CAMBRIDGE
Cambridge University Press
978-0-521-18695-7 - 21st Century: Guidebook to Fungi
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Part I Nature and origins of fungi

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1 21st century fungal communities

In this book we aim to provide a broad understanding of the biology of fungi and the biological systems to which fungi contribute. Our scope ranges from the evolutionary origins of fungi and other eukaryotes more than a billion years ago (though the discussion covers all of time), through to the many contributions that fungi make to our present, everyday, lives. The book provides an all-round view of fungal biology, including ecology, evolution, diversity, cell biology, genetics, biochemistry, molecular biology, biotechnology, genomics and bioinformatics.

Our book emphasises interactions between fungi and other organisms to bring out the functions and behaviours of biological systems:

- we concentrate on integration rather than reduction, which satisfies those who would see systems biology as a paradigm of the scientific method;
- we include computational modelling and bioinformatics for those who view systems biology in terms of operational research protocols;
- and we bring together data about biological systems from diverse interdisciplinary sources.

In this chapter we examine present-day communities; starting with the essential terrestrial habitat and the nature and formation of soil. We emphasise the contributions made by fungi to soil structure and chemistry; and particularly what has come to be called geomycology. We also discuss the diversity of organisms in soil and illustrate interactions between bacteria, amoebae (including slime moulds), fungi, nematodes, microarthropods and larger animals. The origins of agriculture are briefly mentioned and our dependence on fungi illustrated.

1.1 What and where are fungi?

'How many of you think that fungi are bacteria?' is a question asked at a recent Summer School for year 10 pupils (4th year in secondary school, 14 years of age at entry), by one of the pupils who had attended a workshop session of ours. When all attendees (approximately 170 pupils) were asked 'Hands up all those who think fungi are plants,' about 15 hands went up, but when asked 'Hands up all those who think fungi are bacteria,' at least 150 hands went up!

As teachers we are used to battling against the mistaken idea that fungi are plants, but it was a shock to find that so many pupils believe that fungi are bacteria so close to the end of their statutory education. After all, it's a bigger error than for them to think that whales are fish; at least whales and fish are in the same biological kingdom. Does such ignorance matter? We say it does. The practical reason it matters is because the activities of fungi are crucially important in our everyday lives. The educational reason it matters is that fungi form what is arguably the largest kingdom of higher organisms on the planet. Ignorance of this kingdom is a major blot on our personal education.

Fungi are not bacteria, because fungi are eukaryotes and they have the complex cell structures and abilities to make tissues and organs that we expect of higher organisms. Unfortunately, even though fungi make up such a large group of higher organisms, most current biology teaching, from school level upwards, concentrates on animals, with a trickle of information about plants. The result is that the majority of school and college students (and, since they've been through the same system, current university academics) are ignorant of fungal biology and therefore of their own dependence on fungi in everyday life. This institutional ignorance about fungi, generated by the lack of an appropriate treatment of fungal biology in national school curricula, seems to apply throughout Europe, North and South America and Australasia; indeed, most of the world.

The feature which has figured most in our decision to write this textbook is that although fungi comprise what is arguably **the most pivotal kingdom** of organisms on the planet, these organisms are often bypassed and ignored by the majority of biologists. We say 'pivotal' because molecular phylogenies place animals and fungi together at the root of evolutionary trees. It is likely that the first eukaryotes would have been recognised as 'fungal in nature' by features presently associated with that kingdom. So in a sense, those primitive 'fungi' effectively invented the eukaryotic lifestyle.

The contribution that fungi make to human existence is close to crucial, too. Imagine life without bread, without alcohol, without soft drinks, without cheese, coffee or chocolate; without cholesterol-controlling drugs (the 'statins') or without antibiotics, and you are imagining a much less satisfactory existence than we currently enjoy. As we will show in later chapters:

- Fungi (known as anaerobic chytrids) help to digest the grass eaten by cows (and other domesticated grazing animals) and by so doing indirectly provide the milk for our breakfast, the steak for dinner and the leather for shoes.
- Fungi make plant roots work more effectively (more than 95% of all terrestrial plants depend on mycorrhizal fungi) and, even leaving aside the effect of this on the evolution of land plants, by so doing mycorrhizal fungi help provide the corn for our cornflakes, oats for our porridge, potatoes, lettuce, cabbage, peas, celery, herbs, spices, cotton, flax, timber, etc. And even oxygen for our daily breath.
- The characteristic fungal life style is the secretion of enzymes into their environment to digest nutrients externally; and we harness this feature in our biotechnology to produce enzymes to start our cheese-making, clarify our fruit juices, distress denim for 'stone-washed' jeans, and, conversely, provide fabric conditioners to repair day-to-day damage to our clothes in the weekly wash.
- Fungi also produce a range of compounds that enable them to compete with other organisms in their ecosystem; when we harness these for our own purposes we create products like:
  - cyclosporine, which suppresses the immune response in transplant patients and prevents organ rejection;
  - the statins, which help increase the lifespan of so many people these days by controlling cholesterol levels;
  - and even today's most widely used agricultural fungicides, the strobilurins.

But fungi are not always benevolent. There are fungal diseases of all of our crops that we need to understand and control. In many cases crop losses of 20% to 50% are *expected* by the agricultural industry today. As the human population increases such losses in primary production cannot be sustained. And there is more to fungal infection of humans than athlete's foot and a disfigured toenail. Opportunistic fungal infections of patients are an increasing clinical challenge as the majority of patients with chronic immunodeficiency now die of fungal infections; and yet we lack a sufficient range of good drugs to treat fungal infections.

Our answers to the questions in the title of this section 'What and where are fungi?' are that fungi comprise the most crucial kingdom of eukaryotic organisms on the planet, and that they exist everywhere on planet Earth.

1.2 Soil, the essential terrestrial habitat

The conventional estimate is that 75% of the Earth is covered with water; oceans, lakes, rivers, streams. However, less than 1% of the known species of fungi have been found in marine habitats (see pp. 346–351 in Carlile *et al*., 2001). Fresh water is inhabited by many water moulds (an informal grouping that includes the most ancient fungi and fungus-like organisms, which will be discussed in more detail in Chapter 3), but the overwhelming majority of fungi occur in association with soil; where 'in association with' means in or on the soil, or in or on some live or dead plant or animal that is in or on the soil.

As Wikipedia points out 'Soil is also known as **earth**: it is the substance from which our planet takes its name' (http://en.wikipedia.org/wiki/Soil). Soil is, therefore, the essential terrestrial habitat. In saying this we do not underestimate the importance of other categories of habitat. But they are categories: grassland, forest, coastal, desert, tundra and even cities and suburbs, and ultimately all these habitats depend on their soil. Without soil, no grass, so no grassland habitat. Without soil, no trees, so no forest habitat. Few, if any, organisms can be found on bare rock, wind-blown sand or ice. Fundamentally, terrestrial life on Earth depends upon the earth, and to show how fungi contribute to the formation of soil, this is where we choose to start our story.

1.3 How much soil is there and where is it?

Only about 7.5% of the Earth's surface provides the **agricultural soil** on which we depend for the world's food supply (Table 1.1), and this fragment competes, sometimes unsuccessfully, with all other needs: housing, cities, schools, hospitals, shopping centres, landfills, etc.

Indeed, there may not be enough soil in the first place. A **subsistence diet** requires about 180 kg of grain per person per year, and this can be produced on 0.045 hectares of land. In contrast, an affluent high-meat diet requires at least four times more grain (and four times more land, 0.18 hectares) because the animals are fed on grain and conversion of grain to meat is very inefficient.

Table 1.1 **How much soil is there? Broad estimates of the coverage of the Earth's surface by different features**

Surface feature	Percentage coverage
Aquatic: oceans, seas, rivers and lakes	75
Deserts: polar and mountain regions unsuitable for agriculture	12.5
Rocky and other poor-quality terrestrial regions unsuitable for agriculture	5
Terrestrial regions suitable for agriculture	7.5

The Earth has about 0.25 hectares of farmland per person, but only about 0.12 hectares per person of farmland is suitable for producing grain crops. As it stands, the Earth does not have enough land for all inhabitants to enjoy an **affluent diet** as that is presently defined (see Table 1–2 in Miller & Gardiner, 2004, and see Fig. 11.12, p. 275, for a potential alternative).

1.4 The nature of soil and who made it

Soil is that part of the Earth's surface that is composed of fragmented rock and humus. It is made up of solid, liquid and gaseous phases.

- The solid phase is mineral and organic matter and includes many living organisms.
- The liquid phase is the 'soil solution', from which plants and other organisms take up nutrients and water.
- The gaseous phase is the soil atmosphere, supplying oxygen to plant roots and other organisms for respiration.

The solid phase of soil is made up of **minerals** and **organic matter**. Minerals may be either primary or secondary. Primary minerals are those that cooled from a molten mass, and are chemically unchanged from the day they came into existence. Secondary minerals form by chemical modification, precipitation or recrystallisation of chemicals released by the weathering of parental rocks. Rocks are mixtures of minerals. **Igneous rock** forms from molten magma, **sedimentary rocks** are cemented accumulations of minerals; common sedimentary rocks include limestone, sandstone, quartzite and shale. **Metamorphic rocks** include slate (hardened shale) and marble (hardened limestone).

Weathering is the term applied to the processes that cause rocks and minerals to disintegrate into smaller parts. Loose or unconsolidated products of weathering are called soil. Soil minerals may be fragmented versions of primary minerals (e.g. sand is fragmented quartz rock) or may be secondary minerals, like clays, slowly formed through chemical interactions in the soil, then becoming further chemically modified with time. The elements most commonly found in soil minerals are silicon, oxygen and aluminium.

Physical and chemical processes contribute to weathering. The main **physical weathering** effect is the force exerted by the expansion of water as it freezes, so physical weathering is most pronounced in cold climates. In dry climates abrasion by materials suspended in the wind causes weathering (and a similar effect occurs in flowing water). **Chemical weathering** predominates in warm and/or moist climates, and chemical weathering is generally more important for soil formation than physical weathering. Chemical processes include:

- **oxidation** and **reduction** (of great importance for iron-containing minerals);
- **carbonation** (dissolution of minerals in water made acidic by carbon dioxide);
- **hydrolysis** (when water splits into hydrogen and hydroxide, and one or both components participate directly in the chemical process); and
- **hydration** (when water is incorporated into the crystal structure of a mineral, changing the properties of that mineral) (Miller & Gardiner, 2004).

Soils are highly dynamic environments; they change over time, and all the while their particles are moved: downward by the **leaching** effect of rainwater; laterally by wind, water and ice.

The most potent soil-forming factor is often considered to be the **climate**, mainly temperature and rainfall. Temperature affects the rates of chemical reactions, so that soils of warmer climates tend to mature more rapidly than soils of temperate climates. However, living organisms (the soil biota) both affect, and are affected by, soil formation. First thoughts tend to be about the profound effects of vegetation on soil formation. For one thing, the extent of vegetation cover influences water runoff and erosion. Fairly obviously, also, the vegetation type and amount directly affects the type and amount of organic matter that accumulates on and in the soil. Grasslands and forests form different soils, there being more rapid nutrient cycling in grassland.

Organic matter deposited on the surface contributes to soil solids. It is moved downward physically through rainwater leaching, and influences soil chemistry, pH and nutrient supply as it goes. This organic matter is the food source for most microorganisms in the soil, so the vegetation influences soil microbial populations by providing their nutrients. Old soils can lose their ability to produce vegetation fast enough to keep up with microbial decomposition. In healthy agricultural soils organic material is initially decomposed rapidly, but within about a year organic materials like crop residues 'stabilise'; the remaining residues decay very slowly. This slowly decomposing material is composed of **humic substances** (commonly called **humus**). Humic substances are natural non-living organic substances that occur in all aquatic and terrestrial environments, being found in sediments, peat, sewage, composts and other deposits. This soil organic matter represents the main carbon reservoir in the biosphere, estimated at a grand total of 1600×10^{15} g C (Grinhut *et al.*, 2007). The organic matter of soil is crucial to its agricultural value because it aids structure, nutrition and water relations; everything that contributes to soil **tilth** (*tilth* is an Old English word that describes the structure and quality of cultivated soil in the sense that good tilth corresponds to potentially good crop growth).

Decomposing organic matter provides nutrients to other **soil organisms** (including, but not exclusively, crop plants). Stable organic matter does not do this, but it improves the ability of the soil to hold nutrients and water. An organic soil is dominated by organic matter, rather than minerals. Such soils are found in wetlands, especially cold wetlands, where the primary production of organic materials by the plants exceeds the rates of decomposition in the soil. Ultimately, this equation results in **peat** formation.

The spaces between soil particles form the **pore space**, which contains air and water. The water, called the **soil solution**, contains soluble salts, organic solutes and some suspended colloids. The amount and behaviour of soil water is controlled to a great extent by pore size (influenced by proportions of coarse material (like sand) and fine minerals (such as clays). Small pores have a greater affinity for water and hold it very tightly. Larger pores allow water to escape easily, by drainage or into the atmosphere by evaporation. **Soil 'air'** has more CO_2 but less O_2 than the open atmosphere. This is because organisms in the soil consume O_2 and produce CO_2, producing corresponding concentration gradients between the soil and the atmosphere. Similarly, soil air always has a relative **humidity** near 100%. Respiration releases water vapour, which evaporates only slowly into the atmosphere above the soil.

So soil is a **dynamic matrix** of organic and mineral constituents enclosing a network of voids and pores, which contain liquids and gases. It is also a living system. Soil organic matter includes living organisms ranging from bacteria, fungi, algae, protozoa, and multicellular animals from rotifers and microarthropods to worms and small mammals. Although living macroorganisms are usually not considered part of the soil, they can have considerable effect on soil (remember Darwin's experiments on earthworms: Darwin (1881, reprinted 1985 in facsimile)), leaving aside human activities like ploughing, irrigating, mining, clearing, waste-disposing, excavating, levelling, building, draining, flooding, etc.

1.5 Soil biota are extremely varied and numerous

In about 5 cm^3 of agricultural soil you are likely to find:

- At least 5 billion bacteria
- 5 million protozoa
- 5000 nematodes (about 0.3–1.5 mm long); the most common multicellular animals in soil
- About 6 mites and other microarthropods: this equates to up to 600 000 per square metre.

For larger organisms we have to look at quadrats of about 1 square metre:

- Earthworms – maybe 300 per square metre. Earthworm casts add more bacteria back to the soil than the worm eats. More bacteria mean healthier soil.
- There may be around 20 000 kilometres of hyphae per square metre. Above ground, a meadow may look like separate plants. Underground, the plants are interconnected by their fungal associates (mycorrhizas) so they all belong to a single web of living things.
- Small mammals; mice, voles, shrews and moles, which depend on the earthworms, arthropods and fungi for their nutrition, and in their turn feed predators; owls, foxes, etc., so the food web extends from microbes to large animals.

1.6 Microbial diversity in soil

The word '**diversity**' when used in relation to organisms in a habitat describes complexity and variability at different levels of biological organisation:

- genetic variability within taxons (which may be species)
- the number (also called richness) of taxa
- relative abundance (or evenness) of taxa
- and number and abundance of functional groups.

Important aspects of diversity at the ecosystem level are:

- the range of processes
- complexity of interactions
- number of trophic levels.

Thus, measurements of **microbial diversity** must include multiple methods, integrating measures at the total community level and partial approaches that target subsets of the community having specific structural or functional attributes. For example, you might be trying to assess all decomposers, or all leaf-eaters, all root diseases, etc., each of which will give you just a partial view of the community in the habitat.

Simply attempting to count the number of microorganisms in soil raises difficulties. Because they are microscopic counting and identifying them with conventional techniques requires them to be cultivated. Yet not all can be cultivated; some have growth requirements that are so fastidious they may be difficult or impossible to provide and it seems that in many other cases the growth requirements are simply unknown. The filamentous nature of most fungi creates the additional difficulty of recognising an individual fungus, and disentangling an extensive mycelial network from the substratum it is exploring and penetrating. Techniques based on **chemical analysis** to quantify some characteristic component of the fungal cell have been successfully used to quantify fungal biomass in soils, composts (in mushroom farming) and timber. Measurement of chitin (as amino sugar) can be used where confusion with arthropod exoskeletons

Resources Box 1.1 | Life in the soil

Thomas E. Loynachan, Professor of Agronomy and Microbiology at Iowa State University, has created a set of 16 short digital videos showing the scope of life in the soil.

Visit http://www.agron.iastate.edu/~loynachan/mov/ to view these.

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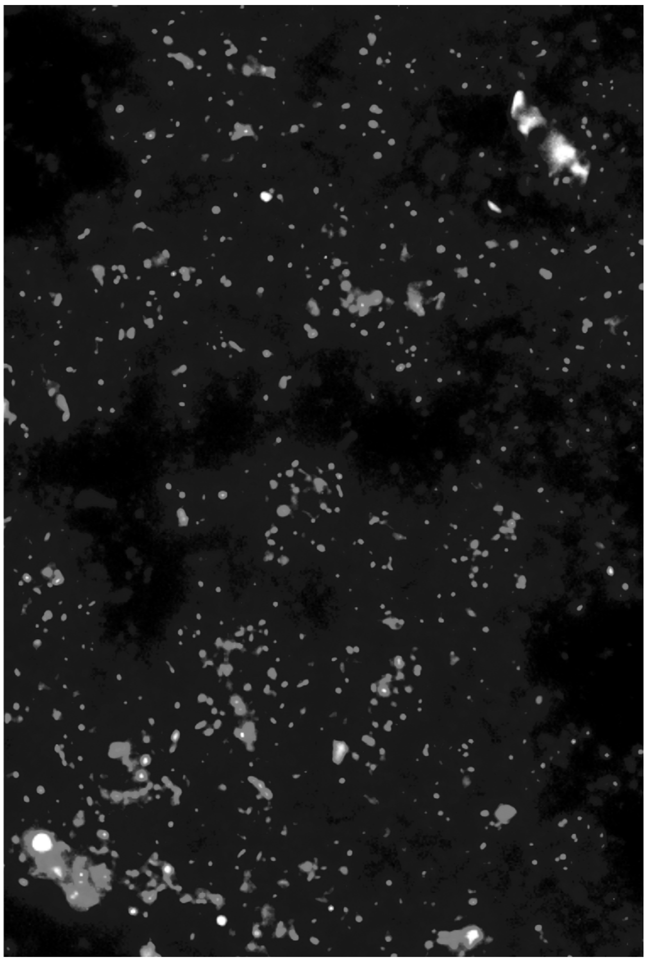

Fig. 1.1 This picture (from Torsvik & Øvreås, 2002) shows an epifluorescence micrograph of soil microorganisms stained with the fluorochrome DAPI (4′-6-diamidino-2-phenylindole), which detects intact DNA. This sample had a **visible** count of 4×10^{10} cells g^{-1} soil (dry weight); but the **viable** count was 4×10^{6} colony-forming units g^{-1} soil (dry weight) when estimated by plating on agar media. (Reproduced with permission from Elsevier.) See Plate section 1 for colour version.

can be excluded; but measurement of ergosterol, which is a characteristic component of fungal membranes, is more generally applicable. More recently, novel methods based on **RNA** and **DNA probes** and **PCR** have been developed to identify particular organisms and to reveal an immense diversity of microbes in natural habitats (Prosser, 2002; Torsvik & Øvreås, 2002; Wellington *et al*., 2003; Anderson & Parkin, 2007). Frequently, less than 1% of the microorganisms detected this way can be cultivated and characterised as live cultures (Fig. 1.1).

This contrast between the **numbers of microbes** (of all sorts) that can be seen to be alive and the numbers that can be cultivated is not unusual, and certainly applies to fungi (Prosser, 2002; Mitchell & Zuccaro, 2006; Anderson & Parkin, 2007). There may be several reasons for it, including fastidious growth requirements of presently unknown nature, and our current inability to break the dormancy of many of the living cells that can be detected.

1.7 Microbial diversity in general

Microorganisms exist in every conceivable place on Earth, even in **extreme environments**. The tropics are considered to be richer in microbial species diversity than the temperate zones, but deserts may feature an equal amount, if not more, microbial diversity, and microbial communities can be found on rocks and within deep rock crevices (e.g. Staley *et al*., 1982). Temperature may be the only limitation as to where they can and cannot exist and/or function (Hunter-Cevera, 1998).

Mycologists estimate that there are 1.5 million species of fungi on Earth, of which only 98 000 species have been isolated or described (Hawksworth, 1997, 2001). The estimate was made by comparing the number of species of fungi and vascular plants described for particular geographic regions. For example, in the British Isles there are about six times more species of fungi than species of vascular plants. Extrapolating this ratio to the 270 000 species of vascular plants in the world gives an estimate of 1 620 000 fungi. Now, this figure needs to be corrected (to 1 504 800) to account for the double-counting of fungal species resulting from the practice of giving separate specific names to the asexual and sexual stages of some fungi (because it may not be known that the two reproductive stages belong to the same fungus).

If you subtract the 98 000 described species from the estimated total 1.5 million species of fungi on Earth, you might well ask: 'Where are the other 1.402 million **undescribed fungi**?'

Part of the answer to that question is that there are not many mycologists in the world today and not much work has been done in several unique geographical regions or habitats. Many 'missing fungi' may be associated with tropical forests, for example. Insects may be another large source of missing fungi as many fungi are already known to be associated with insects. Finally, many missing fungi may be discovered in specialised habitats which have not yet been explored at all, or have been only poorly investigated. The rumen and hindguts of herbivorous animals and the inner surfaces of Antarctic rocks do not sound like very promising **habitats**, but they are examples of habitats that have, unexpectedly, already yielded novel fungi.

Resources Box 1.2 | About the diversity of fungi

We do not intend to expand further on the topic of fungal biodiversity here because we prefer to concentrate on other particular aspects of the fungal contribution to the soil community, but if you wish to investigate fungal diversity further we recommend the following literature references.

Feuerer, T. & Hawksworth, D. L. (2007). Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's Xoristic regions. *Biodiversity and Conservation*, **16**: 85–98. DOI: http://dx.doi.org/10.1007/s10531-006-9142-6.

Gams, W. (2007). Biodiversity of soil-inhabiting fungi. *Biodiversity and Conservation*, **16**: 69–72. DOI: http://dx.doi.org/10.1007/s10531-006-9121-y.

Hyde, K. D., Bussaban, B., Paulus, B., Crous, P. W., Lee, S., Mckenzie, E. H. C., Photita, W. & Lumyong, S. (2007). Diversity of saprobic microfungi. *Biodiversity and Conservation*, **16**: 7–35. DOI: http://dx.doi.org/10.1007/s10531-006-9119-5.

Mueller, G. M. & Schmit, J. P. (2007). Fungal biodiversity: what do we know? What can we predict? *Biodiversity and Conservation*, **16**: 1–5. DOI: http://dx.doi.org/10.1007/s10531-006-9117-7.

Mueller, G. M., Schmit, J. P., Leacock, P. R. Buyck, B., Cifuentes, J., Desjardin, D. E., Halling, R. E, Hjortstam, K., Iturriaga, T., Larsson, K.-H., Lodge, D. J., May, T. J., Minter, D., Rajchenberg, M., Redhead, S. A., Ryvarden, L., Trappe, J. M., Watling, R. & Wu, Q. (2007). Global diversity and distribution of macrofungi. *Biodiversity and Conservation*, **16**: 37–48. DOI: http://dx.doi.org/10.1007/s10531-006-9108-8.

Schmit, J. P. & Mueller, G. M. (2007). An estimate of the lower limit of global fungal diversity. *Biodiversity and Conservation*, **16**: 99–111. DOI: http://dx.doi.org/10.1007/s10531-006-9129-3.

Shearer, C. A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D., Porter, D., Raja, H. A., Schmit, J. P., Thorton, H. A. & Voglmayr, H. (2007). Fungal biodiversity in aquatic habitats. *Biodiversity and Conservation*, **16**: 49–67. DOI: http://dx.doi.org/10.1007/s10531-006-9120-z.

Wherever they occur, fungal communities are very diverse metabolically, physiologically and taxonomically, and given the benefits that man has derived from the fungi we know about, it is surprising, and disappointing, that more efforts have not been made to seek out these still unisolated fungi.

1.8 Geomycology

The fungal contribution to the soil community is usually seen as some aspect of their involvement in **biomass recycling** (releasing nutrients for plants), or direct involvement as components of food webs (as part of the nutrition of some animal, large or small). These aspects of fungal biology are undeniably extremely important and will be discussed in some detail in later chapters in this book. Here we will only mention these points because we want to emphasise something that usually gets much less attention, which is the fungal involvement in the **geological transformations** that produce and modify soils.

Fungi are intimately involved in **biogeochemical transformations** on large and small scales, and although such transformations occur in both aquatic and terrestrial habitats, the terrestrial environment is where fungi have the greatest influence. The areas in which fungi have fundamental importance include:

- organic and inorganic transformations and element cycling (e.g. Lepp *et al.*, 1987),
- rock and mineral transformations,
- **bioweathering**,
- mineral formation,
- fungal–clay interactions,
- and metal–fungal interactions (Fig. 1.2).

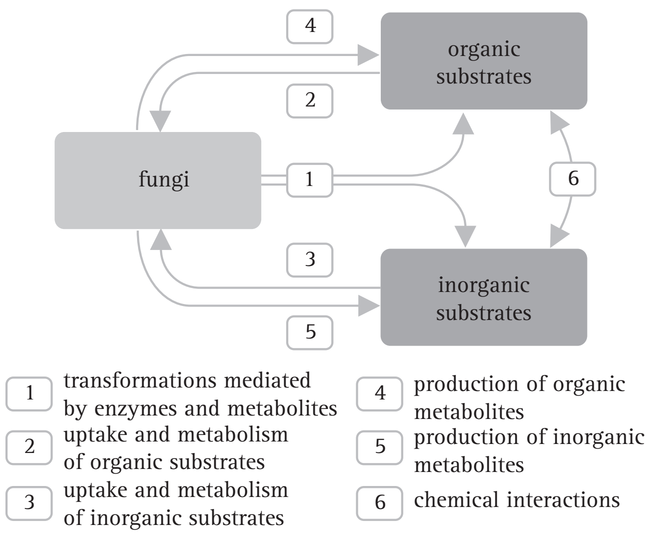

Fig. 1.2 Diagrammatic representation of fungal action on **organic** and **inorganic substrates** which may be naturally occurring and/or man-made. Key: **1**, organic and inorganic transformations mediated by enzymes and metabolites, e.g. H ions, carbon dioxide and organic acids, and physicochemical changes occurring as a result of metabolism; **2**, uptake, metabolism or degradation of organic substrates; **3**, uptake, accumulation, sorption, metabolism of inorganic substrates; **4**, production of organic metabolites, exopolymers and biomass; **5**, production of inorganic metabolites, secondary minerals and transformed metal(loid)s; **6**, chemical interactions between organic and inorganic substances, e.g. complexation and chelation, which can modify bioavailability, toxicity and mobility. Organisms in this model may also translocate nutrients. (Modified from Gadd, 2004.)

Many of these processes are relevant to the potential use of fungi in **environmental biotechnology** such as **bioremediation** (Burford *et al.*, 2003; Gadd, 2004, 2007).

Fungi also affect the **physical structure** of soils at a variety of spatial scales via electrostatic charge, and adhesive and enmeshment mechanisms. They also produce large quantities of extracellular polysaccharides and hydrophobic compounds that affect water infiltration properties of soils. Fungal decomposition of organic matter can also destroy soil structure through effects on soil aggregation. In turn, soil structure affects fungi. The filamentous growth form of fungi is an efficient adaptation for life in a **heterogeneous environment** like soil, but the labyrinthine pore network will itself determine how fungal mycelia can grow through and function within the soil (Fig. 1.3).

The distribution of water within soils plays a crucial role in governing fungal development and activity, as does the spatial distribution of nutrient resources (Ritz & Young, 2004). In aerobic environments fungi are of great importance on **rock** surfaces, in soil and at the plant **root–soil interface** (Table 1.2).

Many fungi can grow **oligotrophically**, which means they can thrive in environments that are low in food sources. They do this by **scavenging nutrients** from the air and rainwater and this ability enables them to survive on stone and rock surfaces. Fungi are able to cause weathering of a wide range of rocks. In Iceland and other subpolar regions bioweathering of basalt outcrops by fungal communities is believed to be chronologically the first weathering process. Lichens are important at early stages of **rock colonisation** and mineral soil formation, while free-living fungi are also major biodeterioration agents of stone, wood, plaster, cement and other building materials. There is increasing evidence that fungi are important components of rock-inhabiting microbial communities with significant roles in **mineral dissolution** and secondary mineral formation.

Several fungi can dissolve minerals and mobilise metals more efficiently than bacteria. Mycorrhizal **fungi** are involved in mineral transformations and redistributions of inorganic nutrients (e.g. essential metal ions and phosphate; Figs 1.4–1.6).

These roles of fungi in soil geochemistry, especially metal cycling, have been included under the term **geomycology**, defined as 'the study of the role fungi have played and are playing in fundamental geological processes' (Burford *et al.*, 2003; Gadd, 2004, 2007).

1.9 The origins of agriculture and our dependence on fungi

As the last ice age came to an end, the consequential climatic and environmental changes forced humans to utilise an ever wider variety of food resources. Although hunting and gathering persisted (and still exists today in certain regions of the world), new food production techniques gained importance. The controlled cultivation of plants, what we might now call **agriculture**, began to be practised in different parts of the world between 14 000 and 11 000 years ago. This was soon followed by the close management and eventual domestication of the animals that are common on farms today. The four major centres from which agriculture evolved were the Middle East and Europe, Africa, the Americas, and China and Southeast Asia.

European agriculture originated in the '**Fertile Crescent**', centred on the Tigris and Euphrates rivers. The region is also known as Mesopotamia, which refers to an area now occupied by modern Iraq, eastern Syria, southeastern Turkey, and southwest Iran. Farmers in Mesopotamia were using