends on soil properties and worm abundance (Fig. 8.8).

Advantages: no use of toxic chemicals, no need of water.

Disadvantages: strong disturbance of soil, labour and time intensive.

Work procedure: Removal of soil by means of a spade or shovel followed by spreading out of soil on a piece of plastic (in the field or a room) and cautiously, searching for the earthworms (by hand or forceps).

Characterisation of Formalin extraction: Use of the same sampling plot as for hand-sorting (= 0.25 m^2); Concentration: 0.5% = diluting 25 mL formalin (37%) in 5 L water.

The formalin extraction works particularly well with anecic earthworms which have burrows connected to the soil surface. When water in the case of rain, or formalin in the case of this extraction methodology enters the burrow, the earthworm detects it through its skin. In the case of water the earthworm moves to the surface as it would drown if its burrow became water logged. In the case of formalin, the earthworm tries to move away and it does this by leaving its burrow by going to the surface, when it arrives at the surface it can then be collected by hand

Work procedure: Application of the formalin solution to the sampling plot. This is repeated until 20 litres are added (the amount can be adapted depending on soil properties) followed by observation of the plot and collection of all worms appearing. End of sampling 30 min after application of the last watering (Fig. 8.8).

Advantages: high efficiency especially for anecic species.

Disadvantages: use of chemicals and the need for a large amount of water.

Handling of the worms after collection: Immediate fixation in 70% ethanol e.g. in 250/500 ml plastic pots, for at least half an hour but not longer than 24 hours. Worms can then be kept in 4% Formalin for at least 4 days (better: 1 or 2 weeks). Afterwards worms can be stored for an unlimited time in 70% Ethanol.

Tropical Soil Biology and Fertility (TSBF)-Method (modification for tropical soils): Hand-sorting of soil monoliths (25 x 25 x 15 cm) for soil macrofauna (body length > 2 mm) at the end of the rainy season. The litter layer is treated separately. All worms (> 10 cm) found in a 20 cm trench are included. The monolith is divided into three layers (each 10 cm high) and each is sprayed with formalin (0.2%) repeatedly at 10 minutes intervals. Worms are preserved in 4% Formaldehyde.

Advantages: high efficiency.

Disadvantages: high number of replicates (time consuming) and efficiency depending on clay content.

Electrical extraction: Eight electrodes (52 cm diameter) are placed in the soil. They generate an electrical field by which the worms are driven out of the soil (Fig. 8.8).

Advantages: no use of toxic chemicals, no need of water.

Disadvantages: expensive equipment, variable results, difficult to use in stony soils, efficiency dependent on soil moisture.

Fig. 8.8: Different techniques for extracting soil fauna from the soil. The techniques shown are: Formalin extraction and hand sorting of earthworms (photos to the **left**); electrical method for earthworm sampling (**above middle**), and a soil corer for extracting mesofauna groups (**right**). (All photos – JR)

Sampling of enchytraeids

Enchytraeids have often been used in ecological and ecotoxicological field studies for different purposes such as indicators for acidification or due to their role in nutrient cycling in the soil. These small worms are sampled from the soil by using a split corer (diameter usually about 5 cm; Fig. 8.8). After sampling, the soil samples containing the enchytraeids are transported to the laboratory. There, they are extracted from soil by means of a wet extraction method (Fig. 8.9); an approach that has been in use for many years. This methodology relies on the fact that enchytraeids preferentially move away from hot and dry environments towards cooler and more moist environments. In the case of the wet extraction soil cores are submerged in water and exposed to light and heat from above for several hours. The enchytraeids usually move away from a light and heat source, such as a light bulb, down through the soil which is usually suspended above a beaker of water. When they pass out of the bottom of the soil they are collected in the water filled container.

Afterwards, they are identified alive and, if required, preserved in a way that they can be stored in a collection indefinitely (e.g. for taxonomical purposes). Finally, abundance and biomass values can be extrapolated from the area of the soil corer or, more rarely, volume parameters.

Fig. 8.9: Wet extraction of enchytraeids. (JR)

Sampling of microarthropods

Out of the many soil microarthropod groups, Collembola and Acarina are the ones most often studied in soil ecology. Due to their high abundance and diversity they are an important part of the soil system, playing influential roles in key biological processes (e.g. acting as catalysts in organic matter decomposition). These features make them suitable organisms to be used as bioindicators of changes in soil quality, especially due to land use practices and pollution. Again, long-used ecological methods have been taken as a starting point for a standard monitoring method.

Fig. 8.10: Collection of microarthropods using the Berlese-Tulgren funnel method. (CG)

These microarthropods are collected using a split corer (Fig. 8.8) where each soil sample can be divided into different sections and studied separately if necessary. After collection, animals are extracted from the soil samples using behavioural methods (e.g. using a Tulgren funnel or a MacFadyen high gradient extractor; Fig. 8.10). These methods takes advantage of the preference of these animals for moist environments; in the MacFadyen extractor soils samples are placed under a temperature gradient and the animals tend to move down and are caught in the receptor vessels (Fig. 8.10).

Sampling of nematodes

Nematodes are an important and major part of the soil fauna. They occur in every place which has sufficient water and organic material. The species diversity and functional variety are impressive.

Nematodes are especially well known as parasites of animals and plants, but the majority of nematode species participate in decomposition processes by bacterial and fungal feeding.

Nematology (being the study of nematodes) has developed strongly from the viewpoint of agriculture, advisory sampling, and phytosanitary regulations, because some terrestrial nematode species cause a lot of damage in crops. With respect to methods, there are several "schools" in different parts of the world with their own history, and practical advantages and disadvantages. The more recently described methods are often developed with specific interest to certain plant-parasitic species.

Nematodes are now used for ecological soil research and monitoring in several countries around the world. Since it is impossible to give a full overview here one common method is described in the following:

Usually, several samples (mixed to create a few composite samples) are taken with a soil corer (diameter 2.5 cm; depth 10 cm). Nematodes are extracted from soil by a sieving and decanting method devised by Cobb in 1918 (Cobb 1918; Fig. 8.11). All nematodes are extracted and fixed in formol (10% formealdehyde in water), followed by an identification at least to the family level (trophic groups) and further data assessment (e.g. Maturity Index).

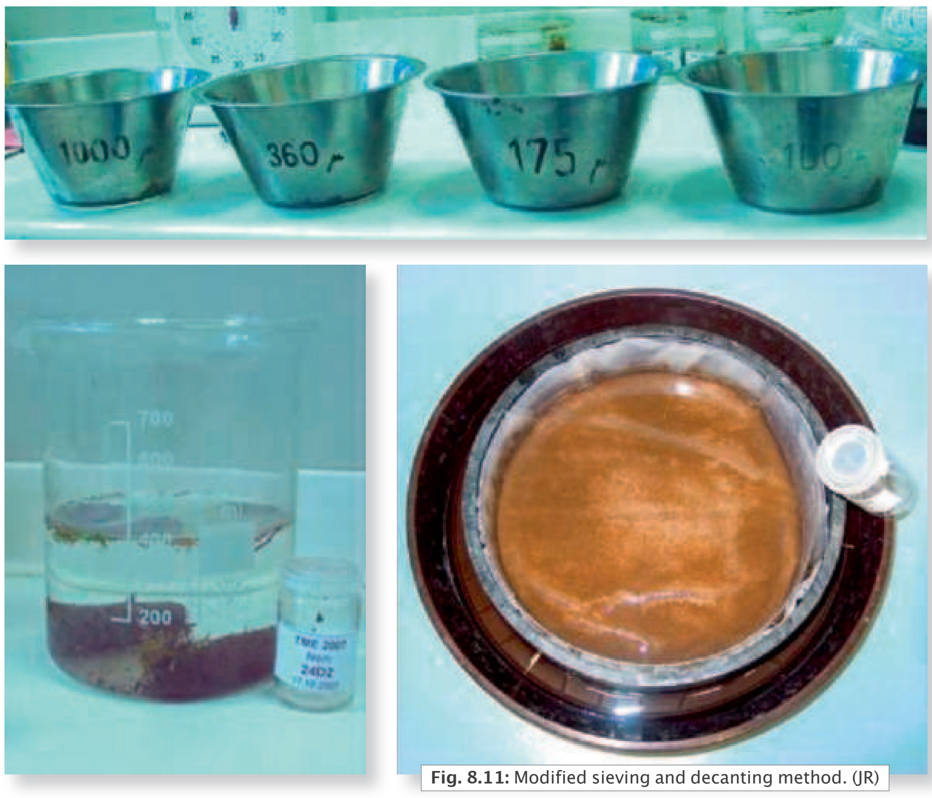


Fig. 8.11: Modified sieving and decanting method. (JR)

How Do You Catch Giant Earthworms?

The standard method on earthworm sampling is suitable almost globally, but in some cases it simply does not work. For example, what do you do when the worms to be caught are two to three times larger than the hole what is used for hand-sorting? While in temperate regions earthworms do usually not grow larger than 50 cm in length, in tropical regions of South America and Africa and also Australia, species occur which are can be more than 1.5 m long (See Section 3.4). Obviously, in these circumstances, the standard method does not work – but two options are left: Digging big holes, which is very labour-consuming and rarely efficient since it is difficult to know where these worms can be found. Or alternatively, a technique successfully used in the tropical Amazonian rainforest (Brazil), is performed as follows: Firstly, an area of at least 2 x 2 m is cleared of litter particles. Secondly, a formalin solution is sprayed on the surface of the mineral soil (preferably, several times) and within the next 30 minutes, these giant worms come to the surface. Finally, they are caught by hand. This must be done carefully since several species are able to shed their tails in case of danger. In France – worms can be up to 1 metre, in Chile – worms can be up to 3 metres long!

8.3 Approaches to Soil Biodiversity Monitoring

Soil monitoring

Soils are one of the fundamental systems for agricultural food production and the living environment, and therefore their functions and quality must be maintained for the survival of mankind. Thus it is essential to observe the functioning of soils and to detect any significant change in soil quality for a general surveillance of our environment. Furthermore, based on surveillance information undesired trends can be reversed through soil conservation and soil protection measures and through sustainable land management. Soil monitoring as part of a general surveillance system can be defined as the systematic determination of soil attributes so as to record their state and their temporal changes.

National monitoring actions are generally made by using a network of sites/areas where changes in soil characteristics can be documented through periodic sampling and analysis of a set of soil parameters. To be recognised as a soil monitoring site, a site has to fulfil the following minimum conditions:

i) the georeference of the site is known with an accuracy fitted to the spatial scale of sampling, and

ii) one or more sampling and measuring campaigns have been conducted or planned.

The raw data should be recorded in an accepted format, transparently stored in database systems and accessible for any sort of analysis or assessment, both for scientific objectives as well as for policy or land management objectives.

Fig. 8.12: Map of earthworm abundance derived from a monitoring network covering the whole of Brittany, France. Such networks are of critical importance in order to monitor changes in biodiversity over time in relation to variations in drivers such as climate and land use practices. (GP) From Cluzeau *et. al.* (2009).

Why monitor soil biodiversity?

In an international context, the need for soil biodiversity monitoring was identified in a recommendation made by the Food and Agriculture Organisation (FAO) to the Conference of Parties for the Convention on Biological Diversity which resulted in the implementation of an International Initiative for the Conservation and Sustainable Use of Soil Biodiversity (COP 6 Decision VI/5). In this agreement, monitoring soil biodiversity is encouraged as a method of assessing soil quality or soil health, in order to better inform management and policies related to the use of soil and land. It is also essential for the early detection of a possible decline and to enable the adoption of measures to reverse such decline.

The adoption of soil biodiversity monitoring programmes is motivated by both the increasing pressures on soil biodiversity and the limited current knowledge. Main drivers impacting soil biodiversity derive from overexploitation of soil, changes of climatic and hydrological regime, changes in land-use, competition from invasive species. Furthermore any degradation of soil as soil erosion or compaction, soil contamination and decrease of soil organic matter can lead to loss of biodiversity (all of these threats are discussed in more depth in Chapter 5).

How to monitor soil biodiversity

For the sampling and analysis of soil attributes related to soil organisms and soil processes, specific methodologies are available. Some of them are routinely applied in monitoring networks, others are also applied in specific cases, like a farmer's request for a soil analysis or for risk assessment of contaminated sites.

The selection of sites for monitoring programmes can be based on a hierarchical design, or a grid-based scheme (regular, irregular, stratified, etc.). In the hierarchical design, factors that mainly affect soil biodiversity are the first-level categories (i.e. land use/cover, soil type, climate conditions, hydrology, etc.). The monitoring starts with the inventory of soil biodiversity (e.g. estimation of taxonomic or functional diversity) and often with the measurement of the activity related to soil organisms (e.g. enzymatic activities, number of burrows) at the selected sites at a given time (see Fig. 8.13). The initial analysis can be used to address the current state of the soils and to address differences from soil types, land use categories, or differences in the intensity of the land use. Subsequent monitoring cycles can also be used to address trends. When changes in land use are known for a long time, initial monitoring analysis can also be used to perform a surrogate trend analysis. For instance, if intensity of ploughing is increased over decades, and one monitoring cycle clearly depicts a relationship between ploughing intensity and a loss of soil biodiversity, it is reasonable to assume a loss of soil biodiversity over decades. The measurements should be based on standardised, quantitative and repeatable protocols of sampling and estimation of soil biodiversity such as those published by the International Organisation for Standardisation (ISO 23611 series). The use of harmonised methodologies is essential to provide data that are comparable among sites and among time. These methodologies should enable representation of both the complexity and the high temporal and spatial variability that characterise soil biota.

Starting at EU level the monitoring of soil biodiversity

A survey of EU soil monitoring practices was recently conducted and it appears that indicators related to soil biodiversity are measured very rarely (e.g. only 5 of 29 European countries have monitoring sites for earthworms) with the exception of the Netherlands (see Box 2) or some other countries (e.g. France, Germany, Ireland, Portugal) where such measurements are being implemented (see Fig. 8.13).

In principle, when considering soil biodiversity, all soil organisms and the biological functions that they provide are relevant for the soil system. Depending on the specific policy or research questions to be answered, it is however not necessary to monitor them all. For practical reasons (e.g. ease of implementation, budget, standardisation and expertise needed), it was recently proposed to start with a minimum set of the following 3 indicators to act as surrogate measures for soil biodiversity: a) abundance, biomass and species diversity of earthworms – macrofauna; b) abundance and species diversity of Collembola – mesofauna; and c) microbial respiration. Basic biodiversity (species level) as well as ecological functions (or services) of soil organisms are covered by these groups and levels. These key indicators were chosen by applying three stringent criteria: a suitable indicator should (i) have a standardised sampling and/or measuring methodology; (ii) be complementary to other indicators; and (iii) be easy to interpret at both scientific and policy levels. Of course if financial and technical resources are available, this minimum set of indicators should be extended, to include the diversity and abundance of macro-fauna, nematodes and microorganisms (bacteria, fungi and protozoa).

Besides the development of national initiatives to involve people in the survey of the soil as a vital aspect of our living environment (see Box 1), the monitoring of soil biodiversity is urgently needed because soil organisms are responsible for the functioning of our soils and the soil ecosystem services they provide to mankind (see Chapter 4). Consequently we should make a start of sampling and analysis across the EU to produce an atlas of the current state of the soil as a basis for protection of our common heritage and for insurance of our future by developing schemes for sustainable land use and restoration of deteriorated soils.

Fig. 8.13: The sequence of steps needed for one possible technique used for soil monitoring: (a) Marking out area; (b) Extracting worms; (c) Collecting worms; (d) Measuring soil respiration; (e) Extracting collembola and (f) Identifying organisms. (CG/RC/JR)

Box 1. We need you to survey soil biodiversity!

Several science based education programmes were designed to teach the soil ecosystem to children and for involving volunteers to monitor soil organisms. All these programmes encourage having some fun outside while collecting and identifying soil organisms like insects and earthworms.

One of the first initiative is the so called "WormWatch" in Canada which started around 2005. The dedicated website describes the importance of worms as an indicator of soil biodiversity, introduces worm anatomy and ecology, and provides tools and resources to enable to collect, identify and monitor worms. (http://www.icewatch.ca/english/wormwatch/). Gardeners, naturalists, farmers, schoolchildren – everyone can participate in this survey. The collected data is uploaded by participants to create a Canadian database of earthworm species and habitat distribution. More recently similar initiatives took place in Europe.

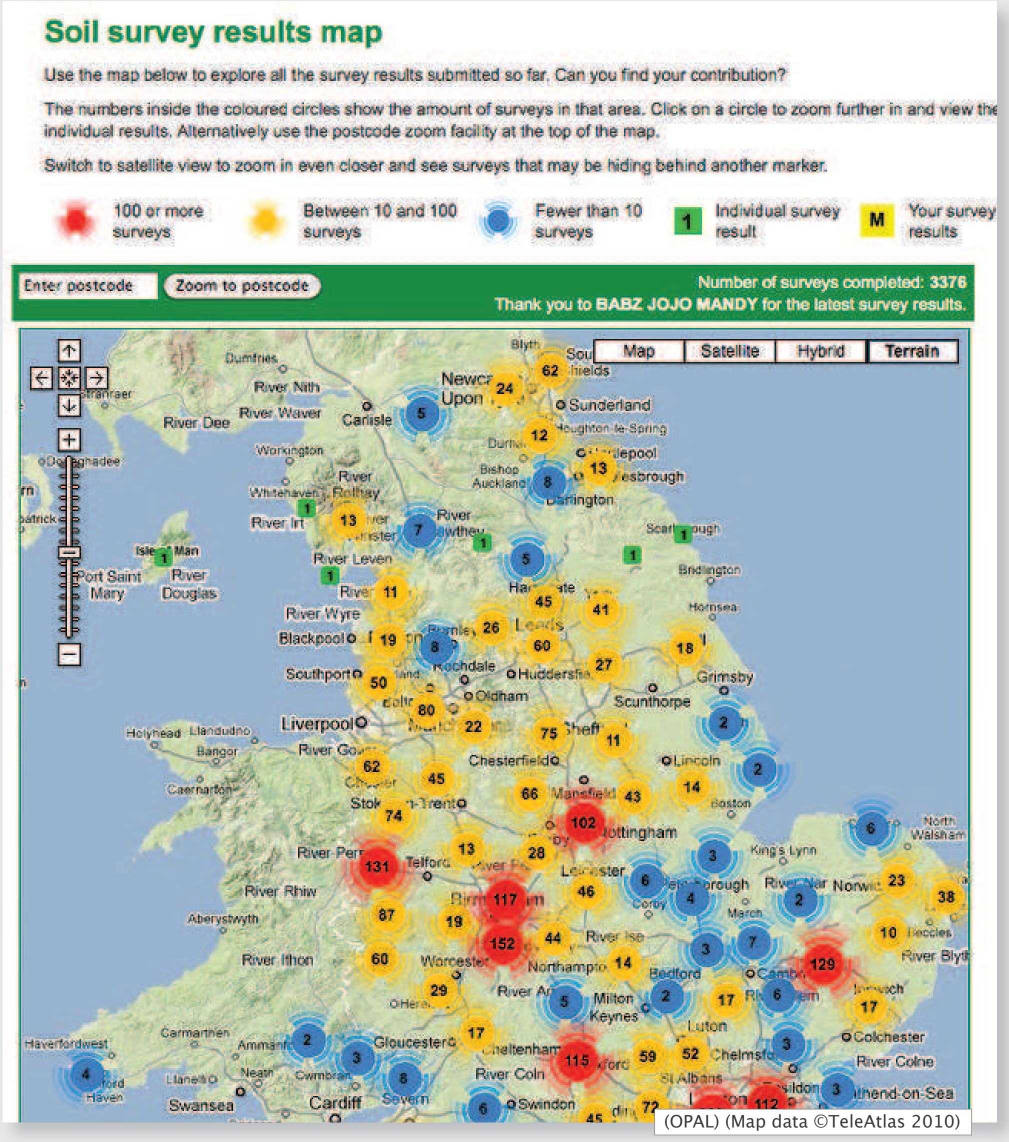
In Portugal, a sampling protocol based on pit falls was designed to collect soil insects and then a web identification key with pictures help children to classify the captured animals. Then they are able to draw the evolutionof soil biodiversity insects according to the land-use and land-cover(http://biotic.bot.uc.pt/index.php?menu=13&language=pt&tabela=geral#44).

In England, the OPAL (Open Air Laboratories) launch the Soil and Earthworm Survey which aims to find out more about soil and earthworms across England. As for the Canadian WormWatch the results are gathered in a database and will help scientists to understand the distribution of each species. Data can also be directly used on the web site (http://www.opalexplorenature.org/?q=soilsurvey) to draw maps and figures (see figure).

In France, a similar initiative, on the survey of snails and slugs in gardens has also been started (http://www.noeconservation.org/index2.php?rub=12&srub=31&ssrub=322&goto=contenu&titre=L%5C%27Op%E9ration+Escargots).

Those initiatives increase our understanding regarding soil biodiversity but the main output is to encourage people to get in touch with nature and soil. It also enables them to explore their local environments and identify the main drivers of species distribution. People become ambassadors of soil biodiversity and help to raise awareness of the living aspects of the soil.

N.B. All internet links were functioning as of April 2010, but future changes may have been made.



(OPAL) (Map data ©TeleAtlas 2010)

Box 2. From monitoring the soil biodiversity to indicating the soil quality

In the Netherlands soil biological measurements are undertaken in a nationwide program based on the Netherlands Soil Monitoring Network (NSMN). About 300 locations (see map, Fig. 8.14) were selected in a random stratified design comprising 35 stringent combinations of land use and soil type. All locations were sampled in a six year cycle.

The role of biodiversity in the maintenance of soil quality is crucial and this was satisfied by designing a biological-indicator system for soil quality (BISQ). Firstly, the most important life support functions of the soil were identified: decomposition of organic matter, nutrient cycling, soil structure formation, plant–soil interactions and ecosystem stability. Subsequently ecological processes linked to these functions were described. Finally the dominant soil organism groups and ecological process parameters were determined and brought together in a practical indicator system to be used in a nationwide soil monitoring program.

BISQ contains the following indicators:

In square soil samples of 20x20x20 cm:

- number, wet weight and community composition of earthworms

In soil columns of 5.8 cm wide and 15 cm tall:

- number and community composition of micro-arthropods (mites and springtails)
- number and community composition of enchytraeids (potworms)

In mixed soil samples (300 cores of 10 cm):

- number and community composition of nematodes (eelworms)
- bacterial and fungal biomass
- thymidine and leucine incorporation rate
- bacterial community metabolic profile
- anaerobic N mineralisation, C and N mineralisation rates

BISQ contains indicators for many, but not all soil organisms and processes. Due to budgetary reasons, samplings and analyses were not replicated, nor repeated during a given year, deepburrowing earthworm species below 20 cm were not sampled, and protozoa were not analyzed. Yet, BISQ includes a relative wide range of soil biological parameters and is running for more than ten consecutive years in a nationwide monitoring program. Besides indicators on soil biological attributes, also many other relevant parameters are monitored in the NSMN, like general soil characteristics (pH, total and heat extractable organic matter, clay content, total nitrogen, several phosphor fractions and metal concentrations), penetration resistance, bulk density, humidity and several soil management characteristics (life stock units, application of manure and fertilizers, tillage, mowing frequency, ground water table, rotation, vegetation, climate conditions, et cetera). Together these data can be used as a starting point to calculate the performance of the ecosystem services of the soil.

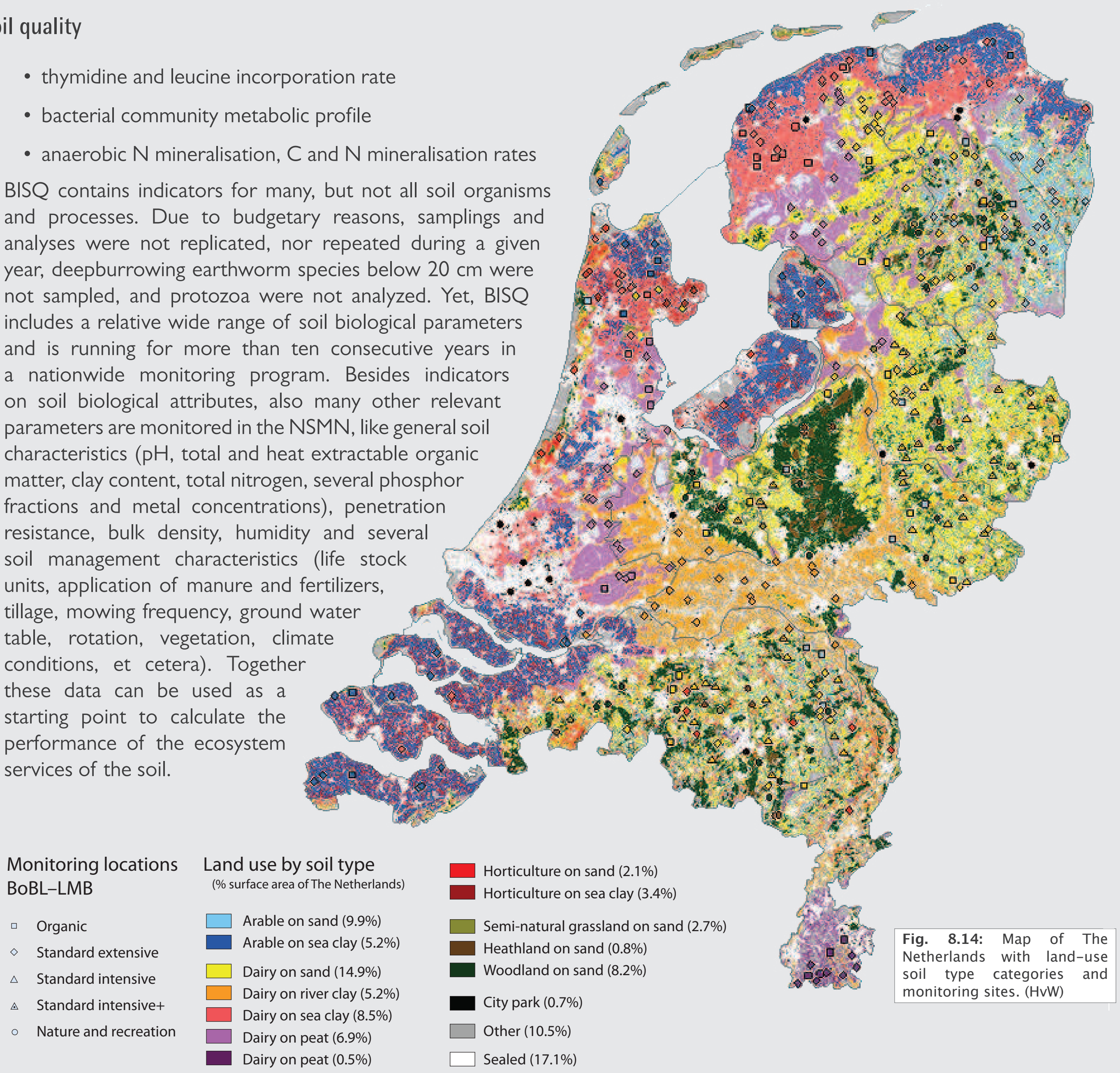


Fig. 8.14: Map of The Netherlands with land-use soil type categories and monitoring sites. (HvW)

Chapter 9 Soil Biodiversity, Policy and Education

9.1 Soil Biodiversity and the Convention on Biological Diversity

Convention on Biological Diversity

The Convention on Biological Diversity (CBD) was inspired by the world community's growing commitment to sustainable development. It arose from the 1992 United Nations Conference on Environment and Development (the Rio "Earth Summit") and came into force in 1993. Currently the CBD has 193 Parties (192 governments plus the European Commission).

The CBD is a legally binding multi-lateral environment agreement with implementation being the responsibility of national governments. The objectives of the CBD are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of benefits arising from the use of genetic resources.

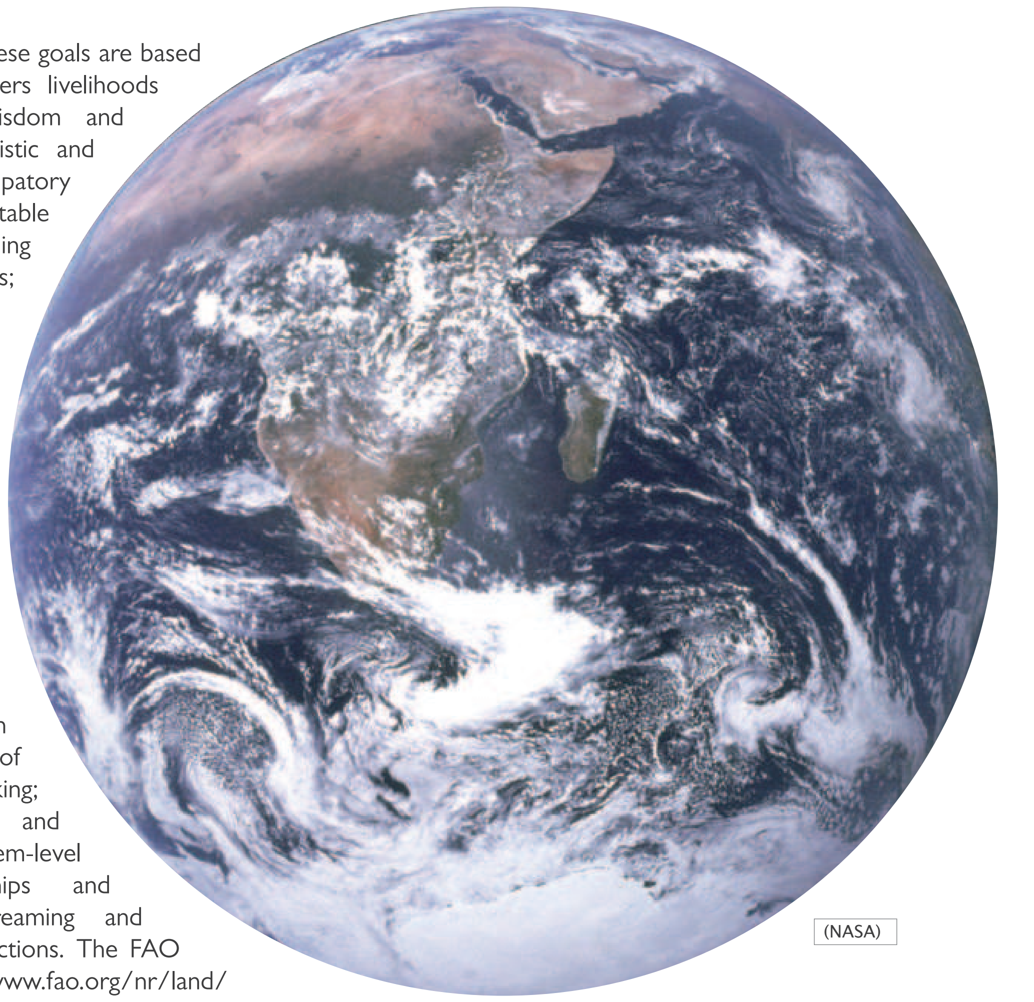
Policy is developed through scientific guidance provided via the Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA). The Articles of the convention itself lay down general principles for the conservation and sustainable use of biodiversity. Decisions adopted during the biannual Conference of the Parties (COP) have added further detail to policies, supplemented in many areas by guidance on how objectives should be achieved. In particular, various programmes of work have been adopted which deal with specific goals, policies and management approaches for specific areas which are biome or sector based, such as agricultural biodiversity, forest biodiversity, biodiversity of dry and sub-humid lands, and issues which are more cross-cutting by nature, such as protected areas, economics, trade and incentives, invasive alien species and sustainable use. The ecosystem approach (a means to integrate all relevant considerations and balance conservation and sustainable use) is the primary framework for implementation. Further details of the CBD, its history, current programmes of work and a full list of relevant decisions, tools and guidance etc. can be found at http://www.cbd.int.

The year 2010 is an important one for the CBD and biodiversity. It has been designated as the International Year for Biodiversity by the United Nations and also represents an opportunity to reflect on our progress towards the achievement of the target to *"achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth"* adopted by the Conference of the Parties to the CBD at its sixth meeting in 2002; subsequently endorsed by the World Summit on Sustainable Development and the United Nations General Assembly. The tenth meeting of the Conference of the Parties to be held in Nagoya, Japan, 18-29 October 2010, will assess this progress and make important commitments to sustain biodiversity for the post 2010 period. This Soil Biodiversity Atlas is an important contribution in these regards by demonstrating and raising awareness of the importance of soil biodiversity.

Soil biodiversity was identified as an area requiring particular attention whilst the programme of work on agricultural biodiversity was being developed between COP-3 (1996) and COP-7 (2004). Special attention was paid to the role of soil and other below ground biodiversity in supporting agricultural production systems, especially in nutrient cycling. Parties were encouraged to conduct case studies on the issue of symbiotic soil microorganisms in agriculture and on the soil biota in general. Many technical agencies and partners contributed to discussions. The Food and Agriculture Organisation of the United Nations (FAO), in collaboration with partners, prepared a detailed summary of the subject for the consideration of SBSTTA prior to COP-7. This eventually led to the adoption at COP-8 (2006) of the International Initiative for the Conservation and Sustainable Use of Soil Biodiversity.

The Soil Biodiversity Initiative is recognised as crosscutting within the programme of work on agricultural biodiversity, through the coordination, and with the technical support, of FAO with appropriate links to other thematic programmes of work of the CBD, particularly those on the biodiversity of dry and sub-humid lands, mountain and forest biological diversity, and with relevant cross-cutting issues, particularly the Global Taxonomy Initiative, and work on technology transfer and cooperation. The Initiative provides an opportunity to apply the ecosystem approach (https://www.cbd.int/ecosystem/) and the Addis Ababa Principles and Guidelines for Sustainable Use (https://www.cbd.int/sustainable/addis.shtml). The Goals of the initiative include the promotion of awareness- raising, knowledge and understanding of the role of soil biodiversity and the mainstreaming of soil biodiversity conservation into land and soil management practices.

Strategic principles to achieve these goals are based on: the improvement of farmers livelihoods and recognition of their wisdom and skills; integrated, adaptive, holistic and flexible local solutions; participatory technology development suitable to local conditions; building partnerships and alliances; promotion of crosssectoral and integrated approaches; and the dissemination and exchange of information and data. Strategic areas of action to achieve implementation include: increasing recognition of the essential services provided by soil biodiversity across all production systems and its relation to land management; research, information management and dissemination; data collection and processing; transfer of technologies and networking; public awareness, education and capacity building; ecosystem-level approaches; and partnerships and cooperation through mainstreaming and cooperative programmes and actions. The FAO Soil Biodiversity Portal (http://www.fao.org/nr/land/sustainable-landmanagement/soil-biodiversity/en/) includes a framework under which soil biodiversity can be assessed, managed and conserved with pointers to research, capacity building and policy and management within the framework of the Soil Biodiversity Initiative Plan of Action.



(NASA)

The soil biodiversity initiative has also been instrumental in bringing the importance of this subject to the attention of inter-governmental processes. For example, the Commission on Genetic Resources for Food and Agriculture has officially recognised the important role of micro-organisms and invertebrates for sustainable agriculture. At its 12th regular session the Commission on Genetic Resources for Food and Agriculture also considered scoping future studies on micro-organisms and invertebrates. In such ways the Soil Biodiversity Initiative is helping to increase awareness and mobilise attention to the importance of soil biodiversity.

The European Commission and many regional and national institutions in Europe provided inputs into the development of the Soil Biodiversity Initiative. European Parties have also provided strong political support throughout the Conference of the Parties. The CBD Soil Biodiversity Initiative and relevant European policies and guidance regarding soil biodiversity have a parallel recent history and are therefore mutually supportive. Beyond Europe, a major contribution of the Soil Biodiversity Initiative is to raise awareness of soil biodiversity and increase attention on the need for its improved management.

Further to the Convention on Biological Diversity, the Conference of the Parties adopted a supplementary agreement in January 2000. This agreement, which is known as the Cartagena Protocol on Biosaftey, seeks to protect biodiversity from potential risks which may be posed by living modified organisms (LMOs – being genetically modified organisms which are still alive). The Protocol established an 'advance informed agreement procedure' to ensure that any country within the Protocol is provided with all of the information necessary to allow the making of fully informed decisions regarding the potential importuning of LMOs into their territory.

On 11th September 2003, the Protocol enetered into force after being ratified by 103 countries. The Protocol itself contains reference to a precautionary approach as well as reaffirming the precautionary language used in the Rio Declaration on Environment and Development, and is aimed at facilitating the exchange of information on LMOs as well as assisting countries in the implementation of the protocol.

The Cartagena Protocol is of particular pertinence to soil biodiversity as many LMOs are crop species which have the potential to impact on soil biodiversity. However, what the extent of any impact of LMOs is likely to be with regards to the soil biota is generally still unclear and this is shown by the relatively low threat weighting given by the experts polled in Section 5.1 (Fig. 5.2)

Fig. 6.1 on the opposite page shows which countries have signed up to the Convention on Biological Diversity, and which countries have also signed up to the Cartagena Protocol.

While the Convention on Biological Diversity and the Cartagena Protocol are international agreements, European States have also been working to multi-laterally conserve biological diversity. Some of the steps that are being taken, and a brief look at future directions are discussed over in the following section.

2010 International Year of Biodiversity

(CBD)

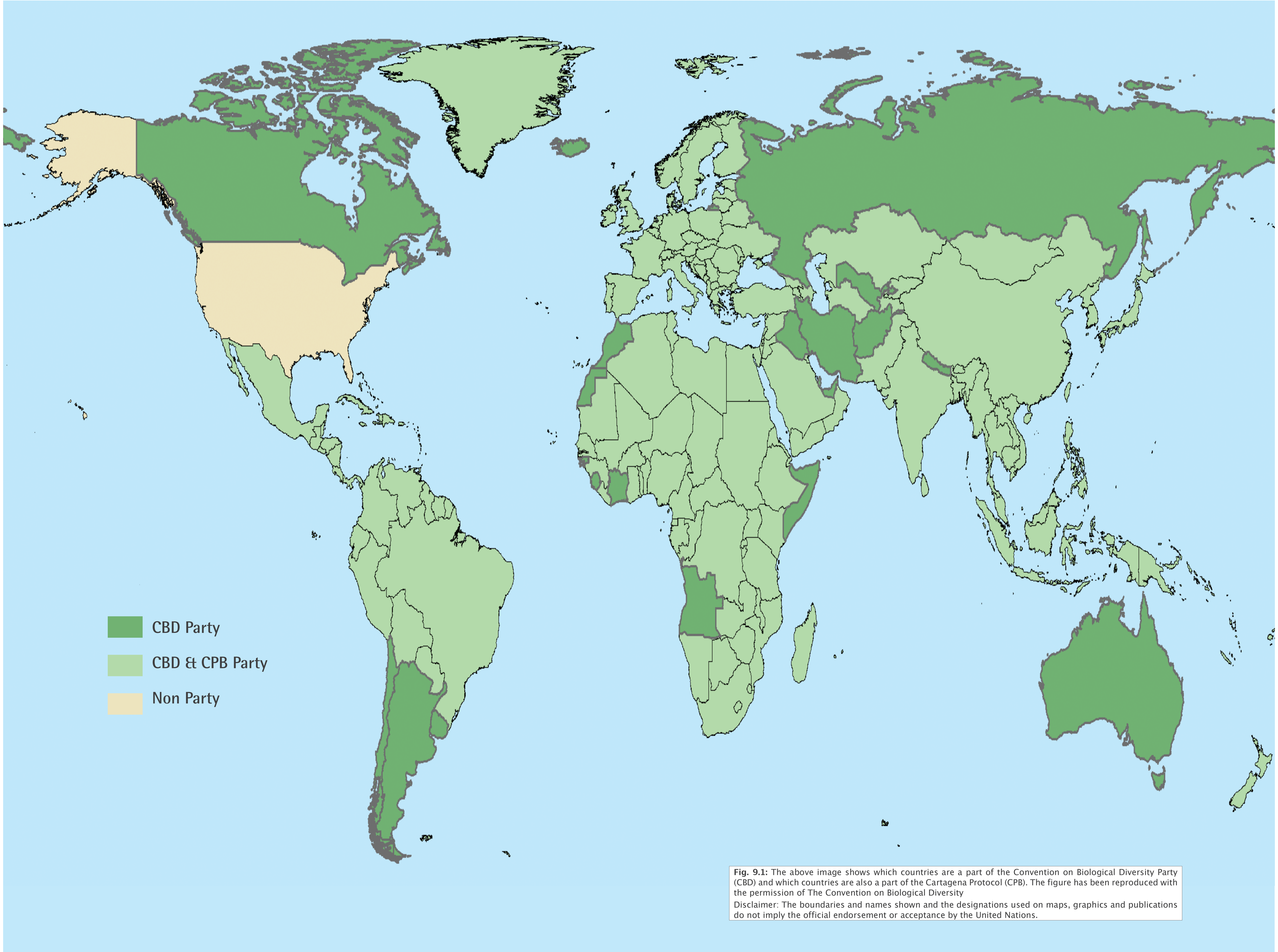


Fig. 9.1: The above image shows which countries are a part of the Convention on Biological Diversity Party (CBD) and which countries are also a part of the Cartagena Protocol (CPB). The figure has been reproduced with the permission of The Convention on Biological Diversity

Disclaimer: The boundaries and names shown and the designations used on maps, graphics and publications do not imply the official endorsement or acceptance by the United Nations.

9.2 Soil Biodiversity and the European Union

Where the CBD functions at a global level, steps are also being taken to protect biodiversity, and soil biodiversity in particular, at a European level.

How much we know about life, about the differences among the different beings, their interactions, their role, their evolution, their risks, in a word their existences, is a difficult debate for scientists and policy makers. However, the aim of protecting life is so important that it is worth being attempted, even if at the expense of some over-simplification and schematisation. That is why nature conservation and biodiversity were among the first, and the most developed European environmental policies, despite the difficulties and complexities which arise due to their attempting to control and regulate life.

Such challenge is even more difficult for soil biodiversity, given its incredible levels of diversity, its complexity and our current relative lack of knowledge. Soils are home to a prodigious diversity of life, which can often be several orders of magnitude greater than that which occurs at a similar unit of land surface above ground or in the canopy of tropical rainforests. Billions of microorganisms are present in just one teaspoon of soil, with one spoonful of grassland soil usually containing more microbes than there are currently humans on planet Earth. One thousand species of invertebrates may live in just one square metre of a European forest and up to 100,000 individuals belonging to some ten thousand species can be found in one square metre of soil. It is also for this reason that the protection of soil biodiversity has lagged behind at international level, including within the European Union (EU).

However, progress is being made with policies and legislative instruments put in place over the last decades which are still currently undergoing development.

Evolution of nature protection and biodiversity policies

Historically, conservation strategies were based on the designation of protected areas where wildlife would be somehow isolated from human activities. National parks were established in the 19th century and in the 20th century were introduced into colonial territories, such as across the British Empire. From the 1930's and after the Second World War they also became more widespread across Europe. In the earlier days of development of nature and wildlife protection, both nationally and at European levels, the measures of conservation were targeted at the most endangered species and habitats, where the agreement and consensus could be more easily reached as the evidence of their decline were readily available and abundant. Examples of this approach are the CITES Convention (Convention on International Trade in Endangered Species of Wild Fauna and Flora http://www.cites.org/index.html), adopted in 1975, and the EU's Birds Directive (Council Directive 79/409/EEC) in 1979 on the conservation of wild birds which clearly identifies certain specific species that should be protected.

This approach has been changing in recent years. With time, it has become clear that species-based conservation management runs the risk of concentrating the attention of the public, and therefore policymakers, on certain so called "flagship" species that act as a symbol for a defined habitat, issue, campaign or environmental cause. The problem with that is that the bigger picture is often lost and the approach may not necessarily result in comprehensive environmental protection. The focus has thus turned to the protection not only of certain species, but also of the habitats that host them. In the EU, this has resulted in the adoption of the Habitats Directive (Council Directive 92/43/EEC) in 1992 on the conservation of natural habitats and of wild fauna and flora, which has produced a network of sites considered worthy of special protection, known as Natura 2000 sites (http://www.natura.org/). By the end of 2008, the Natura 2000 sites made up 17% of the terrestrial area of the EU-27, which is an area of approximately 730,000 km^2.

This evolution of conservation policies is not yet finished. It has given rise to the development of a policy approach based on the conservation of entire ecosystems as well as their functions and the protection of Europe's "Green Infrastructure" within a multifunctional landscape. This approach was crystallised with the adoption of the UN Convention on Biological Diversity as discussed in Section 9.1 (http://www.cbd.int/). The CBD has paved the way to halt biodiversity loss and protect the biological diversity of all species, coupled with a sustainable use of the natural resources. The EU has made significant commitments in this regard. EU Heads of State or Government agreed in 2001 "to halt the decline of biodiversity [in the EU] by 2010" and to "restore habitats and natural systems". In 2002, they joined some 130 world leaders in agreeing "to significantly reduce the rate of biodiversity loss [globally] by 2010".

At European level, biodiversity policy is now largely in place and biodiversity protection concerns have been integrated into the Sustainable Development Strategy (http://ec.europa.eu/environment/eussd/), the so-called Lisbon Strategy (http://ec.europa.eu/growthandjobs/faqs/background/index_en.htm) and into a wide range of environmental and sector policies. A Biodiversity Strategy (COM(98)42, 4.2.1998) was adopted in 1998 and related Action Plans in 2001 (COM(2001)162, 27.3.2001) and (COM(2006)216, 22.5.2006). Most Member States have also developed, or are developing, such strategies and/or action plans. This has called for the development of biodiversity indicators to monitor progress.

Where does soil biodiversity fit in?

With the notable exception of peat soils, which have been the object of some protection since the days of the Ramsar Convention (Convention on Wetlands of International Importance, http://www.ramsar.org) of 1971, nature conservation polices have generally neglected soil and the life within it. This serious shortcoming of current conservation policies can be explained by various reasons. One problem is that the literature on soil science and soil biodiversity in relation to nature conservation is scarce, so policymakers have not been given a sufficient knowledge base as to what should be protected, where, how and why. Another major problem is that neither a protected area nor a species approach is really possible for soil-dwelling organisms. For above ground organisms, the number of species (i.e. the taxonomic diversity) is the most common measure of biodiversity. However, for soil organisms where many species are still are unknown, or difficult to be identified, the traditional taxonomy is less of an anchor for quantifying biodiversity. As a consequence, it has so far proven impossible to identify "hotspots" where soil species are either more valuable, or more at risk than in other areas of the EU. Due to an apparent functional redundancy of species in the soil (as discussed in Section 4.1), it has also not been possible to agree on, or identify, soil species which have a disproportionate effect on their ecosystem. Due to their size or activity (known as keystone species). The same is true of other species (known as umbrella species) which have such demanding habitat and/or area requirements that their conservation would ensure the viability of many other species. The identification of these species below ground may help in prioritising the actions in combating soil biodiversity loss.

For those reasons, the strategies to protect soil biodiversity have rather focused on protecting the functions and services provided by the soil ecosystems. In this way they have embraced earlier concepts and approaches which are gaining weight now for above ground biodiversity. Another major recent achievement is that soil ecologists have shown, through developing the concept of above ground-below ground linkages, that many of the patterns and processes in the visible world are driven and steered by species, interactions, or processes which occur in the soil.

This has helped demonstrate the importance, and raise awareness of below ground biodiversity. However, while specific concepts for soil ecology are now emerging, these developments can only take place once the different fields that sustain them (e.g. soil physics, soil organic matter dynamics, ecology of populations etc.) have reached sufficient maturity.

Fig. 9.2: Night falls across Europe and Northern Africa. The European Union is actively pursuing policies to safeguard and enhance soil biodiversity. (NASA)

The Soil Thematic Strategy of the European Union

Until recently, soil had not been subject to a specific protection policy at EU level, although several Union policies, such as in the field of agriculture or the prevention of industrial pollution, have been contributing to soil protection. In the last five years the need for a coherent approach to soil protection has finally come on the political agenda in Europe. This led to the Soil Thematic Strategy (COM(2006)231, http://ec.europa.eu/environment/soil/index_en.htm) being adopted, with the aim of halting and reversing soil degradation thus ensuring a high level of soil protection across the EU. The strategy underlines that soil is an essential and irreplaceable natural resource that performs a number of fundamental functions which need to be protected.

The objective of the strategy, which accounts for all the different functions that soils can perform, their variability and complexity, and the range of different degradation processes to which soils can be subject, is to define a common and comprehensive approach, focused on the preservation of soil functions. It is based on the principles of preventing further soil degradation and preserving soil functions, and calls for restoring the functional capacity of degraded soils.

The strategy is based around four pillars:

i. framework legislation, in the form of a Soil Framework Directive proposal (COM(2006)232, http://ec.europa.eu/environment/soil/index_en.htm),

ii. the integration of soil protection in other national and Community policies,

iii. increased research on soils as a foundation for policies,

iv. raising public awareness of the need to protect soils. The rationale behind the development of a coherent approach to soil protection is based on the recognition of the vital multi-functionality of soils, which is largely performed by soil biodiversity.

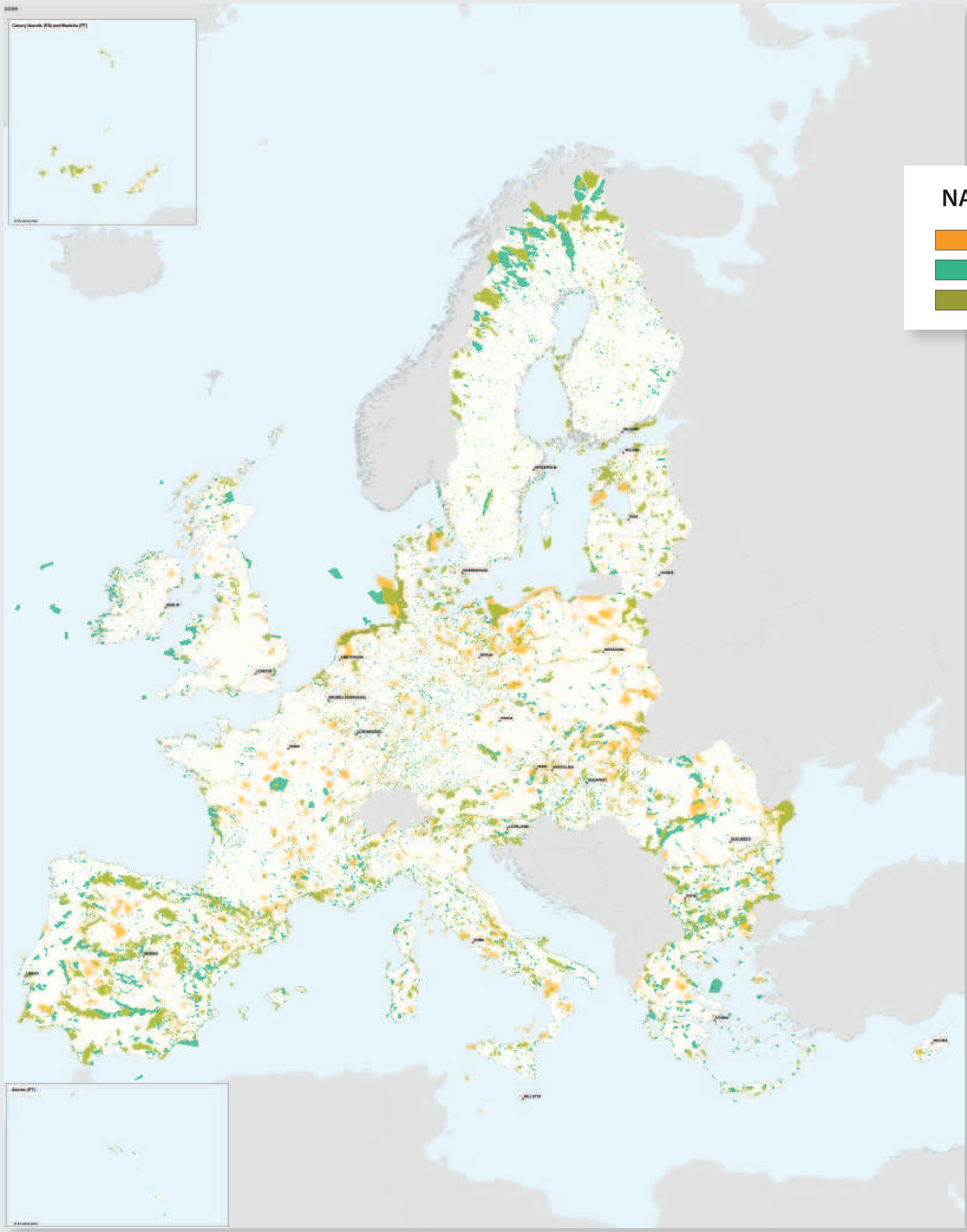
The European Commission, recognising the importance of soil biodiversity, but at the same time aware of current knowledge gaps, has decided to step up the efforts to strengthen the understanding of the function of biodiversity as an environmental service. For example, more funds are being allocated to dedicated calls in the context of the Research Framework Programme.

The way forward

Despite its importance, it is clear that there is little awareness on the role soil biodiversity plays in either ecosystems or in economic development. "Out of sight, out of mind" has been especially true for soil biodiversity. Although soil organisms are necessary to sustain ecosystem functions, they are one of the least known and most neglected components of global biodiversity. However, the adoption of the Soil Thematic Strategy by the European Commission and the flurry of initiatives that have followed are about to change that. The strategy has been instrumental in starting a process of deepening our scientific understanding of soil biodiversity and its link with other soil functions. At the same time, it has called for the development of initiatives to bring to light, as it were, the life under our feet to the general public and policymakers. These new developments are paving the way for integrating soil biodiversity aspects in other EU policies such as the Common Agricultural Policy, where the synergies between soil biodiversity and a sustainable and productive agriculture have become undeniable.

This publication is just an example of what we – European institutions, Member States, scientific community, land users, European citizens – will need to do even more in coming years to improve the way in which life in soil is perceived, so as to generate greater interest in it, and therefore greater care of it.

Natura 2000



NATURA 2000: Birds and Habitats Directives

- Birds Directives (SPA)
- Habitats Directives (pSCI, SCI, SAC)
- Sites - or parts of sites - belonging to both directives

In May 1992 European Union governments adopted legislation called the "Habitats Directive" which was designed to protect the most seriously threatened habitats and species across Europe (see adjacent map). This legislation was designed to complement the Birds Directive which was adopted in 1979. Where the Birds Directive required the establishment of "Special Protection Areas" for birds, the Habitats Directive similarly required "Special Areas of Conservation" to be designated for other species, and for habitats. These areas combined to make up the Natura 2000 network. All EU Member States contribute to the network of sites in a Europe-wide partnership.

Currently there are no specific sites set up within Natura 2000 to protect soil species or habitats specifically. However, as the important ecosystem services provided by various soil organisms, and the threats that they are under as discussed elsewhere in this Atlas, this could change in the future.

Fig. 9.3: A map showing the distribution of Natura 2000 sites, both terrestrial and marine, through the EU25. (JRC)

9.3 Raising awareness of Soil Biodiversity

The need to raise awareness and understanding of the importance of soil and soil biodiversity, both in the urban and rural environments, has been highlighted at both European and Global scales. In Europe a number of threats to soil quality are recognised (e.g. compaction, erosion, loss of organic matter, landslides, contamination, desertification, salinisation and soil sealing) which impact on the functioning of our soils (see Chapters 4 and 5).

However, the loss of soil biodiversity is not explicitly included in the proposed legislation for soil protection in the European Union as we still know so little about the activity and distribution of soil organisms. Therefore, increasing everybody's knowledge about soil biodiversity through research and education is the first logical step to allow society as a whole to understand and appreciate soil biodiversity and its importance.

Fig. 9.5: Soil biodiversity from a different point of view. A child's eye view of life below ground. It is interesting to note the variety of organisms and that the child has drawn a yellow figure with their entire body 'suspended' by their feet in the soil! (KG)

What does soil awareness mean?

Soil awareness means developing a responsible behaviour towards soils and soil management, based on knowledge and attitude. The more we can learn about the role that soil biota play in sustaining the environment, the more we understand how important it is and, hopefully, the more likely we are to look after it.

Who needs to know about soil biodiversity?

It is important that we teach the importance of soil biodiversity to society at large. From young children, school teachers, farmers, gardeners and industrialists to planners and politicians.

Children, of all ages, love playing with soil (Fig. 9.4) and have the capacity to learn so much, with simple "hands-on" activities from comparing textures to making mud pies, building wormeries and looking at what lives in soil under the microscope. A child's perspective on what we think when we talk about soil functions and the role of soil organisms often reflect a clearer appreciation than adults. Drawings done by children show how they perceive soil and perhaps surprisingly they often describe soil as an essential part of the entire ecosystem (Fig. 9.5). Such sketches or paintings, especially by primary school children often show complex messages such as the food chain or the importance of earthworms in increasing the pore network underground, which in turn aids infiltration of rain water.

This is a lesson that soil scientists constantly strive to communicate, but often over complicate. The ecosystem view is, however, apparently inherent to most children who also seem to be fascinated by life in the soil, be it at primary, secondary or even university level (Fig. 9.6, Fig. 9.7).

Other actors that need education and awareness raising are:

University students

The knowledge of soil in general, and soil biology and ecology, is often neglected, even in faculties having a direct connection with the study of terrestrial ecosystems. It is clear that the study of soil biota should be improved at university level, not only in subjects such as agricultural sciences, forestry and environmental sciences, but also in engineering, architecture, land use planning, because they also deal with the management of our planet.

Environmental scientists

Environmental sciences should be characterized by a very holistic approach. These results can be achieved by having a multi-disciplinary team where people specialized in different subjects are able to cooperate and understand each other. However, this optimal situation is threatened by the fact that some disciplines are neglected.

Policy makers

Policy makers are responsible for decisions affecting our every day life. Often the temporal horizon in politics is very limited and more related to the political elections than to real world processes. Increasing the awareness of soil biodiversity in the decision making process could bring enormous benefits.

Farmers and land managers

Farmers generally have a good knowledge and feeling about soil because it represents the most important factor of their activities. However, the functioning of the living soil system is not so obvious and there are some farming practices that should be limited.

A possible further problem is represented by the fact that in many cases the choice of farmers are changing from a long term perspective to a more short-term outlook. This is driven by the switch from traditional systems to more industrial approaches.

Public

At the very end, the most important result is probably to raise the awareness among the general public, because in a democratic system, this is the only way to have a bottom-up driven change in life style, aimed to a more sustainable use of our planet.

Fig. 9.6: Primary school children investigating life in a soil pits close to their school. (KG)

Fig. 9.7: Even university students enjoy sampling soil biodiversity in the field. (CG)

Fig. 9.8: You can discover more life in the soil when it's magnified. (CG)

Fig. 9.9: The European Union is developing policies and legislation to protect biodiversity and, in particular, soil biodiversity. It is just as important to educate politicians and decision makers. Perhaps one days, these children may be in a position to protect what lives in the soil. (AJ)

Fig. 9.4: Children love playing with soil. This scene, taken from the highly influential movie 'Dirt', shows a traditional game played by Indian children in which they cover themselves in soil. (Photograph Courtesy Gene Rosow © Common Ground Media, Inc. From DIRT! The Movie www.dirtthemovie.org)

Where can you learn about soils and soil organisms?

Often the best place to teach people about soils is to go physically in to 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 in to contact with soil biota.

The use of magnifying lenses or microscopes to show the variety of soil organisms found in a few grams of soil is such a simple lesson and is guaranteed to leave a long lasting impression on the person doing the viewing (Fig. 9.8).

A huge amount of educational material is increasingly being available for both students and teachers. This includes computer programmes, lesson plans, supporting materials and activities for both the classroom and outdoors (Fig. 9.12).

The great thing about teaching soil biology is that it is applicable across all ages from young children who make wormeries, to school leavers and university students who discover the importance of soil biology in the global nutrient cycles and ecosystem functions (Fig. 9.10).

Fig. 9.10: Concepts of soil depending on age. (KG)

A number of promising educational initiatives have been developed to reach the general public and, in particular, for children to learn outside the school environment. Examples include interactive museums (Fig 9.11) or at informative nature walks that tell the story of soil and its role within a particular landscape.

Fig. 9.11: Underground soil museum in Osnabrück, Germany. (KG)

Another interesting route is to use images of creatures that live in the soil to help raise public awareness of the importance of life in soil. An obvious candidate is the character of Mole from the book Wind in the Willows (Fig. 9.13). This approach could also work even if the creature is considered as 'ugly'! A naked mole rat (Fig. 9.13) is currently enjoying global recognition as the character 'Rufus'in the Disney cartoon series 'Kim Possible' Many children are terribly disappointed to learn that they cannot have naked rats as pets once they learn that these animals need their special warm and dark habitat in soil. Instead they make do with the soft-toy version which sells so well that it is often out of stock with retailers! These examples show very clearly that soil organisms can compete with other, perhaps more famous and charismatic, animals such as elephants and lions, in raising awareness on soil biodiversity.

More recently the importance of soil has become an international topic with release of the film 'DIRT the movie' (http://www.dirtthemovie.org) and the increased abundance of articles in the press, whether it be in National Geographic or in comic strips (Fig. (9.4, 9.13).

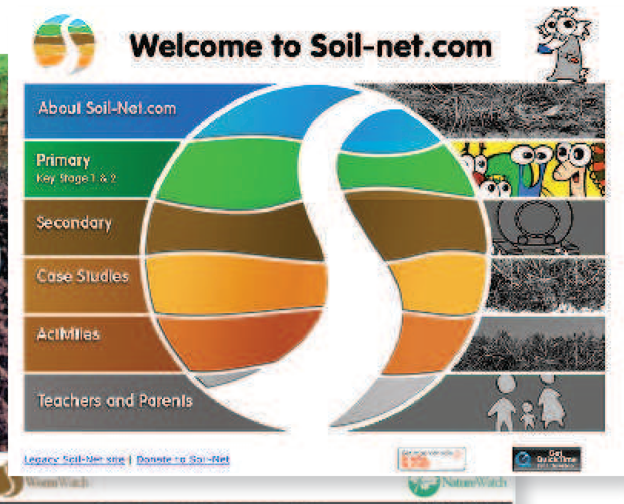
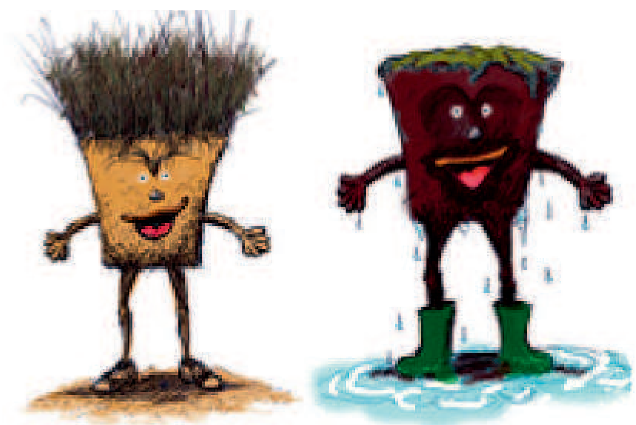


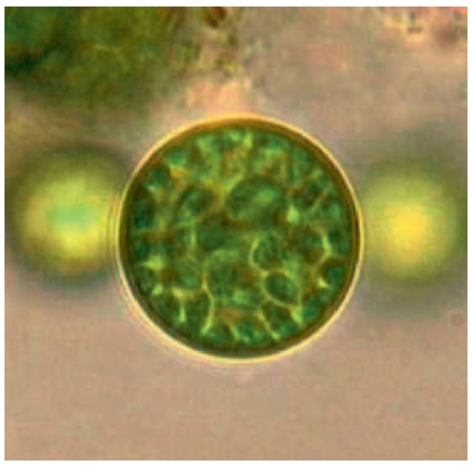
Fig. 9.12: For further information on soil education resources available for teaching about soils and soil biodiversity, please go to the following sites:
http://eusoils.jrc.ec.europa.eu/awareness/Inventory.cfm
http://www.soil-net.com/
http://ec.europa.eu/environment/index_en.htm

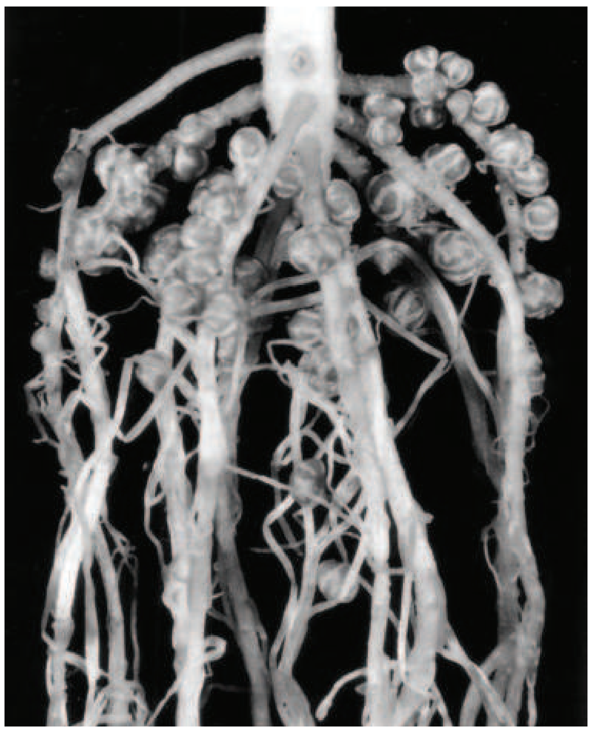


Sandy

Pete

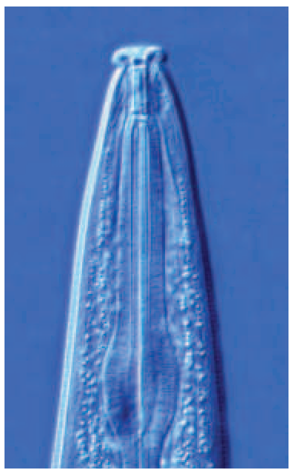
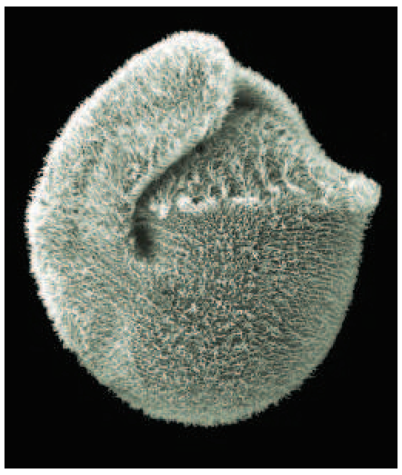
Fig. 9.13: above left: a naked mole rat (RK); **above right:** two cartoon characters used to raise awareness of soil by the Macaulay Land Use Research Institute. (WT); **below:** Mole and Rat from Wind in the Willows. (SBI)

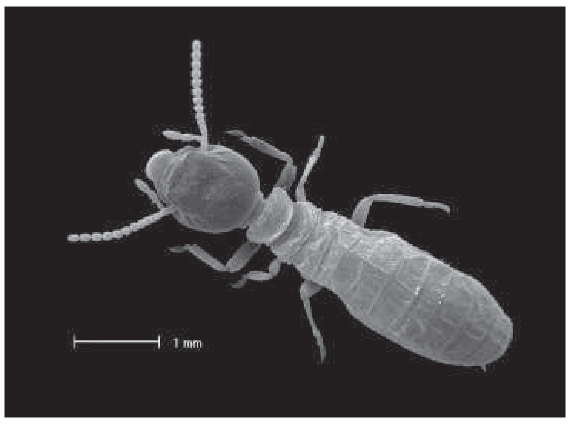






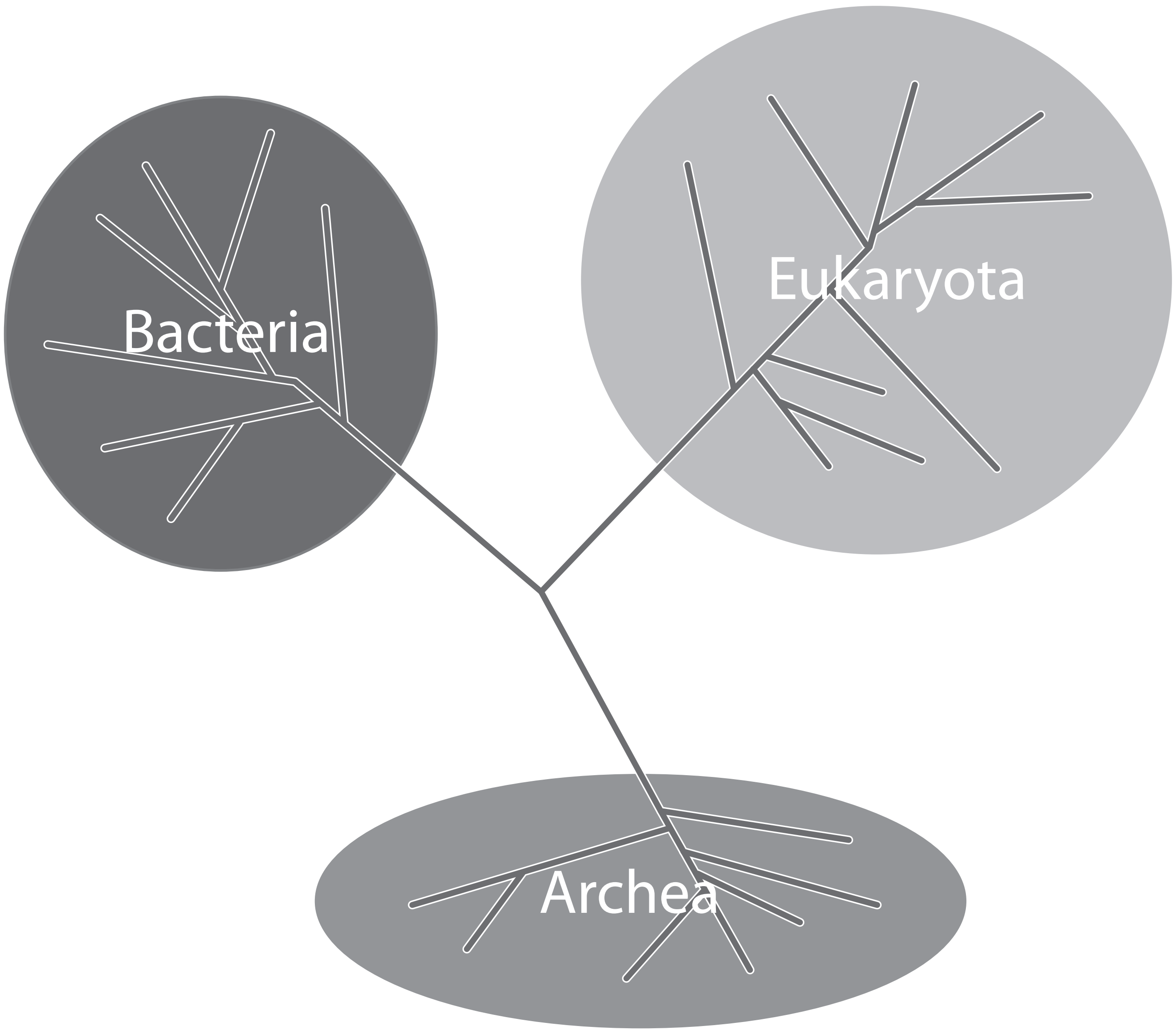




1 mm



SECTION 2

ORGANISMS OF THE SOIL



I Prokaryotes

"Prokaryote" refers to all organisms which lack cell nuclei, which is a clearly defined, generally spherical structure which contains all of the organisms genetic material (as well as lacking other membrane bound organelles). All organisms in this group are single cellular and consist of two of the Domains of life, Bacteria, and Archea. Both Domains of organisms are abundant in soils, with bacteria generally being the more abundant and diverse group of the two in most soils. Relatively little is still known regarding Archea in soil, and indeed until recently it was thought that Archea were only found in very harsh environments such as hot springs. This has since proven to be false and Archea are now known to be found in most habitats. The functional aspects of archea are discussed in Section 3.5 and this section focuses more on bacteria owing to the fact that while archea and bacteria are very disparate groups with regard to their genetics and biochemistry, morphologically they look very similar down a microscope.

With regard to their vertical distribution, prokaryotes are generally found in greater abundance nearer to the soil surface where there they are closely associated with organic matter and the rhizosphere (as discussed in Section 1.4). Their numbers decline markedly with depth.

Prokaryotes are microscopic, being too small to be visible to the naked eye and requiring microscopy to see them. They are very difficult to distinguish morphologically, as they fall into only a relatively small number of groups depending on their cell shapes and the shape that they grow in culture when viewed down a microscope (Fig. I.I)

The study of prokaryotes is complicated by the fact that it is estimated that more than 90% of soil bacteria are not culturable out side of the soil under laboratory conditions. This means that much of the work which is undertaken on bacteria is done at a molecular level. However, some visual research is conducted, some of the results of which are depicted here.

Prokaryotic taxonomy is further complicated by the fact that no clear consensus exists concerning what a bacterial species actually is. This is because bacteria are capable of swapping genetic material between each other, as well as picking it up from the environment and as such do not need to reproduce to become genetically distinct. This would be the equivalent of you picking up some DNA from a carrot, for example, and integrating it into your body! This type of activity is widespread in the bacterial world, leading to difficulties in defining what a bacterial species really is or means. Bacteria are incredibly diverse in the functions that they perform as well as their morphologies. Some of these functions are listed in Section 4.1, along with the names of some of the species which carry out these functions. Furthermore, many different types of soil bacteria, and the compounds that they produce, are used widely for biotechnological applications. These are detailed in Section 4.5.

Symbiotic Relationships

Many prokaryotic organisms are capable of forming symbiotic relationships with other organisms. In fact, some organisms such as Lichens are the result of a symbiosis between a fungus and cyanobacteria, a prokaryotic organism, or in some cases with algae.

Fig. I.II: Actinomycetes are a type of bacteria from the phylum Actinobacteria. The genus *Frankia* is capable of fixing nitrogen and does so by forming root nodules with actinorhizal plants, including many species of tree. The above image shows a cross section though a root nodule taken from the root of an Alder. (PDI)

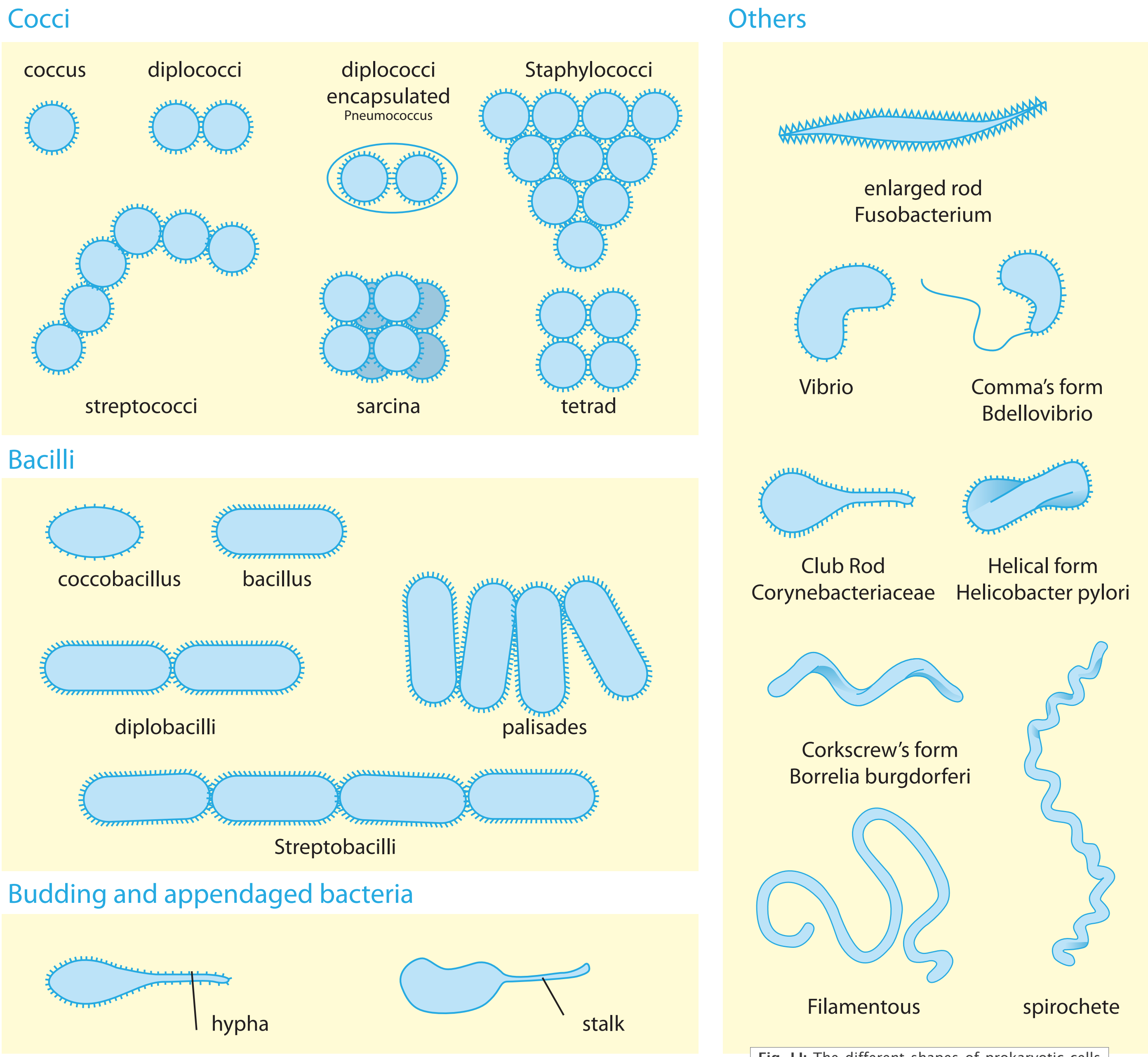


Fig. I.I: The different shapes of prokaryotic cells that can be seen under a microscope. (MRV)

Some of these relationships have very far reaching consequences and drive systems which function on a global scale. One example of this is the nitrogen cycle which relies on nitrogen being fixed and converted into plant useable forms by organisms within the soil. Some of the organisms that play a part in this cycle are free living, existing as independent organisms within the soil, such as some species of algae. Others however, such as cyanobacteria, discussed more in Section II, and actinomycetes, where organisms from the genus Frankia form symbiotic relationships with trees in the form of root nodules, such as those shown in Fig. I.II. Symbiotic relationships such as these, either with actinomycetes forming nodules on tree roots, or species such as *Rhizobium* forming nodules on the roots of legumes (Fig. I.III), play a very important role in maintaining soil fertility due to their ability to move nitrogen from gaseous form from the atmosphere and convert it into a plant usable form such as nitrate.

Pathogens

Prokaryotic organism are not always positive and many species and varieties are capable of producing diseases in both plants and animals, including humans. In fact, the disease Anthrax is caused by the soil bacterium *Bacillus anthracis* which, as well as having been developed as a biological weapon, can cause fatal disease in livestock that are exposed to this organism from the soil. Other well known diseases which can be caused by soil borune prokaryotes include tetanus (*Clostridium Tetani*) and gas gangrene (*Clostridium perfringens*). More specific information on the effects of pathogenic prokaryotic organisms can be found in Section 4.4.

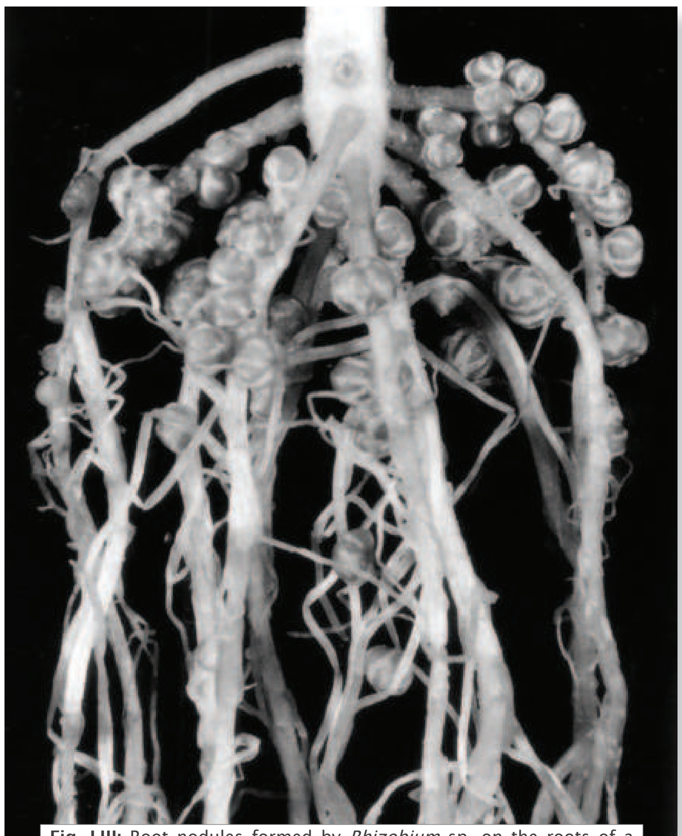


Fig. I.III: Root nodules formed by *Rhizobium* sp. on the roots of a leguminous plant as part of a symbiotic relationship between the bacterium and the plant. The plant provides a safe environment, rich in sugars as food for the bacterium which in turn fixes nitrogen into plant usable forms. (KR)

Bacterial colonies are distributed throughout the soil matrix where they grow in water films in the pore spaces between soil aggregates (Fig. I.IV). Some colonies grow in very restrictive pore spaces (Fig. I.V). This has advantages and disadvantages in that the colony is unable to grow beyond the size of the pore and is reliant on water and nutrients to diffuse through the surrounding soil aggregates. However, the colony is protected from being grazed upon by bacterial feeders such as protozoa. Furthermore, soil is a highly dynamic system, with ever changing pore spaces owing to changes brought on by wetting and drying cycles and in some instances, by freezing thawing cycles, so it is unlikely that the above colony would have been isolated and protected indefinitely.

Nutrients are often limited in the soil system for bacteria, which therefore spend much of their time in an inactive resting state. However, upon increased nutrient availability, most soil bacteria are able to rapidly utilise the available nutrient for increased growth and reproduction before again settling to a more inactive state (Fig. I.VI).

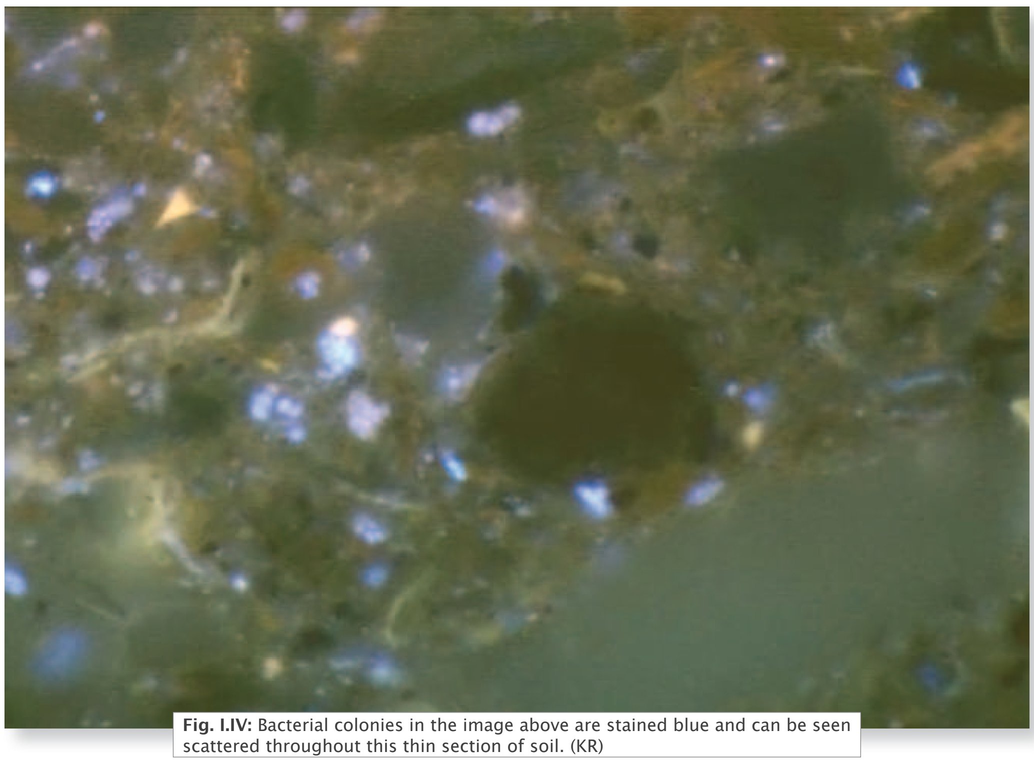


Fig. I.IV: Bacterial colonies in the image above are stained blue and can be seen scattered throughout this thin section of soil. (KR)

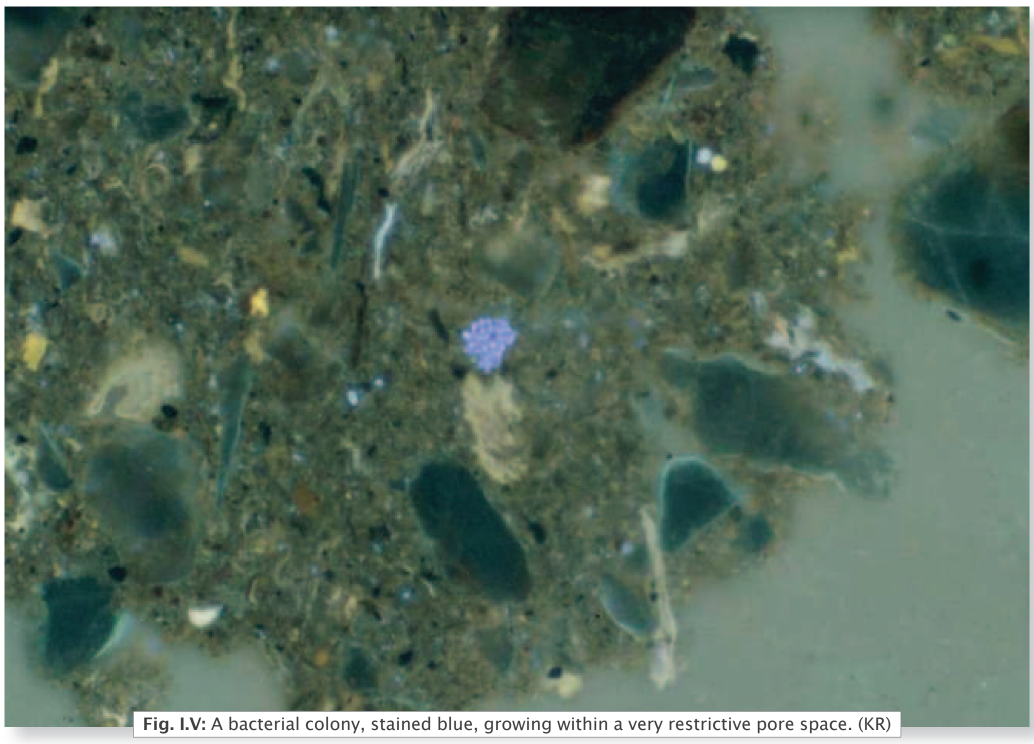


Fig. I.V: A bacterial colony, stained blue, growing within a very restrictive pore space. (KR)

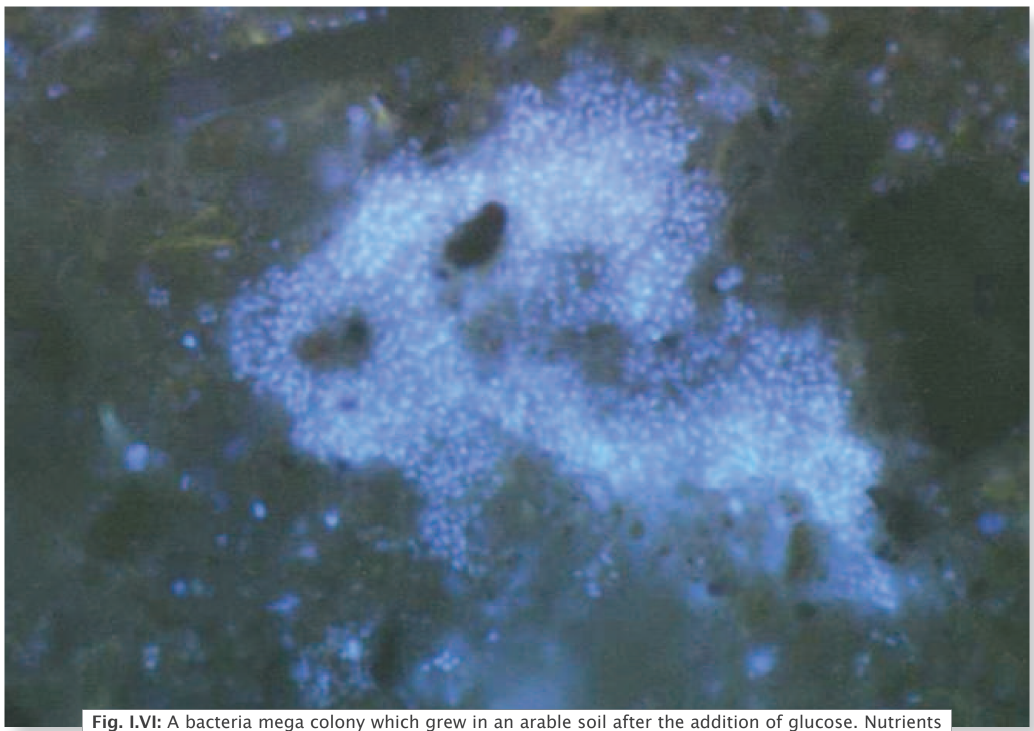


Fig. I.VI: A bacteria mega colony which grew in an arable soil after the addition of glucose. Nutrients are often limited in the soil system for bacteria, which therefore spend much of their time in a dormant or near dormant state, growing much more slowly than under ideal laboratory conditions. (KR)

Fig. I.VII: A range of soil organisms growing in culture in the laboratory produced by repeatedly diluting a sample of soil in water and adding the diluted sample to an agar plate. Each colony is produced by one cell initially, which utilises nutrients in the agar gel and reproduces, growing to build a colony of identical cells over time. Each different shaped and coloured colony represents a different 'species' of microorganism. (RW)

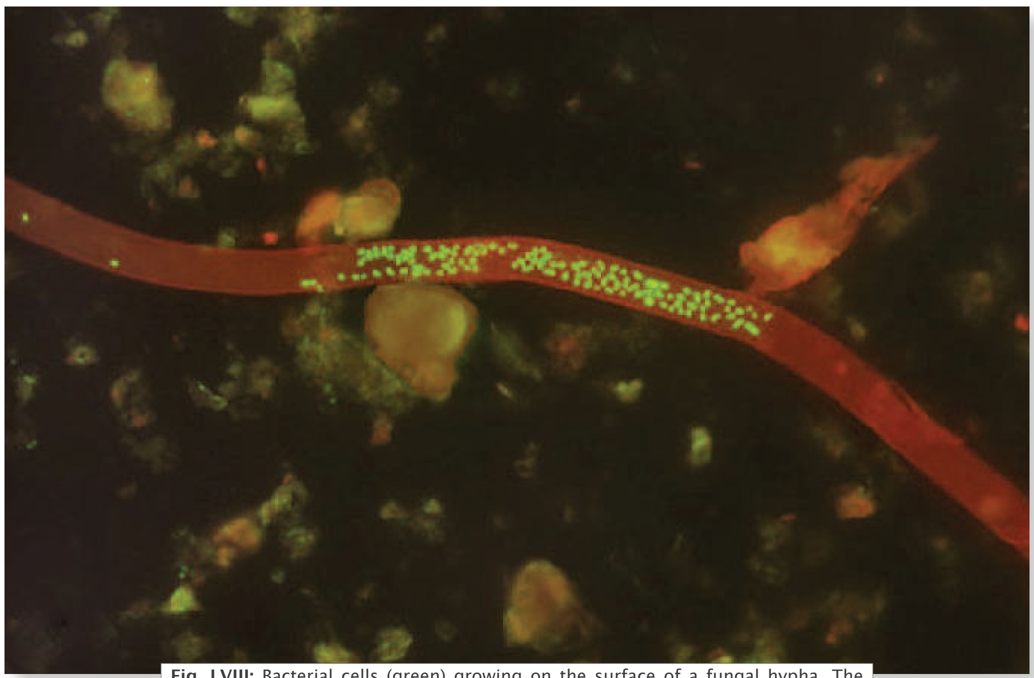


Fig. I.VIII: Bacterial cells (green) growing on the surface of a fungal hypha. The soil is a highly complex biological system, full of interactions between different species, classes and domains of organisms. (KR)

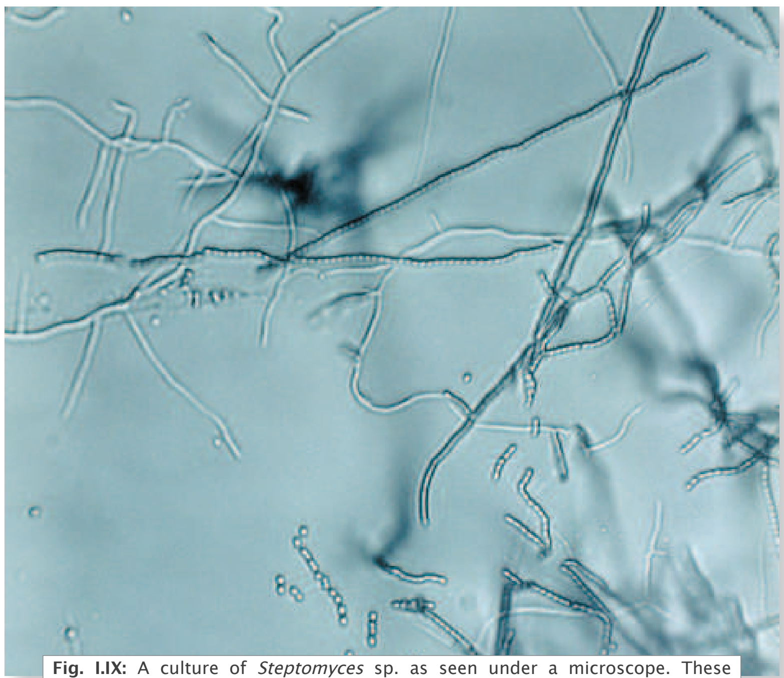


Fig. I.IX: A culture of *Steptomyces* sp. as seen under a microscope. These organisms are responsible for the soil's earthy smell; created by their production of a volatile metabolite called geosim. (PDI)

II Cyanobacteria and Algae

Cyanobacteria and algae are actually very disparate groups of organisms, with cyanobacteria being prokaryotes, the same as bacteria, and algae being eukaryotes, the same as protozoa, higher plants and even humans. However, both are capable of photosynthesis and perform relatively similar ecological functions within the soil and as such they are considered together here.

Cyanobacteria (previously also known as blue-green algae) are photoautotrophic prokaryotes meaning that they play a role in the carbon cycle as they fix atmospheric CO_2 through photosynthesis. Cyanobacteria are relatively robust organisms and have been shown to be capable of photosynthetic growth in extremely arid conditions, down to a dry limit of less than 5 mm precipitation per year, and to be able to resist decadal periods of no rainfall. This means that they can grow on soil surfaces in many areas of the planet, including all but the driest desert environments (Fig. II.I, II.II and II.III). Furthermore, cyanobacteria have been shown to be able to photosynthesize in conditions of very high irradiance, again demonstrating that these microorganisms are very tough and capable of surviving in harsh environments. These adaptations are particularly pertinent to soil surface environments, which are relatively extreme and dynamic compared to deeper soil layers due to the effects of wind, rain and mechanical disturbance. However, it is clearly vital that cyanobacteria can cope with the relative extremes of the soil surface as they need light to grow, and light penetrates only very poorly into soil, generally down to just 1 or 2 mm in even the best case scenarios.

Cyanobacteria have also been shown to play an important role in the nitrogen cycle as non-symbiotic nitrogen fixers (Fig. II.IV, II.V). In fact, nitrogen fixing cyanobacteria are vital for growth of rice in paddy fields, which would be less productive without the nitrogen fixed by the cyanobacteria. Nitrogen fixation rates in arable systems have been found to be in the range of 10 - 25 kg N per hectare per year. As well as increasing soil fertility through the input of nitrogen, cyanobacteria also improve the structure of the soil, significantly reducing bulk density and increasing both the water holding capacity and hydraulic conductivity of the soil.

Fig. II.I: The two figures to the left depict urban soil crusts from Krakow (Poland). Figures II.II and II.III show different representations of cyanobacteria and diatoms found in one sample of soil crust. (KW)

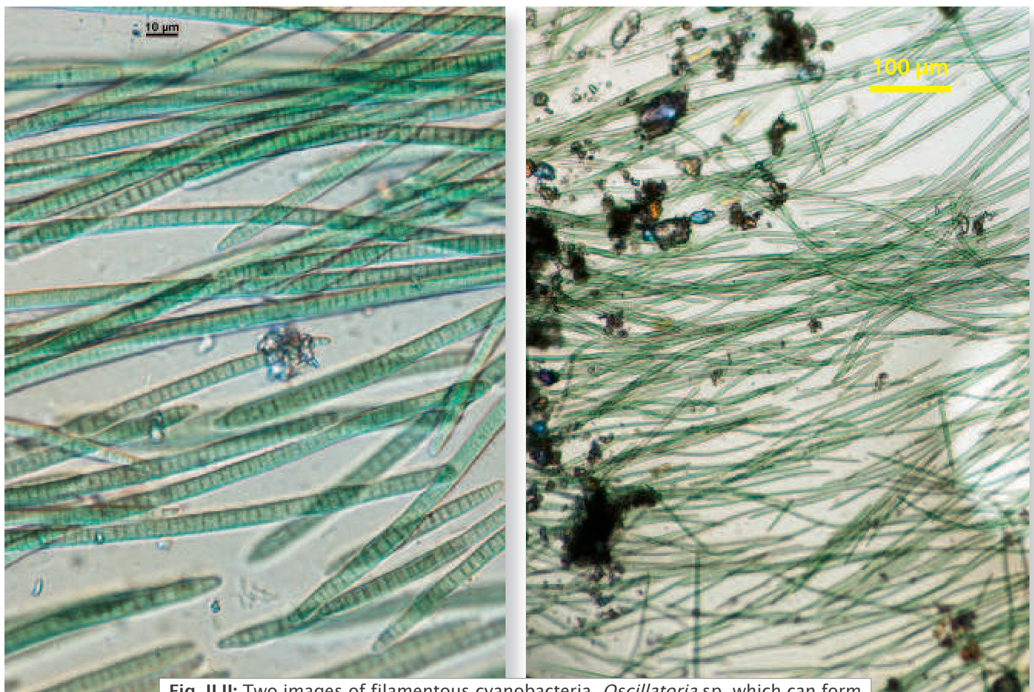


Fig. II.II: Two images of filamentous cyanobacteria, *Oscillatoria* sp. which can form extensive mats on urban soil such as those seen above. (KW)

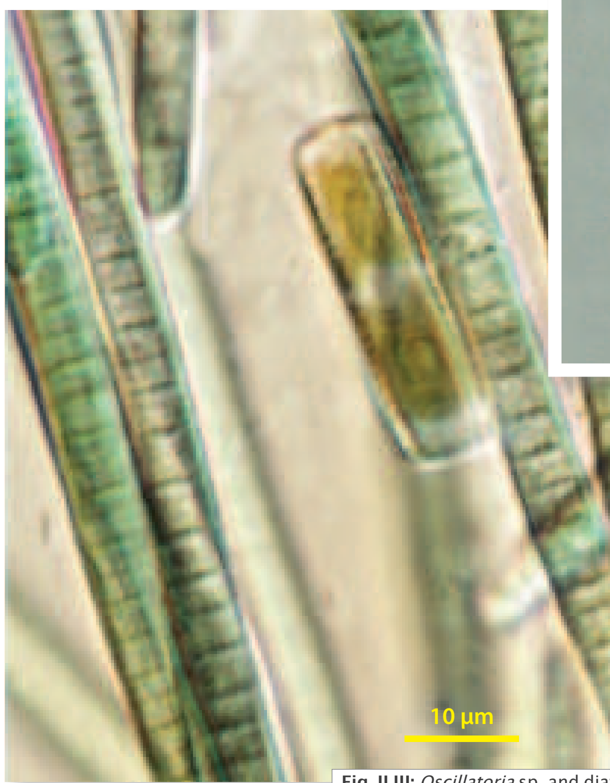


Fig. II.III: *Oscillatoria* sp. and diatoms from urban soil crust (**left**) and (**right**) a single, small frustule of *Luticola* sp. (KW)

Fig. II.IV: Filamentous cyanobacterium *Nostoc commune* which can form macroscopic colonies on wet soil. The larger almost spherical cells which can be seen interspersed with the smaller cells are known as heterocysts which are capable of fixing atmospheric nitrogen and for moving it into the soil in a form which can be used by other organisms including higher plants. (KW)

Fig. II.V: The filamentous cyanobacterium *Nostoc edaphicum* creates spherical colonies. As with all green photosynthetic organisms, the green colour is caused by the molecule chlorophyll and the blue tint by the molecule phycocyanin. (BPS)

Algae are found in soils everywhere. They are generally most abundant at or near the soil surface, although they are also found in lower soil horizons (Fig. II.VI). Like cyanobacteria, algae are photoautotrophs and as such rely on light to allow them to fix CO_2 through the process of photosynthesis. For this reason, it would seem logical to conclude that the vast majority of algae would be found at the soil surface, where light is abundant as is the case for cyanobacteria. However, it has been found that there can be nearly 700 species of algae at 15 to 20 cm depth below the surface in many parts of the world. It is believed that earthworms and rain are the main cause of vertical movement of algae through the soil. Many soil algae, including diatoms and Cyanophyta, are motile and so are often able to return to the surface if they are not buried too deeply.

Algae are an important part of the soil microflora. They act as a reservoir for plant nutrients, incorporate organic carbon and nitrogen into the soil system through photosynthesis and nitrogen fixation, influence soil structure and control the activity of other edaphic organisms. In a similar manner to cyanobacteria, some species of algae are capable of fixing nitrogen within the soil surface in a light-dependent process. Algae have been shown to withstand desiccation to a similar extent as cyanobacteria. This is a useful adaption mechanism in coping with the relative environmental and climatic extremes that can be found at the soil surface. However, the speed of desiccation has been shown to be an important factor in algal survival with many more algal cells surviving 'short and sharp' desiccation events compared to a long and slow drying of the soil (Fig II.VII).

As an active component of biological soil crusts, algae, together with bacteria and fungi, play major role in mineral retention and the primary and secondary succession of plants. Presently over forty prokaryotic and one hundred eukaryotic genera which form soil algae communities are known. Most frequent are representatives of cyanobacteria green algae (Chlorophyta), diatoms (Bacillariophyta), and yellow green algae (Xanthophyta) as well as, slightly less commonly euglenophytes (Euglenophyta) and red algae (Rhodophyta).

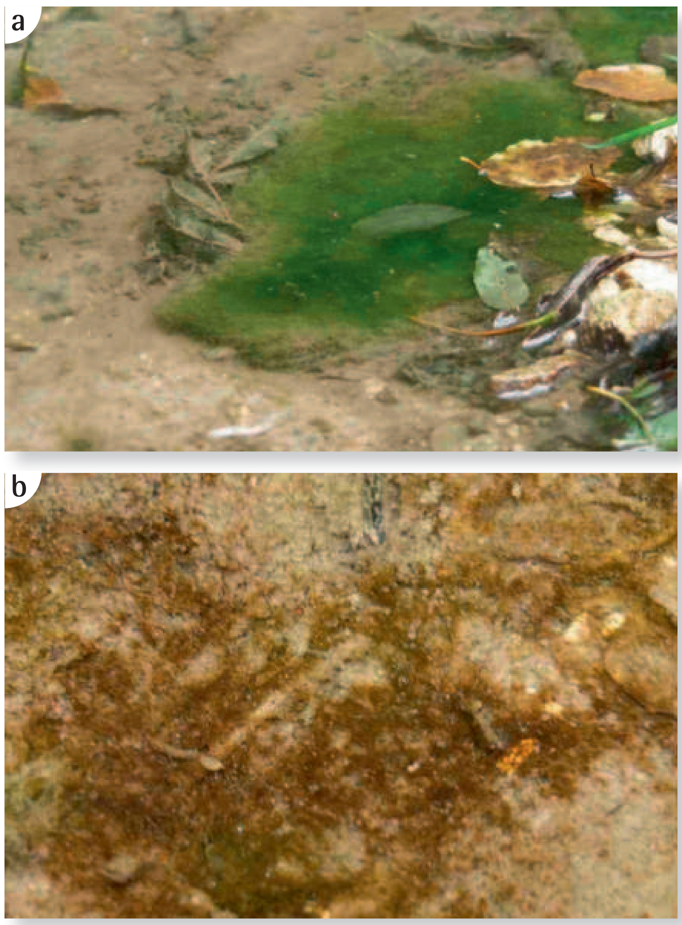


Fig. II.VI: As with cyanobacteria, algae are also capable of forming macroscopic mats on wet soils: (a) a mat on wet soil formed by a yellow green algae (Xanthophyta) called *Vaucheria* sp; (b) a brown mat formed of diatoms is clearly visible.) (KW)

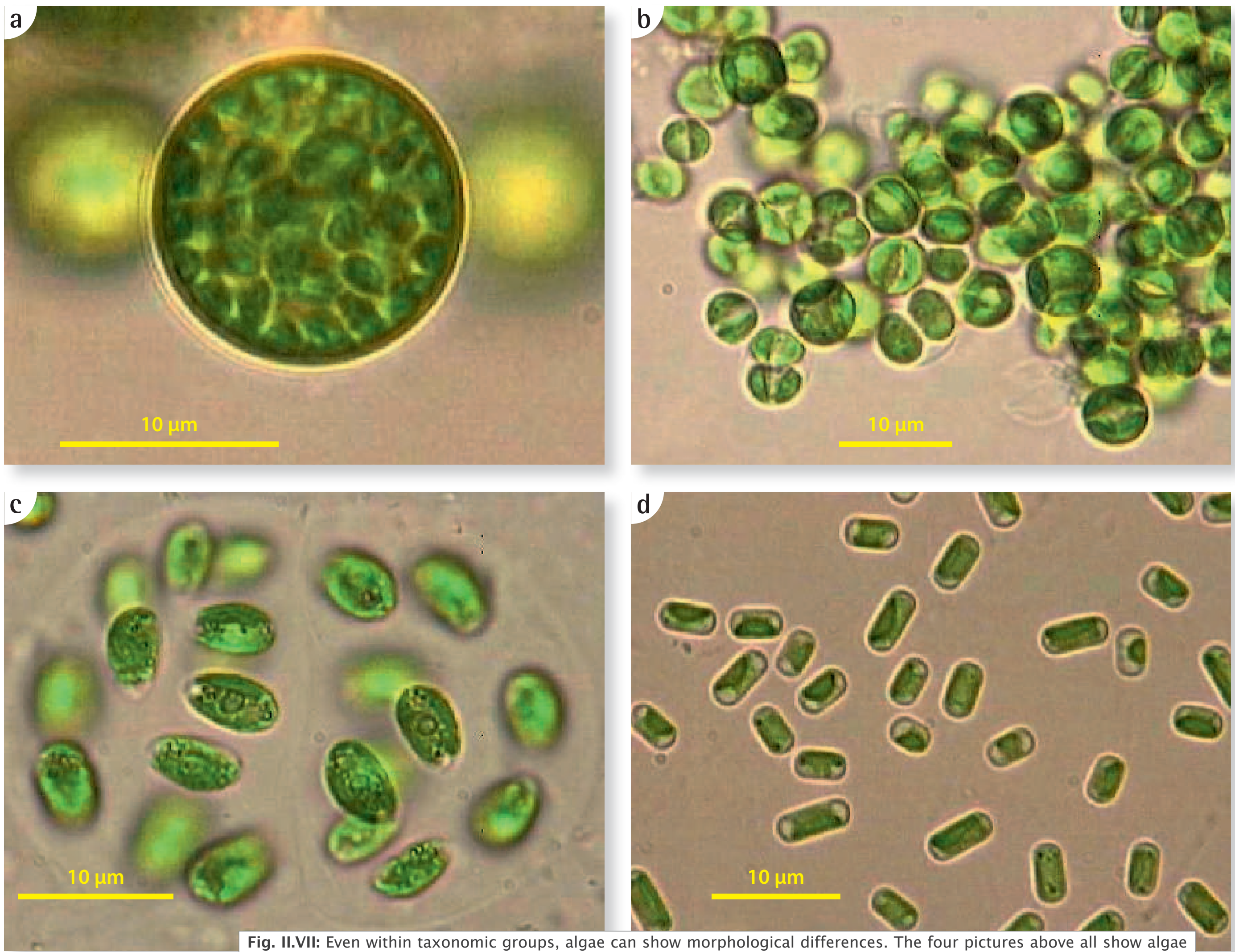


Fig. II.VII: Even within taxonomic groups, algae can show morphological differences. The four pictures above all show algae from the group Chlorophyta (green algae): (a) a cell of the relatively large and spherical species *Dictyococcus* cf. *varians*; (b) the "pea like" *Muriella decolour*; (c) the elliptical species *Chlamydomonas boldii* immersed in a mucilage envelope and (d) the rod like species *Stichococcus minor*. All of these four species were isolated from an industrial area where the soils were polluted with heavy metals, demonstrating these species of algae to be capable of survival in relatively harsh conditions. (BPS)

Biological Crusts:

Biological soil crusts are made by organisms such as cyanobacteria, green algae, microfungi, mosses, liverworts and lichens that live on or close to the surface of soils. These features are common in arid environments.

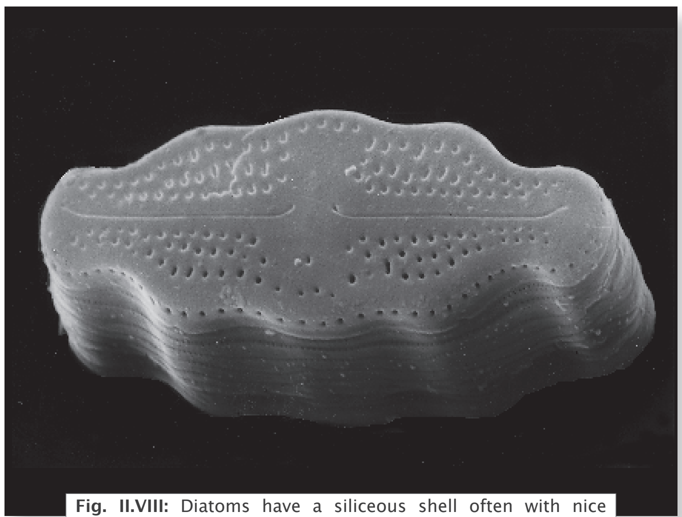


Fig. II.VIII: Diatoms have a siliceous shell often with nice ornamentations. They are autotrophic organisms and thus present mainly in the upper soil layers, especially in deciduous litter. The species shown is about 30 µm long. (WF)

Lichens

Lichens are not individual organisms. Actually they are the result of a symbiotic relationship between an alga and a fungus with the two types of organisms in the relationship being so tightly interwoven that they appear as one organism. More than 18,000 'species' of lichen have been described world wide, with lichens inhabiting some of the most hostile places on Earth such as the rocky outcrops on mountain tops, to the cold and dry soils of the Arctic and Antarctica. Lichens grown very slowly and play an important role in soil formation owing to their ability to make their own food through photosynthesis and then providing organic matter as a substrate for other organisms after their death. Some species are very sensitive to pollution and so can be used as effective indicators regarding the state of their local environment.

a *Lobaria pulmonaria*. (BH)

b *Xanthoparmelia* sp. (BH)

III Fungi

Fungi are familiar to many people in the form of mushrooms, but these structures are just the fruiting bodies of one group of this very diverse range of organisms. Fungi occupy a distinct taxonomic kingdom, separate from prokaryotes, plants and animals. They occur in all soils, and can form the larger part of the biomass below ground, particularly in soils high in organic matter. Fungi are hugely important in the functioning of soil systems, involved in a wide range of roles.

There are two basic growth-forms of fungi, a single-celled yeast-like form, and a more common thread-like structure called a hypha. These filamentous hyphae grow by extending at the tip, and branch periodically to form a larger-scale structure called a mycelium (Fig. III.I).

A metre square of grassland soil will typically contain several kilometres of fungal hyphae. The mycelial growth-form is well adapted to the soil environment, since hyphae can effectively explore the three-dimensional soil pore network, foraging for food resources. Hyphae can aggregate and differentiate in many ways to form diverse structures including long-range foraging cords, microscopic spore-bearing structures, intricately-shaped mushrooms and even nematode-trapping lassoes (Figure III.IIIf).

While fungi are considered to be 'microbes', some mycelia can grow to be huge in extent and form what are arguably the largest single organisms on the planet. There are documented examples of single mycelia of *Armillaria bulbosa* in some forests that are several kilometres in extent and estimated to weigh some hundreds of tonnes (Fig. III.II; see also Section 3.1).

Armillaria bulbosa is common in hardwood forests in America where, in one of the more extreme cases, the mycelium formed by one individual of this species grew through the forest and expanded over and area of more than 890 hectares!

Armillaria is also found in the hardwood forests of Europe and Japan. The fungus is an important part of the ecosystem where it feeds on dead wood.

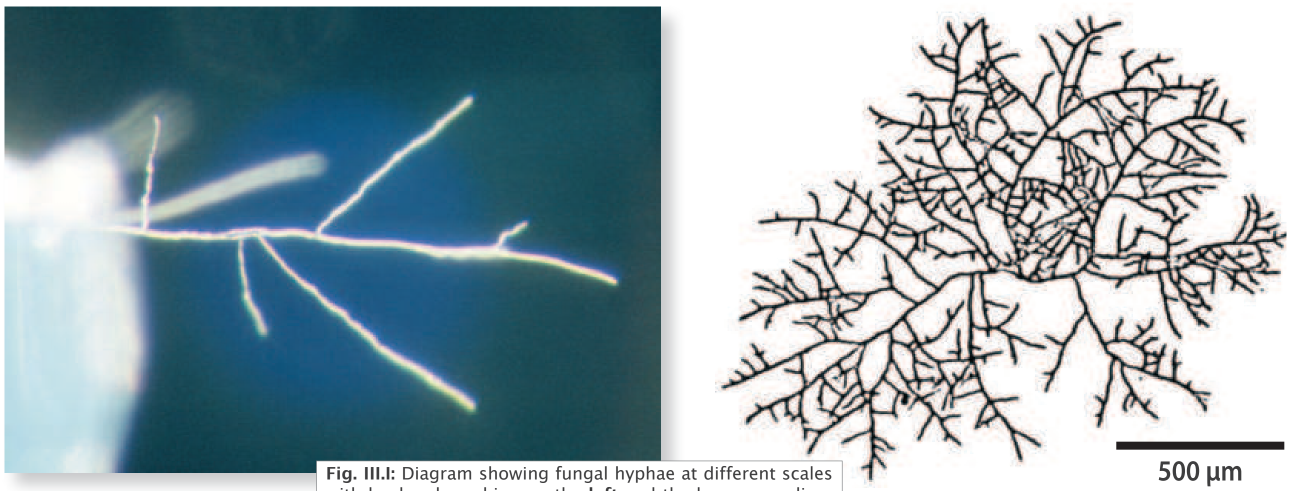


Fig. III.I: Diagram showing fungal hyphae at different scales with hyphae branching on the **left** and the larger mycelium formed by hyphae over time on the **right**. From Ritz (2005)

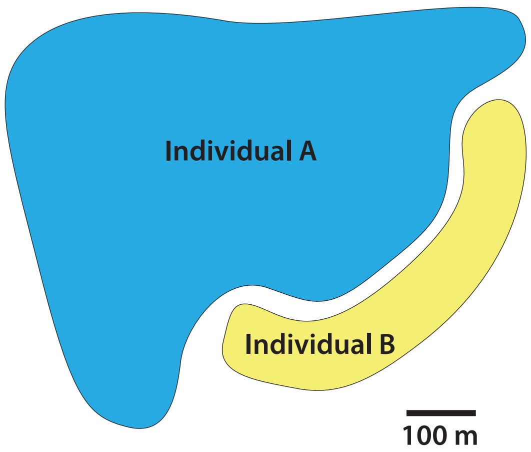


Fig. III.II: The variable sizes of mycelium of two individuals of fungal species *Armillaria bulbosa*. (KR)

Soil fungi and trees:

- Many species of trees cannot grow without a symbiotic relationship with certain soil-based fungi such as arbuscular mycorrhizal fungi (AMF).
- Invasive plant species, landfill and air pollution are causing a decline of AMF in many forests in Europe and North America.
- A possible mass extinction of soil-fungi would affect the health and the survival of forest ecosystems.
- Systematic records of mushrooms species, which have been kept in Europe since the beginning of the 20th century, show a sharp decline in mushroom diversity in several European countries.
- The Swiss Federal Environment Office has published the first-ever 'Red List' of mushrooms detailing 937 known species facing possible extinction in Switzerland.

Fig. III.III: A selection of photographs of different fungi showing a range of diverse structures. (a) shows a thin section viewed down a microscope with fungal hyphae (stained blue) growing through the pore space of a soil; (b) shows a puff ball, the fruiting body *Calvatia gigantea* which is full of spores which are dispersed over a wide area when the puff ball bursts; (c) the fruting bodies of *Pilobilus* sp., which actually produces the fastest acceleration rates in the living world; faster than a missile or a speeding bullet! The black ends are spores which can be shot up to two metres due to the fluid sacks behind each spore filling slowly with fluid until they burst, dispersing the spores; (d) the fruiting body of *Amanita muscari*, the classic 'toadstool' seen in fairytale drawings; (e) the fruiting body of *Lacrymaria* sp. (f) the carnivorous fungi *Drechslerella anchonia* which captures nematodes in rings which grow along its hyphae then penetrates the skin and consumes the nematode from the inside out (g) the fruiting body of *Hygrocybe punicea*.

Fungal Roles in Soil

Nutrient cycling

Soil fungi play a crucial role in nutrient cycling in terrestrial systems due to their ability to break down almost all organic materials and as such act as 'primary decomposers'. Many species possess a wide range of enzymes capable of degrading recalcitrant plant residues such as cellulose and lignin, and complex soil organic matter, and in so doing release nutrient elements which are available for uptake by other soil organisms including plants. Some fungi release organic acids into the soil which solubilise nutrient elements such as phosphorus, and others produce compounds which make iron more available for uptake. Nutrients can also be transported through connected networks of fungal mycelia between different regions of the soil at much greater rates than would occur if they were to diffuse freely.

Biological interactions

Mutualistic associations between plant roots and fungi are extremely common, and the natural state for the majority of root systems in non-flooded soils is to be infected to some extent by symbiotic fungi (Fig. III.IV). These associations are termed 'mycorrhizae'. There are four major types that differ in the plant host ranges and extent of fungal growth inside the root versus a proliferation around the root surface (Table III.I). In the mycorrhizal relationship, the fungus derives carbon and energy from the host, which is used to support extensive mycelial growth into the soil. The fungus absorbs nutrients, notably phosphorus, from the soil and transports this directly into the roots where it is absorbed and utilised by the plant host. A number of soil fungi are pathogenic on other organisms, including nematodes, insects, other fungi, and plants. Soil-borne fungal diseases of crop plants such as 'take-all' of cereals (*Gauemannomyces graminis*), tree pathogens like *Armillaria mellea*, and root rots caused by *Rhizoctonia solani* which attacks a wide range of plants, cause significant yield losses and can be difficult to control. There are also many symbiotic and parasitic relations between soil-dwelling insects and fungi. A number of ant species essentially 'farm' specific fungi in their nests, in highly regulated fungal-based composting systems which provide food for their colonies.

Soil structure

Fungi affect soil structure by a number of mechanisms. Hyphae serve to bind soil particles as they grow through pore networks, and dense mycelia can 'knit' the soil fabric together (Fig. III.V). Many of the biochemicals released by hyphae into the soil environment are adhesive, serving to glue soil particles together; other exudates are highly water-repellent and can stabilise soils by preventing water incursion. However, such repellency can also be a problem in that it can prevent water infiltration into the soil.

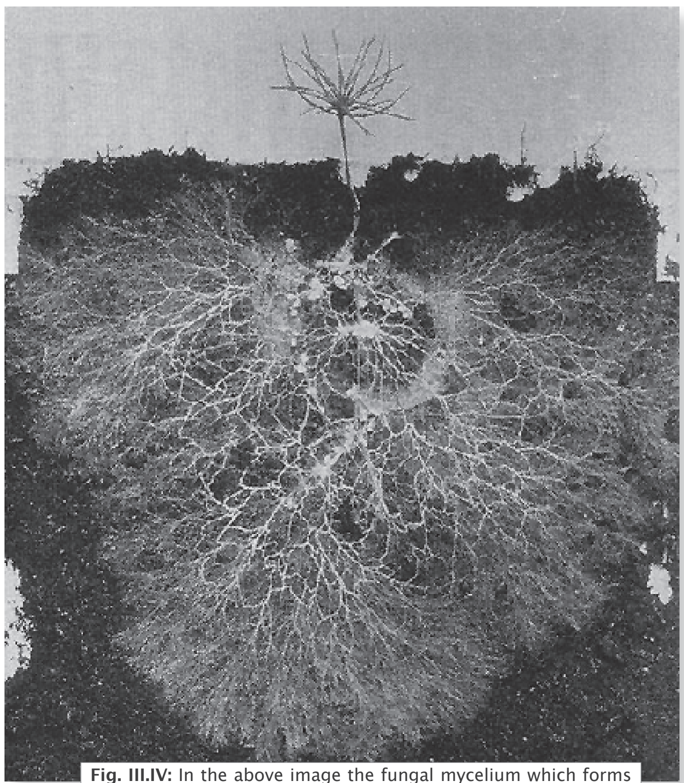


Fig. III.IV: In the above image the fungal mycelium which forms the mycorrhizal association with the plant roots are clearly visible. The white growth is almost all fungi and not plant roots as it may first appear. (PDI)

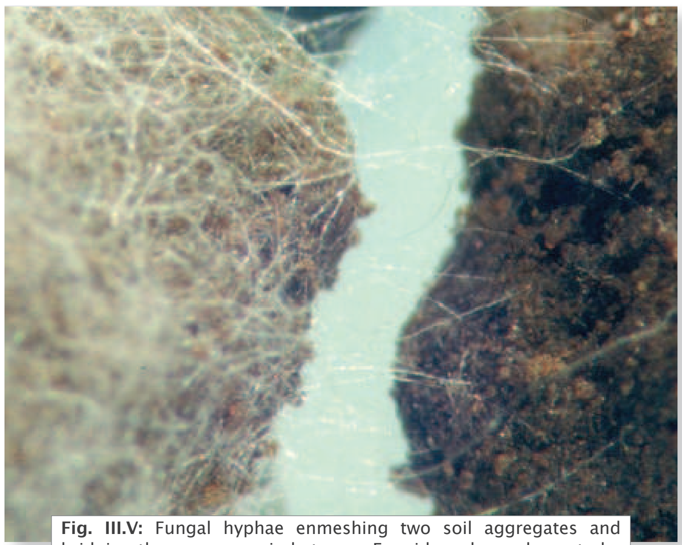


Fig. III.V: Fungal hyphae enmeshing two soil aggregates and bridging the pore space in between. Fungi have been shown to be important in reducing the risk of erosion through this mechanism, as well as others. (KR)

Biotechnological roles of soil fungi

Humans have long exploited edible types of soil fungi as a direct – and delectable – food source. The Perigord truffle (*Tuber melanosporum*; Fig. III.VI) is a fungus that is mycorrhizal on oak trees, and is on occasion the most expensive epicurean food on a weight basis. At the other end of the scale, the mass production of a mycoprotein derived from *Fusarium venenatum*, a fungus isolated from an arable field in England, is used in the manufacture a range of processed food products. Fungi produce a remarkably wide range of biochemicals which have been exploited industrially. These include organic acids, polysaccharides, antibiotics and agrochemicals. Fungi that are antagonistic to pests and weeds are also being used successfully as biocontrol agents in agriculture and horticulture.

Fig. III.VI: A sliced open Perigord truffle. Prices of these truffles can exceed 3000 Euros per kilo. (PDI)

Killer mushrooms:

Chinese scientists have recently discovered that a tiny mushroom belonging the genus Trogia, was responsible for around 400 sudden deaths in China, known as Yunnan Sudden Death Syndrome. During the rainy season, tens of people in Yunnan province died suddenly of cardiac arrest. A five-year investigation by researchers from the Chinese Centre for Disease Control and Prevention in Beijing has identified a mushroom, known as Little White, as the culprit. The mushroom, unknown to the scientific community, contains three toxic amino acids. Families, who make their living by collecting and selling fungi would eat the Little White as it had no commercial value.

Table III.I: The basic characteristics of the four mycorrhizal types. Taken from Ritz (2005)

Mycorrhizal type	Habit	Host Range	Examples	Notes
Arbuscular	Penetrates roots (Endotrophic); forms arbuscules and sometimes vesicles in root cortices	Approximately 90% of plants. Exceptions include plants of the mustard and cabbage family	Exclusively fungi of the order Gloales from the phylum Zygomycota such as *Acaulospora* and *Glomus*	Obligate mutualists; can only be cultured in associating with plants, including root organ tissue culture systems
Ecto- (ECM)	Does not penetrate roots (Ectotrophic); Forms extensive sheath around plant roots	Mainly woody plants such as trees	"Basidomycetes, which includes mushrooms, Ascomycetes and Zygomecetes"	May also grow saprotrophically in absence of host plant and in pure culture
Ericaceous	Endotrophic; extensive intracellular coils formed inside host cortex	Heathers	*Hymenoscyphus*, *Oidioendrum*	May enhance availability of N to host by degradation of soil organic N
Orchidaceous	Endotrophic; short lived intracellular coils in host root cells	Orchids	*Rhizoctinia*, *Marasmius*	Often obligate mutualism required for host plant to enable seedling developing. *Achlorophyllous orchids* are solely dependent on fungus for substrate

IV Mycetozoans (Slime Moulds)

Mycetozoans (commonly called slime moulds) are eukaryotic, spore producing, fungus-like organisms that feed primarily upon bacteria and other microorganisms in terrestrial habitats throughout the world. Although formerly classified as fungi, mycetozoans are not true fungi, and they actually have more in common with protozans such as amoebae than they do with the true fungi. However, mycetozoans are invariably studied by mycologists (the scientists who study fungi). Plasmodial slime moulds (commonly referred to as myxomycetes) are the largest group (with approximately 900 species) and best known of the mycetozoans, as well as the only examples that can be observed directly in nature. The cellular slime molds (also known as dictyostelids) are less familiar organisms only rarely observed under field conditions as they are microscopic in size for much of their lifecycles . Consequently, these organisms must be grown under controlled laboratory conditions in order to be studied.

Myxomycetes

Myxomycetes have a relatively complicated life cycle which was not understood completely until the latter part of the nineteenth century. In brief, the life cycle consists of two very different trophic (or feeding) stages, along with a reproductive stage that is distinctly different from either of the trophic stages. In the first of the two trophic stages the organisms consists of uninucleate (single-nucleus) amoeboid cells that may or may not have flagella. These amoeboid cells, derived from spores which have germinated, feed and divide by binary fission (whereby a cell divides into two, with each new cell having the potential to grow into new individuals) and can build up large populations in the microhabitats in which they occur. Ultimately, the amoeboid cells give rise to a second trophic stage, which consists of a distinctive multinucleate (a cell with many nuclei, not separated by cellular membranes) structure called a plasmodium which gives rise to the common name "plasmodial slime mold" used for this group.

Plasmodia have no cell walls and exist as thin masses of protoplasm, which often appear to be streaming in a fanlike shape in the larger, more commonly encountered examples (Fig. IV.I). Most plasmodia are no more than a few centimetres across, but those of some species can reach sizes of up to a square metre or more and weigh up to between 20 and 30 grams!

Ultimately, under suitable conditions, a plasmodium gives rise to one or more fruiting bodies (also sometimes referred to as sporophores or sporocarps) containing spores. Identification of myxomycetes is based almost entirely upon features of the fruiting bodies and spores. Spores can be dark or light to brightly coloured. The spores of most species are wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboid cells. The fruiting bodies of myxomycetes are somewhat suggestive of those produced by some fungi, although they are considerably smaller (usually no more than 1-2 millimetres tall). However, some can achieve macroscopic dimensions, with the largest known examples occasionally exceeding half a metre across! Fruiting bodies tend to be relatively ephemeral and do not persist in nature for very long (Fig.IV.II and IV.III).

The primary microhabitats for myxomycetes are decaying wood, litter (dead plant matter on the ground) and the bark surface of living trees. However, these organisms are also widespread and common, or even abundant in soils, where they are major predators of other microorganisms such as bacteria, yeasts, cyanobacteria and green algae. They form a significant component of the soil protistan biota and represent a major active part of the soil biomass. This would suggest that these organisms have considerable ecological significance. However, because of their cryptic life cycle and the fact that the number of specialists studying them is relatively small, myxomycetes are among the most understudied groups of soil organisms.

Fig. IV.I: Plasmodium of a myxomycete. (RD)

Fig. IV.II: Fruiting bodies of a myxomycete. (KF)

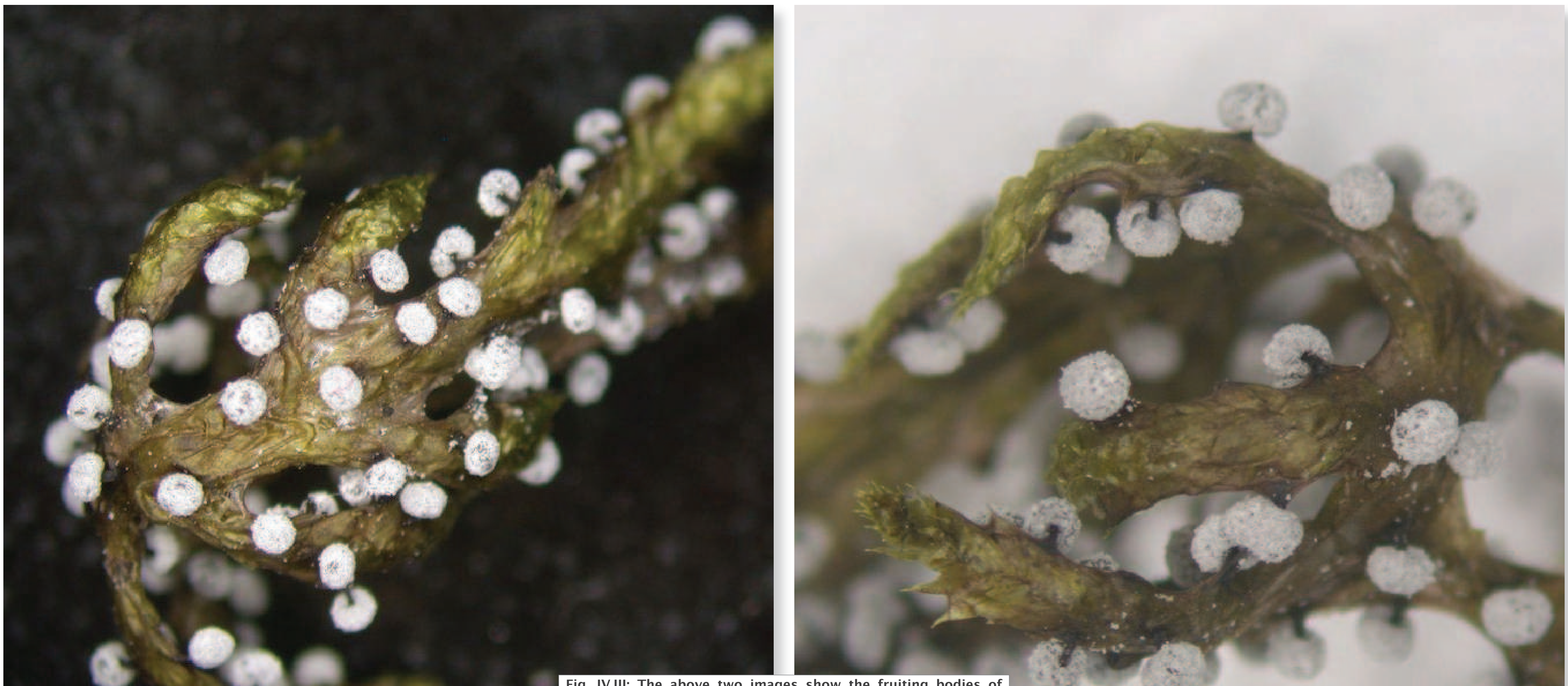


Fig. IV.III: The above two images show the fruiting bodies of myxomycetes which have formed on a moss. (KT)

Dictyostelids

The dictyostelids are easily mistaken for some of the microfungi that commonly occur as contaminants in laboratory cultures, so it is easy to see why they were originally considered to be fungi. Since their discovery by the German mycologist Oskar Brefeld in the late nineteenth century, dictyostelids have intrigued biologists because of their unusual life cycle. When one of their spores germinates, it releases a single amoeboid cell that begins to engulf and digest bacteria in the soil, the usual habitats for these organisms, along with decaying plant debris in the form of soil organic matter. When the amoeboid cell divides, the two cells separate and become completely independent of each other, with each cell continuing to feed and undergo additional divisions for a number of hours or days. Only after the growing population of amoeboid cells depletes the local supply of bacteria is there any indication that a multicellular structure will be produced. In response to the production of chemical signals, thousands of amoeboid cells which have been operating as individual single-celled organisms begin to move, either singly or in streaming masses, to form multicellular clumps, or aggregations (Fig. IV.IV). Shortly thereafter, one or more cigar-shaped structures called pseudoplasmodia emerge from each aggregation. A pseudoplasmodium is a unified collection of thousands of what had once been separate, independent amoeboid cells. The cells remain distinct in the pseudoplasmodium but no longer act independently. Instead, they cooperate as part of a multicellular entity.

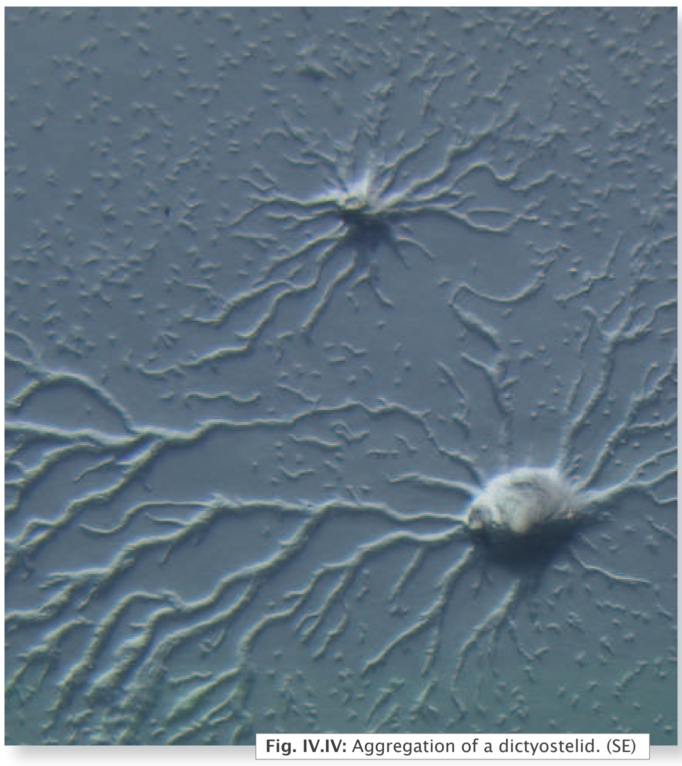


Fig. IV.IV: Aggregation of a dictyostelid. (SE)

Either immediately, or in some species after the entire structure has migrated a short distance towards a light source, cells of the pseudoplasmodium begin to display different patterns of specialisation. Cells that happen to have been positioned near the anterior end of the moving "cigar" begin to secrete a wall of cellulose. These cells bind together to form a slender stalk that grows upward from the surface of the substance upon which the pseudoplasmodium occurs. Other cells, those nearer the posterior end of the pseudoplasmodium, are lifted off the surface on the end of the extending stalk. These cells begin to turn into spores. Only the spores live on and produce another generation of amoeboid cells to feed upon soil bacteria. The cells that produced the stalk in order to elevate the spore cluster above the substratum eventually die, dry up, and decay.

The actual fruiting body produced by a dictyostelid typically consists of elongated, erect to semi-erect stalk (called a sorophore) that bears a mass of spores (sorus) at the tip (Fig. IV.V, Fig. IV.VI). The dimensions and branching patterns of dictyostelids vary greatly in different species. As a group, these organisms are not especially colorful, and the fruiting bodies of most species are white to essentially colorless. However, a few species are strikingly pigmented, ranging from deep purple to bright yellow although these colours fade rapidly. There are about one hundred and fifty described species of dictyostelids. These have been assigned to one of three genera – *Dictyostelium*, *Polysphondylium*, and *Acytostelium*. This classification is based solely upon morphology and does not necessary reflect evolutionary relationships. Indeed, molecular studies have provided evidence that the three genera do not hold together at all, with some species in two different genera seemingly being more closely related to each other than to species currently assigned to the same genus.

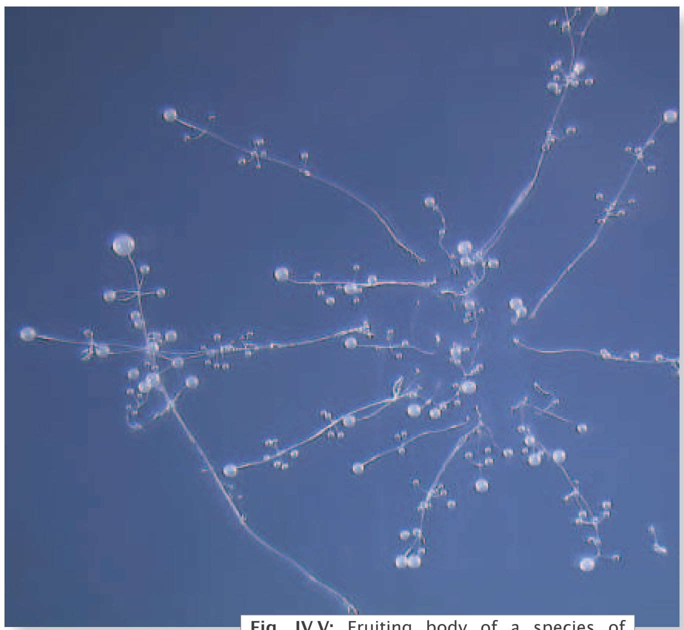


Fig. IV.V: Fruiting body of a species of *Polysphondylium.* (JSh)

Fig. IV.VI: Fruiting bodies of a species of *Dictyostelium.* (JSh)

Distribution and occurrence

Some species of dictyostelids are found in almost all parts of the world, whereas others appear to have a more restricted distribution. Numbers of species appear to be highest in the American tropics, and this suggests that the region represents a centre of evolutionary diversification of the group. More than 35 different species have been found in the small area around the Mayan ruins at Tikal in tropical Guatemala. The highest total known from any region in the temperate zone is 30 species for the Great Smoky Mountains National Park in eastern North America. In general, numbers of species of dictyostelids decrease with increasing elevation and with increasing latitude.

Myxomycetes associated with soil have been studied quantitatively only recently. Results from these studies indicate that they are abundant and widespread in virtually all types of soils, sometimes representing >50% of all of the amoebae present. Myxomycetes appear to be particularly abundant in the rhizosphere of agricultural soils and grasslands but considerable numbers (sometimes >80 plasmodium forming units/gram) also occur in the soils of temperate forests. The myxomycetes associated with soils of tropical forests have not yet been studied to any extent.

A Mycetozoan and a Maze

In a study published in Nature in the year 2000 it was demonstrated that *Physarum polycephalum*, a slime mould, was "intelligent" enough to solve a maze (Fig. IV.VII).

Over a period of four hours an organism of the species *P. polycephalum* was found to be capable of changing its shape into the most efficient form, being the shortest route through the maze. The plasmodium pseudopodia which were in dead ends shrank back leaving only those pseudopodia which spanned the minimum length between the nutrient containing agar blocks. This allowed the plasmodium to consume two different energy sources with minimal waste of energy, supporting unnecessary pseudopodia which did not provide energy to the rest of the organism.

This suggests, claim the authors, that the cells which made up the plasmodium where capable of some limited form of "primitive intelligence".

Nakagaki *et al.* 2000. Intelligence: Maze-solving by an amoeboid organism, Nature 407.
Figure reprinted with permission from Nature Publishing Group.

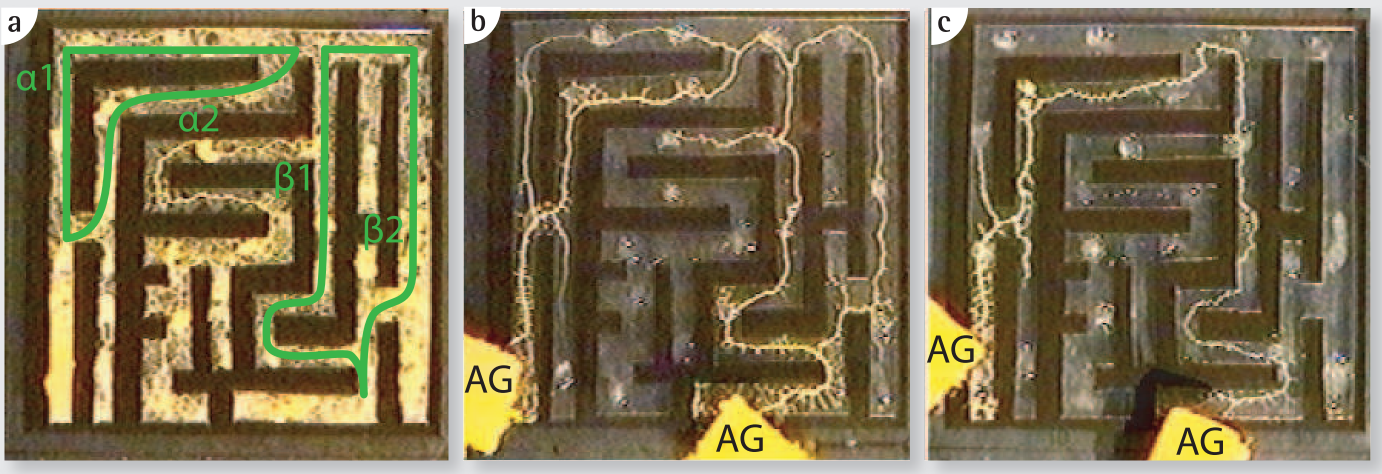


Fig. IV.VII:
a) Structure of the organism before finding the shortest path. Blue lines indicate the shortest paths between two agar blocks containing nutrients.
b) Four hours after the setting of the agar blocks (AG), the dead ends of the plasmodium shrink and the pseudopodia explore all possible connections.
c) Four hours later, the shortest path has been selected.

V Protozoa

Protozoa are a group of microorganisms which are classified as unicellular eukaryotes. Eukaryote refers to all organisms which contain a 'true nucleus', being a structure which can usually be viewed down a light microscope which contains the organisms genetic material (DNA). Furthermore, the cytoplasm of eukaryotes contains other structures called 'organelles' such as mitochondria or chloroplasts.

Protozoa are microscopic, being unicellular, and can grow up to approximately 1 mm in size in some cases. However, they are more usually between 10 and 50 μm in size. They are heterotrophic, meaning that they obtain their energy from organic carbon sources. This can be in the form of organic matter, such as small sections of decomposed plant matter or excreted compounds such as sugars. Alternatively it can also be in the form of bacteria and other small cells such as algae and small fungal cells, up on which the protozoa 'graze'.

Currently, over 30,000 different species of protozoa are known to exist, being found in both aquatic environments and the soil. The numbers of protozoa found in soil is highly variable and depends on many different factors. A low fertility soil may contain 'just' a few thousand cells per teaspoon of soil where as a more fertile soil may contain a million or more cells per teaspoon of soil. Soil moisture is also a big determinant as to which type of protozoa are likely to be present and active in a soil. Protozoa make up four different groups depending on their morphological characteristics. These are:

- Ciliates – being cells which are covered in hair-like organelles on their cellular membranes which are similar to flagella but are shorter and more numerous. As with flagella, cilia are used for locomotion. (Fig. V.I, Fig. V.II)
- Amoeboids – being cells which can deform and control the shape of their cell to produce pseudopodia, being bulges of cellular cytoplasm used for locomotion. (Fig. V.III, Fig. V.IV)
- Flagellates – being cells with 'whip like' organelles called flagella as external cell structures which are used for locomotion. (Fig. V.V)
- Sporozoans – being spore forming cells which are exclusively parasites of animals.

Protozoa are an important part of the soil system, and are both herbivores (consumers of bacteria and other primary producers), as well as being decomposers, break down organic matter. Herbivorous protozoa function to control the microbial biomass by grazing, and thereby release other essential nutrients, into the wider soil environment. When feeding on bacteria, nitrogen in particular is released. This occurs as the grazed bacterial cells contain relatively large amounts of nitrogen, meaning that the protozoa consumes an excess of nitrogen by the time it has consumed a sufficient quantity of carbon via bacteria grazing. This nitrogen is released into the environment in the form of ammonium (NH_4^+) which can then be taken up by other bacteria and higher plants.

As well as grazing on smaller microorganisms and decomposing organic matter, protozoa are themselves a part of the food chain being fed upon by other animals which are higher up the food chain. Furthermore, they are competitors with other bacteria feeding organisms such as some species of nematode, meaning that some soils can have either high numbers of protozoa or high numbers of nematodes, but generally not both. Increased understanding of soil protozoa has possibly strong implications for the sustainability of agriculture and other managed ecosystems due to their influence on both nutrient cycling and disease suppression. For example, one group of amoeba called Vampyrellids eat fungi. They do this by 'drilling' round holes into fungal cell walls through the use of enzymes produced by the amoeba. The amoeba then sucks the cytoplasm from the fungal cell before moving on to the next cell. These amoeba attack many different types of fungi including root pathogens such as *Gaeumannomyces graminis*, the causative agent of Take-all disease in wheat.

Soil Cilliates

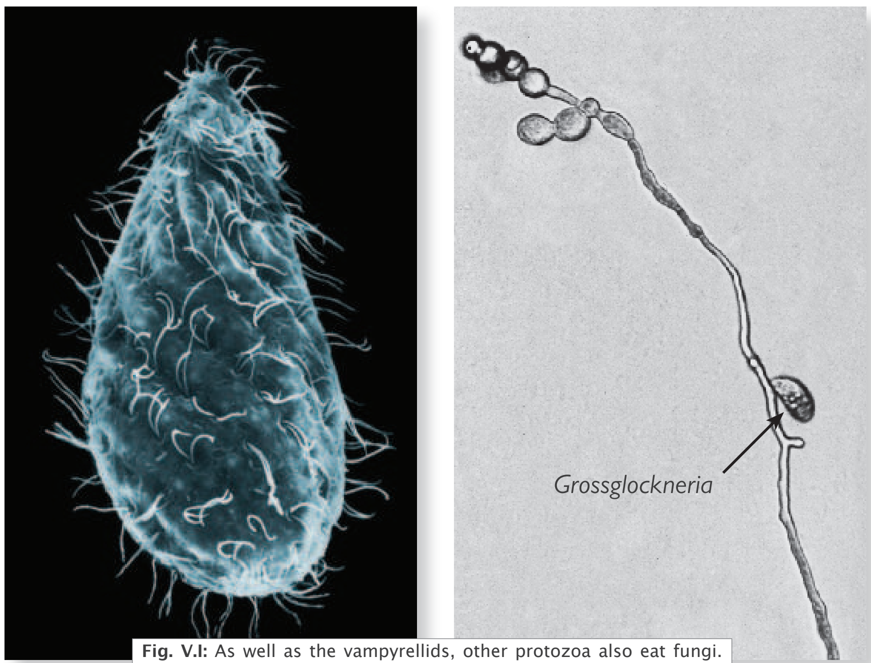


Fig. V.I: As well as the vampyrellids, other protozoa also eat fungi. The *Grossglockneria acuta* (**above left**) is about 70 μm in size and belongs to a ciliate group unique to soil known as Grossglocknerids. It has a special mouth located near the apical end and (**above right**) can be seen feeding on a fungal hyphae. (WF)

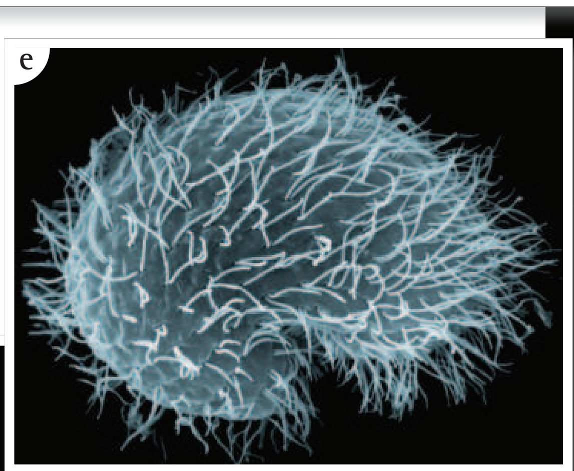


Fig. V.II: These images show various scanning electron micrographs (with post production colour added) of soil ciliates. They range in size from <70 μm up to 600 μm, as in the case of *Bresslauides discoideus* (image a); images are not shown to scale. There are thousands of soil-specific ciliate species, showing a great diversity in morphology, feeding, ecology, and adaptation. For instance, the *mycophagous ciliates* (a) or very slender *Engelmanniella mobilis* (b). Some species, such as *Grossglockneria acuta*, are small enough to exploit the soil pores. However, large species, such as *Pattersoniella vitiphila* (c) and *Bresslauides discoideus* (a) can be found in mosses and fresh leaf litter. Some ciliates are sessile (e.g. *Paracineta lauterborn* (d), a predaceous species which lives in a neat, chitinous 'shell') although these are rare because food is quickly depleted in the soil pores. The most common soil ciliates belong to the genus Colpoda (e) and thus the soil ciliate community is called Colpodetea. The Colpoda group has greatly radiated in the soil environment, producing, *inter alia*, the mycophagous ciliates. (All images: WF)

Naked Amoeba

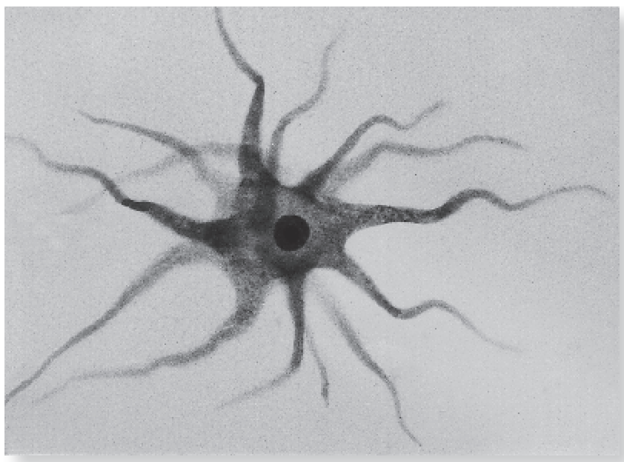
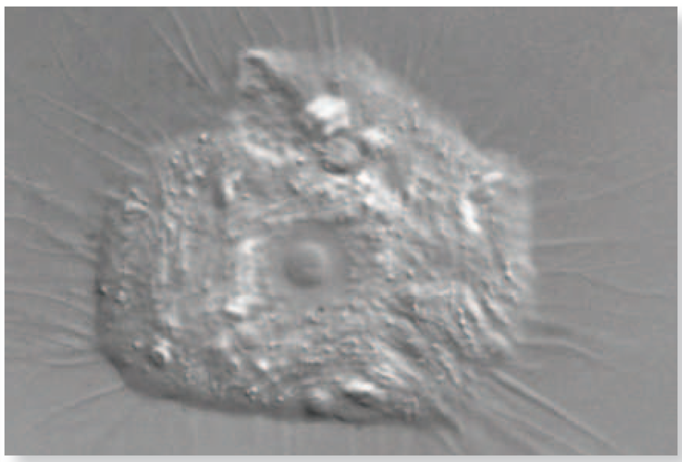
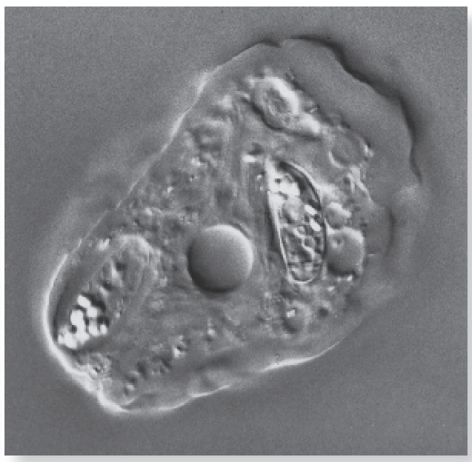
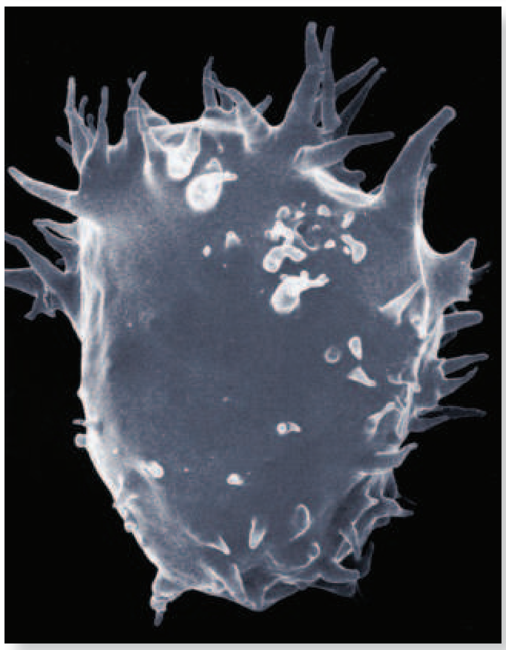
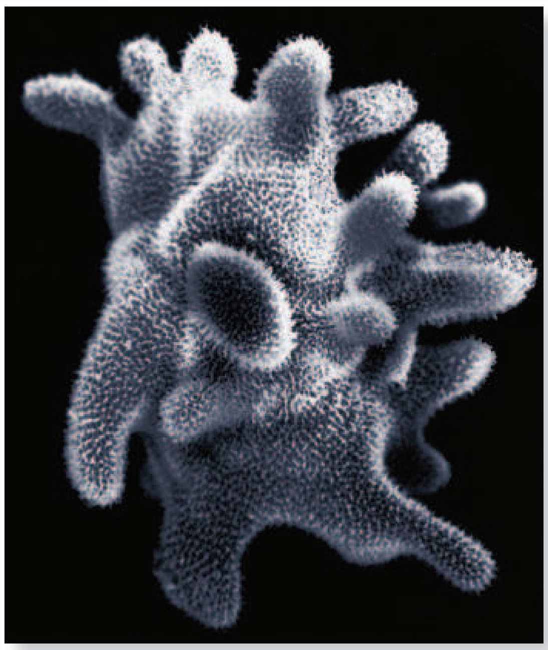






Fig. V.III: These images show various species of naked amoebae. The three above images were taken via light microscopy, with the two images to the left being taken via scanning electron microscopy, with colour added post production.

Soil naked amoebae are small, usually having a size between 10 µm and 100 µm. The cell nucleus is usually in the cell centre, being the circular structure visible in the images **above left** and **middle**.

Some amoeba have very thin and highly flexible pseudopodia, allowing them to exploit even very small soil pores (≤ 0.5 µm) and graze on the bacteria colonising the wall of the pores (**upper left** and **middle** image). However, others have thick pseudopodia, called lobopodia (**lower two images**), and feed on larger food items, such as fungal spores and ciliates. Naked amoebae are very numerous, i.e. there may be up to 40,000 individuals in 1 g of soil and, as such, they are important in soil energy flux. (WF)

All protozoa scanning electron micrographs have had colour added to them in Photoshop as a post production step by N. Frost to help highlight details. All organisms shown appear colourless in nature.

Testate Amoeba

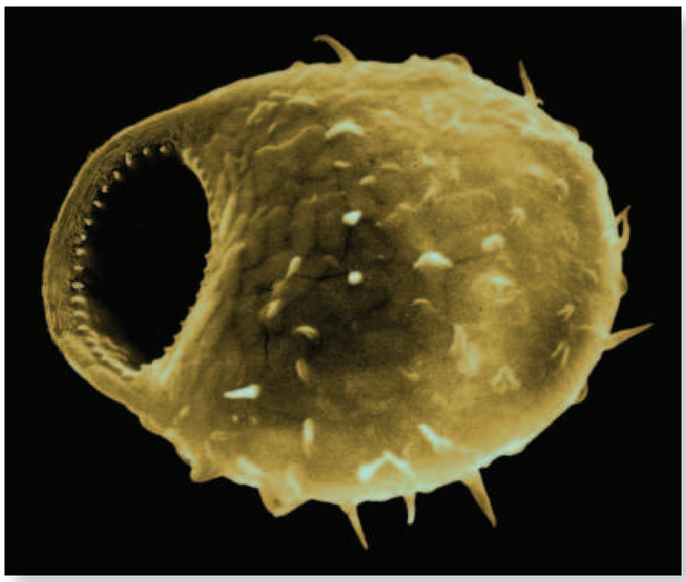
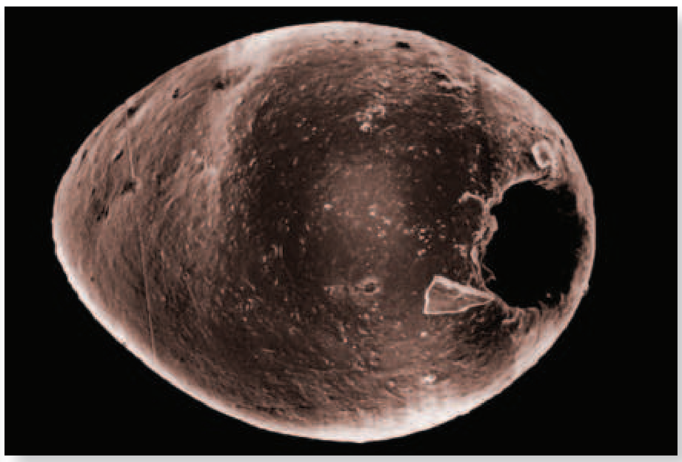
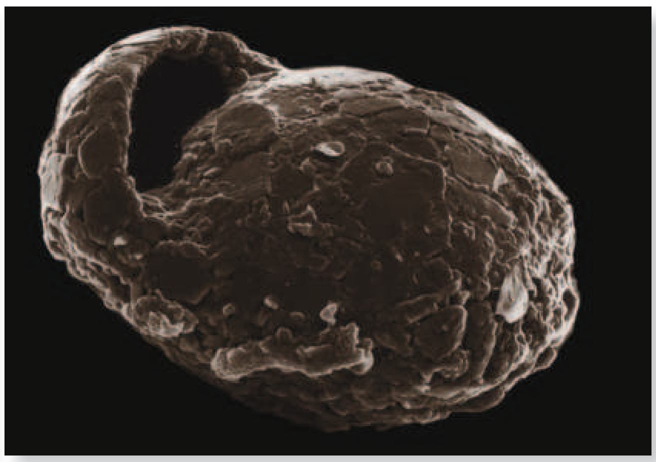
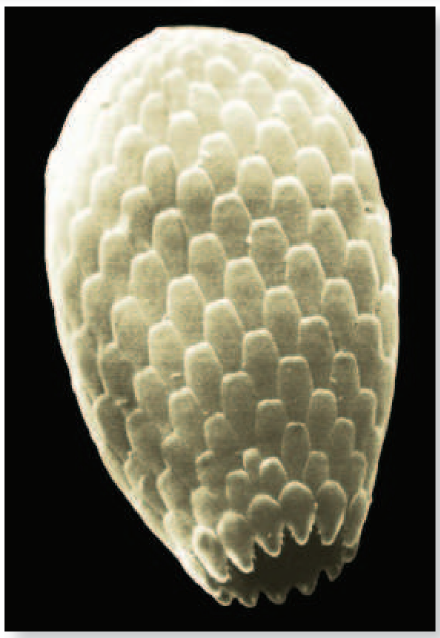
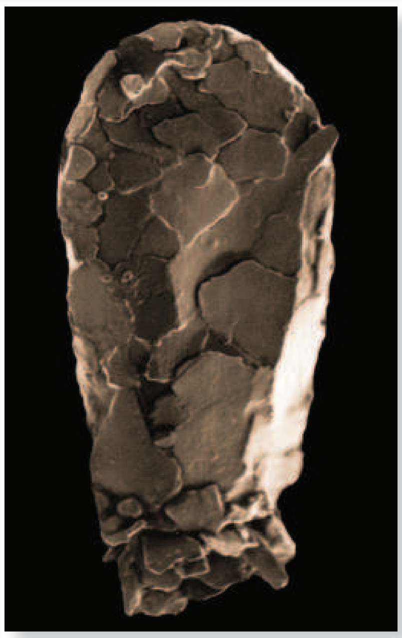




Fig. V.IV: These images show scanning electron micrographs (with post production colour added) of various testate amoebae. Their size ranges between 30 µm and 100 µm. There are usually up to 20,000 individual testate amoeba in just 1 g of soil. Testate amoebae play an important role in the energy flux of the soil and are excellent indicators of soil quality. The testate amoebae are basically similar to the naked amoebae, except of having a shell with a small opening called pseudostome. The shell is either made of siliceous platelets produced by the amoeba, as in *Corythion asperulum* (**top left**) and *Euglypha* (**bottom left**), or of mineralic particles taken from the soil environment, as in *Pseudawerintzewia orbistoma* (**top middle**), *Difflugia lucida* (**bottom right**), and *Centropxsis cryptostoma* (**top right**). The pseudostome of soil testate amoebae is often smaller than that of lake and river dwelling species to minimise loss of water. Accordingly, many of the species occurring in soil are specialised and restricted to the soil environment. (WF)

Soil Flagellates

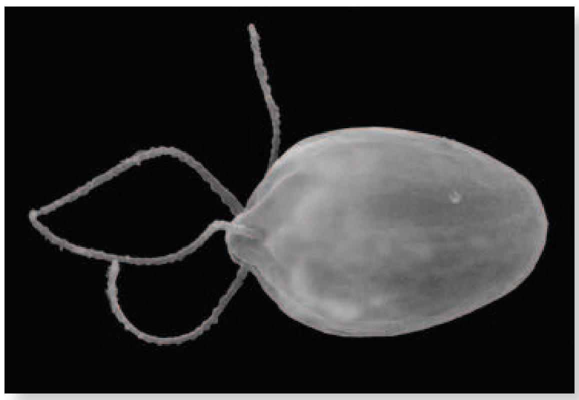
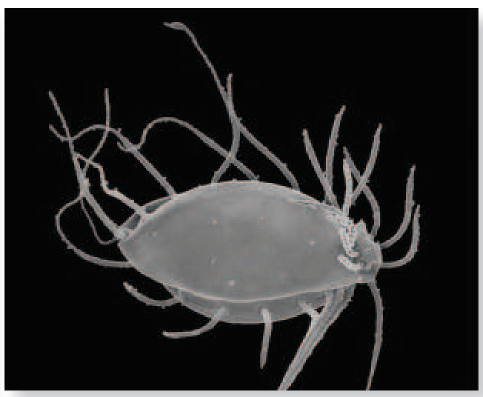



Fig. V.V: The images to the left show electron micrographs (with post production colour added) of two different species of soil flagellates, named for the long tentacle like protrusions called flagella which are used for locomotion. *Polytomella* sp. (**left**) has four flagella and is very common in soil globally. They are usually about 20 µm in size.

Hemimastix amphikineta, a 20 µm-sized flagellate with two rows of flagella, occurs only in soils in central and south America as well as Australia soils, likely being a palaeoendemic, that is it probably used to exist over a much greater range which has become reduced in size over time. The fine structure of this organism is so peculiar that it has been classified in a distinct phylum, the "Hemimastigophora". (WF)

VI Tardigrades

In 1773, a German pastor, Johann August Ephraim Goeze (1731-1793), was the first to describe a new animal in the book "Herrn Karl Bonnets Abhandlungen aus der Insektologie": "… *strange because of its extraordinary anatomy and at first glance its appearance has a strong resemblance to a little bear. It is because of this I will name them small water bears*…" Goeze also included the first drawing of a tardigrade in this book (Fig. VI.I).

Six years after the publication of Goeze, the famous naturalist Lazzaro Spallanzani (1729-1799) made the first scientific description of the water bear. Since then they have been called tardigrades. The name refers to the animal's slow movements (Lat. *tardus* - slow, *grado* - walker).

The group of tardigrades is quite old. Two fossils are known from amber which trapped the creatures and was formed in the Upper Cretaceous period which was 60 – 80 million years ago. Another specimen has been discovered in amber which is approximately 92 million years old. There are also a few specimens known from the mid Cambrian (around 550 million years ago), which have been attributed to a stem-group of the water bears.

The number of known tardigrade species has been increasing steadily over the last decades. In 1972, 301 water bear species were known and had been catalogued, with the number increasing to 531 by 1983, 960 by 2005, and today we know more than 1,000 different species of tardigrades from all over the world. Tardigrades can be found in a variety of habitats including marine, brackish, freshwater and terrestrial ecosystems, ranging from the deep sea to the highest mountains, as well as in many extreme environments ranging from the coldest to the hottest and driest places.

Terrestrial tardigrades mostly live in patches of moss or lichens (Fig. VI.II): they can be up to just over 1 mm in size. They have a cylindrical body with four pairs of clawed legs (Fig. VI.III). Marine tardigrades are often less than 0.5 mm in size, and can have various different appendages in place of claws. The body of tardigrades can also carry appendages. Not much is known about their feeding behaviour in general, although it is known that many tardigrades are carnivorous or at least omnivorous. They typically hunt protozoans, rotifers, and nematodes, living within the same habitat. Within seconds, they pierce their long and sharp-edged stylets into the prey and suck the body fluids. Small prey can be eaten completely (Fig. VI.IV). Although some species have eyes, they are generally poor and do no appear to be used for hunting. Herbivorous tardigrades are able to pierce the cells of moss or green algae whereby they can feed by sucking out the cellular fluids.

Sexual reproduction or mating takes place, but observations are really rare. However, many species are parthenogentic (i.e. the ovum does not require fertilisation to develop into a new individual); therefore no males are known. This may be an evolutionary advantage for colonisation of new habitats as a single female is able to establish a new population. Many tardigrades lay freely single eggs with a miscellaneous egg-shell morphology (Fig. VI.V). But there are also species which lay egg clutches into the exuvium after molting. The embryonic development varies between a few days to several months, depending on species, but all animals molt continuously throughout their life time which varies also between a few months and a couple of years.

Due to their ability to enter a cryptobiotic state (similar to an extreme form of hibernation whereby all metabolism stops) at any developmental stage, tardigrades are capable of surviving extreme conditions for very long periods of time and are able to extend their lifespan significantly.

Drying of cells and whole organisms generally leads to massive damage of cellular properties, which usually results in cell death and, consequently, death of the organism. However, this is not the case of tardigrades. They have the remarkable ability to circumvent such problems by retracting their legs and entering a form known as a tun (from the German word "Tönnchen") (Fig. VI.VI) during periods of desiccation. This is an ametabolic state; a state without visible signs of life. In this state they are able to survive exposures to extreme temperatures over 100°C, they are freezing tolerant and can also survive ionizing radiation, and high pressure. Tardigrades have even been shown to be able to survive in the vacuum of open space. A number of tardigrades were exposed to the vacuum of space in a low earth orbit for 10 days. It was found that on return to earth many of the organisms survived and laid eggs which hatched normally. Currently, the longest known observation of an extended lifespan in the tun state was 20 years.

Due to the fact that tardigrades show extraordinary tolerances to a range of physical extremes they are now being used as a new model organism to study mechanisms of preservation in several fields of research and applied technologies. Tardigrades may eventually tell us something fundamental about the nature of life itself.

Fig. VI.I: The earliest known drawing of a tardigrade by Goeze in 1773.

All images on this page were produced by Eye of Science.

Fig. VI.II: A tardigrade of the species *Paramacrobiotus kenianus* sitting on a moss leaf.

Fig. VI.III: The tardigrade *Echniscus granulatus* has relatively long appendages and strong claws.

Fig. VI.IV: A tardigrade of the species *Paramacrobiotus tonollii* feeding.

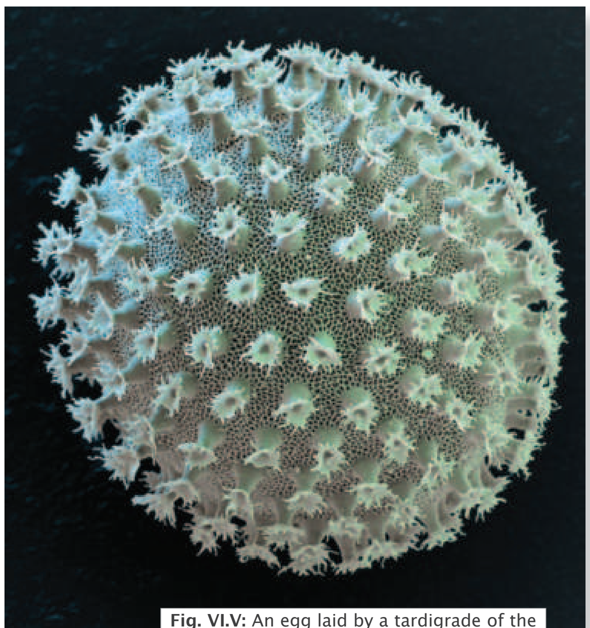


Fig. VI.V: An egg laid by a tardigrade of the species *Marcobiotus sapiens*.

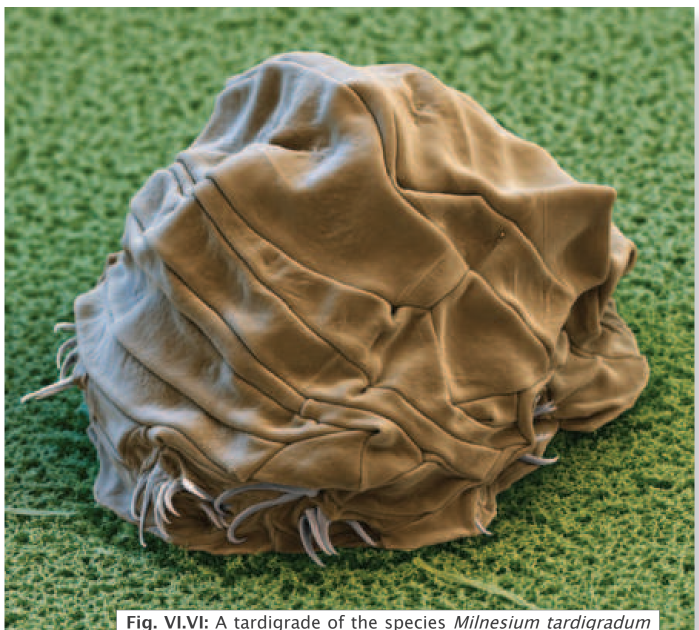


Fig. VI.VI: A tardigrade of the species *Milnesium tardigradum* which has entered a tun state. No signs of life are detectable while tardigrades are in this state, although they are capable of revival when environmental conditions again become suitable.

VII Rotifers

Within the top layer of soil or litter, and in moss growing on the soil, rotifers are one of the most abundant taxa which will be found when looking down a microscope (Fig. VII.I). These minute animals, generally between 0.2 and 0.4 mm in size can be found creeping like miniature leeches, gliding over surfaces, or feeding or swimming through the action of their ciliary corona, a feature which has given them their name, Rotifera or "wheel-bearers" (Fig. VI.II). Rotifers, as many soil microorganisms, require an aqueous matrix for any of their activities. In moist soil habitats, rotifers can occur at densities ranging from about 32,000 up to more than 2 million per m^2! However, the diversity of the rotifers is relatively low, with only about 2030 species currently described, but this is most likely an underestimate considering the occurrence of cryptic diversity, i.e. the possible presence of biologically distinct, but morphologically hardly discernible species, in all morphological species tested so far.

Soil rotifers belong to two groups with very different ecology, reproduction, and physiology. The most abundant and diverse soil rotifers belong to the belloids (Fig. VII.III), a group most renowned by its exclusive parthenogenetic reproduction and ability to undergo anhydrobiosis. All of the approximately 460 known species of bdelloids lay eggs which are capable of growing into adult forms without fertilisation. In fact, no form of sexual reproduction at all is known to occur in this group. This condition makes bdelloids outstandingly interesting model organisms for studies on the evolution of sex. In addition, bdelloids are capable, to a varying degree, of anhydrobiosis (as discussed previously for Tardigrades). This condition enables the animals to survive extended periods of desiccation, which can last up to 20 years, and they may become active again minutes to hours after rehydration of their environment.

In their anhydrobiotic state the animals contract into a minute barrel, by retracting both their head and foot inside the trunk, and by slowing their metabolism to an undetectable level.

The second group, the monogononts (Fig. VII.IV, Fig. VII.V), contains only a few species found in the terrestrial environment, but is the most successful in freshwater ecosystems. These animals alternate parthenogenetic and sexual reproduction, which results in resting stages consisting of encapsulated embryos. The combination of parthenogenetic reproduction, enabling the colonisation of habitats by a single specimen, and ability to form resistant stages determines the dispersal and, therefore, biogeography of both groups of rotifers.

The vast majority of soil rotifers are microphages that feed by grazing the bacterial film which grows on substrates (e.g. *Adineta*), or by filter-feeding on suspended bacteria, yeasts or algae cells and other particulate matter within the soil water where they are present. Only a few species have the ability to ingest larger particles, and only a single one species known as *Abrochtha carnivora* is a predator, mostly of other bdelloids.

A number of peculiar monogononts of the genera *Albertia*, *Balatro*, *Claria* are parasites of annelids such as earthworms, living in the body cavity and intestine of terrestrial earthworms such as *Allolobophora*, and enchytraeids such as *Fridericia* and others. However, the impact on their hosts is poorly known. Rotifers themselves are in turn preyed upon by Turbellaria (flatworms) and predatory nematodes and form an important component of the diet of other ciliated microorganisms such as *Bursaria* and *Spatidium*, and especially tardigrades.

Apart from a few species such as *Colurella*, the vast majority of soil rotifers require live specimens for study and identification. In particular, bdelloids need to be examined during feeding as well as creeping, in order to evaluate characteristic features. This problem is exacerbated by the very active and erratic behaviour of quite a lot of species. As a consequence, studying soil rotifers is often a tedious and time-consuming occupation, which possibly explains why relatively little is known about these animals and the role they play in soil ecosystems. However, they appear to constitute only a small fraction of soil biomass and are therefore in general not considered a keystone group in the functioning of soil ecosystems.

Commercial uses of Rotifers:

Rotifers eat particles of fish waste, dead bacteria, and algae that are up to 10 micrometres in size. Like crustaceans, rotifers contribute to nutrient recycling. For this reason, they are used in aquariums to help clean the water and prevent clouds of waste matter. Rotifers can markedly affect the species composition of algal communities in ecosystems through selective grazing.

Rotifers are also used in sewage treatment plants to clean wastewater. The principal role of rotifers in wastewater treatment is the removal of non-flocculated bacteria and the development of floc. Mucus secreted by rotifers at either the mouth opening or from the foot aids in better floc formation.

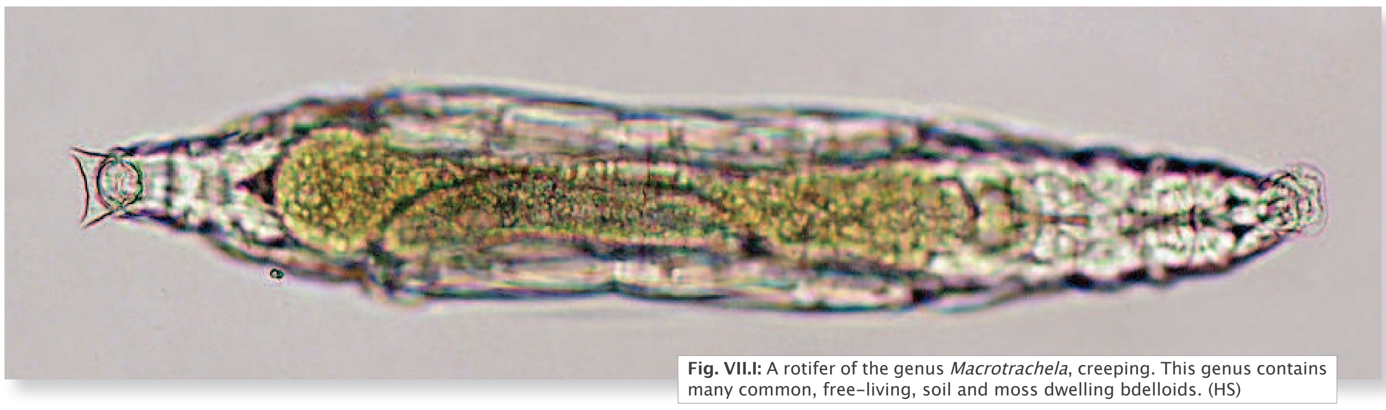


Fig. VII.I: A rotifer of the genus *Macrotrachela*, creeping. This genus contains many common, free-living, soil and moss dwelling bdelloids. (HS)

Fig. VII.IV: This undescribed species of terrestrial *Colurella* is one of several, morphologically similar and minute species of this genus of monogonont rotifer. (HS)

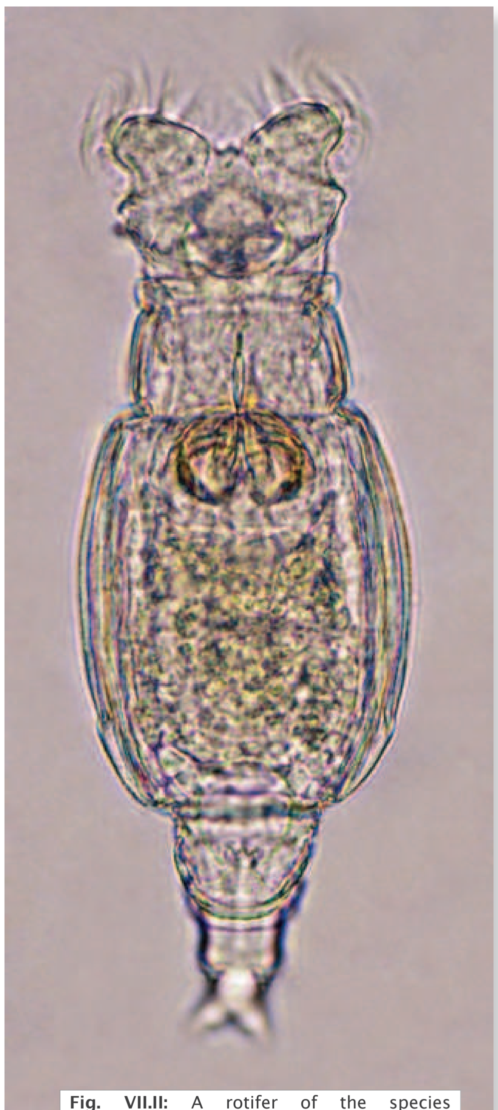


Fig. VII.II: A rotifer of the species *Macrotrachela vanoyei*, feeding, showing the ciliary corona at the top of the organism. (HS)

Fig. VII.III: A bdelloid rotifer of the genus *Habrotrocha*. With over 125 valid species recognised, this genus is one of the most diverse of all bdelloid rotifers. (HS)

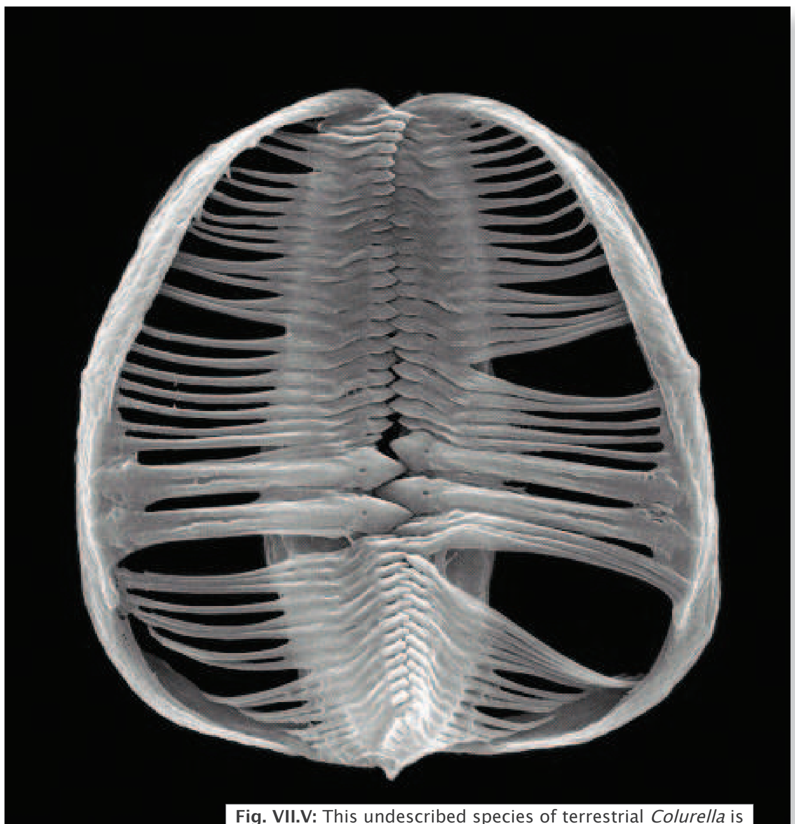


Fig. VII.V: This undescribed species of terrestrial *Colurella* is one of several, morphologically similar and minute species of this genus of monogonont rotifer. (HS)

VIII Nematodes

The name *Nematode* is derived from ancient Greek and means "thread like". This is an apt description as nematodes are essentially thin multi-cellular cylindrical tubes encapsulating all the necessary organs required for survival (Fig. VIII.I). They range in size from a microscopic 80 µm to 8 m in length and from 20 µm to 2.5 cm in diameter (Fig. VIII.II). However, the larger lengths refer to parasitic nematodes with the majority of free living nematodes in soil and water being a few milimetres in length at maximum. Nematodes are considered aquatic organisms and in soil inhabit the water film around soil particles. Nematodes are also sometimes known as roundworms or eelworms.

Fig. VIII.I: A nematode of the genus *Hirschmaniella*. All nematodes species from within this genus are plant parasites. (HvM)

They are arguably the most abundant (ranging from 1 to 10 million per metre square in cultivated soils) multicellular organism phylum on earth with respect to both species richness (number of species) and abundance. Approximately 30,000 nematode species are known to science, but this is considered to be only about 5 % of the estimated global nematode species number.

Nematodes have adapted to survive in the harshest environments from the Antarctic to desert environments and in marine environments too. Depending upon their life cycle, some nematodes can use animals, insects, man and plants as their host. In the developing world, although not exclusively, some serious human diseases are caused by nematode infections e.g. Guinea worm, elephantiasis.

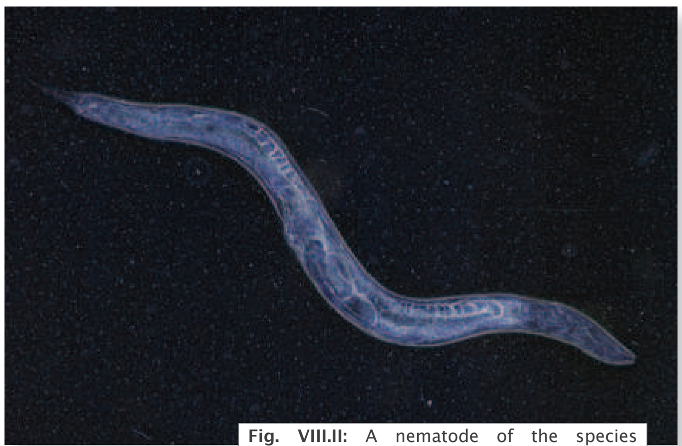


Fig. VIII.II: A nematode of the species *Pristionchus pacificus*. This nematode species is being used as a model nematode in many macro and microevolutionary studies. (MR)

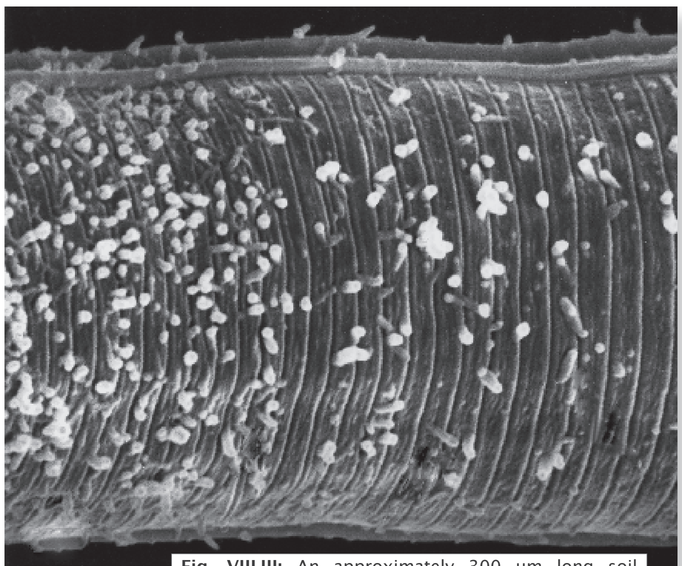


Fig. VIII.III: An approximately 300 µm long soil nematode colonised by about 3 µm long bacteria. (WF)

Free-living nematodes have been classified into eight feeding groups of which the five main feeding types are bacterivores, fungivores, omnivores, plant parasites and predators. These groups are used as indicators of the quality of marine and land environments. It is difficult to identify nematodes to species level, but it is relatively easy to distinguish the different nematode feeding groups based on the shape and size of their mouthparts.

Nematodes are considered very important in the soil food web and are known as keystone species within the soil ecosystem. They perform major roles in many soil processes such as mineralisation and decomposition. Therefore, as well as identification using mouth parts, nematode fauna can also be classified according to other ecological characteristics, such as the 'life history traits'. These traits concern the way in which an organism reacts to its surroundings. For example, species which are able to respond quickly to sudden nutrient-rich conditions are called 'colonisers', due to their fast reproduction. There are also 'persister' organisms, which have long life cycles, low reproduction rates and make specific adaptations to the surroundings. Environmental factors such as food availability, vegetation composition and abiotic conditions (e.g. soil type) determine which combination of nematode species and functional groups are present. Furthermore, nematodes can have perhaps unexpected effects such as moving other soil organisms through the soil. For example, Fig. VIII.III shows a nematodes' skin to be colonised by bacteria and it is possible that the nematodes functions as a 'vehicle' for the immobile bacteria which allows them to get food more easily.

What do they eat?

Different nematode species are usually specialised to feeding on different groups or types of organisms and this can be seen by the different types of mouth parts which have evolved.

Plant Feeders

Some nematodes (Fig.VIII.IV), feed on plants. These species have hollow, needle-like structures that are used to puncture cell walls in plants thereby allowing the nematodes to be able to suck out the nutritious cell contents (**a**, head of *Paratrichodorus*; **b**, head of *Hirschmaniella*). Plant-eating nematodes are mostly known as pests in agriculture and some of these species can have large economic impacts. For example, *Hirschmaniella* can cause considerable yield decreases when it is present in rice fields. *Globodera* (**c**) is a parasite on potato plants and *Pratylenchus* (**d**) is parasitic on many different crops.

Omnivores

The image of Fig.VIII.V shows the head of *Dorylaimus* sp., an omnivorous nematode which is able to feed on different food sources depending on the environmental conditions and food availability. *Dorylaimus* has a big hollow tooth that can be used as a stylet to puncture other organisms or to suck liquids. The nematodes can function as predators, feeding on protozoa and possibly other nematodes when available, but changing to feeding on fungi and bacteria when its primary food source is no longer available. Feeding habits may also change from juvenile to the adult stage, for instance from bacterial feeding in the juvenile stage to becoming predatory in the adult stage.

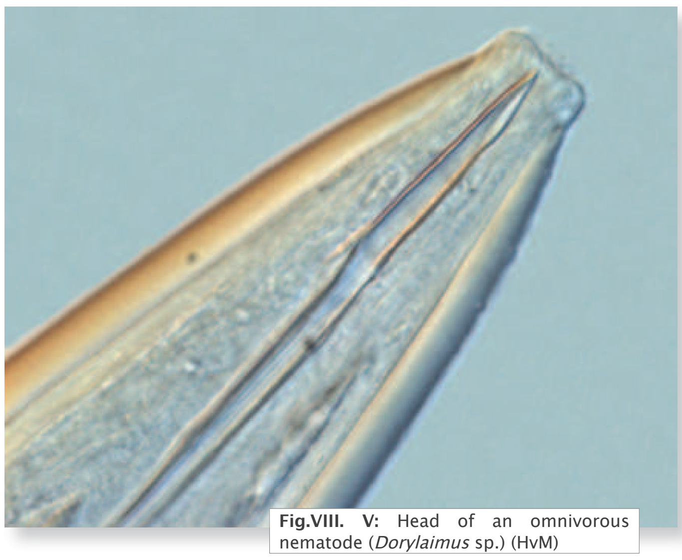


Fig.VIII. V: Head of an omnivorous nematode (*Dorylaimus* sp.) (HvM)

Nematodes and health:

Several nematodes are parasitic to mammals. Common examples include filarias, hookworms, pinworms (*Enterobius*) and whipworms (*Trichuris trichiura*). *Baylisascaris* usually infests wild animals but can be deadly to humans as well. *Dirofilaria immitus* are Heartworms known for causing Heartworm disease by inhabiting the hearts, arteries, and lungs of dogs and some cats. In contrast, entomopathogenic nematodes parasitize insects and are considered by humans to be beneficial.

Nematodes can also cause severe damage to both cultivated and wild plants by both directly infecting the plant or by the transmission of viruses.

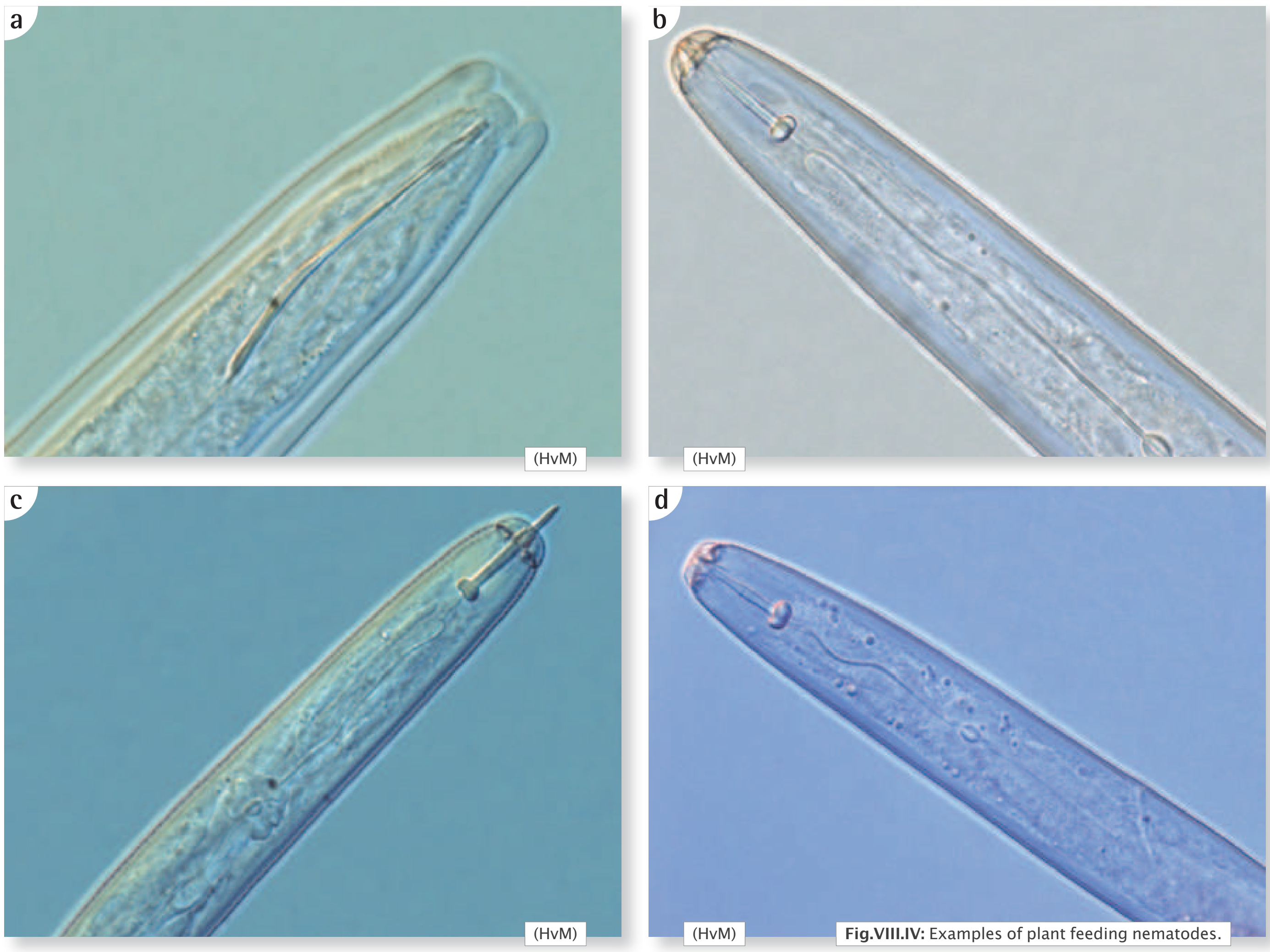


Fig.VIII.IV: Examples of plant feeding nematodes.

Bacteria feeding nematodes

Some species of nematode feed on bacteria. Nematodes such as *Acrobeles* sp. (Fig. VIII.VII a) have outgrowths on the anterior end called probolae which are possibly used to scrape bacteria off of soil particles. However, the probolae cannot move independently and so there is another alternative hypothesis that the probolae are used to filter water and that the particles are caught by the outgrowths. *Acrobeles* are restricted to sandy soils as in clayey soils, which have much smaller particles, the probolae seem to be less functional.

However, many bacterial feeding nematodes do not have probolae. *Acrobeles complexus* (Fig. VIII.VII b) and other nematodes from the order Rhabditida, for example have no outgrowths but have a tube shaped mouth which is used to swallow bacteria.

There is some preliminary scientific evidence that, as well as being responsible for turn over of carbon and nitrogen in the soil through grazing on bacteria, bacteria feeding nematodes can stimulate plant root growth through the stimulation of plant hormone production. This occurs due to changes in the soil microbial community as a result of nematode grazing.

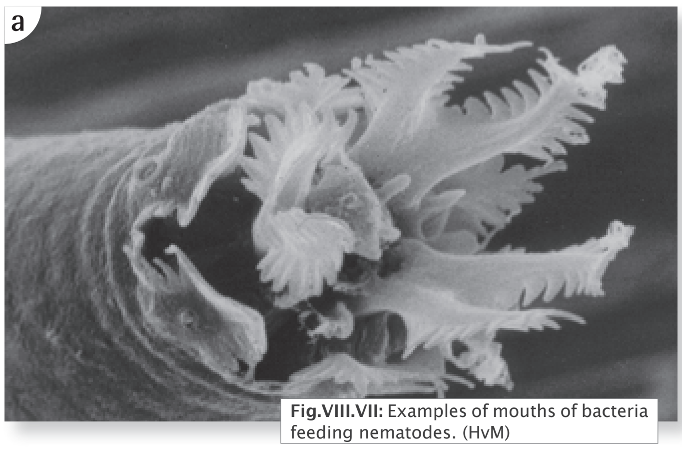
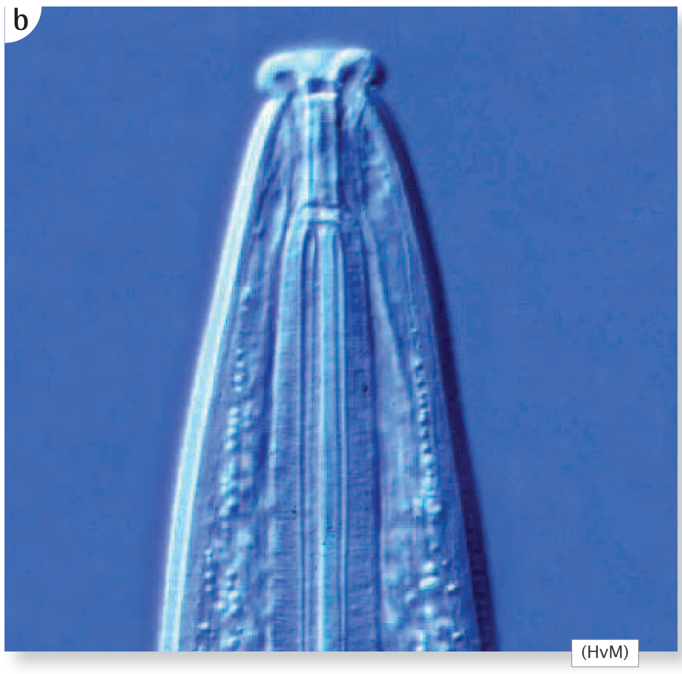
a


Fig.VIII.VII: Examples of mouths of bacteria feeding nematodes. (HvM)

b


(HvM)

Fungivore nematodes

Some nematodes feed on fungi. Species include *Tylencholaimellus* sp. (Fig. VIII.VIII b) and *Anomyctus xenurus* (Fig. VIII.VIII a). Fungiverous nematodes can affect plant growth via the destruction of arbuscular mycorrhizal fungi leading to reduced nutrient availability for the plant. However, some species can be beneficial for pest control through destruction of pest fungal species. Fungal feeding nematodes are generally less abundant than bacterial feeding nematodes especially in highly disturbed soil systems such as convential agricultural soils. Fungivore nematodes also contribute to nutrient mineralisation by releasing important plant nutrients such as nitrogen from fungal tissue. However, the contribution of nutrients such as nitrogen in agricultural systems is usually much greater by bacterivore nematodes than fungivore nematodes.

a

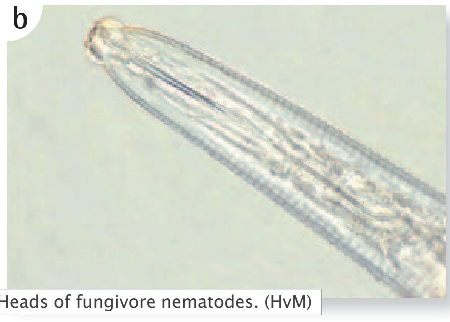

b


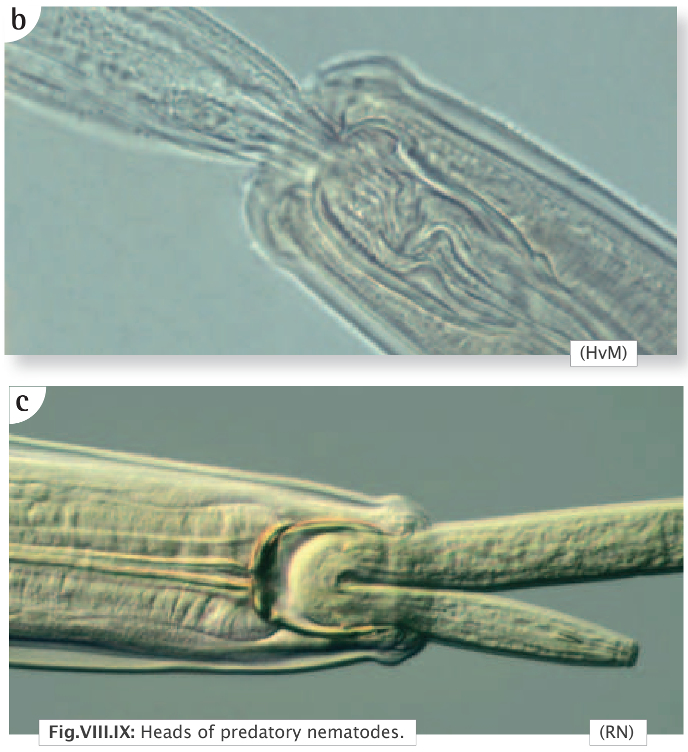
Fig.VIII.VIII: Heads of fungivore nematodes. (HvM)

Predatory nematodes

Other nematodes are able to suck or injest other nematodes or other small animals (Fig.VIII.IX). Predatory nematodes represent approximately 5% of the overall soil nematode community. In soils, predatory nematodes vary in physical size whereas, in contrast, in the marine environment predators are frequently the largest nematodes: a) predatory nematode *Mononchoides*; b) close-up of *Prionchulus* with prey; c) *Anatonchus tridentatus* feeding on an unsuspecting nematode.

a


(HvM)

b


(HvM)

c

Fig.VIII.IX: Heads of predatory nematodes. (RN)

Pest Control

Only a few nematodes species are pest organisms, even if some of them can cause severe damage to crops. Most nematodes are beneficial to mankind by stimulating nutrient cycling, controlling insect pests or even for scientific research. One group of nematodes is so useful that they are actually cultured and commercially available: the entomopathogenic nematodes. This group contains nematodes that are able to infect insects. This may not sound very appealing, but it is a very effective way of controlling insect pests without using pesticides (Fig. VIII.X).

The nematode itself does not kill the insect; they do not have special structures in their head to attack and kill. Instead they use biological warfare: once they have entered the insect via natural openings, bacteria are released that produce toxins which will eventually kill the insect. These entomopathogenic nematodes have a special structure for storing the bacteria that will kill the insect host (Fig. VIII.XI). Once all of the resources within the host's body are consumed the infective juveniles escape and enter the soil where they wait for a new host to become available to allow them to complete their lifecycle.

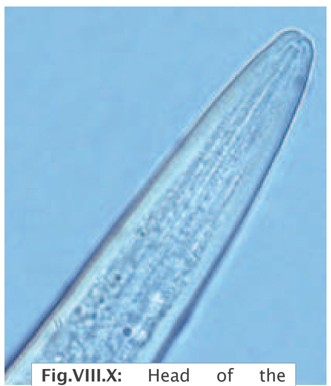


Fig.VIII.X: Head of the entomopathogenic nematode *Steinernema*. (HvM)

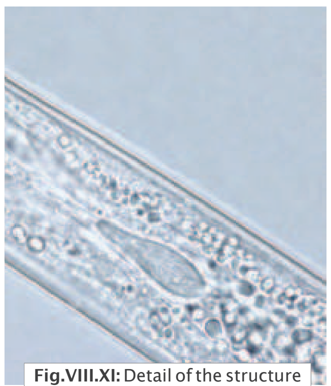


Fig.VIII.XI: Detail of the structure used by entomopathogenic nematodes, to store the infecting bacteria. (HvM)

Harsh Environments

As previously mentioned, nematodes are found in almost all ecosystems on Earth ranging from Antarctic soils through to hot volcanic springs. Species such as *Scottnema lindsayae* (shown **right**), *Plectus antarcticus*, and *Eudorylaimus antarcticus* have all been found in the McMurdo Dry Valleys of Antarctica where annual mean temperatures are around –20°C, with temperatures only hovering around freezing during the summer, and annual rain (or snow) fall of between only 2 and 50 mm water equivalent.

However, perhaps an even harsher environment to cope with are deeper layers within river and estuarine mud flats, where oxygen can be limited or non-existent. This is normally not a problem for many species of bacteria which thrive in an oxygen free environment and in fact can be killed by oxygen. However, very few multicellular organisms are able to survive in anaerobic (without oxygen) environments. *Tobrilus*, (shown on the **far right**), is a genus of nematodes often found in mud layers, which can be oxygen deficient. Metabolic analysis suggests that at least some species from this genus are able to function anaerobically and that even when oxygen is available they continue to function as partial anaerobes.

(MMu)

(HvM)

IX Collembola

Collembola are also known as springtails as many species have a furcula at the end of their abdominal section. This is usually folded beneath the organisms and held under tension which can be released when the organism is threatened causing the 'springtail' to spring and throw the organism into the air. Collembola are small arthropods which are found in soil environments throughout the world, even in the Arctic and Antarctica (Fig. IX.I, Fig. IX.II)! They are classified as 'hexapods', being the largest group of arthropods, including all six legged arthropods, including insects. Collembola (along with protura and diplura) are no longer considered insects. Collembola are thought to be the most abundant hexapods on Earth and are found in soil, leaf litter, fallen branches and even shorelines. There are over 6000 known species of collembola, and in just one handful of grassland soil there can be hundreds or thousands of individual collembola, representing hundreds of different species. Collembola are primarily detritivores and microbivores feeding on fungal hyphae and other organic detritus. Along with nematodes, collembola are one of the main biocontrol agents on microbial populations.

The distribution of collembola in the soil is stratified vertically as well as being variable horizontally. Some species are better adapted to living in the leaf litter and at the soil surface (Fig. IX.III), and there organisms are usually pigmented with relatively long limbs and scales or hairs to help prevent dessication. Those species which live in deeper soil layers usually have diminished eyes and limbs as well as lacking pigmentation. The evolutionary roots of these differences is discussed in more depth in Section 7.3.

Collembola are highly sensitive to desiccation, with the precise level of sensitivity being variable between species. Those that live at depth in soil are usually more sensitive to desiccation than those that live at the soil surface. Collembola play an important role in nutrient cycling through their influence of microbial decomposition. This is because they graze on fungi and bacteria and therefore affect decomposition rates. A few species have been shown to be pest organisms with the species *Sminthurus viridis* having been shown to cause extensive damage to agricultural crops in Australia.

Recent data on population genetics of the Artic species suggests that there has been a glacier refugia in the North West Canadian Arctic which has served as a dispersal source back into more Southern areas. The dark colour of the many Arctic species is probably an adaptation to survive the high UV radiation which is present during the Arctic summers. Most Arctic species lives in mosses, between rocks and can probably feed on cyanobacteria and other types of microorganisms. Arctic species survive Arctic winters through being inactive in times of particularly harsh environmental conditions and by producing a range of sugars that prevents them from freezing.

Fig. IX.I: *Hypogastrura concolor*. This collembolan is widespread in the high Arctic and probably has a circumpolar distribution. During a research expedition to the Canadian Arctic, Nunavut, this species was found to be highly abundant. Although its size is only about 1 mm it has managed to disperse over the Artic region since the last glaciation. However, how it acheived this long range dispersal through such as harsh environment as the Arctic is not known, although it has been found that some collembolans have managed to disperse over 700 km across oceans in the Arctic. (SH)

Fig. IX.II: *Desoria* sp. Some species of Collembola, particularly *Hypogastrura harveyi* and *Hypogastrura nivicola* are often referred to as 'Snow fleas'. This is because they can sometimes be seen jumping around on the surface of snow on warm days, as in the case of *Desoria* sp., shown on the **right**. Actually, they are collembola and not fleas at all, but the fact that they can survive and are mobile on snow, as well as being distributed around the Arctic (as the species shown above) highlights the amazing adaptability of collembola which has allowed them to colonise virtually every terrestrial ecosystem on Earth. (UT)

Fig. IX.III: *Entomobrya nivalis* is an epigeic collembolan living on the soil surface. They are usually approximately 1-2 mm in length, are very common and have a very wide distribution throughout the world. They can often be found on branches and flowers and are relatively resistant to desiccation. (UT)

Collembolans and transfer of moss sperm

We all know that insects or wind can help plants in bringing pollen from one plant to another and in that way ensure sexual reproduction of the plant. But how about other land plants like mosses that are, in evolutionary terms, older than vascular plants and are fertilised by sperm which need wet conditions in order to swim from one moss to another? Scientists have long believed that moss spores needed to be carried by water and that insects or other invertebrates were not responsible for transporting the sperm between mosses.

From a simple experiment it has now been shown that fertile moss shoots attract collembolans and mites, which carry moss sperm in an accidental manner after having come into contact with the sperm, similar to bees with pollen in flowering plants, thereby enhancing the fertilisation process. In one experiment, patches of male and female mosses were placed apart at various distances and collembolans were allowed to freely move among the moss patches. Fertilisation occurred only in mosses that were kept apart when collembolans were present confirming the important role of collembolans in moss fertilisation.

The role of collembolans in moss fertilisation is analogous to the role of animals as pollinators of flowering plants, but may be much older due to the antiquity of the organism groups involved. Mosses and collembolans are extant representatives of groups of organisms that originated and radiated after the early phase of land colonisation (440-470 million years ago). Animal-mediated fertilisation in mosses therefore potentially pre-dates similar interactions in other plant groups.

Fig. IX.IV: A Collembola of the species *Isotoma caerulea* passing over a moss where moss sperm can become attached to its body and be translocated to other mosses leading to fertilization. (KH)

Fig. IX.V: Assessing the numbers of collembolans is done with a split corer which does not compress the soil. The collected soil sample is kept in a cylinder and brought to a high gradient extractor that dries out the soil. At which point the collembola leave the soil core allowing them to be collected, counted and identified (for more details see Chapter 8.2). (PHK)

Fig. IX.VI: Another epigeic collembolan, of the species *Isotoma viridis* s.l. (UT)

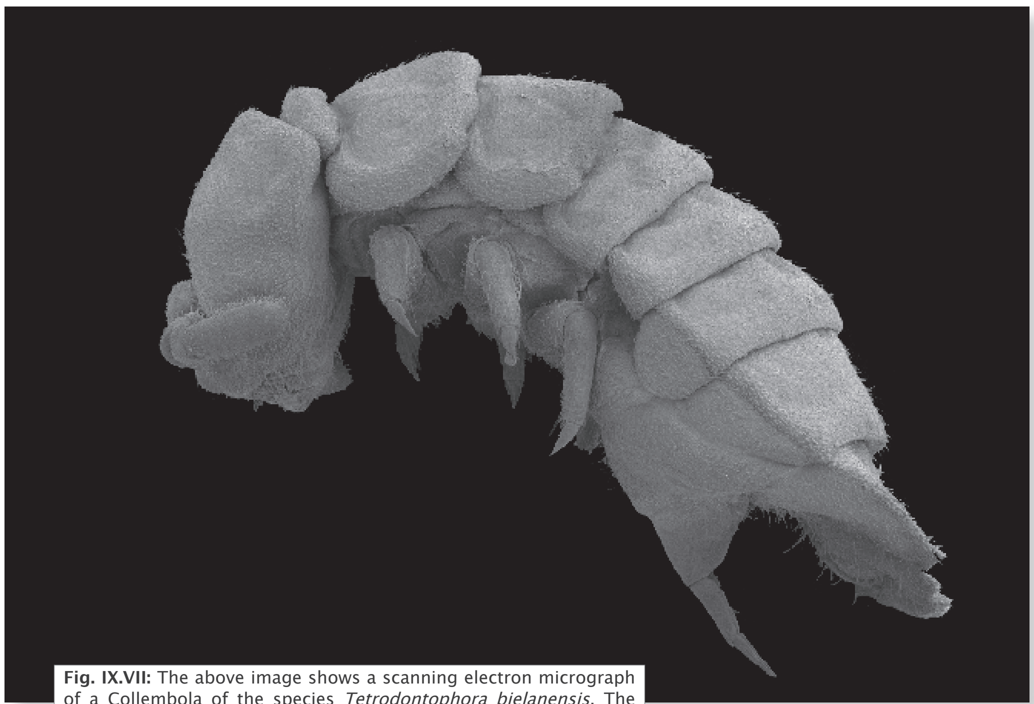


Fig. IX.VII: The above image shows a scanning electron micrograph of a Collembola of the species *Tetrodontophora bielanensis*. The image clearly shows the extended furcula under the abdominal section of the organism. This is usually folded and when extended rapidly is the 'spring' in the 'springtail'. The above shown species is relatively large and as well as having the springtail is able to excrete small droplets of a sticky defensive liquid when attacked. (JM)

Fig. IX.VIII: As discussed previously, Collembola show morphological adaptions depending on their preferred living depth in the soil. Those collembola shown on the opposite page, as well as above (Fig.IX.VI), are all pigmented, probably to provide protection from UV radiation as well as possibly as camouflage from predators. However, those organisms that live generally deeper within the soil, such as *Protaphorura fimata* – a true soil dweller shown above (the larger of the two species present) – need neither protection from UV radiation which penetrates very poorly into soil (<2 mm), nor from predators that live within the soil as they do not use sight to hunt, owing to the lack of light and, therefore, the collembola that live at depth would not have been exposed to evolutionary selection pressure favouring camouflage. As well as several *Protaphorura fimata*, the above picture shows several individuals of *Proisotoma minuta*, which are on average approximately 1.3 mm in length. They often live in flower pots and in organic matter, where they can be found in large numbers. (PHK)

Fig. IX.IX: The above picture shows a closer image of a *Protaphorura fimata* which is approximately 2.5 mm in length. These species is both white and blind, two consequences of it spending a large portion of its life below ground. (PHK)

Fig. IX.X: The above image shows many *Mesaphorura macrochaeta*. They average between 0.6 and 0.7 mm in length and are a true soil dwelling species meaning they spend all of their life cycle living within the soil. It is a very slim and slender collembola and so has access to very small pores within the soil pore system. It is non-pigmented, blind and does not have a springtail. (PHK)

X Acari

Soil mites are, together with collembolans, the most numerous arthropods in the soil with usually thousands or tens of thousands, but possibly even up to several hundreds of thousands of individuals per square metre in a given habitat. They are present in all types of soils throughout the world, including extreme arctic and antarctic soil habitats (see Section 3.7). In addition, they also inhabit many other microhabitats where dead organic matter is present such as peat, mosses, lichens, tree bark, rotting wood etc. Mites are also numerous in above ground ecosystems, mostly living as parasites on animals (eg. ticks, gamasid mites, bee-mites) or plants (e.g. spider-mites, gall and rust mites, etc.). Others feed on different kinds of organic detritus (e.g. feather-mites, dust- and house-mites) or are free living and predatory. A large and diverse group of mites also lives in water habitats (i.e. water mites, suborder Hydracarina). Soil mites, with the body being generally between 0.2 and 0.8 mm, and rarely above 1 mm in size, are considered to be an important group of soil mesofauna. Mites as a group are evolutionary very old. Oribatid mites, very similar to those still living today from the group of primitive oribatids, have been found as fossils in Devonian deposits. The presence of the same forms throughout the hundreds of millions of years demonstrates both the very high relative stability of ecological conditions in soil, and the very high value of soil biodiversity at both genetic and species level.

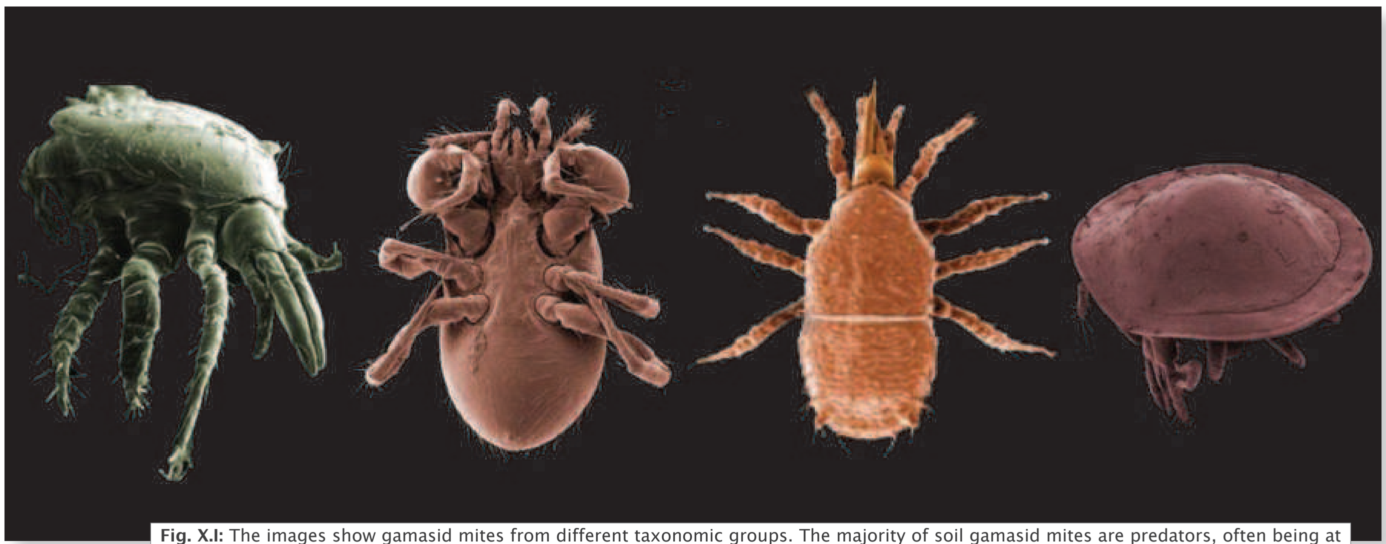


Fig. X.I: The images show gamasid mites from different taxonomic groups. The majority of soil gamasid mites are predators, often being at the top of the soil food webs, preying on Collembola, nematodes, insect larvae or even larvae and nymphs of other mites. On the **far left** is a lateral view on the species *Hypoaspis aculeifer*. This is an approx. 2 mm long predatory species which is present in soils in Europe and which is used for the biological control of plant pests in greenhouses. Using its first pair of legs as antennae , it can detect its collembolan prey in soil by detecting odour, not only from the collembolans, but also from fungi, the prefered food of the collembolans, even recognizing the smell of the preferred food species of fungi. As well as collembolans, *Hypoaspis aculeifer* can feed on enchytraids as shown in Section XIX. Mouthparts of predatory species are usually raptorial, armed with multiple teeth, and often very big (as can be seen here). In the middle are two other predatory species in ventral (**left**) and dorsal (**right**) views. Specific group of so called turtle mites from the tribe Uropodina (on the far right) show a variety of feeding habits from predation or detritivory. The body is lens-like and is strongly sclerotized, with special space for attachment of legs. This protective covering most probably helps protect the species from attack by predators. Photos: left (EH), left middle and far right (JM), right middle (DW).

Taxonomically, mites belong to the Arachnids and are therefore related to spiders, scorpions, harvestmen and pseudoscopions. They were originally classified as single order, but modern studies have shown that they are most probably not monophyletic and actually consist of several different taxons. The systematics of mites is still under development and therefore still under discussion. The most widely accepted view is that taxonomically there are two major groups of mites, classified as subclasses, superorders or orders and known as acariform and parasitiform mites. While the further classification is complicated, it can be simplified in that, in the soil, the highly diverse group of acariform mites (Acariformes or also Actinotrichida) is mostly represented by numerous species of prostigmatid mites (Prostigmata) and oribatid mites (Oribatida). The second group, parasitiform mites (Parasitiformes or also Anactinotrichida) is represented by mostly predaceous mesostigmatid or also gamasid mites (Mesostigmata or Gamasida), with specific non-predatory subgroup of turtle mites (Uropodina) (Fig. X.I).

Mite development is very complex, typically consisting of egg, larva (with no more than 3 pairs of legs) and several nymphal stages. Adults may be similar to nymphs or quite different (e.g. in many oribatid mite species). Many mite species does not need to mate to reproduce as they are parthenogenetic (i.e. only females exist which lay unfertilised eggs which are capable of developing into adult mites without the input of a male). Even sexual species of soil mites (e.g. oribatids) do not necessarily copulate, males produce and excrete sparmatophores, which are afterwards collected by females.

Fig. X.II: Two surface dwelling species of prostigmatid mites. Both species are relatively big, clearly pigmented as well as having long legs which aid mobility over the surface. A soft body surface covered by numerous small hairs is a typical feature of many Prostigmata. (UT)

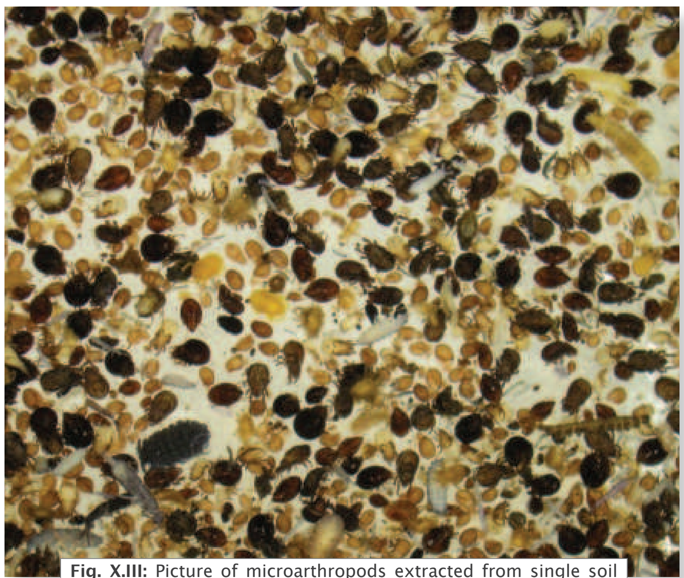


Fig. X.III: Picture of microarthropods extracted from single soil sample from forest soil, taken by a sampling device with 6 cm diameter. The image shows very high variety of size, shape and colour of microarthropods, among which mites and particularly oribatid mites clearly dominate. (LM)

Fig. X.IV: Examples of oribatid mites from deeper layers of soil (from left to right: *Quadroppia monstruosa*, representative of the family Brachychthoniidae and representative of the genus *Suctobelbella*) These are predominantly euedaphic species, with shorter legs and small compact body (about 0.25 mm). Body surface can be strengthened and protected by well developed ribs and spines. *Suctobelbella* mites have mouth parts (chelicerae) elongated and acute, probably adapted to sucking out the liquid contents of cells such as fungal hyphae. The contrast with soil surface dwelling mites is clear when comparing the images with those in Fig. X.II which are much larger and have much longer legs. Photos: left and right (JM) and middle (DW)

Parasitic Acari:

Some parasitic Acari, feed on vertebrate hair or blood. These often carry disease organisms, such as spirochete bacteria which are responsible for illnesses such as Lyme disease (the most common tick-borne disease in the Northern Hemisphere). Because ticks can carry more than one disease-causing agent, patients can be infected with more than one pathogen at the same time, compounding the difficulty in diagnosis and treatment. Ticks tend to be more active during warmer months, though this can vary. Areas with woods, bushes, high grass or leaf litter are likely to have more ticks.

All colour on the scanning electron micrographs was added post production in Photoshop by N. Frost with the exception of images attributed to DW.

As with other arachnids, adult mites usually have four pairs of legs and a body organised into two main parts (with the two parts being different in mites than in other arachnid groups). However, segmentation of these two parts is strongly reduced, and thus invisible, and in some cases the two main segments are even fused. The body surface (cuticle) of many soil mites is often thickened, forming an armour like protection which functions to protect body from both drought and also from predator attacks (Fig. X.V). The most peculiar structure of some oribatid mites are the blades called pteromorphs, resembling wings of insects, but not used for flying but rather to cover and protect retracted legs (Fig. X.VII). The mouthparts of mites are highly variable, being adapted according to the usual diet of the mite species, i.e. for biting, stinging, sawing or sucking. Soil mites are blind, owing to their edaphic lifestyle, and only few of them have one or few simple eyes. Some other surface-, litter- or moss-living species have developed a single, dorsal, unpaired light-percepting area. Conversely, other receptors (mostly being mechanoreceptors or chemoreceptors) are very well developed, usually as sensory hairs (setae, or sensilli – see Fig.X.VII) and pore-like or cup-like formations on the cuticle (known as bothridia). These sensory organs are present on various parts of the body, often on the distal part of legs or on anterior and dorsal part of the body.

The distribution of mites within the soil profile is unequal, both horizontally and vertically. Mites are most numerous in surface layers, which are richest in organic matter and soil bacteria and fungi. However, some species may be found very deep within the mineral soil layers. Surface dwelling and euedaphic mites are adapted to their lifestyles similarly to other soil microarthropods (see also Section 8.4). Horizontally, they usually appear in clusters, depending on the soil humidity, vegetation cover and presence and distribution of dead organic matter. Mites usually move very slowly and only over short distances, but still they are able to colonise almost every soil relatively rapidly. This is possible due to different strategies for travelling larger distances. Mites may move passively in the air (wind) or water, or they may actively attach to the body of different animals which cover much larger distances than the mite would alone (so called phoresy). The most common phoresy is on the body of larger insect species such as flies or beetles, but mites also can also be transported in the feathers of birds or in the fur of small mammals.

Mites are extremely species-rich, over 48,000 species are already described and the total number of species is estimated to be somewhere between 400 - 900,000! In European countries, soil mites are usually represented by several hundreds to few thousands of species per country, with the highest levels of species richness being found in the Mediterranean and Balkan areas. Ecologically, different species of mites are adapted to almost all environmental conditions found on Earth, and have developed virtually all possible feeding strategies, underlining their ecological importance. Predatory species regulate the numbers of their prey. Other species may be parasitic or semi-parasitic and feed either on plant roots or on the bodies of soil dwelling mammals or other animals. Most soil species are, however, involved in decomposition of dead organic matter, preferably consuming either larger parts of plant tissues (macrophytophages) or finer detritus together with fungi or bacteria decomposing it (microphytophages, or also fungivores, bacterivores). Some species distribute fungi and bacteria on the surface of their bodies and so help to inoculate organic matter. Not all mites are necessarily positive from an anthropogenic viewpoint. Parasitic species of mites may be important pests of farm animals and agricultural crops.

Almost all mites contribute to the formation of soil structure and soil humus; directly through fragmenting the organic matter and the production of finely structured faeces (sometimes called fecal pellets), and indirectly by regulating the population of other decomposers, mostly fungi and bacteria. Soils which have lost large part of their mite and other microarthropod communities tend to be degraded much faster and lose a large part of their important functions (e.g. holding cacapcity for water or nutrients, keeping carbon sequestrated in soil etc.). This, combined with their high species richness and ecological variability, makes mites a very good target for biological indication.

Fig. X.V: *Eupelops torulosus*, a species of oribatid mite which feeds by hollowing out the cells of decaying plant leaves. The body is strongly sclerotized and covered by thick irregular layer of cerotegument, which provides protection against both desiccation and predators. Ear-like pteromorphs are clearly visible on lateral side of the body, as well as lamellar structures and setae on the anterior part of the body. (JM)

Fig. X.VI: *Gymnodamaeus bicostatus*, a species of surface dwelling oribatid mite. The body is rather big (0.7 mm), well sclerotised, and legs are long. On the posterior part of prodorsum are two cup-like openings (so called bothridia) with a specific, large sensory seta – so called sensillus. A pair of sensilli growing from bothridia are typical for oribatid mites (see also Fig. X.VII). (JM)

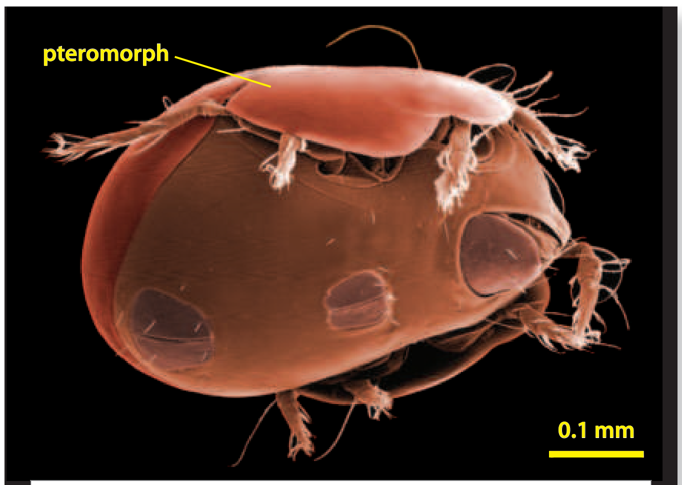


Fig. X.VII: Oribatid mite of genus *Galumna* with well developed, movable blades resempling insect wings – pteromorphes. These are nevertheless not used for flying, but for protecting body appendages. (DW)

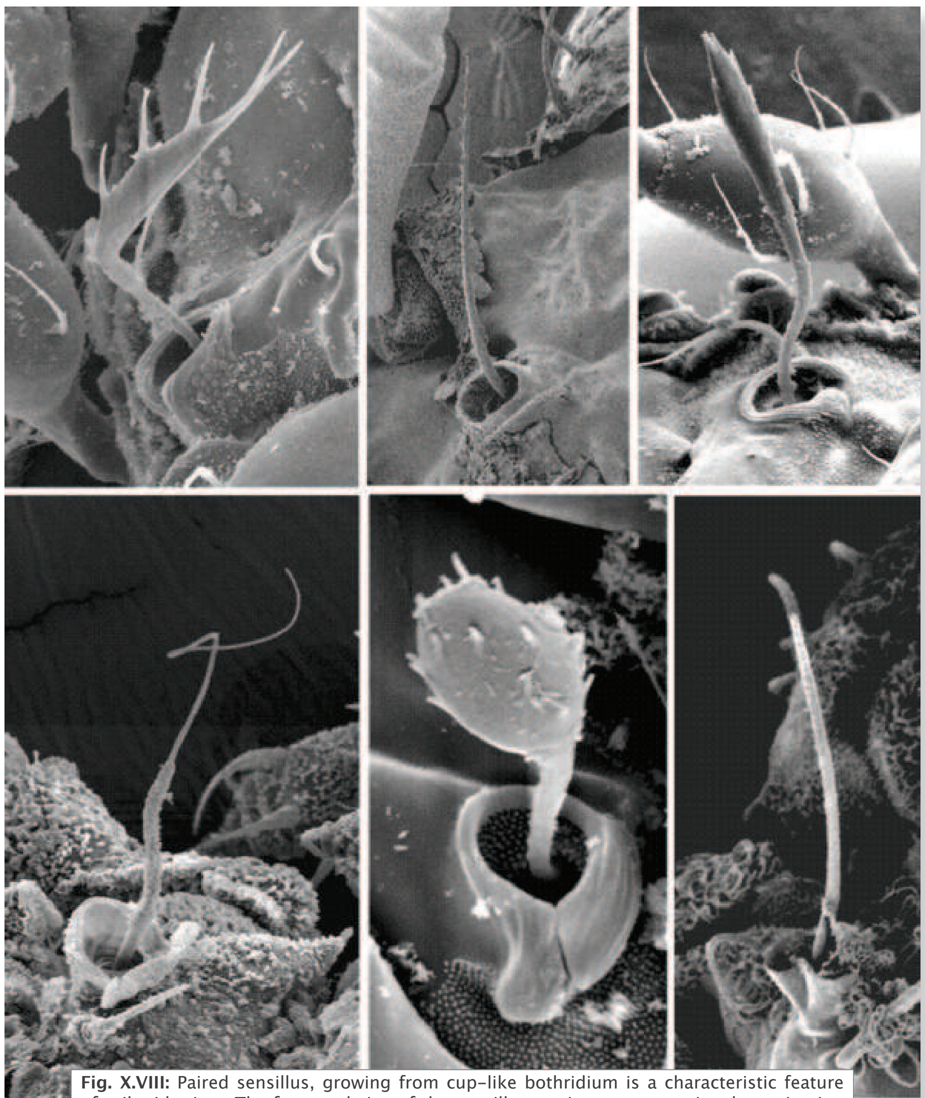


Fig. X.VIII: Paired sensillus, growing from cup-like bothridium is a characteristic feature of oribatid mites. The form and size of the sensillus are important species determination characteristics, and may be very variable – from simple or filiform seta, smooth or covered by small hairs or spines to globular, clavate, or pectiniform shape. (JM)

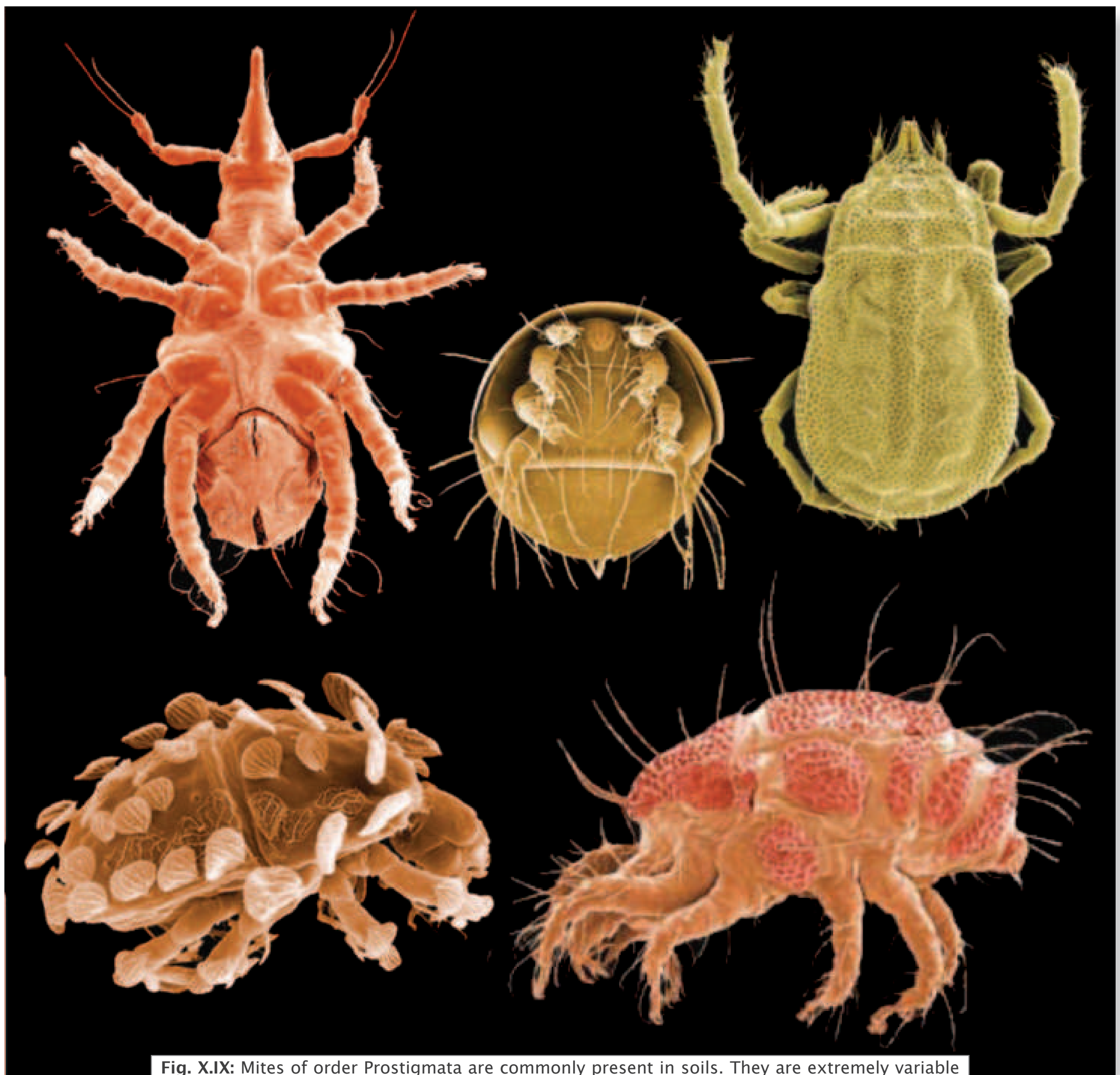


Fig. X.IX: Mites of order Prostigmata are commonly present in soils. They are extremely variable in shapes, size and sclerotization,and also very diverse in feeding habits. Figure shows some of this morphological variability. (DW)

XI Enchytraeids

The Enchytraeidae, or potworms as they are commonly known, are a globally distributed family within the phylum Annelida, the same phylum as the more commonly known earthworms. They can be found in soils as well as in freshwater and marine habitats. Their size and generally whitish appearance distinguishes them from their larger relatives, the earthworms (Fig. XI.I). Most species are between 2 and 20 mm long, although some species may reach up to 50 mm. Due to their narrow body diameter they are classified as soil mesofauna. Enchytraeids occur in almost all soil types in abundances ranging from several hundreds per square metre in dry habitats to 200,000 m^{-2} in coniferous forest soils. About 700 species have been described, but this number is expanding steadily. In particular, many new species are thought to wait to be detected in tropical soils and marine sediments which have received less study to date than temperate soils. The identification of enchytraeid species requires some expertise due to the fact that the worms have to be identified while alive, shortly after extraction from soil. This is because identification of conserved specimens is more difficult and so is very time-consuming.

Enchytraeids have not developed any special protection against desiccation and, consequently, they always need a minimum of soil moisture to survive. The wet skin of enchytraeids is further covered by a secondary water film with which the animals maintain direct contact with water within the soil. Enchytraeids are hermaphroditic and most species reproduce sexually, although parthenogenesis, self-fertilization, and asexual reproduction (fragmentation) occur as well. Enchytraeid species can be classified according to the way they react to environmental conditions. For example, some species are opportunists reproducing very fast when nutrient-rich organic matter is available. Only these species can be easily grown in the laboratory. Others, which have low reproduction rates, are adapted to more stable surroundings. A third group consists of species that are resistant to adverse environmental conditions such as strong soil acidity or oxygen deficiency. There are also some species of the genus *Mesenchytraeus*, known as ice worms, that live in glacial ice.

The diet of enchytraeids is rather uniform. Being both saprovores (i.e. feeding on dead or decaying organic matter) and microbivores they are considered primary and secondary decomposers. In fact, they are substrate feeders that ingest large amounts of microbially active organic matter and mineral soil. In acidic forest soils, where soil mixing earthworms are absent, enchytraeids play a dominant role in litter degradation (Fig. XI.II). In compact soils enchytraeids deposit their casts at the soil surface like earthworms, yet at a smaller scale (Fig. XI.III). However, in other soils, enchytraeid faeces can make up a large proportion of the organic horizons.

Many different predators such as chilopods (i.e. centipedes), nematodes, mites, dipteran fly larvae or carabid beetles prey on enchytraeids. Probably the most important group in this context are predatory mites. These prey on enchytraeids by first penetrating the skin of an enchytraeid. After penetrating the skin of the enchytraeid, the inner content of the worm is liquefied and sucked-out (Fig. XI.IV). In addition, several parasites are regularly found in enchytraeids, e.g. ciliates and other protozoa (which can also be commensals in the gut of enchytraeids), and nematodes. Pathogenic infections with viruses, bacteria, fungi and protozoa seem to increase in enchytraeids living in polluted soils, probably as a result of the organisms being stressed by the pollutants and so more vulnerable to attack and infection.

How do they find their way in the soil?

Enchytraeids do not have eyes but are able to react to light, usually trying to avoid it. Their bodies are covered with different types of chemo and tactile receptors, which are especially abundant in the head region (Fig. XI.VI; Fig. XI.VII). Based on the information provided by these sense organs enchytraeids are able to identify food sources and find their mating partners, as well as able to detect and try to avoid potentially hazardous chemicals. This latter behaviour type can be used as an effect parameter in ecotoxicological effect tests.

Enchytraeids as ecotoxicologicol test species

With the exception of the fragmenting species *Cognettia sphagnetorum*, typical for acid soils of Central and Northern Europe, only members of the genus Enchytraeus have been used in standardised ecotoxicological laboratory tests so far. This genus is unique within the family Enchytraeidae, since some (but not all) species have wide ecological preferences. These species are typical for "stressed" sites (e.g. roadside soils) and can easily be kept in mass cultures. The best-known (and one of the largest) species of this genus is *E. albidus*, which is clearly distinguishable from other enchytraeid species. World-wide it occurs at places with a large amount of organic material (Fig. XI.V), but can rarely also be found at forest and crop sites. Individuals of *E. albidus* reproduce quickly, can be kept in various substrates and be fed with different foods. Some smaller Enchytraeus species like *E. crypticus* or *E. luxuriosus*, are also well suited as test organisms, especially, due to its short generation cycle and large number of juveniles *E. crypticus*. Unfortunately it is not known from where this species originates, since it was described from a compost plant. Today, standard test guidelines with enchytraeids, measuring both acute and chronic effects as well as bioaccumulation, have been published by international standardisation organisations such as ISO and OECD.

Fig. XI.I: The thin, white organism on the left of the photograph is an enchytraeid (*Mesenchytraeus* sp.:) laying alongside a small earthworm (*Dendrobaena attemsi*: on the centre/right). The image clearly demonstrates the differences in size and appearance between both related groups. (HCF)

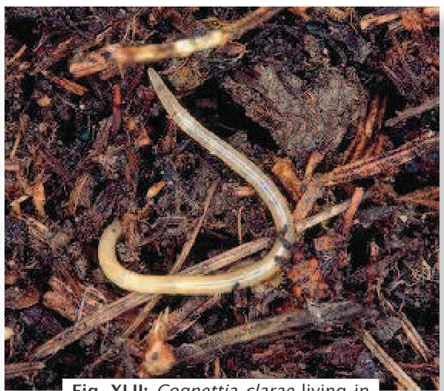


Fig. XI.II: *Cognettia clarae* living in the organic horizons under spruce in the Italian Alps. (DZ)

Fig. XI.IIb: Eggs of the species *Enchytraeus albidus* within a cocoon. (MA)

Fig. XI.III: Casts of a geophagous enchytraeid (*Fridericia* sp.) deposited at the soil surface. (OE)

Fig. XI.IV: Attack of a predatory mite, *Hypoaspis aculeifer*, on an individual of the species *Enchytraeus* sp. in a laboratory test vessel. (TM)

Usage of Enchytraeidae

Enchytraeids are increasingly used as indicators in ecological soil classification and assessment concepts. Their occurrence in a wide range of soil conditions allows the biological assessment of soils, sites and regions where earthworms are absent or less abundant. For example, in Scandinavian coniferous forests where earthworms are rare the enchytraeid species *Cognettia sphagnetorum* (Fig. XI.VI, Fig. XI.VII, Fig. XI.VIII) dominates the whole soil invertebrate community, reaching densities of several hundred thousand individuals per square metre, and playing a key role in processes such as the decomposition of organic matter and nutrient cycling. Consequently, it is considered to be one of the rare examples of an ecosystem engineer among the soil mesofauna. Due to its mode of reproduction (fragmentation) it can react very quickly to environmental changes such as clear-cutting.

Enchytreaids can be used commercially, primarily as a food source for fish in aquariums. Due to their high lipid content they are a favoured food for many fish, but due to these lipids many fish are not able to tolerate them as a permanent and sole food source.

Fig. XI.VI: Scanning Electron Microscopic picture of the head of the species *Cognettia sphagnetorum* showing a high number of chemo and tactile receptors, especially around the mouth. (JR)

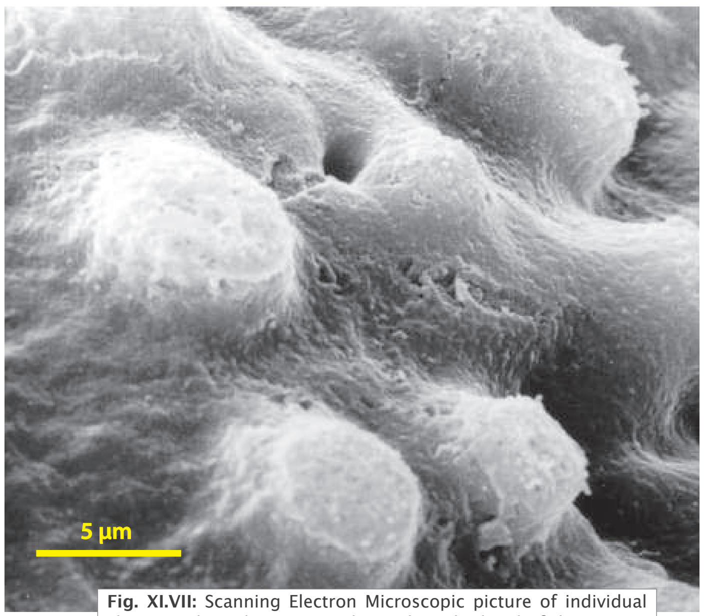


Fig. XI.VII: Scanning Electron Microscopic picture of individual chemo and tactile receptors located on the head of the species *Cognettia sphagnetorum*. (JR)

Ice worms:

Ice worms, a species of the worm genus *Mesenchytraeus*, have been found in glacial ice in north-western USA and Canada. The worms are several centimetres long and feed on snow algae. They come to the surface at night or on cool days before retreating underneath the ice before the sun rises. Enzymes in the bodies of ice worms have a very low optimal temperature which can melt if the temperature rises just a few degrees above 0°C. This causes the worm to liquefy. Some scientists believe that ice worms secrete a chemical which can melt ice by lowering its freezing point, like an antifreeze. Studies on the Suiattle Glacier in the North Cascades Mountains (USA) recorded a population of over 7 billion ice worms on that glacier alone.

Fig. XI.V: Picture of the individuals of the species *Enchytraeus albidus* cultured in a mixture of garden soil and cow manure. The largest individuals have a length of 1 cm. (JR)

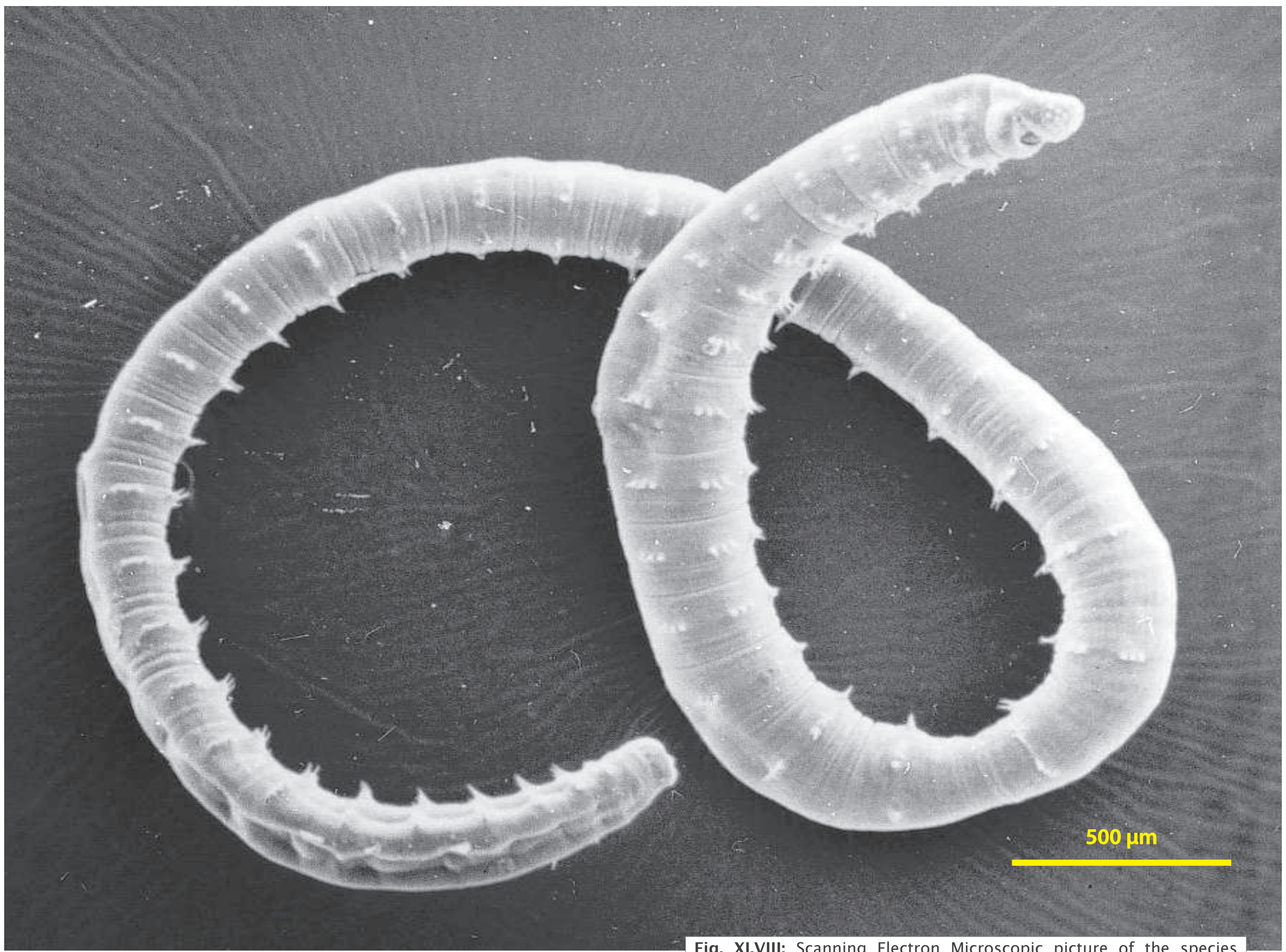
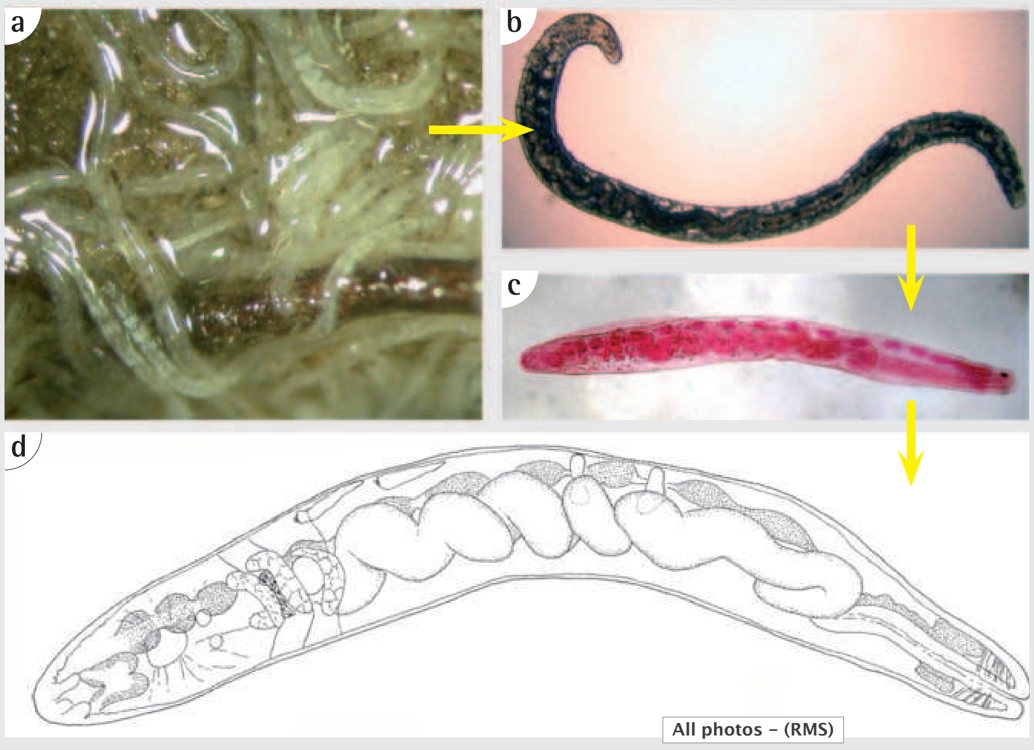


Fig. XI.VIII: Scanning Electron Microscopic picture of the species *Cognettia sphagnetorum*. Length of the specimen: about 1 cm. (JR)

Identification of enchytraeids

Working with enchytraeids at the species level involves several steps.

a. Observing size, habitus and behaviour of living worms extracted from soil with a top light.
b. Scrutinising taxonomic characters in living worms with a light microscope (transmittent light), identification to species.
c. Detailed reinvestigation of voucher specimens or specimens belonging to new species, fixed, stained, and whole-mounted.
d. Scientific drawing of key characters to recognize the new species.



All photos – (RMS)

The annelids:

The annelids are a large phylum of segmented worms, with over 17,000 species including ragworms, earthworms and leeches.

They are found in marine and freshwater environments, hydrothermal vents and in moist terrestrial environments.

Annelids are divided into polychaetes (almost all marine) and oligochaetes (which include earthworms and, recently, leeches).

XII Other Soil Mesofauna

While it is true that the majority of the soil mesofauna is represented by collembolans, soil mites and enchytraeids, there are many other arthropod groups of similar size present in soil. Although these groups are usually less numerous, and therefore contribute less to the soil functions, they may be very sensitive to various disturbances. As they are usually considered to be euedaphic, i.e. true soil inhabitants, they are dependent on rather limited range of conditions, such as, for example, the higher humidity, limited range of pH, relatively stable temperature and presence or absence of some dissolved chemicals that are found in deeper soil zones. Therefore, they may serve as useful indicators of soil health. They are formed by two major groups, the first being hexapods, forming the closely related group (Endognatha) together with collembolans, and second representing small euedaphic myriapods (see also Section XIV).

Proturans (Protura) are primitive hexapods, lacking wings, antennae and eyes. Their bodies are elongated and cylindrical, and is tapered to points at both ends. They are usually colorless, whitish or pale, and range in size from approximately 0.5 to 2 mm. Their first pair of legs is utilised as tactile organs, replacing missing antennae, with distal segments covered by many receptors (Fig. XII.I, Fig. XII.II).

Protura are common in the moist soils of forest and grasslands, preferring soils with high organic matter content and where the pH is not too acidic. Their dietary requirements are partially unknown, but considering the shape of the mouth parts it seems likely that they mainly consume fluids. However, some hypotheses state that they may feed on mycorrhizae and other microflora. As with all soft-bodied arthropods, they are also important prey for predatory species such as mites, spiders, centipedes etc.

Their density is highly variable. In disturbed soils they may be all but absent. However, in less disturbed soils their number usually ranges between 1,000 to 7,000 individuals per m^2, and in some cases can reach up to 90,000 indivudals m^2! More than 700 protura species have been described so far, but usually only several species are present in a single place.

Like proturans, **diplurans** (order Diplura) also belong to the primitive hexapods (Fig. XII.III). They range in size between 1 and 5 mm. They have elongated, colorless, apple or yellowish bodies, with long antennae and two abdominal "cerci" which can be developed either as two long articulated filaments resembling antennae, or they may be pincer-like and in some cases used to capture the prey. Diplura are often euedaphic, living in deeper layers of soil, or in the litter layer. They have biting mouthparts (mandibles) indicating that they are predators, usually of other small arthropods such as collembolans and mites, as well as nematodes and enchytraeids, although they also can consume fungal mycelia and plant detritus. They are present in a range of soils and biomes, preferring soils with relatively high and stable moisture contents. Although they do not have specific habitat restrictions, they never reach very high density: generally in the range of up to 50 individuals m^2. Around 800 species have been described worldwide, but they are rarely more than one to several species at the same place.

Arthropods:

An arthropod is an invertebrate organism (an animal without a backbone) having a rigid external skeleton (exoskeleton), a segmented body and jointed appendages. The exoskeleton is made of chiton, a non-cellular material secreted by the epidermis. As the rigid exoskeleton inhibits growth, arthropods replace it periodically by moulting. Arthropods include insects, arachnids and crustaceans and can range in size from microscopic plankton up to several metres long.

Fig. XII.I: A scanning electron micrograph (SEM) showing an individual Acerentomid proturan of the genus *Parajapygidae*. (DW)

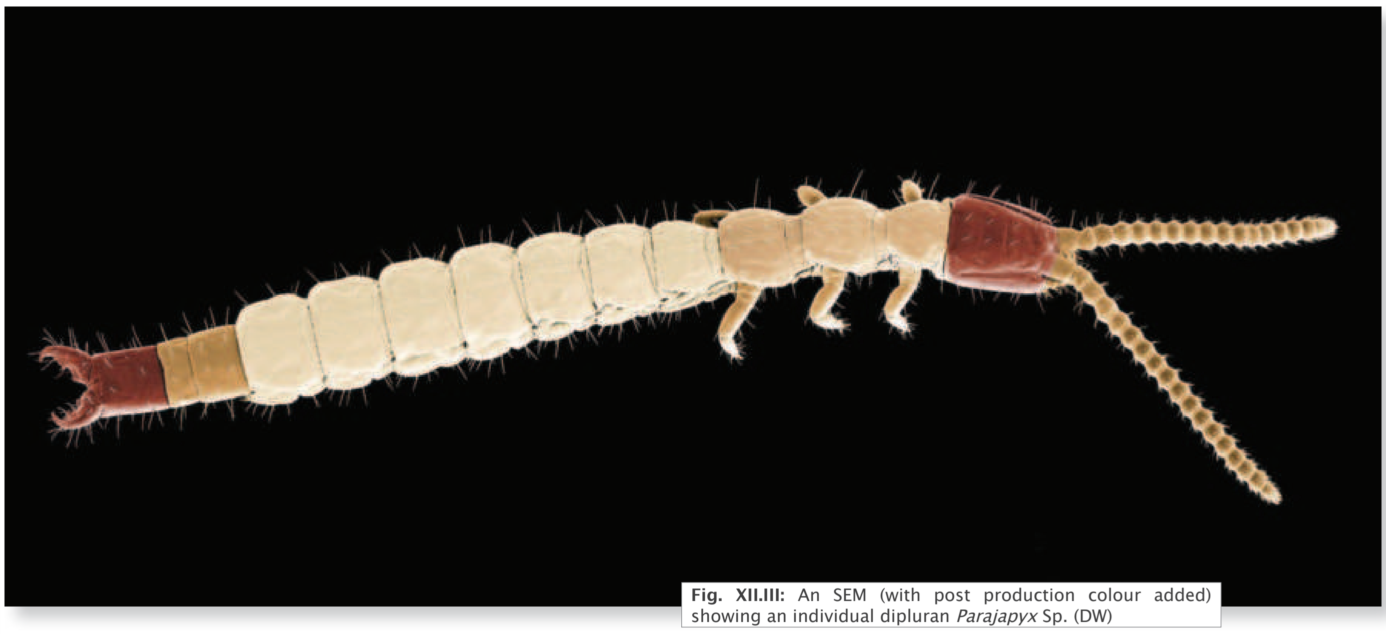


Fig. XII.III: An SEM (with post production colour added) showing an individual dipluran *Parajapyx* Sp. (DW)

Fig. XII.IV: A palpigrade from the genus *Eukoenenia*, a very rare animal in Europe. The group Palpigradi is common in tropical soils while in Europe they are usually only found in caves. It has a very primitive characteristics including a segmented body with "tail-like" posterior part. The first pair of legs is relatively large and serve as antennae, while the palpes developed as pair of legs (so called pedipalpes) and so the animal looks like it had 5 pairs of legs. (LK, GCz)

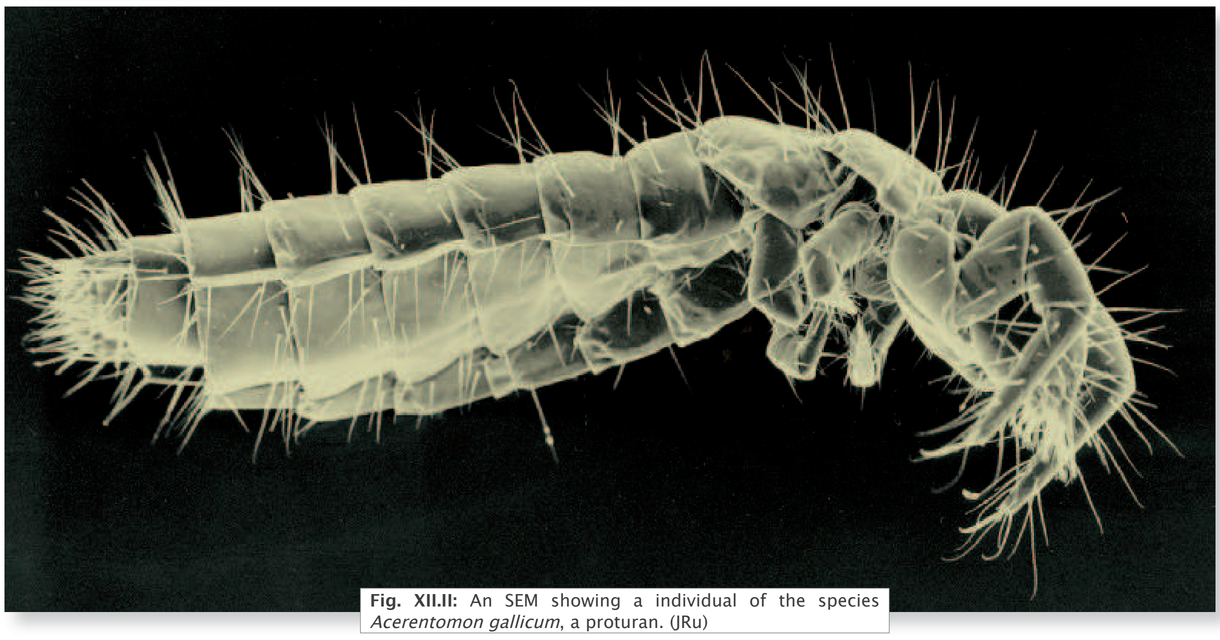


Fig. XII.II: An SEM showing a individual of the species *Acerentomon gallicum*, a proturan. (JRu)

As well as the larger myriapods discussed in Section XIV small myriapods, are represented by two related groups, Pauropoda and Symphyla are also relatively common in soils.

Symphyla are another small group of soil-dwelling myriapods, also known as garden centipedes or glasshouse symphylans (Fig. XII.V, Fig. XII.VI). They resemble centipedes, but are smaller and, unlike centipedes, are translucent. The body size is generally in the range of few millimetres. They have twelve pair of legs, of which the first are generally reduced in size; the head has long, segmented antennae, and the last segment of their body is slender, lacks legs, and possesses a pair of cerci with silk glands. They have several characteristics in common with the less evolved insects, such as the Diplura. They eat mainly decaying vegetation and microorganisms, but can cause damage in agricultural settings by consuming seeds, roots, and root hairs in cultivated soil. They can move rapidly through into the soil and can be found from the surface down to a depth of about 50 cm. As with their larger relatives, centipedes, their reproduction does not involve copulation: males deposit 150 to 450 spermatophores, on small stalks, and the female picks up and store these in her mouth. When the female lays her eggs, she usually attaches them to the sides of moss or lichen with her mouth and smears the sperm over them. The eggs are laid in groups of 8 to 12.

Density of symphylans can vary similarly as in pauropods, and may reach up to 20,000 individuals per m^2 in the greenhouse soil, or 7-8,000 individuals per m^2 in agricultural soils. About 200 species are known worldwide.

Pauropoda reach the size between 0.5 and 2 mm. They have a soft, elongated body with nine pairs of legs in adult (Fig. XII.VII). From an evolutionary point of view, they appear to be closely related to millipedes (Diplopoda, see Section XIV). Like other organisms that are adapted to the life below ground they are blind, but they have a pair of organs which are sensitive to vibrations called pseudoculi. The antennae are typically very well developed. After the first segment they are divided in two branches, one ending with a flagellum, while the other ends with two flagellae, and on the end of one of these there is another sensor organ called a globulus. Their diet is generally dead plant matter and fungi, but occasionally they can also became predators. Due to their low density (generally not exceeding 100 individuals per m^2, although rarely they can reach 600 individuals per m^2) and small size, their contribution to soil functioning is thought to be relatively limited. Approximately 500 species have been described in the world.

Among the soil mesofauna, some of the smallest representatives of insects may also be found. Several families of beetles may be represented by minute euedaphic representatives, such as Staphylinid beetles of the subfamily Leptotyphlinae for example. These beeetles do not have eyes or wings and strongly shortened elytrae (the hardend forewing which covers the delicate rear wings in beetles). In this manner they resemble other soil microarthropods showing evidence of evolutionary convergence as discussed in Section 8.4.

A further group are the **thrips** (Thysanoptera), also known as thunderflies or corn lice (Fig. XII.VIII). These have fringed wings and body form again similar to other soil microarthropods. Individuals from this group are usually just about 1 mm long and can be found living in both above ground and below ground ecosystems. In the soil, they feed on broad variety of living or decaying plant and animal material, usually by perforation of cell walls and sucking up the contents. Some may also feed on specific food sources such as fungal spores, algae or pollen. Others may be predatory or parasitic (e.g. on soil mites). Given their feeding habits, this group may be important pests of commercial plants, as well as vectors of virual diseases. Density of thrips is highly variable; in the right environmental conditions their numbers may rise exponentially within a short period. About 5000 species have been described worldwide so far.

Thrips:

Thrips have asymmetrical mouthparts where the right mandible is reduced or sometimes species completely absent.

The left mandible is larger and is used to pierce the cell wall of tissues.

Some species inject a digestive enzymes into the piercing of plants to drain cellular fluids.

Fig. XII.V: *Symphylella major*, a representative of the symphylans. This group of myriapod is closely relatede to centipedes, but has smaller and pale body, a lower number of leg pairs, and typical silk glands in two flattened appendages at the posterior body segment. (LK, GCz)

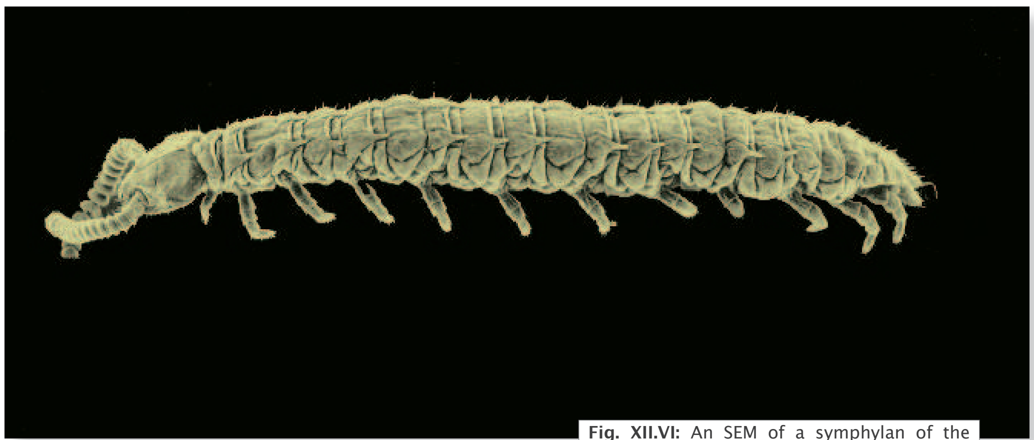


Fig. XII.VI: An SEM of a symphylan of the species *Scolopendrellopsis microcolpa*. (JRu)

Fig. XII.VII: A pauropod of unknown species (DM)

Fig. XII.VIII: A Thrip of the species *Ponticulothrips diospyrosi*. (OpenCage)

XIII Earthworms

Earthworms are found in soils all over the world, even in Antarctica, and are very important organisms in maintaining soil fertility. They feed on organic matter in the soil but don't have the digestive enzymes to break down the cellular structure of plant material. This means that they must rely on other organisms in the soil biota to start to digestion. To reach their daily calorific intake earthworms generally have to eat between 10 and 30 times their own body weight in soil. The soil passes through the earthworm and for species such as *Lumbricus terrestris* is what is deposited on the surface as an earthworm cast. Soils that contain lots of earthworms is regularly mixed by this activity, and up to 5 mm of fresh soil material can be brought to the surface every year by this action.

Earthworms can be divided into three separate ecological groups based on their distribution within the soil (Fig. XIII.I). These groups are:

- Epigeic species – also called litter species or surface-dwelling species live at the soil surface, in leaf litter, humus layers, manure, compost and sometimes within the first few centimetres of the soil (Fig. XIII.II). They are generally small, being 1 - 5 cm in length, and are a dark red in colour. They are important factors regarding the turn over and biodegradation of organic matter. They form no or only few burrows, and feed on decomposing litter on soil surface. They have relatively short life spans balanced by high reproductive rates (100 cocoons per year) and fast maturation (45 days). They survive drought in the cocoon stage. They are submitted to very high predation from birds, mammals (boar, mole, badger) and predatory arthropods. Species include *Dendrobaena octaedra*, *Lumbricus castaneus* and *Eisenia fetida*.
- Anecic species – also called topsoil species or soil-dwelling species live in permanent, vertical (or close to vertical) burrows which are connected to the soil surface and can be 5 - 6 m in length. Anecic species are generally the longest earthworms being 10-110 cm in length. They are variable in colour, being either red, dark grey or brown. They emerge on the soil surface, usually during the night, to feed on dead organic materials (decomposing litter, leaves) which is mixed with ingested soil, creating casts. They deposit casts on the soil surface (30 T/ha/year under meadow) and play an important role in mixing organic matter into the soil system. The casts on soil surface could be associated to organic matter residues and thus form "middens". They have relative long life but with a low reproductive rates (12 cocoons/year) and a long generation time (9 months). They are predated when on soil surface, and are strongly affected by tillage (a cut-earthworm will never end in two earthworms). Species include, *Aporrectodea giardi*, *Lumbricus terrestris* and *Lumbricus rubellus rubellus*.
- Endogeic species – subsoil species or soil-dwelling species live within the soil, almost never going to the soil surface. These species are generally medium to large, being 1 - 20 cm in length (Fig. XIII.III). They are usually slightly coloured, being pink to light grey. They feed on soil ("geophagous"), and derive their nourishment from humified organic matter in the soil. They have produce a temporary burrow system, horizontally oriented, that they refilled with their casts (190 T/ha/year under meadow) ending in granular structure. They have intermediate longevity with a short generation time. They submit to relatively low predation, limited to ground-dwelling birds, predatory arthropods and mammals. The burrows they produce are temporary, very ramified and horizontally orientated within the soil system. Casts which they produce are deposited within the soil. Species include *Allolobophora icterica*, *Octolasium cyaneum* and *Aporrectodea caliginosus*.

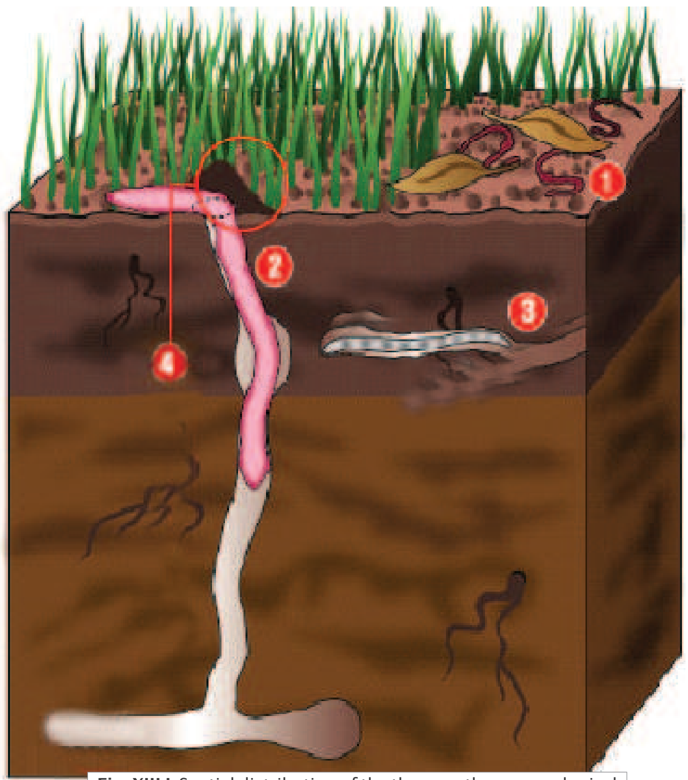


Fig. XIII.I: Spatial distribution of the three earthworm ecological groups. 1 = epigeic specis, 2 = anecic species, 3 = endogeic specis and 4 = cast deposition on the soil surface. (DC)

Fig. XIII.II: The photo to the **left** shows *Allolobophoridella eiseni*, an epigeic species which lives in the leaf litter and mulch layer and only sometimes moves down into the top few centimetres of the soil. The photo on the **right** shows *Aporrectodea giardi*, an anecic earthworm of a different genus. Photos: left (MBo) and right (DC)

Fig. XIII.III: Above are three different species of endogeic earthworms (**Left** – *Aporrectodea icterica*; **middle** – *Octalasium cyaneum*; and **right** – *Allolobophora c. chlorotica albanica*. While all three species fall into the same ecological group, clear morphological differences can be seen in both the pigmentation, size, shape and position of the clitellum (saddle). (DC)

(MB)

(EHo)

Fig. XIII.IV: The picture to the **left** shows two earthworms mating on the surface of the soil. Earthworms are hermaphroditic, but are in capable of self fertilisation. Mating is triggered by external environmental conditions (**right**), such as the soil temperature and moisture. These conditions become optimal in spring and autumn. The earthworms mate by exchanging sperm through the male pores onto the clitellum. Fertilisation takes place outside of the body and sometime after the earthworms have separated a cocoon is secreted by the clitellum into the soil which contains the fertilised egg. The earthworm embryo develops within the cocoon (below), which is resistant to both hot and cold and drying out. The cocoon hatches as a small, but complete earthworm which is sexually active within 4 to 6 months. An earthworm next to two types of eggs. The colourless eggs are from a slug while the smaller light brown egg cocoons are from the earthworm.

Fig. XIII.V: The above images show *Lumbricus terrestris* foraging at the surface (**above left**) and an earthworm cast (**top middle**). Casts such as this at the soil surface are produced by anecic species of earthworms . The image on the **top right** shows a Lumbricus terrestris forming a new burrow into a highly managed grassland. *L. terrestris* burrows can extend up to 2-3 m in depth, although 60-90 cm is more common. Their burrows are this deep so that during the summer, when the upper horizons of the soil profile dry out the earthworm can still reach moist soil. *L. terrestris* feed on organic matter such as leaf material found on the soil surface. When they feed they often remain anchored in their burrow, with specially adapted rear segments. By contracting their external muscular structure they can rapidly withdraw into their burrow as the perceive risk of predation. The picture to the **right** shows *Aporrectodea giardi*, an anecic earthworm of a different genus. (MB)

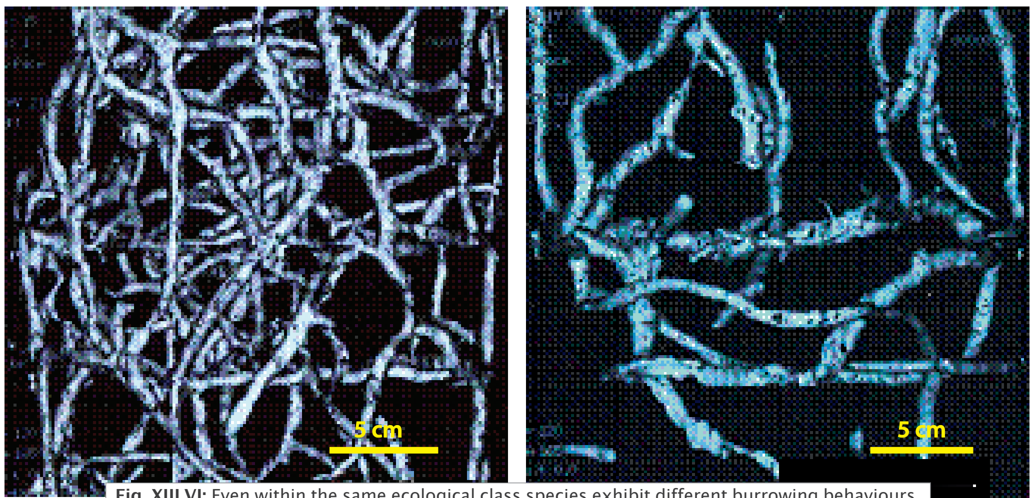


Fig. XIII.VI: Even within the same ecological class species exhibit different burrowing behaviours. The images **above** show the differences in burrow structures between *L. terrestris* and *A. giardi*, both of which are anecic species. *L. terrestris* generally produces fewer, thicker burrow whereas *A. giardi* builds a more extensive range of slightly narrow burrows. (GP)

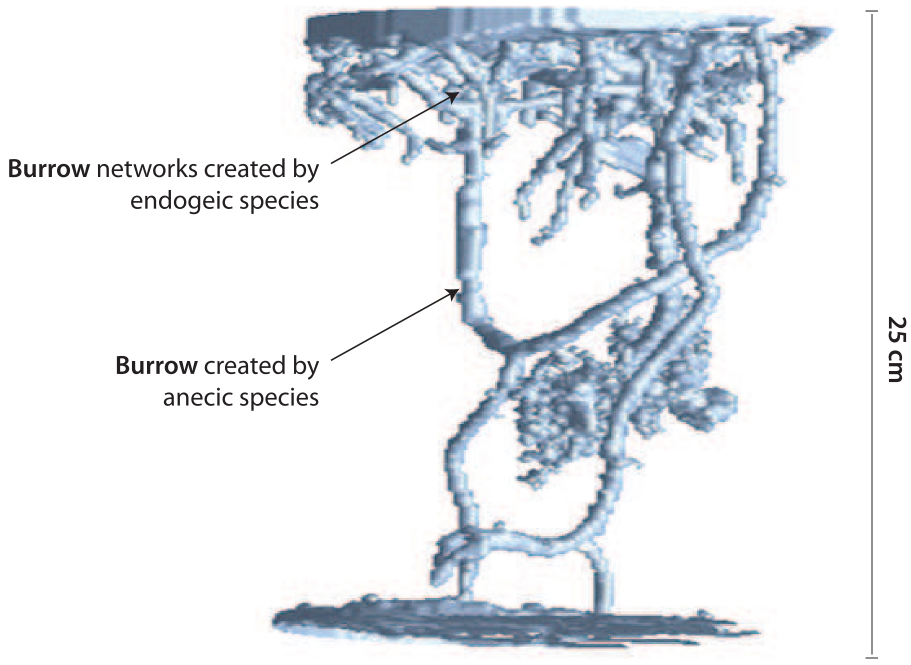


Fig. XIII.VII: The image above shows a 3 dimensional reconstruction of a natural burrow network created by earthworms. The image is constructed from a group of images obtained by x-ray tomography. (GP)

Fig. XIII.VIII: Shows earthworm casts which have been deposited at the soil surface (**left**). Images **below** show cast deposition in soil. In some instances this can create a crumble structure at soil pit scale (**A**), and in other cases the cast itself covers the inside of the burrow walls (**B**). (DC)

Fig. XIII.IX: Earthworms are not always active within the soil. In times of environmental stress such as being too cold, too hot or too dry, earthworms are capable of entering a state of hibernation or estivation (summer time hibernation). The image to the **right** shows *A. giardi* having curled up in a state of estivation. (DC)

XIV Myriapods

Myriapods are arthropods which are characterised by an elongated body with several, up to several tens, of similarly shaped segments bearing one or two pairs of legs, therefore having more than six legs in the adult phase. Two classes of Myriapods (Pauropoda and Symphyla) are small, mostly euedaphic microarthropods and have been presented among the representatives of soil mesofauna (Section XII). The two other classes of Myriapods are larger, present in broad range of ecosystems and classified as soil macrofauna. These are commonly known as millipedes (Diplopoda) and centipedes (Chilopoda).

Millipedes (**Diplopoda**) are arthropods which range in size between 2 and 280 mm. They can be easily distinguished from other terrestrial arthropods as for most of their length they have two pairs of uniform legs in length (Fig. XIII.III). The exceptions are the first segment behind the head, which does not have any appendages at all, and the next few segments which only have one pair of legs. Millipedes are evolutionary very old. Evidence from fossil studies, have shown *Pneumodesmus newmani*, a 1 centimetre long millipede living approximately 428 million years ago, to be the oldest known land creature. While typical millipedes (subclass Helminthomorpha) have very elongated and regularly cylindrical bodies, there are also many species with ventrally or dorsoventrally flattened body. With the exception of some of the more primitive families, the cuticle is well sclerotized and often incrusted by calcareous salts; this being a reason why they are more common in calcareous soils. As well as sclerotization, millipedes have developed several self-defence mechanisms. Some are capable of rolling up into a spiral and some, in the case of the more squat species, into a ball (subclass Pentazonia) similarly to isopods. Small, more primitive species bear longer hairs, which defend the body against ants. Millipedes can also use a chemical defense through secreteing substances produced by glands on lateral side of the body which have a repugnatory effect.

Diplopoda generally live within the litter layers and in the upper part of the soil. They are slow moving detritivores that eat decaying leaves and other dead plant matter, contributing to diminution and destruction of detritus as part of the first phases of decomposition. There are also few omnivorous or carnivorous species, and these may prey on small arthropods, such as insects and centipedes, or on earthworms. Some species have piercing mouthparts that allow them to feed on plant juices. Millipedes excreta contribute to creation of coprogenic humus. Many species are adapted to the life in deeper soil horizons, microcaverns and caves. These species show high level of adaptation, many being much smaller, having lost their eyes and developed specialised receptors for sensing humidity and chemical properties of the environment. Despite of their defensive adaptations, millipedes are an important prey group for many larger predators.

Reproduction activity generally involves copulation, even though a few species can be parthenogenetic.

Around 10,000 species have been described so far. The density of these organisms can vary broadly dependent on conditions and presence of calcareous substances. Population density usually ranges from 15 to 800 individuals per m^2. Due to their relatively large and robust body, the overall biomass of millipedes may reach up to 4-8 g per m^2.

Fig. XIV.I: A Rusty Millipede (*Trigoniulus corallinus*) which is native to Southeast Asia. (EG)

Fig. XIV.II: Photograph looking through a microscope at a fossil of *Pneumodesmus newmani* from the Silurian Period, found in Cowie Harbour, Stonehaven, Aberdeenshire, Scotland, UK. (JMa)

Fig. XIV.III: The head of a North American Millipede (*Narceus americanus*) on which two eyes are clearly visible. (JM)

Fig. XIV.IV: Diplopods evolved a high morphological variability. Body may be regularly cylindrical (as in *Strongylosoma stigmatosum*, **bottom left**), flattened ventrally (*Polyzonium germanicum*, **bottom right**) or dorsoventrally (*Polydesmus complanatus*, **above left**) , or similar to isopods (**above middle and right**). *Glomeris tetrasticha* (**above right**) is even able to roll into a ball. Almost unpigmented species *Trachysphaera gibbula* (**above middle**) is adapted to life in deeper soil horizons, in microcaverns and caves. (FT/IHT)

Chilopoda, or centipedes as they are more commonly known, are common predators in soil and litter habitats. Their size can range from a few millimetres up to about 30 cm in length (Fig. XIV.V - VII). Centipedes have an ancestry dating back 430 million years to the late Silurian, being, together with millipedes, among the earliest terrestrial animals.

The body of centipedes is elongated, composed of several segments, each of which has a single pair of legs. The first segment of the body holds a pair of forcipules (maxilipedes) which are very strong organs that have poison ducts at their tips. These are used for catching the prey. Two main body forms evolved: Larger species living usually close to soil surface, in the rotting wood or in litter have usually flattened body with lower number of segments, with longer and stronger legs allowing very fast movement (common centipedes from the order Lithobiomorpha and giant centipedes from the order Scolopendromorpha). On the other hand, species from the order Geophilomorpha are specialised to life in deeper layers of the soil, with their body usually being smaller, or at least narrower, almost cylindrical, having very high numner of segments and minute, gracile legs. The colours of euedaphic species are generally more pale, and in some cases can be pigmentless.

Centipedes are known as generalist predators, adapted to hunt a variety of different available prey, but they can also occasionally feed on leaf litter , especially in starving conditions. In the soil, they usually prey on small insects and their larvae, on collembolans, acari, spiders, nematodes, enchytraeids and even earthworms. The largest centipedes have also been observed feeding on reptiles, amphibians, small mammals, bats and birds.

Reproduction does not involve copulation. Instead, males deposit a spermatophore in a web, and the male encourages the female to engulf his sperm, undertaking a courtship dance.

Centipedes occur in a wide range of biomes, from forests to deserts. As well as leaf litter and soil, they can also occur in specific microhabitats such as in rotting wood, under the bark of the trees, in crevices of rocks, in ruderal areas, as well as living trees. It is estimated that there are approximately 8000 species worldwide, 3000 of which have been already described by science. Their abundance in litter and soil may vary, usually within the range of 20-300 individuals per m^2.

Centipedes:

Centipedes are predators and generally nocturnal.

Centipedes and spiders may frequently prey on one another.

Centipedes form an important item of diet for many species and are eaten by mice, beetles and snakes.

Some species of centipedes can be hazardous to humans because of their sting. The stings of some centipede species are among the most painful stings that exist in nature.

Fig. XIV.V: A centipede of the species *Scutigera coleoptrata*, one of several species of chilopoda commonly known as house centipedes. They feed on spiders, termites, cockroaches and ants, and other small insects. (FT/IHT)

Fig. XIV.VI: A scanning electron micrograph showing the underside of a centipedes head and first four body segments. Clearly visible are the forcipules, a feature unique to centipedes. These are modified front legs which form a pincer like appendage just behind the head. These are used for capturing prey and are capable of injecting venom. (JM)

Fig. XIV.VII: The species in the photograph above give some impression of the high levels of morphological and colour variation found in this group. Surface dwelling species as *Orya barbarica* (**bottom right**) and *Eupolybothrus tridentinus* (**above left**) are usually well pigmented, larger and more flattened. Above ground living house centipedes (as *Scutigerella coleoptrata*, **above middle**) have very long body appendages. Species living in deeper soil layers (as *Clinopodes flavidus*, **bottom left** or *Henia illyrica*, **above right**) are usually narrow, pale, with a relatively narrow body, high number of segments and short, minute legs. (FT/IHT)

XV Ants

Ants are insects belonging to the order Hymenoptera (as bees and wasps) and to the family Formicidae. In mid-Cretaceous period (110-130 million years ago), they evolved from a wasp-like ancestor, but they became dominant only after an adaptive radiation after the rise of flowering plants at the beginning of the Tertiary period (60 million years ago). These data were confirmed in 1966 when E.O. Wilson and colleagues discovered a fossil ant (*Sphecomyrma freyi*) trapped in amber. The ant dates back to more than 80 million years ago and has features of both ants and wasps. This ant was probably a ground forager but comparative analyses of ancient groups such as Leptanillinae suggest that primitive ants were probably predators under the soil surface. Ants should not be confused with Termites (sometimes called white ants). These latter insects belong to the order Isoptera and are more closely related to cockroaches and mantids. Ants and Termites are both eusocial but this similarity is probably due to a convergent evolution.

Distribution and Diversity

Today more than 12,500 species are known representing between 15 and 25% of the terrestrial animal biomass. They are found on all continents except for Antarctica, Greenland, Iceland and parts of Polynesia and the Hawaiian Islands. They occupy a wide range of ecological niches as different ant species fulfil the roles of direct or indirect herbivores, predators, scavengers, mutualists, social parasites and also plant, fungi, and homopteran (an order of insects) breeders (Fig. XV.I).

Fig. XV.I: Ants are highly social organisms and as such it is relatively rare to see lone individuals far from the nest. This 'teamwork' is apparent in the above three images which show: (**top left**) Foragers of *Formica cunicularia* cutting pieces from a dead grasshopper that will be carried back to the nest as food for the colony; (**left**) *Messor minor* workers carrying seeds; (**above**) Workers of *Aphaenogaster campana* foraging on a fruit. These granivorous ants are abundant in dry areas of Central Southern Italy. (AMo/DG)

Morphology

Ant size varies form 0.75 to 53 mm with the majority of the species are red or black and only a few species being yellow, green or with a metallic lustre. As all the insects, an ant body is divided into three parts: head, thorax (or mesosoma) and abdomen (gaster or metasoma) (Fig. XV.II). The head is characterised by the presence of compound eyes, antennae and mandibles; the thorax is characterised by three pairs of legs and eventually wings; whereas the gaster is the last segment sometimes with a sting at the end. Elbowed antennae on the head, metapleural glands in the thorax and a strong constriction of the second abdominal segment into a node-like structure (petiole) are the three features that discriminate the ants from the other insects.

Fig. XV.II: All insects have three body sections and six legs, as shown by individual above, but the elbowed antennae are ant specific. This photo shows a worker of the species *Crematogaster scutellaris*. (AMo/DG)

Ants across Europe:

A group of Swiss, French and Danish scientists have found that a species of Argentine ant (*Linepithema humile*), introduced into Europe on imported plants about 90 years ago, has developed the largest supercolony ever recorded, stretching approximately 6,000 kilometres from northern Italy, through the south of France to the Atlantic coast of Spain. The colony is made up of billions of related ants occupying millions of nests. While ants from rival nests normally fight each other, ants from the supercolony recognise each other and co-operate.

Ant Facts:

All ants belong to one systematic family (Formicidae).

Ants have two stomachs: one for itself and one for sharing food with other ants.

Ant biomass was found to exceed vertebrates by four times in a Brazilian rainforest.

An ant can carry 20 times its weight.

43 ant species were found on a single tree in Peru while 668 species were found in 4 hectares of forest in Borneo.

Social Behaviour

Ants form colonies that range in size from a few dozen individuals living in small natural cavities (Fig. XV.III) to highly organised colonies which may occupy large territories and consist of millions of individuals. According to E.O. Wilson's definition, ants (with termites and some species of wasps, bees and aphids) are considered eusocial insects because their social organisation is characterised by the presence of three important conditions: reproductive division of labour (with specific individuals devoted to reproduction and often almost the total sterility of the rest of the colony members), overlapping of more than two generations living inside the nest and cooperative care of young. The division of labour (called polyethism) is associated with a differentiation of morphological traits among the different groups known as castes (this differentiation within a species is known as polymorphism). Generally, there are three different castes in ant colonies: workers (sterile wingless females), queens (fertile females) and drones (fertile males) (Fig. XV.V). Workers, according to their specific tasks (brood-care, nest building and maintenance, foraging, defence, etc), can have a continuous variation in the size, or distinct size-classes (minor, median and major workers). The colonies are sometimes described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.

Fig. XV.III: Ants live in most of the terrestrial environments and nest in many different habitats and form colonies in a variety of substrate such as these *Camponotus* sp. ants living in a dead tree. **Above** shows an ant leaving through the nest entrance and **below** shows the internal portion of a *Crematogaster* sp. colony within a dead tree. (AMo/DG)

Fig. XV.IV: Different species of ants can have very different heads (below). From left to right the species are: *Cyphomyrmex laevigatus, Camponotus sp., Acanthognathus brevicornis, Thaumatomyrmex mutilatus, Basiceros convexiceps, Pheidole sp., Solenopsis germinate, Pachycondyla striata, Eciton burchellii, Cephalotes angustus.* (JB)

Relationships with other organisms

Several ant species belonging to different genera (e.g. *Lasius, Formica, Linepithema*) engage in mutualistic relationships with homopteran insects (such as aphids, mealybugs, scale insects, treehoppers) (Fig. XV.VII). The ants generally keep predators away and may even move their partners between different feeding locations according to their needs. In return the homopterans secrete a sweet liquid (honeydew) which is a high-energy food source for the ants. There is a similar relationship between ants and some Myrmecophilous (ant-loving) butterflies of the family Lycaenidae (e.g. blues, coppers, or hairstreaks), which also includes several parasitic species.

Other arthropods can actively enter ant nests using several forms of morphological and/or chemical mimicry and exploit them eating their larvae, eggs or adults.

Fig. XV.VI: *Messor wasmanni* polymorphic workers transporting seeds of different size. (AMo/DG)

Fig. XV.V: Winged queens of *Messor structor* assisted by workers on grass blades before leaving for their nuptial flight. (AMo/DG)

Fig. XV.VII: *Linepitema humile* worker tending a colony of mealybugs. (AMo/DG)

Army ants (e.g. *Dorylus* sp. or *Eciton* sp.) are nomadic and form huge foraging armies of more than 1,000,000 ants which simultaneously cover a specific area, attacking all they can find (invertebrates as well as small vertebrates). These predatory "raids" are often followed by birds (such as antbirds and woodcreepers) that take advantage from the panic created by the ants to capture escaping insects. Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus of the genera *Leucoagaricus* or *Leucocoprinus* or of the Agaricaceae family. Lemon ants make "devil's gardens" by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees (*Duroia hirsuta*). Seed dispersal by ants (myrmecochory) is widespread in several continents as is the case of *Messor* sp. in Europe and other Mediterranean areas or *Pogonomyrmex* sp. in North America.

Ants and humans

In some areas ants are used as biological pest control agent. For example, ants of *Formica* sp. were used in Italy for the control of Pine Processionary (*Thaumetopoea pityocampa*), the larva of which is a major forest pest and weaver ants have been used in citrus cultivation in southern China. Sometimes ants become pest themselves, particularly when are imported in new areas. A famous example of this is the fire ant (*Solenopsis invicta*) in North America or the Argentinean ant (*Linepithema humile*) in Europe and several other regions. Some species of the family Ponerinae, Myrmeciinae and Myrmicinae have very toxic venoms and are of medical importance. The high organisation of ant societies thorough division of labour and efficient communication among individuals has helped to produce some algorithms in order to solve complex problems of human daily life (e.g. The Ant Colony Optimisation algorithm). Furthermore, ants have also been used to produce robots (BILL Ants: Biological Inspired Legged Locomotion Ants) which are able to orient, freely move and localize object.

Ants as Bioindicators

Ants are increasingly being recognized as useful tools for land managers to monitor ecosystems for many reasons. These reasons for this include their high diversity (more than 12,000 species) as well as their numerical and biomass dominance in almost every habitat. Their systematics are well known and their sampling is generally easy and cheap (Fig. XV.VIII). Most species have stationary, perennial nests with fairly restricted foraging ranges. Therefore, they are generally a constant presence at a site and can thus be more reliably sampled and monitored. Furthermore, ants are present in many different trophic levels (predators, prays, detritivores, mutualists, parasites and herbivores) and play many important roles in ecosystem functioning. Physical soil modification (Fig. XV.IX), chemical changes in the soil, and changes in nutrients, energy fluxes and vegetation are all consequences of the presence of ants. They are often defined as "ecological engineers" because they directly or indirectly control the resource availability for other organisms. Some ants are true keystone species because they disproportionately impact their community, as is the case when whole groups of harvesting ants control the seed dispersal of several plants (Fig. XV.X). Ant impact on the ecosystem is clearly evident when introduced ants disrupt communities. Ants transported away from their native ecosystems can disrupt the ecosystems of their new homes as the well known examples of the Argentine ant *Linepithema humile* and the Fire ant *Solenopsis invicta* demonstrate. Sensitivity to environmental change is another important feature that makes ants an ideal bioindicator. Many ant species have narrow tolerances and respond quickly to environmental change. Their small size and the reliance on relatively high temperatures make them sensitive to climate and microclimate change. In addition, long-lived species allow the monitoring of the health of a colony and the environment changes around it, whereas short-lived ant species may show high turnover and thus an immediate response to a stressor. Therefore, ant assemblages allow monitoring programs to check environmental changes on different temporal scales and further investigation on ants as bioindicators in Europe's temperate regions may yield promising results.

Fig. XV.VIII: Workers of the species *Crematogaster scutellaris.* An example of a very simple food bait trap filled with tuna. Food baits and pitfall traps are commonly used to monitor ant biodiversity. (CC)

Fig. XV.IX: The External aspect of *Messor minor*'s nest showing evidence of the soil modification due to ant activities. (DDE)

Fig. XV.X: Worker of the species *Messor wasmanni.* The worker is a forager collecting plant fragments. (DDE)

XVI Termites

The common name Termite, of Latin origin, can be translated as "woodworm" and it refers to the diet of many species of this order (Fig. XVI.I). The order name Isoptera, which derives from the Greek ísos (same) and *pterón* (wing), refers to the two pairs of straight and very similar wings that termites have as reproductive adults. Termites are small insects (5-15 mm on average), white to tan or sometimes black in colour. As with all insects, they have three-body parts: head, thorax, abdomen, and six legs. They are hemimetabolous, having an "incomplete metamorphosis": meaning that their development starts with an egg, followed by different instars of nymphs, and ends with the adult, also known as imago, which is the final, winged stage of the insects. Termites are closely related to cockroaches and their roots go back more than 180 million years. There are more than 2600 species of termites worldwide with the greatest diversity being found in Africa, with over 1000 species. North America has 50 species and Europe only 10. They are particularly abundant in the tropical and subtropical regions and it is estimated that termites represent about 15-33% of the Earth's terrestrial animal biomass.

The two main factors which are thought to be behind the success of termites are their social organisation and their highly efficient digestive system, including very effective mouthparts, combined with a gut which contains symbiotic microorganisms which makes it possible to gain energy and nutrients efficiently from the highly abundant but recalcitrant food source, lignocellulose, which is found in woody plants and is indigestible to virtually all other animals.

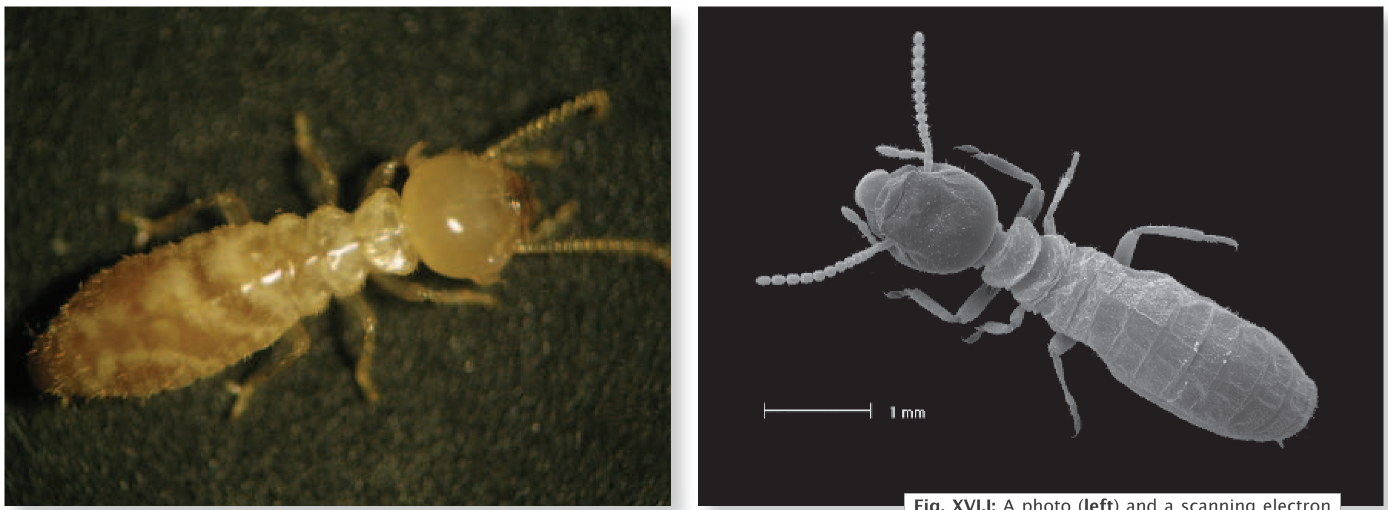
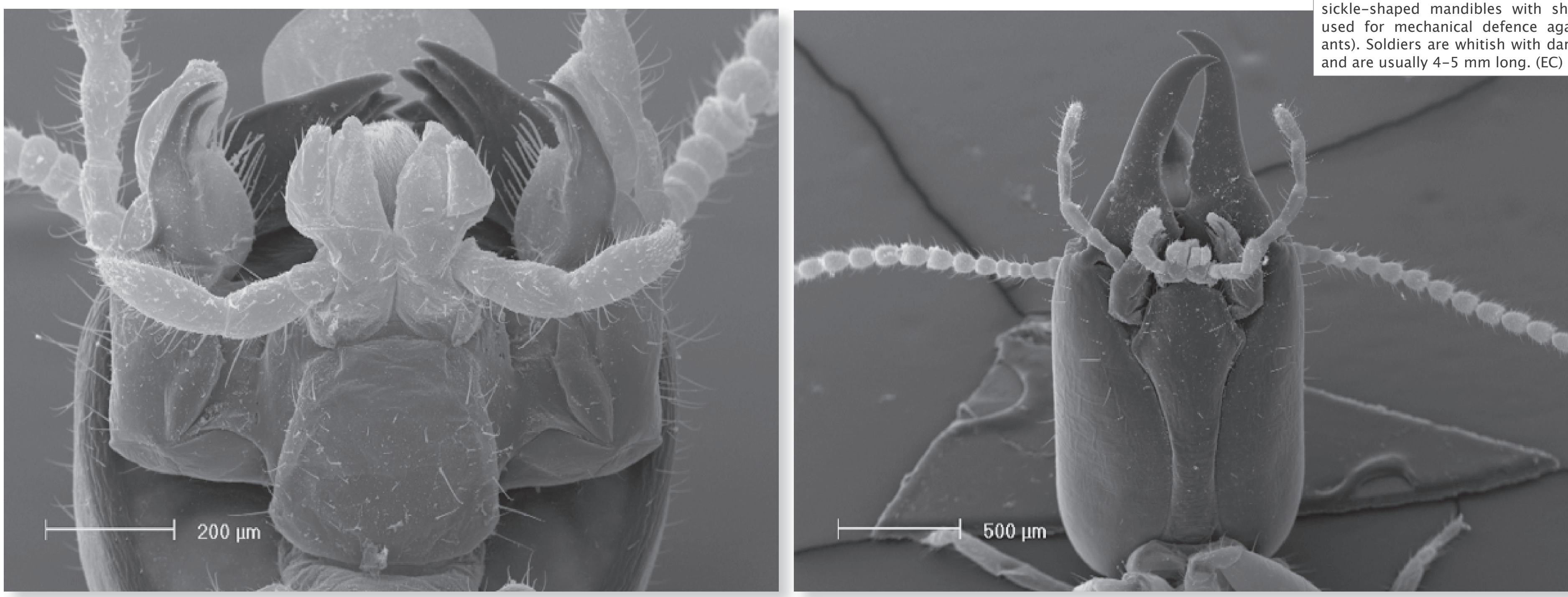


Fig. XVI.I: A photo (**left**) and a scanning electron micrograph (**right**) showing workers (about 5 mm in length) of the species *Reticulitermes lucifugus*. This is a subterranean termite species commonly found in Italy that can be a serious pest of wooden/paper materials in urban areas. Images: left (LMa); right (EC).

Termite society is unique among social insects as members of all castes can be either males or females. The foundation of new colonies occurs after the swarming performed by the winged imagoes (all dark in colour, with long grey-black wings), called 'alates' (Fig. XVI.III), also known as 'swarmers', which are the only individuals to complete the developmental pathway. Alates leave the original colony nest by flight. When they land on the ground they shed their wings and form couples. The newly formed pairs then head out to search for suitable nesting sites, usually near or inside a wooden material. After mating, the queen begins to lay eggs.

Fig. XVI.II: Two scanning electron micrographs showing a comparison of the head regions of a worker (**left**) and a soldier (**right**) of termites of the species *R. lucifugus*. The worker has a rounded head capsule and short, strong, toothlike mandibles (darkest elements) which are used for chewing wood and for nest construction/repair In contrast, the soldier has an elongated-rectangular shaped head capsule and the long slender sickle-shaped mandibles with sharp cutting edges, used for mechanical defence against enemies (e.g. ants). Soldiers are whitish with dark brown mandibles and are usually 4-5 mm long. (EC)



Termites are social insects that live in colonies of thousands or sometimes millions of individuals. These communities are organised in a caste system based on division of labour, with morphologically and functionally different individuals (Fig. XVI.II): nymphs, workers, soldiers and reproductive termites (known as reproductives). Nymphs hatch from eggs and molt at least three times before becoming functional workers. Workers are wingless and do not lay eggs. They are the most numerous individuals in a colony and perform most of the tasks including foraging, building and maintaining the nest, and feeding and taking care of all of the other nest-mates (Fig. XVI.I, Fig. XVI.V).

Soldiers are morphologically and behaviourally specialised to defend the colony against predators and competitors (Fig. XVI. II, Fig. XVI.IV). They perform their task by means of fearsome mandibles and/or squirting sticky or toxic chemicals. Soldiers cannot feed by themselves due to their large mandibles, therefore they are completely dependent on workers to receive food.

Reproductives are the only individuals able to reproduce in a colony. They consist of a royal couple (queen and king), the original colony founders, and supplementary or replacement reproductives (known as neotenics) may also be generated from immature forms (larvae, workers or nymphs) in case of death of the original pair or other pheromonal cues or environmental factors.

Once nymphs and workers are produced, the new colony starts to grow. Queens are the largest individuals in the colonies (up to 5-6 cm) and, depending on the species, they can lay from 10 to thousands of eggs per day. The king is always by the queen's side and mates intermittently to provide sperm to the queen. The reproductive adults have functional eyes whereas nymphs, workers and soldiers that live all their lives deep inside the nests, soil or mounds, are blind. Termites communicate through acoustic, tactile and chemical signals with many behaviours being mediated by pheromones (i.e. trail following, alarm and sexual communication). The exchange of food among colony members (from workers to all other nestmates) is called 'trophallaxis' and termites use the 'proctodeal' method (from anus to mouth) for food and symbiont exchange between each other.

Termites are herbivores, fungivores and humivores (feeding on humous). They are among the few animals able to feed on lignocellulose, directly from both dead or living plants or indirectly from fungus growing on decaying material. For lignocellulose digestion termites rely on a unique community of species-specific symbiont microorganisms (protist flagellates and/or bacteria) hosted in their hindgut and the efficiency of this system is so high that termite gut is considered nature's most efficient bioreactor, able to convert up to 95% of the cellulose material into simple sugars within 24 hrs. Moreover, some of the symbiotic bacteria play a significant role in nitrogen fixation.

Fig. XVI.III: An alate (adult reproductive with wings) of the species *Kalotermes flavicollis*. In alate form this species has a dark-brown body and head, a yellowish pronotum (neck) and transparent long brownish wings and are usually 10-12 mm long, (with wings). In this species usually alates perform swarming flights during late summer. (LP)

All living termites can be divided into 7 families (Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae, Rhinotermitidae, Serritermidae, Termitidae) and, based on ecological traits, they can be lumped into 4 groups: dampwood, drywood, subterranean, and mound builders.

- Dampwood termites live and feed in very moist wood, especially in tree stumps and fallen trees.
- Drywood termites have moderate size colonies that nest and feed in wood (either dead or alive) above the soil and can tolerate dry conditions for prolonged periods.
- Subterranean termites are very numerous in many parts of the world and have very large colonies ranging from a few thousands to millions of members. They nest in or close to the soil. They require moderate to high levels of humidity and search for their food (foraging) by tunnelling to form subterranean galleries or by building mud shelter tubes (using their faeces, saliva and soil) over almost any surface.
- Mound builders occur mainly in the tropics. They have very large colonies and feed on grass, litter or soil and build above ground mounds as nests that have a very complex architecture and can be up to 8 m in height.

Among the termite species present in Europe, the most common belong to the genus *Reticulitermes* (Rhinotermitidae; Fig. XVI.I). These are subterranean termites that are widespread around the Mediterranean and Black Sea and can be found both in natural habitats and as pests in urban environments.

Another common species is *Kalotermes flavicollis* Fabr. (Kalotermitidae) which is a drywood termite living in regions across the Mediterranean basin. They are able to attack living plants and so are potentially dangerous for some arboreal crops (e.g. grapevines, fruit trees).

Some termites are invasive species. For example, *Cryptotermes brevis* (Walker) (Kalotermitidae), is a drywood termite which was initially imported with manufactured wood products and is now present in urban areas in Italy, The Canaries Islands and The Azores.

Impacts of Termites

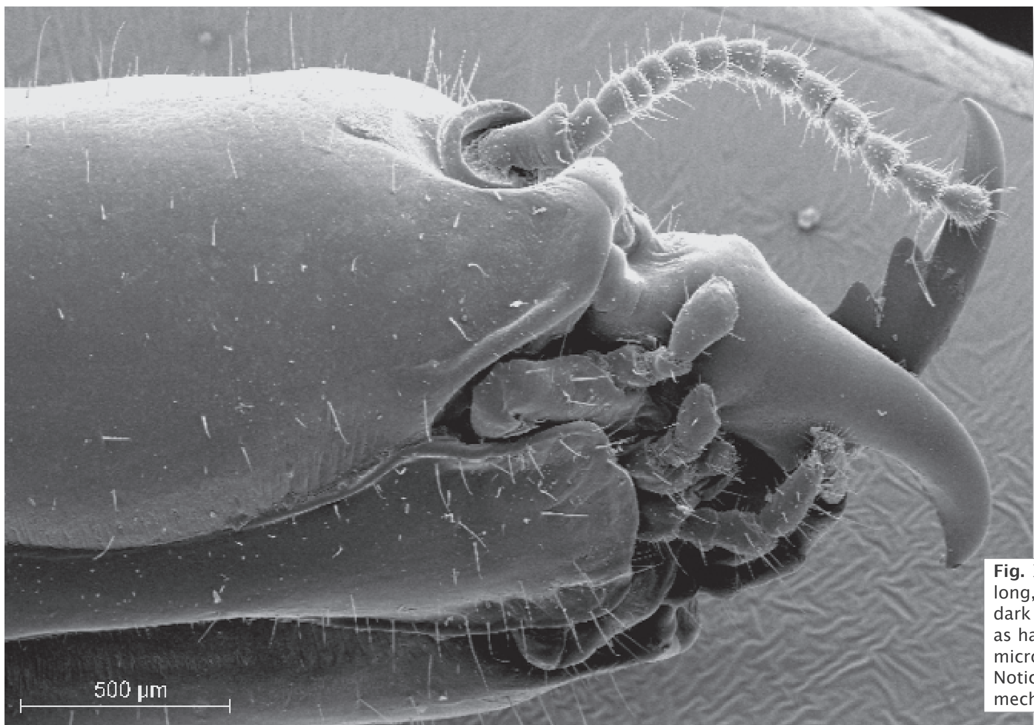
Due to the highly evolved mutualism with microbes, termites play a major role in decomposition processes and nutrient recycling: it is estimated that every year about 1/3 of all plant produced material is consumed by these insects! Being the world's best bioconverters, termite guts make a very good model to study energy access from wood or plant litter. Investigating the termite-gut community reveals a vast collection of biological pathways that may be used for multiple energy applications, such as by scaling up the metabolic processes for industrial biofuel production.

Termites are considered as soil ecosystem engineers due to the highly significant impact on pedogenesis, soil properties and soil functions they have over large areas of the tropics and sub-tropics. This impact arises from their frequent high abundance and biomass, combined with the habit of creating extensive underground gallery systems (tunnelling) and the use of excavated mineral material to build their nests. Soils which are well populated by termites are better drained, more stable and likely to have a higher retained organic content than counterpart soils which are do not have termites present, either for natural reasons or because of anthropogenic land-use change. Termite activity in the desert areas of west and north Africa help to reclaim soils damaged by overgrazing. Termites represent an important food source for many animals, including other insects, reptiles, birds, mammals. However, they become a problem when they interfere with human interests related to wood/cellulose products and in the agro-forestry field (Fig. XVI.VI), Fig. XVI.VII). Some species, especially subterranean termites such as *Coptotermes formosanus* and *Reticulitermes* sp., can be serious pest of structural timber, furniture, works of art, paper products etc. The annual cost for termite damage and management is estimated 3-5 billion US$ in the U.S.A. and about 1 million € in Europe. In tropical-subtropical regions some species of Termitidae can also attack annual and perennial crops causing significant yield losses.

Fig. XVI.V: A group of workers and soldiers of *Coptotermes formosanus*. Workers are whitish with rounded heads and short dark mandibles. Soldiers (5-7 mm length) are white-yellowish with orangebrown, tear-drop shaped heads and have dark brown, sickle-shaped mandibles. Beside biting, they exude a white, glue-like secretion from the top of their head during fights or when disturbed. This subterranean species is native of China but has been introduced by man activities in almost all continents (except Europe) and is considered the most destructive pest termite in the world. (LMa)

Fig. XVI.VI: Some of the damage that termites can do to wood. The above image shows wood which has been eaten by drywood termites. (VRL)

(LMa)



(GS)

Fig. XVI.VII: A group of four pseudergates (= false workers, functionally acting as workers) of *K. flavicollis*, together with a queen (female reproductive). Pseudergates are faded yellow-whitish with short robust dark chewing mandibles, the queen is dark-brown with a yellowish neck and is usually 6-8 mm long. This drywood termite species is commonly found in coastal regions of the Mediterranean basin, nesting and feeding inside dead wood, but can attack also living plants, becoming an occasional pest of fruit and ornamental trees. (LP)

Fig. XVI.IV. A soldier of *K. flavicollis* (**top left**). Soldiers are 6-8 mm long, with grey-yellowish body, ochre-yellow pronotum and head and dark brown mandibles. The head capsule is rectangular and as long as half of the body. (LMa) The image on the **left** is a scanning electron micrograph showing the detail of the head of a soldier of *K. flavicollis*. Notice the long tough mandibles with internal toothed edges, used for mechanical defence against enemies (e.g. ants). (GS)

XVII Terrestrial Isopods

The terrestrial isopods are a monophyletic suborder (Oniscidea) of the order Isopoda which also includes aquatic groups. The name Isopoda is derived from the ancient Greek *isos* meaning "equal" and *podes* meaning "feet" and refers to the seven pairs of legs of more or less of the same size and morphology. The Oniscidea are the only group of crustaceans fully adapted to live on land and are derived from marine ancestors. They are commonly known as woodlice, pill bugs, sow bugs, or slaters. With over 3,600 species currently known, they represent the largest suborder of Isopoda, and this number has been increasing greatly, year after year, as numerous new species are discovered and described, particularly from tropical regions, but also from temperate regions.

As all the other Isopoda, which live in marine or fresh water environments, the terrestrial isopods are segmented animals with a rigid exoskeleton and jointed limbs. They range in length from approximately 1.5 mm to 60 mm, but most of the species do not exceed 20 mm in length. However, some marine relatives such as species of genus *Bathynomus* can reach a length of nearly 50 cm! The body of isopods is dorso-ventrally flattened and divided in three distinct parts: the head (or cephalon), the thorax (or pereion) and the abdomen (or pleon) (Fig. XVII.I). The main substances found in the exoskeleton are calcium carbonate and chitin. The dorsal surface is often smooth, but in some species there are tubercles, ribs and spines of different shape and development.

Fig. XVII.I: Adult specimen of *Porcellio pumicatus* from Italy showing main body parts. (RI)

The head consists of segments which are fused together and contains one pair of compound eyes, two pairs of antennae and the mouthparts. The eyes are sessile (unstalked), with a variable number of ommatidia, which range from one to a few hundred. In some species adapted to live in underground environments the eyes are often reduced or absent (Fig. XVII.II). The first pair of antennae (or antennulae) are vestigial, consisting only of one to three segments, and can only be distinguished under a microscope. The second antennae are well developed, and consist of a 5-jointed basal part and a distal part (the flagellum) with a variable number of segments. The flagellar sections show a progressive reduction in number from the most primitive forms such as Ligia with more than 10 segments (Fig. XVII.III) similar to marine isopods, to the higher Oniscidea with only 3 segments as in *Philoscia* or 2 segments as in *Porcellio* (Fig. XVII.IV) and *Armadillidium*. The biting and chewing mouthparts are inserted on the underside of the head and include one pair of mandibles, two pairs of maxillae, and a pair of maxillipeds.

Fig. XVII.II: *Titanethes albus*, a blind and depigmented Trichoniscidae from Postojna Cave. (SPo)

Fig. XVII.III: *Ligia oceanica*, a littoral species common along the coasts of Atlantic Europe. (ST)

The pereion consists of 7 segments (pereionites) and each segment has a pair of legs (pereiopods) which are adapted for running and sometimes for burrowing. The number of legs (7 pairs) easily distinguishes the Oniscidea from all the other soil arthropods and especially from some millipedes (Diplopoda Glomerida) with which they are often confused for having the same ability to roll up into a ball.

The pleon is always much shorter than the pereion, consisting of 5 segments (pleonites) and ends in a "telson". Each pereionite bears a pair of double-branched flattened appendages called pleopods. The outer branch of the pleopod is the exopod and the inner branch the endopod. The telson is variable in shape, from rounded to triangular, trapezoidal or even hourglass-shaped, and its appendages are known as the uropods.

Respiration

The transition from an aquatic to a terrestrial environment has brought a big change in the way of breathing in the terrestrial isopods. Respiration mainly takes place in the abdominal appendages, the pleopods. In the most primitive groups which are still linked to a very damp environment (as for instance in the Ligiidae and the Trichoniscidae), the pleopods act as gills, the same as in all the other aquatic isopods, while in the more derived groups, adapted to live in more arid habitats, the pleopodal exopods bear respiratory structures that function as lungs that, as their function is similar to that of the tracheae of insects, are also known as pseudotracheae. These lungs are present on 1st and 2nd, 1st to 3rd, or 1st to 5th pleopodal exopods, according to the different families and genera. Their morphology is also variable; in the more primitive forms the respiratory surface is on the external surface (uncovered pleopodal lungs) while in the species adapted to more xeric environments the respiratory surface is inside the exopod (covered pleopodal lungs) with one or more openings on the external surface.

Reproduction

In male specimens of the Oniscidea, the endopods of the 1st and 2nd pleopods are styliform (Fig. XVII.V) and are used to transfer the spermatophores from the genital papilla to the female oviducts. The shape of the male pleopods is one of the most important characteristics used to distinguish the different species in most of the oniscidean families. The female delivers the eggs in a brood pouch (or marsupium) on the ventral side of the pereion, where the mancas (larvae) develop until they hatch out. When they emerge from the marsupium they look like miniature adults and their growth proceeds through successive moults. The fact that the early development takes place in the marsupium allows terrestrial isopods to be independent from water, unlike the few other terrestrial crustaceans groups. In general terrestrial isopods do not show any parental care, except in the desert genus *Hemilepistus* (Fig. XVII.VI). Species of this genus form single families and burrow a nest in the ground where they house their offspring.

Fig. XVII.IV: *Porcellio dilatatus*, a typical "clinger" isopod. (RI)

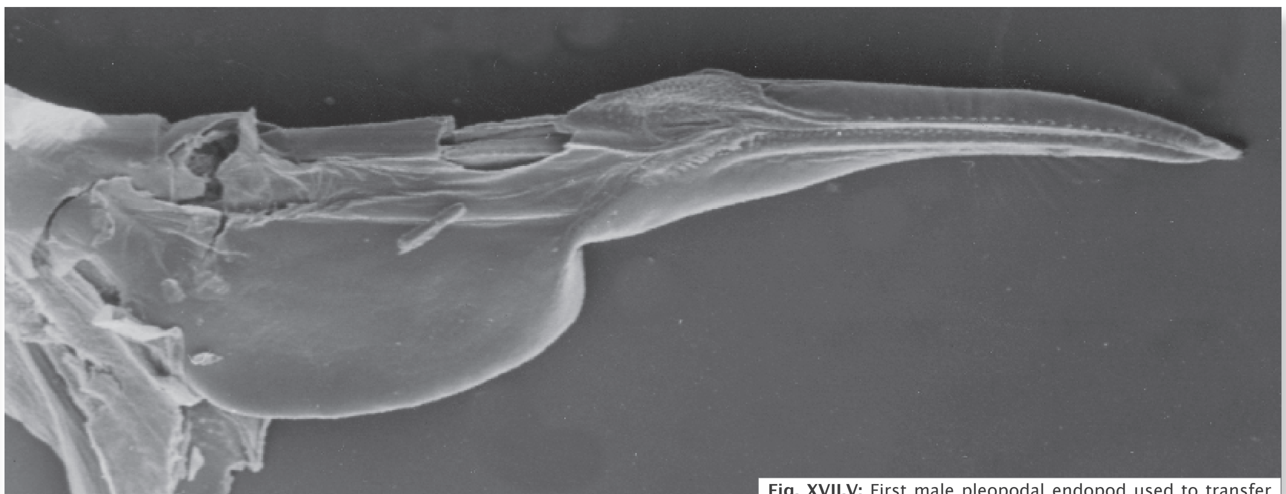


Fig. XVII.V: First male pleopodal endopod used to transfer the spermatophores into the female oviducts. (ST)

Ecology

Terrestrial isopods occur in all kinds of terrestrial habitats, from littoral to high mountains, from forests to very dry areas like sub-deserts and even deserts. They are commonly found under stones, tree logs, in the leaf litter of the woods, among grass in meadows, and even on bushes and in the tree canopy. Some species are strictly littoral and occur along sandy and rocky shores, while a few species, such as *Porcellionides pruinosus* and *Armadillidium vulgare*, are adapted to live in anthropic sites as gardens, houses and cellars. Many species inhabit caves and crevices deep in the ground and are usually blind and colourless, while a few species live in symbiosis with termites and ants (e.g. *Platyarthrus*) and present the same morphological characteristics of cavernicolous forms.

As with other terrestrial crustaceans, most terrestrial isopods live in environments with a high degree of relative humidity and are active during the night in order to limit water loss due to evaporation. Terrestrial isopods have a water-conducting system on the ventral side of the body consisting of narrow grooves and large scales with which they recycle the water of excretion, as in the genus *Porcellio*, or they uptake water from an external source with the grooves on the 6th and 7th pereiopod, as in the case of the littoral genus *Ligia*. The water circulating in this conducting system is very important to keep the correct humidity within the body, particularly in the pleopods, and it can also be reabsorbed by the gut. In general woodlice are decomposers and feed on dead plant material. However, they also feed, sometimes extensively, on living bacteria, fungi, live plants, animal remains and dung, as well as on their own fecal pellets.

Predators and defensive strategies

A large variety of animals are known to eat woodlice. The majority of the predators belong to arthropods such as carabid beetles, spiders, scorpions, opilionids and chilopods. Some vertebrates, such as shrews, frogs, toads and some birds, are also known to feed on woodlice. As a protection against predation the Oniscidea have adopted body morphologies correlated to different defensive strategies which can be grouped in five main categories:

1. the "runners", have an elongated, slightly convex body, smooth dorsum and long pereiopods (e.g. *Ligia* and *Philoscia*);
2. the "clingers", have a flat broad body and short strong pereiopods with which they cling tightly to a solid substratum (e.g. *Trachelipus* and *Porcellio*);
3. the "spiny forms", have a dorsum covered by conspicuous spines as in some tropical species (e.g. *Polyacanthus aculeatus*, Fig. XVII.VII);
4. the "creepers", with small size, convex and elongate body, dorsum with longitudinal ribs, and slow movements (e.g. *Bathytropa* and *Haplophthalmus*), adapted to live in below ground habitats such as deep crevices in rocky biotopes and the lower stratum of deep layers of leaf litter;
5. the "rollers", with a very convex body able to roll up into a ball. Rollers show two different types of conglobation, i.e. keeping the antennae out of the ball (exonantennal conglobation) as in *Cylisticus* or inside the ball (endoantennal conglobation) as in *Armadillidium* (Fig. XVII.VIII).

Distribution

Terrestrial isopods are very good ecological and biogeographical indicators, because most of them are closely linked to the soil, have a low dispersal ability, and have numerous below ground and cave dwelling species. Only a very limited number have been introduced with human activities to many part of the world: most of these species are of Mediterranean or Atlantic origin (e.g. *Agabiformius lentus*, *Porcellionides pruinosus*, *Porcellio laevis*, *P. scaber*, *P. dilatatus*, *Armadillidium vulgare*) and only a few of tropical origin (e.g. *Nagurus cristatus*, *N. nanus*, *Cubaris murina*, *Venezillo parvus*) which are widespread in the tropics and also occur in hothouses in temperate regions. The largest diversity of terrestrial isopods is found in the Mediterranean region and particularly in Italy (approximately 350 species, over 60% of which are endemic) and the Balkan Peninsula, while the northern part of Europe and North America host only a relatively limited number of species.

Fig. XVII.VI: *Hemilepistus reaumurii*, a species from sub-desert areas in northern Africa. This species is exception from other terrestrial isopods in that parents care for their young in specially constructed burrows. (ST)

Fig. XVII.VII: *Polyacanthus aculeatus*, a spiny form of Armadillidae from Africa. (SB)

Fig. XVII.VIII: *Cylisticus gracilipennis* (**left**), a typical exoantennal "roller" and *Armadillidium granulatum* (**right**), an endoantennal "roller", both are from the Mediterranean area. (RI)

XVIII Carabid Beetles

Carabid beetles (Fig. XVIII.I), also known as ground beetles, belong to a very species rich family of the order Coleoptera, and are included in a small group of terrestrial or aquatic predatory taxa that form the suborder Adephaga, together with Dytiscidae, and Gyrinidae. The name is thought to probably derive from "Caribbean cannibals" and refers to their predatory habits.

Carabid beetle distribution is worldwide, with the exception of Antarctica, with about 1,500 genera and 40,000 species currently described, about 3,000 of which are found in Europe. They live in almost all terrestrial habitats, from mountain tops to sea shores, and most are typical soil dwellers, showing epigeic running activity especially in adults.

The preimaginal stages live hidden within the soil or in leaf litter, but many species, especially in the tropics, climb or live on trees or in the canopies, whereas other subgroups such as Trechini, Anillini, Platynini inhabit caves or deep soil cracks in mountain areas.

Ground beetle populations often show high abundance or density values in several ecosystem types: forests, pastures, wetlands, riverine habitats, and also in anthropogenic habitats such as cropland or urban areas although in these habitats, species diversity is usually lower. Carabid beetles and their communities (represented by species-abundance distributions) are currently used as bioindicators for a wide variety of targets: ecological successions and population dynamics, forest management, habitat/soil quality, evaluation for conservation, non-intensive cropland management and diversity assessment, pesticide impact and alternative biological control, landscape management and planning, global change.

Fig. XVIII.I: First male pleopodal endopod used to transfer the spermatophores into the female oviducts. (PB)

Fig. XVIII.II: Carabid larvae are, in most cases, less pigmented than adults, and are subject to predation in the leaf litter or in the humus layer of the soil. The preimaginal development passes through three larval phases. This image shows, here the third "instar" stage of a forest species, *Pterostichus burmeisteri.* (PB)

Carabids are usually univoltine (i.e. produce one brood per year). Eggs are usually laid in spring (species with summer larvae) or in autumn (winter larvae) (Fig. XVIII.II); in this second case the larva needs 5-8 months for its development and pupation takes place in the spring after (Fig. XVIII.III). Population activity and life cycle events vary depending on climate and habitat. In wet or hydromorphic soils species with summer larvae prevail.

The most pronounced morphological variations in adult beetles are connected with specialised modes of feeding. Normally prey is detected by olfactive/tactile cues. Olfactive predators may be polyphagous (feeding on various different types of food source), as are most species, or highly specialised as is the case of the snail feeders of the genus *Cychrus* or the "snail crusher" *Licinines*. In some genera, the head is swollen and the mandibles allow the crushing of very hard preys (e.g. *Scarites*, *Thermophilum*). A few genera are visual hunters (e.g. *Cicindela*, *Elaphrus*) and show enlarged eyes with high numbers of ommatidia, the structural elements of a compound eye. The visual hunter *Notiophilus* is a selective predator of Collembola. The well adapted mouthparts of *Leistus* and the antennal setae of *Loricera* also show preference of Collembola as prey. In some tribes (Amarini, Harpalini) the predatory habits are partially or entirely (e.g. *Ophonus*, *Carterus*) substituted by seed eating and seeds may be stored also in the soil as food supply for the larvae (some *Ditomines*).

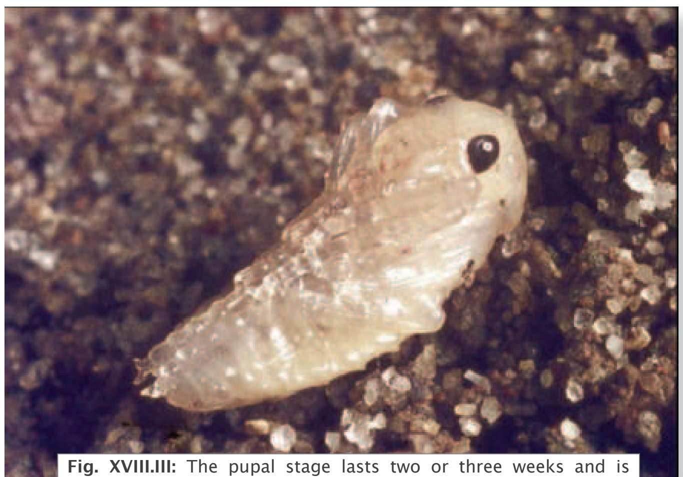


Fig. XVIII.III: The pupal stage lasts two or three weeks and is protected in a subterranean hole that the larva digs out before metamorphosis. Despite its harmless look, the pupa is strongly protected against predators and fungal attacks by manifold chemical substances, including ketones, aldehydes, alcohols, esters and carboxylic acids secreted by lateral exocrine glands. (PB)

Beetles:

About 40% of all described insect species are beetles. Beetles often feed on plants and fungi, break down organic matter and eat other invertebrates. Certain species (such as the boll weevil, *Anthonomus grandis*) are agricultural pests while other species of beetles are used as important controls of agricultural pests (e.g. ladybirds that consume aphids).

Faster than a cheetah!:

Some tiger beetles (Cicindelinae) can run at a speed of 8 km/hour. In proportion to its size, this technically makes them the fastest running land animals. If humans would have this capability, they would be running at speeds greater than 200 km/hour. Tiger beetles have large eyes and hunt by sight.

Fig.XVIII.IV: Two blind cave dwelling carabid beetles. The individual on the left is from the genus *Aphaenops* and the one on the right is of the species *Duvalius krasnohorska* found in a cave in Slovakia. (GC and JSi)

The habitat choice of Carabids is strictly connected to soil features, especially the presence of water in the subsoil, as well as showing textural soil preferences. Ground beetle fauna (or species groupings) can be assessed using "life history traits". These traits concern basic adaptations of species independent from their affinity with related taxa and/or geographical origin, and define the way they react to habitat changes. Therefore, in unstable (ephemeral) habitats taxa with high dispersal power are usually found and are easily recognisable by the presence of well developed hind wings. In stable habitats, such as forests or mountains, brachypterous (i.e. having poorly developed wings) individuals and species generally dominate the community.

Fig. XVIII.V: *Zabrus costai*, a phytophagous carabid, feeds on graminaceous seeds in a pasture of the Italian Appennines. (GC)

Fig. XVIII.VI: *Cicindela sylvicola*, a species of carabid beetle native to Europe. (KKu)

Fig. XVIII.VII: *Anchomenus dorsalis* is a muddy soil dweller common in riparian woods and in cultivated fields. It feeds on small, soft preys, e.g. on aphids. (GC)

The impact of humans on ecosystems is often revealed by the amount of opportunistic feeders in the species assemblage: specialised predators are the most affected by disturbance whereas omnivorous carabids are generally the most numerous in cropland and cities. Species with restricted distribution ranges (endemic chorotypes) often show lower dispersal power, low reproduction rates and are dominant in forest or mountain soils. Carabids represent an important predatory guild of terrestrial ecosystems, ranging from the tropics to higher latitudes, and in mountains until the altitudinal belt of the alpine mats, but also around glaciers and even on the ice itself or on the bare stone fields. Like spiders, they transform minute animal biomass into larger prey palatable for birds, hedgehogs, shrews, moles, bats, frogs and toads. Their role in pest control as generalist predators in cultivated fields is increasingly acknowledged by international scientific research and by EU authorities responsible for pesticide registration. For example, tests with the species *Poecilus cupreus* as a representative of beneficial arthropods can be required in order to assess the environmental risk of a new product.

Chemical Defense

The defenses of carabid adults against predation are mainly chemical. Almost all species produce defensive secretions by abdominal glands, in the so called "bombardier beetles" the secretions are particularly toxic (hydroquinones) and expelled at a very high temperature trough a sort of "explosion chamber". The image on the right shows an Australian Bombardier Beetle (*Pheropsophus verticalis*).

When a bombardier beetle is threatened by a predator, it swings its tail-end around and hot, noxious gases, heated to 100°C are released in an explosive manner from twin combustion tubes into the face of the attacker. The ejection is accompanied by a distinct 'pop'.

The gland openings of some African bombardier beetles can swivel through 270° and thrust between the insect's legs so it can be discharged in all sorts of directions with considerable accuracy.

(PH)

Fig. XVIII.VIII: The most impressive weapons of carabid larvae are the mandibles, which show often very sharp cutting edges. The third stage larva of *Epomis circumscriptus* has a head of about 3 mm width and predates on young toads (*Bufo viridis*) on wet mudflats around Mediterranean ponds. (PB)

XIX Other Soil Macrofauna

While it goes beyond the scope of this atlas to provide a detailed and comprehensive overview of all soil living organisms, as well as those organisms which have been introduced in previous sections, there is a whole set of others organisms which may be commonly found in soil, and may even be of high ecological importance. Many of these fall within the group of soil macrofauna. Within the group of soil macrofauna, in addition to permanent soil inhabitants, such as earthworms, there are other groups that only spend a portion of their time below ground and are more normally found in above ground ecosystems. Furthermore, some macrofauna are a true soil inhabitants, but only during immature stages of their development. Organisms from these groups may still be responsible for playing an important role in various soil functions, and may also be important as bioindicators of soil health.

Spiders (Araneida) are the most well known arachnids (Fig. XIX.I), and play a very similar role in the soil as carabid beetles (Section XIX). They are very mobile predators, feeding on almost all soil inhabitants, including nematodes, earthworms and enchytraeids, and different groups of soil arthropods. Spiders are well adapted to predatory life, having usually long legs, well developed eyes and chelicerae (the mouth parts on which the fangs are found) adapted to predation, as well as the ability to produce venom. As is well known, spiders have silk glands which enable them to create webs which aid many spider species in catching prey. Larger species are mostly found on soil surface or in litter, often hiding or sheltering under rocks and fallen wood. Some species burrow holes into the soil from which they catch their prey. There is also a significant number of small species which inhabit soil pores and cavities (e.g. from family Linyphiidae). Spiders are abundant in almost all types of habitats with up to 200 individuals being present per m^2 of soil in some environments. They are also relatively species rich with altogether 34,000 species currently known. It is thought that spiders may be used as good bioindicators.

Harvestmen (Opilionida) are arachnids similar to spiders, but their abdomen is still articulated (Fig. XIX.II). Most species of Harvestmen have very long legs, and live mostly on the soil surface (Fig. XIX.III). Only a few species penetrate into upper layers of litter. Unlike spiders, they are omnivorous and as well as predation they also feed on detritus, fungi or even excrements of other soil fauna.

Pseudoscorpions (Pseudoscorpionida), which resemble scorpions but do not have elongated abdomen with a venomous sting at the end and are smaller, are also generally true soil inhabitants (Fig. XIX.IV). They are mostly predaceous, as is the case of many soil arachnids. They are generally considered beneficial to humans as they prey on various species which can be pests such as carpet beetle larvae.

Other groups of mostly predatory arachnids that live on the soil surface in a similar way to spiders and ground beetles are scorpions (Scorpionida) and camel spiders (Solifugae) which may be found in warmer and often semiarid or arid conditions. In Europe these groups are mostly found in southern areas such as the Mediterranean.

Fig. XIX.III: Harvestmen of the genus *Trogulus* with large and flattened body and relatively short legs, living in soil litter. They are more similar in appearance to rather large mites than classical harvestmen. (LM)

Fig. XIX.I: Some spiders, such as the majority of wolf spiders, an example of which is shown above (*Acantholycosa lignaria*), do not make webs but rather live in, and hunt from, burrows in the soil or shelter under rocks. (FT)

Fig. XIX.II: Although they make look similar to spiders, harvestmen, such as *Oligolophus tridens* are actually from a different taxonomic order. (FT)

Fig. XIX.IV: An Asian forest scorpion (*Heterometrus longimanus*; **right**). These scorpions are generally nocturnal, spending the majority of the day in cool areas such as in holes in the soil or under rocks and only coming out to hunt at night. **Above** shows a photo of *Ischyropsalis helwigii*, a species of harvestman. It should be noted that the cheliceres of this harvestmen with "pinchers" at the end are not homologous with pinchers of scorpions and pseudoscorpions. (FT) **Far right** shows a pseudoscorpion. Pseudoscorpions are arachnids which have pinchers that resemble those of scorpions but have a small and rounded abdomen in contrast to the segmented tail and stinger which true scorpions have. (FT)

A very important part of soil macrofauna group is made up from different groups of **insects**. Probably the most important are larvae of Diptera (flies), often referred to as maggots (Fig. XIX.V). These can inhabit the soil in very numerous populations, reaching up to several thousands of individuals per square metre. Flies are very species rich with approximately 120,000 species currently known. However, not all of these have soil living larvae. That said, there are still thousands of species which do live in soil (e.g. families Sciaridae, Sciophilidae, Bibionidae, Chironomidae, Simulidae etc.). Diptera larvae are very heterogenous ecologically, being predatory, parasitic, omnivorous, coprophagous, phytophagous or often saprophagous, feeding on dead organic matter. They may fundamentally contribute to the fragmentation and decomposition of dead organic material. In some types of soils such as wet meadows they are one of the most important parts of decomposer food chains. Due to their high abundance and biomass, diptera larvae also serve as an important prey of soil predators. Soil organic matter, when passaging through the intestines of Dipteran larvae, is not only decomposed, but the pH may also be affected, becoming more neutral or even basic. Therefore, the faeces of larvae still support enzymatic activity and contribute to the fermentation processes in organic layers of soil.

Beetles (Coleoptera) are represented by several families, with very different feeding habits (Fig. XIX.VI). Among predatory species, the staphylinids (Staphylinidae) are most numerous, some of which are even adapted for life within the deeper soil layers. The bodies of euedaphic species resemble collembolans, proturans or other microarthropods. They do not have eyes, have very short legs and other appendages, and the body size is reduced and elongated. Other beetle families are specialised detritivores that spend only their larval stages in soil. The most well known of these groups are the numerous species of dung beetles (several families within the superfamily of scarab beetles, Scarabaeoidea), which feed on dung of herbivores and also bury it within the soil to be used as food for larvae. This helps to recycle the organic matter in dung which is still rich in energy. Another group of beetles, often known as carrion beetles or burying beetles (family Silphidae and some others, e.g. Trogidae), is saprophagous, the larvae of which feed on dead animal bodies. They are capable of burying the dead bodies, up to the size of small mammals, into the soil and again contribute to decomposition and recycling of dead organic matter. Larvae of many species of beetles from several families (Scarabaeidae, Lucanidae, Elateridae, Curculionidae, Chrysomelidae, Cerambycidae, etc.) are known as white grubs or wire-worms and inhabit soil or soil surface, feeding on roots of plants or decaying plant organic material (mostly wood or litter). As well as ants and termites, some other social insects may also be found soils, such as bees, bumblebees, wasps etc. Other orders of insects which may be found in the soil include Heteroptera, Psocoptera, Blattodea etc., either as adults or, more often in immatures forms.

Another large group of non-arthropod invertebrates related to soil is **Gastropoda**, which includes slugs (Fig. XIX.VII) and snails (Fig. XIX.VIII). Snails are dependent on the presence of carbonates for their shells. Therefore, they may be very important in calcareous soils, where they may reach abundance up to several hundreds of individuals per square metre. The presence of shells makes them a very good indicator, not only of current ecological quality, but also that of fossil soils. In soils, both species living on the soil surface as well as in the litter can be found. Among snails, many are important phytophages. However, many species are detritophagous. Their excrements may contribute significantly to the formation of soil humus and consequently to the soil structure. Also of high importance is a production of slime, which is energy rich and used as food source by many soil microorganisms. Some species are intermediate hosts of parasites of mammals and birds.

Fig. XIX.V: As well as the more well known maggots (**top**), soil living Diptera larvae can be as morphologically varied as the adult flies that they become. (GP) **Bottom** image shows the larvae of *Metriocnemus* sp. (2 on the left) and *Forcipomia* sp. (**right**). (JF)

Fig. XIX.VI: A highly variable group of dung beetles use dung as food source for their larvae, processing and laying dung into the soil where it can decompose, as other organic matter in the soil, contributing to the cycling of soil nutrients. Some of the dung beetles are small and less distinct, but some may be large or variably coloured and/or having different horn- or thorn-like formations on their bodies, especially in males. The first pair of their legs is always dentated, which is an adaptation helping them to dig holes in the soil. European species from upper to bottom row and from left to right: *Ontohphagus vacca*, *Aphodius conspurcatus*, *Bolboceras armiger* (male), *Bolbelasmus unicornis* (male), *Geotrupes mutator* and *Sisyphus schaefferi*. (FT)

Fig. XIX.VII: A slug of the genus *Ario*. (GB)

Fig. XIX.VIII: A snail of the species *Helix pomatia*, also known as the Grapevine snail. (JS)

Fig. XIX.IX: As well as the more well known larger snail species, many small gastropods live in upper layers of soil. These may have very variable forms of shells, being broad, very long and narrow or flat, as in the species on the image (from left to right): *Succinea putris*, *Alinda biplicata* and *Oxychilus inopinatus*. (LJU and MH)

Glossary

This page explains some of the more technical words and phrases used in the atlas. Readers can avail themselves of additional explanations from the many comprehensive glossaries that can be purchased or found on the Internet.

Technical definitions of soil terms:

- https://www.soils.org/publications/soils-glossary
- *Soil and Environmental Science Dictionary , 2001, Edited by E.G. Gregorich, L.W. Turchenek, M.R. Carter & D.A. Angers, Publisher: CRC Press Boca Raton; 600 pages, ISBN 0849331153*

Soil terms explained for children/general public:

- http://www.soilnet.com

Texts relating to biology:

- http://www.emc.maricopa.edu/faculty/farabee/biobk/biobookgloss.html
- *Biology for Dummies, Donna Rae Siegfried, John Wiley & Sons 384 pages ISBN: 978-0764553264*

Introductory texts on soil ecology:

- *Biological Diversity and Functions in Soils (2005), Ed. R.D. Bargett, M.B. Usher, D.W. Hopkins, Cambridge University Press, Cambridge, UK, pp. 411*
- *Fundamentals of Soil Ecology (2004) D.C. Coleman, D.A. Crossley Jr., P.F. Hendrix, Elsevier Academic Press, San Francisco, USA, pp. 386*
- *Sustaining Biodiversity and Ecosystem Services in Soils and Sediments (2004) Ed. D.H. Wall, Island Press, Washington, USA, pp. 275*

Definitions

Aerobic: Living or occurring only in the presence of oxygen

Agroecosystem: Land used for crops, pasture or livestock

Algae: predominantly aquatic-based, chlorophyll-containing eukaryotic organism

Anaerobic: Living or occurring only in the absence of oxygen

Anhydrobiotic: A type of cryptobiosis induced by a lack of water

Anthropogenic: Caused or created by humans

Antibiosis: An association between two or more organisms that is detrimental to at least one of them

Apomorphic: A trait which characterises an ancestral species and its descendants.

Arbuscular mycorrhizal fungi: Fungi that form symbiotic relationships in and on the roots of host plants that are capable of producing tree-shaped (arbuscular) structures which are unique to these types of fungi

Archea: Organisms forming one of the three domains of the phylogenetic system along with Bacteria and Eukaryota

Autoclave: A device for sterilising equipment by exposing it to pressurised steam at high temperatures

Autotroph: An organism which uses light or chemical energy to synthesize sugars and proteins from inorganic substances. Green plants are by far the most common autotrophes

Bait-lamina assay: An ecological screening method for measuring the feeding activity of the soil biota

Biodiversity: Defined by the Millennium ecosystem assessment as "the diversity among living organisms in terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part. It includes diversity within and between species and the diversity of ecosystems"

Biome: A major community of organisms which is adapted to a particular environmental or climatic condition

Biota: All of the living organisms within a given region

Carnivore: An organism which gains nutrients by eating other organisms

Chlamidospores: A thick walled asexual spore which can function as a resting spore

Coniferous forest: Woodland consisting of mainly needle or scale leaved trees which are generally evergreen

Cryptobiotic: A condition in which the metabolism of an organism is reduced to an imperceptible state. Similar to an extreme form of hibernation

Cytoplasm: The main inner constituent of a cell, a jelly like substance which contains all the structures within a cell that performs specific functions (organelles)

Deciduous forest: Woodland consisting of mainly broad leafed trees where the trees lose their leaves every autumn

Ecosystem: The resulting system of interactions between organisms and their environment, functioning as a unit within a given area

Ecosystem engineers: Any organism that is capable of creating or modifying the local habitat

Edaphic: Of, or relating to, the soil

Endophyte: An organism that lives inside a plant either as a parasite or in a mutually beneficial relationship

Epigeous: Living on or near the soil surface

Euedaphic: Being a 'true' soil organism (i.e. particularly adapted to the soil environment)

Eukaryote: An organism, either single or multi-cellular, the cells of which contain a distinct membrane bound nucleus

Flagellates: Microorganisms containing one or more flagellum

Flagellum: A long threadlike appendage of some cells or microorganisms which can be used for locomotion

Fungi: (sing. fungus) a spore-bearing, unicellular or multicellular organism lacking chlorophyll and feeding on organic matter (mushrooms are the spore-bearing fruiting body of a specific group of fungi)

Fungivore: An organism that eats fungi

Gene: A hereditary unit consisting of a sequence of DNA that determines a particular characteristic of an organisms

Genotype: The genetic make up of an organism or group of organisms

Georeference: Information that relates different sources of geographical data so that they can be linked to a specific point on the Earth's surface

Herbivore: An organism that eats plants

Hermaphrodite: An organism which contains both male and female reproductive organs

Humivore: An organism that feeds on humus

Hydromorphic soils: Soils which are waterlogged, as generally found in bogs and marshes

Ion: An atom (or group of atoms) which have an electric charge through having either gained or lost an electron

Keystone species: A species which is critical for maintaining the structure and functioning of an ecosystem

Lyse: To split open or cause to disintegrate

Micro, meso, macro, megafauna: Groupings of animal groups by size. Size increases from micro, through meso and macro and up to megafauna

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)

Microarthropods: Small organisms from the phylum Arthropoda that range in size from 1-10 mm

Microbivore: An organism that feeds on microorganisms

Microflora: Microscopic plants such as algae, also includes bacteria

Micromorphology: The microscopic structure of a material or organism

Mineralisation: The process of forming a mineral by combination with another element such as metals or oxygen

Mycorrhizosphere: The zone in soil which is influenced by the physical, chemical and biological processes of plant roots and their associated mychorrhizal fungi

Niche: The place or function of an organism within an ecosystem

Omnivore: An organism that eats both plants and other animals

Ontogeny: The origin and development of an organism from embryo to adult

Oospore: A type of fertilised fungal (or algal) spore

Organic-chemistry: The branch of chemistry studying compounds containing carbon

Organic-farming: A form of agriculture whereby no synthetic chemicals such as fertilizers or herbicides are used

Organism: Any living entity

Parasitism: A form of interaction between two different species of organism whereby one organisms gains a benefit at the expense of the other organism

Parasitoids: Types of insects that lay eggs in other organisms that the larvae parasitise after hatching, usually resulting in the death of that organism

Parthenogenesis: A form of reproduction in which an unfertilised egg develops into a new individual

Pedogenesis: The process of soil formation

Pedology: The study of soils in their natural environment

Phenotype: The appearance or characteristics of an organism that result of the interactions of that organism's genes with environmental influences

Phoresy: A relationship between two organisms of different species whereby an organism of one

Photoautotroph: organisms that synthesize organic materials using energy derived from sunlight in the process of photosynthesis

Photosynthesis: The process whereby plants use energy from sunlight to combine carbon dioxide and water to make carbohydrates

Phyllosphere: The micro-environment on and below the surface of a leaf

Phytopathogens: Pathogens which infect plants

Predators: Organisms which hunt other species of organisms for food

Prey: Organisms which are hunted by predators to be used as food

Prokaryote: Single cells organisms which do not contain a distinct membrane bound nucleus

Propagules: Portions of a plant such as a bud, which aid the dispersal of that organism and is capable of growing into a new individual

Protista: A proposed taxonomic kingdom consisting of unicellular, eukaryotic organisms such as algae and fungi

Pseudopodia: A temporary projection of a unicellular organism to create an appendage like protrusion for use in locomotion and for taking in food

Recalcitrant: Something which is difficult to break down

Rhizodeposition: The release of compounds from living plant roots

Rhizosphere: The zone in soil which is influenced by the physical, chemical and biological processes of plant roots

Sclerotia: Fungal mycelium which have hardened into a compact mass, with a store of reserve food material that in some higher fungi becomes detached and remains dormant until favorable environmental conditions for growth occur

Senescence: Change in the biology of an organism as it ages after its maturity

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, preservation of archeological remains, habitat etc.

Spore: a small usually single-celled asexual reproductive organism produced by many non-flowering plants and fungi that are capable of developing into a new individual without sexual fusion

Sylviculture: The care and cultivation of trees

Symbiosis: A close and prolonged association between organisms of two different species which may result in benefits to either or both organisms

Trophic: Relating to nutrition or involving the feeding habits of different organisms within an ecosystem

Univoltine: Referring to organisms which have one brood per year

Weathering: Changes in the chemical or physical make up of rocks due to being exposed to weather

EUROPEAN COMMISSION JRC

Institute for Environment and Sustainability

JRC mission statement:

The mission of the JRC is to provide customer-driven scientific and technical support for the conception, development, implementation and monitoring of EU policies.

As a service of the European Commission, the JRC functions as a reference centre of science and technology for the Union. Close to the policy-making process, it serves the common interest of the Member States, while being independent of special interests, whether private or national.

Robust science for policymaking

The Joint Research Centre is a research based policy support organisation and an integral part of the European Commission. The JRC provides scientific advice and technical know-how to support a wide range of EU policies. Our status as a Commission service, which guarantees our independence from private or national interests, is crucial for pursuing our mission.

The JRC has seven scientific institutes, located at five different sites in Belgium, Germany, Italy, the Netherlands and Spain, with a wide range of laboratories and unique research facilities. Through numerous collaborations, access to many facilities is granted to scientists from partner organisations.

JRC value statement:

"The JRC aims to operate to the highest standards of quality, efficiency and integrity with respect to the society as a whole, to its customers and to its own staff." Our work ranges from detecting and measuring genetically modified organisms (GMO) in food and feed to developing nuclear forensics technology for combating illicit trafficking of nuclear material and to using satellite technologies for monitoring land use and emergency situations such as forest fires and floods. Our activities also involve the definition of food safety standards, research into new energy technologies and evaluating policy options, for instance related to climate change.

The JRC employs around 2750 staff coming from throughout the EU, and its budget comprises €330 million annually, coming from the EU's research budget. Further income is generated through the JRC's participation in indirect actions, additional work for Commission services and contract work for third parties, such as regional authorities and industry. The latest figures are available in the JRC annual report.

http://www.jrc.ec.europa.eu./

A research-based policy support organisation

More than 25% of EU legislation has a technical or scientific basis and this trend is likely to grow as increasingly policies cut across several disciplines. The JRC as the Commission's in-house research based policy support centre works to provide such support throughout the policy process, while maintaining a strong science base. The JRC's Multi-Annual Work programme for the Seventh Framework Programme (2007-2013) reflects this user emphasis while also allowing the development of new scientific competence to meet emerging trends.

JRC research-based policy support is grouped around five themes:

- Prosperity in a knowledge intensive society includes growth, employment, knowledge, and competitiveness. The JRC will focus on the regulatory context, the development of measurement standards and data harmonisation; and support to key policy areas such as energy, transport, information, chemicals and biotechnologies.
- The sustainable management of resources is a long-standing work priority for the JRC, particularly in areas of agriculture and environment. The 'environment and health' theme is emerging as a new focus of attention while climate change remains a key feature.
- Security and freedom is an area of growing concern for the Union. The JRC will focus on providing technical support on internal security issues where interactions between the European Commission and Member States are expanding. Activities will continue in well established policy areas where many new challenges lie ahead, including the safety of food and feed and response to disasters.
- Europe as a world partner involves the JRC supporting a range of external policies (e.g. international trade/anti-fraud, Community action relevant to stability, non-proliferation and common foreign and security policy; development cooperation policy and humanitarian aid; European neighbourhood policy etc).
- The EURATOM programme for the JRC entails developing and assembling knowledge, providing crucial scientific/technical data and support for safety/security, reliability, sustainability, and control of nuclear energy; including the assessment of safety and security aspects related to innovative/future systems.

Located in Ispra (a small town on the shores of lake Maggiore in Northern Italy), the Institute for Environment and Sustainability (IES) is one of the institutes that constitute the Joint Research Centre of the European Commission. In line with the JRC mission, the aim of IES is to provide scientific and technical support to European Union strategies for the protection of the environment contributing to a sustainable development.

IES works in close collaboration with official laboratories, research centres and industries of the EU's Member States, creating a bridge between the EU's policies and the European citizen.

The combination of complementary expertise in the fields of experimental and analytical sciences, modelling, GIS and remote sensing puts the IES in a strong position to contribute to the implementation of the European Research Area and to the achievement of a sustainable environment.

The mission of the Institute for Environment and Sustainability is to provide scientific and technical support to EU policies for the protection of the environment contributing to a sustainable development in Europe.

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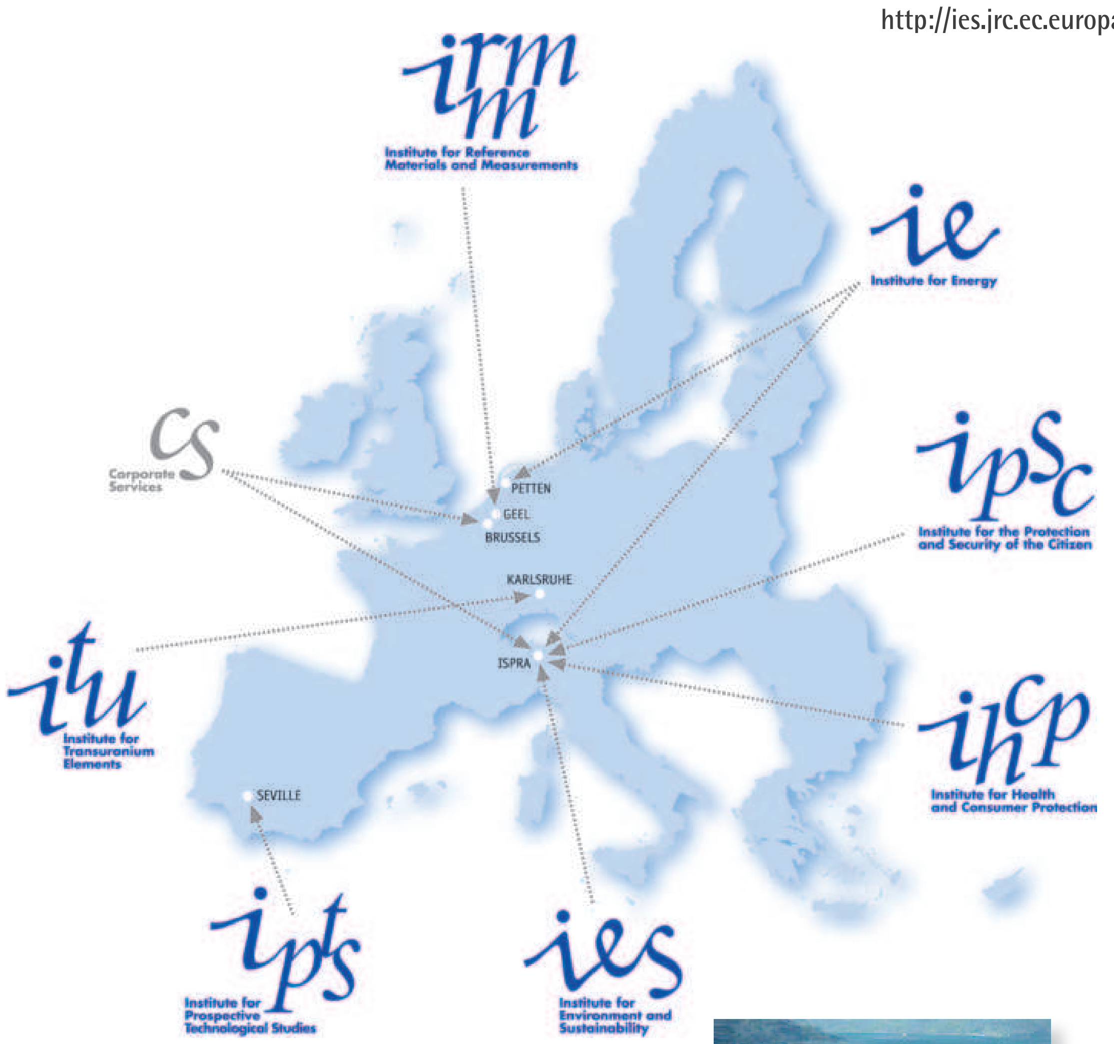
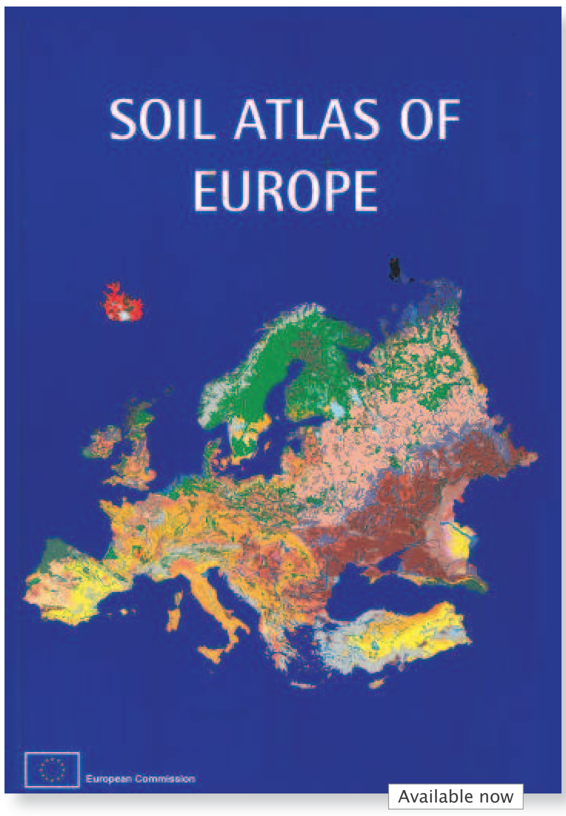


Atlas Series

The European Commission Joint Research Centre is collaborating 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 web site (http://eusoils.jrc.ec.europa.eu).



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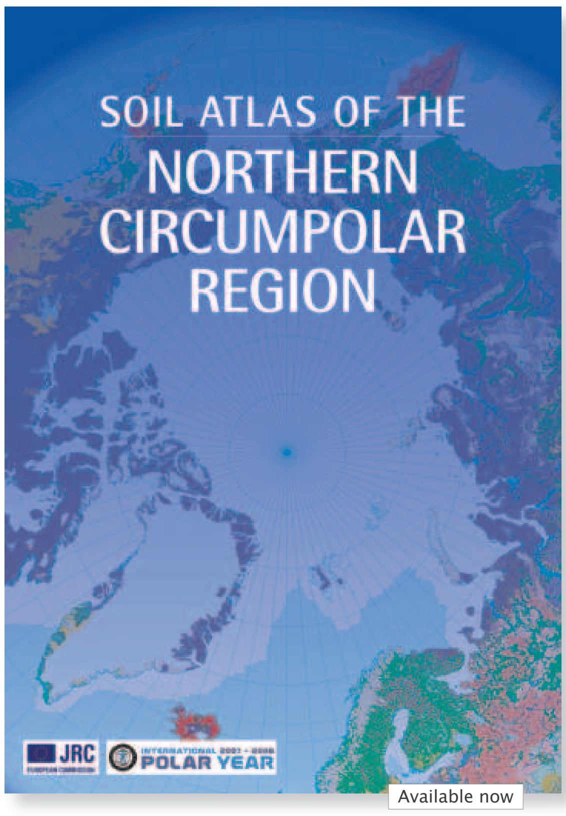

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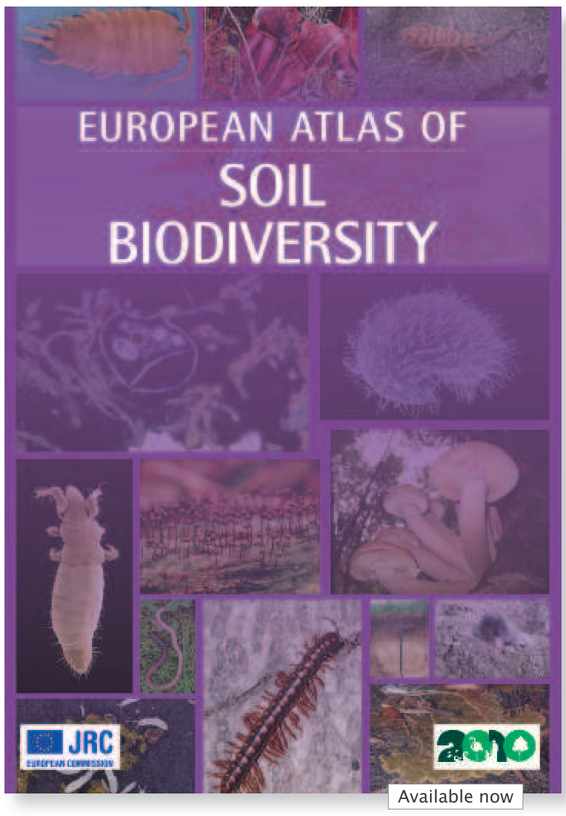

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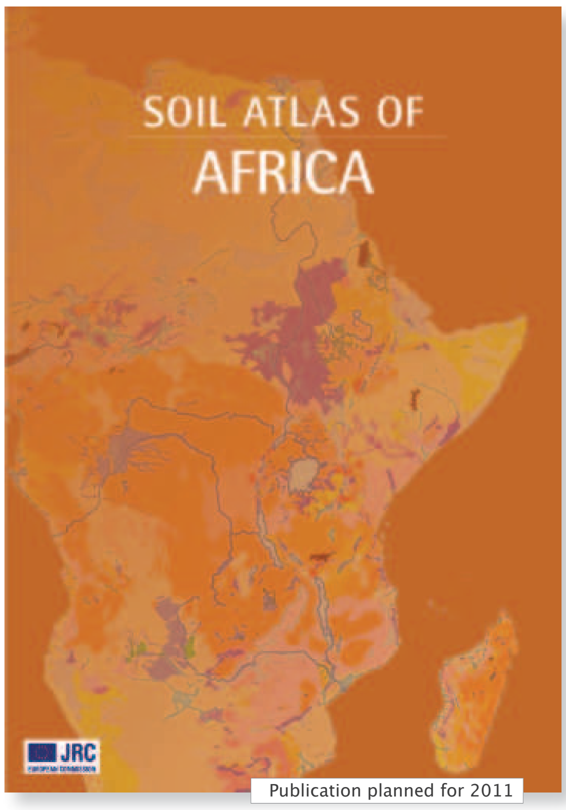

Publication planned for 2011

Publication planned for 2013

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Soil is one of the fundamental components for supporting life on Earth. Most ecosystem processes and global functions that occur within soil are driven by living organisms that, in turn, sustain life above ground. However, despite the fact that soils are home to a quarter of all living species on Earth, life within the soil is often hidden away and suffers by being 'out of sight and out of mind'.

LB-NA-24375-EN-C

What kind of life is there in soil? What do we mean by soil biodiversity? What is special about soil biology? How do our activities affect soil ecosystems? What are the links between soil biota and climate change?

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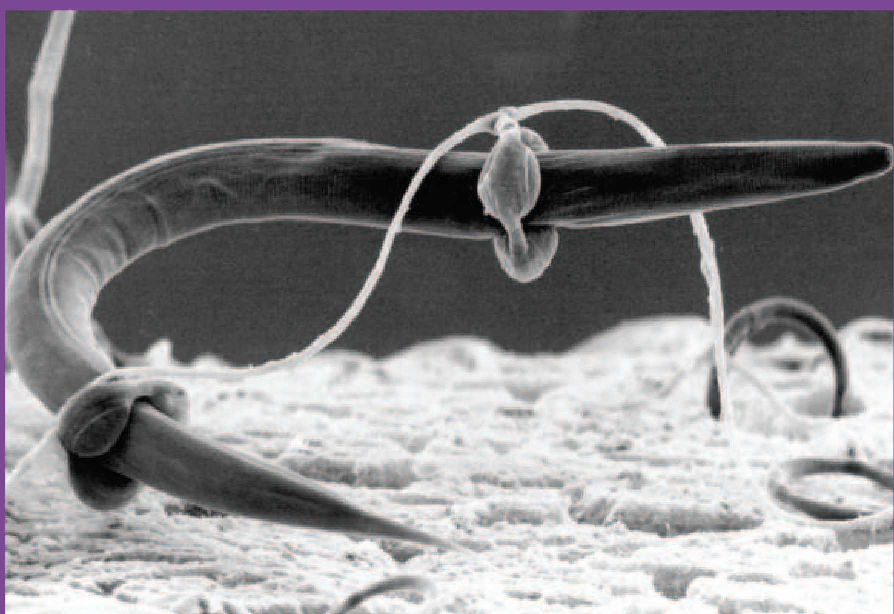
The EUROPEAN ATLAS OF SOIL BIODIVERSITY is an essential reference to the many and varied aspects of soil. The overall goal of this work is to convey the fundamental necessity to safeguard soil biodiversity in order to guarantee life on this planet.



Soil organisms represent around a quarter of all biodiversity on Earth, yet are widely neglected in conservation efforts. Worldwide, only eight soil species are protected under CITES, the international rules on trade in endangered species: three scorpions, four tarantulas and one beetle. This is not because soil species are not endangered: it is simply because they are so little known and because their habitat and functioning are complex. However, taking steps to protect them may be doubly useful as efforts to protect soil communities are very likely to help above ground habitats.

ISBN 978-92-79-15806-3

European Commission

Publications Office

EUR 24375 EN
Price (excluding VAT)
in Luxembourg €25