CAMBRIDGE
Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

CHAPTER 1

Twenty-First Century Fungal Communities

This second edition of our book continues to emphasise interactions between fungi and other organisms to bring out the functions and behaviours of biological systems; but this edition features a thorough section-by-section update from the mycology of the years 2008/10 to the mycology of 2018/20. However, we continue to maintain our aim to:

- concentrate on integration rather than reduction, to satisfy those who would see systems biology as a paradigm of scientific method;
- include computational modelling and bioinformatics for those who view systems biology in terms of operational research protocols;
- bring together data about biological systems from diverse interdisciplinary sources;
- offer our readers a comprehensive, all-embracing view of today's fungal biology.

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, 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 briefly illustrated.

1.1 WHAT AND WHERE ARE FUNGI?

'How many of you think that fungi are bacteria?' is a question asked at a 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!

When teaching mycology, we were used to battling against the mistaken idea that fungi are plants, but it was a shock to find that so many pupils believed 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, South and Central America, and Australasia; indeed, most of the world. We have a history of writing about this institutional ignorance of fungi, in several formats, in several arenas and at several academic levels. We stated in the first edition of this book that although fungi comprise what is arguably the most pivotal kingdom of organisms on the planet, these organisms are

Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

often bypassed and ignored by the majority of biologists. We say 'pivotal' here 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 currently associated with that kingdom. So, in a sense, those primitive 'fungi' effectively invented the eukaryotic lifestyle.

We will not tax our readers further, except to say that this tragic situation clearly persists. To quote Lozano Garza and Reynaga Peña (2017): 'Even in specialised Biology books, the issue of fungi, as compared to plants or animals, is not given equal importance. The results of this analysis partially explain the reasons for the common but scientifically incorrect belief that fungi are bacteria or plants.' This institutional ignorance is the feature which figured most in our decision to write the first edition of this textbook and its persistence fuelled the desire to write the second edition.

It is also worth emphasising that 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 lifestyle is the secretion of enzymes into their environment to digest nutrients externally; 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 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 Earth. Remember this: 'when looking for nature-based solutions to some of our most critical global challenges, fungi could provide many of the answers' (Willis, 2018).

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 we will discuss 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.

The soil environment is the most complex on Earth and provides a range of habitats that support an enormous population of soil organisms. Soil is characterised by a heterogeneity, which is measured across physical scales varying from nanometres to kilometres, and differs in chemical, physical and biological characteristics in both space and time. The nature of soil is determined by the interaction of geology, climate and vegetation, and is a biochemical product of the organisms participating in its formation (Voroney & Heck, 2015).

As Wikipedia points out (https://en.wikipedia.org/wiki/Soil) 'Soil is commonly referred to as earth,' so it is the substance from which our planet takes its name. Soil is, therefore, essential to terrestrial habitats.

But they are categories: grassland, forest, coastal, desert, tundra and even cities and suburbs, and ultimately all these environments 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 'earth', and showing how fungi contribute to the formation of soil is where we choose to start our story.

Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

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). This fragment competes, sometimes unsuccessfully, with all other needs: housing, cities, schools, hospitals, shopping centres, land fills, 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. This can be produced on 0.045 ha of land. In contrast, an affluent high-meat diet requires at least four times more grain (and four times more land, 0.18 ha) because the animals are fed on grain and conversion of grain to meat is very inefficient.

The Earth has about 0.25 ha of farmland per person, but only about 0.12 ha 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 Figure 12.12, in section 12.4 below, for a potential alternative).

This chapter describes the key physical and chemical features of the soil habitat that govern the biodiversity and activity of soil organisms.

1.4 THE NATURE OF SOIL AND WHO MADE IT

Soil is that part of the Earth's surface comprised of fragmented rock and humus. It is made up of solid, liquid and gaseous phases (Needelman, 2013).

- 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 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. If the magma cools slowly it forms a network of large crystals as in granite, if it cools rapidly it forms small crystals as in basalt. Sedimentary rocks are cemented accumulations of minerals: common sedimentary rocks include limestone, sandstone, quartzite, and shale. Metamorphic rocks, which arise when an existing rock is transformed by exposure to high temperatures and pressures, include slate (hardened shale) and marble (hardened limestone).

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	75.0
Deserts: polar and mountain regions unsuitable for agriculture	12.5
Rocky and other poor-quality terrestrial regions unsuitable for agriculture	5.0
Terrestrial regions suitable for agriculture	7.5

Weathering is the term applied to the processes that cause rocks to disintegrate into smaller parts. Loose or unconsolidated products of weathering are called soil minerals. These 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 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 (a similar effect occurs in flowing water). Chemical weathering predominates in warm and/or moist climates. It is generally more important for soil formation than physical. 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, as their particles are moved downward by the leaching effect of rainwater and 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. 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, the vegetation type and amount directly affect the type and amount of organic matter that accumulates on and in the soil. Grasslands and forests form different soils, as there is more rapid nutrient cycling in grassland.

Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

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' and the remaining residues decay very slowly. This slowly decomposing material is comprised of 'humic substances' (commonly called humus). Humic substances are natural non-living organic substances that occur in all aquatic and terrestrial environments. They are 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 1,600 × 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 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.

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: bacteria, fungi, algae, protozoa and multicellular animals, from rotifers and microarthropods to worms and small mammals (Haynes, 2014). The soil biota is extremely important to soil processes. Although living macroorganisms are usually not considered part of the soil, they can have considerable effect on soil; remember Darwin's experiments on earthworms, animals that excrete more bacteria into the soil than they consume (Darwin, 1881). This is true even if we leave 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;
- 5,000 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 m^{-2}.

For larger organisms we must look at quadrats of about 1 m^2:

- 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 km 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) that 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.

RESOURCES BOX 1.1 Life in the Soil

Deep Down & Dirty: the Science of Soil. A close-up of creatures living beneath the soil, made by the British Broadcasting Corporation (BBC): https://www.youtube.com/watch?v=gYXoXiQ3vC0

The Living Soil Beneath Our Feet, made by the California Academy of Sciences: https://www.youtube.com/watch?v=MlREaT9hFCw

The development of communities of soil biota is characterised by progressive addition with many pioneer species remaining throughout soil development. Size and diversity of soil biota communities increases rapidly during the first 20 to 50 years and then more or less stabilises after hundreds of years. Plant biomass and soil organic matter content do not reach a peak for many hundreds or even thousands of years (Haynes, 2014). Development of communities of soil fauna is less rapid than that of the microbial communities because dispersal is slower, and some faunal species require a certain depth of organic topsoil and/or litter layer before high populations can develop. With increasing time, the food web, which is based on organic detritus, becomes increasingly complex (Haynes, 2014). Organism abundance, diversity and activity vary in a patchy fashion both

Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

horizontally across a landscape and vertically through the soil profile. Different groups of soil organisms exhibit different spatial patterns, with the spatial heterogeneity in microbial properties being an inherent feature of soils (Frey, 2015).

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 taxa (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 with 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. 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 can be excluded, but measurement of ergosterol, which is a characteristic component of fungal membranes, is more generally applicable. Methods based on RNA and DNA probes and polymerase chain reaction (PCR) were initially developed to *identify* organisms, but they revealed 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 (Figure 1.1).

This contrast between the numbers of microbes (of all sorts) that are known to exist 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 this discrepancy, including the unknown growth requirements of the uncultured organisms and the intractable dormancy of their resistant structures. For example, it has been demonstrated that *arbuscular mycorrhizal fungi are fatty acid auxotrophs*; that is, they depend on their host plants to synthesise and transfer, from the plant to the mycorrhizal fungus, essential substrates for the production of fungal lipids that the fungus cannot make for itself (Luginbuehl *et al.*, 2017). Also, there are many obligately biotrophic fungi that cause serious and widespread diseases of crop plants, but which cannot be cultured *in vitro* (Tang *et al.*, 2018). Today, the numerical discrepancy between living presence and culturability (as illustrated in Figure 1.1) is most likely to be detected by environmental DNA testing (Taberlet *et al.*, 2018), although the use of environmental DNA samples to define sequence based taxa without physical specimens and formal nomenclature is hotly debated (Hongsanan *et al.*, 2018).

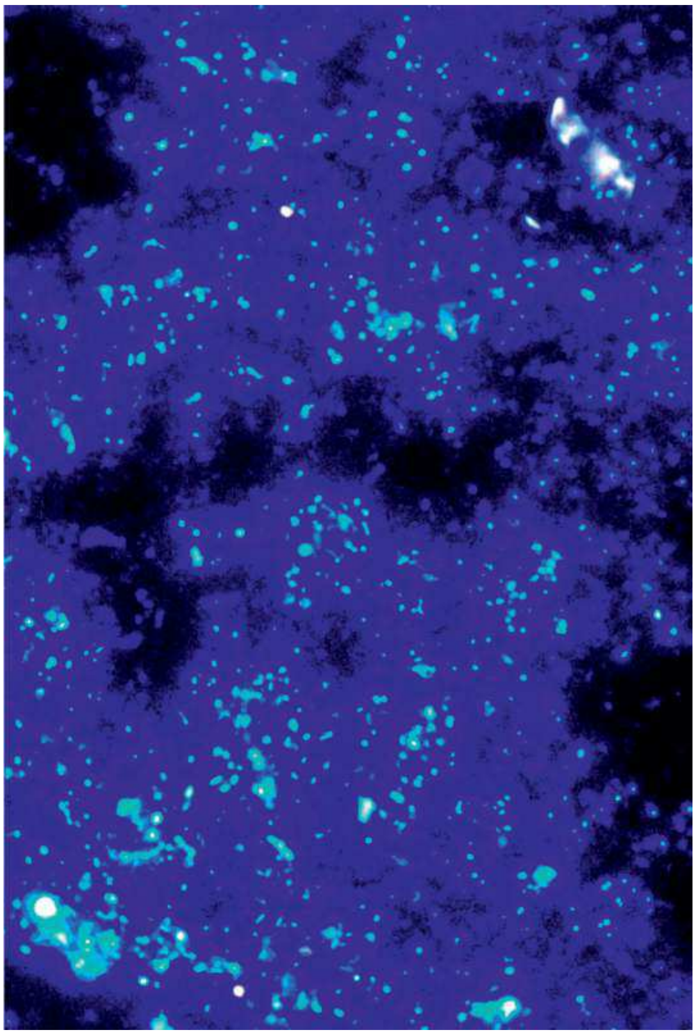

Figure 1.1. This picture (from Torsvik & Øvreås, 2002) shows an epifluorescence micrograph of soil microorganisms stained with the fluorochrome DAPI (4′-6-diamidino-2-phenylindole), which detects intact DNA. This sample had a visible count of 4 × 10^{10} cells g^{-1} soil (dry weight); but the viable 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.

1.7 MICROBIAL DIVERSITY IN GENERAL

Microorganisms exist in every conceivable place on Earth, even in extreme environments. The tropics are 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 (Hunter-Cevera, 1998).

The conservative estimate is that there are 1.5 million species of fungi on Earth, of which only 120,000 species have been isolated or described (Hawksworth, 1997, 2001; Hawksworth & Lücking, 2017). The former estimate was made by comparing the number of species of fungi and vascular plants described for 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). In recent years molecular approaches to species recognition, together with the recognition of new habitats, hyperdiverse environments and unstudied collections have prompted revision of this conservative estimate of fungal diversity. Hawksworth and Lücking (2017) conclude that the range 2.2–3.8 million species of fungi on Earth is a better estimate. They point out that this means that 'at best just 8%, and in the worst case scenario just 3%' of the world's fungi have been formally described and named so far.

You might ask: 'Where are the other 92 to 97% of undescribed fungi?' In fact, recent developments of molecular phylogeny have revealed an unexpected diversity, many times greater than this, among fungi, and indeed, most other organisms. We mentioned in the previous Section the numerical discrepancy between living presence detected by environmental DNA testing and culturability (as illustrated in Fig. 1.1). Applying molecular phylogenetics to the DNA testing identifies many cryptic species (species recognised only by analysis of DNA sequences). Based on such data, the number of fungal species on the Earth has been estimated to be **12 (11.7–13.2) million** compared to the estimate of **2.2–3.8 million** species indicated above (Wu *et al.*, 2019).

Intensive studies of specific fungal genera and families have demonstrated that in countries and areas that were hitherto neglected by mycological taxonomists, up to over 90% of the collected specimens may constitute undescribed species (Hyde *et al.*, 2018). But the novelty goes beyond recognising more species; a number of novel taxa including new divisions, classes, orders and new families have been established in the last decade by molecular phylogenetics, and many of these ***dark matter fungi*** belong to early diverging branches of the fungal evolutionary tree (Grossart *et al.*, 2016).

The range and prevalence of the genetic material being detected has led to it being called **biological dark matter** [https://en.wikipedia.org/wiki/Biological_dark_matter] by (informal) analogy with cosmological dark matter, which is a form of invisible matter thought to account for approximately 85% of the matter in the universe because of its gravitational influences. Biological dark matter is an extremely active and important research topic, which we cannot pursue further here but we do suggest a few representative references: Wu *et al.*, 2011; Carey, 2015; Lok, 2015; Wu *et al.*, 2019.

Part of the answer to our question about the location of all those undescribed fungi 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,

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 aspects of the fungal contribution to the soil community, but if you wish to investigate fungal diversity further we recommend the following literature references (and the papers referenced in them). Many of these topics will be discussed later in this book.

Aptroot, A., Cáceres, M.E.S., Johnston, M.K. & Lücking R. (2016). How diverse is the lichenized fungal Family Trypetheliaceae (Ascomycota: Dothideomycetes): a quantitative prediction of global species richness. *Lichenologist*, 48: 983–1011. DOI: https://doi.org/10.1017/S0024282916000463.

Bass, D. & Richards, T.A. (2011). Three reasons to re-evaluate fungal diversity 'on Earth and in the ocean'. *Fungal Biology Reviews*, 25: 159–164. DOI: https://doi.org/10.1016/j.fbr.2011.10.003.

Hawksworth, D.L., Hibbett, D.S., Kirk, P.M. & Lücking, R. (2016). (308–310) Proposals to permit DNA sequence data to serve as types of names of fungi. *Taxon*, 65: 899–900. DOI: https://doi.org/10.12705/654.31.

Hawksworth, D.L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. In *The Fungal Kingdom*, ed. J. Heitman, B. Howlett, P. Crous *et al.* Washington, DC: ASM Press, pp. 79–95. DOI: https://doi.org/10.1128/microbiolspec.FUNK-0052-2016.

Hibbett, D.S. (2016). The invisible dimension of fungal diversity. *Science*, 351: 1150–1151. DOI: https://doi.org/10.1126/science.aae0380.

Hyde, K.D., Bussaban, B., Paulus, B. *et al.* (2007). Diversity of saprobic microfungi. *Biodiversity and Conservation*, 16: 7–35. DOI: https://doi.org/10.1007/s10531-006-9119-5.

box continues

Leavitt, S. D., Divakar, P. K, Crespo, A. & Lumbsch, H. T. (2016). A matter of time: understanding the limits of the power of molecular data for delimiting species boundaries. *Herzogia*, 29: 479–492. DOI: https://doi.org/10.13158/heia.29.2.2016.479.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How many species are there on Earth and in the ocean? *PLoS Biology*, 9: article e1001127. DOI: https://doi.org/10.1371/journal.pbio.1001127.

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

Mueller, G.M., Schmit, J.P., Leacock, P.R. *et al.* (2007). Global diversity and distribution of macrofungi. *Biodiversity and Conservation*, 16: 37–48. DOI: https://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: https://doi.org/10.1007/s10531-006-9129-3.

Schoch, C.L., Seifert, K.A., Huhndorf, S *et al.* (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 6241–6246. DOI: https://doi.org/10.1073/pnas.1117018109.

Shearer, C.A., Descals, E. Kohlmeyer, B *et al.* (2007). Fungal biodiversity in aquatic habitats. *Biodiversity and Conservation*, 16: 49–67. DOI: https://doi.org/10.1007/s10531-006-9120-z.

Taberlet, P., Bonin, A., Zinger, L. & Coissac, E. (2018). *Environmental DNA For Biodiversity Research and Monitoring.* Oxford, UK: Oxford University Press. ISBN-10: 0198767285, ISBN-13: 978-0198767282.

Tedersoo, L., Bahram, M., Põlme, S. *et al.* (2014). Global diversity and geography of soil fungi. *Science*, 346: article 1256688. DOI: http://dx.doi.org/10.1126/science.1256688.

Tedersoo, L., Bahram, M., Puusepp, R., Nilsson, R.H., James, T.Y. (2017). Novel soil-inhabiting clades fill gaps in the fungal tree of life. *Microbiome*, 5: article 42 (10 pp.). DOI: https://doi.org/10.1186/s40168-017-0259-5.

Truong, C., Mujic, A.B., Healy, R *et al.* (2017). How to know the fungi: combining field inventories and DNA-barcoding to document fungal diversity. *New Phytologist*, 214: 913–919. DOI: https://doi.org/10.1111/nph.14509.

A greater understanding of Earth's biodiversity, coupled with the responsible stewarding of its resources, are among the most crucial aims and challenges of the Earth BioGenome Project as described in the following:

Lewin, H.A., Robinson, G.E., Kress, W.J *et al.* (2018). Earth BioGenome Project: sequencing life for the future of life. *Proceedings of the National Academy of Sciences of the United States of America*, 115: 4325–4333. DOI: https://doi.org/10.1073/pnas.1720115115.

See also the *Earth BioGenome Project* website at https://www.earthbiogenome.org/ and the *Darwin Tree of Life Project* at https://www.sanger.ac.uk/news/view/genetic-code-66000-uk-species-be-sequenced.

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.

Wherever they occur, fungal communities are very diverse metabolically, physiologically and taxonomically (Bass & Richards, 2011; Money, 2014). 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 unknown fungi (see section 3.9 for discussion of the species concept in 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 fungal involvement in the geological transformations that produce and modify soils (Gadd, 2016, 2017; Robson, 2017).

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 (Kirtzel *et al.,* 2017, 2018);
- mineral formation (Robson, 2017);
- fungal–clay interactions; and
- metal–fungal interactions (Robson, 2017; and see Figure 1.2).

Many of these processes are relevant to the potential use of fungi in environmental biotechnology such as bioremediation (Burford *et al.*, 2003; Conceição *et al.,* 2019; Gadd, 2004, 2007, 2016, 2017; Robson, 2017) and recovery of high-value rare earth elements or other precious metals from wastes (Boczonádi *et al.*, 2019).

Fungi 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

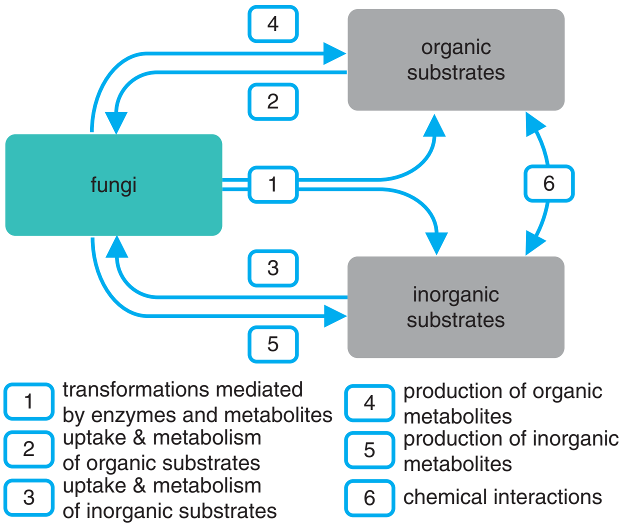

Figure 1.2. Diagrammatic representation of fungal action on organic and inorganic substrates which may be naturally occurring and/or synthetic. Full key: (1) organic and inorganic transformations mediated by enzymes and metabolites, e.g. H-ions, carbon dioxide, and organic acids, and physicochemical 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; and see Gadd, 2016, 2017).

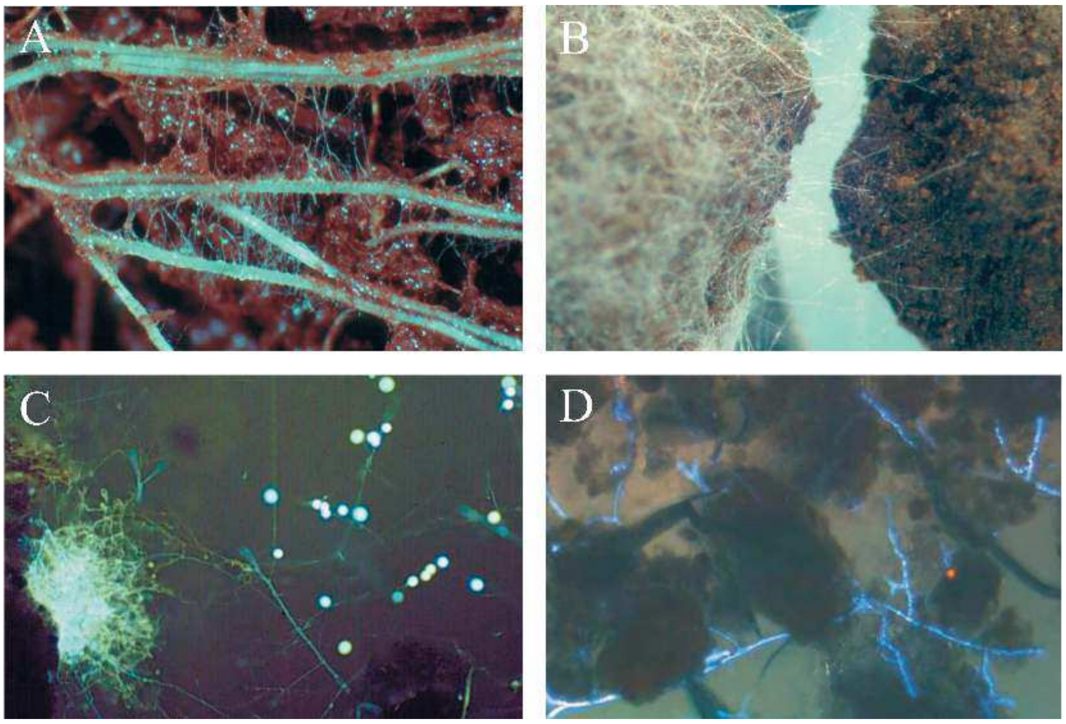

Figure 1.3. Fungal mycelia visualised in the soil environment. (A) Unidentified hyphae bridging roots of *Plantago lanceolata* growing in non-sterile field soil. Note the shiny films of mucilage; image width, 2 cm. (B) Hyphae of *Fusarium oxysporum* f. sp. *raphani* colonising a pair of adjacent soil aggregates. Aggregate on left is sterile, hence extensive mycelial development. Aggregate on right is non-sterile; reduced mycelial growth is due to competition from other microorganisms and reduced nutrients; image width, 1 cm. (C) Unidentified mycelium growing in soil pore, visualised in a thin-section of undisturbed pasture soil with a fluorescent stain. Note proliferation of hyphae on pore wall in left of image. Bright spherical objects are sporangia; image width, 150 μm. (D) Mycelium of *Rhizoctonia solani* growing in sterilised arable soil, visualised in thin-section with a fluorescent stain; image width, 150 μm. Modified from Ritz and Young (2004) using images kindly supplied by Professor Karl Ritz, Cranfield University, UK. Reproduced with permission from Elsevier.

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 (Figure 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).

Cambridge University Press
978-1-108-74568-0 — 21st Century Guidebook to Fungi
David Moore , Geoffrey D. Robson , Anthony P. J. Trinci
Excerpt
More Information

Table 1.2. Roles and activities of fungi in biogeochemical processes

Fungal role and/or activity	Biogeochemical consequences
Growth and mycelium development	Stabilisation of soil structure; soil particulate aggregation; penetration of pores, fissures and grain boundaries in rocks and minerals; mineral tunnelling; biomechanical disruption of solid substrates; plant colonisation and/or infection (mycorrhizas, pathogens, parasites); animal colonisation and/or infection (symbiotic, pathogens, parasites); translocation of inorganic and organic nutrients; assisted redistribution of bacteria; production of exopolymeric substances (serve as nutrient resource for other organisms); water retention and translocation; surfaces for bacterial growth, transport and migration; cord formation (enhanced nutrient translocation); mycelium acting as a reservoir of nitrogen and/or other elements (e.g. wood-decay fungi).
Metabolism: carbon and energy metabolism	Organic matter decomposition; cycling and/or transformations of component elements of organic compounds and biomass: carbon, hydrogen, oxygen, nitrogen, phosphorus, sulfur, metals, metalloids, radionuclides (natural and accumulated from anthropogenic sources); breakdown of polymers; altered geochemistry of local environment, e.g. changes in redox, oxygen, pH; production of inorganic and organic metabolites, e.g. protons, carbon dioxide, organic acids, with resultant effects on the substrate; extracellular enzyme production; fossil fuel degradation; oxalate formation; metalloid methylation (e.g. arsenic, selenium); xenobiotic degradation (e.g. polynuclear aromatic hydrocarbons); organometal formation and/or degradation (note: lack of fungal decomposition in anaerobic conditions caused by waterlogging can lead to organic soil formation, e.g. peat).
Inorganic nutrition	Altered distribution and cycling of inorganic nutrient species, e.g. nitrogen, sulfur, phosphorus, essential and inessential metals, by transport and accumulation; transformation and incorporation of inorganic elements into macromolecules; alterations in oxidation state; metal(loid) oxido-reductions; heterotrophic nitrification; siderophore production for iron(III) capture; translocation of nitrogen, phosphorus, calcium, magnesium, sodium, potassium through mycelium and/or to plant hosts; water transport to and from plant hosts; metalloid oxyanion transport and accumulation; degradation of organic and inorganic sulfur compounds.
Mineral dissolution	Rock and mineral deterioration and bioweathering including carbonates, silicates, phosphates and sulfides; bioleaching of metals and other components; manganese dioxide reduction; element redistributions including transfer from terrestrial to aquatic systems; altered bioavailability of e.g. metals, phosphorus, sulfur, silicon, aluminium; altered plant and microbial nutrition or toxicity; early stages of mineral soil formation; deterioration of building stone, cement, plaster, concrete, etc.
Mineral formation	Element immobilisation including metals, radionuclides, carbon, phosphorus, and sulfur; mycogenic carbonate formation; limestone calcrete cementation; mycogenic metal oxalate formation; metal detoxification; contribution to patinas on rocks (e.g. 'desert varnish'); soil storage of carbon and other elements.
Physicochemical properties Sorption of soluble and particulate metal species Exopolysaccharide production	Altered metal distribution and bioavailability; metal detoxification; metal-loaded food source for invertebrates; prelude to secondary mineral formation. Complexation of cations; provision of hydrated matrix for mineral formation; enhanced adherence to substrate; clay mineral binding; stabilisation of soil aggregates; matrix for bacterial growth; chemical interactions of exopolysaccharide with mineral substrates.
Mutualistic symbiotic associations: mycorrhizas, lichens, insects and other invertebrates	Altered mobility and bioavailability of nutrient and inessential metals, nitrogen, phosphorus, sulfur, etc.; altered carbon flow and transfer between plant, fungus and rhizosphere organisms; altered plant productivity; mineral dissolution and metal and nutrient release from bound and mineral sources; altered biogeochemistry in soil–plant root region; altered microbial activity in plant root region; altered metal distributions between plant and fungus; water transport to and from the plant.

table continues

Fungal role and/or activity	Biogeochemical consequences
	Pioneer colonisation of rocks and minerals; bioweathering; mineral dissolution and/or formation; metal accumulation and redistribution; metal accumulation by dry or wet deposition, particulate entrapment; metal sorption; enrichment of carbon, nitrogen, etc.; early stages of mineral soil formation; development of geochemically-active microbial populations; mineral dissolution by metabolites including 'lichen acids'; biophysical disruption of substrate. Fungal populations in gut aid degradation of plant material; invertebrates mechanically render plant residues more amenable for decomposition; cultivation of fungal gardens by certain insects (organic matter decomposition and recycling); transfer of fungi between plant hosts by insects (aiding infection and disease).
Pathogenic effects: plant and animal pathogenicity	Plant infection and colonisation; animal predation (e.g. nematodes) and infection (e.g. insects, etc.); redistribution of elements and nutrients; increased supply of organic material for decomposition; stimulation of other geochemically-active microbial populations.

Such activities take place in aquatic and terrestrial ecosystems, as well as in artificial and anthropogenic systems, their relative importance depending on the species present and physicochemical factors that affect activity. The terrestrial environment is the main locale of fungal-mediated biogeochemical change, especially in mineral soils and the plant root zone, and on exposed rocks and mineral surfaces. There is rather a limited amount of knowledge on fungal biogeochemistry in freshwater and marine systems, sediments, and the deep subsurface. Fungal roles have been arbitrarily split into categories based on growth, organic and inorganic metabolism, physicochemical attributes and symbiotic relationships. However, it should be noted that many, if not all, of these are interlinked, and almost all directly or indirectly depend on the mode of fungal growth (including symbiotic relationships) and accompanying heterotrophic metabolism. This, in turn, is dependent on a utilisable carbon source for biosynthesis and energy, and other essential elements, such as nitrogen, oxygen, phosphorus, sulfur and many metals, for structural and cellular components. Mineral dissolution and formation are outlined separately although these processes clearly depend on metabolic activity and growth form (modified from Table 1 in Gadd, 2007; and see Gadd, 2016, 2017).

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. This ability enables them to survive on stone and rock surfaces. Fungi can 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 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; Figures 1.4–1.6). Proteomics analysis has demonstrated that bioweathering of black slate, which can contain up to 20% organic carbon, is caused by the laccase enzymes of the white-rot basidiomycete fungus, *Schizophyllum commune* (Kirtzel *et al.*, 2017, 2018).

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

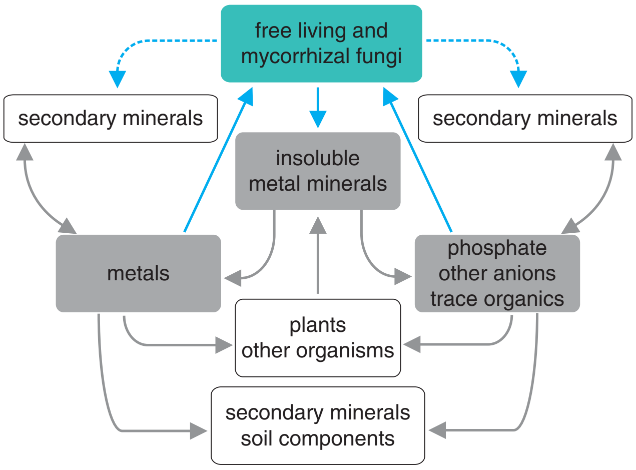

Figure 1.4. Action of free-living and mycorrhizal fungi on insoluble metal minerals in the terrestrial environment resulting in release of mineral components; metal(s), anionic substances, trace organics and other impurities. These can be taken up by living organisms (biota) as well as forming secondary minerals with soil components or fungal metabolites and/or biomass. Released minerals can also be absorbed or adsorbed or otherwise removed by organic and inorganic soil components. The dashed arrows imply secondary mineral formation because of secreted metabolites as well as fungal action on non-biogenic minerals. Possible losses to groundwater are not shown. Blue arrows indicate processes driven by the fungi. Modified from Gadd (2004; and see Gadd, 2016, 2017).