Royal Botanic Gardens Kew

State of the World's Fungi

2018

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Introduction to State of the World's Fungi 2018

The facts and figures contained in the pages of this report and accompanying website (stateoftheworldsfungi.org) will probably come as a total revelation to many people. The first of its kind outlining the state of the world's fungi, the report highlights just how important fungi are to all life on Earth.

Despite early recognition of the importance of fungi for human well-being, and archaeological evidence for human uses of fungi in food, drinks and medicines going back at least 6,000 years, historically they have remained in the shadows when compared with research on plants and animals. In fact, many of the early writings on fungi assumed that they were simple or lower plants. It wasn't until detailed work on fungal features including the cell wall, methods for digesting and storing food, and DNA, that it became apparent that they are in fact a kingdom in their own right, closer to animals than plants. For example, most fungi have a cell wall composed primarily of chitin, a substance that is also found in the exoskeletons of insects and shells of crabs and lobsters.

The realisation that fungi are closer to animals than plants is, however, only one of a number of remarkable facts to emerge in the past few decades. It is now becoming apparent that these organisms, which often cannot be seen with the naked eye and spend vast parts of their life cycle underground or inside plants and animals, are responsible for incredibly important processes; these include global cycling of nutrients, carbon sequestration, and even the prevention of desertification in some drought-prone regions of the world. Fungi also underpin products and processes that we rely heavily on in aspects of everyday life, from critical drugs (including statins, the class of medication used to lower blood cholesterol), to synthesis of biofuels, to cleaning up the environment through bioremediation. Some have multiple uses; for example, species of *Penicillium* have uses as diverse as in antibiotics, the synthesis of third-generation contraceptive pills and cheese production. The global market in edible mushrooms is also huge and increasing.

But some species of fungi can wreak havoc. Many gardeners will know only too well the problems with rusts, wilts and mildews caused by certain species of fungi, and throughout the world there is significant concern related to the spread of fungal pathogens that are devastating crops and wild plant communities – a threat which seems to be increasing with climate change. Understanding the pathogenicity, hosts and methods of spread of fungal pathogens is of critical importance to global biosecurity.

The Royal Botanic Gardens, Kew has housed a Fungarium since 1879. In fact, many notable figures came to examine specimens within it, including Charles Darwin and the children's author Beatrix Potter (who was a keen mycologist). The Fungarium at Kew is the largest in the world and now has over 1.25 million specimens, a number that is growing daily as the global significance of this kingdom becomes more and more apparent. It therefore seemed appropriate that Kew should lead this endeavour to examine the current status of knowledge of Kingdom Fungi. In devising this volume, however, we have worked extensively in global partnership to pull together leading mycological researchers from across the world to provide an up-to-date synthesis of our current knowledge of the state of the world's fungi.

This volume is split into three parts. First, we present an understanding of current knowledge of the diversity and distribution of fungi, new discoveries and evolutionary relationships. Next, we examine some of the key and potential uses of fungi for everyday life, we look at the global impact of positive plant–fungal interactions, and we review the vast insights gained from knowledge of their genomes. For our country focus, we turn our attention to what is known about fungi in China; fungi have been an integral part of Chinese medicine, food and culture for thousands of years resulting in a knowledge base that is probably the best in the world. Finally, we look at the state of knowledge of some of the global challenges associated with fungi, including plant diseases, the impacts of climate change on fungi, and global efforts to conserve them.

From this volume it is clear that Fungi should definitely be viewed on a par with the plant and animal kingdoms and that we have only just started to scratch the surface of knowledge of this incredible and diverse group of organisms. What also becomes apparent is that when looking for nature-based solutions to some of our most critical global challenges, fungi could provide many of the answers.

Professor Katherine J. Willis CBE
Director of Science
Royal Botanic Gardens, Kew

"IT IS CLEAR THAT FUNGI SHOULD BE VIEWED ON A PAR WITH THE PLANT AND ANIMAL KINGDOMS ... WE HAVE ONLY JUST STARTED TO SCRATCH THE SURFACE OF KNOWLEDGE OF THIS INCREDIBLE AND DIVERSE GROUP OF ORGANISMS"

MAIN QUESTIONS ADDRESSED IN THIS REPORT

What are fungi and why are they important? How many species, families and phyla are currently known to science and why is it so difficult to work these numbers out?

How are different species of fungi related to each other? What do we know about the major steps in fungal evolution and when they occurred? What are we doing about filling the knowledge gaps in the fungal tree of life?

How many new species of fungi were described in 2017? Which groups do they represent, where were they found and what are some of the more surprising discoveries?

What makes a species of fungus economically valuable? What daily products utilise fungi and what are the useful fungi of the future for food, medicines and fungal enzymes?

How do plants benefit from fungal interactions and vice-versa? What is the role of these positive interactions in supporting vital ecosystem processes?

How many whole fungal genomes have been sequenced to date? How is this information being used to enhance our insights into medicine and climate change resilience and to find new fungi for use in everyday life, from food to antibiotics and biofuels?

What is the current status of knowledge of fungi in China? How many different Chinese fungal species are currently known, where are they distributed, which are most important economically, and how do they help combat the effects of desertification?

Which fungal diseases pose the greatest threats to global ecosystems? Why are these threats on the increase and what biosecurity is urgently needed to reduce their global spread?

What impact is climate change having on fungal communities across the globe and where are our greatest knowledge gaps?

How many species of fungi are threatened with extinction and why are they so difficult to assess? What threats are fungi facing and what are the conservation challenges?

DEFINITION AND DIVERSITY

FUNGI ARE MORE CLOSELY RELATED TO ANIMALS THAN TO PLANTS

What are fungi and why are they important? How many species, families and phyla are currently known to science and why is it so difficult to work these numbers out?

stateoftheworldsfungi.org/2018/definition-and-diversity.html

THE MORE WE LEARN ABOUT FUNGI, THE MORE WE REALISE HOW THIS INTRIGUING KINGDOM OF ORGANISMS UNDERPINS ALL LIFE ON EARTH. NOT ONLY ARE THEY CRITICAL FOR DECOMPOSING DEAD MATTER AND RECYCLING NUTRIENTS, THEY ALSO PROVIDE MANY DIRECT BENEFITS TO HUMANS – FROM EDIBLE MUSHROOMS AND TRUFFLES, TO BREAD AND DRINKS MADE USING YEASTS, TO ANTIBIOTICS.

In contrast, they can also cause devastating plant and animal diseases resulting from fungal pathogens such as mildews, rusts and chytrids.

Fungi were once regarded as merely simple or lower plants and were assigned fewer than fifty of the 1,200 pages in Linnaeus' *Species Plantarum*[1]. As time has moved on and more has been learned about fungi and their relationships to other forms of life, they are now rightly placed in their own kingdom[2], more closely related to animals than to plants[3–5] (see Figure 1). In this chapter, we provide a synthesis of current knowledge of what defines fungi, their origins and diversity, the number of species currently known to science, their rapidly changing classification and the challenges ahead.

WHAT ARE FUNGI?

Fungi are distinctive organisms that digest their food externally by secreting enzymes into the environment and absorbing the dissolved organic matter back into their cells. Most have cell walls composed primarily of chitin (a substance that is also found in the animal kingdom, for example in the exoskeletons of insects and shells of crabs and lobsters). They also store food reserves as glycogen and lipids (not starch as in plants). Thus, despite the superficial resemblance of some fungi to plants (e.g. having rooted, stalked structures), their non-photosynthetic, absorptive method of feeding and their different cell walls, cell membrane chemistry, methods of food storage and DNA indicate that they form an independent kingdom[e.g. 3,4,5].

Some fungi exist as microscopic, single-celled yeasts (e.g. the bloom on the skin of a plum or grape), while the most complex forms have a far more elaborate multicellular body comprising an interconnected network, or mycelium, of minute, protoplasm-filled tubes called hyphae. The individual thread-like tubes extend at their tips and form branches that explore their environment, fight with other fungi to occupy territory, or interact with other organisms. These activities can occur inside a few cells of a leaf, in a column of decay extending for several metres inside a tree trunk, or in the soil, for example forming a giant 'fairy ring' of mushrooms in ancient grassland.

Other fungi live as lichens – a symbiotic association between a fungus (the mycobiont) and at least one photosynthetic partner (the photobiont), which can be an alga, a cyanobacterium or both. Lichens are often referred to as the ultimate example of mutualism (a type of symbiosis in which both partners benefit), given their ability to form distinct biological entities so well integrated that they resemble one single organism. They grow almost everywhere; they can be found in most terrestrial habitats, even in extreme conditions such as Antarctic deserts, growing on rocks, bark, soil, leaves, mosses, man-made materials and even on top of other lichens.

FUNGAL NUTRITION AND NUTRIENT CYCLING

Whereas human beings digest food within an internal tube (our alimentary tract) and absorb the resulting products into our blood to circulate throughout our bodies, fungal hyphae do it differently: enzymes produced inside the tubular hyphae are exuded into the surrounding environment, where they digest organic matter, and the nutrients are then absorbed back through the cell walls and membranes into the hyphae.

Fungi are associated with the roots of almost all plants, including forest trees and most food crops – the fungi act as living intermediaries between the plant and the surrounding soil. This type of root–fungal interaction is known as a mycorrhiza (see Chapter 5) and, like lichens, the partners engage in a mutualistic relationship. The plant benefits from the greater capacity of the fungus to absorb water and nutrients and to mobilise minerals that would otherwise be unavailable, and the fungus benefits from a steady source of carbohydrates from the plant.

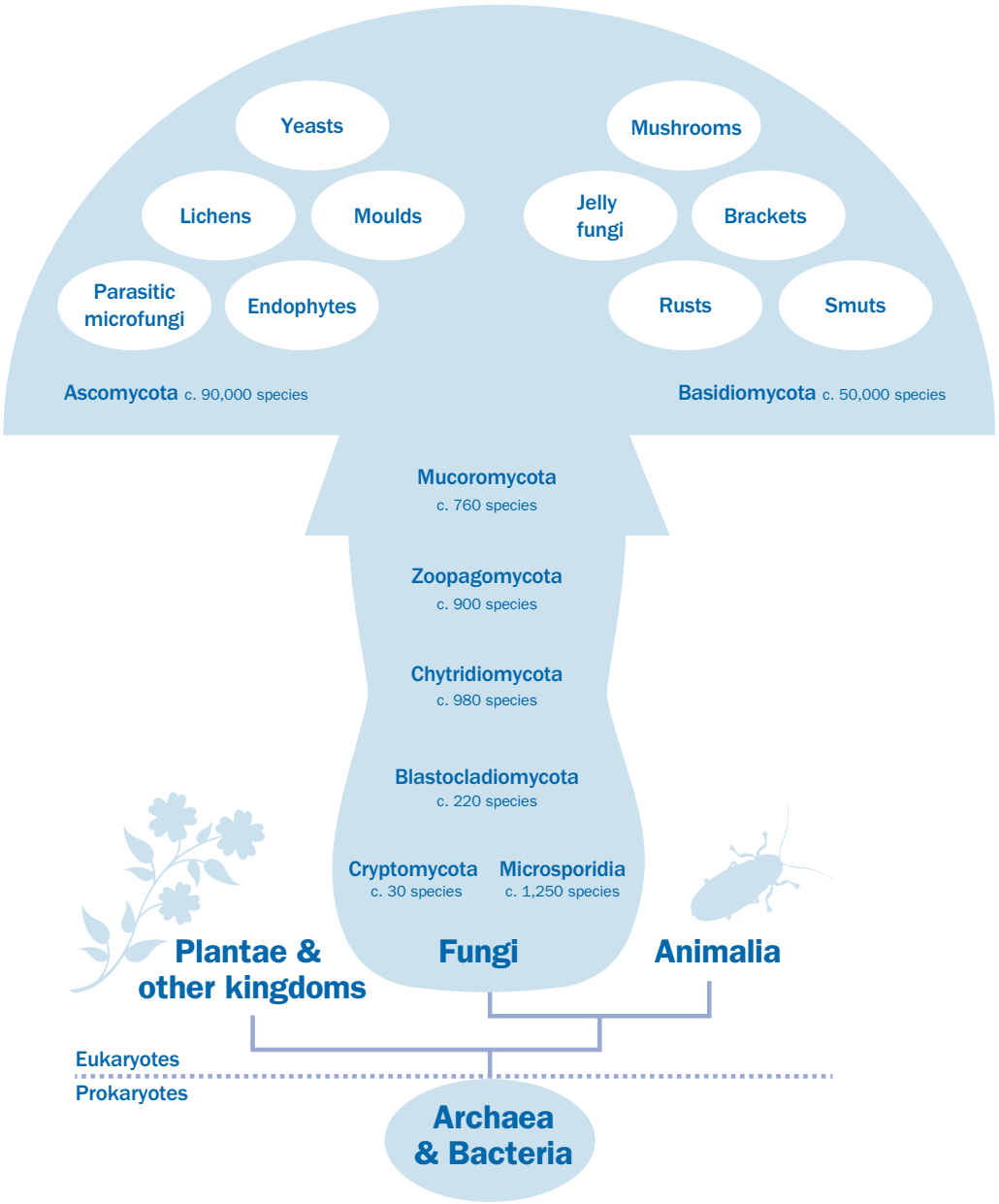
Fungi are also the most significant organisms that break down cellulose, hemicellulose and lignin. These are the tough polymers in plant cell walls that give wood its great strength and durability. Their decomposition by wood-decaying fungi releases key plant nutrients back into the soil, thereby allowing the next generation of seedlings to grow. Without nutrient cycling, life on Earth as we know it would not exist; nutrients would be in such short supply that biological growth would be severely limited right across the globe.

FUNGAL LIFE CYCLES

Fungi have diverse, complex life cycles and can reproduce sexually, asexually and/or parasexually (which involves combining genes from different individuals without forming sexual cells and structures). They can do this through the production of different kinds of spores and/or through fragmenting hyphae. For most of their life cycles, the majority of animals and plants are built of diploid cells (i.e. combining one genome from each parent) and form bodies with determinate growth. In contrast, many fungal lineages are more complex, and for much of their life cycle their cells may be haploid (with just one genome), diploid, dikaryotic (two nuclei per cell) or multikaryotic (multiple nuclei per cell). In addition, many fungi have indeterminate growth, which means they can continue to grow as long as resources and conditions are suitable and enables them to take the shape of their environment (e.g. a leaf, a cheese, a lung). Thus, piecing together a fungal life cycle is complex and involves much detective work.

FIGURE 1: SCHEMATIC REPRESENTATION OF KINGDOM FUNGI IN THE TREE OF LIFE

Evolutionary studies have shown that Fungi and Animalia are more closely related to each other than to any of the other kingdoms of life. The eight fungal phyla are shown here, along with estimates of the number of described species in each. Well-known examples of fungi from Ascomycota and Basidiomycota are also displayed. [Schematic based on [3,24,32]]



The interconnected network of hyphae is critically important for the life cycle of most fungi. It is usually hidden within soil or inside the tissues of living or dead plants, animals or other fungi and is often overlooked. However, once sufficient nutrients have been absorbed from the substrate, fungi usually reproduce and disperse to new sites by means of spores – it is at this point that they may become more visible to us. The spores themselves are usually microscopic and dust- or pollen-like, often measured in microns (thousandths of a millimetre). They may be formed asexually on specialised branches of the mycelium (as seen on mouldy food items or damp shower curtains) or after mating has occurred and elaborate spore-bearing reproductive structures have been developed, such as mushrooms. Mycologists sometimes refer to these as sporocarps, fruit bodies or fruiting bodies – in this report we use the term 'spore-bearing structures'.

Fungi that produce spore-bearing structures visible to the naked eye are often referred to as macrofungi, and these structures are variously known as morels, mushrooms, brackets, puffballs, stinkhorns and earthstars to name just a few. Those that don't produce spore-bearing structures at all, or where they are too small to be seen without a microscope, are often referred to as microfungi.

Myriostoma coliforme, UK

Clavariaceae, Bhutan

Helvella lacunosa, Iceland

Umbilicaria cylindrica, UK

Ravenelia macowaniana, South Africa

Sticta humboldtii, Ecuador

Heterodermia sp., Bhutan

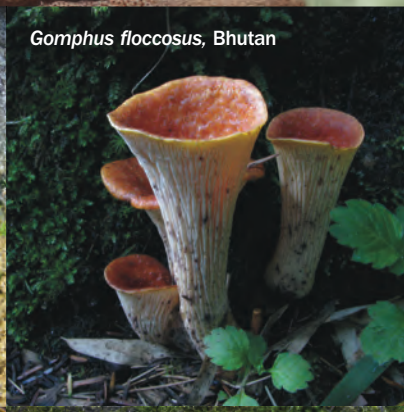
Hypocreopsis rhododendri, UK

Letrouitia domingensis, Costa Rica

Microbotryum silenes-dioicae, UK

Phallus impudicus, UK

Scutellinia aff. *scutellata*, UK


Gomphus floccosus, Bhutan

Crucibulum laeve, USA

Fistulina hepatica, UK

THE ORIGINS AND IMMENSE DIVERSITY OF FUNGI

Fungi have ancient origins, with evidence indicating they first appeared around 1 billion years ago[6–8]. Fossil fungi are difficult to find and study due to their perishable structure, but organisms recognisable as fungi (remarkably similar to modern species) are known from the Ordovician period around 450 million years ago (Mya)[9] onwards, with evidence of lichens, plant and fungal parasites, and mycorrhiza-like associations[10]. A remarkable fossil is the late-Silurian (443–416 Mya) *Prototaxites*, which grew up to 8 m tall. It was originally assumed to have been a tree, but more recent analysis indicates that it was a fungus[11].

Fungi and plants have been intricately linked through much of their evolutionary history. Without fungi, plants may have never colonised land. It is thought that the earliest rootless land plants evolved from freshwater algae, solving the problem of obtaining water and scarce mineral nutrients such as nitrogen and phosphorus in dry land masses by forming intimate associations with ground-dwelling filamentous fungi[12]. Exchanges of fungal-foraged minerals for plant photosynthetic products probably allowed land plants to dominate continents from around 450 Mya onwards, transforming the lithosphere (the Earth's outer shell), biosphere (the Earth's living systems) and atmosphere into what they are today.

Fungi are immensely diverse, with 144,000 species named and classified so far at a current rate of around 2,000 per year (see Chapter 3); this is comparable to the rate of species discovery of new plants[13]. However, it is estimated that the vast majority (over 93%) of fungal species are currently unknown to science. The latest best estimate suggests that the total number of fungal species on Earth is somewhere between 2.2 and 3.8 million, a number that exceeds the estimated number of plants by more than 6 times[14]. This broad range is based on extrapolations of plant/fungus species ratios supplemented by DNA studies of environmental samples (see Chapter 2: Box 4).

There were 536 accepted families of fungi in 2007[15] and that number has risen to 886 in the last ten years. This reflects the large number of new taxa being recognised on a yearly basis (see Figure 2; see also Chapter 3), mainly as a result of the recent rapid increase in the availability, affordability and efficiency of DNA-based methods for detection and identification of fungi. Among the largest families are Mycosphaerellaceae with around 6,400 species (mainly facultative plant pathogens, i.e. those that don't rely on infecting a host to complete their life cycle), and Pucciniaceae with around 5,000 species (obligate plant pathogens, i.e. those that must infect a host to survive and spread; see Box 1). Other large families include two that form mushroom-shaped spore-bearing structures (Agaricaceae and Cortinariaceae), each containing about 3,000 accepted species, and a further 32 families harbouring more than 1,000 species. Conversely, there are also 57 families that currently include only a single known species (known as monotypic families). Most are probably this way due to under-sampling, but some appear to be all that remain of an entire lineage – so-called 'living fossils'. Examples of the latter include Bartheletiaceae, with a single species restricted to leaves of another living fossil, the tree *Ginkgo biloba*[16,17] (see Box 2), and *Mixia osmundae*, which only occurs in leaves of the fern genus *Osmunda*[18].

Some families may be regarded as hyperdiverse partly because they have been sampled and studied more than others. This can be the case if the spore-bearing structures are large and conspicuous, such as those within Agaricaceae (mushrooms and allies), Polyporaceae (bracket fungi and allies) and the lichen family Parmeliaceae (see Box 3), or if the fungi are of economic importance, such as Aspergillaceae, whose members (including the familiar moulds *Aspergillus* and *Penicillium*) are important as producers of toxins and antibiotics (see Figure 2b).

BOX 1: PUCCINIACEAE (RUST FUNGI)

Pucciniaceae (Basidiomycota) is one of the most species-rich families of fungi and contains economically important plant pathogens, common in many crops including cereals and coffee. It has a widespread distribution across the globe. Many Pucciniaceae are the causal agents of disease epidemics, but they have also been tested as biological control agents of invasive species. Traditionally, they were classified based on their hosts, as many rust fungi are host specific, and on some morphological (physical) characteristics. DNA data suggest that the high species diversity we see today may have been facilitated by their ability to jump between hosts[33]. Rust fungi have very complex life cycles that can include up to five different spore stages, as in stem rust (*Puccinia graminis*). In some instances, two unrelated hosts are necessary for the different stages.

Puccinia buxi, a common leaf rust of the box tree (*Buxus sempervirens*)

SHIFTING CLASSIFICATIONS AND NEW DISCOVERIES

The modern classification of fungi is mostly based on groups defined by the common descent of their DNA sequences, with other characteristics providing supporting evidence. Traditional classifications, however, were based purely on morphological and physiological characteristics that did not necessarily reflect evolutionary history. DNA analyses have therefore overturned traditional classification schemes, particularly with the finding that not all fungi with similar spore-bearing structures have evolved from the same ancestral lineages (convergent evolution; see Chapter 2: Box 1). A number of species that were once taxonomically 'lumped' together, due to the difficulties in distinguishing them using morphological characters, are also now known from DNA studies to be distinct species (so-called cryptic species because they appear identical). Similarly, fungal pathogens, such as rusts (Pucciniales), found on the same genus or species of host plant were often assumed to be members of the same species of fungus. However, this assumption is increasingly being challenged by molecular studies, which are detecting new species even in this relatively well-studied and species-rich group[19–21].

It seems likely that as molecular approaches are applied more widely, along with global sampling of fungal specimens, the number of cryptic species is likely to rise rapidly. Even now, for every species traditionally recognised, around 11 new species on average are distinguished using DNA analyses[14]; in some cases, the number is much higher than this. For example, in the genus *Cora*, which was originally thought to include a single neotropical lichenised species, 189 species are now recognised[22,23]. Frequently, the use of molecular data to distinguish between different species also leads to the recognition of differences in physical characteristics that were previously missed or not thought to be significant.

Throughout the classification hierarchy, the number of accepted taxa and/or the number of taxonomic levels they are grouped into (e.g. phyla, subphyla, classes) can therefore vary greatly. For example, a 2017 study recognised eight fungal phyla[24] whereas just one year later another study delimited nine subkingdoms and no fewer than 18 phyla[25], although time will tell if this will be supported by further data (see Box 4).

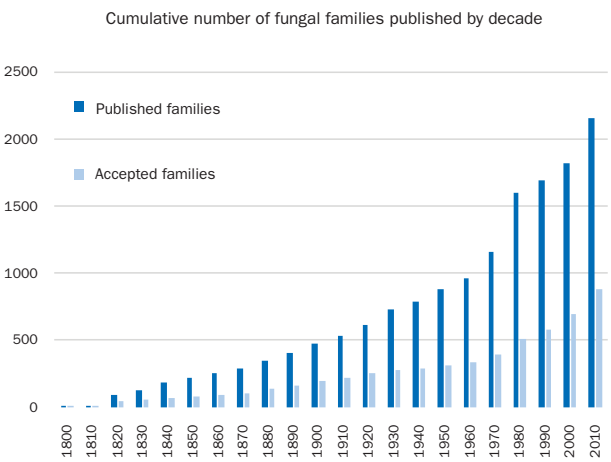
Searching for molecular evidence of fungi in soils, water and airborne particles (environmental DNA sequencing) has also proved a major source of potentially novel taxa, suggesting the existence of a huge amount of unrecognised fungal diversity. Even in environments that have been comprehensively sampled using traditional methods, large numbers of previously undetected taxa with distinctive molecular signatures (dark taxa; see Chapter 2: Box 4) are emerging. There are environments from which almost no sequences can be assigned to a taxonomic category – for example, some marine samples yielded fungi that could not even be identified to the taxonomic rank of order, let alone family, genus or species[26].

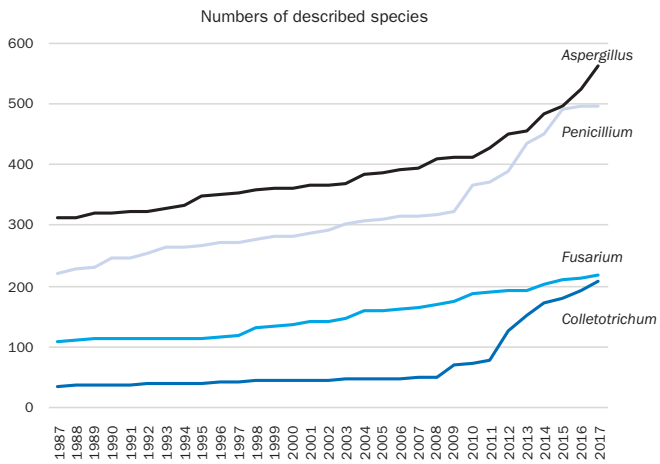
Nevertheless, it is also recognised that there are many potential issues that need to be addressed when dealing with these newly emerging molecular data, particularly in terms of reproducibility between environmental samples[27,28] and protocols for naming species known only from DNA sequences[27,29–31]. The challenge for the future will be to reach consensus across the community of scientists who work on fungi on how these exciting new discoveries of fungal diversity, based purely on DNA sequence data, are incorporated into existing fungal classification systems. Only then will it be possible to reach a truly comprehensive understanding of the full extent of global fungal diversity.

FIGURE 2: THE IMPACT OF DNA SEQUENCE-BASED CLASSIFICATION ON FUNGAL FAMILY AND SPECIES RECOGNITION

2a: Cumulative numbers of fungal families published each decade since 1800. [Data from *Index Fungorum* (indexfungorum.org)]

2b: The increase in numbers of accepted species from 1987 to 2017 for four economically important fungal genera. Molecular sequence data started to become extensively used in species recognition from 2000 onwards. [Data from *Species Fungorum* (speciesfungorum.org)]





BOX 2: THE MONOTYPIC FAMILY BARTHELETIACEAE

Many fungal families (as currently recognised) contain only a single species (i.e. they are monotypic), but in most cases it is suspected that this is due to under-sampling. *Bartheletia paradoxa*, however, is the only member of Bartheletiaceae and due to its 'living fossil' status it is likely that this family is genuinely monotypic.

Black spore-producing structures of the living fossil, *Bartheletia paradoxa*, developing on dead leaves of *Ginkgo biloba*.

BOX 3: THE LICHEN FAMILY PARMELIACEAE

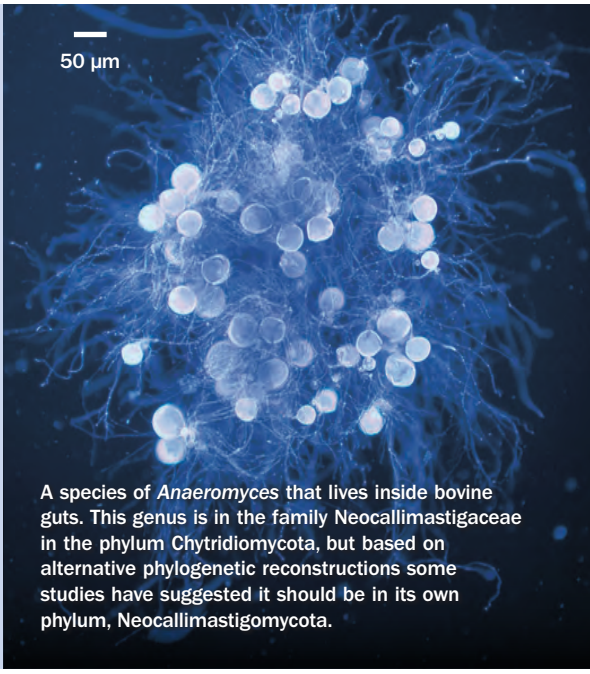
Lichens are a symbiotic association between a fungus and at least one photosynthetic partner. Parmeliaceae is the largest and most morphologically diverse family of lichens, including around 2,750 species in 77 genera, with a single genus *Xanthoparmelia* currently containing about 820 species. The family has a worldwide distribution, occupying and sometimes dominating habitats as diverse as Antarctic rocks and tree bark in tropical montane forests, and is particularly prominent in southern hemisphere temperate regions. Species of Parmeliaceae contain a plethora of complex chemicals that may help to protect against UV radiation and predation, and they also play a part in human nutrition as one of the principal components of the spice mix garam masala. Their varied coloration partly reflects their internal chemistry, and some species are used in traditional fabric dyeing. Most species are foliose (leafy) in form, but many are shrubby in appearance and some have pendent, beard-like thalli, occasionally reaching several metres in length. The earliest-diverging lineages are crustose (resembling a crust).

Parmelia saxatilis, one of the most widespread species on acid rocks in temperate areas.

BOX 4: SHAKING UP FUNGAL CLASSIFICATION

The last decade has seen a surge in production of fungal molecular data due to rapidly evolving DNA technologies, increasingly sophisticated methods of analysis and an improved ability to detect hitherto unsuspected levels of fungal diversity from environmental sequencing. Together, these studies are uncovering entirely new branches in the fungal tree of life (see Chapter 2: Box 4) and prompting novel and interesting proposals on how fungi are related to each other and how they should be classified. In one recent study, a group of intracellular parasites of microscopic algae, considered by some to be more closely related to animals and historically named in accordance with animal nomenclature, has been promoted to the rank of a fungal subkingdom (Aphelidiomyceta)[25].

It is still early days for assessing the acceptability of these new classifications, and further studies could result in even more upheaval. Nevertheless, they highlight how rapidly our understanding of what it means to be a fungus is changing and how new discoveries are shaking up fungal classification and the fungal tree of life. Truly, these are interesting times for fungal taxonomy!

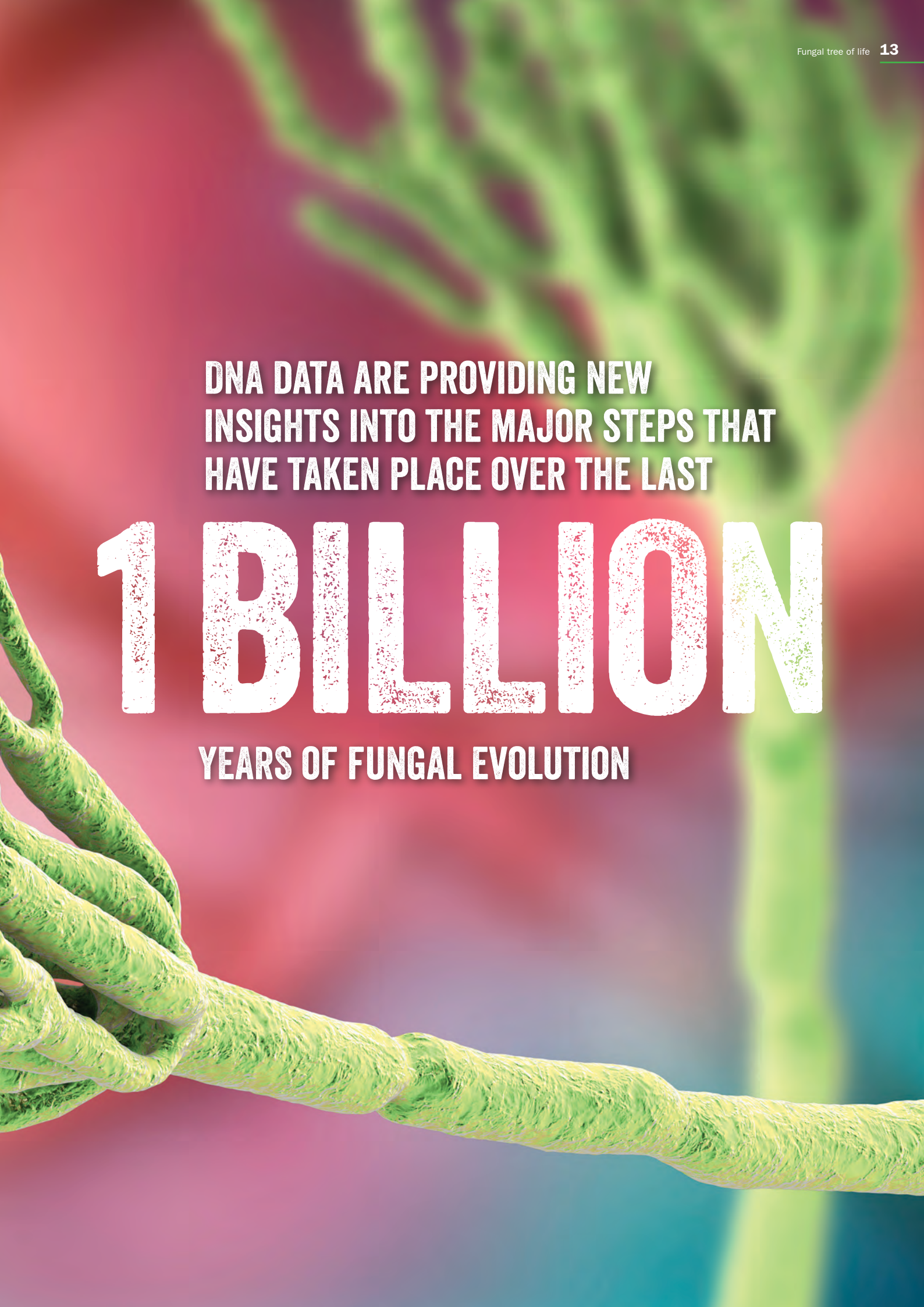


A species of *Anaeromyces* that lives inside bovine guts. This genus is in the family Neocallimastigaceae in the phylum Chytridiomycota, but based on alternative phylogenetic reconstructions some studies have suggested it should be in its own phylum, Neocallimastigomycota.

FUNGAL TREE OF LIFE

How are different species of fungi related to each other? What do we know about the major steps in fungal evolution and when they occurred? What are we doing about filling the knowledge gaps in the fungal tree of life?

stateoftheworldsfungi.org/2018/fungal-tree-of-life.html



DNA DATA ARE PROVIDING NEW INSIGHTS INTO THE MAJOR STEPS THAT HAVE TAKEN PLACE OVER THE LAST

1 BILLION

YEARS OF FUNGAL EVOLUTION

HOW ARE DIFFERENT SPECIES RELATED TO EACH OTHER? THIS SIMPLE YET CRITICALLY IMPORTANT QUESTION, WHICH IS ROUTINELY ASKED ABOUT SPECIES IN ALL KINGDOMS OF LIFE, IS ONE OF THE MOST DIFFICULT TO ANSWER FOR FUNGI.

This is because building the fungal tree of life has several significant challenges. First, similarities in the physical features of fungi, such as the shape of the spore-bearing structures (e.g. mushrooms), can be misleading – species that occupy similar habitats or adopt a similar life strategy can evolve to look superficially similar even though they are not (see Box 1). Second, many fungi live unseen underground or within the cells of plants, animals or other fungi for most, or all, of their lives, often without visible reproductive structures or mycelium. It is therefore often hard, if not impossible, to find distinctive physical features to use. In this chapter, we address this question by examining the increasing evidence emerging from the rapid advances being made in DNA sequencing technologies (see also Chapter 6).

UNCOVERING THE MAJOR STEPS IN THE EVOLUTION OF FUNGI

Identifying similarities and differences in DNA sequences between fungi is helping us to understand how the branches of the fungal tree of life fit together – i.e. the evolutionary relationships between species and how they are grouped together into higher levels of classification (e.g. orders, classes and phyla)[1–5]. This has given rise to many new classifications, including a recent recognition of eight fungal phyla[5], which we follow in this volume. In addition, these data are providing new insights into the major steps that have taken place over the last 1 billion years of fungal evolution[5–7] (see Figure 1).

1. The earliest fungi. The earliest fungi are thought to have evolved around 1 billion years ago and to have been simple, single-celled organisms living in water and reproducing using motile asexual spores (zoospores) propelled by a posterior whip-like structure called the flagellum[8,9]. Indeed, these earliest fungi may well have been similar to the modern-day fungi that have been placed in the early-diverging branches of the fungal tree of life (i.e. the phyla Cryptomycota, Chytridiomycota and Blastocladiomycota; see Figure 1) because they also produce motile spores and predominantly adopt an aquatic life (see Box 2). However, while the phylum Microsporidia is also placed among these early diverging branches[5], all known species lack motile spores.

Despite their simplicity, these phyla include species capable of causing diseases not only in humans but also in many other organisms. For example, at least 15 species of Microsporidia cause a diverse set of symptoms in humans collectively known as microsporidiosis, resulting in reduced longevity, weight loss and a general reduction in health and well-being. Another microsporidian, *Nosema ceranae,* is a globally widespread parasite of honey bees that not only shortens the life of individuals but may well be a key player in the devastating Colony Collapse Disorder of beehives around the world[10]. Perhaps even more devastating is a fungus belonging to the phylum Chytridiomycota, *Batrachochytrium dendrobatidis*, which is responsible for the death of many amphibians. Indeed, it is estimated that over 30% of amphibian species across the globe may suffer extinction or severe decline, with no known treatment in sight[11,12].

BOX 1: APPEARANCES CAN BE DECEPTIVE

When studying evolution, scientists distinguish between convergent evolution (where distantly related species look similar) and divergent evolution (where closely related species look different). Spore-bearing structures of fungi come in many different shapes and forms and confusion can arise when convergent evolution results in similar shapes and forms in distantly related fungi. When that happens, the appearance of the spore-bearing structure can be misleading for taxonomists aiming to predict the relationships between fungi. For example, the black truffle or Périgord truffle (*Tuber melanosporum*), one of the most expensive edible mushrooms in the world and from the phylum Ascomycota, has a spore-bearing structure that resembles the false truffle (*Melanogaster tuberiformis*), which belongs to the phylum Basidiomycota. However, these two species are separated by over 600 million years of evolution.

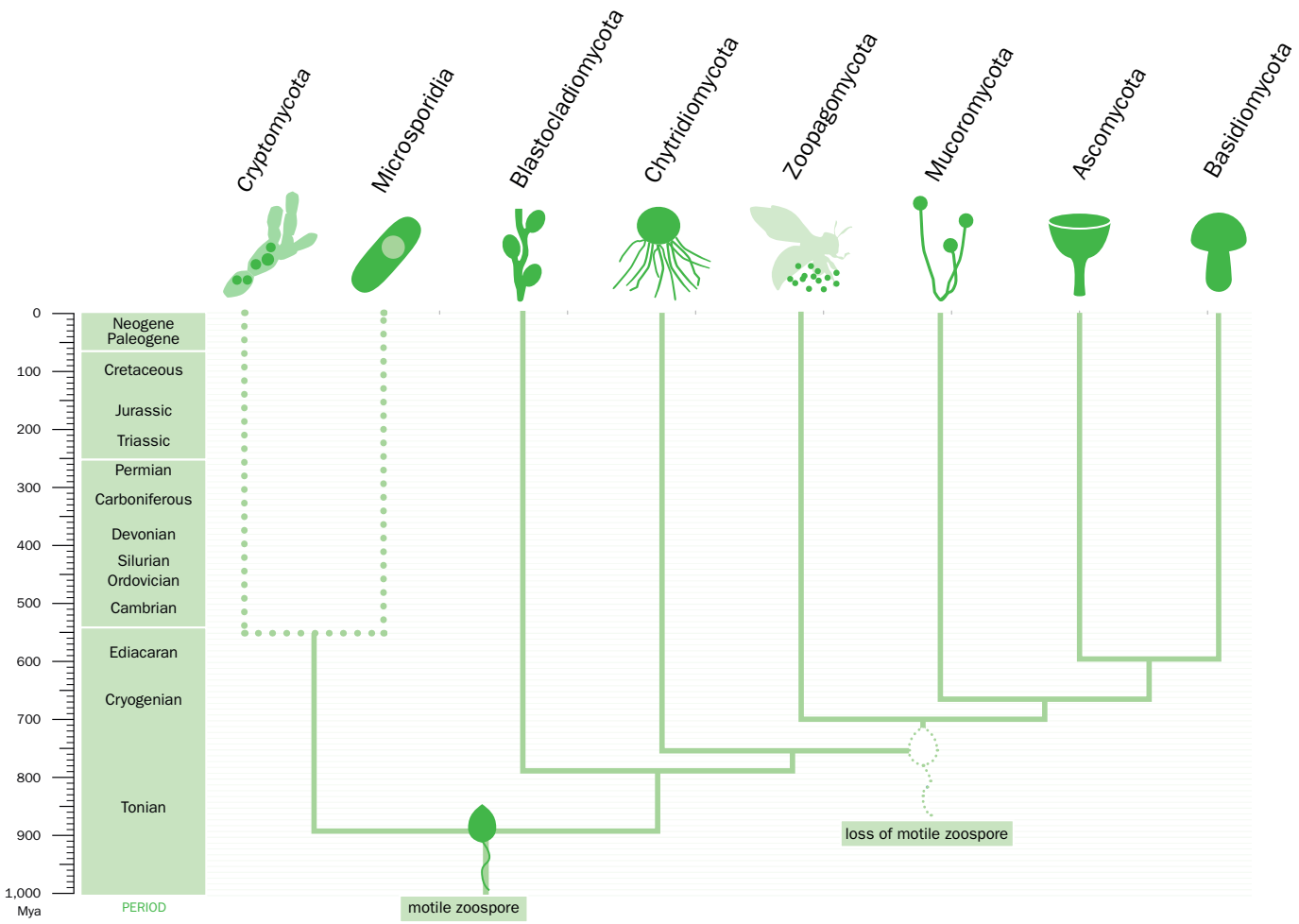
In contrast, divergent evolution occurs when the appearance of the spore-bearing structure evolves so rapidly between closely related groups, that they no longer look similar. This gives the erroneous impression that such species are distantly related. For example, three distinctive types of mushroom can be found in relatively closely related species belonging to the family Agaricaceae (Basidiomycota). These are: i) the agaricoid or parasol-shaped mushrooms; ii) the gasteroid or puffball-shaped mushrooms; and iii) mushrooms shaped like a bird's nest (e.g. fluted bird's nest, *Cyathus striatus*).

Convergent evolution: the black truffle (*Tuber melanosporum*; Ascomycota) **(A)** and false truffle (*Melanogaster tuberiformis*; Basidiomycota) **(B)** have a similar appearance despite belonging to different phyla.

Divergent evolution: three different spore-bearing structures in Agaricaceae (Basidiomycota). Field mushroom (*Agaricus campestris*) **(C)**, giant puffball (*Calvatia gigantea*) **(D)** and fluted bird's nest (*Cyathus striatus*) **(E)**.

FIGURE 1: THE FUNGAL TREE OF LIFE

The figure shows the order in which the major fungal phyla are considered to have appeared over evolutionary time[5]. The divergence times of the branches are approximations based on fossil and molecular data, as there is considerable uncertainty over the precise timings of these events[6,7].



2. The evolution of land-dwelling fungi. The evolutionary transition from predominantly aquatic to land-dwelling fungi is estimated to have taken place around 700 million years ago (Mya)[7]. The first two groups of fungi to evolve that lacked motile spores were the Zoopagomycota and Mucoromycota. Both of these are characterised by the production of a unique thick-walled spore called the zygospore[13].

The fungi belonging to the phylum Zoopagomycota are almost exclusively pathogens, parasites or living on or within animals and other fungi[14]. In contrast, Mucoromycota almost exclusively obtain their nutrition by plant associations and include those species that live inside plant cells (i.e. endophytes; see Chapter 5)[15–17], those that decompose common foods[18], such as the all-too-familiar black bread mould (*Rhizopus stolonifer*) that also attacks a broad array of fruits and vegetables, and those that form underground root associations (mycorrhizas; see Chapter 5)[19,20]. Indeed, the discovery of c. 400-million-year-old fossils that have mycorrhizal-like structures similar to Mucoromycota species living today, has led to the suggestion that fungi may well have been essential for enabling the successful transition of plants onto land[6,7,19,21] (see Box 3 and also Chapter 1).

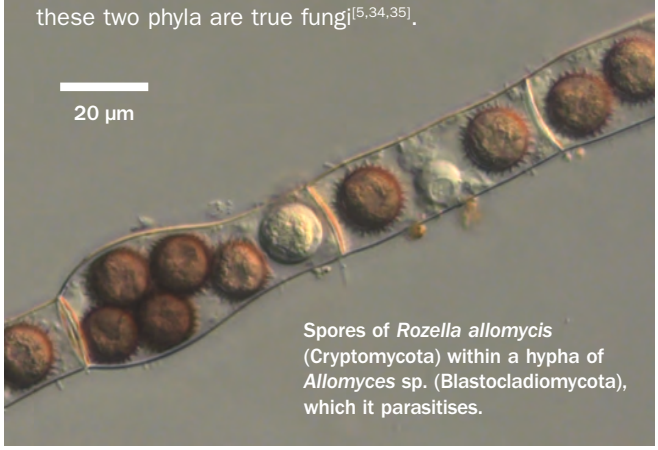
3. Evolution of complexity in body structure. The evolution of the two fungal groups that contain species capable of forming highly complex spore-bearing structures (i.e. Ascomycota and Basidiomycota) is considered to have occurred around 600–700 Mya. Together they contain the vast majority of known fungal species diversity – c. 90,000 species in Ascomycota and c. 50,000 species in Basidiomycota. They contain not only most of the more familiar groups of fungi with visible spore-bearing structures, but also the single-celled yeasts and other microscopic fungi (see Chapter 1).

The phylum Ascomycota includes species that were among the first to be domesticated by humans. For example, there is evidence to suggest that yeasts were being used to produce the alcoholic drink mead as far back as 9,000 years ago[22]. Most medicines of fungal origin are also found in this group (see Chapter 4), as are some of the most expensive foods on Earth, the white truffle (*Tuber magnatum*) and the black truffle (*Tuber melanosporum*)[23]. Yet there is another side to this phylum since it also contains some of the most economically damaging pathogens; these can bring devastation to farms and threaten food security (e.g. *Fusarium* wilt diseases[24]) or transform entire ecosystems (e.g. *Hymenoscyphus fraxineus,* which is the fungus responsible for ash dieback[25], a destructive disease of ash trees (*Fraxinus* spp.) in Europe; see Chapter 8).

The phylum Basidiomycota also includes a diverse array of species that have a major impact on humanity. Among them are some of the major players that perform a vital role in decomposing and recycling wood and leaf litter[26], unlocking and releasing the stored carbon and other nutrients back into the environment. Basidiomycota, like Ascomycota, includes species that are devastating plant pathogens, such as those belonging to the rusts and allies (Pucciniomycotina) and smuts (Ustilaginomycotina). Basidiomycota also includes the iconic mushroom-forming fungi (Agaricomycotina) that are consumed in large quantities by humans, such as the familiar button mushroom (*Agaricus bisporus*) as well as the shiitake mushroom (*Lentinula edodes*) and chanterelle (*Cantharellus cibarius*).

BOX 2: FUNGI OR NOT FUNGI?

One of the characters that is widely used to define a fungus is the presence of chitin (a carbohydrate) in the cell walls (see Chapter 1). Thus, the absence of chitin in most stages of the life cycle in members of Cryptomycota and Microsporidia led to a debate as to whether these species were actually fungi. Nevertheless, genomic data have now revealed that Cryptomycota and Microsporidia contain the genes needed for making chitin, while anatomical analyses show that chitin can be detected in their resting spores. It is now, therefore, generally accepted that these two phyla are true fungi[5,34,35].

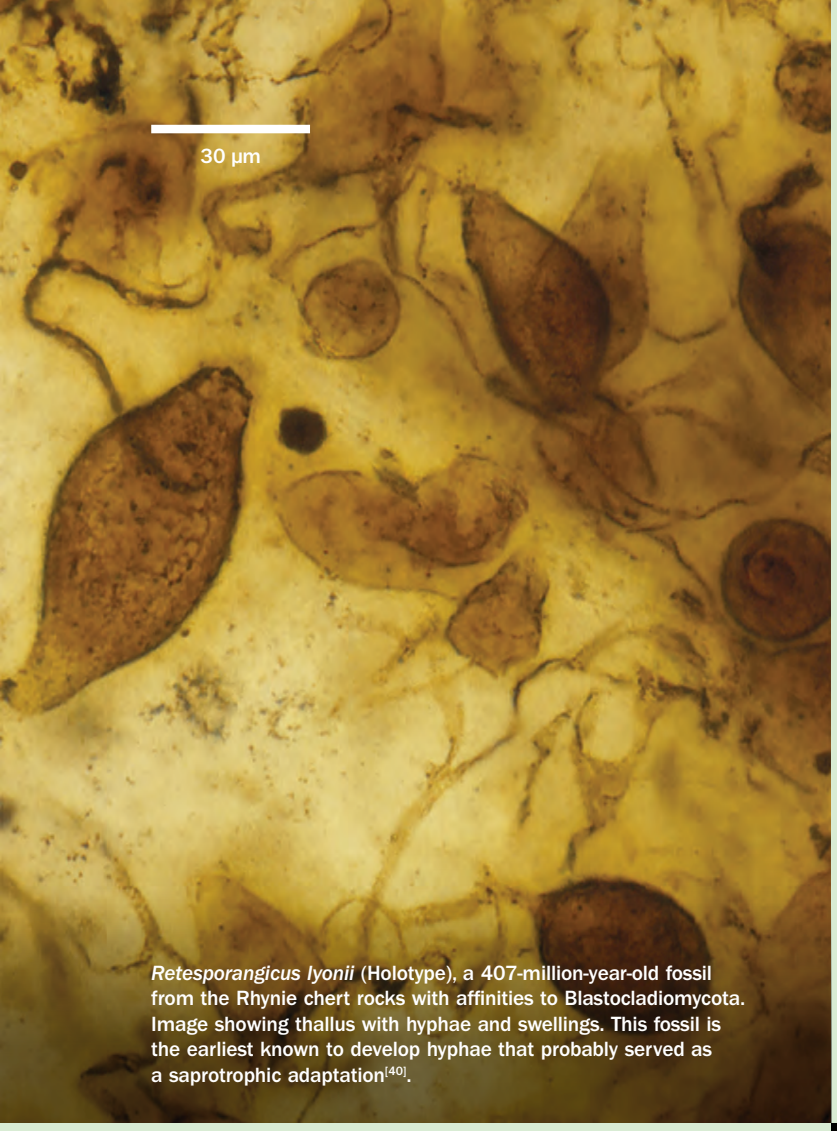


Spores of *Rozella allomycis* (Cryptomycota) within a hypha of *Allomyces* sp. (Blastocladiomycota), which it parasitises.

CHALLENGES AND OPPORTUNITIES IN COMPLETING THE FUNGAL TREE OF LIFE

Although there is now a reasonably good understanding of the evolutionary relationships between the fungal phyla (even if the naming of the different lineages is still much debated – see Chapter 1: Box 4), relationships at the family, genus and species levels are still largely unresolved. In addition, while the technology for generating molecular data continues to advance[27–29], there are still many issues arising from the ever-increasing rate at which fungal species are being discovered from environmental sequencing (see Box 4). These approaches are revealing a whole new 'invisible dimension of fungal diversity' in our soils, bodies and waterways[30].

The challenge for the future will be not only to continue to enhance the understanding of evolutionary relationships based on currently described species but also to see how the full diversity of fungal species, including the so-called dark taxa (see Box 4), fits onto the branches of the fungal tree of life. With advances in DNA sequencing technologies, opportunities to exploit the vast archives in fungaria around the world[31], and projects focused specifically on building the fungal tree of life (e.g. the *Plant and Fungal Trees of Life*[32] and the *1000 Fungal Genomes* project[33]), our understanding of the tree of life for all fungi is likely to improve significantly and rapidly in the near future. This will provide us with exciting and unparalleled opportunities to predict the fungal properties that will enable them to be best utilised, exploited and conserved.



Retesporangicus lyonii (Holotype), a 407-million-year-old fossil from the Rhynie chert rocks with affinities to Blastocladiomycota. Image showing thallus with hyphae and swellings. This fossil is the earliest known to develop hyphae that probably served as a saprotrophic adaptation[40].

BOX 3: DATING THE FUNGAL TREE OF LIFE AND THE DEARTH OF FUNGAL FOSSILS

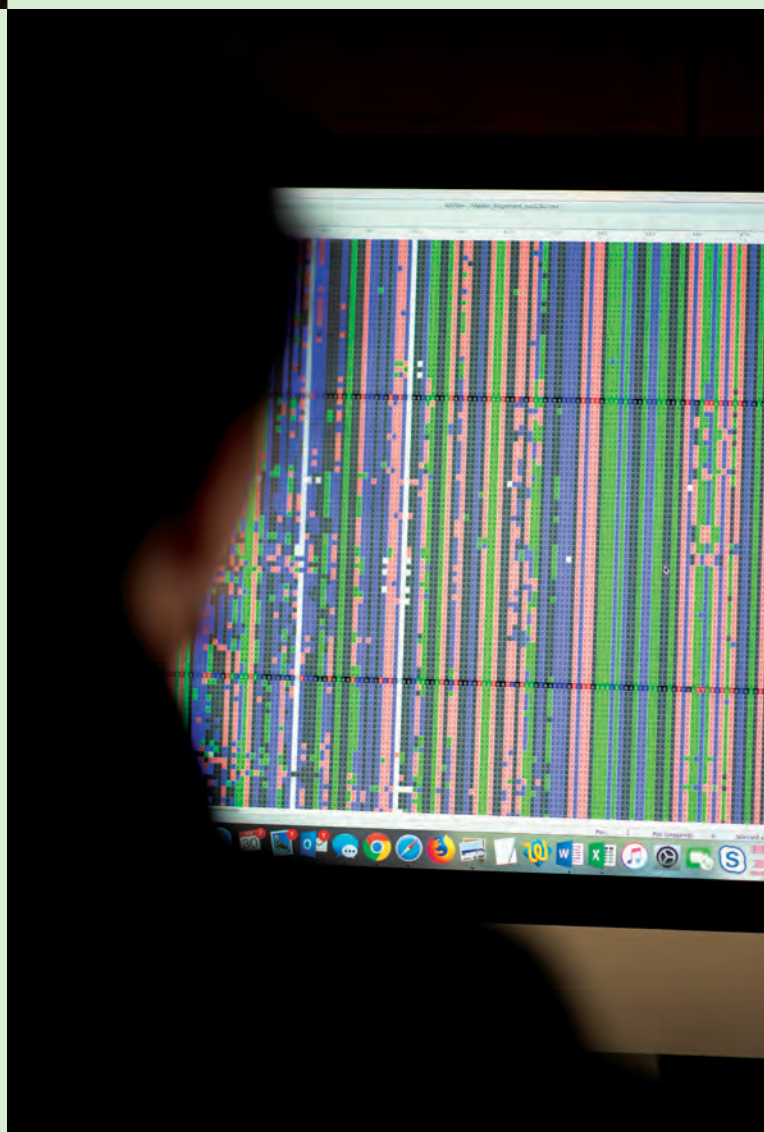
Estimating when fungal lineages diverged on the fungal tree of life is not an easy task. The estimates require the conversion of the rate at which molecular changes take place in the DNA sequence (=mutation rate) into measures of geological time (called molecular clocks). However, since the mutation rate can vary considerably between fungal lineages, fungal fossils are also critical to the analysis, as the age of the rock in which the fossil is found provides an estimate of the minimum age of the fungus within[36].

Unfortunately, the fungal fossil record is not as extensive as for plants and animals and this has led to far greater uncertainty in establishing when the major events of fungal evolution took place. Nevertheless, new fungal fossil discoveries are continually being made[6,21,37,38]. For example, several exquisitely preserved fossils from the c. 400-million-year-old Rhynie chert rocks in Scotland appear to show fungi associated with some of the earliest known land plants[39]. Such discoveries, combined with molecular clock analyses[7,26], suggest that some of the fungal lineages we find today were already present with the earliest land plants; indeed they may well have played an essential role in the early colonisation of land.

BOX 4: THE DARK TAXA – IMPLICATIONS OF ENVIRONMENTAL SEQUENCING FOR THE FUNGAL TREE OF LIFE

In recent years, there has been a huge increase in the amount of data generated from sequencing DNA present in environmental samples (e.g. soil, water, air or tissues of other organisms) rather than individual fungi. This approach is revealing a hitherto unsuspected level of fungal diversity, with the identification of potentially thousands to hundreds of thousands of new species[30,41–43] (see also Chapters 1 and 3). For example, a study of dust samples across the USA recovered nearly 40,000 distinct molecular signatures, of which around 40% could not be correlated with known species in gene bank databases[43,44]. These 'dark taxa' are only known from their DNA sequence and as yet have no known physical specimen for reference.

While these new data are enhancing our understanding of fungal diversity, they are also opening up new challenges – how do we place hundreds or thousands of fungal sequences into the fungal tree of life? While the analytical methods that can cope with these data are still being developed, it is already clear that many of the newly identified fungi are so distinctive that they are being assigned to entirely new orders and classes across the fungal tree of life[42,43,45]. For example, a recent analysis of soil samples from a broad geographical range detected over 40 previously unrecognised major lineages and even a new phylum[42,46]. These new discoveries will not only substantially impact estimates of the total number of fungal species on Earth (see Chapter 1) but will also considerably modify the current fungal tree of life[30,43,47,48].



NEW DISCOVERIES: SPECIES OF FUNGI DESCRIBED IN 2017

How many new species of fungi were described in 2017? Which groups do they represent, where were they found and what are some of the more surprising discoveries?

stateoftheworldsfungi.org/2018/new-discoveries.html

2,189

NEW SPECIES OF FUNGI WERE DESCRIBED DURING 2017

Cora galapagoensis, Galápagos

Gymnosporangium przewalskii, China

Herpothallon tricolor, Brazil

<< A new, colourful lichen described from a coastal tropical forest in Brazil

>> A new, drought-tolerant decomposer found on native *Euphorbia* in the Canary Islands

Orbilia beltraniae, Canary Islands

Pseudofibroporia citrinella, China

Inocybe araneosa, Australia

Trichomerium eucalypti, Australia

An elegant spore of a new sooty mould, feeding off 'honeydew' from sap-sucking insects

>> A new mould, belonging to a new genus, discovered in rotten wood from an apartment in Paris, France

Zasmidium podocarpi, Australia

Planamyces parisiensis, France

WITH AT LEAST 2 MILLION SPECIES OF FUNGI YET TO BE DESCRIBED[1], AND POTENTIALLY MANY MORE, DISCOVERING AND NAMING FUNGAL DIVERSITY IS OF FUNDAMENTAL IMPORTANCE TO OUR UNDERSTANDING OF BIODIVERSITY AND ITS ECOLOGICAL FUNCTIONS.

In this chapter, we report on some of the 2,189 new species of fungi described during 2017 as recorded in *Index Fungorum*[2].

Over the past two decades, the rate of description of fungal species has increased from 1,000–1,500 new species per year to the current rate of more than 2,000 per year (see Figure 1). This is largely due to the increased use of DNA-based techniques, which have improved the ability to detect fungi in the environment and to distinguish between very similar-looking species.

The 2,189 newly described species in 2017 ranged from conspicuous, large macrofungi, such as mushrooms and bracket fungi, to those with tiny and inconspicuous spore-bearing structures, such as moulds. The new discoveries were predominantly from the phylum Ascomycota, which was represented by 68% (1,481 species) of new fungi, followed by Basidiomycota represented by 31% (684 species). Other phyla were poorly represented, making up the final 1% (24 species).

Many of the new species were found in historically under-studied regions and habitats, but well-studied regions in Europe were also shown to have considerable undocumented fungal diversity[3,4]. The description of the new discoveries involved many hundreds of researchers from all over the world, and the published accounts range from studies of single species to major taxonomic revisions of genera.

NEW MYCORRHIZAL FUNGI

Around 90% of all land plant species engage in mutualistic relationships with fungi, which form mycorrhizas in their roots (see Chapters 1 and 5). A single plant species can have several, tens or even more than a hundred species of fungi associated with its roots.

Of the 2,189 species of fungi named in 2017, an impressive 179 were fibrecaps (*Inocybe*) from Australia[5], Europe[6] and India[7]. Species in this genus form mycorrhizal associations with vascular plants and, interestingly, also produce compounds such as muscarine (a toxin) and psilocybin (a hallucinogen; see Chapter 4), both of which have medical applications.

Forty new species of webcaps (*Cortinarius*) were described in 2017[e.g. 8]; this large genus comprises over 3,000 species worldwide and includes important mycorrhizal partners of trees in boreal (subarctic), temperate and subtropical forest ecosystems in both the northern and southern hemispheres. Nine species of false truffles (*Elaphomyces*) were also described, from the USA (New Hampshire)[9], Spain and Greece[4]; this genus forms mycorrhizal associations with a large diversity of tree species and its truffle-like, subterranean spore-bearing structures are eaten and dispersed by rodents and other animals.

Arbuscular mycorrhizal fungi (Glomeromycotina) are found in a diverse range of habitats, forming mycorrhizas with many crop species and also with tropical forest trees. An interesting new discovery from this group was *Dominikia emiratia*, first isolated from a sandy desert in the United Arab Emirates. It was found in soil in the vicinity of key lime (*Citrus* × *aurantiifolia*), pomegranate (*Punica granatum*) and grape (*Vitis vinifera*). This species may be endemic and is potentially of interest as a subject for research because it could be helping these crops to survive under extremely harsh desert conditions[10].

NEW PATHOGENIC FUNGI

Many new species of fungi associated with plant diseases (see Chapter 8) were named in 2017[e.g.11]. These fungi infect plants of economic importance, such as those used in agriculture, forestry, and as ornamentals, as well as those in natural ecosystems.

For example, 14 species of *Colletotrichum* were described; species in this genus can cause anthracnose, foliar disease, rot and post-bloom fruit drop in many important crops, including citrus trees (*Citrus* spp.)[e.g. 12], peppers (*Capsicum* spp.)[13] and other hosts. As highlighted in *State of the World's Plants 2016*, *Colletotrichum* has been ranked in the top ten fungal pathogens of plants[14,15].

Twenty-nine new species of *Diaporthe*, a genus causing root, stem and leaf diseases, were named, many from China and Italy. They were discovered affecting host plants including peach (*Prunus persica*)[16], Manchurian walnut (*Jugulans mandshurica*)[17], lemon (*Citrus limon*)[18], coffee (*Coffea* sp.) and tea (*Camellia sinensis*)[19]. Surveys of tea plants in China also revealed new species of fungi: eight of *Pestalotiopsis* and three of *Pseudopestalotiopsis*[20].

New species of smut and rust fungi, which parasitise living plants (including plants of agricultural importance), were also described – among these were ten species of *Macalpinomyces* (smut fungi) from inflorescences of the grass genus *Eriachne* in Australia[21] and a further four smut fungi from grass or sedge hosts from China[22]. Fifteen species of rust fungi were also described – four from *Panicum* (switchgrass)[23], a genus widely used as forage, biofuel feedstock, for soil conservation, and as ornamentals across the world.

NEW DECOMPOSERS

Decomposer fungi recycle nutrients from nearly all types of organic material, which can then be used by other organisms. Some are generalists and decompose a wide array of organic material, whereas others are more selective.

Decomposers such as bracket or crust fungi (polypores and corticioids), which often produce large conspicuous spore-bearing structures, can be extremely important recyclers of woody material. In 2017, over 70 new species from 38 genera of bracket and crust fungi were described, including eight new species of brown rot fungi in *Antrodia*[e.g. 24], white rot polypores in *Polyporus*[25], *Fomitiporia*[26] and *Fomitiporella*[27], and crust fungi in the genus *Lyomyces*[28].

Lichenomphalia altoandina, Chile

FIGURE 1: NUMBER OF NEW FUNGAL SPECIES DESCRIBED PER YEAR OVER THE PAST TWO DECADES

Note that names published in 2017 are still being added and this number is therefore likely to rise.
[Data from *Index Fungorum* (indexfungorum.org)]

Fungi with very small sexual spore-bearing structures or mould-like asexual states (commonly known as microfungi) can also be extremely important and ecologically diverse decomposers. In 2017, 37 new species of the ubiquitous mould genus *Aspergillus* were described from samples from an extraordinary array of different environments, including soils, plant tissues, a cave wall biofilm, a baby-carrier backpack, an oil painting, a fingernail and house dust[e.g. 29]. Nineteen species of the genus *Talaromyces* (related to the mould genus *Penicillium*) were also discovered from soil, indoor air samples, seeds, and dead twigs and bark[e.g. 30].

Many species of lesser known microfungi were also described in 2017, some revealing links between asexual and sexual forms and helping to improve knowledge of their life cycles. The description of *Epicoccum mackenziei* was particularly astonishing: this discovery revealed the first sexual stage ever reported for this genus[31], 201 years after the genus was first described based on asexual structures.

NEW LICHENS AND LICHEN-INHABITING FUNGI

Lichen-forming fungi are important primary colonisers of ecosystems and diverse microhabitats. They are involved in the weathering of rocks to release mineral nutrients, they capture nutrients from the air and are important components of many food webs. Other fungi, some closely related to lichen-forming fungi, are found only on lichens (many are parasitic) and are therefore called lichenicolous fungi.

Over 200 new lichen-forming and lichenicolous fungi were described in 2017, in over 95 genera. These were found on rocks, bark, twigs, leaves, a range of microhabitats and on other lichens, from over 34 countries globally. New discoveries of lichen-forming fungi included crust-like button lichens (*Buellia* and *Amandinea*[e.g. 32,33]); warty crust-like lichens (*Pertusaria*[34,35]; and frond-like or bushy lichens (*Usnea* and *Heterodermia*[36,37]). Twenty-one tropical species in the Arthoniales, an old but little-studied fungal order exhibiting very varied habitat preferences and morphological characters, were also described[e.g. 38]. Potentially endemic lichens were reported from the Galapagos Islands[39], the Seychelles[40], and Hawaii[41]. *Lichenomphalia altoandina*, a strikingly orange, salt-tolerant lichen-forming mushroom, was described from the Andes in Chile[42].

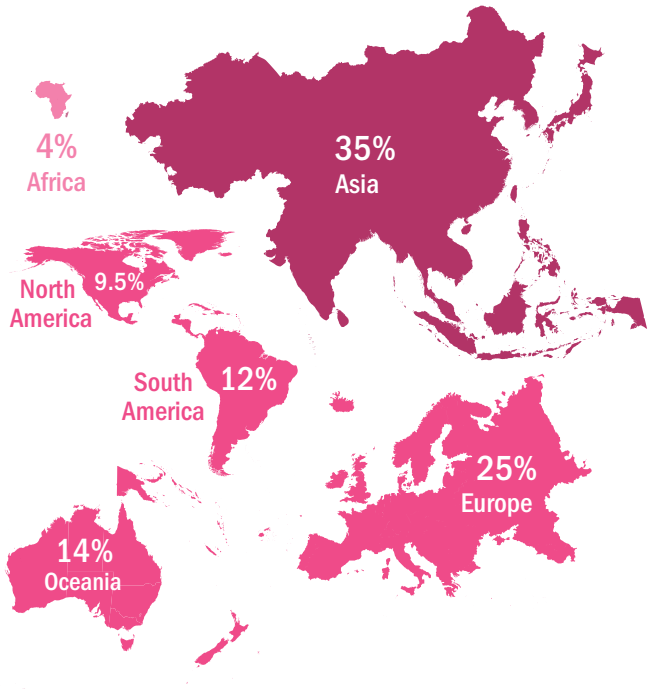
Examples of newly described lichenicolous fungi include *Talpapellis mahensis*, a presumed lichenicolous mould known only from one unidentified lichen on a coconut tree, and *Stictographa dirinariicola*, consisting of tiny, black, sexual spore-bearing structures immersed in a lichen on coconut bark (both from the Seychelles)[40].

NEW RELATIVES OF EDIBLE FUNGI

In 2017, a number of new species related to edible fungi were described. New species of chanterelles (*Cantharellus*) were discovered from Canada[43], the Central African Republic[44] and South Korea[45], and a new porcini mushroom was found in India (*Boletus indoedulis*)[46]. Two new species of truffles (*Tuber*) were described from Hungary[47]. Thirty-three new species of *Agaricus* were described from China, Thailand, Brazil, Spain and Italy[e.g. 48]; this genus includes the widely cultivated button mushroom (*Agaricus bisporus*), also marketed as portobello mushroom when the caps are fully expanded, or chestnut mushrooms when the caps are brown.

FIGURE 2: GEOGRAPHIC DISTRIBUTION OF NEW SPECIES DESCRIBED IN 2017

Schematic showing the proportion of new species described from each continent (Antarctica not shown – 0.5%). Very few new species were described from Africa even though it is one of the most poorly known areas.



WHERE HAVE NEW FUNGI BEEN FOUND?

At the continental level, the best represented areas for new species of fungi described in 2017 were Asia (35% of the new species) and Europe (25%), while the fewest species (4%) were described from Africa (Figure 2). New species are usually discovered in areas where most fungal taxonomists are working, and hotspot areas for recently described species reflect this research bias. At the country level, China was the leader in newly described species of fungi, with a total of 362 described in 2017 (see also Chapter 7). These included a very wide diversity of species, ranging from *Agaricus* mushrooms from forests[48] to karst cave fungi such as *Amphichorda guana*, which was isolated from bat guano[49]. Australia was the second most prolific area, with 259 new species described, including fibrecap mushrooms (Inocybaceae), microfungi and lichens[e.g. 5,32,50]. Third was Thailand with 180 species, including 39 new species from submerged wood[e.g. 51].

The environments in which the fungi were found ranged from the extreme to the commonplace. Those in unusual environments included the mould *Cadophora antarctica*, discovered from diesel-contaminated soil in Antarctica[52], and *Aegeanispora elanii*, found producing tiny spore-bearing structures on decaying driftwood in the Aegean Sea[53]. Conversely, new species of fungi can also be found very close to home. Surveys of house dust[e.g. 54], garden soils[e.g. 52] and other urban environments revealed more than 40 new species. One new species was even isolated from a human fingernail[52]! With undescribed fungal diversity being uncovered in such a wide variety of habitats, new discoveries are set to continue for the foreseeable future and beyond.

USEFUL FUNGI

THE GLOBAL MARKET FOR EDIBLE MUSHROOMS IS ESTIMATED TO BE WORTH

US$42 BILLION

PER YEAR

What makes a species of fungus economically valuable? What daily products utilise fungi and what are the useful fungi of the future for food, medicines and fungal enzymes?

stateoftheworldsfungi.org/2018/useful-fungi.html

FUNGI ARE A SOURCE OF NUTRITIOUS FOOD, LIFESAVING MEDICINES AND ENZYMES FOR BIOTECHNOLOGY.

Most people would be able to name a few species of edible mushrooms but how many are aware of the full diversity of edible species in nature, still less the enormous contribution fungi have made to pharmaceuticals and biotechnology? In fact, the co-opting of fungi for the production of wine and leavened bread possibly marks the point where humans first learned to use the natural world to perform useful chemical reactions. It is part of a story that continues into the present day – the notion of fungi as factories that can produce valuable chemical compounds is the bedrock of modern biotechnology. In this chapter, we look specifically at edible fungi, medicines and enzymes and draw out the major applications that provide significant societal benefits. Other significant uses and applications not covered in this chapter are summarised in Table 1.

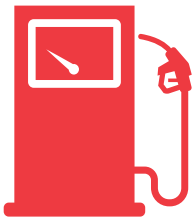
EDIBLE FUNGI

The global market for edible mushrooms is estimated to be worth US$42 billion per year[1]. At least 350 species of fungi are collected and eaten as food, although the exact number is likely to be higher as this information is not available for many countries[2]. These edible species come from just 18 orders of fungi, which is a small fraction of total fungal diversity (see Figure 1). Among wild-collected fungi, the species most commonly consumed and traded are brittlegills (*Russula* spp.), milkcaps (*Lactarius* spp.), chanterelles (*Cantharellus* spp.), agarics (*Amanita* spp.) and boletes (*Boletus* spp.)[2]. Most wild-collected species cannot be cultivated because of complex nutritional dependencies (they depend on living plants to grow), whereas cultivated species have been selected to feed on dead organic matter, which makes them easier to grow in large quantities[2,3]. The rise of the suite of cultivated mushrooms seen on supermarket shelves today, including button mushrooms (*Agaricus bisporus*), began relatively recently in the 1960s[3]. The majority of these cultivated mushrooms (85%) come from just five genera: *Lentinula*, *Pleurotus*, *Auricularia*, *Agaricus* and *Flammulina*[4] (see Figure 2).

Fungi also play a pivotal role in the production of food and drinks. Brewer's or baker's yeast, *Saccharomyces cerevisiae*, underpins almost all bread and alcoholic drink production and is a key ingredient in Marmite™ and Vegemite™. The meat substitute Quorn™ is also manufactured using a fungus (*Fusarium venenatum*), in carefully controlled fermentation vessels that yield 300 kg of the fungus per hour[5]. Fungi are also essential to the production of some types of cheese, with moulds such as *Penicillium camemberti* and *P. roqueforti* used to ripen and give flavour to the cheese. While these two species can be found in many types of cheese, the wider diversity of fungi involved is currently unknown[6]. Furthermore, the type of cheese produced is not necessarily dependent on the species involved. A DNA analysis of 44 types of cheese revealed that aside from *P. roqueforti*, which is specific to blue-veined cheese, there was little correlation between the fungal species detected and the type of cheese[7]. Interestingly, analysis of a collection of *P. roqueforti* from 120 different blue-veined cheeses found distinct populations of the fungus that corresponded to the different cheese varieties[8], so cheese production appears to have shaped the population structure of this species[9].

At least 350 species are consumed as foods

15% of all vaccines and therapeutic proteins are made in yeast



Fungi are being used to turn crop waste into bioethanol

216 species of fungi are thought to be hallucinogenic

Itaconic acid from fungi is used to make Lego®

TABLE 1: AN OVERVIEW OF THE HUMAN APPLICATIONS OF FUNGI

AGRICULTURE	Species of *Trichoderma* are used to enhance the growth of crops and as a source of enzymes added to improve animal feeds[49,50]. Fungi are also the source of an important class of agricultural fungicides called strobilurins[51]. *Aspergillus flavus* is used as a biocontrol agent on peanut crops to out-compete aflatoxin-producing fungi[52].
BEVERAGES	Yeasts underpin alcoholic drink production from beer to wine to spirits. Soft drinks contain citric acid that is produced from the fermentation of *Aspergillus niger*[53]. Glucoamylase from species of *Aspergillus* is used to convert starch to high-fructose corn syrup, which is used as a sweetener in soft drinks[54].
BIOFUELS	Second-generation bioethanol makes use of species of *Trichoderma* to break down agricultural waste such as maize straw into sugars that can be fermented using yeast to produce ethanol[42].
BIOREMEDIATION	White rot fungi, including *Pleurotus ostreatus* and *Trametes versicolor*, can degrade toxic polychlorinated biphenyl (PCB) chemicals in soil and polluted wastewaters[55,56].
COTTON PROCESSING	Catalase enzymes from species of *Aspergillus* are used to break down excess bleach in the wastewater from cotton processing[57]. *Trichoderma* cellulases are used to remove fine cotton threads, which prevents the fibre aggregating into pills[57].
FOOD	At least 350 edible mushroom species are known to be collected for food[2]. The meat substitute Quorn™ is manufactured using a fungus (*Fusarium venenatum*)[5]. Moulds such as *Penicillium camemberti* and *P. roqueforti* are integral to the ripening process in many types of cheese[6]. Live yeast and fungal enzymes are used in breadmaking[58]. The food colourings lycopene and beta-carotene are now produced from the fungus *Blakeslea trispora*[59]. Soy sauce is produced using koji (*Aspergillus oryzae*) and the Asian snack tempeh makes use of *Rhizopus microsporus*[60,61].
HALLUCINOGENS	Worldwide, 216 species of fungi are believed to be hallucinogenic – of these, 116 species belong to the genus *Psilocybe*[62].
LEATHER PROCESSING	Leather hides are degreased with lipase enzymes from *Aspergillus oryzae*[63,64].
MEDICINES	Many drugs come from fungi. Penicillin from *Penicillium rubens* revolutionised the treatment of bacterial infections and cyclosporine from *Tolypocladium inflatum* made organ transplantation possible[11–13]. Gestodene is an active ingredient in third-generation contraceptive pills; a key step in its synthesis is achieved using fungal fermentation with *Penicillium raistrickii*[65].
PAPER MANUFACTURING	Cellulase enzymes produced by species of *Trichoderma* and *Humicola* are used to speed up the pulping process thereby reducing water usage[37,38].
PLASTICS AND BIOMATERIALS	Plastic car parts, synthetic rubber and Lego™ are made using itaconic acid derived from species of *Aspergillus*[66,67]. Additionally, fungal mycelium-based products are now being used as replacements for polystyrene foam, leather and building materials[68–70].
RESEARCH	Since 2010, more than a quarter of Nobel prizes for physiology or medicine were awarded for work based on yeast[71].
VITAMINS	The vitamin B2 used for vitamin supplements is produced by fermentation of the fungus *Eremothecium gossypii*[72].
WASHING DETERGENTS	Cellulase enzymes produced by the thermophilic fungus *Humicola insolens* are added to washing powders and liquids. They trim the fine cotton threads on the surface of cotton fabric to produce a smoother, newer feel[41,73]. Lipase enzymes from the same species are also added to break down fat stains[40,41].

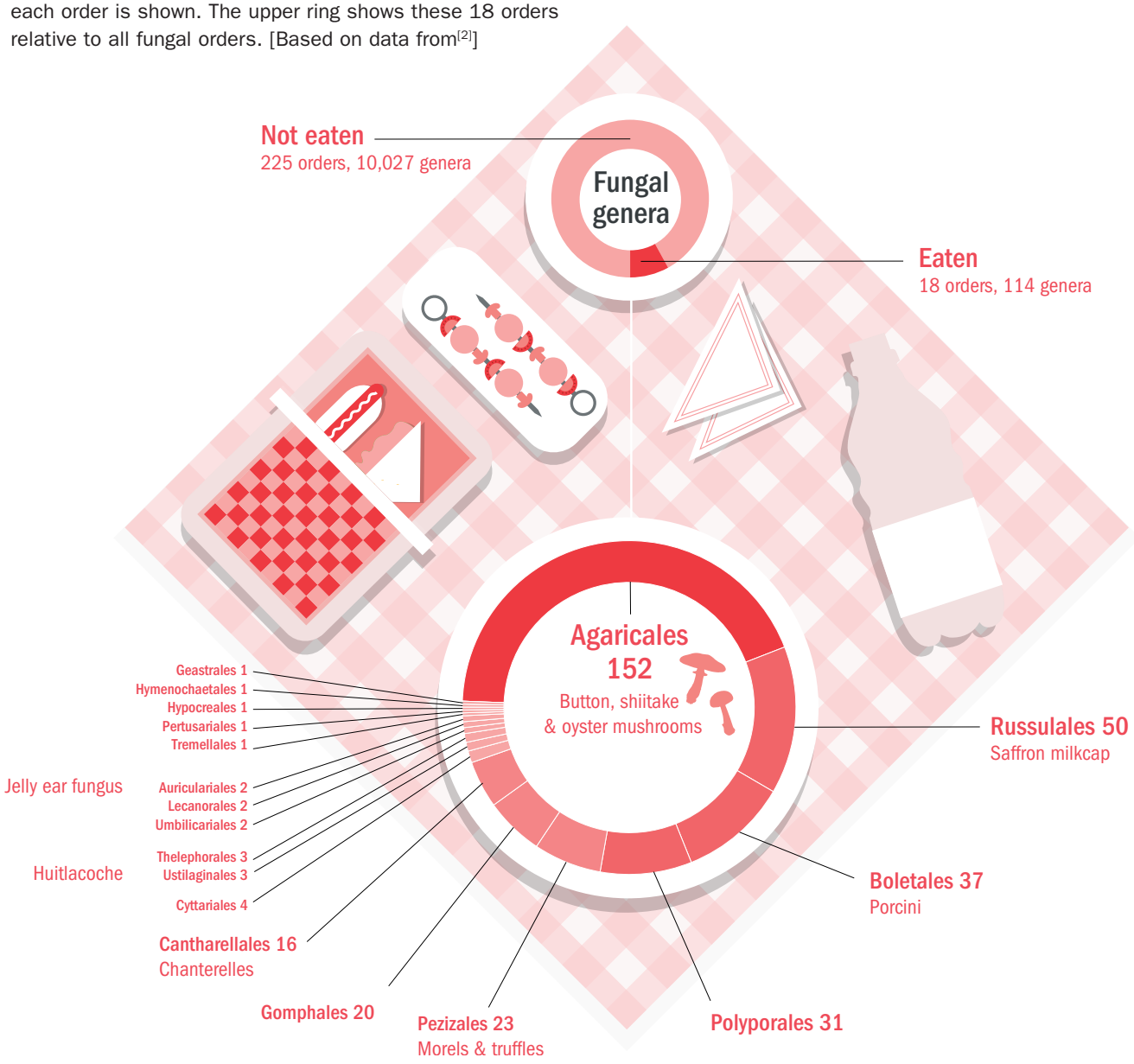
As is the case for other areas of mycology, identifying and naming species of edible mushrooms can be problematic. For example, in a study conducted at Kew, DNA was extracted from a packet of dried porcini mushrooms bought from a shop in London. Analysis of the DNA revealed that rather than being from a single known species (*Boletus edulis*), the chopped pieces of mushroom in the packet came from three different species, each of which was new to science[10]. This demonstrates that not only do we eat just a small fraction of the edible mushrooms available in nature, we can't even be sure of the identity of those that we do eat!

FUNGAL PHARMACEUTICALS

Fungi have made major contributions to the world of medicine. For example, penicillin from the fungus *Penicillium rubens* revolutionised the treatment of bacterial infections, while cyclosporine from the fungus *Tolypocladium inflatum* made organ transplantation possible by helping to prevent rejection of the donated organs[11–13]. Other notable examples include the cholesterol-lowering drug lovastatin, from *Aspergillus terreus*, and fingolimod, which is used to treat multiple sclerosis (see Figure 3). The chemical structure of fingolimod took inspiration from myriocin, a chemical compound produced by *Isaria sinclairii*.

FIGURE 1: EDIBLE FUNGAL DIVERSITY IN COMPARISON TO TOTAL FUNGAL DIVERSITY

The fungi that are recorded as being eaten for food represent a small fraction of total fungal diversity. The lower ring shows the species distribution of 350 confirmed fungal food species in 18 fungal orders. The number of edible species in each order is shown. The upper ring shows these 18 orders relative to all fungal orders. [Based on data from[2]]



Additionally, several chemotherapy drugs, or their natural precursors, that were originally isolated from plants have since been discovered to be produced by fungi too[14–16]. One example is the cancer drug paclitaxel: it was originally discovered as a chemical compound synthesised by the Pacific yew tree (*Taxus brevifolia*) but has since been reported to be synthesised independently by two different fungal species, *Taxomyces andreanae* and *Penicillium raistrickii*, that live inside the yew tree[14]. This curious phenomenon has been observed with other plant-derived chemotherapy drugs. For example, it was recently discovered that the cancer drugs vinblastine and vincristine, originally isolated from the Madagascan periwinkle (*Catharanthus roseus*), are also synthesised by an endophytic *Fusarium* species, a fungus that lives inside the plant[16].

Aside from the chemical compounds produced naturally by fungi, genetically engineered yeasts also play an important role in medicine – as living factories for the production of protein-based medicines such as vaccines and human therapeutic proteins[17]. The ability of yeast species such as *Saccharomyces cerevisiae* and *Komagataella pastoris* (formerly known as *Pichia pastoris*) to efficiently produce human proteins, means that 15% of biopharmaceuticals are now produced using yeast cells[18]. Notable examples include insulin and the hepatitis B vaccine[19,20].

A key question is: Why do fungi make medicines that are so beneficial to humans? Fungi live in competitive environments and they cannot easily move to new niches when competition for resources is high. They therefore need to defend their patch, and one means of fighting off competitor fungi or bacteria is the production of antibiotics. The majority of the fungal chemical compounds in Figure 3 are antibiotics that inhibit the growth of either bacteria or fungi. Even the immunosuppressant drugs cyclosporine, mycophenolic acid and myriocin (which are not used as antibiotics) display potent antifungal activity[21–23], as does the statin drug lovastatin[24]. This suggests that the role of these chemical compounds in nature is to protect the fungi that produce them from microbial competitors, and this role is exploited by humans – we benefit from the fundamental biochemical similarities between fungi and humans. This also explains why antifungal chemical compounds such as statins have unintended benefits in human medicine[25,26]. Similarly, biochemical pathways that control activation of immune cells in humans are also present in fungi[27–29].

Humans can also benefit from compounds that are produced by fungi to enable them to invade the bodies of other organisms. Cyclosporine and myriocin, both of which act as immunosuppressants in humans, are produced by fungal species that are able to invade insects' bodies. The fungus *Tolypocladium inflatum*, which produces cyclosporine, is able to infect beetle larvae – an infected larva actually becomes the base of the fungus from which the spore-bearing structure emerges[30]. Similarly, the fungus *Isaria sinclairii*, which produces myriocin, infects cicada larvae[31] (see Box 1). It has been suggested that for these fungi to survive inside insect larvae, they must produce immunosuppressant chemical compounds to evade the host's immune system. Experiments with insect larvae models do indeed show that cyclosporine and myriocin cause immunosuppression in insect larvae[32,33]. This example demonstrates the importance to drug discovery of tapping into new and unusual sources of fungi, such as those that live inside insects and plants[34,35].

APPLICATIONS OF FUNGAL ENZYMES

Enzymes are natural molecules that catalyse (cause or speed up) chemical reactions. A particularly important use of enzymes is in industry, where they are changing the way industrial chemical processes are conducted. Industrial processes that would normally require high temperatures or harsh chemicals can be carried out under far milder conditions using enzymes[36] and fungi have proved a useful source: 60% of the enzymes used in industry come from fungi and 70% of these are derived from just seven fungal species (see Figure 4).

In natural environments, fungi produce efficient cellulase enzymes to break down wood and leaves into digestible components and this makes them ideal for paper manufacturing, where wood needs to be broken down into a soft pulp. Cellulase enzymes produced by species of *Trichoderma* and *Humicola* are used to speed up the pulping process thereby reducing water usage[37,38].

FIGURE 2: THE MAJOR GENERA OF CULTIVATED EDIBLE MUSHROOMS

85% of cultivated edible mushrooms come from just five genera: *Lentinula* **(A)**, *Pleurotus* **(B)**, *Auricularia* **(C)**, *Agaricus* **(D)** and *Flammulina* **(E)**

THE FUNGAL GENUS PENICILLIUM HAS USES AS DIVERSE AS CHEESE PRODUCTION, ANTIBIOTICS AND THE SYNTHESIS OF THIRD-GENERATION CONTRACEPTIVE PILLS

Penicillium

BOX 1: FROM FUNGAL IMMUNOSUPPRESSANT TO BILLION-DOLLAR DRUG

The entomopathogenic fungus *Isaria sinclairii* infects cicada larvae; it grows inside its host, initially without killing it but instead replacing the host tissue with fungal mycelium. Eventually its spore-bearing structures emerge from the dead larvae. *Isaria sinclairii* produces an immunosuppressant chemical compound called myriocin. Extensive chemical redesign of myriocin resulted in the immunosuppressive multiple sclerosis treatment fingolimod. Fingolimod is a blockbuster drug with sales of US$2.48 billion in 2018[83].

FIGURE 3: DRUGS OR CLASSES OF DRUGS USED IN HUMAN MEDICINE THAT OWE THEIR DISCOVERY TO CHEMICAL COMPOUNDS ISOLATED FROM FUNGI

[Information compiled from [11,74–82]]

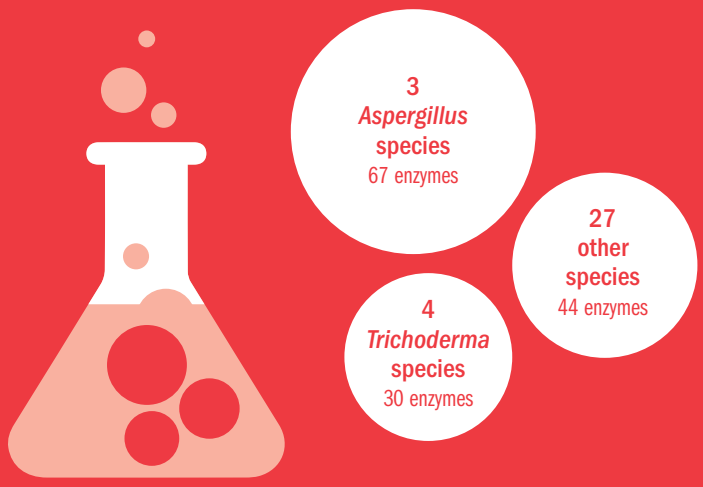
Paper production also makes use of cultures of fungi of the genus *Ophiostoma* to remove lipophilic compounds that would reduce paper quality[39]. In another application, cellulase enzymes from the fungus *Humicola insolens* are added to washing detergents. The enzymes dissolve tiny, fine cotton strands on the fabric exterior, which gives cotton fabrics a renewed appearance; lipase enzymes from the same species are also added to help remove fat stains[40,41].

The production of bioethanol, which is used increasingly as a fuel for cars, also makes use of cellulases from species of *Trichoderma*, to break down agricultural cellulose waste into sugars[42,43]. This has enabled the development of so-called second-generation biofuels that do not compete with food crops. Instead of using starch from food, agricultural waste (for example stalks, leaves and husks from crops such as maize) is broken down by fungal cellulases into sugars and then fermented by yeast into ethanol[44]. The recent development of electric cars powered by ethanol fuel cells will help keep interest in bioethanol production alive for the foreseeable future[45].

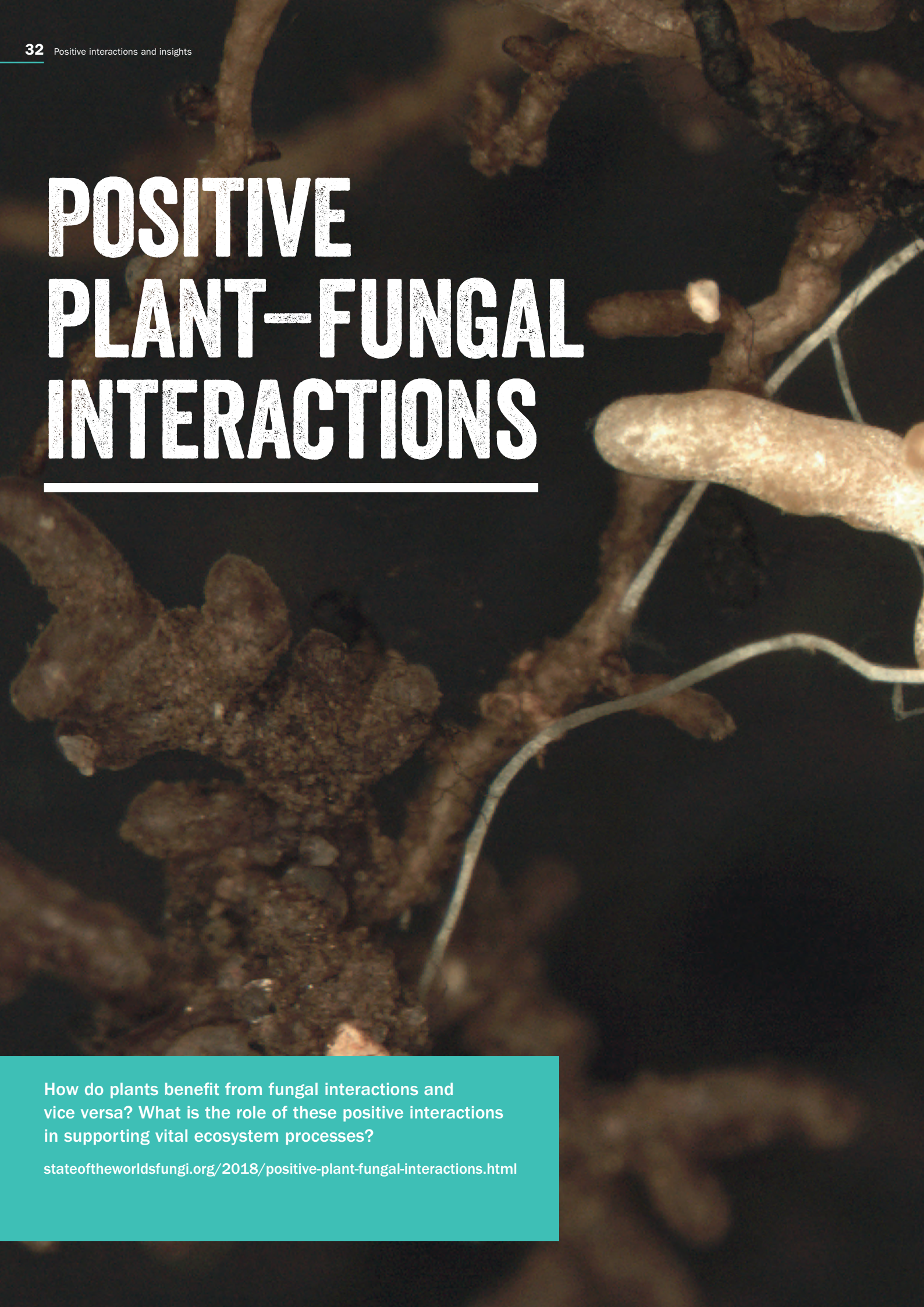
Fungal biotechnology is also likely to be greatly influenced by research in the new field of synthetic biology, which involves building artificial biological systems for research and for applications in engineering and medicine. An international team of collaborators is currently working on producing yeasts with synthetic genomes[46,47] and these organisms are anticipated to have enhanced biosynthetic potential[48]. In the future, it is likely that a wider range of pharmaceuticals, high-value chemicals and enzymes will be made in yeast or other fungal production platforms.

FIGURE 4: FUNGAL ENZYMES IN INDUSTRY

Nearly 70% of all industrially used fungal enzymes are derived from just seven species of fungi. [Data from the Association of Manufacturers and Formulators of Enzyme Products[84]]



POSITIVE PLANT–FUNGAL INTERACTIONS



How do plants benefit from fungal interactions and vice versa? What is the role of these positive interactions in supporting vital ecosystem processes?

stateoftheworldsfungi.org/2018/positive-plant-fungal-interactions.html

IT IS ESTIMATED THAT AROUND

90%

OF LIVING PLANT SPECIES HAVE MYCORRHIZAL FUNGI ASSOCIATED WITH THEIR ROOTS

THROUGHOUT THEIR EXISTENCE ON EARTH, FUNGI AND PLANTS HAVE BEEN INTRICATELY LINKED, AND THEIR INTERACTIONS SPAN A VAST CONTINUUM FROM DETRIMENTAL TO BENEFICIAL[1–3].

Although negative interactions have received more attention, due in part to their impacts on crops, forests and horticulturally important plants, positive plant–fungal interactions are not only ubiquitous but also vitally important to sustaining life on this planet. In this chapter, we highlight what is currently known about the beneficial interactions resulting from fungi that form symbiotic[4,5] relationships with plants.

PLANT–FUNGAL MUTUALISMS

Fungi and bacteria are now widely acknowledged as playing a central role in the health of all organisms, including plants and humans. In plants, beneficial symbiotic fungi live at least partly within the plant and fall broadly within two groups – endophytic fungi (endophyte meaning 'within plant') and mycorrhizal fungi (mycorrhiza meaning 'fungus root'). These symbiotic fungi, found growing within or between cells in plant shoots and/or roots, provide a variety of benefits to their host plants. These range from improved access to nutrients and increased plant growth to enhancing plant defence mechanisms to herbivory and disease. In return, the fungi obtain nutrition (sugars, lipids) from the plant and a host to live in. Both endophytes and mycorrhizal fungi are ancient symbioses between plants and fungi and are functionally and ecologically very diverse. Endophytes are found in roots and/or shoots, where they are often symptomless. Mycorrhizal fungi are found only in roots, where they form specialised structures for nutritional exchange with plants (see Box 1).

1. Endophytes. It appears that all plants harbour endophytic fungi[3], from the Arctic to the tropics[6]. There are four classes of fungal endophytes, differentiated by host range, transmission and symbiotic functionality[3]. They are found between and within cells in plant shoots and/or roots[6–9] (see Figure 1) and can be beneficial to plant growth, especially in harsh environments[3,10]. For example, endophytic fungi such as *Trichoderma* (Ascomycota), used as a seed treatment in agriculture, can induce plant resistance to diseases, water deficits, salinity and also heat stress[11,12]. They do this by altering the expression of the genes involved in root growth, nutrient uptake or protection against oxidative damage[13].

2. Mycorrhizas. Evidence from the fossil record suggests that mycorrhizas are found even in some of the earliest land plants from around 400 million years ago; the extinct spore-bearing plant *Aglaophyton major* from the Rhynie chert in Scotland is a characteristic example[14]. These plant–fungal mutualisms have arisen many times in the evolutionary history of different groups of plants and fungi[2]. It is estimated that around 90% of living plant species have mycorrhizal fungi associated with their roots. In contrast, less than 2% of fungal species enter into mycorrhizal partnerships[15,16]. Through becoming specialised to co-exist with plants, the fungi involved rely on their plant hosts for their supply of carbon, having lost the ability of their ancestors to decompose dead organic matter[17]. In return for their photosynthetic carbon, the plants receive water and mineral nutrients from the soil via the fungi. Most mycorrhizal fungi are dependent on their hosts for survival, just as many plants are dependent on their fungal partners.

Different plants associate with different groups of fungi to form mycorrhizas (see Table 1), which can be broadly described as ectomycorrhizas (where the fungus remains between the plant root cells) or endomycorrhizas (where the fungus penetrates the root cells). Only around 2% of plants form ectomycorrhizas but they are mostly ecologically and economically important trees that dominate temperate, boreal and some tropical ecosystems (e.g. oaks (*Quercus* spp.), beech (*Fagus* spp.), pines (*Pinus* spp.), spruces (*Picea* spp.), eucalypts (*Eucalyptus* spp.) and dipterocarps (e.g. *Shorea* spp.)); it is therefore important to understand the relationships between these plant species and their fungal partners.

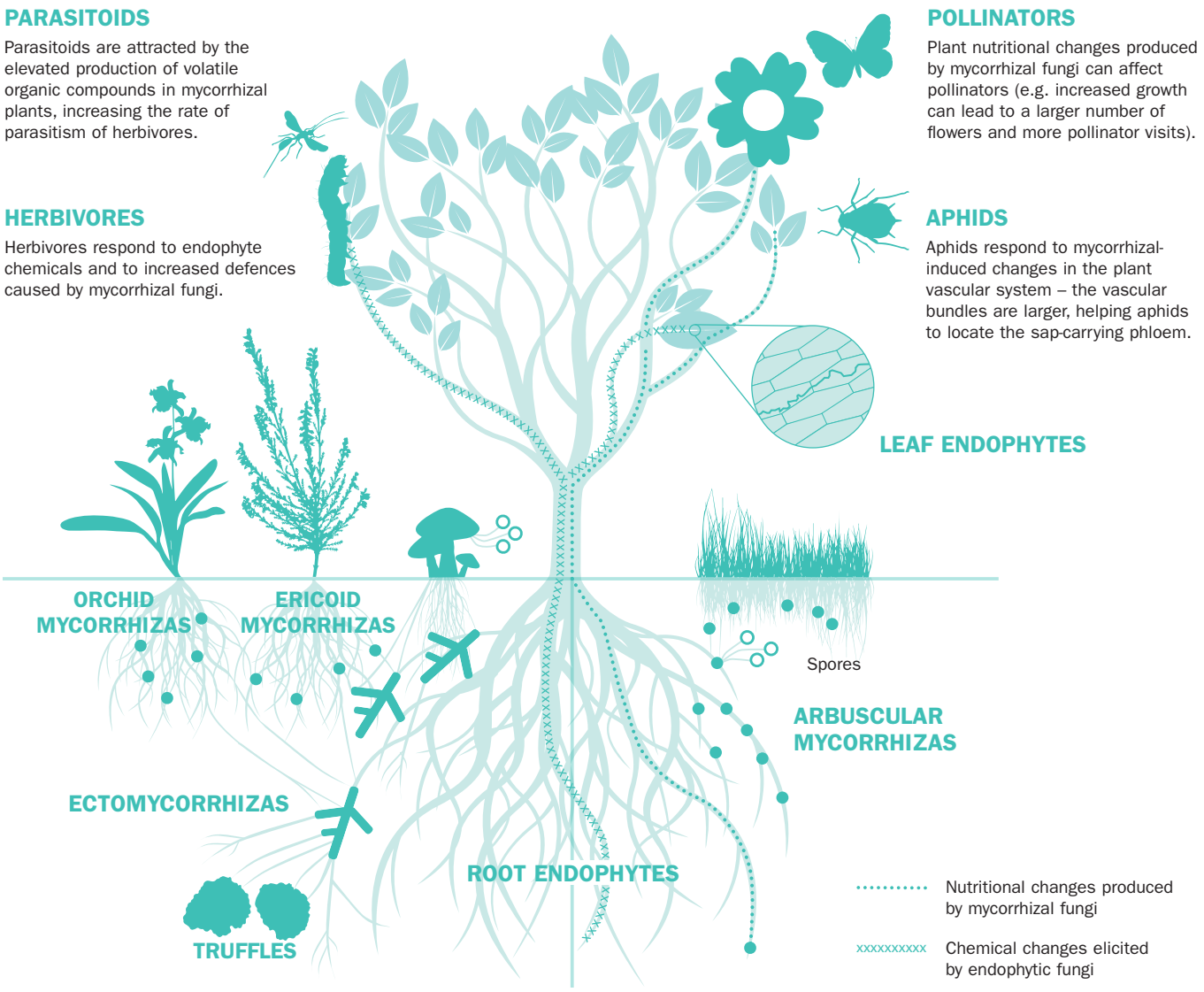
Endomycorrhizas are subdivided into arbuscular mycorrhizas (forming tree-like and/or coiled structures within root cells), ericoid mycorrhizas (forming coils within root cells in members of the heather family, the Ericaceae), and orchid mycorrhizas (forming coils within root cells of orchids) (see Box 1). Approximately 80% of plant species from across the plant tree of life have interactions with arbuscular mycorrhizal fungi (e.g. most food crops, as well as grasses, herbs and trees like junipers (*Juniperus* spp.), maple (*Acer* spp.), apple (*Malus* spp.) and cherry (*Prunus* spp.)). In contrast, the other two groups of endomycorrhizas are plant–fungal associations specific to one plant family each (Ericaceae and Orchidaceae). The fungi forming these different relationships are specialised in different roles in the different ecosystems in which they occur, helping the plants they associate with to thrive (see Boxes 2 and 3).

THE FOUNDATIONS OF TERRESTRIAL ECOSYSTEMS

It is now known that mycorrhizal fungi provide a number of key benefits to terrestrial ecosystems, including: (i) enhanced nutrient uptake, by provisioning plants with mineral nutrients from soil; (ii) soil structure, through the formation of soil aggregates and pores; and (iii) carbon sequestration, acting as sinks for plant carbon and slowing down decomposition by competing with free-living decomposer organisms in soil for organic nitrogen, known as the Gadgil Effect[18–21]. Another benefit of the mycorrhizal association is that the enhanced acquisition of resources by mycorrhizal plants leads to larger external structures (such as flowers), increasing the attractiveness of plants to pollinators[22] (see Figure 1).

Ectomycorrhizal fungi include some well-known edible species such as chanterelles (*Cantharellus* spp.), truffles (*Tuber* spp.), milkcaps (*Lactarius* spp.) and boletes (*Boletus* spp.), and all of them are specialised in the

FIGURE 1: INTERACTIONS ABOVE AND BELOW GROUND



uptake of inorganic and organic nitrogen – often the most limiting nutrient in temperate and boreal forests. Crucially, ectomycorrhizas are known to mediate ecosystem processes such as carbon storage. In fact, ecosystems dominated by ectomycorrhizal plants contain 70% more carbon per unit of nitrogen than ecosystems dominated by arbuscular mycorrhizal plants[19]. They are also key players in nutrient cycling: in exchange for 15% of plant carbon, they provide water and up to 80% of the soil nitrogen needed by the plant[16,23]. Overall, ectomycorrhizal fungi are directly involved in plant nutrition, growth and survival[24–26].

PLANT PROTECTION – FUNGAL 'BODYGUARDS'

Arbuscular mycorrhizal fungi (see Table 1) and fungal endophytes have another important interaction with plants and that is providing plants with increased resistance to plant pests and diseases. They are therefore often described as fungal 'bodyguards'[27].

Arbuscular mycorrhizal fungi are specialised in the uptake of phosphorus from the soil[2] and have a major role in the regulation of plant diversity[16,28,29]. Moreover, they can alter the chemical composition of their plant host, including increasing levels of plant chemical defences against insect herbivores[30] (see Figure 1).

This has the effect of reducing the performance of generalist 'chewing' insects while increasing that of 'sucking' specialists, which are more attuned to their host chemistry[31]. These fungi also change the release of volatile compounds from the leaves, which attract organisms higher up the food chain resulting in increased parasitism rates of herbivores[32] (see Figure 1).

Endophytic fungi can also play an important role in plant defences. For example, fungal endophytes in grasses and herbs produce an array of chemicals, some of which are antagonistic to insect herbivores[33–35]. Endophytes can also produce plant hormones, regulating plant gene expression to alter chemical pathways in the plants[30]. Recent research shows that insect-killing fungi (entomopathogens), can also exist as endophytes in both grasses and other herbaceous plants, providing a novel method of plant protection against pests and diseases[36].

BENEFITS TO AGRICULTURE

Endophytes and mycorrhizal fungi have the potential to improve the sustainability of agriculture by reducing the need for costly and environmentally damaging chemical inputs such as fertilisers and pesticides – the fungi enhance nutrient uptake by crops and increase resilience to environmental stresses[37,38]. Seeds can be coated with fungi to inoculate the germinating plant, which allows the beneficial interaction to begin as soon as the plant germinates.

Methods for large-scale production and seed-coating for arbuscular mycorrhizal fungi have been developed[39–41] to make their application in horticulture and agriculture cheaper and more reliable for crops with high mycorrhizal dependence, such as corn and soybeans. For instance, inoculation with propagules of arbuscular mycorrhizal fungi led to significant yield increase in the globally important crop cassava[42]. The fungus facilitates phosphate uptake from the low available levels in tropical soils – it does this by releasing carbon-rich compounds that stimulate microbial activity (especially phosphate-solubilising bacteria) in the surrounding soil[43] and by greatly increasing a plant's root absorptive network through elongation and branching of hyphae.

Fungal endophytes, applied even in small amounts as a seed treatment (e.g. 500 mg per hectare), have also been shown to provide significant advantages, including systemic resistance to diseases on a wide variety of monocot and dicot crops[44]. However, much of the potential remains untapped, providing a significant resource for future development. Selecting endophytes for crop improvement is a challenge because the diversity of microorganisms associated with any plant (the microbiome diversity) is huge, and because the roles of endophytes are not yet fully understood. However, endophytic fungi identified as harmful to insect pests and those able to enhance plant tolerance to elevated temperature and salinity[36] are significant potential resources.

Crop wild relatives (CWR, which broadly speaking are the cousins of crops and the ancestral species from which our current crops have evolved/are derived) offer potential in the hunt for fungi that may provide benefits to crops. Undomesticated relatives of the target crop, sampled from the wild, are a suitable source of endophytes because they are locally adapted to the niche from which they were taken and are closely related to the target crop. Their fungi are also likely to show high compatibility when applied as crop treatments. Many of the fungal endophytes found in CWRs are poorly studied microorganisms compared with the better known mycorrhizal fungi; there is therefore untapped potential that could lead to the discovery of new fungal species and further benefits for crops[46]. A 'pipeline' approach to integrated agricultural practice has been proposed[38] that involves sampling endophytes from CWRs, selection of focal taxa, field trials, and then scaling-up for agriculture (see Figure 2).

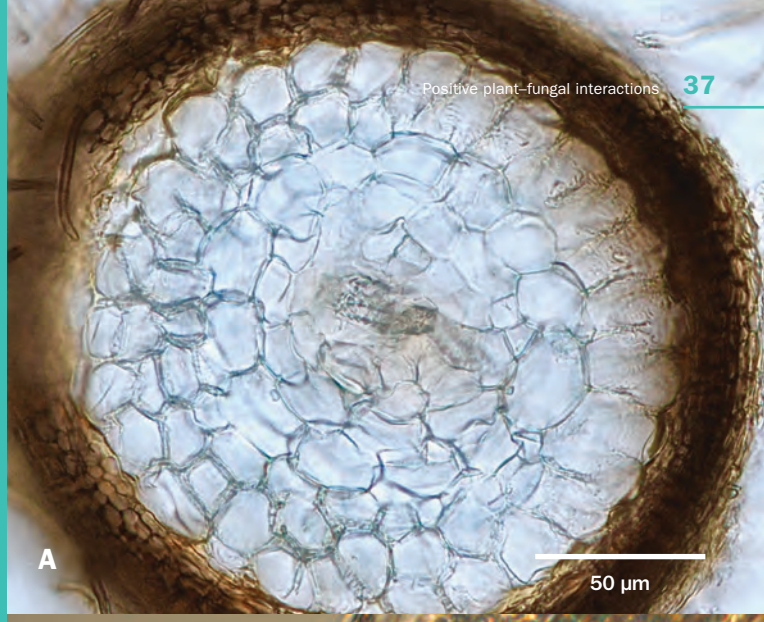
TABLE 1: MAIN TYPES OF MYCORRHIZAL FUNGI AND THEIR PLANT PARTNERS

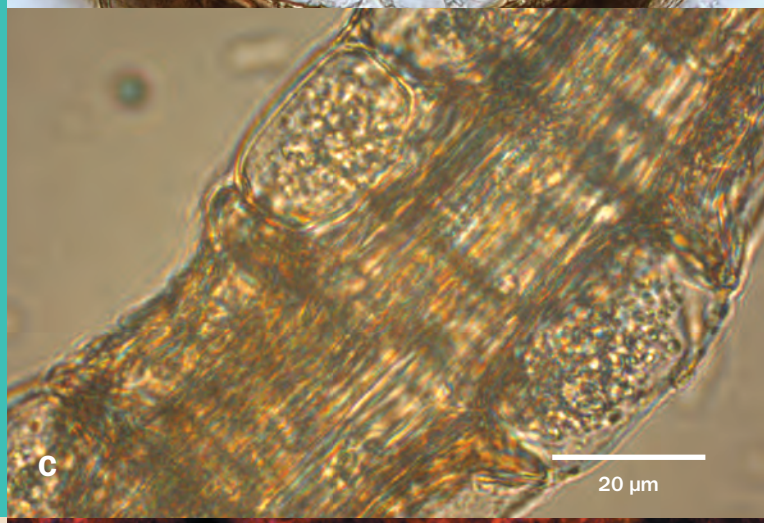
MYCORRHIZAL TYPE	PLANT PARTNER	FUNGAL PARTNER	MAIN ECOSYSTEMS
Ectomycorrhizal fungi	2.2% of plant species, especially woody species; Pinaceae (e.g. pine, spruce, fir, larch) and angiosperms (e.g. beech, oak, chestnut, hazelnut, rockrose)	20,000 Basidiomycota and Ascomycota species	Temperate, boreal, mediterranean, and some tropical forests
Arbuscular mycorrhizal fungi	78% of plant species; Herbs, shrubs, trees, liverworts, hornworts, lycopods and ferns	300–1,600 Mucoromycota (Glomeromycotina) species	Tropical and temperate forests, grasslands, savannas, shrublands, deserts, agricultural crops
Ericoid mycorrhizal fungi	1.5% of plant species; Ericaceae (e.g. heather, rhododendron, blueberry) and liverworts	>150 Ascomycota and some Basidiomycota species	Heathlands, tundra, boreal and temperate forests
Orchid mycorrhizal fungi	10% of plant species; Orchidaceae (orchids)	25,000 Basidiomycota and some Ascomycota species	Tropical, temperate, mediterranean

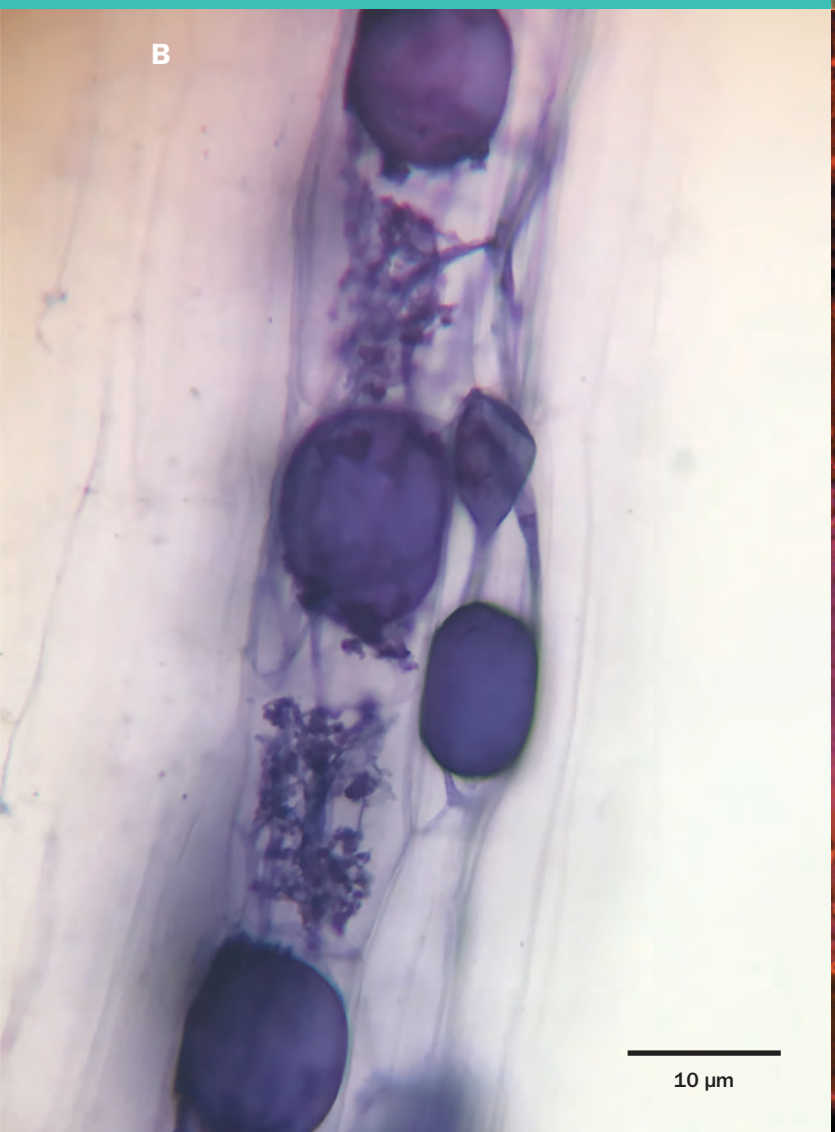
[Information extended from [15,16,55]]

BOX 1: FUNCTIONAL DIVERSITY OF MYCORRHIZAL FUNGI

Based on the groups of plants and fungi that form these nutritional partnerships and the extent of fungal penetration into roots, mycorrhizas are generally classified into four main types: ectomycorrhizas, arbuscular mycorrhizas, ericoid mycorrhizas and orchid mycorrhizas[2]. In ectomycorrhizas **(A)**, the fungal filaments envelop the fine roots of the plant forming a sheath of fungal tissue. They also form what is called the Hartig net, a network of hyphae that runs in between the root cortical cells to facilitate nutrient exchange between the fungus and plant. In arbuscular mycorrhizas **(B)**, the fungal filaments run in parallel to the endodermis inside the root cortex, forming tree-like structures (arbuscules) and/or vesicles penetrating plant cell walls but not cell membranes. In ericoid mycorrhizas **(C)**, fungal filaments penetrate root epidermal cell walls forming coils, while in orchid mycorrhizas **(D)**, fungal filaments form coils called pelotons.







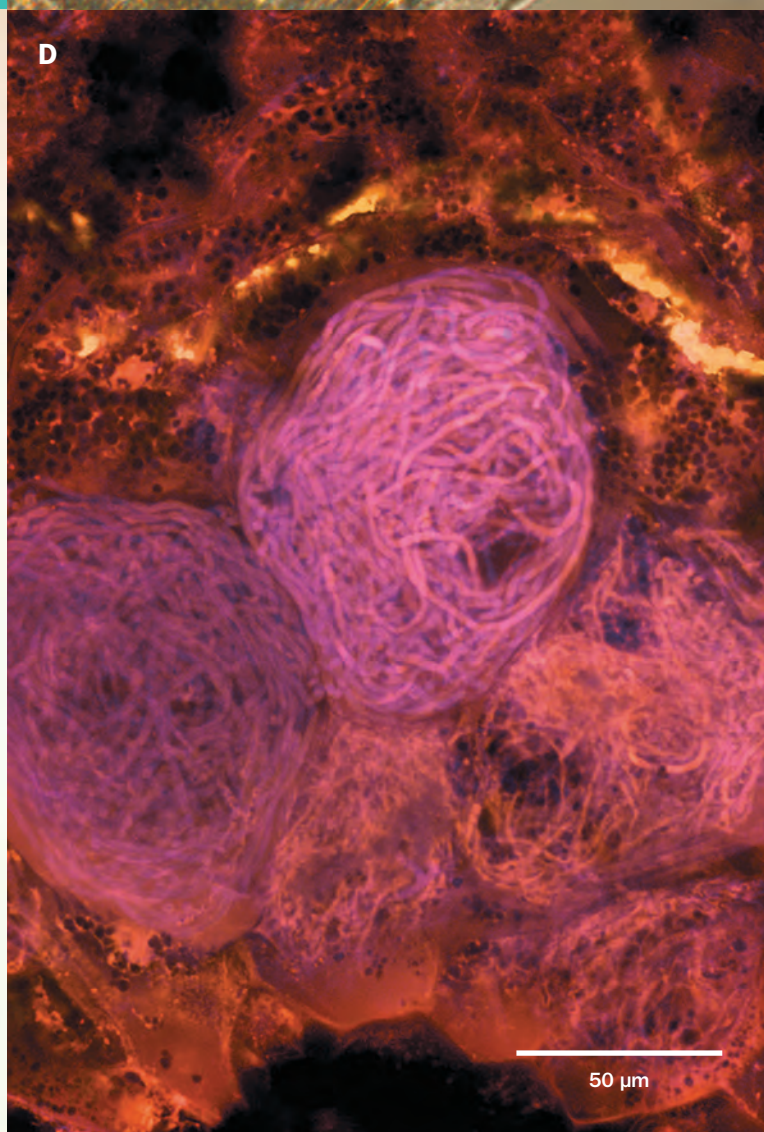
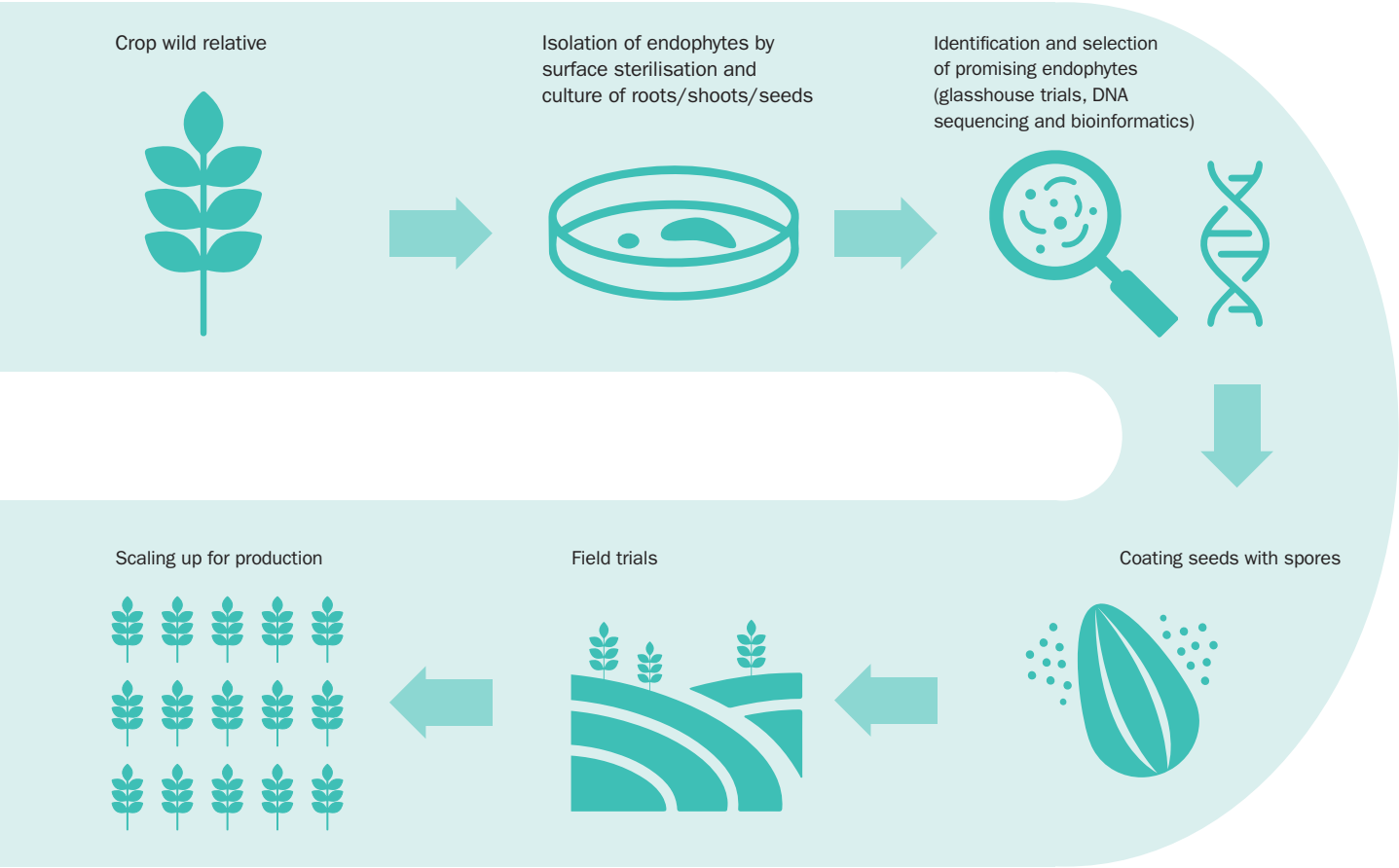


FIGURE 2: PIPELINE FOR ENDOPHYTE DISCOVERY AND APPLICATION

The fungal endophytes of crop wild relatives are relatively poorly studied and may hold the potential to provide benefits to crops. A pipeline approach can help to accelerate the discovery of useful endophytes. Endophytic fungi are isolated from crop wild relatives, cultured *in vitro* for identification and later scaled up for seed-coating and field trials. [Adapted from [38]]



RESPONSE TO GLOBAL CHANGE

In the face of global environmental change, endophytes and mycorrhizas can act as useful tools in helping plants to respond to stresses such as increased temperature and drought. For example, interaction with these fungi can result in increased tolerance to drought and salinity[16,47–49]. A meta-analysis of 434 studies has demonstrated that the presence of endophytic and mycorrhizal fungi can enhance plant biomass under drought conditions[50] by either decreasing water consumption or by increasing water absorption and mobilising water from deeper layers of soil (in the case of mycorrhizas)[51,52]. An innovative study has shown that plants inoculated with liverworts harbouring mycorrhizal fungi can cope better with the effects of flooding[53].

Environmental stress trials are demonstrating that endophytes may also be useful ameliorators of the effects of heat and drought stress for some crops; including grasses, wheat, sweetcorn, cotton and mung bean[45,54]. Advances in mycorrhizal and endophyte agricultural applications therefore have the potential to translate into improved food security, environmental sustainability and increased production revenues.

As global change continues to affect ecosystems and agricultural systems worldwide, the beneficial interactions of plant–fungal symbioses provide resilience and the opportunity to survive and adapt.

SYMBIOTIC FUNGI HAVE THE POTENTIAL TO IMPROVE GLOBAL FOOD SECURITY

BOX 2: ORCHID MYCORRHIZAS

Orchids, representing around 7% of plant species, are dependent on mycorrhizal fungi for germination and survival. Orchid seeds lack food reserves, so they rely on orchid mycorrhizal fungi for both carbon and nutrients during germination and early development[59–61]. The orchid mycorrhizal fungi (see Table 1 and Box 1) also support further growth and successful orchid establishment[62–64]. Orchids are more threatened than any other flowering plant family. Culturing and identifying orchid mycorrhizal fungi is therefore critical, to augment populations in the wild. This involves the use of mycorrhizal fungi to germinate orchid seeds and produce seedlings that can be reintroduced into the wild[64,65].

BOX 3: RESTORATION OF HEATHLANDS

Ericoid mycorrhizal fungi (see Table 1 and Box 1) colonise the root cortical cells of Ericaceae (e.g. heathers, blueberries, cranberries) and extend into the soil, unlocking nutrients for their host plants in exchange for sugars. They are diverse, globally distributed and play a major role in carbon and nutrient cycling in ecosystems with harsh soil environments, such as heathlands, tundra and boreal forests[56]. Heathlands, where nitrogen and phosphorus are extremely limited, are habitats of global conservation importance. By associating with ericoid mycorrhizal fungi in these challenging environments, ericaceous plants can access organic forms of nitrogen, allowing them to bypass competition for inorganic nitrogen[57]. Recent research demonstrated a nutritionally mutualistic symbiosis between a non-vascular plant (a liverwort) and an ericoid mycorrhizal fungus[58], opening up the possibility of using mycorrhizal fungi hosted by non-vascular plants in threatened lowland heathland restoration to facilitate heather growth and resilience[53].

FUNGAL GENOMES: EXPLORING, UNDERSTANDING AND UTILISING THEIR DIVERSITY

How many whole fungal genomes have been sequenced to date? How is this information being used to enhance our insights into medicine and climate change resilience and to find new fungi for use in everyday life, from food to antibiotics and biofuels?

stateoftheworldsfungi.org/2018/fungal-genomes.html

WHOLE GENOMES HAVE BEEN SEQUENCED FOR OVER

1,500

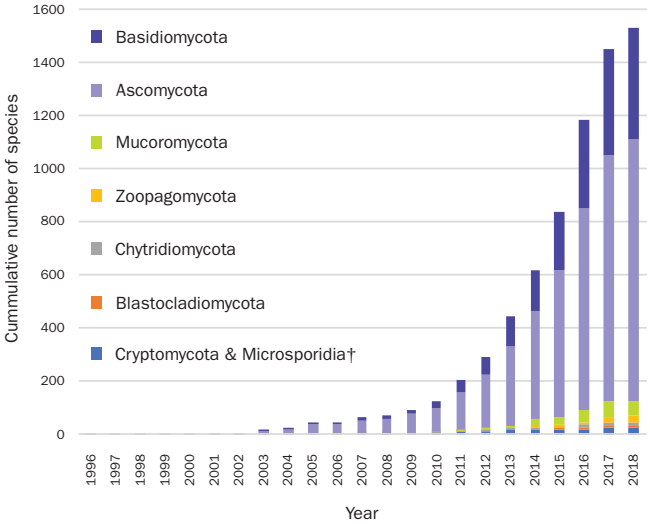
SPECIES OF FUNGI, MORE THAN THE NUMBER SEQUENCED FOR PLANT AND ANIMAL SPECIES COMBINED

THE GENOMES OF FUNGI HAVE LONG BEEN OF INTEREST TO GENETICISTS BECAUSE MANY SPECIES ARE QUICK AND EASY TO GROW, THEIR DNA CAN BE EASILY MANIPULATED, AND BECAUSE MANY OF THEIR ESSENTIAL CELL PROCESSES ARE THE SAME AS IN ALL EUKARYOTES*, INCLUDING HUMANS.

Indeed, some of the earliest insights into how DNA encodes the information needed to build life came from research on the fungus *Neurospora crassa*[1]. More recent studies using baker's yeast (*Saccharomyces cerevisiae*) and fission yeast (*Schizosaccharomyces pombe*) have led to many further breakthroughs in our understanding of human biology and disease[2,3] (see Box 1 and Chapter 4). In this chapter, we review the current status of our knowledge of fungal DNA and how this is being utilised to address some of the most pressing challenges facing humanity, such as climate change, food security and human health[4–8].

FIGURE 1: CUMULATIVE NUMBER OF FUNGAL SPECIES WITH WHOLE-GENOME SEQUENCES

[Data collated from online genome databases including NCBI Genome database (ncbi.nlm.nih.gov/genome), JGI Genome Portal: MycoCosm (genome.jgi.doe.gov/fungi), and EnsembleFungi (fungi.ensembl.org)]



† The current fungal status of species belonging to Cryptomycota and Microsporidia is still debated by some mycologists as they possess some characters that suggest they fall outside Kingdom Fungi. However, increasing amounts of genomic data support the inclusion of these phyla within Kingdom Fungi (see Chapter 2: Box 2).

WHOLE-GENOME SEQUENCING

Baker's yeast was the first eukaryote to have its whole genome sequenced (published in 1996[9]). Since then, the number of whole-genome sequences available for fungi has risen exponentially (see Figure 1). This has been driven by several factors, including: (i) rapid advances in DNA sequencing technologies; (ii) the drop in sequencing costs; (iii) the typically small size of fungal genomes compared with other eukaryotes (see Box 2); and (iv) several large-scale sequencing initiatives (e.g. the *Fungal Genome Initiative* by the Broad Institute[10] and projects like the *1000 Fungal Genomes*[11,12] and the *Mycorrhizal Genomics Initiative*[13] from the US Department of Energy Joint Genome Institute (JGI)).

Currently there are more whole-genome sequences for species of fungi than for plants and animals combined. By 31 March 2018, the number of fungal species with publicly available whole-genome sequences was 1,532 (most available online in JGI's MycoCosm[14]). This is in comparison to just 326 plant and 868 animal species with whole genome sequences available in the National Center for Biotechnology Information (NCBI) genome database[15]. However these fungal data still represent just a tiny fraction of the estimated 2.2 to 3.8 million species[16]. Most data come from species in the phyla Ascomycota and Basidiomycota (see Figure 1), which is hardly surprising since together they contain >90% of the currently described species[17] (see Chapter 1). Nevertheless, species with whole-genome sequences also include representatives across the fungal tree of life, with data for species from all eight phyla (see Figure 1) and all 12 subphyla[18,19].

In addition to ensuring full coverage across the spectrum of fungal diversity, many other factors have been important in driving the choice of species for sequencing. The insights that can arise from a knowledge of fungal genomes can be applied to many different challenges, as we now describe.

1. INSIGHTS THAT ENHANCE OUR UNDERSTANDING OF FUNGAL DISEASES AND HOW TO TREAT THEM

Applications in medicine and human health

Many of the first fungal species sequenced were those of medical importance, including *Candida albicans* – the most commonly encountered human fungal pathogen, causing, for example, skin and mucosal infections such as nappy rash and thrush[20]. Whole-genome sequences have since been generated for over 100 additional fungal pathogens of humans. They include genome sequences for the top ten invasive fungal species, such as *Pneumocystis jirovecii*, which causes a type of pneumonia with mortality rates that can reach 80% in immunocompromised patients[21]. Together it is estimated that these ten species may be responsible for more human deaths each year than are caused by either tuberculosis or malaria[21].

The emerging knowledge of the underpinning genes and metabolic pathways is also proving to be invaluable for designing effective therapies that target the fungus while minimising toxic side effects in humans[22], and in the search for new antibiotics and other bioactive compounds with potential as new pharmaceuticals[23].

* Eukaryotes comprise any organism that packages the bulk of its DNA into chromosomes located within a membrane-bound nucleus. Eukaryotes include animals, fungi, plants and a huge diversity of single-celled organisms that are loosely referred to as protists. Eukaryotes are distinct from prokaryotes, which include Bacteria and Archaea.

BOX 1: FUNGAL GENOMES AS GATEWAYS TO UNDERSTANDING HUMAN BIOLOGY AND DISEASE

Fungi, in particular the unicellular yeasts such as baker's yeast (*Saccharomyces cerevisiae*) and fission yeast (*Schizosaccharomyces pombe*), have been hugely important for understanding many aspects of human biology. This is because many of the genes involved in regulating molecular, metabolic and cellular processes in humans have equivalent genes in these yeasts[2,40]. They can therefore be used as powerful models to shed light on a diverse range of biological processes and on how errors in these genes and processes lead to diseases.

The study of genes that are involved in controlling when cells divide in *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* has been pivotal in revealing how the cell cycle is regulated at the genomic level. Such discoveries have pioneered the development of a diverse array of treatments for cancer that are widely used today.

Saccharomyces cerevisiae was recently used to uncover some of the molecular processes underpinning ageing and longevity. Given the high similarity of these processes in yeast and humans, these findings are now being explored to identify potential features of the genome that can be used to focus the development of new approaches for extending the lifespans of humans[41].

As several major drugs have been shown to hit the same gene targets and elicit the same responses in *Saccharomyces cerevisiae* as they do in humans, this yeast is currently being used as a living test tube to test the efficacy of possible therapeutic toxins in the treatment of Parkinson's disease[3].

Cells of the fission yeast *Schizosaccharomyces pombe*[2]

In addition, the increasing availability of multiple genome sequences for different strains of the same species is providing insights into the rapid genomic evolution that can occur during disease progression and treatment. This enables the development of rapid diagnostic tools and identification of drug resistance and hence the delivery of tailor-made treatments for patients[24].

In the field of public health, recent analysis of genomic data from studies of the gut microbiome (the sum of all the microbes such as bacteria and fungi that live in the gut) suggests that changes in the abundance of specific fungi and their interactions with gut bacteria may be associated with high fat diets and may therefore play an important role in influencing the risk of developing obesity and obesity-related disorders such as diabetes[25]. One of the fungi involved is *Aspergillus terreus*, which produces lovastatin, the cholesterol-reducing chemical (see Chapter 4). These new insights, which highlight the importance of fungi in the microbiome, promise to develop into an active research field where genomic data will have a significant impact by enabling, for example, the rapid identification of which fungal species are key to maintaining a functional gut microbiome.

Applications in plant pathology

A recent analysis of whole-genome data for over 500 pathogenic species included some of the most devastating plant fungal pathogens, such as the rice blast fungus *Pyricularia oryzae* (syn. *Magnaporthe oryzae*)[26]. While this fungus causes devastation to many grass crops, including wheat and barley, it is most notorious for its impact on rice, where it is capable of destroying quantities of rice that would otherwise feed hundreds of millions of people each year[27]. The insights gained from these genomic data are starting to enhance understanding in areas such as: (i) how and why pathogenicity evolves in some species and not others; (ii) the genomic mechanisms underpinning the evolution of fungicide resistance; and (iii) how to develop diagnostic tools that enable rapid and effective responses to disease outbreaks and minimise impact on food security and ecosystems[7,28,29]. For example, a recent study comparing the whole-genome sequences of over 70 individuals of the rice blast fungus from across the globe is shedding light on how this devastating fungus evolves and spreads between different host plant species. Such understanding is key to helping predict the emergence and likely spread of new diseases caused by this fungus, and ensuring that appropriate plant health surveillance schemes are in place to limit impact on food security[30].

2. INSIGHTS INTO THE ROLE OF FUNGI IN ECOSYSTEM FUNCTIONING AND RESILIENCE

Many species have been chosen for genome sequencing to enhance understanding of how fungi impact and influence ecosystem functioning. Species receiving particular attention are those that form mutualistic relationships with plants through mycorrhizal associations (see Chapter 5), given their importance in influencing plant health and resilience, the flow of nutrients through ecosystems and global carbon sequestration dynamics[e.g. 31–33] (see also Chapter 5). They include species such as the basidiomycete *Pisolithus tinctorius*, which forms mycorrhizal associations with pine species and is used in commercial forestry to inoculate plantations in order to enhance their growth and health. The growing volumes of genomic data are opening up new opportunities to explore how mycorrhizal fungi can be manipulated to enhance plant health, environmental sustainability and ecosystem resilience in the face of environmental change[34].

While mycorrhizal species have been targeted for whole-genome sequencing[13], the genomes of endophytic fungi (i.e. those that grow inside plants – see Chapter 5) have received less attention. However, some endophytes, particularly those of crop species, are attracting genomic research to shed light on how they interact and influence their host plant genome[35,36]. Such understanding is anticipated to lead to the development of novel approaches for more sustainable agricultural systems[37], as it could contribute to relieving farmers' reliance on pesticides, fertilisers and irrigation (see Chapter 5).

3. INSIGHTS THAT CONTRIBUTE TO SOLVING SOME OF THE MAJOR CHALLENGES FACING HUMANITY

Fungi are already widely used in industry for the large-scale production of a diverse array of chemicals (e.g. food products, existing antibiotics, pharmaceuticals – see Chapter 4), yet there remains much fungal diversity that is unexplored.

In recent years, the exploration of fungal diversity for its potential exploitation has been enhanced by the growing availability of whole-genome sequences. Such data are providing insights into the diversity of genes, enzymes and biochemical pathways that fungi use for their survival, which in turn are leading to novel ways of using fungi to solve major challenges facing humanity (see Boxes 3 and 4).

INTO THE FUTURE – NOVEL APPROACHES TO INCREASE OUR UNDERSTANDING OF FUNGAL GENOME DIVERSITY, EVOLUTION AND UTILISATION

In the future, fungal genomics is likely to continue its exponential trajectory, particularly given recent advances in genomic sequencing technologies and bioinformatic (analysis) tools. These include the increasing use of novel sequencing approaches that can generate gigabases (1,000,000,000 bp) to terabases (1,000,000,000,000 bp) of data in a single experiment. Nevertheless, there are still many challenges since current methods rely on being able to obtain sufficient quantities of DNA for sequencing – this is an issue for many fungi that currently can't be cultured. Yet even these hurdles seem likely to be overcome in the next few years as methods that can sequence whole fungal genomes from minimal amounts of material, and possibly even from single cells, are being developed[38,39].

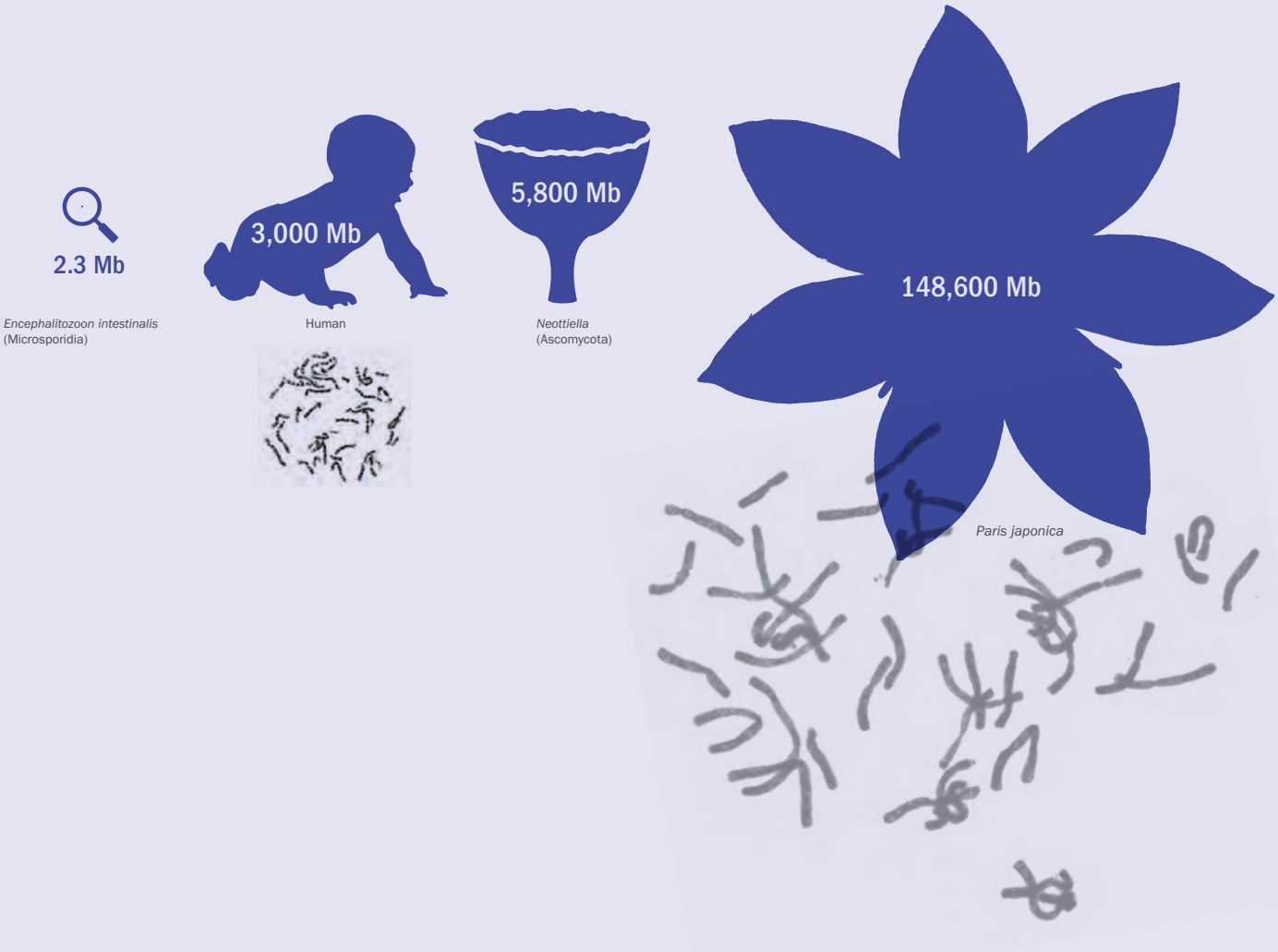
Such advances will not only increase our genomic knowledge of the many fungi yet to be even described (see Chapter 1 and Chapter 2: Box 4) but will also increase the speed at which data are generated so there is more time to explore and utilise the remarkable evolutionary diversity and functional complexity of fungi.

BOX 2: THE SIZE OF FUNGAL GENOMES – SMALL BUT DIVERSE

One of the genomic features that makes fungi particularly amenable to whole-genome sequencing is their small genome size (i.e. the total amount of DNA that makes up a genome). This means the cost of generating sequence data and the time needed to assemble them into a whole genome are typically lower compared with other eukaryotic groups that are characterised by larger genomes. For example, the average genome size of fungi is just 44 Mb (megabases)[42], compared with c. 3,400 Mb for mammals and c. 5,020 Mb for flowering plants[43,44].

Fungi are also notable as they include the species with the smallest genome so far reported for any eukaryote. This species is the obligate intracellular parasite *Encephalitozoon intestinalis*, whose genome comprises just 2.3 Mb of DNA – i.e. over 1000x smaller than the human genome. The sequencing of 23 microsporidian fungi has been instrumental in uncovering the genomic processes and dynamics leading to such highly compact genomes, with only c. 2,000 genes and minimal repetitive and intergenic DNA in some species[45–47]. In addition, since all microsporidians are obligate parasites, their genomes are being used as models for studying host–parasite interactions[48].

At the upper end, the largest genome measured without sequencing for any fungus is 5,800 Mb, found in *Neottiella*, an ascomycete that parasitises mosses[49,50]. Yet the largest fungal genome sequenced so far is just 335.7 Mb, from the rust fungus *Melampsora allii-populina*. Given that whole-genome sequences have been generated from animals and plants whose genomes are c. 95x bigger (i.e. the Mexican axolotl (*Ambystoma mexicanum*)[51] and the sugar cone pine (*Pinus lambertiana*)[52]), there is no reason why similar data cannot be generated for species that encompass the full 2,500-fold range of genome sizes in fungi.



Genome sizes vary over 64,000-fold across eukaryotes, from the smallest found in the fungus *Encephalitozoon intestinalis* to the largest in the flowering plant *Paris japonica*. (The 46 chromosomes of a human and the 40 chromosomes of *P. japonica* are shown at the same magnification.)

BOX 3: HARNESSING FUNGI TO MAKE SUSTAINABLE BIOFUELS OF THE FUTURE

The unique ability of fungi to break down the molecules in plant cell walls (e.g. pectin, cellulose, hemicellulose and lignin) is already exploited in the synthesis of current biofuels. Nevertheless, issues associated with sustainability and cost are leading scientists to search for new solutions. The discovery that some endophytic fungi can convert lignocellulose directly into chemicals with similar properties to diesel (so-called 'mycodiesel') has raised the potential of utilising them to generate biofuels more economically and sustainably[53]. Consequently, genomes of numerous endophytic fungi are now being sequenced to uncover the full genomic repertoire underpinning mycodiesel production and hence design approaches for its sustainable production on an industrial scale[8,54,55].

Daldinia eschscholzii – one of the endophytic fungi being sequenced to explore its potential to produce mycodiesel.

BOX 4: UTILISING THE ABILITY OF FUNGI TO CLEAN UP THE ENVIRONMENT

Fungi are remarkable in the diversity of substrates they use as food sources. This has led to a growing list of species being used for the bioremediation of environments contaminated by pollutants such as oil spills and toxic chemicals (e.g. TNT, sarin nerve gas, pesticides)[56,57]. Nevertheless, their use for cleaning up sites contaminated by acidic radioactive waste is only just starting to be realised, following the discovery of a fungus (*Rhodotorula taiwanensis*) that not only grows in extremely acidic conditions (pH 2.3) but can also tolerate such high levels of gamma radiation that it is one of the most radiation-resistant organisms on Earth[58]. Its genome has recently been sequenced to decipher the genomic machinery enabling it to survive and to determine how this can be utilised to develop new ways to clean up soils contaminated by radioactive waste[58].

Similar approaches are also proposed in a recent study that has discovered a fungus (*Aspergillus tubingensis*) capable of breaking down plastics such as polyester polyurethane (used in a wide diversity of products such as refrigerator insulation and synthetic leather) in weeks rather than years. This ability thus has potential to be developed into one of the tools desperately needed to address the growing environmental problem of plastic waste[59].

Cells of *Rhodotorula taiwanensis* growing under high levels of chronic ionising radiation (36 Gy/h) in highly acid conditions (i.e. pH 2.3)[58].

Visualisation of a DNA sequence from part of the genome of baker's yeast (*Saccharomyces cerevisiae*) using the program DNASkittle (dnaskittle.com).

COUNTRY FOCUS: CHINA

What is the current status of knowledge of fungi in China? How many different Chinese fungal species are currently known, where are they distributed, which are most important economically, and how do they help combat the effects of desertification?

stateoftheworldsfungi.org/2018/country-focus.html

THERE ARE

1,789

EDIBLE AND

798

MEDICINAL FUNGI REPORTED FROM CHINA

ARCHAEOLOGICAL EVIDENCE INDICATES THAT THE USE OF FUNGI BY HUMANS BEGAN IN CHINA AT LEAST 6,000 YEARS AGO[1–3]. SINCE THIS TIME, FUNGI HAVE BEEN AN INTEGRAL PART OF CHINESE MEDICINE, FOOD AND CULTURE, RESULTING IN A KNOWLEDGE BASE OF FUNGI IN CHINA THAT IS PROBABLY THE BEST IN THE WORLD.

In this chapter, we describe the current knowledge of the names of Chinese fungi, their distribution, economic importance, ecological importance and conservation.

TOWARDS A CHECKLIST OF THE FUNGI OF CHINA

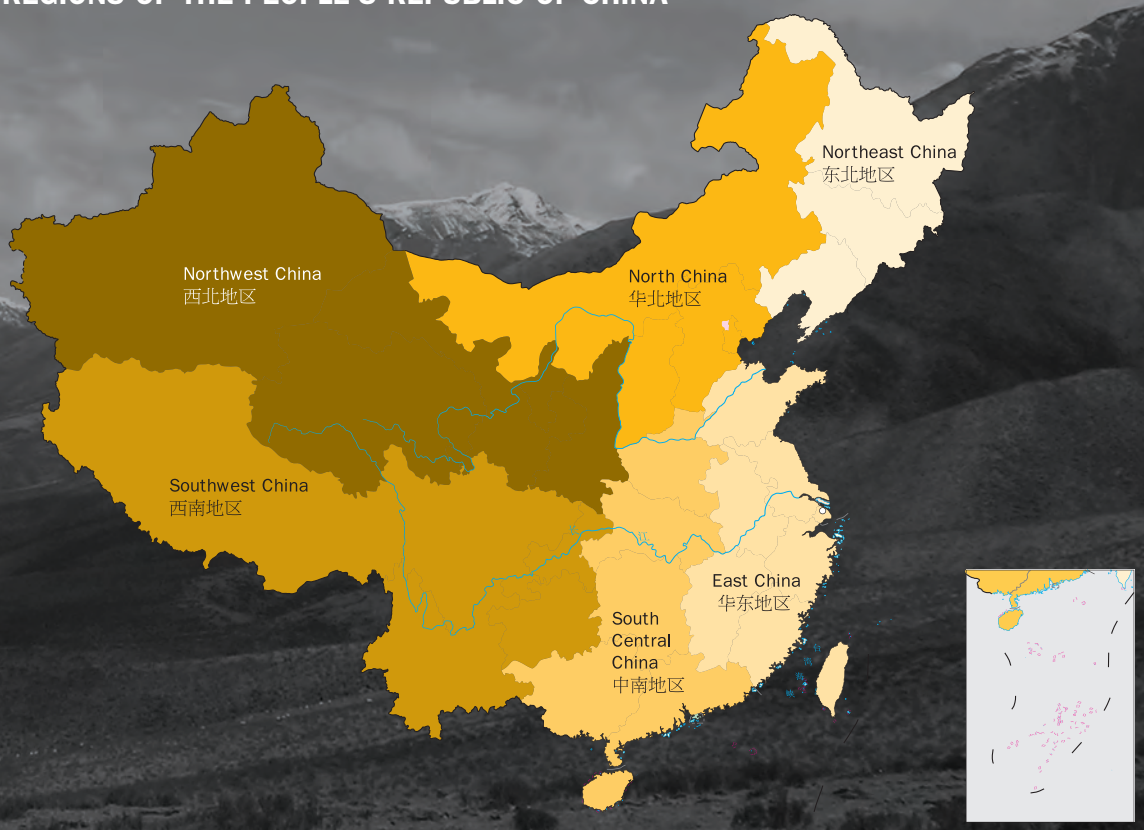
Chinese fungi and their uses were first documented in an ancient Chinese book from the second century, entitled *Shen Nong Ben Cao Jing* (*The Divine Farmer's Materia Medica*). In this book, 14 fungi are included among a total of 365 herbal medicines. The first Chinese monograph of fungi was created over 1,000 years later, in 1245, and contained descriptions of 15 species. Although the modern study of fungi was brought to China by Europeans in the mid-eighteenth century[1,2], it wasn't until the early twentieth century that Chinese authors started to publish their research on fungi in China[4]. Since then, a large amount of work has been carried out by Chinese mycologists, resulting in published studies on more than 6,700 species[5]. A suite of fungal research journals published from China have also become well-known academic journals, including *Fungal Diversity*, *Mycology* and *Mycosystema*.

With so much information being published on Chinese fungi, a major project to gather information for updating the checklist of fungal species in China was started in 2011[6]. At the time of writing this report, over 231,000 fungal records derived from over 7,200 publications since 1970 have been databased, and over 7,000 species have been compiled for publication as the third volume in the *Species Catalogue of China*.

DIVERSITY AND DISTRIBUTION OF CHINESE FUNGI

The database for the *Checklist of Fungi in China*[6] currently contains around 27,900 species and intraspecific names of fungi belonging to 15 phyla, 56 classes, 192 orders, 585 families and 3,534 genera. In addition, over 7,000 specific and intraspecific taxa have been described, and many illustrated, in the *Flora Fungorum Sinicorum* series (50 volumes so far). Based on these available fungal records, it would appear that the distribution of fungal species in China is remarkably uneven. In particular, species discovery in Northwest China (see Figure 1), which includes the provinces of Xinjiang, Qinghai, Gansu, Ningxia and Shaanxi and accounts for over 30% of the territory of the country, has yielded only 3,887 species in 759 genera of fungi (including slime moulds and oomycetes in the broad sense) despite a long period of comprehensive survey[7].

FIGURE 1: REGIONS OF THE PEOPLE'S REPUBLIC OF CHINA



In contrast, 5,056 species in 1,192 genera were recorded in the tropical regions of South Central China and Southwest China, which include the provinces of Hainan, Guangdong, Guangxi and Yunnan and account for less than 5% of the country's territory[7]. There is a significant difference between the precipitation of the two regions: Northwest China has <200 mm of rainfall per year[8], while the tropical regions of China are characterised by a warm and humid climate with up to 2,491 mm of rainfall per year[7]. It is therefore possible that climatic and geographical differences have played an important role in shaping the fungal diversity in these two regions of China. Agricultural and industrial development, and other factors such as pollution and habitat destruction, may also have had strong effects on fungal distribution – for example in central and eastern China, where fungi are less well recorded.

Southwest China is also the richest for plant and animal diversity due to its diverse ecology and favourable climate; as so many fungi are restricted to particular plants, these factors may have similarly influenced fungal diversity.

ECONOMIC IMPORTANCE OF FUNGI IN CHINA

Cultivated mushrooms have become one of the most important crops in Chinese agriculture[9], and China is the largest edible mushroom producer in the world, reaching an estimated annual yield of 38.42 million tonnes. This accounts for around 75% of the total global output, providing over 25 million jobs and generating an estimated income of ¥268.3 billion for growers in 2017[9]. The export of edible mushrooms also amounted to US$3.84 billion in 2017[10].

The history of the cultivation of fungi for food and medicines in China can be traced back to the Tang Dynasty (600–900 CE)[11]. Today, there are 1,789 edible and 798 medicinal fungi reported from China, with 561 being both edible and medicinal[6]. Over 100 species of fungi have been domesticated for cultivation and around 60% of them are commercially produced[11]. In particular, one of the most sought-after delicacies and the most difficult to cultivate, *Morchella importuna* (a black morel), has been successfully cultivated[12] and commercialised in recent years.

Mushroom cultivation plays a very important role in ecology and social development in China. It is not only important for food and nutrition, but also provides jobs and generates incomes for local communities. In rural areas, edible and medicinal fungi are grown in the traditional manner to help alleviate poverty[13]. However, this sector has attracted huge capital investment and this has accelerated its growth onto an industrial scale. More and more species are being grown in large environmental control compartments for quick, high yields and high-quality production. These include button mushroom (*Agaricus bisporus*), velvet shank (*Flammulina velutipes*), king oyster (*Pleurotus eryginii*) and shiitake (*Lentinula edodes*) among others[14].

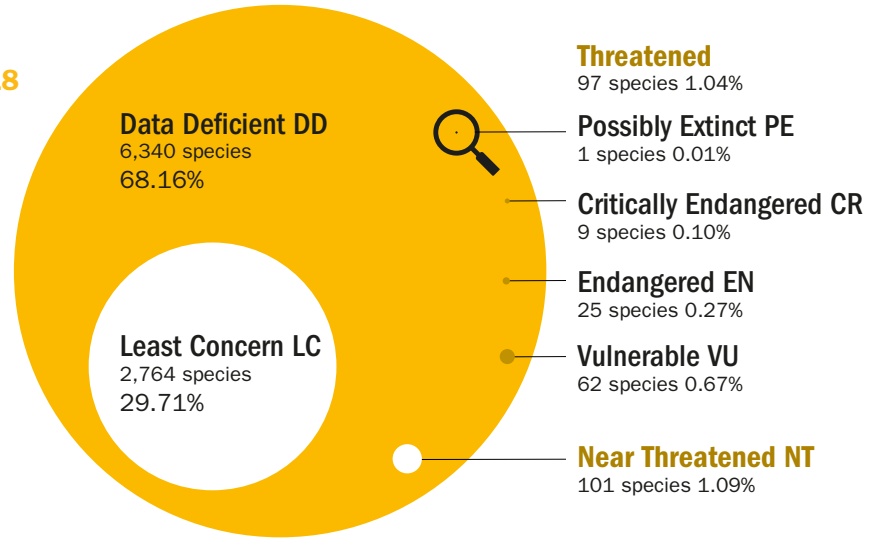
ECOLOGICAL IMPORTANCE OF LICHENS IN COMBATTING DESERTIFICATION IN CHINA

With up to 58% of the land area being classified as arid or semi-arid, nearly one-third of the land in China suffers from the effects of desertification; increased sand and dust storms are a consequence of this and also a cause of further desertification[15]. A large amount of research effort has gone into studying ways to combat this process, and traditional afforestation through planting trees and shrubs has proved to be ineffective in desert areas with annual precipitation of <200 mm[16]. In comparison, some fungi appear to thrive in these environments. For example, after a 48-year trial of afforestation in the southeast of the Tengger Desert (and since 1956 in the Shapotou area), biological soil crusts with dominant lichens largely replaced the planted shrubs in 90% of the afforestation area, developing naturally up to a thickness of 11 mm[17].

Work on desert fungi has also revealed some interesting mechanisms of drought tolerance. The fungus *Endocarpon pusillum* (Verrucariales, Ascomycota) forms a lichen that is ecologically dominant in the desert in Northwest China. Investigations indicated that this lichen is extremely drought-tolerant[18], due in part to a gene called EpANN that is expressed when the lichen encounters drought stress. Transgenic organisms generated using this gene showed stronger stress tolerance, and this work suggests that it may be possible to combat desertification using drought-resistant transgenic turf[19].

Morchella sextelata **(a black morel) has been successfully cultivated and commercialised in recent years.**

FIGURE 2: RESULT OF THE RED LIST ASSESSMENT OF MACROFUNGI IN CHINA, 2018



CONSERVATION STATUS OF FUNGI IN CHINA

With the development of the Chinese economy and associated improvements in the standard of living, market demands for fungal products in China increased significantly in the 1990s and grew even more rapidly in the beginning of the twenty-first century. Overharvesting by humans, coupled with urban expansion and environmental change, has caused significant declines in wild fungal populations. For example, the annual yield of the Chinese caterpillar fungus (*Ophiocordyceps sinensis*) is reported to have declined from more than 100 tonnes in the 1950s to 5–15 tonnes in the 1990s[20]. Similarly, the annual export volume of the pine mushroom (*Tricholoma matsutake*) dropped from more than 6,000 tonnes at its peak in 1996[21] to 1,000–1,500 tonnes in the last two years[10]. Consequently, they have been listed as threatened species under the second category of state protection in China since 1999 (State Forestry Administration and Ministry of Agriculture, 1999) – the only two fungal species to be listed.

To assess the wider threat to fungal diversity, a Red List assessment of macrofungi in China was recently carried out, led by the Ministry of Ecology and Environment and the Chinese Academy of Sciences. A total of 140 Chinese mycologists participated in the evaluation. Around 229,000 records of nearly 10,000 species of fungi, of which 3,015 were Ascomycota (two-thirds of which were lichenised species) and 6,287 Basidiomycota, were evaluated according to the International Union for the Conservation of Nature (IUCN) Red List categories and criteria (see Figure 2).

Among these species, 97 were classified as threatened, including 9 Critically Endangered (CR), 25 Endangered (EN) and 62 Vulnerable (VU). There were 101 species classified as Near Threatened (NT) and 2,764 as Least Concern (LC). No species were identified as Extinct (EX) or Extinct in the Wild (EW), but one Critically Endangered species was tagged with Possibly Extinct (PE) because the species has not been re-found since it was first described about 130 years ago. Over 68% of the total assessed species (6,340 fungi) were considered as Data Deficient (DD) due to the lack of information available for assessment.

This assessment of macrofungi in China could be regarded as the most extensive fungal Red List assessment in any country and involved a large team of mycologists. The results have implications for conservation policy and the implementation of fungal conservation measures in China. It was the first attempt at a national assessment on fungi and rigorous follow-up is now needed for the effective conservation of fungi in China.

China is a country with a 1,400-year history of the cultivation of fungi for food and medicine and an incredibly rich natural diversity of fungi. Chinese mycologists are working hard to promote the understanding and conservation of this vitally important resource, and initiatives such as the multicentre fungal collection network, the *Checklist of Fungi in China* (sharing data worldwide), and the new Red List assessment of macrofungi in China are ensuring that fungi remain at the forefront of scientific study and are conserved for the benefit of future generations.

CHINA IS A COUNTRY WITH A 1,400-YEAR HISTORY OF THE CULTIVATION OF FUNGI FOR FOOD AND MEDICINE

BOX 1: KEY REPOSITORIES FOR FUNGAL RESEARCH IN CHINA

Fungal collections have been accumulating at a rapid rate in recent years, reaching a total of one million specimens housed in several major fungaria and research institutes around China. The Fungarium of the Chinese Academy of Sciences (Herbarium Mycologicum Academiae Sinicae: HMAS) is the most comprehensive fungarium in China, holding the largest fungal collection in Asia. Currently, there are more than 520,000 specimens in this fungarium, including 2,776 types (the definitive specimens that act as standards for identifying the correct name for a fungus). The collections, gathered from all 34 provinces of China and 111 other countries and regions around the world, cover all the major groups of fungi, representing 15,000 species in 2,000 genera.

The other five major fungaria include: Kunming Institute of Botany, Chinese Academy of Sciences CAS (HKAS); Xinjiang University (XJU-NALH); Northwest A&F University (HMUABO); Guangdong Institute of Microbiology (GDGM); and Jilin Agricultural University (HMJAU), which together hold about 500,000 collections. The main collection of Southwest China, with over 160,000 specimens (including 50,000 of lichen-forming fungi) is deposited in HKAS. A few small fungaria keep collections of 8,000–9,000 specimens, for example the Alpine Fungarium, Tibet Plateau Institute of Biology (AF); Fungi Collection, Tarim University (HMUT); and Lichen Collection, Liaocheng University (LCU-L).

Amanita exitialis is the species responsible for the largest number of mushroom-associated human poisonings and fatalities in South China. Its lethal cyclic peptide toxins cannot be destroyed by cooking. (South Central China – tropical.)

BOX 2: BIODIVERSITY, ENDEMISM AND GEOGRAPHY OF THE TRUFFLE GENUS *TUBER* IN CHINA

As a result of its underground habit, *Tuber* (the important species-rich genus of truffles), was among the least studied groups of fungi until recent years, even though they are fairly common in some areas in China and around the world. DNA technology stimulated the study of this group, particularly after 2010, revealing many cryptic species previously unrecognised by morphological study alone. Based on analyses of multiple gene sequences, 12 evolving lineages worldwide were revealed in *Tuber*[22–24] and a total of 76 species have been described from China, with 70 of these found only in China[23–25]. Of the 12 defined lineages, nine are found in China, with seven of these occurring worldwide and two unique to China and Asia[22–24]. Some European species previously reported from China were found to have been misidentified; only two species, *T. anniae* and *T. maculatum* are thought to be non-native[25].

Species of *Tuber* are ectomycorrhizal (see Chapter 5) and the Chinese species are associated with a wide range of host plants, including conifers and broadleaved trees and mostly with the dominant species of temperate forest; these include pine (*Pinus* spp.), larch (*Larix* spp.), spruce (*Picea* spp.), poplar (*Populus* spp.), oak (*Quercus* spp.), chestnut (*Castanea* spp.), beech (*Fagus* spp.) and hazel (*Corylus* spp.)[23,24] and are most species-rich in the southwest. The important species, economically or ecologically, are *T. sinense*, *T. sinoaestivum*, *T. pseudohimalayense*, *T. panzhihuaense*, *T. pseudosphaerosporum*, *T. sinosphaerosporum*, *T. liyuanum*, *T. taiyuanense* and *T. xuanhuaense*[26].

Tuber sinense

Auricularia heimuer is one of the most important edible and medicinal mushrooms in China. (Northeast China – forest.)

Ophiocordyceps sinensis is a fungus that grows on the larvae of ghost moths. As it is a highly valuable traditional Chinese medicine, it has become the most important source of income in rural Tibet.

PLANT-KILLERS: FUNGAL THREATS TO ECOSYSTEMS

THE RAPID SPREAD OF FUNGAL DISEASES AROUND THE WORLD IS DAMAGING NATURAL ECOSYSTEMS

Which fungal diseases pose the greatest threats to global ecosystems? Why are these threats on the increase and what biosecurity is urgently needed to reduce their global spread?

stateoftheworldsfungi.org/2018/plant-killers.html

FUNGI AND PLANT–FUNGAL INTERACTIONS PROVIDE GREAT BENEFITS TO HUMANS. HOWEVER, THEY ALSO PROVIDE SOME OF THE GREATEST THREATS.

In *State of the World's Plants 2016*[1], we reported the devastating impacts of the top ten fungal diseases globally. These all reduce the yields of crops and are a major challenge to food security. This year, we explore the threats that fungi pose to non-crop plants and especially plants in natural ecosystems. We discuss how and why these threats emerge and their broad impact on the natural environment.

FUNGAL DISEASES AS A WORLDWIDE THREAT TO ECOSYSTEMS

The impact of fungal diseases on plants and animals is increasing worldwide[2,3], and detrimental effects on plants in natural ecosystems are an important part of this worrying global trend[4,5]. These fungal pathogens have wide-ranging effects due to the large number of species they affect directly as hosts or indirectly via ecological interactions. The impacts can be long term and can severely affect ecosystem functions such as carbon sequestration[6]. Long-established pathogens cause ongoing impacts, such as northern hemisphere species of *Armillaria* (e.g. honey fungus) and *Heterobasidion* that cause root rots of many tree species. However, much of the global increase in fungal impacts is driven by newly emerging pathogens, of which we now give some key examples (see also Boxes 1–3).

Until 2010, myrtle rust (*Austropuccinia psidii*) was mainly known as a problem in plantations of introduced plants in South America[7]. However, in 2010 it was detected in Australia where it has the potential to infect over 1,000 different native species in the Myrtaceae family, including eucalyptus (*Eucalyptus* spp.) and paperbark/tea trees (*Melaleuca* spp.)[8]. It has now escaped eradication attempts and has spread along the entire east coast, where it has had severe effects on native forests[7]. The spread of myrtle rust has continued; in 2013 it was detected in South Africa and New Caledonia, and it was found in New Zealand for the first time in 2017 (see Figure 1).

The ash dieback fungus (*Hymenoscyphus fraxineus*) is more restricted in its host range than myrtle rust, with severe effects only known from ash trees (*Fraxinus* spp.). However, ash trees are abundant in continental Europe and a key component of native woodlands. Ash dieback was first found in Poland in the early 1990s and over the subsequent years has spread rapidly east to west across Europe. However, it is not just the ash tree itself that is at risk. There are around 955 other species, including 68 fungal species, that live in association with ash[9] and are thus also under threat. A recent study has reported the presence of *H. fraxineus* on three new species outside the ash genus (but still within the same family, Oleaceae); these are *Chionanthus virginicus*, *Phillyrea angustifolia* and *Phillyrea latifolia* (N. Spence (Defra), pers. comm., 19 July 2018). It remains to be seen whether these new hosts will develop the disease or contribute to its spread.

BOX 1: DOGWOOD ANTHRACNOSE

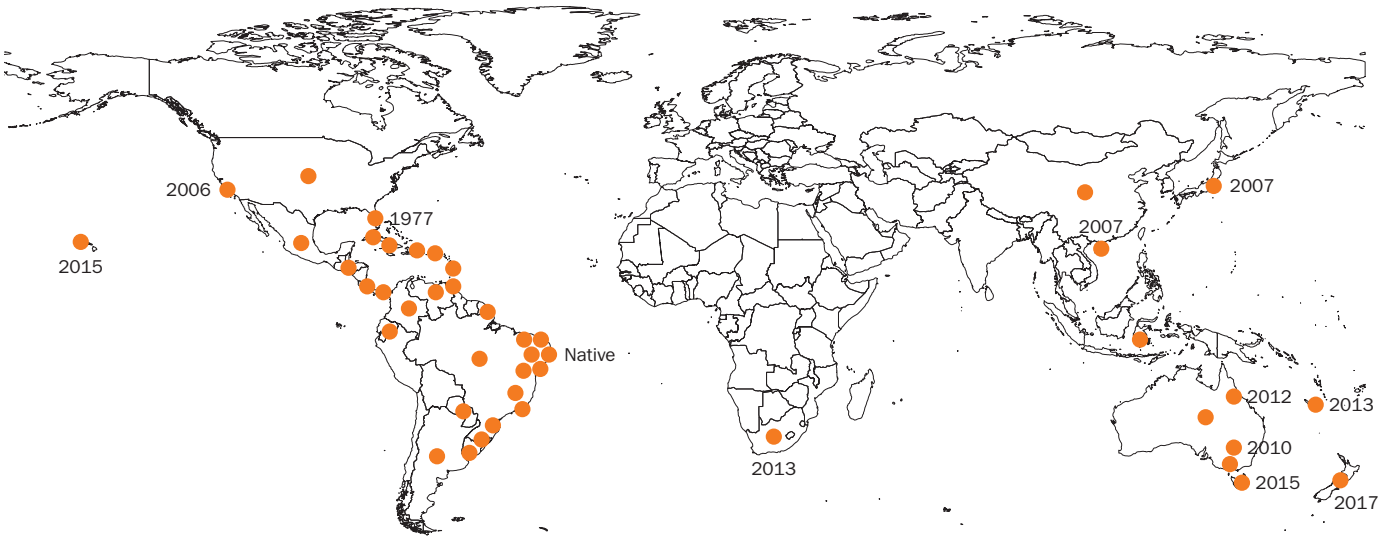
Dogwood anthracnose is a lethal disease of native dogwoods (*Cornus* spp.) in the USA and is caused by the fungus *Discula destructiva*. Dogwoods are found in the understorey of woodlands and are important for their fruits, which provide autumn food for many birds and mammals[37].

BOX 2: BEECH BARK DISEASE

Beech bark disease is caused by *Neonectria* fungal species and an insect pest. Modelling suggests that replacement of American beech (*Fagus grandifolila*) by another tree species would lead to 13% less carbon storage in plants and the forest floor after a century as compared to a healthy beech stand[38].

FIGURE 1: THE SPREAD OF MYRTLE RUST GLOBALLY

Myrtle rust (*Austropuccinia psidii*) is native in South America, from where it has spread across the globe. Each orange dot is a record of myrtle rust, with the year it was first reported shown alongside (where known). [Based on data from CABI (cabi.org) and CRC Plant Biosecurity (pbcrc.com.au)]



FUNGAL DISEASES CAN REMOVE KEYSTONE TREE SPECIES FROM ECOSYSTEMS, WITH DEVASTATING EFFECTS

BOX 3: WHITE PINE BLISTER RUST

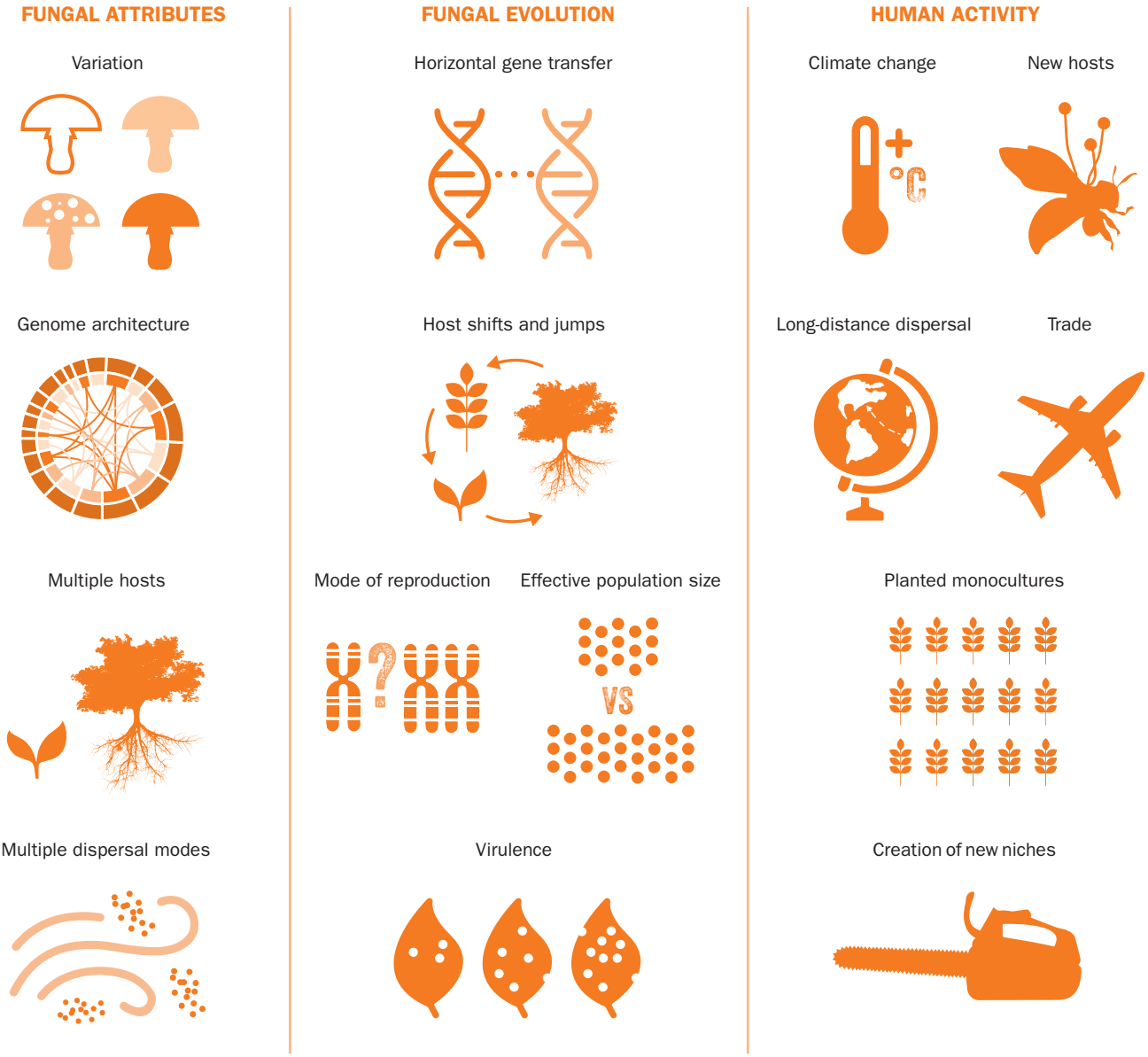
Extensive natural stands of white pines (*Pinus strobus*) can be seen in North America that are dead or dying due to white pine blister rust (*Cronartium ribicola*), with severe impacts on local ecosystems and grizzly bear habitat[39].

The fungus *Raffaelea lauricola*, which was first found in the USA in 2002, has a symbiotic relationship with the ambrosia beetle (*Xyleborus glabratus*). Together, the fungus and beetle cause laurel wilt[10] and are now devastating natural stands of redbay (*Persea borbonia*) in the southeastern USA, as well as three Critically Endangered native plant species: pondberry (*Lindera melissifolia*), pondspice (*Litsea aestivalis*) and Florida licaria (*Licaria triandra*)[10].

The long-term devastation that can be caused to ecosystems by emerging fungal diseases is demonstrated by the effects of Dutch elm disease (*Ophiostoma novo-ulmi*) in Europe and chestnut blight (*Cryphonectria parasitica*) in North America. Decades ago, these pathogens effectively eliminated keystone tree species from ecosystems and these trees have so far been unable to return to their former function[11,12]. This has knock-on effects for other organisms; for example, bird communities have shown substantial changes in the ten years since the habitat disturbance that resulted from Dutch elm disease in northern Minnesota[13]. In southern Appalachian riparian forests, the demise of chestnuts due to blight has led to the spread of *Rhododendron maximum* and consequent reduction in the species richness of forest vegetation[14].

FIGURE 2: FACTORS AFFECTING THE EMERGENCE OF FUNGAL DISEASES

[Adapted from [5]]



WHY ARE FUNGAL THREATS EMERGING?

There are many factors that can lead to the emergence of fungal threats and increase their impact (see Figure 2). A major factor in the recent increase in the impacts of fungal diseases globally is the movement of fungal pathogens around the world, often by humans[2]. All of the examples outlined previously owe their emerging impact to accidental introduction into geographic regions where native plants have not been previously exposed to the pathogen and don't have the tools to combat the infection, allowing rapid spread and severe damage to occur. As we reported in *State of the World's Plants 2017*[15], this is also true of insect pests of plants. Climate change also opens up new regions for fungal pathogens[16]. One study indicates that fungi are now moving towards the poles, following their plant hosts at a rate of 6–7 km/year as the Earth warms[17]. The planting of monocultures, producing local ecosystems with high environmental and genetic uniformity, can provide cradles for the evolution of fungal pathogenicity[18,19].

Fungi may be particularly good at invasion for several reasons. They have multiple ways of associating with plants, which means they can easily hitchhike on plant species moving around the globe[20]. For example, a fungus could enter a country as a harmless, symptomless endophyte of one host species, then move to another host species on which it is pathogenic. Fungi also have multiple ways of reproducing, including clonally, which allows rapid multiplication of a single invader[21]. Rapid dispersal can therefore occur by the production of different spore types (many of which are capable of long-distance airborne dispersal) or by vegetative spread. In addition, some are also associated with insects, which enhance their dispersal and propagation.

HOW DO FUNGAL PATHOGENS EVOLVE?

Fungi are able to recombine genetic information within species through both sexual and parasexual reproduction (see Chapter 1). They can also gain genetic information from other species via hybridisation and horizontal gene transfer. These processes allow new pathogen variants to be continually generated[22]. Some fungal pathogens possess 'two-speed' genomes, which means that while essential genes evolve slowly, the genes involved in pathogenicity and virulence occupy genomic regions that evolve more quickly[23]. This may be accelerated by a process known as repeat-induced point mutation, which appears to be unique to fungi[24].

Understanding how fungi cause disease in plants has benefitted in recent years from the generation of genetic information provided by the recent sequencing of over 500 fungal genomes (see Chapter 6). This has also helped identify and characterise the fungal pathogen genes that code for so-called 'effector' proteins[25]. These proteins are transferred by fungal pathogens into their hosts and contribute to virulence by manipulating the host's immune system. This makes the hosts more susceptible to infection, leading to rapid progression of the disease. Transfer of effector genes between fungal species can lead to the emergence of new diseases[26].

For certain fungal pathogens such as *Fusarium oxysporum* (which causes vascular wilt diseases, such as the devastating Panama disease of bananas (*Musa* spp.)), the ability of different strains to infect specific host plants can be linked to the gain or loss of entire chromosomes[27,28]. Hybridisation can also lead to new pathogenic forms; for example, the flow of genes between populations of the fungal pathogens *Ophiostoma ulmi* and *O. novo-ulmi* seems to have contributed to the rapid evolution of Dutch elm disease[29]. The ash dieback fungus population in Europe appears to have passed through a bottleneck of just two individuals, but sexual reproduction among their offspring has generated diversity via recombination[30].

WHAT CAN WE DO TO REDUCE THE IMPACTS OF FUNGAL DISEASES?

There is clearly a need for greater biosecurity in global trade. But even with stringent checks, pathogenic fungi can move across borders undetected – for example as spores on clothing, vehicles or packaging, or via birds. It is sobering to reflect that myrtle rust has successfully entered Australia and New Zealand, despite the exceptional vigilance of their biosecurity systems compared to many other countries. Long-term solutions could include a drastic reduction in global trade in live plants, improved detection and removal of contaminated and infected plants and improved decontamination treatments.

Integrated approaches that include risk assessments, surveillance, population genomics, practical epidemiology and climate forecasting are needed, so that effective disease prevention strategies can be developed. Response strategies are also needed for the control, detection and eradication of new outbreaks. Such disease prevention and response strategies are already in place in some countries, including the UK, but they need to be adopted more widely to be effective across the range of problem pathogens.

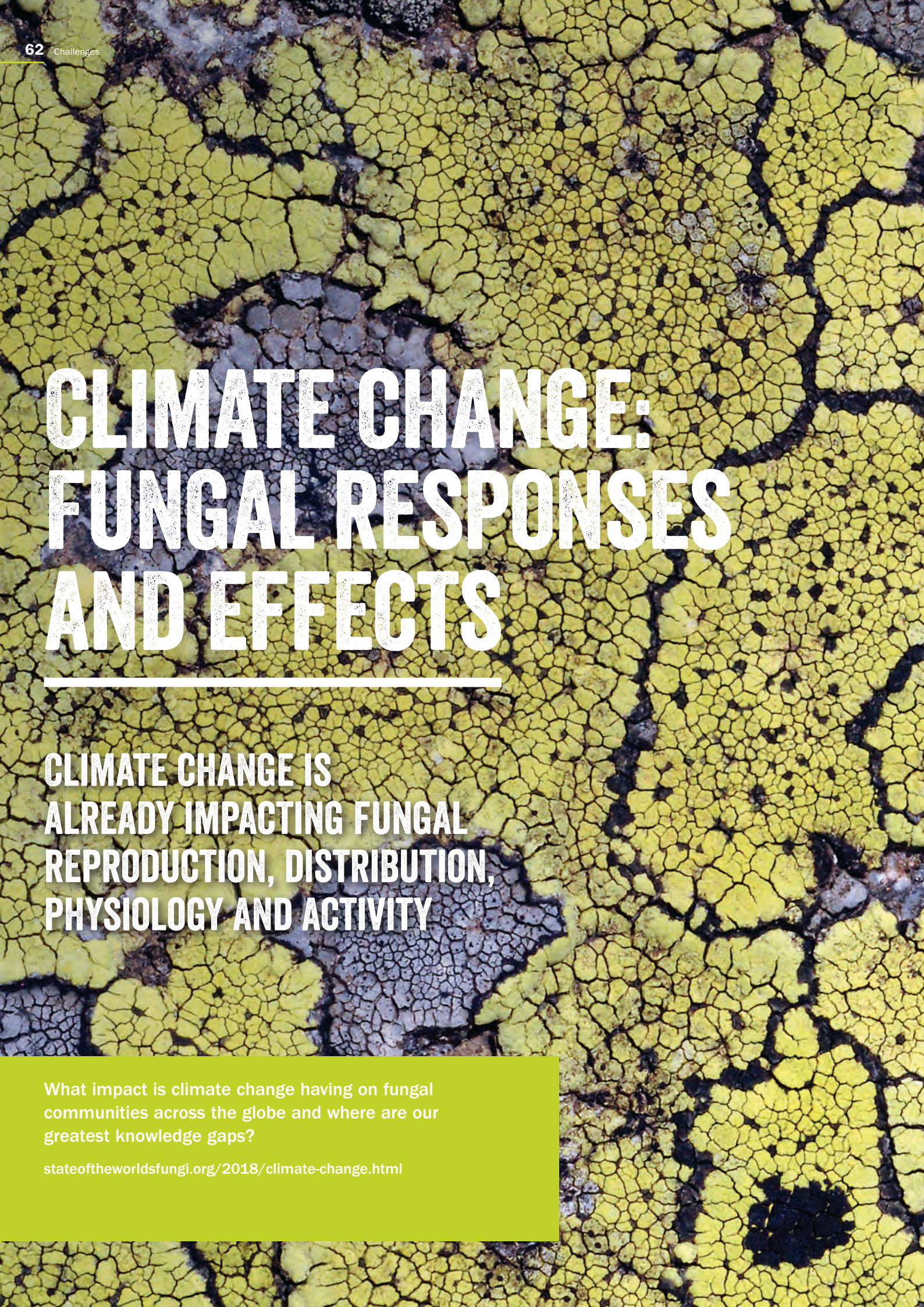
Improved diagnostic methods may help the situation, particularly DNA-based approaches that can detect asymptomatic infections or provide reliable diagnoses for ambiguous symptoms. For example, an in-field diagnostic process was developed for the ash dieback fungus[31], which allowed accurate diagnoses in the early stages of pathogen spread in the UK.

It is hoped that increased knowledge of the genomes of fungal pathogens will lead to the production of new fungicides[32], including RNA-based fungicides[33]. If these are very specifically targeted, deployment may be possible in natural ecosystems without damaging populations of non-pathogenic fungi. Increasing knowledge of the genomes of the hosts of fungal pathogens may also enhance our ability to breed resistance in host plants, as has been done in important crop species. For example, there are several long-term breeding programmes for American chestnut trees resistant to chestnut blight[34] and these are now being enhanced by studies that map resistant genes and allow trees to be scanned for the presence of these useful genes in their genomes[35].

The impacts of fungal diseases on the services provided by natural ecosystems can affect everyone, and increased public awareness is needed if we are to tackle this problem effectively. The willingness of the public to get involved can be seen, for example, in the crowdsourcing of genomic analyses on ash dieback[36] and the fund-raising by organisations such as The American Chestnut Foundation in the USA and Action Oak in the UK. Translating huge public concern into effective citizen action is key to halting the spread of damaging fungal pathogens and reducing their impacts on natural ecosystems.

FIGURE 3: WORDCLOUD OF TOP FUNGAL PATHOGENS AFFECTING NATURAL ECOSYSTEMS CONTAINED IN SCIENTIFIC CITATIONS

[For details of the method, see supplementary material on website: stateoftheworldsfungi.org]



CLIMATE CHANGE: FUNGAL RESPONSES AND EFFECTS

CLIMATE CHANGE IS ALREADY IMPACTING FUNGAL REPRODUCTION, DISTRIBUTION, PHYSIOLOGY AND ACTIVITY

What impact is climate change having on fungal communities across the globe and where are our greatest knowledge gaps?

stateoftheworldsfungi.org/2018/climate-change.html

GIVEN THE IMPORTANT ROLES, BOTH BENEFICIAL AND DETRIMENTAL, THAT FUNGI PLAY IN ALL ASPECTS OF LIFE ON EARTH, IT IS CRITICAL TO CONSIDER THE IMPACT OF CLIMATE CHANGE ON THIS KINGDOM.

The Earth's climate has been changing rapidly since the mid-twentieth century[1] and this has consequences for all living organisms. Last year's *State of the World's Plants* focused on how these climate impacts are already affecting vascular plants across the globe and how they are likely to affect them in the future[2]. This chapter provides a broad overview of the current status of knowledge of how fungi are responding to climate change and how their ecological functions and interactions may affect ecosystem responses to current and future change.

THE IMPACTS OF CLIMATE CHANGE

By 2100, global temperature increases in the range of 1 to 5°C are predicted. High-latitude temperature increases are, and will continue to be, of greater magnitude than average, with rapid changes in boreal (subarctic) and Arctic ecosystems[3]. The consequences of these rapid changes are likely to be significant, and in temperate mountain zones a 1°C increase will result in an upward shift of mean annual temperature isotherms by nearly 200 m. Hot days will increase and cold days will decrease. Patterns of rainfall and snowfall are also shifting, and extreme disturbance events such as hurricanes and fires are also likely to increase. These changes will affect the evolution of species and their ability to adapt to, migrate between, and reside within ecosystems. In fact, some climate impact is already apparent: fungal reproduction, geographic distributions, physiology and activity have changed markedly in the last few decades, through direct climate change effects on fungal growth and indirect effects on their habitats[e.g. 4–8].

Because fungi play a dominant role in terrestrial decomposition and nutrient cycling, as well as plant nutrient uptake (see Chapter 5), plant health (see Chapter 8), and the diet of many animals[9,10], changes in fungal growth resulting from climate change will have considerable knock-on effects for ecosystem functions. Fungi are uniquely able to exploit living and dead plant tissues that make up 95% of terrestrial biomass[11]. They are also a major component in the regulation of atmospheric carbon dioxide (CO_2); in Scandinavia, for example, it was estimated that 50–70% of carbon stored in boreal forest soils was derived from dead roots and associated fungi[12]. A changing climate will have significant effects on these processes. In addition, global patterns of fungal disease are changing and although the main driver in the spread of fungal pathogens is considered to be trade, climate change will have an increasingly important role to play (see Chapter 8).

FIGURE 1: QUESTIONS AND KNOWLEDGE GAPS

KEY UNRESOLVED QUESTIONS:

- What is the relative importance of fungal adaptation, migration and acclimatisation?
- How does climate change affect the yield of fungal spore-bearing structures?
- How does climate change affect fungal growth and activity?
- How do fungi mediate ecosystem responses to climate change?
- How do changes in the phenology of spore-bearing structure production reflect changes in activity, abundance, biomass and distribution?
- Can fungi track climate space shifts?

KEY INFORMATION GAPS:

- Long-term data
- Large-scale data
- Data from tropical, subtropical and warm temperate ecosystems
- Experimental data from fungi associated with trees, rather than seedlings
- Fungal response and effect traits
- Data from multiple simultaneous drivers of change (nitrogen deposition, carbon dioxide, ozone, UV, temperature, drought, fire)

OBSERVING HOW FUNGI RESPOND

Because fungi feed and live within substrates or underground, direct observation and measurement of their responses to climate change are challenging. Crucially, this limits our ability to predict change in ecosystem properties such as global carbon stocks[13,14]. For practical reasons, more readily observable shifts in the timing of reproduction – when some fungi emerge from wood, litter and soil to make spore-bearing structures such as mushrooms – have been more intensively documented (see Box 1). Even though evidence of changes in distribution, physiology and activity are emerging (see Box 2), or can be predicted from models (see Box 3), for fungi it is not yet possible to comprehensively assess the importance of the four possible outcomes of global change: adaptation, migration, acclimatisation or extinction.

Studies of individual species in laboratory conditions show that fungal growth increases with temperature until reaching a maximum and then decreases. Moisture levels also have an effect, causing a decrease in fungal growth when moisture is insufficient or excessive[15]. But how do fungi respond to changes in the real world? For mushrooms (basidiomycete agarics), there are abundant long-term datasets available from citizen science and fungarium collections showing that reproduction has been dramatically impacted by climate change: length of the reproductive season and timing of the production of spore-bearing structures have been shown to be affected by temperature and rainfall, as have diversity and range, in studies from Europe, Japan and the USA[5,8,16–31]. For example, in some European countries, the mushroom season has up to doubled in length for many fungal species since 1950[20,26]. Similar changes have been reported elsewhere in Europe, Asia and North America, but variation in fungal phenology and fungal biomass exists among species and locations. Overall, the higher temperatures and increased moisture levels have become more conducive to reproduction, and growth within soils and plant biomass potentially occurs over a longer period each year. Consequently, inputs of dead vegetation, decomposition and the resulting release of carbon dioxide from soil, wood and leaf litter can be expected to rise, although data are still limited on the capacity for plant-mutualistic fungi to store carbon in soils, which may counterbalance this effect.

The dominant plant nutritional mutualists – mycorrhizal fungi – increase plant access to limiting soil nitrogen and thus drive global soil carbon storage by mediating competition between plants and decomposers[32] and controlling the CO_2 fertilisation effect[33]. The strongest evidence of change for this group comes again from surveys of mushrooms (including edible porcini (*Boletus edulis*) and chanterelles (*Cantharellus* spp.)) from forest understoreys. Reproduction is now considerably later in the season than in the 1950s[7]. There is also evidence of changes in fungal communities in warmer soils, with mycorrhizal species that produce abundant filaments in the soil and consume more plant host carbon becoming more dominant[6,34,35]. Though considerably less studied, leaf endophytes (fungi living within the leaf cells of plants; see Chapter 5) also respond to global change and can ameliorate the effects of drought in their host plants[36,37]. However, there are still large knowledge gaps and unresolved questions relating to how fungi will respond to current and future climate change (Figure 1).

MYCORRHIZAL INTERACTIONS AND FEEDBACK

Human-induced changes in the atmosphere are known to affect fungi in a variety of ways. In general, studies have found that elevated atmospheric CO_2 enhances the abundance and activity of mycorrhizal fungi, particularly in relation to the production of spore-bearing structures, while warmer temperatures increase fungal abundance but decrease activities such as soil nutrient transfer to plants[6]. Mycorrhizal fungi reduce plant stress and increase productivity during drought, so the effect of fungal shifts on plant community dynamics is likely to be important[6]; shifts in mycorrhizal diversity are directly linked with tree tolerance to climate change[38]. Carbon dioxide fertilisation of plants[39] might also increase resources for decomposer fungi. In general, depending on their characteristics, different fungi are likely to be variously impacted (see Figure 2).

In addition to climate change, nitrogen (an essential nutrient that mycorrhizal fungi have specialised in scavenging for plants from mineral and organic sources) has reached unnaturally high concentrations in industrialised regions. Low nitrogen deposition levels (up to 5–10 kg/ha/yr of nitrate and/or ammonium) can be favourable to fungal growth. Higher levels (increasingly more widespread globally), shift the proportion of mycorrhizal fungi in ecosystems and negatively impact their diversity, growth and reproduction. Dutch studies conducted since the 1950s provide striking evidence that fungal fruiting declines with increased nitrogen pollution[35,40]. Some mycorrhizal fungi in Europe have benefited from environmental measures to reduce nitrogen deposition[41], yet nitrogen pollution is increasing in the developing world, especially Asia. Considering these complex responses to climate change and other factors such as pollution, it is not yet known how shifts in mycorrhizal species, abundance and activity will affect ecosystems[42,43].

CHANGES IN FUNGAL GROWTH RESULTING FROM CLIMATE CHANGE WILL HAVE CONSIDERABLE KNOCK-ON EFFECTS FOR ECOSYSTEMS

BOX 1: FUNGARIUM RECORDS FOR UNDERSTANDING HOW GLOBAL CHANGE IMPACTS FUNGI

The ClimFun database[16] combines national-scale records of fungal spore-bearing structures (from fungaria, such as Kew, citizen science and surveys) into one dataset of over six million records. Originally supported by the Norwegian Research Council and later by the Swiss National Science Foundation, it has helped us to understand how fungal reproduction has responded to global change. Fungal reproductive timing (phenology) has become seasonally extended and mean annual temperature changes of as little as 0.2°C can shift the production of spore-bearing structures by one day (especially for fungi that reproduce in autumn)[8]. Temperature also drives compositional patterns across Europe, suggesting feedback effects as the climate changes further[17]. Drought, in general, reduces the length of the reproductive season[8].

BOX 2: UNCOVERING BELOW-GROUND FUNGAL RESPONSES TO ENVIRONMENTAL CHANGE

Air pollution impacts forests and the mycorrhizal fungi that provide tree roots with soil mineral nutrients and water in exchange for carbon. Alarming declines in tree nutritional status are occurring across Europe's forests[58]. Since 2006, a collaboration between Kew, Imperial College London and ICP Forests (icp-forests.net), supported by the UK Natural Environmental Research Council and the European Union, has been busy generating the first high-resolution, large-scale underground baseline datasets at national[59] and continental[60,61] scales across pine (*Pinus sylvestris*), spruce (*Picea abies*), beech (*Fagus sylvatica*) and oak (*Quercus robur* and *Q. petraea*) forests in Europe. So far, these studies have revealed: (i) widespread damaging effects of nitrogen deposition on fungal taxonomic and functional diversity; (ii) that European emissions controls require strong adjustment; and (iii) that the morphological variability of keystone fungi and the degree to which they are specific to the host tree species have been underestimated.

BOX 3: MODELLING CLIMATE CHANGE EFFECTS ON LICHENS

In general, lichens can be more easily recorded during field surveys than other fungi, and the wealth of distribution records available make them good candidates for predicting the effects of climate change. It is possible to describe lichen distributions as an outcome of climate[62] and then project models under future climate change scenarios to predict losses, gains or shifts in suitable climate space[63,64]. These pioneering analyses highlight threats to species in mountain environments[65] and coastal zones caught between rising sea levels and intensively managed land[66], and problems caused by fragmented habitat for species needing to migrate northwards[63] – as much as 60 km north per decade for the UK[67]. The threat of climate change is exacerbated by pollution and habitat loss[68]. Practical solutions include improving habitat quality to create microclimate refugia[69].

FIGURE 2: POTENTIAL OF DIFFERENT STRUCTURES AND TRAITS TO COMBAT SOME OF THE EFFECTS OF CLIMATE CHANGE

THICK-WALLED SPORES

Spores with thick walls are better able to withstand environmental stresses. The thick walls provide protection from drought and temperature-related desiccation, and incineration[70].

DROUGHT TEMPERATURE FIRE

MELANISATION

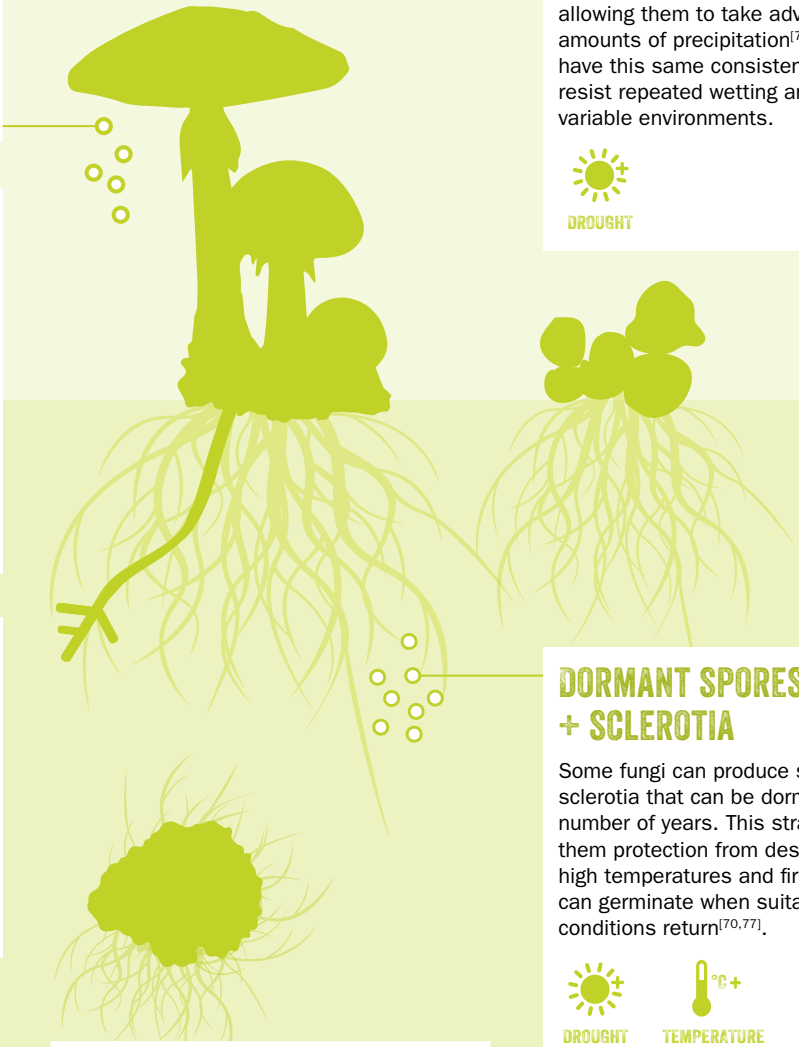
Melanin is a complex pigment found in some fungi. It can provide resistance to desiccation, high temperatures and UV radiation[71]. It also provides strength, allowing hyphae to penetrate deeper into the soil to access water and to transport water over larger distances without leaks[70,71].

DROUGHT TEMPERATURE

RHIZOMORPHS

Rhizomorphs are root-like fungal structures that act as pipelines to transport water, carbohydrates and minerals over long distances (up to metres) through soil. Fungi with rhizomorphs are better able to survive drought conditions[72–74].

DROUGHT



JELLY FUNGI

Species of jelly fungi have cell walls that can contract down to become hard and resistant when dry but can expand rapidly and become gelatinous when wet, allowing them to take advantage of small amounts of precipitation[76]. Their spores have this same consistency and can resist repeated wetting and drying in variable environments.

DROUGHT

DORMANT SPORES + SCLEROTIA

Some fungi can produce spores or sclerotia that can be dormant for a number of years. This strategy gives them protection from desiccation, high temperatures and fire, and they can germinate when suitable conditions return[70,77].

DROUGHT TEMPERATURE FIRE

TRUFFLES AND FALSE TRUFFLES

Truffles and false truffles are spore-bearing structures that are formed below ground by some species of fungi[75]. Their underground habit minimises water loss in dry environments and means they are buffered from high air temperatures and protected from fire.

DROUGHT TEMPERATURE FIRE

FUNGAL PESTS AND PATHOGENS

The movements of some fungi can be tracked because of their negative effects on other organisms, and many such fungi are known to have undergone major geographic range changes over several decades. This is evidenced by their emergence where previously unknown (e.g. *Batrachochytrium dendrobatidis*, responsible for amphibian decline worldwide, and *Pseudogymnoascus destructans*, causing bat white-nose syndrome in North America) and by their expansion (e.g. *Hymenoscyphus fraxineus*, spreading ash dieback across Europe, and death cap (*Amanita phalloides*) spreading to North America and beyond from its native Europe)[4,44,45]. Environmental change can drive the emergence of infectious fungal diseases, particularly those of plants[4] (see Chapter 8).

THE CASE OF LICHENS

Lichens can resemble plants but they are fungi with photosynthetic partners (algae and/or cyanobacteria) and live on a variety of substrates (e.g. trees, rocks, buildings) exposed to the environment. The fungi extract food from their partners in exchange for providing them with nutrients and shelter. Can lichens survive climate change? A lichen species' vulnerability to climate change can be assessed through understanding its potential to adapt, acclimatise or migrate (see Box 3). Local populations of the same lichen can be adapted to different climatic settings[46]; perhaps they can adapt to a changing climate if their genes can flow from warm-adapted to cold-adapted populations. However, individual lichen fungi can also acclimatise to a changing climate through shifts in their morphology (e.g. increased mass-per-area can improve water storage)[47]. A fungus might also change photosynthetic partners over time as a mechanism to promote survival[48]. Lichen morphology and photosynthetic partners vary among species and monitoring these attributes may be useful in tracking climate change impacts[49]. Finally, a species can migrate to escape the changing conditions; for example, some southern European lichens have been expanding northwards into southern England and the Netherlands[50].

Dispersal and migration of lichens in response to climate change are often confounded with effects such as pollution response; for example, lichens were severely affected by fossil fuel burning causing sulphur pollution during the Industrial Revolution[51,52]. As sulphur pollution has declined and species have expanded their ranges, some lichen communities have recovered but are skewed towards species tolerant of already high and/or increasing nitrogen pollution[53].

There is evidence for direct sensitivity of lichens to climate change[50,54,55]; however, direct climate change responses may in some cases be less important than indirect community-scale effects, such as the overshading of Arctic/alpine lichens by increased vascular plant growth[56], causing lichen decline. These direct and indirect climatic effects on lichens have the potential to adversely impact ecosystem functions such as weathering and subsequent soil stabilisation, the provision of habitat for invertebrates, and nitrogen-fixation and primary productivity in support of food-webs[57]. The prominence and visibility of lichens in the habitats in which they occur and their sensitivity to change have made them convenient models for monitoring responses to global climate change.

CONSERVATION OF FUNGI

ONLY

56

SPECIES OF FUNGI HAVE HAD THEIR CONSERVATION STATUS GLOBALLY EVALUATED FOR THE IUCN RED LIST, COMPARED WITH 25,452 PLANTS AND 68,054 ANIMALS

How many species of fungi are threatened with extinction and why are they so difficult to assess? What threats are fungi facing and what are the conservation challenges?

stateoftheworldsfungi.org/2018/conservation-of-fungi.html

THERE IS A STRIKING TAXONOMIC IMBALANCE WITHIN THE FIELD OF BIOLOGICAL CONSERVATION. IT WAS NOTED FROM A REVIEW OF PAPERS PUBLISHED IN THE TOP TWELVE MAINSTREAM CONSERVATION JOURNALS THAT ONLY AROUND 3% DISCUSSED FUNGI[1].

Furthermore, this meagre coverage was mostly concerned with the threats that these organisms pose to other wildlife. This sends the incorrect message that it is only within the animal and plant kingdoms that populations are threatened, declining or becoming extinct, and therefore worthy of conservation. Data from the International Union for Conservation of Nature (IUCN) on the number of species that have had their global conservation status evaluated also reflect the imbalance between the kingdoms[2] (see Figure 1). In fact, fungi, animals and plants all face similar threats resulting from climate change, pollution, over-exploitation, and habitat destruction and fragmentation[3–5]. In this chapter, we discuss why there has been so little attention paid to the conservation of fungi, we look at the merits of species and habitat-based conservation and we highlight the potential for using new and exciting approaches to tackle this critical subject.

WHY HAVE FUNGI OFTEN BEEN NEGLECTED?

Collaboration between mycologists and conservationists has been hampered by the knowledge gaps in fungal distributional and ecological data. These persist chiefly because fungi are frequently invisible, of indeterminate form and show a propensity to switch between forms[6]. Fungi, although ubiquitous, hyperdiverse and fascinating, are challenging and frustratingly elusive. Despite the eye-catching and prolific displays of spore-bearing structures (e.g. mushrooms) produced by some species, they are generally regarded as difficult to detect and count because, when not sporulating, most are composed of nothing more substantial than a wispy network of mycelium (see Chapter 1).

Fungi therefore constitute a large, and yet largely hidden, presence within soil and inside other living things. This makes them difficult subjects to characterise, survey and monitor. A comparison with plants illustrates the disparity: work on the first IUCN Red List of Threatened Plants was initiated by Sir Peter Scott in the 1960s[7], but it was another four decades before the first mushroom was globally recognised as threatened, in 2006[8].

Despite some welcome recent progress in the conservation of fungi with larger spore-bearing structures (macrofungi)[3,6], the unseen microfungal majority remains largely neglected[3,9]. Fortunately, a general shift towards conserving whole ecosystems is now underway and, due to their ecological importance in nutrient cycling, this should ensure a higher profile for fungi[10]. One group is already ahead of the pack – the lichenised fungi. Most lichens are relatively conspicuous in the wild and have thalli which are visible throughout the year, making them relatively amenable to conservation-related studies (see Box 1).

HOW AND WHERE DID FUNGAL CONSERVATION START?

The origins of organised fungal conservation lie within Europe, where long traditions of recording and classifying wild fungi exist within several countries. Therefore, when significant declines were reported during the 1970s and 80s they were taken very seriously. This led to the establishment of the European Council for the Conservation of Fungi (ECCF), whose inaugural meeting[11] was held in Poland in 1988. A second meeting[12] followed in Germany in 1991 and the theme was taken up in the following year's Congress of European Mycologists, at Kew[13]. The apparent decline in populations of fungi was reported across Europe, for example in former Czechoslovakia[14–16], Denmark[17], Germany[18–20], the Netherlands[21–27] and Sweden[28]. These reported changes were mainly associated with increasing levels of air pollution affecting the mycorrhizal partners of trees, clearcutting of old-growth forests and the loss of waxcap-rich grasslands[29]. The realisation that European fungal populations were rapidly deteriorating led to the recognition that fungal conservation research and communication were of great importance[29].

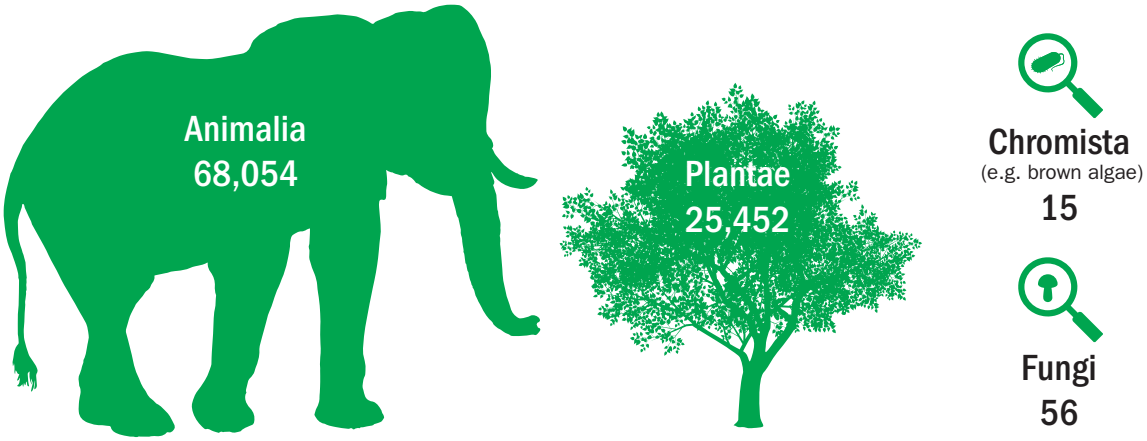
HOW HAS SPECIES-BASED CONSERVATION OF FUNGI DEVELOPED?

Species-based conservation assessment based on IUCN criteria (a process called Red-Listing), reveals the relative level of extinction risk faced by each species, either globally or within a particular geographic region. Traditionally, it has formed part of an internationally recognised early warning system highlighting those species in greatest need of help. The declining wild mushroom yields across Europe therefore generated much interest in national Red-Listing projects. Starting in 1982 in the former German Democratic Republic[30], by 1993 ten countries had published conservation assessments for at least some macrofungi[29].

AT LEAST 10% OF EUROPEAN MACROFUNGI ARE THREATENED WITH EXTINCTION, MAINLY DUE TO CHANGING LAND USE AND INCREASING NITROGEN DEPOSITION[5]

FIGURE 1: CHART SHOWING THE NUMBER OF SPECIES EVALUATED FOR THE GLOBAL IUCN RED LIST BY KINGDOM

[Based on data from [2]]



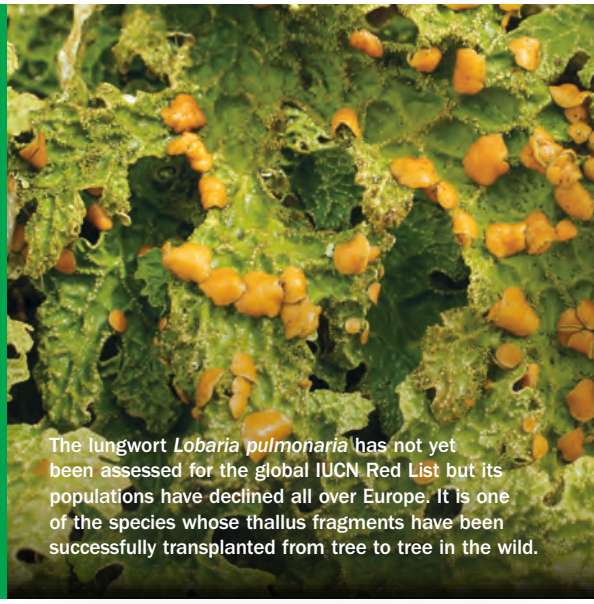
These preliminary assessments, often drawing heavily on expert opinion and species lists generated by fungus forays[31], were soon routinely underpinned by national recording databases and mapping projects. Indeed, the combination of increased digitisation, data accessibility and availability of improved identification guides stimulated such an upsurge in fungal recording that an uncritical glance at the data could suggest that populations of almost all species were increasing. Only when a statistical correction had been applied to the data to allow for this increase in general recording activity, did the gradual decline in some Dutch species become apparent[27]. Sweden established permanent Red-Listing teams in 1990[32] and is now one of the role models for national Red-Listing.

National Red Lists became more objective and standardised with the adoption of IUCN criteria and, where appropriate, the use of some IUCN-approved, fungi-specific assumptions to help fungal conservationists grapple with such unfamiliar and difficult concepts as the mature fungal individual[6,33]. Although the most comprehensive national conservation assessments for non-lichenised fungi still rely on records of spore-bearing structures, and are therefore far from complete, some pan-European data analysis has already occurred and a European Red List is a long-term goal[3,5,29,34–38]. To illustrate the scale and challenge of such a project, a 14-year project recently culminated in the publication of species accounts and dot-maps for 51 European macrofungi[39]. Compiling and publishing such fungal distribution data supported by appropriate taxonomic studies, are not only essential prerequisites for Red-Listing at a continental scale, but the resulting maps can also highlight some conservation priorities for the countries covered[39].

Outside Europe, however, the Red List picture is bleaker[40] (see Figure 2). This is due to a lack of fungal inventories, reference collections, taxonomists and other resources.

BOX 1: LICHEN CONSERVATION

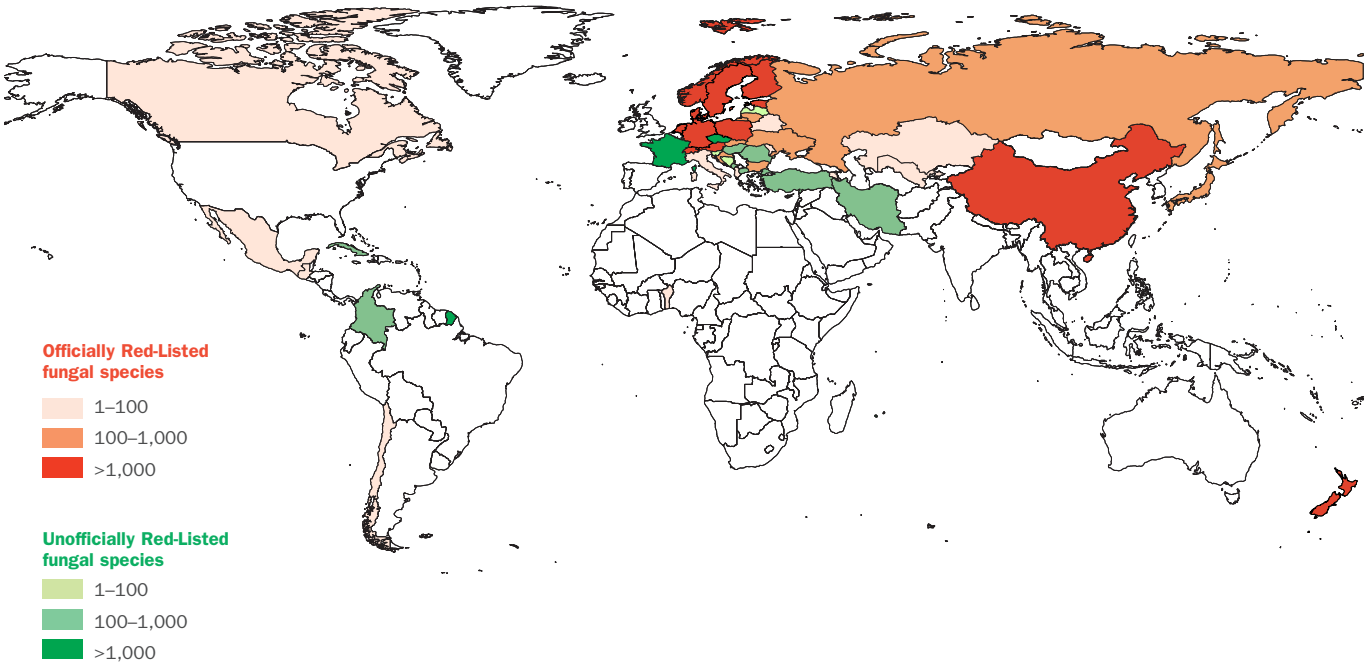
The ease with which lichens can generally be found, studied and experimentally manipulated in the field has helped to ensure that they are relatively well surveyed, monitored, protected and managed. Methods of lichen conservation largely depend on the nature and durability of the various supporting substrata, from fragile soil crusts to rocks and ancient tree trunks, but regulating light and shelter and mitigating air pollution are key to success. Grazing by the right animals at the right density is essential to keep the surrounding vegetation in check while minimising damage to the lichens themselves. Many threatened lichens depend on veteran trees and a long history of grazing, essential for maintenance of a glade-and-grove mosaic of lighting conditions. Some species produce vegetative diaspores comprising fungal and photosynthetic partners, but these are bulky and tend to not travel far. An innovative lichen-specific conservation technique has been developed involving transplantation of diaspores, or other fragments, to suitable substrata to increase the size of small, fragmented and threatened populations.



The lungwort *Lobaria pulmonaria* has not yet been assessed for the global IUCN Red List but its populations have declined all over Europe. It is one of the species whose thallus fragments have been successfully transplanted from tree to tree in the wild.

FIGURE 2: COUNTRIES WITH PUBLISHED NATIONAL FUNGAL RED LISTS

Officially approved Red Lists (those acknowledging appropriate government agency endorsement) are shaded red, with increasing intensity indicating greater numbers of taxa assessed. Corresponding shading in green highlights countries with unofficial Lists. Only Red Lists covering entire ISO-coded countries are shown (hence no shading for the UK although some official Red-Listing has occurred in Great Britain). [For more information and sources of data, see supplementary material on website: stateoftheworldsfungi.org]



Several countries have initiated online national mapping schemes for selected macrofungal target species but only a few have done so outside Europe, for example the Australian *Fungimap* project[41]. A similar citizen science approach is at the heart of the *Lost and Found Fungi* project[42], which aims to distinguish those fungi that are genuinely rare from those that are merely rarely recorded (see Box 2).

National legislation enacted to prohibit fungal picking and destruction can be difficult to enforce due to resourcing issues, but one remarkably successful fungal flagship was created by the US Northwest Forest Plan in 1994. Each tree supporting the noble polypore (*Bridgeoporus nobilissimus*) was surrounded by a 240-hectare exclusion zone in which disturbance was prohibited and habitat was thereby conserved[43]. Similar areas also exist for the protection of lichens, such as the globally Critically Endangered boreal felt lichen (*Erioderma pedicellatum*) in Canada[44–46].

HOW HAS HABITAT-BASED CONSERVATION DEVELOPED?

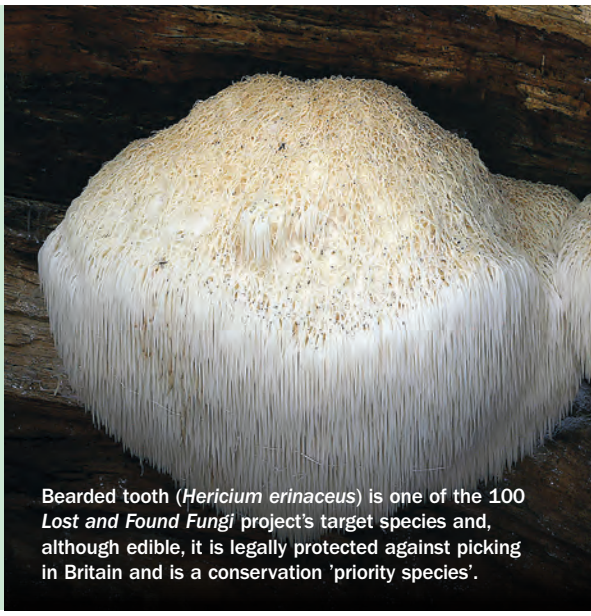
Fungal communities inevitably gain a degree of indirect protection when they inhabit sites that are legally protected and/or managed in order to conserve other forms of wildlife. Although such protection is largely beneficial to fungi, some species of conservation concern can be damaged and destroyed by routine management activities when neither their importance nor their precise locations are known to site owners/managers. Indeed, management for the benefit of other groups of organisms can be unintentionally highly detrimental to populations of fungi officially recognised as national conservation priorities. This can occur, for example, when bonfires are situated directly above threatened litter-inhabiting fungi or when fallen branches occupied by protected wood decomposers are fragmented by tractor-drawn machinery due to a lack of awareness of a site's special mycological interest.

The process of ranking sites for protection based on their fungal species diversity has its roots in the concepts of indicator species[47] and, in the UK, Important Fungus Areas[48]. Before 2018, the only British habitat that could gain legal protection in this way was nutrient-poor grassland[49], but a revised and expanded set of site selection guidelines[50] should help to ensure that a wider range of fungal habitats is protected in future. In countries where sufficient knowledge exists, fungi of conservation interest are now being considered beyond the boundaries of protected areas and their requirements are helping to shape agricultural and forestry land management more generally, for example within the Forest Stewardship Council (FSC)[51] forestry certification system in northern Europe.

At a continental level, a project to add 33 fungal species to the European Union's list of plants and animals of conservation concern[37] unfortunately had to be withdrawn for political reasons and no further attempts have been forthcoming.

BOX 2: ENGAGING VOLUNTEERS

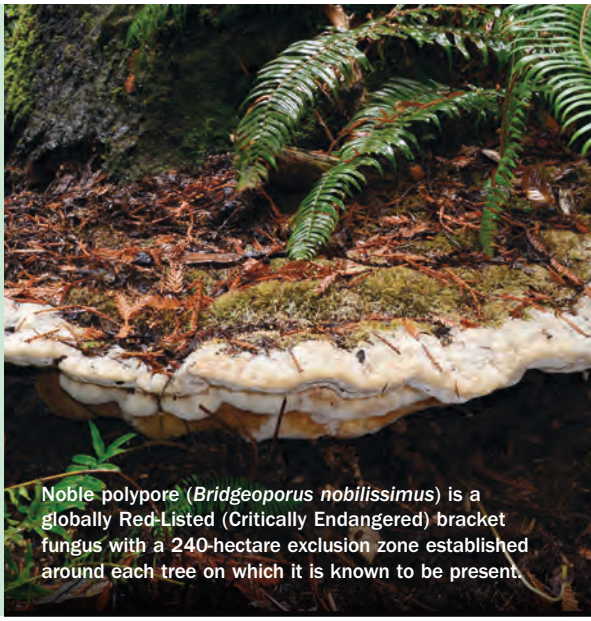
The *Lost and Found Fungi* project (fungi.myspecies.info/content/lost-found-fungi-project) is a volunteer-based fungal conservation project (2014–2019) coordinated at Kew and funded by the Esmée Fairbairn Foundation. It aims to increase awareness, recording and knowledge of 100 target species of current or potential conservation concern in the UK, while at the same time developing identification skills and encouraging greater engagement with fungi within and beyond the UK's volunteer fungal recording community. Focusing on a diverse range of distinctive but rarely recorded fungi, the project team has: compiled a curated dataset of over 1,200 new records (28% of the known records and sites for these species in Great Britain and Ireland), which will be used in conservation (Red-Listing) assessments; mentored and advised groups and individuals; rediscovered species 'lost' for over 50 years; investigated the distribution of recently described fungi and recent arrivals; undertaken population surveillance; resolved taxonomic difficulties; and described species new to science.



Bearded tooth (*Hericium erinaceus*) is one of the 100 *Lost and Found Fungi* project's target species and, although edible, it is legally protected against picking in Britain and is a conservation 'priority species'.

BOX 3: ONLINE GLOBAL RED-LISTING

Established in 2013 by the IUCN's five Fungal Specialist Groups in collaboration with its Species Survival Commission and Red List Unit with funding provided by the Mohamed bin Zayed Species Conservation Fund, the *Global Fungal Red List Initiative* (iucn.ekoo.se/en/iucn) is assessing a global representation of fungi for publication in the IUCN Red List (iucnredlist.org). It is raising awareness of fungal conservation among mycologists, the conservation community, policymakers and the general public, while serving as a forum to educate, inspire and engage the mycological community. It identifies knowledge gaps that impede fungal Red-Listing and is integrating fungi into general conservation initiatives. A total of 255 individuals from 60 countries have nominated over 500 species for consideration as of spring 2018. Experts assess these nominations during sponsored Red-Listing workshops, utilising their knowledge along with data made available through the digitisation of preserved collections and citizen science recording initiatives. To date, over 200 species have received at least a preliminary assessment of their conservation status.



Noble polypore (*Bridgeoporus nobilissimus*) is a globally Red-Listed (Critically Endangered) bracket fungus with a 240-hectare exclusion zone established around each tree on which it is known to be present.

WHAT ELSE IS HAPPENING?

Responding to the dismal message conveyed by having a solitary mushroom species on the global IUCN Red List between 2006 and 2015, an online wiki-based approach to fungal assessments has resulted in many new international collaborations (see Boxes 3 and 4). This effort has already yielded positive and very encouraging results. There are now 56 species of fungi that have been globally evaluated under the IUCN Red List criteria, of which 13 are lichens or lichen associates. The total includes 43 that are listed as threatened (Critically Endangered, Endangered or Vulnerable)[2]. This will create new opportunities for the inclusion of globally threatened species within the criteria used to select sites for protection at regional levels and, furthermore, it will help to ensure such species are embedded within international conservation initiatives such as the EU's *LIFE* and *Natura 2000* projects.

Another exciting new development is the increasing use of fungal DNA analysis to resolve taxonomic issues, provide more reliable identifications and explore community and population ecology, all of which are required to support improved conservation assessments and site management plans. There are innovative country-level approaches too, such as the promotion of Chilean mycology and conservation following pioneering legislation requiring the inclusion of fungi in environmental impact assessments (see Box 5) and an increasing number of national biodiversity portals that include fungi[52–57]. There are also encouraging signs that the equally important political aspects of fungal conservation are starting to be developed at an international level, courtesy of the International Society for Fungal Conservation (fungal-conservation.org).

BOX 4: ONLY ONE GLOBALLY THREATENED MUSHROOM SPECIES? NOT ANY MORE

Natural populations of animals, fungi and plants face similar threats. Nonetheless, between 2006 and 2015 a relative of the cultivated oyster mushroom, white ferula mushroom (*Pleurotus nebrodensis* subsp. *nebrodensis*), was the only non-lichenised fungus to be included on the global IUCN Red List of Threatened Species[8,58]. It was originally listed as a species, *P. nebrodensis*, but since its reclassification as a subspecies it is no longer included in the IUCN species totals. Fortunately, the misleading conservation message that there was only one globally threatened mushroom species is now being addressed and corrected (see Box 3). A total of 56 species of non-lichenised and lichenised fungi have been evaluated and 43 are currently listed by the IUCN as threatened. A global effort is underway to rapidly increase the number of species evaluated to ensure threatened species are listed and afforded appropriate protection.

BOX 5: CHILEAN MYCOLOGY, CONSERVATION AND THE LAW

In 2010, fungi were incorporated into Chile's Environmental Law (Nº.19,300, General Bases of the Environment, 1994) such that the Ministry of Environment must ensure fungi are classified in a national inventory using scientific and IUCN Red-Listing criteria. In addition, regulations must be developed to design management, conservation and recovery plans for species under threat. In late 2013, the Environmental Impact Assessment System Regulation came into effect, which ruled that fungi be included in both environmental impact assessments and declarations in all terrestrial ecosystems. In effect, every terrestrial project seeking an environmental permit must include fungal baseline studies and analyse the threats posed to the species found. This was partly possible because of The Fungi Foundation – a Chilean non-governmental organisation (NGO) working exclusively for the conservation, research, and promotion of fungi – who took it upon themselves to trigger, defend and develop the legal inclusion. This is already resulting in increasing numbers of mycologists and taxonomists being employed in Chile to satisfy demand.

Loyo (*Butyriboletus loyo*) is a highly esteemed wild edible mushroom associated with southern beech (*Nothofagus* spp.) in the temperate southern rainforests of Chile. It is of cultural importance to the Mapuche people but is now nationally assessed as Endangered and under threat from habitat loss and overharvesting.

Contributors and references

Authors are affiliated to RBG Kew unless otherwise stated. The production of this report has been supported by numerous staff members at Kew and in our partner organisations and by many other individuals.

1. Definition and diversity

Authors: Paul F. Cannon, Begoña Aguirre-Hudson, M. Catherine Aime (Purdue University), A. Martyn Ainsworth, Martin I. Bidartondo (Imperial College London & RBG Kew), Ester Gaya, David Hawksworth (Natural History Museum, London, RBG Kew & Jilin Agricultural University), Paul Kirk (RBG Kew & Institute of Microbiology, Chinese Academy of Sciences), Ilia J. Leitch and Robert Lücking (Botanical Garden and Botanical Museum Berlin).

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References: **[1]** Linnaeus, C. (1753). *Species Plantarum, exhibentes plantas rite cognitas ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas.* Laurentius Salvius, Stockholm; **[2]** Hibbett, D. S., et al. (2007). A higher-level phylogenetic classification of the Fungi. *Mycological Research* 111(5): 509–547; **[3]** Wainright, P., et al. (1993). Monophyletic origins of the metazoa: an evolutionary link with fungi. *Science* 260(5106): 340–342; **[4]** Woese, C. R., Kandler, O. & Wheelis, M. L. (1990). Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences* 87(12): 4576–4579; **[5]** Shalchian-Tabrizi, K., et al. (2008). Multigene phylogeny of Choanozoa and the origin of animals. *PLoS ONE* 3(5): e2098; **[6]** Lücking, R. & Nelsen, M. P. (2018). Ediacarans, protolichens, and lichen-derived *Penicillium*. A critical reassessment of the evolution of lichenization in fungi. In: M. Krings et al. (eds), *Transformative Paleobotany*. *Papers to Commemorate the Life and Legacy of Thomas N. Taylor*. Academic Press, London. pp. 551–590; **[7]** Prieto, M. & Wedin, M. (2013). Dating the diversification of the major lineages of Ascomycota (Fungi). *PLoS ONE* 8(6): e65576; **[8]** Lücking, R., et al. (2009). Fungi evolved right on track. *Mycologia* 101(6): 810–822; **[9]** Redecker, D., Kodner, R. & Graham, L. E. (2000). Glomalean fungi from the Ordovician. *Science* 289(5486): 1920–1921; **[10]** Taylor, T. N., et al. (2007). Fungi from the Rhynie chert: a view from the dark side. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 94(4): 457–473; **[11]** Honegger, R., et al. (2018). Fertile *Prototaxites taiti*: a basal ascomycete with inoperculate, polysporous asci lacking croziers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1739): 20170146; **[12]** Field, K. J., et al. (2015). Functional analysis of liverworts in dual symbiosis with Glomeromycota and Mucoromycotina fungi under a simulated Palaeozoic CO_2 decline. *The ISME Journal* 10: 1514; **[13]** Willis, K. J. (ed.) (2017). *State of the World's Plants 2017*. Report. Royal Botanic Gardens, Kew. Available from: https://stateoftheworldsplants.org; **[14]** Hawksworth, D. L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4): FUNK-0052-2016; **[15]** Cannon, P. F. & Kirk, P. M. (2007). *Fungal families of the world.* CABI Publishing, Wallingford; **[16]** Scheuer, C., et al. (2008). *Bartheletia paradoxa* is a living fossil on *Ginkgo* leaf litter with a unique septal structure in the Basidiomycota. *Mycological Research* 112(11): 1265–1279; **[17]** Mishra, B., Choi, Y.-J. & Thines, M. (2018). Phylogenomics of *Bartheletia paradoxa* reveals its basal position in Agaricomycotina and that the early evolutionary history of basidiomycetes was rapid and probably not strictly bifurcating. *Mycological Progress* 17(3): 333–341; **[18]** Merje, T., et al. (2014). Genome sequencing provides insight into the reproductive biology, nutritional mode and ploidy of the fern pathogen *Mixia osmundae*. *New Phytologist* 202(2): 554–564; **[19]** Liu, M., Rodrigue, N. & Kolmer, J. (2013). Population divergence in the wheat leaf rust fungus *Puccinia triticina* is correlated with wheat evolution. *Heredity* 112: 443–453; **[20]** McTaggart, A. R., et al. (2015). A co-evolutionary relationship exists between *Endoraecium* (Pucciniales) and its *Acacia* hosts in Australia. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 35: 50–62; **[21]** Bennett, C., Aime, M. C. & Newcombe, G. (2011). Molecular and pathogenic variation within *Melampsora* on *Salix* in western North America reveals numerous cryptic species. *Mycologia* 103(5): 1004–1018; **[22]** Lücking, R., et al. (2017). Turbo-taxonomy to assemble a megadiverse lichen genus: seventy new species of *Cora* (Basidiomycota: Agaricales: Hygrophoraceae), honouring David Leslie Hawksworth's seventieth birthday. *Fungal Diversity* 84(1): 139–207; **[23]** Lücking, R., et al. (2014). A single macrolichen constitutes hundreds of unrecognized species. *Proceedings of the National Academy of Sciences* 111(30): 11091–11096; **[24]** Spatafora, J. W., et al. (2017). The fungal tree of life: from molecular systematics to genome-scale phylogenies. *Microbiology Spectrum* 5(5): FUNK-0053-2016; **[25]** Tedersoo, L., et al. (2018). High-level classification of the Fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90(1): 135–159; **[26]** Richards, T. A., et al. (2015). Molecular diversity and distribution of marine fungi across 130 European environmental samples. *Proceedings of the Royal Society B: Biological Sciences* 282: 20152243; **[27]** Lücking, R. & Hawksworth, D. L. (2018). Formal description of sequence-based, voucherless Fungi: Promises and pitfalls, and how to resolve them. *IMA Fungus* 9(1): 143–166; **[28]** Urbina, H. & Aime, M. C. (2018). A closer look at Sporidiobolales: Ubiquitous microbial community members of plant and food biospheres. *Mycologia* 110(1): 79–92; **[29]** Hawksworth, D. L., et al. (2018). (F-005-006) Proposals to permit DNA sequence data to be used as types of names of fungi. *IMA Fungus* 9(1:Myconames): v–vi; **[30]** Zamora, J. C., et al. (2018). Considerations and consequences of allowing DNA sequence data as types of fungal taxa. *IMA Fungus* 9(1): 167–175; **[31]** Thines, M., et al. (2018). Ten reasons why a sequence-based nomenclature is not useful for fungi anytime soon. *IMA Fungus* 9: 177–183; **[32]** Baldauf, S. L. & Palmer, J. D. (1993). Animals and fungi are each other's closest relatives: congruent evidence from multiple proteins. *Proceedings of the National Academy of Sciences* 90(24): 11558–11562; **[33]** Aime, M. C., McTaggart, A. R., Mondo, S. J. & Duplessis, S. (2017). Chapter 7 – Phylogenetics and phylogenomics of rust fungi. In: J. P. Townsend & Z. Wang (eds), *Fungal Phylogenetics and Phylogenomics*. Academic Press, Cambridge, MA. *Advances in Genetics* 100: 267–307.

2. Fungal tree of life

Authors: Ester Gaya, Pepijn Kooij, Bryn Dentinger (Natural History Museum of Utah), Igor V. Grigoriev (U.S. Department of Energy, Joint Genome Institute), László Nagy (Biological Research Centre, Hungarian Academy of Sciences), Jason Stajich (University of California, Riverside), Timothy Coker and Ilia J. Leitch.

References: **[1]** James, T. Y., et al. (2006). Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443(7113): 818–822; **[2]** Lutzoni, F., et al. (2004). Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *American Journal of Botany* 91(10): 1446–1480; **[3]** McLaughlin, D. J., et al. (2009). The search for the fungal tree of life. *Trends in Microbiology* 17(11): 488–497; **[4]** Hibbett, D. S., Stajich, J. E. & Spatafora, J. W. (2013). Toward genome-enabled mycology. *Mycologia* 105(6): 1339–1349; **[5]** Spatafora, J. W., et al. (2017). The fungal tree of life: From molecular systematics to genome-scale phylogenies. *Microbiology Spectrum* 5(5): 1–32; **[6]** Berbee, M. L., James, T. Y. & Strullu-Derrien, C. (2017). Early diverging fungi: Diversity and impact at the dawn of terrestrial life. *Annual Review of Microbiology* 71(1): 41–60; **[7]** Chang, Y., et al. (2015). Phylogenomic analyses indicate that early fungi evolved digesting cell walls of algal ancestors of land plants. *Genome Biology and Evolution* 7(6): 1590–1601; **[8]** Paps, J., et al. (2013). Molecular phylogeny of Unikonts: New insights into the position of Apusomonads and Ancyromonads and the internal relationships of Opisthokonts. *Protist* 164(1): 2–12; **[9]** Torruella, G., et al. (2015). Phylogenomics reveals convergent evolution of lifestyles in close relatives of animals and fungi. *Current Biology* 25(18): 2404–2410; **[10]** Lee, K. V., et al. (2015). A national survey of managed honey bee 2013–2014 annual colony losses in the USA. *Apidologie* 46(3): 292–305; **[11]** Stuart, S. N., et al. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* 306(5702): 1783–1786; **[12]** Lips, K. R. (2016). Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1709): 20150465; **[13]** Spatafora, J. W., et al. (2017). A phylum-level phylogenetic classification

of zygomycete fungi based on genome-scale data. *Mycologia* 108(5): 1028–1046; **[14]** Benny, G. L., et al. (2016). Challenges and future perspectives in the systematics of Kickxellomycotina, Mortierellomycotina, Mucoromycotina, and Zoopagomycotina. In: D-W Li (ed.), *Biology of Microfungi*. Springer International Publishing, Cham. pp. 65–126; **[15]** Hoff, J. A., et al. (2004). Fungal endophytes in woody roots of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). *Forest Pathology* 34(4): 255–271; **[16]** Summerbell, R. C. (2005). Root endophyte and mycorrhizosphere fungi of black spruce, *Picea mariana*, in a boreal forest habitat: Influence of site factors on fungal distributions. *Studies in Mycology* 53: 121–145; **[17]** Terhonen, E., et al. (2014). Endophytic fungi of Norway spruce roots in boreal pristine mire, drained peatland and mineral soil and their inhibitory effect on *Heterobasidion parviporum in vitro*. *Fungal Ecology* 9(1): 17–26; **[18]** Benny, G. L., Humber, R. A. & Voigt, K. (2014). 8 Zygomycetous Fungi: Phylum Entomophthoromycota and Subphyla Kickxellomycotina, Mortierellomycotina, Mucoromycotina, and Zoopagomycotina. In: D. J. McLaughlin & J. W. Spatafora (eds), *Systematics and Evolution*. Springer, Berlin. pp. 209–250; **[19]** Bidartondo, M. I., et al. (2011). The dawn of symbiosis between plants and fungi. *Biology Letters* 7(4): 574–577; **[20]** Redecker, D. & Schüßler, A. (2014). 9 Glomeromycota. In: D. J. McLaughlin & J. W. Spatafora (eds), *Systematics and Evolution*. Springer, Berlin. pp. 251–269; **[21]** Strullu-Derrien, C., et al. (2014). Fungal associations in *Horneophyton ligneri* from the Rhynie Chert (c. 407 million year old) closely resemble those in extant lower land plants: novel insights into ancestral plant-fungus symbioses. *New Phytologist* 203(3): 964–979; **[22]** Vidrih, R. & Hribar, J. (2016). Mead: The oldest alcoholic beverage. In: K. Kristbergsson & J. Oliveira (eds), *Traditional Foods: General and Consumer Aspects*. Springer US, Boston, MA. pp. 325–338; **[23]** Bohannon, J (2009). Genetics: Rooting around the truffle genome. *Science* 323(5917): 1006–1007; **[24]** Dale, J., et al. (2017). Transgenic Cavendish bananas with resistance to *Fusarium* wilt tropical race 4. *Nature Communications* 8(1): 1496; **[25]** McMullan, M., et al. (2018). The ash dieback invasion of Europe was founded by two genetically divergent individuals. *Nature Ecology & Evolution* 381: 1–9; **[26]** Floudas, D., et al. (2012). The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 Fungal Genomes. *Science* 336(6089): 1715–1719; **[27]** Philippe, H., et al. (2011). Resolving difficult phylogenetic questions: Why more sequences are not enough. *PLoS Biol* 9(3): 1–10; **[28]** Delsuc, F., Brinkmann, H. & Philippe, H. (2005). Phylogenomics and the reconstruction of the tree of life. *Nature Reviews Genetics* 6(5): 361–375; **[29]** Kumar, S., et al. (2012). Statistics and truth in phylogenomics. *Molecular Biology and* Evolution 29(2): 457–472; **[30]** Hibbett, D. (2016). The invisible dimension of fungal diversity. *Science* 351(6278): 1148–1150; **[31]** Dentinger, B. T. M., et al. (2016). Tales from the crypt: Genome mining from fungarium specimens improves resolution of the mushroom tree of life. *Biological Journal of the Linnean Society* 117(1): 11–32; **[32]** Royal Botanic Gardens Kew. (2015). *2020 Strategic Outputs: Plant and Fungal Trees of Life 2015–2020*. Available from: http://www.kew.org/science/who-we-are-and-what-we-do/strategicoutputs-2020; **[33]** Joint Genome Institute. (2018). *1000 Fungal Genomes*. Available from: https://jgi.doe.gov/our-science/science-programs/fungal-genomics/1000-fungal-genomes/; **[34]** James, T. Y. & Berbee, M. L. (2011). No jacket required – new fungal lineage defies dress code. *BioEssays* 34(2): 94–102; **[35]** James, T. Y., et al. (2013). Shared signatures of parasitism and phylogenomics unite Cryptomycota and Microsporidia. *Curbio* 23(16): 1548–1553; **[36]** Berbee, M. L. & Taylor, J. W. (2010). Dating the molecular clock in fungi – how close are we? *Fungal Biology Reviews* 24(1-2): 1–16; **[37]** Taylor, T. N., Krings, M. & Taylor, E. L. (2014). *Fossil fungi*. Academic Press, San Diego, CA; **[38]** Cai, C., et al. (2017). Mycophagous rove beetles highlight diverse mushrooms in the Cretaceous. *Nature Communications* 8: 1–7; **[39]** Taylor, T. N., et al. (1995). Fossil arbuscular mycorrhizae from the Early Devonian. *Mycologia* 87(4):560–573; **[40]** Strullu-Derrien, C., et al. (2017). New insights into the evolutionary history of Fungi from a 407 Ma Blastocladiomycota fossil showing a complex hyphal thallus. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1739): 20160502; **[41]** Tedersoo, L., et al. (2014). Global diversity and geography of soil fungi. *Science* 346(6213): 1256688–8; **[42]** Tedersoo, L., et al. (2017). Novel soil-inhabiting clades fill gaps in the fungal tree of life. *Microbiome* 5(1): 42; **[43]** Hawksworth, D. L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4): FUNK-0052-2016; **[44]** Grantham, N. S., et al. (2015). Fungi identify the geographic origin of dust samples. *PLoS ONE* 10(4): e0122605; **[45]** Rosling, A., et al. (2011). Archaeorhizomycetes: Unearthing an ancient class of ubiquitous soil fungi. *Science* 333: 876–879; **[46]** Jones, M. D. M., et al. (2011). Discovery of novel intermediate forms redefines the fungal tree of life. *Nature* 474(7350): 200–203; **[47]** Nagy, L.G., et al. (2011). Where is the unseen fungal diversity hidden? A study of *Mortierella* reveals a large contribution of reference collections to the identification of fungal environmental sequences. *New Phytologist* 191(3): 789–794; **[48]** Grube, M., et al. (2017). The next generation fungal diversity researcher. *Fungal Biology Reviews* 31(3): 124–130.

3. New discoveries: Species of fungi described in 2017

Authors: Tuula Niskanen, Brian Douglas, Paul Kirk (RBG Kew & Institute of Microbiology, Chinese Academy of Sciences), Pedro Crous (Westerdijk Fungal Biodiversity Institute), Robert Lücking (Botanical Garden and Botanical Museum Berlin), P. Brandon Matheny (Department of Ecology and Evolutionary Biology, University of Tennessee), Lei Cai (State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences), Kevin Hyde (Center of Excellence in Fungal Research, Mae Fah Luang University) and Martin Cheek.

References: **[1]** Hawksworth, D. L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4): FUNK-0052-2016; **[2]** Index Fungorum Partnership (2018). *Index Fungorum*. Available from www.indexfungorum.org [Accessed 2 March 2018]; **[3]** Kučera, V., Lizoň, P. & Tomšovský, M. (2017). Taxonomic divergence of the green naked-stipe members of the genus *Microglossum* (Helotiales). *Mycologia* 109(1): 46–54; **[4]** Paz, A., et al. (2017). The genus *Elaphomyces* (Ascomycota, Eurotiales): a ribosomal DNA-based phylogeny and revised systematics of European 'deer truffles'. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 38: 197–239; **[5]** Matheny, P. B. & Bougher, N. L. (2017). *Fungi of Australia: Inocybaceae*. CSIRO Publishing, Clayton, VIC; **[6]** Ludwig, E. E. (2017). *Pilzkompendium, Band 4: Beschreibungen (Text Volume): Cortinariaceae (Galerina, Hebeloma, Hebelomina, Inocybe, Phaeogalera, Cortinarius Teil I mit den Untergattungen Cortinarius, Dermocybe, Leprocybe, Phlegmacium).* Fungicon-Verlag, Berlin; **[7]** Latha, K. P. D. & Manimohan, P. (2017). *Inocybes of Kerala*, SporePrint Books, Calicut; **[8]** Ammirati, J. F., et al. (2017). Spring and early summer species of *Cortinarius*, subgenus *Telamonia*, section *Colymbadini* and/ *Flavobasilis*, in the mountains of western North America. *Mycologia* 109(3): 443–458; **[9]** Castellano, M. A. & Stephens, R. B. (2017). *Elaphomyces* species (Elaphomycetaceae, Eurotiales) from Bartlett Experimental Forest, New Hampshire, USA. *IMA fungus* 8(1): 49–63; **[10]** Al-Yahya'ei, M. N., et al. (2017). *Dominikia emiratia* and *Rhizoglomus dunense*, two new species in the Glomeromycota. *Botany* 95(7): 629–639; **[11]** Marin-Felix, Y., et al. (2017). Genera of phytopathogenic fungi: GOPHY 1. *Studies in Mycology* 86: 99–216; **[12]** Guarnaccia, V., et al. (2017). High species diversity in *Colletotrichum* associated with citrus diseases in Europe. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 39: 32–50; **[13]** Diao, Y.-Z., et al. (2017). *Colletotrichum* species causing anthracnose disease of chili in China. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 38: 20; **[14]** Dean, R., et al. (2012). The Top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* 13(4): 414–430; **[15]** Willis, K. J. (ed.) (2016). *State of the World's Plants 2016*. Report. Royal Botanic Gardens Kew. Available from: https://stateoftheworldsplants.org; **[16]** Dissanayake, A., et al. (2017). The current status of species in *Diaporthe*. *Mycosphere* 8: 1106–1156; **[17]** Yang, Q., et al. (2017). *Diaporthe juglandicola* sp. nov. (Diaporthales, Ascomycetes), evidenced by morphological characters and phylogenetic analysis. *Mycosphere* 8: 817–826; **[18]** Guarnaccia, V. & Crous, P. W. (2017). Emerging citrus diseases in Europe caused by species of *Diaporthe*. *IMA fungus* 8(2): 317–334; **[19]** Gao, Y., et al. (2017). *Diaporthe* is paraphyletic. *IMA fungus* 8(1): 153–187; **[20]** Liu, F., et al. (2017). *Pestalotiopsis* and allied genera from *Camellia*, with description of 11 new species from China. *Scientific Reports* 7(1): 866; **[21]** Li, Y.-M., et al. (2017). Ten new species of *Macalpinomyces* on *Eriachne* in northern Australia. *Mycologia* 109 (3): 408-421; **[22]** Li, Y.-M., et al. (2017). Cryptic diversity in *Tranzscheliella* spp. (Ustilaginales) is driven by host switches. *Scientific Reports* 7: 43549; **[23]** Demers, J. E., et al. (2017). Rust fungi on *Panicum*. *Mycologia* 109(1): 1–17; **[24]** Spirin, V., Vlasák, J. & Miettinen, O. (2017). Studies in the *Antrodia serialis* group (Polyporales, Basidiomycota). *Mycologia* 109(2): 217–230; **[25]**

Tibpromma, S., et al. (2017). Fungal diversity notes 491–602: Taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 83(1): 1–261; **[26]** Chen, H. & Cui, B.-K. (2017). Multi-locus phylogeny and morphology reveal five new species of *Fomitiporia* (Hymenochaetaceae) from China. *Mycological Progress* 16(7): 687–701; **[27]** Ji, X.-H., et al. (2017). Phylogeny and diversity of *Fomitiporella* (Hymenochaetales, Basidiomycota). *Mycologia* 109(2): 308–322; **[28]** Yurchenko, E., Riebesehl, J. & Langer, E. (2017). Clarification of *Lyomyces sambuci* complex with the descriptions of four new species. *Mycological Progress* 16(9): 865–876; **[29]** Sklenář, F., et al. (2017). Phylogeny of xerophilic aspergilli (subgenus *Aspergillus*) and taxonomic revision of section *Restricti*. *Studies in Mycology* 88: 161–236; **[30]** Peterson, S. W. & Jurjević, Ž. (2017). New species of *Talaromyces* isolated from maize, indoor air, and other substrates. *Mycologia* 109(4): 537–556; **[31]** Jayasiri, S., et al. (2017). Taxonomy and multigene phylogenetic evaluation of novel species in *Boeremia* and *Epicoccum* with new records of *Ascochyta* and *Didymella* (Didymellaceae). *Mycosphere* 8(8): 1080–1101; **[32]** Elix, J. A., Kantvilas, G. & McCarthy, P. M. (2017). Thirteen new species and a key to buellioid lichens (Caliciaceae, Ascomycota) in Australia. *Australasian Lichenology* 81: 26–67; **[33]** Elix, J. A., Knight, A. & Blanchon, D. J. (2017). New species and new records of buellioid lichens (Physciaceae, Ascomycota) from New Zealand and Tasmania. *Australasian Lichenology* 80: 46–52; **[34]** Archer, A. W. & Elix, J. A. (2017). Seven new species and a new record in the lichen genus *Pertusaria* (Pertusariales, lichenized Ascomycota) from eastern Australia. *Australasian Lichenology* 80: 3–15; **[35]** Archer, A. W. & Elix, J. A. (2017). Seven new species of Australian *Pertusaria* (Pertusariales, lichenised Ascomycota) from New South Wales. *Telopea* 20: 325–333; **[36]** Gerlach, A., Clerc, P. & Borges da Silveira, R. (2017). Taxonomy of the corticolous, shrubby, esorediate, neotropical species of *Usnea* Adans. (Parmeliaceae) with an emphasis on southern Brazil. *The Lichenologist* 49(3): 199–238; **[37]** Michlig, A., et al. (2017). New species of the *Heterodermia comosa* group (Physciaceae, lichenized Ascomycota) from southern South America. *Cryptogamie Mycologie* 38(2): 155–167; **[38]** Aptroot, A., Gumboski, E. L. & da Silva Cáceres, M. E. (2017). New Arthoniales from Santa Catarina (South Brazil). *Cryptogamie Mycologie* 38(2): 275–281; **[39]** Dal Forno, M., et al. (2017). High levels of endemism among Galapagos basidiolichens. *Fungal Diversity* 85(1): 45–73; **[40]** Diederich, P., et al. (2017). New species and new records of lichens and lichenicolous fungi from the Seychelles. *Herzogia* 30(1): 182–236; **[41]** Luecking, R., Moncada, B. & Smith, C. W. (2017). The genus *Lobariella* (Ascomycota: Lobariaceae) in Hawaii: late colonization, high inferred endemism and three new species resulting from "micro-radiation". *The Lichenologist* 49(6): 673–691; **[42]** Sandoval-Leiva, P., et al. (2017). *Lichenomphalia altoandina*, a new species of Hygrophoraceae from the Chilean Altiplano. *Mycologia* 109(1): 92–99; **[43]** Thorn, R. G., et al. (2017). The golden chanterelles of Newfoundland and Labrador: a new species, a new record for North America, and a lost species rediscovered. *Botany* 95(6): 547–560; **[44]** Buyck, B., et al. (2017). Fungal Biodiversity Profiles 21–30. *Cryptogamie Mycologie* 38(1): 101–146; **[45]** Antonín, V., et al. (2017). New *Cantharellus* species from the Republic of Korea. *Mycological Progress* 16(8): 753–759; **[46]** Chakraborty, D., et al. (2017). A new species of porcini mushroom from India with morphology and phylogeny. *Nova Hedwigia*: 197–204; **[47]** Merényi, Z., Varga, T. & Bratek, Z. (2016). *Tuber brumale*: A Controversial *Tuber* Species. In: A. Zambonelli, M. Iotti & C. Murat (eds), *True Truffle (Tuber spp.) in the World*. Springer, Berlin. pp. 49–68; **[48]** He, M.-Q., et al. (2017). Tropic origins, a dispersal model for saprotrophic mushrooms in *Agaricus* section *Minores* with descriptions of sixteen new species. *Scientific Reports* 7(1): 5122; **[49]** Zhang, Z., et al. (2017). Culturable mycobiota from Karst caves in China, with descriptions of 20 new species. Persoonia – Molecular Phylogeny and Evolution of Fungi 39(1): 1–31; **[50]** Crous, P., et al. (2017). Fungal Planet description sheets: 558–624. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 38: 240–384; **[51]** Hyde, K. D., et al. (2017). Fungal diversity notes 603–708: taxonomic and phylogenetic notes on genera and species. *Fungal Diversity* 87(1): 1–235; **[52]** Crous, P. W., et al. (2017). Fungal Planet description sheets: 625–715. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 39: 270–467; **[53]** Mohamed, A., et al. (2017). New saprobic marine fungi and a new combination. *Botanica Marina* 60(4): 469–488; **[54]** Tanney, J., et al. (2017). *Aspergillus* subgenus *Polypaecilum* from the built environment. *Studies in Mycology* 88: 237–267.

4. Useful fungi

Authors: Thomas Prescott, Joanne Wong (Novartis Institutes for BioMedical Research), Barry Panaretou (King's College London), Eric Boa (University of Aberdeen), Angela Bond, Shaheenara Chowdhury, Lee Davies and Lars Østergaard (Novozymes A/S).

References: **[1]** Knowledge Sourcing Intelligence. (2017). Global edible mushrooms market – Industry trends, opportunities and forecasts to 2023. Report. Available from: https://www.knowledge-sourcing.com/products/global-edible-mushrooms-market-industry-trends-opportunities-and-forecasts-to-2023; **[2]** Boa, E. R. (2004). *Non-wood Forest Products. Wild edible fungi: A global overview of their use and importance to people*. Technical paper. Food and Agriculture Organization of the United Nations, Rome. Available from: http://www.fao.org/docrep/018/y5489e/y5489e.pdf; **[3]** Baars, J. (2017). Fungi as Food. In: K. Kavanagh (ed.), *Fungi: Biology and Applications*. 3rd ed. John Wiley & Sons, Hoboken, NJ; **[4]** Royse, D. J., Baars, J. & Tan, Q. (2017). Current overview of mushroom production in the world. In: D. C. Zied & A. Pardo-Giménez (eds), *Edible and Medicinal Mushrooms: Technology and Applications.* John Wiley & Sons, NJ. pp. 5–13; **[5]** Wiebe, M. G. (2002). Myco-protein from *Fusarium venenatum*: A well-established product for human consumption. *Applied Microbiology and Biotechnology* 58(4): 421–427; **[6]** Ropars, J., et al. (2012). A taxonomic and ecological overview of cheese fungi. *International Journal of Food Microbiology* 155(3): 199–210; **[7]** Banjara, N., Suhr, M. J. & Hallen-Adams, H. E. (2015). Diversity of yeast and mold species from a variety of cheese types. *Current microbiology* 70(6): 792–800; **[8]** Gillot, G., et al. (2015). Insights into *Penicillium roqueforti* morphological and genetic diversity. *PLoS One* 10(6): e0129849; **[9]** Ropars, J., et al. (2017). Blue cheese-making has shaped the population genetic structure of the mould *Penicillium roqueforti*. *PLoS One* 12(3): e0171387; **[10]** Dentinger, B. T. & Suz, L. M. (2014). What's for dinner? Undescribed species of porcini in a commercial packet. *PeerJ* 2: e570; **[11]** Aly, A. H., Debbab, A. & Proksch, P. (2011). Fifty years of drug discovery from fungi. *Fungal Diversity* 50: 3–19; **[12]** Borel, J. F., Kis, Z. L. & Beveridge, T. (1995). The history of the discovery and development of cyclosporine (Sandimmune®). In: V. J. Merluzzi & J. Adams (eds), *The Search for Anti-Inflammatory Drugs*. Birkhäuser, Boston. pp. 27–63; **[13]** Houbraken, J., Frisvad, J. C. & Samson, R. A. (2011). Fleming's penicillin producing strain is not *Penicillium chrysogenum* but *P. rubens*. *IMA Fungus* 2(1): 87–95; **[14]** Stierle, A. A. & Stierle, D. B. (2015). Bioactive secondary metabolites produced by the fungal endophytes of conifers. *Natural Product Communications* 10(10): 1671–1682; **[15]** Kusari, S., Zuhlke, S. & Spiteller, M. (2009). An endophytic fungus from *Camptotheca acuminata* that produces camptothecin and analogues. *Journal of Natural Products* 72(1): 2–7; **[16]** Kumar, A., et al. (2013). Isolation, purification and characterization of vinblastine and vincristine from endophytic fungus *Fusarium oxysporum* isolated from *Catharanthus roseus*. *PLoS One* 8(9): e71805; **[17]** Nielsen, J. (2013). Production of biopharmaceutical proteins by yeast: advances through metabolic engineering. *Bioengineered* 4(4): 207–211; **[18]** Berlec, A. & Strukelj, B. (2013). Current state and recent advances in biopharmaceutical production in *Escherichia coli*, yeasts and mammalian cells. *Journal of Industrial Microbiology & Biotechnology* 40(3–4): 257–274; **[19]** McAleer, W. J., et al. (1984). Human hepatitis B vaccine from recombinant yeast. *Nature* 307(5947): 178–180; **[20]** Raskin, P. & Clements, R. S. Jr. (1991). The use of human insulin derived from baker's yeast by recombinant DNA technology. *Clinical Therapeutics* 13(5): 569–578; **[21]** Perdoni, F., et al. (2015). Antifungal activity of Myriocin on clinically relevant *Aspergillus fumigatus* strains producing biofilm. *BMC Microbiology* 15: 248; **[22]** Dreyfuss, M., et al. (1976). Cyclosporin A and C. New metabolites from *Trichoderma polysporum*. *European Journal of Applied Microbiology* 3(2): 125–133; **[23]** Schneweis, I., et al. (2000). Mycophenolic acid in silage. *Applied Environmental Microbiology* 66(8): 3639–3641; **[24]** Qiao, J., et al. (2007). Antifungal activity of statins against *Aspergillus* species. *Medical Mycology* 45(7): 589–593; **[25]** Kachroo, A. H., et al. (2015). Evolution. Systematic humanization of yeast genes reveals conserved functions and genetic modularity. *Science* 348(6237): 921–925; **[26]** Leszczynska, A., et al. (2009). Investigating the effects of statins on cellular lipid metabolism using a yeast expression system. *PLoS One*

4(12): e8499; **[27]** Rusnak, F. & Mertz, P. (2000). Calcineurin: form and function. *Physiological Reviews* 80(4): 1483–1521; **[28]** Chen, J. K., Lane, W. S. & Schreiber, S. L. (1999). The identification of myriocin-binding proteins. *Chemistry & Biology* 6(4): 221–235; **[29]** Desmoucelles, C., et al. (2002). Screening the yeast "disruptome" for mutants affecting resistance to the immunosuppressive drug, mycophenolic acid. *Journal of Biological Chemistry* 277(30): 27036–27044; **[30]** Hodge, K., et al (1996). *Tolypocladium inflatum* is the anamorph of *Cordyceps subsessilis*. *Micologia* 88: 715–719; **[31]** Adachi, K. & Chiba, K. (2007). FTY720 story. Its discovery and the following accelerated development of sphingosine 1-phosphate receptor agonists as immunomodulators based on reverse pharmacology. *Perspectives in Medicinal Chemistry* 1: 11–23; **[32]** Fiolka, M. J. (2008). Immunosuppressive effect of cyclosporin A on insect humoral immune response. *Journal of Invertebrate Pathology* 98(3): 287–292; **[33]** de Melo, N. R., et al. (2013). Myriocin significantly increases the mortality of a non-mammalian model host during *Candida* pathogenesis. *PLoS One* 8(11): e78905; **[34]** Higginbotham, S. J., et al. (2013). Bioactivity of fungal endophytes as a function of endophyte taxonomy and the taxonomy and distribution of their host plants. *PLoS One* 8(9): e73192; **[35]** HyphaDiscovery (2018). Natural Product Libraries. Available from: http://www.hyphadiscovery.co.uk/our-services/natural-product-libraries/ [Accessed 19 March 2018]; **[36]** Abate, T. (2003). *The Biotech Investor: How to Profit from the Coming Boom in Biotechnology*, Henry Holt & Company, NY. pp. 147–167; **[37]** Imran, M., et al. (2016). Cellulase production from species of fungi and bacteria from agricultural wastes and its utilization in industry: A review. *Advances in Enzyme Research* 4: 44–55; **[38]** Sajith, S., et al. (2016). An overview on fungal cellulases with an industrial perspective. *Journal of Nutrition & Food Sciences* 6: 461; **[39]** Dunn, C., Wolfaardt, F. & Wingfield, M. J. (2002). Pathogenicity of *Ophiostoma piliferum* (Cartapip 97®) compared with that of other South African sap-staining fungi. *South African Journal of Science* 98(7–8): 401–403; **[40]** Hasan, F., et al. (2010). Enzymes used in detergents: lipases. *African Journal of Biotechnology* 9(31): 4836–4844; **[41]** Bhat, M. K. (2000). Cellulases and related enzymes in biotechnology. *Biotechnology Advances* 18(5): 355–383; **[42]** Tolan, J. (2002). Iogen's process for producing ethanol from cellulosic biomass. *Clean Technologies and Environmental Policy* 3: 339–345; **[43]** Mathew, G., et al (2008). Progress in research on fungal cellulases for lignocellulose degradation. *Journal of Scientific and Industrial Research* 67: 898–907; **[44]** Saini, J. K., Saini, R. & Tewari, L. (2015). Lignocellulosic agriculture wastes as biomass feedstocks for second-generation bioethanol production: concepts and recent developments. *3 Biotech* 5(4): 337–353; **[45]** Automotive Design & Production. (2016). *Nissan's ethanol-powered fuel cell vehicle*. Available from https://www.adandp.media/articles/nissans-ethanol–powered-fuel-cell-vehicle. [Accessed 19 March 2018]; **[46]** Zahn, L. M. & Riddihough, G. (2017). Building on nature's design. *Science* 355(6329): 1038–1039; **[47]** Richardson, S. M., et al. (2017). Design of a synthetic yeast genome. *Science* 355(6329): 1040–1044; **[48]** Holmes, B. (2017). Five designer chromosomes bring synthetic life a step closer. *New Scientist*, Daily News 9 March 2017. Available from: https://www.newscientist.com/article/2124052-five-designer-chromosomes-bring-synthetic-life-a-step-closer/; **[49]** Näsi, M., Partanen, K. & Piironen, J. (1999). Comparison of *Aspergillus niger* phytase and *Trichoderma reesei* phytase and acid phosphatase on phytate phosphorus availability in pigs fed on maize-soybean meal or barley-soybean meal diets. *Archives of Animal Nutrition* 52(1): 15–27; **[50]** Kashyap, P. L., et al. (2017). *Trichoderma* for climate resilient agriculture. *World Journal of Microbiology and Biotechnology* 33(8): 155; **[51]** Van Dingenen, J., et al. (2017). Strobilurins as growth-promoting compounds: How Stroby regulates *Arabidopsis* leaf growth. *Plant, Cell & Environment* 40(9): 1748–1760; **[52]** Dorner, J. W. & Lamb, M. C. (2006). Development and commercial use of afla-Guard® , an aflatoxin biocontrol agent. *Mycotoxin Research* 22(1): 33–38; **[53]** Show, P. L., et al. (2015). Overview of citric acid production from *Aspergillus niger*. *Frontiers in Life Science* 8(3): 271–283; **[54]** Pavezzi, F. C., Gomes, E. & da Silva, R. (2008). Production and characterization of glucoamylase from fungus *Aspergillus awamori* expressed in yeast *Saccharomyces cerevisiae* using different carbon sources. *Brazilian Journal of Microbiology* 39(1): 108–114; **[55]** Stella, T., et al. (2017). Bioremediation of long-term PCB-contaminated soil by white-rot fungi. *Journal of Hazardous Materials* 324(Pt B): 701–710; **[56]** Walter, M., et al. (2005). Field-scale bioremediation of pentachlorophenol by *Trametes versicolor*. *International Biodeterioration & Biodegradation* 56(1): 51–57; **[57]** Østergaard, L. H. & Olsen, H. S. (2011). *Industrial applications of fungal enzymes*. Springer, Heidelberg; **[58]** Poutanen, K. (1997). Enzymes: An important tool in the improvement of the quality of cereal foods. *Trends in Food Science & Technology* 8(9): 300–306; **[59]** Dufosse, L., et al. (2014). Filamentous fungi are large-scale producers of pigments and colorants for the food industry. *Current Opinions in Biotechnology* 26: 56–61; **[60]** Bull, S. M., Yong, F. M. & Wong, H. A. (1985). The production of aroma by *Aspergillus oryzae* during the preparation of soy sauce koji. *Food chemistry* 17(4): 251–264; **[61]** Wang, H. L., Swain, E.W. & Hessel Tine, C.W. (1975). Mass production of *Rhizopus oligosporus* spores and their application in tempeh fermentation. *Journal of Food Science* 40(1): 168–170; **[62]** Guzmán, G., Allen, J. W. & Gartz, J. (2000). A worldwide geographical distribution of the neurotropic fungi, an analysis and discussion. *Annali del Museo Civico di Rovereto: Sezione: Archeologia, Storia, Scienze Naturali* 14: 189–280; **[63]** Thanikaivelan, P., et al. (2004). Progress and recent trends in biotechnological methods for leather processing. *Trends in Biotechnology* 22(4): 181–188; **[64]** Singh, R., et al. (2016). Microbial enzymes: industrial progress in 21st century. *3 Biotech* 6(2): 174; **[65]** Jia, L., et al. (2017). Identification and characterization of the steroid 15alpha-hydroxylase gene from *Penicillium raistrickii*. *Applied Microbiology and Biotechnology* 101(16): 6409–6418; **[66]** Al-Imam, A. (2014). Fermentative itaconic acid production. *Journal of Biodiversity, Bioprospecting and Development* 1(1): 1–8; **[67]** Kristiansen, S. (2018). *The LEGO Group 2030 sustainable materials challenge. The approach and learnings*. Available from: https://universe.ida.dk/meetupfiles/download/?meetupNumber=325506&fileid=236ed46f-07ba-4c91-bdbc-3a208ac7d83d; **[68]** Schiffman, R. (2013). Mushrooms are the new styrofoam. *New Scientist* (2921). Interview, 12 June 2013. Available from: https://www.newscientist.com/article/mg21829210-300-mushrooms-are-the-new-styrofoam/; **[69]** Mycoworks. (2017). Available from: http://www.mycoworks.com/ [Accessed 19 March 2018]; **[70]** Haneef, M., et al. (2017). Advanced materials from fungal mycelium: Fabrication and tuning of physical properties. *Scientific Reports* 7: 41292; **[71]** Nobel Media AB 2014. (2018). All Nobel laureates in physiology or medicine. Available from: https://www.nobelprize.org/nobel_prizes/medicine/laureates/ [Accessed 19 March 2018]; **[72]** Kato, T. & Park, E. Y. (2012). Riboflavin production by *Ashbya gossypii*. *Biotechnology Letters* 34(4): 611–618; **[73]** Maheshwari, R., Bharadwaj, G. & Bhat, M.K. (2000). Thermophilic fungi: their physiology and enzymes. *Microbiology and Molecular Biology Reviews* 64(3): 461–488; **[74]** Eschenauer, G., Depestel, D. D. & Carver, P. L. (2007). Comparison of echinocandin antifungals. *Therapeutics and Clinical Risk Management* 3(1): 71–97; **[75]** van den Heever, J. P., et al. (2014). Fumagillin: An overview of recent scientific advances and their significance for apiculture. *Journal of Agricultural and Food Chemistry* 62(13): 2728–2737; **[76]** Jekkel, A., et al (2001). Microbiological transformation of mycophenolic acid. *Journal of Molecular Catalysis B: Enzymatic* 11: 423–426; **[77]** El Enshasy, H. (2010). *Immunomodulators*. Springer, Heidelberg; **[78]** Mizuno, K., et al. (1974). Studies on bredinin. I. Isolation, characterization and biological properties. *Journal of Antibiotics (Tokyo)* 27(10): 775–782; **[79]** Zécri, F. J. (2016). From natural product to the first oral treatment for multiple sclerosis: The discovery of FTY720 (Gilenya™)? *Current Opinions in Chemical Biology* 32: 60–66; **[80]** Tfelt-Hansen, P., et al. (2000). Ergotamine in the acute treatment of migraine: a review and European consensus. *Brain* 123(Pt 1): 9–18; **[81]** Paukner, S. & Riedl, R. (2017). Pleuromutilins: Potent drugs for resistant bugs-mode of action and resistance. *Cold Spring Harbor Perspectives in Medicine* 7(1): a027110; **[82]** Ina, K., Kataoka, T. & Ando, T. (2013). The use of lentinan for treating gastric cancer. *Anticancer Agents in Medicinal Chemistry* 13(5): 681–688; **[83]** Palmer, E. (2018). Gilenya – Novartis. Online report. Available from: https://www.fiercepharma.com/special-report/gilenya-novartis [Accessed 19 March 2018]; **[84]** Association of Manufacturers and Formulators of Enzyme Products. (2015). List of commercial enzymes. Available from: https://amfep.org/_library/_files/Amfep_List_of_Enzymes_update_May_2015.pdf [Accessed 19 March 2018].

5. Positive plant–fungal interactions

Authors: Laura M. Suz, Viswambharan Sarasan, James A. Wearn, Martin I. Bidartondo (Imperial College London & RBG Kew) Trevor R. Hodkinson (Trinity College Dublin), Jill Kowal (Natural History Museum, London), Brian R. Murphy (Trinity College Dublin), Rusty J. Rodriguez (University of Washington) and Alan Gange (Royal Holloway, University of London).

References: **[1]** Schulz, C. & Boyle, C. (2005). The endophytic continuum. *Mycological Research* 109: 661–686; **[2]** Smith, S. E. & Read, D. E. (2008). *Mycorrhizal symbiosis*. 3rd ed. Academic Press, London; **[3]** Rodriguez, R. J., et al. (2009). Fungal endophytes: diversity and functional roles. *New Phytologist* 182: 314–330; **[4]** Frank, A. (1877). Über die biologishen Verhältnisse des Thalles eininger Krustenflechten. *Beitrage zur biologie der Pflanzen* 2: 123–200; **[5]** De Bary, A. (1879). *Die Erscheinung der Symbiose*. Karl J. Trübner, Strassbourg; **[6]** Arnold, A. E. (2007). Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. *Fungal Biology Reviews* 21: 51–66; **[7]** Clay, K. & Holah, J. (1999). Fungal endophyte symbiosis and plant diversity in successional fields. *Science* 285: 1742–1744; **[8]** Redman, R. S., et al. (2002). Thermotolerance generated by plant/fungal symbiosis. *Science* 298: 1581–1581; **[9]** Selosse, M. A. & Schardl, C. L. (2007). Fungal endophytes of grasses: hybrids rescued by vertical transmission? An evolutionary perspective. *New Phytologist* 173: 452–458; **[10]** Jumpponen, A. (2001). Dark septate endophytes: a review of facultative biotrophic root colonizing fungi. *New Phytologist* 140: 295–310; **[11]** Mastouri, F., Björkman, T. & Harman, G. E. (2010). Seed treatment with *Trichoderma harzianum* alleviates biotic, abiotic, and physiological stresses in germinating seeds and seedlings. *Phytopathology* 100: 1213–1221; **[12]** Shoresh, M., Harman, G. E. & Mastouri, F. (2010). Induced systemic resistance and plant responses to fungal biocontrol agents. *Annual Review of Phytopathology* 48: 21–43; **[13]** Hidangmayum, A. & Dwivedi, P. (2018). Plant responses to *Trichoderma* spp. and their tolerance to abiotic stresses: A review. *Journal of Pharmacognosy and Phytochemistry* 7(1): 758–66; **[14]** Willis, K. J. & McElwain, J. C. (2013). *The Evolution of Plants*. Oxford University Press; **[15]** Brundrett, M. C., Tedersoo, L., (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*. Advance online publication, 22 January 2018. doi: https://doi.org/10.1111/nph.14976; **[16]** van der Heijden, M. G. A., et al. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytologist* 205: 1406–1423; **[17]** Kohler, A., et al. (2015). Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics* 47(4): 410–415; **[18]** Clemmensen, K. E., et al. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339: 1615–1618; **[19]** Averill, C., Turner, B. L. & Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505: 543–545; **[20]** Fernandez, C. W. & Kennedy, P. G. (2015). Revisiting the 'Gadgil effect': Do interguild fungal interactions control carbon cycling in forest soils? *New Phytologist* 209: 1382–1394; **[21]** Abbott, L. K. & Johnson, N. C. (2017). Chapter 6 – Introduction: Perspectives on mycorrhizas and soil fertility. In: N. Johnson, C. Gehring & J. Jansa (eds), *Mycorrhizal Mediation of Soil. Fertility, Structure, and Carbon Storage*. Elsevier, Amsterdam. pp. 93–105. doi: https://doi.org/10.1016/B978-0-12-804312-7.00006-1; **[22]** Gange, A. C. & Smith, A. K. (2005). Arbuscular mycorrhizal fungi influence visitation rates of pollinating insects. *Ecological Entomology* 30: 600–606; **[23]** Hobbie, J. E. & Hobbie, E. A. (2006). N-15 in symbiotic fungi and plants estimates nitrogen and carbon flux rates in Arctic tundra. *Ecology* 87, 816–822; **[24]** Booth M. G. (2004). Mycorrhizal networks mediate overstorey-understorey competition in a temperate forest. *Ecology Letters* 7: 538–546; **[25]** Teste, F. P. & Simard, S. W. (2008). Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia* 158: 193–203; **[26]** van der Heijden, M. G. A. & Horton, T. R. (2009). Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* 97: 1139–1150; **[27]** Moore, B. D. & Johnson, S. N. (2017). Get tough, get toxic, or get a bodyguard: Identifying candidate traits conferring belowground resistance to herbivores in grasses. *Frontiers in Plant Science* 7: 1925. Published online 5 January 2017. doi: https://doi.org/10.3389/fpls.2016.01925; **[28]** van der Heijden, M. G. A., et al. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72; **[29]** Kernaghan, G. (2005). Mycorrhizal diversity: Cause and effect? *Pedobiologia* 49: 511–520; **[30]** Rasmann, S., et al. (2017). Root symbionts: Powerful drivers of plant above- and belowground indirect defenses. *Insect Science* 24: 947–960; **[31]** Gange, A. C., Stagg, P. G. & Ward, L. K. (2002). Arbuscular mycorrhizal fungi affect phytophagous insect specialism. *Ecology Letters* 5: 11–15; **[32]** Gange, A. C., Brown, V. K. & Aplin, D. M. (2003). Multitrophic links between arbuscular mycorrhizal fungi and insect parasitoids. *Ecology Letters* 6: 1051–1055; **[33]** Gange, A. C., et al. (2012). Differential effects of foliar endophytic fungi on insect herbivores attacking a herbaceous plant. *Oecologia* 168: 1023–1031; **[34]** Saikkonen, K., Gundel, P. E. & Helander, M. (2013). Chemical ecology mediated by fungal endophytes in grasses. *Journal of Chemical Ecology* 39: 962–968; **[35]** Hartley, S. E., et al. (2015). Infection by a foliar endophyte elicits novel arabidopside-based plant defence reactions in its host, *Cirsium arvense*. *New Phytologist* 205: 816–827; **[36]** Jaber, L. R. & Ownley, B. H. (2018). Can we use entomopathogenic fungi as endophytes for dual biological control of insect pests and plant pathogens? *Biological Control* 116: 36–45; **[37]** Le Cocq, K., et al. (2017). Exploitation of endophytes for sustainable agricultural intensification. *Molecular Plant Pathology* 18: 469–473; **[38]** Murphy, B. R., Doohan, F. M. & Hodkinson, T. R. (2018). From concept to commerce: developing a successful fungal endophyte inoculant for agricultural crops. *Journal of Fungi* 4: 24. Published online 11 February 2018. doi: https://doi.org/10.3390/jof4010024; **[39]** Ijdo, M., Cranenbrouck, S. & Declerck, S. (2011). Methods for large-scale production of AM fungi: past, present, and future. *Mycorrhiza* 21: 1–16; **[40]** Vosatka, M., et al. (2012). Development of arbuscular mycorrhizal biotechnology and industry: current achievements and bottlenecks. *Symbiosis* 58: 29–37; **[41]** Rocha, I., et al. (2018). Seed coating with inocula of arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria for nutritional enhancement of maize under different fertilisation regimes. *Archives of Agronomy and Soil Science*. Published online 31 May 2018. doi: https://doi.org/10.1080/03650340.2018.1479061; **[42]** Ceballos, I., et al. (2013). The *in vitro* mass-produced model mycorrhizal fungus, *Rhizophagus irregularis*, significantly increases yields of the globally important food security crop *Cassava*. *PLoS ONE* 8(8): e70633; **[43]** Zhang, L., et al. (2016). Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. *New Phytologist* 210(3): 1022–1032; **[44]** Harman, G. E. (2011). Multifunctional fungal plant symbionts: new tools to enhance plant growth and productivity. *New Phytologist* 189: 647–649; **[45]** Hubbard, M., Germida, J. J. & Vujanovic, V. (2014). Fungal endophytes enhance wheat heat and drought tolerance in terms of grain yield and second-generation seed viability. *Journal of Applied Microbiology.* 116: 109–122; **[46]** Murphy, B. R., et al. (2015). Profundae diversitas: the uncharted genetic diversity in a newly studied group of fungal root endophytes. *Mycology* 6, 139–150; **[47]** Lacava, P. T. & Azevedo, J. L. (2014). Biological control of insect-pest and diseases by endophytes. In: V. C. Verma & A. C. Gange (eds), *Advances in Endophytic Research*. Springer, New Delhi. pp. 231–256. doi: https://doi.org/10.1007/978-81-322-1575-2_13; **[48]** Griffin, M. R. (2014). Biocontrol and bioremediation: Two areas of endophytic research which hold great promise. In: V. C. Verma & A. C. Gange (eds), *Advances in Endophytic Research*. Springer, New Delhi. pp. 257–282. doi: https://doi.org/10.1007/978-81-322-1575-2_14; **[49]** Essahibi, A., et al. (2018). Influence of arbuscular mycorrhizal fungi on the functional mechanisms associated with drought tolerance in carob (*Ceratonia siliqua* L.). *Trees* 32: 87–97; **[50]** Kivlin, S. N., Emery, S. M. & Rudgers, J. A. (2013). Fungal symbionts alter plant responses to global change. *American Journal of Botany*: 100: 1445–1457; **[51]** Querejeta, J. I., Egerton-Warburton, L. M. & Allen, M. F. (2007). Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. *Soil Biology and Biochemistry* 39: 409–417; **[52]** Egerton-Warburton, L. M., Querejeta, J. I. & Allen, M. F. (2007). Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *Journal of Experimental Botany* 58: 1473–1483; **[53]** Kowal, J., et al. (2016). Liverworts to the rescue: an investigation of their efficacy as mycorrhizal inoculum for vascular plants. *Functional Ecology* 30: 1014–1023; **[54]** Redman, R. S. & Rodriguez. R. J. (2017). The symbiogenic tango: achieving climate-resilient crops via mutualistic plant-fungal relationships. In: S. L. Doty (ed), *Functional Importance of the Plant*

Microbiome. Springer International Publishing, Cham. pp. 71–87; **[55]** Johnson, N. C. & Jansa, J. (2017). Chapter 1 – Mycorrhizas: At the interface of biological, soil, and earth sciences. In: N. Johnson, C. Gehring & J. Jansa (eds), *Mycorrhizal Mediation of Soil. Fertility, Structure, and Carbon Storage*. Elsevier, Amsterdam. pp. 1–6. doi: https://doi.org/10.1016/B978-0-12-804312-7.00001-2; **[56]** Leopold, D. R. (2016). Ericoid fungal diversity: Challenges and opportunities for mycorrhizal research. *Fungal Ecology* 24: 114–123; **[57]** Walker, J. F., et al. (2011). Diverse Helotiales associated with the roots of three species of Arctic Ericaceae provide no evidence for host specificity. *New Phytologist* 191: 515–527; **[58]** Kowal, J., et al. (2018). From rhizoids to roots? Experimental evidence of mutualism between liverworts and ascomycete fungi. *Annals of Botany* 121: 221–227; **[59]** Bidartondo, M. I. & Read, D. J. (2008). Fungal specificity bottlenecks during orchid germination and development. *Molecular Ecology* 17: 3707–3716; **[60]** Stöckel M., et al. (2014). Carbon and nitrogen gain during the growth of orchid seedlings in nature. *New Phytologist* 202: 606–615; **[61]** Fochi V., et al. (2016). Fungal and plant gene expression in the *Tulasnella calospora–Serapias vomeracea* symbiosis provides clues about nitrogen pathways in orchid mycorrhizas. *New Phytologist* 213: 365–379; **[62]** Rasmussen, H. N., et al. (2015). Germination and seedling establishment in orchids: a complex of requirements. *Annals of Botany* 116(3): 391–402; **[63]** Swarts, N. D. & Dixon, K. W. (2009). Terrestrial orchid conservation in the age of extinction. *Annals of Botany* 104: 543–556; **[64]** Rafter, M., et al. (2016). Non-specific symbiotic germination of *Cynorkis purpurea* (Thouars) Kraezl., a habitat-specific terrestrial orchid from the Central Highlands of Madagascar. *Mycorrhiza* 26(6): 541–552; **[65]** Yokoya, K., et al. (2015). Preliminary findings on identification of mycorrhizal fungi from diverse orchids in the Central Highlands of Madagascar. *Mycorrhiza* 25: 611–625.

6. Fungal genomes: Exploring, understanding and utilising their diversity

Authors: Ilia J. Leitch, Pepijn Kooij, Timothy Coker, Igor V. Grigoriev (U.S. Department of Energy, Joint Genome Institute), László Nagy (Biological Research Centre, Hungarian Academy of Sciences), Francis Martin (INRA Université de Lorraine), Jason Stajich (University of California, Riverside), Bryn Dentinger (University of Utah) and Ester Gaya.

References: **[1]** Beadle, G. W. & Tatum, E. L. (1941). Genetic control of biochemical reactions in *Neurospora*. *Proceedings of the National Academy of Sciences (USA)* 27: 499–506; **[2]** Hoffman, C. S., Wood, V. & Fantes, P. A. (2015). An ancient yeast for young geneticists: A primer on the *Schizosaccharomyces pombe* model system. *Genetics* 201(2): 403–423; **[3]** Menezes, R., et al. (2015). From the baker to the bedside: yeast models of Parkinson's disease. *Microbial Cell* 8(2): 262–279; **[4]** Stajich, J., E. (2017). Fungal genomes and insights into the evolution of the Kingdom. *Microbiol Spectrum* 5(4): FUNK-0055-2016; **[5]** Galagan, J. E., et al. (2005). Genomics of the fungal kingdom: Insights into eukaryotic biology. *Genome Research* 15(12): 1620–1631; **[6]** Grigoriev, I. V., et al. (2011). Fueling the future with fungal genomics. *Mycology* 2(3): 192–209; **[7]** Aylward, J., et al. (2017). A plant pathology perspective of fungal genome sequencing. *IMA Fungus* 8(1): 1–15; **[8]** Wu, W., et al. (2016). Rapid discovery and functional characterization of terpene synthases from four endophytic Xylariaceae. *PLoS ONE* 11(2): e0146983; **[9]** Goffeau, A., et al. (1996). Life with 6000 genes. *Science* 274(5287): 546–567; **[10]** Broad Institute. (2018). *Fungal Genomics*. Available from: https://www.broadinstitute.org/fungal-genome-initiative [Accessed 15 April 2018]; **[11]** Spatafora, J. (2011). 1000 fungal genomes to be sequenced. *IMA Fungus* 2: 41–45; **[12]** Joint Genome Institute. (2018). *1000 Fungal Genomes*. Available from: https://jgi.doe.gov/our-science/science-programs/fungal-genomics/1000-fungal-genomes/ [Accessed April 2018]; **[13]** Mycorrhizal Genomics Initiative. (2012). JGI CSP 2011: Exploring the genome diversity of mycorrhizal fungi to understand the evolution and functioning of symbiosis in woody shrubs and trees. Available from http://mycor.nancy.inra.fr/IMGC/MycoGenomes/ [Posted October 4 2012; Accessed April 2018]; **[14]** Grigoriev, I. V., et al. (2014). MycoCosm portal: gearing up for 1000 fungal genomes. *Nucleic Acids Research* 42(D1): D699–D704; **[15]** National Center for Biotechnology Information. (2018). *NCBI Genome Database* (2018). Available from: https://www.ncbi.nlm.nih.gov/genome/ [Accessed 31 March 2018]; **[16]** Hawksworth, D. L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4): FUNK-0052-2016; **[17]** Kirk, P. M., et al. (eds) (2008). *Ainsworth & Bisby's Dictionary of the Fungi*. 10th Ed. CAB International, Wallingford; **[18]** Spatafora, J. W., et al. (2017). The fungal tree of life: from molecular systematics to genome-scale phylogenies. *Microbiology Spectrum* 5(5): FUNK-0053-2016; **[19]** Nagy, L. G. & Szöllősi, G. (2017). Fungal phylogeny in the age of genomics: Insights into phylogenetic inference from genome-scale datasets. In: J. P. Townsend & Z. Wang (eds), *Fungal Phylogenetics and Phylogenomics*. Academic Press, Cambridge, MA. *Advances in Genetics* 100: 49–72; **[20]** Jones, T., et al. (2004). The diploid genome sequence of *Candida albicans*. *Proceedings of the National Academy of Sciences of the United States of America* 101(19): 7329–7334; **[21]** Brown, G. D., et al. (2012). Hidden killers: Human fungal infections. *Science Translational Medicine* 4: 165rv113; **[22]** Goranov, A. I. & Madhani, H. D. (2015). Functional profiling of human fungal pathogen genomes. *Cold Spring Harbor Perspectives in Medicine* 5(3): a019596; **[23]** Nielsen, J. C., et al. (2017). Global analysis of biosynthetic gene clusters reveals vast potential of secondary metabolite production in *Penicillium* species. *Nature Microbiology* 2: 17044; **[24]** Cuomo, C. A. (2017). Harnessing whole genome sequencing in medical mycology. *Current Fungal Infection Reports* 11(2): 52–59; **[25]** Heisel, T., et al. (2017). High-fat diet changes fungal microbiomes and interkingdom relationships in the murine gut. *mSphere* 2(5): e00351–00317; **[26]** Dean, R., et al. (2012). The Top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology* 13(4): 414–430; **[27]** Langner, T., Bialas, A. & Kamoun, S. (2018). The Blast Fungus decoded: Genomes in flux. *mBio* 9(2): e00571–00518; **[28]** Plissonneau, C., et al. (2017). Using population and comparative genomics to understand the genetic basis of effector-driven fungal pathogen evolution. *Frontiers in Plant Science* 8: 119; **[29]** Möller, M. & Stukenbrock, E. H. (2017). Evolution and genome architecture in fungal plant pathogens. *Nature Reviews Microbiology* 15: 756–771; **[30]** Gladieuxa, P., et al. (2018). Gene flow between divergent cereal- and grass-specific lineages of the rice blast fungus *Magnaporthe oryzae*. *mBio* 9: e01219–01217; **[31]** Strullu-Derrien, C., et al. (2018). The origin and evolution of mycorrhizal symbioses: from palaeomycology to phylogenomics. *New Phytologist*. Advance online publication, 24 March 2018. doi: https://doi.org/10.1111/nph.15076; **[32]** Martino, E., et al. (2018). Comparative genomics and transcriptomics depict ericoid mycorrhizal fungi as versatile saprotrophs and plant mutualists. *New Phytologist* 217(3): 1213–1229; **[33]** Martin, F., et al. (2016). Unearthing the roots of ectomycorrhizal symbioses. *Nature Reviews Microbiology* 14: 760–773; **[34]** Looney, B. P., et al. (2018). Russulaceae: a new genomic dataset to study ecosystem function and evolutionary diversification of ectomycorrhizal fungi with their tree associates. *New Phytologist* 218(1): 54–65; **[35]** Firrincieli, A., et al. (2015). Genome sequence of the plant growth promoting endophytic yeast *Rhodotorula graminis* WP1. *Frontiers in Microbiology* 6: 978; **[36]** Mandyam, K. G. & Jumpponen, A. (2015). Mutualism–parasitism paradigm synthesized from results of root-endophyte models. *Frontiers in Microbiology* 5: 776; **[37]** Tejesvi, M. V., Pirttilä, A. M. & Frank, A. C. (2017). Emerging tools for emerging symbioses—using genomics applications to studying endophytes. *Frontiers in Microbiology* 8: 859; **[38]** Meiser, A., et al. (2017). Sequencing genomes from mixed DNA samples – evaluating the metagenome skimming approach in lichenized fungi. *Scientific Reports* 7(1): 14881; **[39]** Gawad, C., Koh, W. & Quake, S. R. (2016). Single-cell genome sequencing: current state of the science. *Nature Reviews Genetics* 17: 175–188; **[40]** Duina, A. A., Miller, M. E. & Keeney, J. B. (2014). Budding yeast for budding geneticists: A primer on the *Saccharomyces cerevisiae* model system. *Genetics* 197(1): 33–48; **[41]** Filer, D., et al. (2017). RNA polymerase III limits longevity downstream of TORC1. *Nature* 552: 263–267; **[42]** Tavares, S., et al. (2014). Genome size analyses of Pucciniales reveal the largest fungal genomes. *Frontiers in Plant Science* 5: 422; **[43]** Gregory, T. R., (ed.) (2005). *The Evolution of the Genome*. Elsevier, San Diego; **[44]** Pellicer, J., et al. (2018). Genome size diversity and its impact on the evolution of land plants. *Genes* 9(2): 88; **[45]** Corradi, N., et al. (2010). The complete sequence of the smallest known nuclear genome from the microsporidian *Encephalitozoon intestinalis*. *Nature Communications* 1: 77; **[46]** Pombert, J.-F., et al. (2015). The *Ordospora colligata* genome: Evolution of extreme reduction in Microsporidia and host-to-parasite horizontal gene transfer. *mBio* 6(1): e02400–02414; **[47]** Corradi, N.

(2015). Microsporidia: Eukaryotic intracellular parasites shaped by gene loss and horizontal gene transfers. *Annual Review of Microbiology* 69(1): 167–183; **[48]** Ndikumana, S., et al. (2017). Genome analysis of *Pseudoloma neurophilia*: a microsporidian parasite of Zebrafish (*Danio rerio*). *The Journal of Eukaryotic Microbiology* 64(1): 18–30; **[49]** Kullman, B., Tamm, H. & Kullman, K. (2005). *Fungal Genome Size Database*. Available from http://www.zbi.ee/fungal-genomesize; **[50]** Kullman, B. (2008). Peak genome size in fungi. In: I. Saar & A. Suija (eds), *XVII Symposium of the Baltic Mycologists and Lichenologists. Estonia, Saaremaa, Mändjala, 17–21 September 2008*. Tartu University Publishing, Tartu. p. 25; **[51]** Nowoshilow, S., et al. (2018). The axolotl genome and the evolution of key tissue formation regulators. *Nature* 554: 50–55; **[52]** Stevens, K. A., et al. (2016). Sequence of the sugar pine megagenome. *Genetics* 204(4): 1613–1626; **[53]** Strobel, G. (2014). The use of endophytic fungi for the conversion of agricultural wastes to hydrocarbons. *Biofuels* 5(4): 447–455; **[54]** Gianoulis, T. A., et al. (2012). Genomic analysis of the hydrocarbon-producing, cellulolytic, endophytic fungus *Ascocoryne sarcoides*. *PLoS Genetics* 8(3): e1002558; **[55]** Wu, W., et al. (2017). Characterization of four endophytic fungi as potential consolidated bioprocessing hosts for conversion of lignocellulose into advanced biofuels. *Applied Microbiology and Biotechnology* 101(6): 2603–2618; **[56]** Rhodes, C. J. (2014). Mycoremediation (bioremediation with fungi) – growing mushrooms to clean the earth. *Chemical Speciation & Bioavailability* 26(3): 196–198; **[57]** Varjani, S. J. & Patel, R. K. (2017). Fungi: A remedy to eliminate environmental pollutants. In: R. Prasad (ed.) *Mycoremediation and Environmental Sustainability*. Springer International Publishing, Cham. pp. 53–67; **[58]** Tkavc, R., et al. (2018). Prospects for fungal bioremediation of acidic radioactive waste sites: Characterization and genome sequence of *Rhodotorula taiwanensis* MD1149. *Frontiers in Microbiology* 8: 2528; **[59]** Khan, S., et al. (2017). Biodegradation of polyester polyurethane by *Aspergillus tubingensis*. *Environmental Pollution* 225: 469–480.

7. Country focus: China

Authors: 方睿 (Rui Fang), Paul Kirk (RBG Kew & Institute of Microbiology, Chinese Academy of Sciences), 魏江春 (Jiang-Chun Wei; Institute of Microbiology, Chinese Academy of Sciences), 李玉 (Yu Li; Jilin Agricultural University), 蔡磊 (Lei Cai; Institute of Microbiology, Chinese Academy of Sciences), 范黎 (Li Fan; Capital Normal University), 魏铁铮 (Tie-Zheng Wei; Institute of Microbiology, Chinese Academy of Sciences), 赵瑞琳 (Rui-Lin Zhao; Institute of Microbiology, Chinese Academy of Sciences), 王科 (Ke Wang; Institute of Microbiology, Chinese Academy of Sciences), 杨祝良 (Zhu-Liang Yang; Kunming Institute of Botany, Chinese Academy of Sciences), 李泰辉 (Tai-Hui Li; Guandong Institute of Microbiology), 李熠 (Yi Li; College of Food Science and Engineering, Yangzhou University), 普布多吉 (Phurbu-Dorji; Tibet Plateau Institute of Biology) and 姚一建 (Yi-Jian Yao; University of the Chinese Academy of Sciences).

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References: **[1]** Wang, Y.-C. (1985). Mycology in China with emphasis on review of the ancient literature. *Acta Mycologica Sinica* 4(3): 133–140; **[2]** Wang, Y.-C. (1987). Mycology in ancient China. *Mycologist* 1(2): 59–61; **[3]** Yuan, Y., et al. (2018). Archaeological evidence suggests earlier use of Ganoderma in Neolithic China. *Chinese Science Bulletin* 63(13): 1180–1188; **[4]** Zhang, Z. C. (1916). Questionnaire of most prosperous plant disease around Beijing. *Report of the National Agricultural Farm of the Ministry of Agriculture* (3): 1–6; **[5]** Tai, F. L. (1979). *Sylloge fungorum sinicorum*. Science Press, Beijing; **[6]** Institute of Microbiology, Chinese Academy of Sciences. (2018). *Checklist of Fungi in China*. Available from: http://124.16.146.175:8080/checklist/checklist.html. [Accessed 10 May 2018]; **[7]** Zhuang, W.-Y. (2001). *Higher Fungi of Tropical China*. Mycotaxon Limited, Ithaca, NY; **[8]** Zhuang, W.-Y. (2005). *Fungi of Northwestern China*. Mycotaxon Limited, Ithaca, NY; **[9]** China Business Research Institute (15 December 2017). 2017 Market Research Report of Edible Fungi Industry in China (short version). Available from: http://www.askci.com/news/chanye/20171215/175617114071.shtml; **[10]** CCCFNA Edible Mushroom Branch (2018). Statistics on the global export of various edible and medicinal mushroom products from China in 2017. *Edible and Medicinal Mushrooms* 26(2): 114; **[11]** Zhang, J.-X., et al. (2015). History, current situation and trend of edible mushroom industry development. *Mycosystema* 34(4): 524; **[12]** Du, X.-H., Zhao, Q. & Yang, Z.-L. (2014). Diversity, evolutionary history and cultivation of morels: a review. *Mycosystema* 33(2): 183–197; **[13]** Huang, N. L. (2004). Development status and prospects of modern mushroom industry in China. *Edible Fungi*(4): 2–3; **[14]** Royse, D. J., Baars, J. & Tan, Q. (2017). Current overview of mushroom production in the world. In: C. Z. Diego & A. Pardo-Giménez (eds), *Edible and Medicinal Mushrooms*. John Wiley & Sons, NJ. p. 5; **[15]** Youlin, Y., Squires, V. & Qi, L. (2002). *Global alarm: dust and sandstorms from the world's drylands*. United Nations Convention to Combat Desertification (UNCCD); **[16]** Wei, J.-C. (2005). Desert biological carpet engineering – a new approach to desert management. *Arid Zone Research* 22(3): 287–288; **[17]** Li, S.-Z., et al., (2005). Regulation effect of microbiotic crusts on soil hydrological process in Shapotou vegetated sanddunes. *Journal of Desert Research* 25(2): 228–233; **[18]** Zhang, T. & Wei, J.-C. (2011). Survival analyses of symbionts isolated from *Endocarpon pusillum* Hedwig to desiccation and starvation stress. *Science China Life Sciences* 54(5): 480–489; **[19]** Zhang, Y., et al. (2017). The calcium-binding protein EpANN from the lichenized fungus *Endocarpon pusillum* enhances stress tolerance in yeast and plants. *Fungal Genetics and Biology* 108: 36–43; **[20]** Li, H.-K. (1998). Research progress on resources of *Cordyceps* species. *World Agriculture* (225): 35; **[21]** Ge, S.-L. (2017). Export of main products of mushrooms from China in 1996. *Edible Fungi of China* 16(6): 42; **[22]** Bonito, G., et al. (2013). Historical biogeography and diversification of truffles in the Tuberaceae and their newly identified southern hemisphere sister lineage. *PloS one* 8(1): e52765; **[23]** Fan, L., et al. (2016). Molecular analysis of Chinese truffles resembling *Tuber californicum* in morphology reveals a rich pattern of species diversity with emphasis on four new species. *Mycologia* 108(2): 344–353; **[24]** Fan, L., et al. (2016). Phylogenetic analyses of Chinese *Tuber* species that resemble *T. borchii* reveal the existence of the new species *T. hubeiense* and *T. wumengense*. *Mycologia* 108(2): 354–362; **[25]** Fan, L. (in prep.). Diversity and phylogeny of truffles in China; **[26]** Fan, L., et al. (2018). Chinese black truffles: *Tuber yigongense* sp. nov., taxonomic reassessment of *T. indicum* and re-examination of the *T. sinense* isotype. *Mycotaxon* 133: 183–196.

8. Plant-killers: Fungal threats to ecosystems

Authors: Maryam Rafiqi, Diane Saunders (John Innes Centre), Mark McMullan (Earlham Institute), Richard Oliver (Curtin University and University of Nottingham), Ruth Bone, Helen Fones (University of Exeter), Sarah Gurr (University of Exeter), Delphine Vincent (Agriculture Victoria Research), Timothy Coker and Richard Buggs.

References: **[1]** Willis, K. J. (ed.) (2016). *State of the World's Plants 2016*. Report. Royal Botanic Gardens, Kew. Available from: https://stateoftheworldsplants.org; **[2]** Fisher, M. C., et al. (2012). Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484(7393): 186–194; **[3]** International Society for Infectious Diseases. (2018). *ProMEDmail*. Available from: https://www.promedmail.org; **[4]** Loo, J. A. (2009). Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biological Invasions* 11(1): 81–96; **[5]** Fones, H. N., Fisher, M. C. & Gurr, S. J. (2017). Emerging fungal threats to plants and animals challenge agriculture and ecosystem resilience. *Microbiological Spectrum* 5(2): FUNK-0027-2016; **[6]** Boyd, I., et al. (2013). The consequence of tree pests and diseases for ecosystem services. *Science* 342(6160): 1235773; **[7]** Carnegie, A. J., et al. (2016). Impact of the invasive rust *Puccinia psidii* (myrtle rust) on native Myrtaceae in natural ecosystems in Australia. *Biological Invasions* 18(1): 127–144; **[8]** Berthon, K., et al. (2018). Assessment and prioritisation of plant species at risk from myrtle rust (*Austropuccinia psidii*) under current and future climates in Australia. *Biological Conservation* 218: 154–162; **[9]** Mitchell, R., et al. (2014). Ash dieback in the UK: A review of the ecological and conservation implications and potential management options. *Biological*

Conservation 175: 95–109; **[10]** Hughes, M. A., et al. (2017). No rest for the laurels: symbiotic invaders cause unprecedented damage to southern USA forests. *Biological Invasions* 19(7): 2143–2157; **[11]** Gibbs J, Brasier, C. M. & Webber, J. (1994). *Dutch Elm Disease in Britain*. Issue 252 of Research information note. Great Britain, Forest Authority, Research Division, Farnham, UK; **[12]** Anderson, P. K., et al. (2004). Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19(10): 535–544; **[13]** Canterbury, G. E. & Blockstein, D. E. (1997). Local changes in a breeding bird community following forest disturbance. *Journal of Field Ornithology*: 537–546; **[14]** Vandermast, D. & Van Lear, D. (2002). Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecology and Management* 155(1–3): 97–106; **[15]** Willis, K. J. (ed.) (2017). *State of the World's Plants 2017*. Report. Royal Botanic Gardens, Kew. Available from: https://stateoftheworldsplants.org; **[16]** Harvell, C. D., et al. (2002). Climate warming and disease risks for terrestrial and marine biota. *Science* 296(5576): 2158–2162; **[17]** Bebber, D. P., Ramotowski, M. A. T. & Gurr, S. J. (2013). Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* 3: 985; **[18]** Stukenbrock, E. H. & McDonald, B. A. (2008). The origins of plant pathogens in agro-ecosystems. *Annual Review of Phytopathology* 46: 75–100; **[19]** Wingfield, M., et al. (2015). Planted forest health: the need for a global strategy. *Science* 349(6250): 832–836; **[20]** Burgess, T. I., et al. (2016). Tree invasions and biosecurity: eco-evolutionary dynamics of hitchhiking fungi. *AoB Plants* 8(1): plw076; **[21]** Wingfield, M. J., et al. (2017). The unified framework for biological invasions: a forest fungal pathogen perspective. *Biological Invasions* 19(11): 3201–3214; **[22]** Calo, S., Billmyre, R. B. & Heitman, J. (2013). Generators of phenotypic diversity in the evolution of pathogenic microorganisms. *PLoS Pathogens* 9(3): e1003181; **[23]** Dong, S., Raffaele, S. & Kamoun, S. (2015). The two-speed genomes of filamentous pathogens: waltz with plants. *Current Opinion in Genetics & Development* 35: 57–65; **[24]** Hane, J. K., et al. (2015). Repeat-induced point mutation: a fungal-specific, endogenous mutagenesis process. In: M. A. van den Berg & K. Maruthachalam (eds), *Genetic Transformation Systems in Fungi, Volume 2*. Springer International Publishing, Cham. pp. 55–68; **[25]** Rafiqi, M., et al. (2012). Challenges and progress towards understanding the role of effectors in plant-fungal interactions. *Current Opinion in Plant Biology* 15(4): 477–482; **[26]** Friesen, T. L., et al. (2006). Emergence of a new disease as a result of interspecific virulence gene transfer. *Nature Genetics* 38(8): 953; **[27]** Ma, L. J., et al. (2010). Comparative genomics reveals mobile pathogenicity chromosomes in *Fusarium*. *Nature* 464(7287): 367–373; **[28]** van der Does, H. C., et al. (2016). Transcription factors encoded on core and accessory chromosomes of *Fusarium oxysporum* induce expression of effector genes. *PLoS Genetics* 12(11): e1006401; **[29]** Brasier, C. M. (2001). Rapid evolution of introduced plant pathogens via interspecific hybridization: Hybridization is leading to rapid evolution of Dutch elm disease and other fungal plant pathogens. *BioScience* 51(2): 123–133; **[30]** McMullan, M., et al. (2018). The ash dieback invasion of Europe was founded by two genetically divergent individuals. *Nature Ecology & Evolution* 2: 1000-1008; **[31]** Tomlinson, J. & Boonham, N. (2015). Real-time LAMP for *Chalara fraxinea* diagnosis. In: C. Lacomme (ed), *Plant Pathology: Techniques and Protocols.* 2nd ed. *Methods in Molecular Biology* series, vol. 1302. Humana Press, NY. pp. 75–83; **[32]** Cools, H. J. & Hammond-Kosack, K. E. (2013). Exploitation of genomics in fungicide research: current status and future perspectives. *Molecular Plant Pathology* 14(2): 197–210; **[33]** Wang, M. & Jin, H. (2017). Spray-induced gene silencing: a powerful innovative strategy for crop protection. *Trends in Microbiology* 25(1): 4–6; **[34]** Jacobs, D. F., Dalgleish, H. J. & Nelson, C. D. (2013). A conceptual framework for restoration of threatened plants: The effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist* 197(2): 378–393; **[35]** Steiner, K. C., et al. (2017). Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48(2): 317–336; **[36]** MacLean, D., et al. (2013). Crowdsourcing genomic analyses of ash and ash dieback–power to the people. *GigaScience* 2(1): 2; **[37]** Rossell, I. M., et al. (2001). Impacts of dogwood anthracnose (*Discula destructiva* Redlin) on the fruits of flowering dogwood (*Cornus florida* L.): implications for wildlife. *The American Midland Naturalist* 146(2): 379–387; **[38]** Crowley, K. F., et al. (2016). Long-term effects of pest-induced tree species change on carbon and nitrogen cycling in northeastern US forests: a modeling analysis. *Forest Ecology and Management* 372: 269–290; **[39]** Tomback, D. F. & Achuff, P. (2010). Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *Forest Pathology* 40(3-4): 186–225.

9. Climate change: Fungal responses and effects

Authors: Martin I. Bidartondo (Imperial College London & RBG Kew), Christopher Ellis (RBG Edinburgh), Håvard Kauserud (University of Oslo), Peter G. Kennedy (University of Minnesota), Erik A. Lilleskov (U.S. Forest Service), Laura M. Suz and Carrie Andrew (Swiss Federal Research Institute).

References: **[1]** Loarie, S. R., et al. (2009). The velocity of climate change. *Nature* 462: 1052–1055; **[2]** Willis, K. J. (ed.) (2017). *State of the World's Plants 2017*. Report. Royal Botanic Gardens, Kew. Available from: https://stateoftheworldsplants.org; **[3]** IPCC (2013). *Climate Change 2013: The Physical Science Basis.* Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., et al. (eds)]. Cambridge University Press, UK. doi: https://doi.org/doi:10.1017/CBO9781107415324 [Accessed 10 May 2018]; **[4]** Fisher, M. C., et al. (2012). Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484: 186–194; **[5]** Büntgen, U., Kauserud, H. & Egli, S. (2012). Linking climate variability to mushroom productivity and phenology. *Frontiers in Ecology and the Environment:* 14–19; **[6]** Mohan, J. E., et al. (2014). Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change. *Fungal Ecology*; **[7]** Boddy, L., et al. (2014). Climate variation effects on fungal fruiting. *Fungal Ecology* 10: 20–33; **[8]** Andrew, C., et al. (2018). Continental-scale macro-fungal assemblage patterns correlate with climate, soil carbon and nitrogen deposition. *Journal of Biogeography*. Advance online publication, 19 March 2018. doi: https://doi.org/10.1111/jbi.13374; **[9]** Hammond, P. M. & Lawrence, J. F. (1989). Mycophagy in insects: A summary. In: N. Wilding, et al. (eds). *Insect-fungus Interactions*. Symposium of the Royal Entomological Society of London. Academic Press, London. pp. 275–324; **[10]** Claridge, A. W. & May, T. W. (1994). Mycophagy among Australian mammals. *Australian Journal of Ecology* 19: 251–275; **[11]** Moore, D., Robson, G. D. & Trinci, A. P. J. (2011). *21st Century Guidebook to Fungi*. Cambridge University Press, UK; **[12]** Clemmensen, K. E., et al. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 29: 1615–1618; **[13]** Peay, K. G., Kennedy, P. G. & Bruns, T. D. (2008). Fungal community ecology: a hybrid beast with a molecular master. *Bioscience* 58: 799–810; **[14]** Treseder, K. K. (2016). Model behavior of arbuscular mycorrhizal fungi: predicting soil carbon dynamics under climate change. *Botany* 94: 417–423 doi: 10.1139/cjb-2015-0245; **[15]** Webster, J. & Weber, R. (2007). *Introduction to Fungi.* 3rd ed. Cambridge University Press, UK; **[16]** Andrew, C., et al. (2017). Big data integration: Pan-European fungal species observations' assembly for addressing contemporary questions in ecology and global change biology. *Fungal Biology Reviews* 31(2): 88–98; **[17]** Andrew, C., et al. (2018). Explaining European fungal fruiting phenology with climate variability. *Ecology* 99(6): 1306–1315; **[18]** Büntgen, U., et al. (2015). Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. *Fungal Ecology* 16: 6–18; **[19]** Diez, J. M., et al. (2013). Predicting species-specific responses of fungi to climatic variation using historical records. *Global Change Biology* 19: 3145–3154; **[20]** Gange, A. C., et al. (2007). Rapid and recent changes in fungal fruiting patterns. *Science* 316: 71; **[21]** Gange, A. C., et al. (2011). Host shifts in fungi caused by climate change? *Fungal Ecology* 4: 184–190; **[22]** Gange, A. C., et al. (2018). Trait-dependent distributional shifts in fruiting of common British fungi. *Ecography*: 41: 51–61; **[23]** Heegaard, E., et al. (2016). Fine-scale spatiotemporal dynamics of fungal fruiting: prevalence, amplitude, range and continuity. *Ecography* 40: 947–959; **[24]** Kauserud, H., Mathiesen, C. & Ohlson, M. (2008). High diversity of fungi associated with living parts of boreal forest bryophytes. *Botany (Botanique)* 86: 1326–33; **[25]** Kauserud, H., et al. (2010). Climate change and spring-fruiting fungi. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 277: 1169–1177; **[26]** Kauserud, H., et al. (2012). Warming-induced shift in European mushroom fruiting phenology. *PNAS USA* 109: 14488–14493; **[27]** Mattock, G., Gange, A.C. & Gange, E.G. (2007). Spring fungi are fruiting earlier. *British Wildlife* 18: 267–272; **[28]** Sato, H., Morimoto, S. & Hattori, T. (2012). A thirty-year survey

reveals that ecosystem function of fungi predicts phenology of mushroom fruiting. *PLOS ONE* 7(11): e49777; **[29]** Straatsma, G., Ayer, F. & Egli, S. (2001). Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. *Mycological Research* 105: 515–523; **[30]** Wollan, A.K., et al. (2008). Modelling and predicting fungal distribution patterns using herbarium data. *Journal of Biogeography* 35: 2298–2310; **[31]** Yang, X., et al. (2012). Climate change effects fruiting of the prize matsutake mushroom in China. *Fungal Diversity* 56(1): 189–198; **[32]** Averill, C., Turner, B. L. & Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* 505: 543–545; **[33]** Terrer, C. et al. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* 353: 72–74; **[34]** Deslippe, J. R., et al. (2011). Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra. *Global Change Biology* 17: 1625–1636; **[35]** Lilleskov, E. A., Hobbie, E. A. & Horton, T. R. (2011). Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology* 4: 174–183; **[36]** Kivlin, S. N., et al. (2013). Fungal symbionts alter plant responses to global change. *American Journal of Botany* 100: 1445–1457; **[37]** Giauque, H. & Hawkes, C. V. (2013). Climate affects symbiotic fungal endophyte diversity and performance. *American Journal of Botany* 100: 1435–1444; **[38]** Fernandez, C. W., et al. (2016). Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal-temperate ecotone. *Global Change Biology* 23: 1598–1609; **[39]** Körner, C. (2003). Ecological impacts of atmospheric CO_2 enrichment on terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* 361(1810): 2023–2041; **[40]** Arnolds, E. (1991). Decline of ectomycorrhizal fungi in Europe. *Agriculture Ecosystems & Environment* 35: 209–244; **[41]** van Strien, A. J., et al. (2018). Woodland ectomycorrhizal fungi benefit from large-scale reduction in nitrogen deposition in the Netherlands. *Journal of Applied Ecology* 55: 290–298; **[42]** Treseder, K. K. (2004). A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytologist* 164: 347–355; **[43]** Allen, M. F. & Allen, E. B. (2017). Chapter 12 – Mycorrhizal mediation of soil fertility amidst nitrogen eutrophication and climate change. In: N. Johnson, C. Gehring & J. Jansa (eds), *Mycorrhizal Mediation of Soil. Fertility, Structure, and Carbon Storage*. Elsevier, Amsterdam. pp. 213–231. doi: https://doi.org/10.1016/B978-0-12-804312-7.00012-7; **[44]** Bebber, D. P., Holmes, T. & Gurr, S. J. (2014). The global spread of crop pests and pathogens. *Global Ecology and Biogeography* 23: 1398–1407; **[45]** Wolfe, B. E., et al. (2009). Distribution and abundance of the introduced ectomycorrhizal fungus *Amanita phalloides* in North America. *New Phytologist* 185: 803–816; **[46]** Murtagh, G. J., et al. (2002). Molecular and physiological diversity in the bipolar lichen-forming fungus *Xanthoria elegans*. *Mycological Research* 106: 1277–1286; **[47]** Larsson, P., Solhaug, K. A. & Gauslaa, Y. (2012). Seasonal partitioning of growth into biomass and area expansion in a cephalolichen and a cyanolichen of the old forest genus *Lobaria*. *The New Phytologist* 194: 991–1000; **[48]** Dal Grande, F., et al. (2018). Environment and host identity structure communities of green algal symbionts in lichens. *New Phytologist* 217: 277–289; **[49]** Matos, P., et al. (2015). Lichen traits responding to aridity. *Journal of Ecology* 103: 451–458; **[50]** von Herk, C. M., Aptroot A. & van Dobben, H. F. (2002). Long-term monitoring in the Netherlands suggest that lichens respond to global warming. *The Lichenologist* 34: 141–154; **[51]** Hawksworth D. L. & Rose, F. (1970). Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature* 227: 145–148; **[52]** Hill, D. J. (1971). Experimental study of the effect of sulphite on lichens with reference to atmospheric pollution. *New Phytologist* 70: 831–836; **[53]** Sutton, M.A., et al. (2009). Estimation of the ammonia critical level for epiphytic lichens based on observations at farm, landscape and national scales. In: Sutton M. A., Reis S. & Baker S. M. (eds), *Atmospheric Ammonia*. Springer, Dordrecht. pp. 71–86; **[54]** Braidwood, D. & Ellis, C. J. (2012). Bioclimatic equilibrium for lichen distributions on disjunct continental landmasses. *Botany* 90: 1316–1325; **[55]** Aptroot, A. & Van Herk, C. M. (2007). Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environmental Pollution* 146: 293–298; **[56]** Lang, S. L., et al. (2012). Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology* 18: 1096–1107; **[57]** Asplund, J. & Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* 92: 1720–1738; **[58]** Jonard, M., et al. (2015). Tree mineral nutrition is deteriorating in Europe. *Global Change Biology* 21: 418–430; **[59]** Cox, F., et al. (2010). Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. *Ecology Letters* 13: 1103–1113; **[60]** Suz, L. M., et al. (2014). Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. *Molecular Ecology* 23: 5628–5644; **[61]** van der Linde, S., (2018). Environment and host as large-scale controls of ectomycorrhizal fungi. *Nature* 558: 243–248; **[62]** Eaton, S. & Ellis, C. J. (2012). Local experimental growth rates respond to macroclimate for the lichen epiphyte *Lobaria pulmonaria*. *Plant Ecology and Diversity* 5: 365–372; **[63]** Ellis, C. J., et al. (2007). Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biological Conservation* 140: 217–235; **[64]** Nascimbene, J., et al. (2016). Climate change fosters the decline of epiphytic *Lobaria* species in Italy. *Biological Conservation* 201: 377–384; **[65]** Allen, J. L. & Lendemer, J. C. (2016). Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. *Biodiversity and Conservation* 25: 555–568; **[66]** Lendemer, J. C. & Allen, J. L. (2014). Lichen biodiversity under threat from sea-level rise in the Atlantic Coastal Plain. *Bioscience* 64: 923–931; **[67]** Ellis, C. J. & Eaton S. (2016). Future non-analogue climates for Scotland's temperate rainforest. *Scottish Geographical Journal* 132: 257–268; **[68]** Geiser, L. H. & Neitlich, P. N. (2007). Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens. *Environmental Pollution* 145: 203–218; **[69]** Ellis, C. J. (2018). A mechanistic model of climate change risk: growth rates and microhabitat specificity for conservation priority woodland epiphytes. *Perspectives in Plant Ecology, Evolution & Systematics* 32: 38–48; **[70]** Koide, R. T., Fernandez. C. & Malcolm, G. (2014). Determining place and process: Functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. *New Phytologist* 201: 433–439; **[71]** Fernandez, C. W. & Koide, R. T. (2013). The function of melanin in the ectomycorrhizal fungus *Cenococcum geophilum* under water stress. *Fungal Ecology* 6: 479–486; **[72]** Yafetto, L., Davis, D. J. & Money, N. P. (2009). Biomechanics of invasive growth by *Armillaria* rhizomorphs. *Fungal Genetics Biology* 46: 688–694. **[73]** Agerer, R. (2001). Exploration types of ectomycorrhizae. *Mycorrhiza* 11: 107–114; **[74]** Agerer, R. (2006). Fungal relationships and structural identity of their ectomycorrhizae. *Mycological Progress* 5: 67–107; **[75]** Buntgen, U., et al. (2011). Truffles and climate change. *Frontiers in Ecology and the Environment* 9: 150–151; **[76]** Webster, J. & Weber, R. (2007). *Introduction to Fungi*. 3rd ed. Cambridge University Press, Cambridge, UK; **[77]** Money, N. P. (2016). Spore production, discharge, and dispersal. In: S. C. Watkinson, L. Boddy & N. P. Money (eds), *The Fungi*, 3rd ed. Associated Press, New York, NY. pp. 67–98.

10. Conservation of fungi

Authors: A. Martyn Ainsworth, Cátia Canteiro, Anders Dahlberg (Swedish University of Agricultural Sciences), Brian Douglas, Giuliana Furci (Fundación Fungi, Santiago), David Minter (CABI), Gregory M. Mueller (Chicago Botanic Garden), Christoph Scheidegger (Swiss Federal Institute for Forest, Snow and Landscape Research WSL), Beatrice Senn-Irlet (Swiss Federal Institute for Forest, Snow and Landscape Research WSL), Tim Wilkins (Natural England) and Emma Williams.

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References: **[1]** Griffith, G. W. (2011). Do we need a global strategy for microbial conservation? *Trends in Ecology & Evolution* 27(1): 1–2 [supplemented by pers. comm.]; **[2]** International Union for Conservation of Nature. (2018). Table 1: Numbers of threatened species by major groups of organisms (1996–2018). Available from: http://www.iucnredlist.org/about/summary-statistics [Accessed 6 July 2018]; **[3]** Senn-Irlet, B., et al. (2007). *Guidance for the Conservation of Macrofungi in Europe.* Document prepared for the Directorate of Culture and Cultural Heritage, Council of Europe. Document T-PVS (2007) 13 (rev). Strasbourg 17 Oct 2007. Available from: https://www.wsl.ch/eccf/Guidance_Fungi.

pdf [Accessed 9 February 2018]; **[4]** Minter, D. W. (2010). Safeguarding the future. In: Boddy, L. & Coleman, M. (eds), *From Another Kingdom*. Royal Botanic Garden Edinburgh. pp. 144–153; **[5]** Dahlberg, A., Genney, D. R. & Heilmann-Clausen, J. (2010). Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. *Fungal Ecology* 3: 50–64; **[6]** Dahlberg, A. & Mueller, G. M. (2011). Applying IUCN red-listing criteria for assessing and reporting on the conservation status of fungal species. *Fungal Ecology* 4: 147–162; **[7]** Walter, K. S. & Gillett, H. J. (eds) (1998). *1997 IUCN Red List of threatened plants*. Compiled by the World Conservation Monitoring Centre. IUCN, Cambridge; **[8]** Venturella, G. (2006). *Pleurotus nebrodensis*. The IUCN Red List of Threatened Species 2006: e.T61597A12506882. Available from: http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T61597A102952148.en [Accessed 2 May 2018]; **[9]** Anon. (2010). *Global Sampled Red List Index of the Ascomycota: Baseline Evaluation.* Darwin Initiative Project. Available from: www.cybertruffle.org.uk/redlidat [Accessed 9 February 2018]; **[10]** Heilmann-Clausen, J., et al. (2014). A fungal perspective on conservation biology. *Conservation Biology* 29(1): 61–68; **[11]** Jansen, A. E. & Ławrynowicz, M. (1991). *Conservation of Fungi and Other Cryptogams in Europe.* Łódź Society of Sciences and Arts – science tracks no 18. European Council for the Conservation of Fungi; **[12]** Arnolds, E. J. M. & Kreisel, H. (1993). *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald; **[13]** Pegler, D. N., et al. (eds) (1993). *Fungi of Europe: Investigation, Recording & Conservation*. Royal Botanic Gardens, Kew; **[14]** Fellner, R. (1993). Report on the present situation of decline and conservation of fungi in Czechoslovakia. In: E. J. M. Arnolds & H. Kreisel (eds), *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald. p. 15; **[15]** Fellner, R. (1993). Results of the mycological monitoring in stands of spruce, beech and swiss-pine in the Czech Republic in 1986–1990. In: E. J. M. Arnolds & H. Kreisel (eds), *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald. p. 50; **[16]** Fellner, R. (1993). Air pollution and mycorrhizal fungi in central Europe. In: D. N. Pegler, et al. (eds), *Fungi of Europe: Investigation, Recording & Conservation*. Royal Botanic Gardens, Kew. pp. 239–250; **[17]** Rald, E. (1985). Vokshatte som indikatorarter for mykologisk vaerdifulde overdrevslokaliteter. *Svampe* 11: 1–9; **[18]** Winterhoff, W. (1978). Bemerkenswerte Pilze in Trockenrasen des nördlichen Oberrheingebietes. *Hessische floristische Briefe* 27(1): 2–8; 27(3): 41–47; **[19]** Derbsch, H. & Schmitt, J. A. (1984). *Atlas der Pilze des Saarlandes, Teil 1. Verbreitung und Gefährdung*. Minister für Umwelt des Saarlandes, Saarbrücken; **[20]** Derbsch, H. & Schmitt, J. A. (1987). *Atlas der Pilze des Saarlandes, Teil 2. Nachweise, Ökologie, Vorkommen und Beschreibungen*. Minister für Umwelt des Saarlandes, Saarbrücken; **[21]** Arnolds, E. J. M. (1985). Veranderingen in de paddestoelenflora (mycoflora). *Wetensch. Meded. Kon. Ned. Natuurhist. Ver.* 167: 1–101; **[22]** Jansen, E. & van Dobben, H. F. (1987). Is decline of *Cantharellus cibarius* in the Netherlands due to air pollution? *Ambio* 16: 211–213; **[23]** Arnolds, E. J. M. (1988). The changing macromycete flora in the Netherlands. *Transactions of the British Mycological Society* 90: 391–406; **[24]** Arnolds, E. J. M. & Jansen, E. (1992). New evidence for changes in the macromycete flora of the Netherlands. *Nova Hedwigia* 55: 325–351; **[25]** Arnolds, E. J. M. (1993). Conservation of macrofungi in the Netherlands: recent developments. In: E. J. M. Arnolds & H. Kreisel (eds), *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald. pp. 8–13; **[26]** Arnolds, E. J. M. & Jansen, E. (1993). Recent studies on the changing mycoflora in the Netherlands. In: E. J. M. Arnolds & H. Kreisel (eds), *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald. pp. 38–49; **[27]** Nauta, M. & Vellinga, E. C. (1993). Distribution & decline of macrofungi in the Netherlands. In: D. N. Pegler, et al. (eds), *Fungi of Europe: Investigation, Recording & Conservation*. Royal Botanic Gardens, Kew. pp. 21–46; **[28]** Nitare, J. (1988). Jordtungor, en svampgrupp påtillbakegång I naturlige fodermarker. *Svensk Botanisk Tidskrift* 82: 341–368; **[29]** Arnolds, E. J. M. & de Vries, B. (1993). Conservation of fungi in Europe. In: D. N. Pegler, et al. (eds), *Fungi of Europe: Investigation, Recording & Conservation*. Royal Botanic Gardens, Kew. pp. 211–230; **[30]** Benkert, D. (1982). Vorläufige Liste der verschollenen und gefährdeten Grosspilzarten der DDR. *Boletus* 6: 21–32; **[31]** Ing, B. (1992). A provisional Red Data List of British fungi. *Mycologist* 6: 124–128; **[32]** Svensson, S. (1993). Red Data Lists, mapping, monitoring and conservation of fungi in Sweden. In: E. J. M. Arnolds & H. Kreisel (eds), *Conservation of Fungi in Europe.* Proceedings of the second meeting of the European Council for the Conservation of Fungi, Vilm, Germany, 13–18 September 1991. Universität Greifswald. pp. 31–34; **[33]** Scheidegger, C. & Goward, T. (2002). Monitoring lichens for conservation: Red Lists and conservation action plans. In: P. L. Nimis, C. Scheidegger & P. Wolseley (eds), *Lichen Monitoring – Monitoring Lichens*. Kluwer Academic Publishers, Dodrecht. pp. 163–181; **[34]** Sérusiaux, E. (1989). *Liste rouge des macrolichens dans la Communauté Européenne* [Red List of macrolichens in the European Community]. Centre de Recherches sur les Lichens, Departement de Botanique, Sart-Tilman, Liege; **[35]** Ing, B. (1993). Towards a Red List of endangered European macrofungi. In: D. N. Pegler, et al. (eds), *Fungi of Europe: Investigation, Recording & Conservation*. Royal Botanic Gardens, Kew. pp. 231–237; **[36]** Lizon, P. (1995). *Macrofungi reported as extinct/missing or threatened with extinction in European Red Data Lists.* Fungi and Conservation Newsletter No. 3. IUCN Species Survival Commission Committee for Fungi, Gland; **[37]** Dahlberg, A. & Croneborg, H. (2006). *The 33 threatened fungi in Europe (Nature and environment, No. 136).* Council of Europe, Strasbourg; **[38]** Senn-Irlet, B. (2005). The role of the ECCF in studies and conservation of fungi in Europe. *Mycologia Balcanica* 2: 185–192; **[39]** Fraiture, A. & Otto, P. (2015). *Distribution, ecology and status of 51 macromycetes in Europe*. Meise Botanic Garden, Meise; **[40]** IUCN / Zoological Society of London. National Red List Project. Available from: http://www.nationalredlist.org/ [Accessed 11 February 2018]; **[41]** Fungimap Inc. (2018). Australian *Fungimap* Project. Available from: https://fungimap.org.au/ [Accessed 11 February 2018]; **[42]** UK Lost and Found Fungi Project (2014). Available from: http://fungi.myspecies.info/content/lost-found-fungi-project [Accessed 11 February 2018] **[43]** Castellano, M. A., et al. (1999). *Handbook to Strategy 1 Fungal Taxa from the Northwest Forest Plan.* General technical report PNW-GTR-476. United States Department of Agriculture, Portland, OR; **[44]** Scheidegger, C. (1998). *Erioderma pedicellatum*: a critically endangered lichen species. *Species: Newsletter of the IUCN Species Survival Commission 1998(June)*: 68–69; **[45]** Environment Canada. (2010). *Management Plan for the Boreal Felt Lichen – Boreal Population (Erioderma pedicellatum) in Canada*. Species at Risk Act management plan series. Environment Canada, Ottawa; **[46]** Goudie, R. I., et al. (2011). New population models help explain declines in the globally rare boreal felt lichen *Erioderma pedicellatum* in Newfoundland. *Endangered Species Research* 13: 181–189; **[47]** Nitare, J. (2000). *Signalarter: indikatorer på skyddsvärd skog: Flora over kryptogamer*. Skogsstyrelsens Förlag, Jönköping; **[48]** Evans, S., Marren, P. & Harper, M. (2001). *Important Fungus Areas*. Plantlife report. Plantlife International, London; **[49]** Genney, D. R., et al. (2009). Grassland fungi. In: I. Bainbridge, et al. (eds), *Guidelines for the Selection of Biological SSSIs. Rationale, operational approach and criteria: Detailed guidelines for habitats and species groups*. Joint Nature Conservation Committee, Peterborough; **[50]** Bosanquet, S., et al. (2018). *Guidelines for the Selection of Biological SSSIs. Part 2: Detailed Guidelines for Habitats and Species Groups. Chapter 14 Non-lichenised Fungi.* Joint Nature Conservation Committee, Peterborough; **[51]** Forest Stewardship Council. Available from: https://ic.fsc.org/en [Accessed 21 March 2018]; **[52]** Finnish Biodiversity Information Facility. *Laji.fi Portal*. Available from: https://laji.fi/en; **[53]** Info Species, Schweizerisches Informationszentrum für Arten. Available from: www.infospecies.ch; **[54]** National Biodiversity Network. (2018). *National Biodiversity Network Gateway* (UK). Available from: https://nbn.org.uk/national-biodiversity-network/archive-information/nbn-gateway/; **[55]** Netherlands Biodiversity Information Facility. (2013). Available from: https://www.nlbif.nl/en; **[56]** Norwegian Biodiversity Information Centre. Available from: https://www.biodiversity.no/Pages/135580; **[57]** Swedish Species Observation System (2018). *Artportalen*. Available from: https://www.artportalen.se/Home/About; **[58]** International Union for Conservation of Nature. (2018). *The IUCN Red List of Threatened Species, 2018-1*. Available from: http://www.iucnredlist.org/ [Accessed 12 Feb 2018].

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Report editor: Katherine J. Willis CBE

Website project manager and data assimilator: Abigail Barker

Design: Jeff Eden and Ines Stuart-Davidson

Production editor: Rhian J. Smith

Website producer: Numiko

Website infographics: Numiko, Jeff Eden and Amanda Cooper

Research support: David Baines, Catia Canteiro, Julia Carretero, Timothy Coker, Amanda Cooper, Nicola Kuhn, Gillian Petrokofsky (University of Oxford) and Emma Williams

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