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Fungi, Ecosystems, and Global Change

Lynne Boddy

Cardiff University, Cardiff, UK

INTRODUCTION

Autotrophic plants and heterotrophic fungi colonised the land together between 600 and 460 million years ago (mya), and Ascomycota and Basidiomycota diverged around 550 mya, according to molecular clock data. Evolution of trees and forests from the Devonian to the Jurassic period provided a wealth of nutritional and spatial niches which fungi diversified to fill. Today, hundreds of thousands of fungi are associated with plants as essential mutualistic symbionts (Chapter 7), as pathogens (Chapter 8), and as decomposers that break down dead wood, leaves, and other plant tissues, and conserve and recycle their nutrients. Moreover, there are many mutualistic interactions between fungi and animals (Chapter 9), and fungi are pathogens and decomposers of these, too. So while fungi are widely associated with rot, mould, blight, and disease, they are less appreciated than they deserve for their essential part in the evolution, productivity and sustainability of life on land. Without the contributions of fungi to ecosystem processes, life as we know it would never have begun and would soon cease.

Uses of fungi in pharmaceutical, chemical, food, drink, decontamination, biorefinery, and biofuel applications (Chapter 12) stem from unique processes and products evolved by fungi in the course of adapting to their niches in the environment. Understanding how fungi operate in ecosystems helps to predict promising locations and fungal groups to explore among the estimated 5 million undiscovered species.

In this chapter, we firstly outline the part played by fungal processes in element cycles, bioconversions and energy flows in the Earth's biosphere, and then we briefly consider the global distribution of fungi – their biogeography. We then concentrate on how fungi and fungal communities are being affected by global change, how in turn this will affect ecosystems, and finally the need for, and difficulties faced in, fungal conservation.

THE ROLES OF FUNGI IN ELEMENT CYCLES, BIOCONVERSIONS, AND ENERGY FLOWS

From what we have already said in other chapters it should be evident that fungi are essential to the functioning of the planet's ecosystems. Here we pull together knowledge of the many and varied ways in which fungi live and feed, so that we can understand the major roles that fungi play in the flow of energy and carbon through ecosystems, and in mineral nutrient cycling and soil. Ecosystems can be considered to operate as three interconnected subsystems dominated by the activities of autotrophs, herbivores, or decomposers (Figure 11.1). The autotrophic subsystem in most terrestrial ecosystems is dominated mainly by photosynthetic plants or in the Arctic and Antarctic by lichens (Chapter 7). Even in this subsystem where plants dominate, fungi are major players, as all plant species examined so far contain fungal endophytes (Chapter 7) and over 85% have mycorrhizal associations (Chapter 7) with their roots; the mycorrhizal fungi absorbing water and mineral nutrients from soil, as well as playing protective roles. Further, pathogenic fungi can reduce plant productivity but increase plant species diversity (Chapter 8). In marine ecosystems, algae are major contributors to photosynthetic energy input, and again these have fungal endosymbionts.

The herbivore subsystem largely comprises animals that feed directly on photosynthetic organisms, or that feed on organisms that have already fed on autotrophs, ranging from microscopic nematodes to large ruminant mammals, and the carnivores that feed on them. In this sense, some fungi can be considered to be part of the herbivore subsystem, feeding directly on photosynthetic organisms, and on herbivorous and carnivorous animals. These fungi are the biotrophic and necrotrophic pathogens (Chapters 8 and 9) that abstract nutrients from their host at a cost to the host. Like herbivores and carnivores, the bodies of these fungi will eventually enter the decomposer subsystem where they will be decomposed by other fungi and bacteria.

In the decomposer subsystem, energy flows from plant and animal remains through a trophic web of heterotrophic organisms. Fungi dominate the decomposer subsystem in habitats where the main inputs are lignocellulosic plant remains. These are combined in the upper layers of soil with other detritus – the dead bodies, tissues, cells, and exudates of other organisms. The fungi of this habitat include not only those that specialise in saprotrophy (feeding from dead organic matter), but also many mycorrhizal fungi that have some saprotrophic ability (Chapter 7), and necrotrophic pathogens that continue feeding saprotrophically in the tissues that they have killed (Chapters 8 and 9). The mycelial nature of fungi (Chapter 2) allows them to ramify not only over the surface, but also to penetrate within bulky substrata, which sets them apart from unicellular organisms. Further, the ability of many species, especially basidiomycetes, to break down recalcitrant compounds (e.g. cellulose and lignin, described in detail in Chapter 5) means that fungi are the major agents of decomposition of dead organic matter, and hence of recycling of the mineral nutrients bound within dead organic matter in terrestrial ecosystems.

Without decomposer fungi, life on earth would probably cease after a few decades because carbon and mineral nutrients would be locked up in dead tissues and unavailable to autotrophs for continued primary production. While some plant remains are decomposed by bacteria or combusted in fires, most are decomposed by fungi which can depolymerise lignin and cellulose synthesised by plants, thereby replenishing the carbon dioxide of the

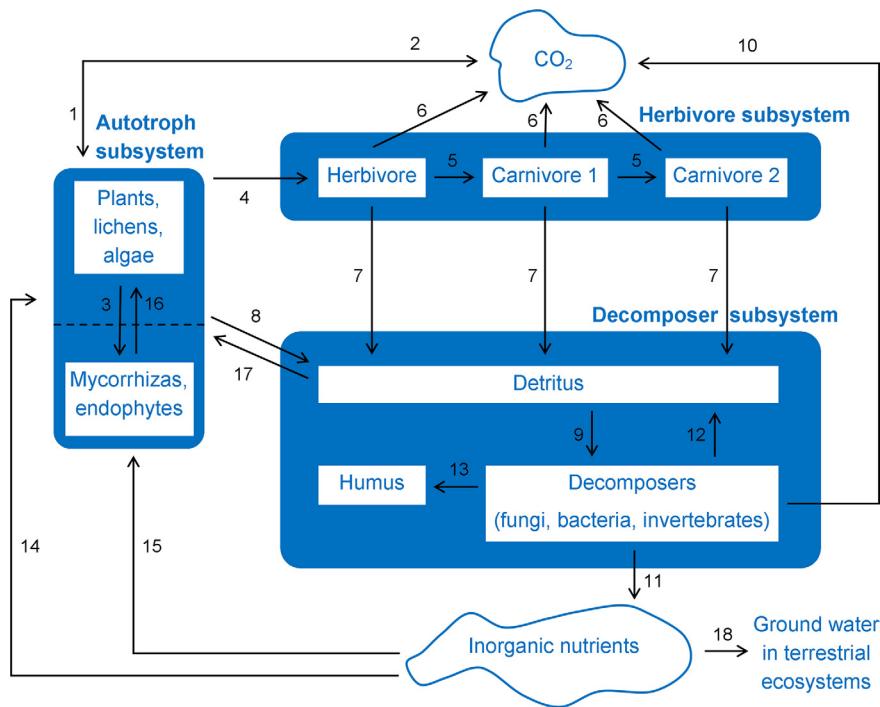


FIGURE 11.1 A general model of ecosystem structure comprising the autotroph, herbivore, and decomposer subsystems. Autotrophs fix carbon from CO_2 during photosynthesis (1). Some photosynthate is respiration and returns to the atmosphere as CO_2 (2), up to 20% supports mycorrhizal growth and activity (3), and the remainder forms plant biomass – net primary production (NPP). Living material from autotrophs enters the herbivore subsystem, by vertebrate and invertebrate grazing, and plant pathogens (4). In forests, usually <5% above ground NPP is grazed, though occasionally it is >10%, and complete defoliation can sometimes occur during pathogen outbreaks or population explosions of grazing invertebrates. In grasslands, up to 50% NPP can be grazed, though usually it is <25%. Within the herbivore subsystem, organisms are consumed by others (5), C is lost to the atmospheric pool by respiration (6), and dead animals and pathogens, excreta, sloughed cells, skin, hair, etc. enter the decomposer subsystem (7). Dead organic matter from the autotroph subsystem will go directly to the decomposer subsystem (8), where it and that from the herbivore subsystem (7) is broken down by decomposers (9) ultimately to CO_2 (10) and H_2O with the release of mineral nutrients (11). Within the decomposer subsystem, the bodies of decomposers themselves die (12) and are decomposed. Decomposer bacteria and fungi also produce humus (13). Mineral nutrients released during decomposition are taken up by the autotrophs, occasionally directly (14), but usually via mycorrhizal mycelium (15) and then passed to the plant (16), and mycorrhizal fungi can also decompose organic materials to some extent, effectively short-circuiting the system (17). Some nutrients released into the soil nutrient pool may be lost via ground water (18), but the presence of mycorrhizal fungi keeps this to a minimum. Source: Adapted from: Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell, Oxford.

atmosphere (Figure 11.2). Bacteria and nematodes are important in decomposing animal tissues, including bodies of vertebrates, and plant remains in aquatic and in less aerobic environments. Invertebrates do not, however, have the enzymatic ability to catabolise as many complex molecules, though some have significant roles in the decomposition of wood and leaf litter. For example, some invertebrates have mutualistic partnerships with fungi (e.g. the attine ants and higher termites, Chapter 9), while hundreds of other arthropods are associated

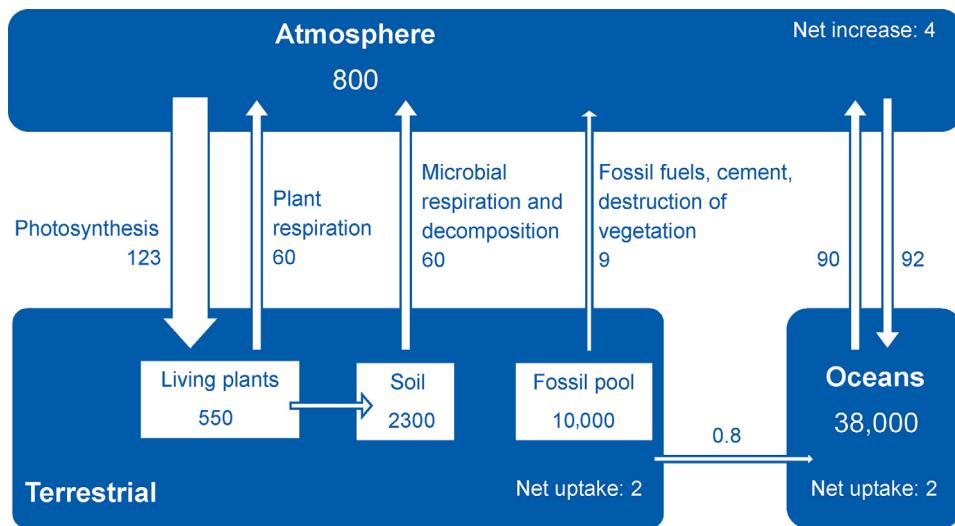


FIGURE 11.2 The global carbon cycle. The numbers in boxes are values for pools expressed as 10^{15} g C and the fluxes (indicated by arrows) and net uptake are expressed as 10^{15} g C/year. Atmospheric carbon is in the form of CO₂, and that in plants is largely lignified cellulose. The fungi make major direct contributions in transfer from living plants to soil as pathogens and mycorrhizas, and from soil to the atmosphere via decomposition. In boreal and arctic regions, lichens make major contributions to photosynthesis. Source: DOE, 2010. *Grand Challenges for Biological and Environmental Research: A Long-Term Vision; A Report from the Biological and Environmental Research Advisory Committee March 2010 Workshop. US Department of Energy Genomic Science: Biological and Environmental Research Information System (BERIS)*.

with wood decay fungi as commensals. The main role of invertebrates is in comminution – the physical (not chemical) breakdown of large litter components into small particles that can be decomposed more quickly and alter the community of decomposer microorganisms and fungi.

Within the decomposer subsystem fungi, together with bacteria, produce humus, which at 1600×10^{15} g globally, represents the main carbon reservoir in terrestrial ecosystems. Humus is not just the slowly decomposing remains of complex organic materials; its accumulation also involves synthesis of complex molecules based on substances such as lignin, though its biochemistry is still poorly understood. The importance of humus lies in its water-holding capacity, its capacity for cation exchange and nitrogen binding and hence ability to store nutrients, and its improvement of soil structure. Fungi, particularly those that form arbuscular mycorrhizas (Chapter 7), also play a direct role in promoting soil aggregation and improving soil structure. Not only do their extensive hyphal networks entwine soil particles, they also produce the carbon-, nitrogen-, and iron-rich glycoprotein glomalin, which joins small soil particles promoting aggregation and stability (see also p. 215).

The huge importance of fungi to carbon cycling in terrestrial ecosystems is evident when we consider the quantities involved. Photosynthetic carbon, entering the soil via mycorrhizal fungi, fuels half of the belowground microbial activity, the other half coming from dead organic matter. Between 27% and 68% of plant net primary productivity (NPP) is allocated

belowground to roots and mycorrhizal fungi, 1–21% of NPP being allocated directly to mycorrhizal fungi. The soil carbon pool is three times greater than the atmospheric carbon pool and four times greater than the plant carbon pool. Fungal processes thus represent a potential control point in the global carbon cycle, and the implications of environmental change for the contributions of fungi to ecosystems are considered later in this chapter. The huge role of fungi in mineral nutrient cycling is evident from the forgoing, since it is the fungi that release nutrients from lignocellulosic substrata, and the nutrient requirements of most plants are met via mycorrhizal mycelium that sequesters nutrients from soil solution, and sometimes directly by decomposition of dead plant material and from inorganic rock phosphate (Chapters 5 and 7). Some fungi also perform transformation of inorganic nitrogen, phosphorus, and sulphur oxides (pp. 157–159), though in ecosystem terms this is usually negligible compared with prokaryote transformations. Geotransformation processes effected by fungi (pp. 181–184), on the other hand, including transformations of rocks and minerals, bioweathering, mycogenic mineral formation, and the interactions between fungi and clay particles and between fungi and metals, can be of major significance.

BIODIVERSITY AND BIOGEOGRAPHY OF FUNGI

The biogeography of plants and animals has been studied in detail for over a century, but patterns of fungal biogeography have only started to emerge in the last few years. One major impediment has been our lack of knowledge of fungal phylogeny, and our inability to discriminate between morphologically similar taxa (pp. 107–109). For example, the wood decay fungus *Hyphoderma setigerum* was considered to have a worldwide distribution, but it is now clear from molecular phylogenetic studies that, although fruit bodies are morphologically indistinguishable, this morphological ‘species’ actually comprises at least nine taxa. These have geographically distinct ranges: four restricted to northern Europe, two to North America, two to East Asia, one to Greenland, and one found in the Caucasus, East Asia, Greenland, and North America. Another hurdle to realising that fungi do exhibit biogeographic differences was the incorrect perception that fungi have few barriers for dispersal because they have airborne spores. The dictum of microbial ecology ‘everything is everywhere, the environment selects’ is now seen not to apply to fungi.

Species of fungi can have different geographical distributions, and to some extent these distributions do depend on the environment. Thus, fungal distributional patterns at geographical scales from landscape to continents depend on suitable conditions for establishment and growth, and these are determined by climate and vegetation (Figure 11.3). Not surprisingly, geographical distributions of mycorrhizal fungi (Chapter 7), biotrophic pathogens (Chapter 8), and saprotrophs with substrate preferences (Chapter 5) match that of their hosts and/or preferred resources. Superimposed on this are direct climatic effects on fungal growth and reproduction. Finally, biogeographic distribution also reflects the ability of fungi to disperse.

Our knowledge of how these patterns have changed historically is even more scant. The poor fungus fossil record has not helped; however, historical accumulations of fungal spores are an important component of palynological records that are dominated

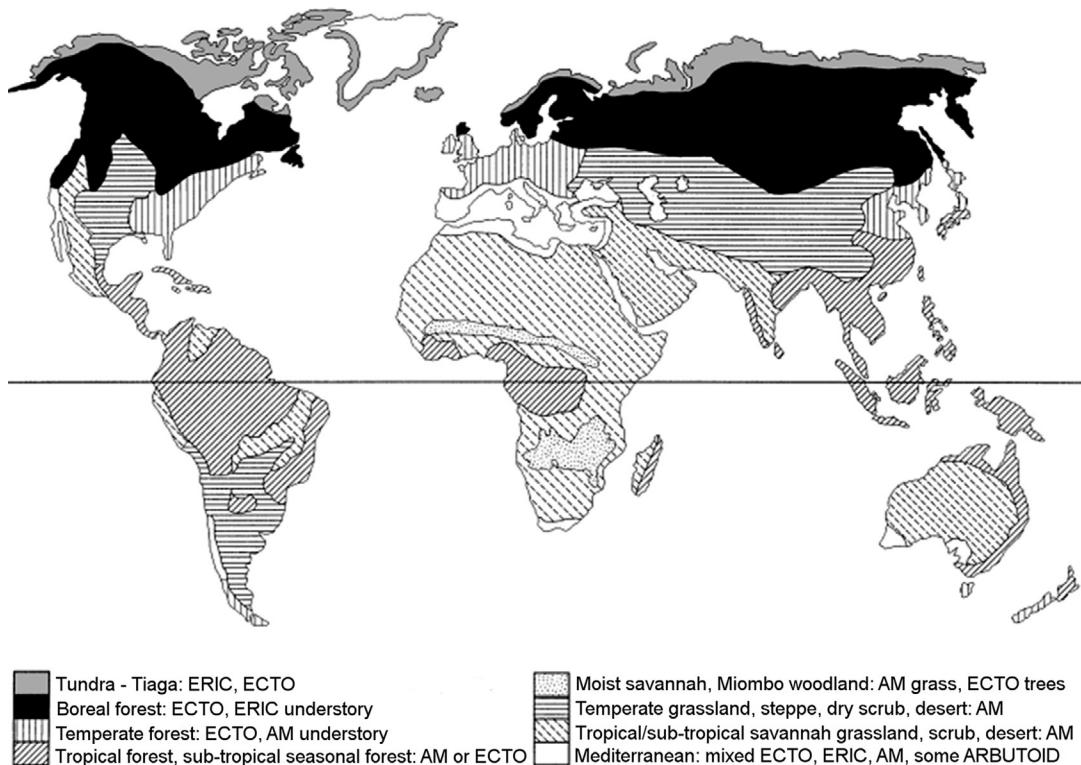


FIGURE 11.3 Biomes are regions where climate and vegetation are relatively constant over an area of land surface, largely reflecting climate. Fungal diversity and function are believed to be characteristic of different biomes. The figure gives types of mycorrhizas found in different biomes as an example. In very broad terms, arbuscular mycorrhizal symbioses (pp. 206–215), for example, predominate where decomposition is rapid and nitrogen supply is good relative to that of phosphorus, notably tropical regions and temperate grasslands. Major exceptions are the dipterocarp forests of Southeast Asia that are dominated by ectomycorrhizal symbioses (pp. 215–225). Ectomycorrhizal symbioses dominate the cool temperate and boreal forests of deciduous angiosperms and evergreen conifers, where decomposition is slower and nitrogen is usually limiting. Ericaceous mycorrhizas dominate in tundra and heathlands where the vegetation is largely Ericales, and decomposition and nitrogen cycling are extremely slow. The distribution of major forest types has a strong influence on distribution patterns of ectomycorrhizal and wood decay species, differences occurring amongst, for example, Betulaceae, Fagaceae, and Pinaceae. The types of decay performed by the dominant fungi vary too, with white rot (pp. 146–150) predominating in angiosperm woodlands and brown rot (pp. 150–152) in conifers. In the boreal zone, many species have a circumpolar distribution occurring in North America, Europe, and Siberia, reflecting the long time that the taiga zone has been coherent. Many wood decay species of temperate forests in Europe appear also to be found in similar forest types in East Asia and North America. Likewise, many species of the Mediterranean are also listed in subtropical and tropical regions. On the other hand, many species have been recorded only in geographically small areas, though this may reflect insufficient searching elsewhere. Source: Read, D.J., Leake, J.R., Perez-Moreno, J., 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Can. J. Bot.* 82, 1243–1263.

otherwise by spores produced by seedless plants and pollen from seed plants. Changes in the proportions of different kinds of fungal spores can provide crucial information on the biological communities and climatic conditions that supported these fungi. The abundance of ascospores of the dung-fungus *Sporormiella* serves as a proxy for the mass extinction of mega-herbivores toward the end of the Pleistocene (12,000–13,000 years ago). In North America, sediment samples from lakes and wetlands show a precipitous decline in the abundance of these ascospores, which is thought to have been caused by the decimation of the woolly mammoth (*Mammuthus primigenius*), mastodon (*Elephas americanus*), and rhinoceros by human hunters and consequent disappearance of their dung. A rich, 130,000 year old palynological record from Queensland, Australia, shows an abrupt loss of *Sporormiella* spores 41,000 years ago, following human immigration. Human hunters are identified as the cause of the collapse of animal populations. Changes in the concentrations of *Sporormiella* ascospores have also been linked to the extinction of Madagascan mega-herbivores 1700 years ago and the seventeenth century extirpation of species of moa (*Dinornis*) – the giant flightless birds of New Zealand.

The distribution of fungi is changing as a result of man's activities. The current geological epoch is sometimes described as the anthropocene, reflecting the huge changes that man has made to the planet. The start of the anthropocene is perhaps best defined as about the time when James Watt invented the steam engine. Though man has changed the environment on a local scale for thousands of years (e.g. by gradual forest clearance for agriculture), major features of the anthropocene are changes on a global scale, with land use change, climate change, nitrogen deposition, movement of biota and CO₂ increase threatening biodiversity in decreasing order of impact. The relative importance of these threats, however, varies between ecosystems (Figure 11.4). Land use change is by far the strongest driver of biodiversity loss in tropical forests and the temperate forests of South America, the weakest driver in Arctic and alpine ecosystems, and intermediate in grasslands and Mediterranean ecosystems. Climatic warming is expected to be most dramatic at high latitudes and least in the tropics. Nitrogen deposition is greatest in the northern temperate zone in the vicinity of cities, and, perhaps surprisingly, is predicted to be the biggest driver of biodiversity change in this region.

While large scale loss of habitat (e.g. for creation of agricultural land, p. 381), and large scale pollution (e.g. from burning fossil fuels, (p. 383), are obvious causes of species loss, small scale habitat loss and pollution can also endanger species. For example, *Poronia punctata* (whose sexual fruit bodies look like the heads of carpenter's nails; Figure 11.5a) is one of the few ascomycetes worldwide to be recognised as needing conservation (though there are likely to be very many not yet recognised). Its demise follows the rise in automobiles, not because of pollution but because of loss of habitat – it is found in old dung of horses, donkey, ponies, and exceptionally, elephants, none of which are much used now for transport! Further, it seems only to thrive in dung from animals feeding on 'unimproved' pasture (p.382) (i.e. meadows to which no fertilisers, pesticides or high yield grass varieties have been introduced). The effects of global change on fungi are considered below under three headings: (1) climate change responses of fungi; (2) land use change; and (3) pollution, pesticides, fertilisers, nutrient distribution, and recycling. However, none of these factors act in isolation.

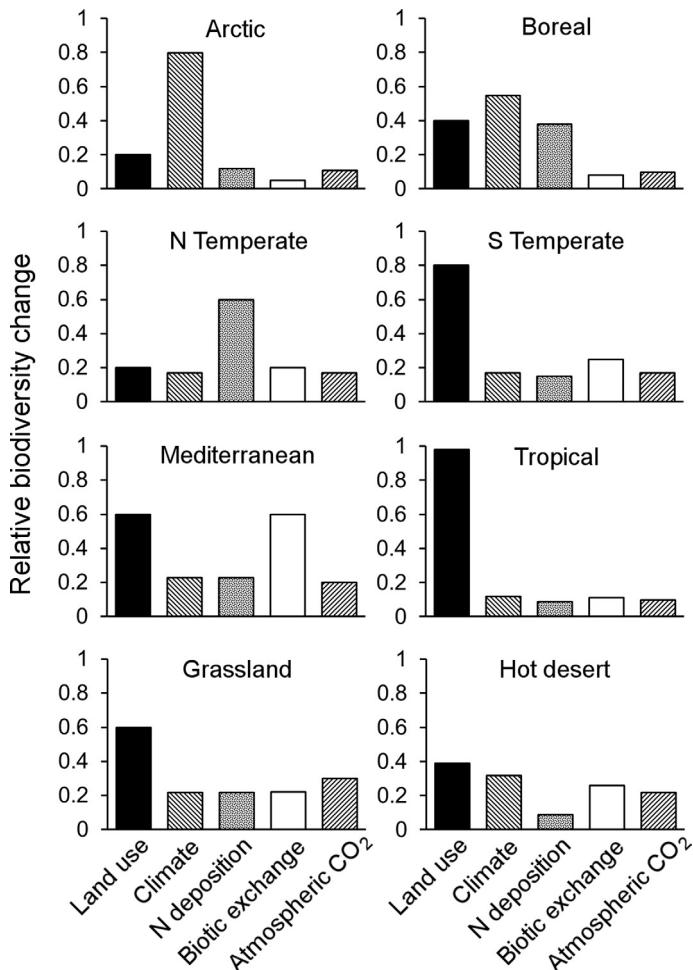


FIGURE 11.4 Many factors affect biodiversity loss. The predicted relative effect of changes in land use, climate, nitrogen deposition, biotic exchange, and atmospheric CO₂ on total biodiversity change, in major biome types is shown. Estimates were obtained by multiplying the expected change caused by each driver by the predicted impact of a large change in each driver. The scale is relative to the maximum possible value. *Source: Modified from: Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. et al., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.*

CLIMATE CHANGE RESPONSES OF FUNGI

There is no doubt that Earth's climate is changing, and that this has largely been brought about by man. By 2100, atmospheric CO₂ concentration is predicted to reach 540–970 ppm. This rise in CO₂ and some other gases (e.g. CH₄) is the cause of the so-called greenhouse effect, which results in a rise in surface temperature. Temperature increases ranging between 1.1 and 6.4°C are predicted, varying across the globe. A 1°C increase in mean annual temperature in the temperate zone will result in a northward shift in isotherms of approximately 140 km, and



FIGURE 11.5 Rare and endangered species. (a) The nail fungus *Poronia punctata* on the Red List of many European countries © Martyn Ainsworth; (b) The wax cap *Hygrocybe collucera* endangered in New South Wales Australia © Ray and Elma Kearney; (c) *Ramariopsis pulchella* near threatened in the British Red List © Martyn Ainsworth; (d) *Hericium coralloides* © Martyn Ainsworth; (e) *Hericium erinaceus* protected by law in the UK © Martyn Ainsworth; (f) *Hygrocybe lanecovensis* endangered in New South Wales Australia © Ray and Elma Kearney; (g) *Phellodon melaleucus* © Martyn Ainsworth; (h) young *Piptoporus quercinus* © Martyn Ainsworth; (i) *Zeus olympius* (Ascomycota) found only on Bosnian Pine (*Pinus heldreichii*) in northern Greece © Stephanos Diamandis; (j) *Pleurotus nebrodensis* found only in Sicily © David Minter; (k) *Ophiocordyceps sinensis* (Ascomycota) on a caterpillar (arrowed) © Paul Cannon (CABI/RBG Kew); (l) critically endangered *Erioderma pedicellatum* (boreal felt lichen) © Christoph Scheidegger.

an upward altitude shift of 170m. The incidence of extremely hot days is likely to increase and extremely cold days to decrease. Patterns and amount of precipitation will alter dramatically, and UV-B penetration and the incidence of extreme events will increase, though the magnitude of these changes is uncertain. 30–50% of glacier mass is predicted to disappear by 2100, and permafrost will shrink by 16%. Sea level will rise by 15–95 cm by 2100.

Effects on fungal distribution, community composition, ecophysiology, activity, and times and extent of reproduction are all likely to alter in response to climate change, both directly through effects on physiology and indirectly through changes in habitat and interactions with other organisms. Since fungi are major agents of decomposition and nutrient cycling (pp. 362–365), are mycorrhizal with about 90% of plants (Chapter 7) and can cause diseases of plants (Chapter 8) and animals (pp. 310–325), changes in their activity will have major knock-on effects to ecosystem functioning.

On a global scale the distribution of plant communities is likely to change dramatically as a result of climate change, and associated saprotrophic, mycorrhizal and pathogenic fungi are likely to change with them. For example, over the next century in the northern hemisphere, boreal and temperate forests are likely to move northwards with huge reduction in taiga and Arctic tundra. Concomitantly, grassland and shrubland will expand northwards. For a 4 °C increase in temperature over the next century plants will probably have to move 500 km northwards or 500 m upwards to remain in the same climatic envelope as now. This far outpaces historical tree migration rates of 100–200 m per annum at low altitude.

Effects on Saprotophosphates

The general effects of temperature, moisture, and CO₂ on the metabolic activity and timing of different events within the fungal lifecycle (e.g. growth and spore production) are well known (Chapters 3 and 5). For example, metabolic activity increases with rise in temperature up to an optimum, above which it decreases, as a result of effects on enzyme catalysed reactions. Moisture inhibits activity when there is both too little and too much: low water potential inhibits water uptake and retention, and enzyme function; high water is inhibitory because it decreases rate of diffusion of O₂ to hyphae and of CO₂ away from hyphae. However, despite understanding the ecophysiology of effects of individual abiotic factors on individual fungal species, it is extremely hard to extrapolate to effects of climate change on fungi in the field, in mixed communities, and in fluctuating environments. That dramatic changes are occurring is clear from long-term datasets on fruiting of macrofungi. For example, the first of this type of study analysed records of 200 saprotrophic basidiomycetes within a 30-mile radius of Salisbury, in the south of the UK between 1950 and 2005. For autumn fruiting, this revealed that the mean date when fruiting of a species was first recorded (averaged across all species) is now significantly earlier than it was prior to the late 1970s, while the mean last fruiting date is significantly later, resulting in a doubling of the length of the fruiting season (Figure 11.6). Response varies between species even within genera, 47% showing an advancement and 55% continuing fruiting later. The response also differs depending on habitat type, with only 13% of grassland species fruiting earlier and 48% having later last fruiting, but with 53% of wood decay fungi fruiting earlier and 20% having later last fruiting. These changes in autumn fruiting times are correlated with late summer temperature and rainfall. Changes in fruiting time have also been reported in other European countries, China and Japan, and are likely occurring worldwide, though there is often considerable variation between countries.

As well as changes to autumn fruiting patterns, many species that previously only fruited in autumn now also fruit in spring, and spring fruiting is getting earlier in northern Europe. Times and extent of basidiomycete fruiting depend on environmental triggers that initiate the various processes, plus sufficient water, nutrients, and energy sources. Earlier autumn

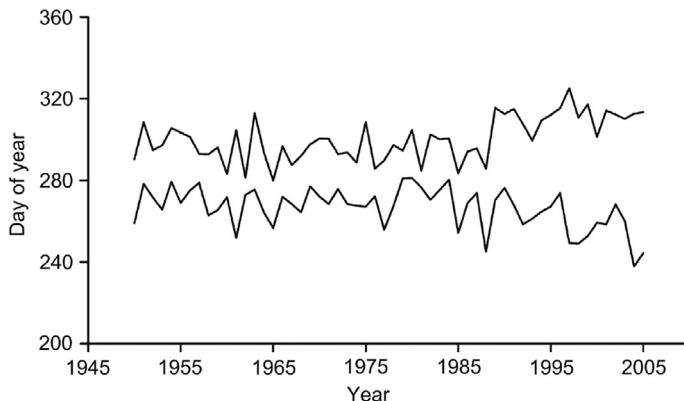


FIGURE 11.6 Fungal fruiting phenology has changed dramatically in the last 30 years or so as a result of climate change. This is shown for the mean first fruiting date (lower line) and mean last fruiting date (upper line) for 200 saprotrophic basidiomycetes around Salisbury in the south of the UK, over 56 years. The fruiting season is now significantly longer than it was pre-1970s. This change is correlated with changes in temperature and rainfall. *Source: Moore, D., Gange, A.C., Gange, E.G., Boddy, L., 2008. Fruit bodies: their production and development in relation to environment. In: Boddy, L., Frankland, J.C., van West, P. (Eds.), Ecology of Saprotrophic Basidiomycetes. Elsevier, Amsterdam, pp. 79–102.*

fruiting is likely to relate to changes in the timing of triggers to fruiting, but may also reflect the fact that mycelia have already acquired sufficient resources to fruit. Extended fruiting implies that environmental conditions remain conducive to fruiting for longer – hard frosts come later, and fungi can obtain water, nutrients, and energy to maintain fruit body production for longer. Spring fruiting suggests that some fungi are now more active in winter and spring than they were in the past. So these phenological changes that are related to climate change imply that decomposer activity of fungi is increasing. It follows that decay rate of organic matter is increasing, as is evolution of CO₂. Provided that plant primary productivity increases at the same rate then this will not be a problem, but if decay rate increases more than primary productivity then the greenhouse effect will be exacerbated. The latter may well occur in soils which are very high in organic matter, such as boreal forests, tundra soils and peat, where in the past decay has been limited by low temperature and/or lack of aeration due to high water content; because of elevated temperatures, these ecosystems may become warmer and drier. There is now evidence that Arctic soils are changing from being net carbon sinks to net carbon sources, with the worrying potential to amplify climate change.

Overall decay rate of dead organic matter in ecosystems depends on the sum of the decay rates brought about by all of the individual fungi. However, climate change will create different niches; plants grown in CO₂ enriched atmospheres tend to release more labile compounds into soil and tissues are more lignified, have greater phenolic content and higher C:N ratios, making them more recalcitrant. Also, the relative competitiveness of species will change and will affect the outcome of combative interactions (pp. 339–354), and hence fungal community composition will change. If the new communities predominantly comprise fungi more active in decomposition, then organic matter will decay more rapidly, and vice versa.

Fungi in aquatic environments are also affected by climate. Temperature preferences of species are broadly correlated with their geographical distribution. On a more local scale, distinct winter and summer communities are often evident; for example, *Flagellospora penicilliooides*

and *Lunulospora curvula* do not grow at less than 5 °C, and disappear from streams in colder seasons. In temperate streams, where temperatures are below the optimum for fungal growth, an experiment in which the temperature was artificially raised by 4.3 °C increased the rate of litter decomposition, decreased the number of leaf fragments (the main substrata of aquatic hyphomycetes), and decreased the number of fungal species on leaf fragments. As in terrestrial environments, climate-induced changes to riparian vegetation communities will affect the composition and diversity of the fungal decomposers of this litter in water.

Mycorrhizal Responses

Climate change affects both plants and their root symbionts. Ectomycorrhizal (ECM) associations are formed with forest trees, and the distribution of tree species within tropical, temperate, and boreal biomes will alter as climate changes, as paleoecological studies have shown for the past. In the Quaternary, trees migrated or adapted in the face of ecological change. Those that did not become locally extirpated or extinct globally. Trees move towards the poles and higher elevations when climate warms and in the opposite direction when it cools. In the southern Santa Rosa Mountains, California, United States, white fir (*Abies concolor*) and Jeffrey pine (*Pinus jeffreyi*) have moved about 96 and 28 m upwards, respectively, in the last 30 years. The current dominance of ECM associations in temperate and boreal forests is clearly a result of their dispersal patterns in response to changing climate over millennia, and changes in their distribution will continue. In tundra, warming experiments show that shrub biomass and cover will increase, and moss and lichen cover will decrease. Successful plant migration and survival of mycorrhizal fungi will depend on successful co-migration of the latter. This may not pose a problem for fungi that produce copious wind-dispersed spores in above ground fruit bodies. However, for resupinate forms that produce spores in the organic soil horizon dispersed by soil invertebrates, and also for hypogeous fungi, such as truffles, that are dispersed by small mammals, migration may depend on the ability of their animal dispersal agents to move too.

Since altitudinal gradients are paralleled by climatic and vegetation gradients, they can be used as models of communities that might be expected following climate change. Studies in the Canadian Rocky Mountains have shown that ECM species richness and diversity decreases with increasing altitude; host-specific ECM are present in subalpine forests, but in alpine regions ECM tend to be generalists. This reflects not only climate but also the plant communities present. However, there are also clear differences in mycorrhizal communities on a single plant species, depending on elevation. The ericaceous shrub *Vaccinium membranaceum* grows from valley bottoms to alpine habitats; at lower elevations the alpha diversity is lower than at higher elevations and the most frequently isolated species is *Phialocephala fortinii*, whereas at higher altitudes *Rhizoscyphus ericae* dominates.

The activity of mycorrhizal fungi is also changing, and immediately evident from changes in timing of fruit body production. Like saprotrophs, ECM basidiomycete fruiting phenology has changed since the late 1970s, but in different ways. Also there are differences between those in association with conifers and deciduous trees; in the UK, 59% of deciduous mycorrhizal species now fruit later than in the 1970s, but coniferous mycorrhizal species have changed little. This is probably because mycorrhizal fruiting responds to cues from the host trees, rather than environmental factors alone, and cues from evergreens are different to those

from deciduous trees. Deciduous trees now frequently remain in leaf, and hence supply fixed carbon to their fungal partners, for much longer; thus any cue for fruiting when photosynthate declines is delayed, and carbohydrates to fuel mycelia and fruiting are available for longer. This implies that, as with saprotrophic fungi, fungi ECM with deciduous trees are active for much longer periods.

Combinations of increasing temperature and changing water regimes will impact directly on mycorrhizal fungal activity and interactions with each other and their hosts. Climatic changes and increasing CO₂ will also affect photosynthesis, elevated CO₂ causing increases; this will in turn affect the mutualistic symbioses. As a result of increased photosynthesis, mycorrhizal abundance is increasing by an average of 47% with a much larger increase for arbuscular mycorrhizal (AM) fungi (84%) than for ECM fungi (19%). However, abundance is not increasing for all species (e.g. ECM in black spruce, *Picea mariana*). There appear to be functional shifts in mycorrhizal community composition. An increase in ECM species that are long-range explorers (i.e. produce copious mycelial cords (p. 217), was found in *Betula nana* root tips in warmed Arctic tundra soils, and Douglas fir (*Pseudotsuga menziesii*) in warmer sites. Experiments show that elevated CO₂ also results in a shift in ECM community composition, again favouring morphotypes that produce large amounts of extraradical mycelium, cords and/or thicker mantles; later successional species dominate fruit body production. With elevated CO₂, mycorrhizal biomass increases, as does plant and fungal exudates and carbon inputs to soil. Soil respiration rate increases, as a result of increased mycorrhizal activity and activity of other microbes capitalising on increased carbon inputs.

Effects on Lichens

Climate largely exerts effects on lichens by affecting the amount of time that thalli are fully hydrated, and by temperature effects on metabolic processes including photosynthesis. Though lichens are autotrophic, their responses to climate will differ from those of higher plants, since lichens are poikilohydric. Climate change effects on lichens are likely to be particularly important in the Arctic and Antarctic where they are dominant primary producers. Though lichen physiological activity in the Antarctic is limited by low temperature, long-term monitoring of the most prominent fruticose lichen, *Usnea aurantiaco-atra*, has revealed that counterintuitively, an increase in thallus temperature of 0.5–1 °C may lead to a 90% reduction of annual biomass increase, due to increased losses through respiration. This occurs particularly in winter where solar radiation, and hence photosynthesis, is almost zero but respiration is higher because of elevated temperature. Also, when there is light for photosynthesis, elevated temperature results in lower atmospheric humidity, and hence longer periods when thalli are not hydrated sufficiently for photosynthesis to occur. In the long-term, *Usnea-Himantormia*-lichen heath may be replaced by competitive grass species that do benefit from elevated temperature.

The distribution of lichens that live on inorganic substrata will be influenced by direct effects of climate on a particular species and indirectly by effects on interacting species. The distribution of lichens that live on particular living substrata will additionally be affected by changes in host distribution and tree species composition in forests. Northward shifts in the boundary between taiga and tundra, will lead to northward shifts in lichens, and upward shifts in snowline and glacial fronts will provide new habitats for lichens.

The strong correlation between lichen communities and climate has been clearly shown in large- and small-scale monitoring along environmental gradients. With harsher conditions lichen cover increases, and in alpine areas lichen species richness is usually higher than plant species richness. In the Northern Ural Mountains, lichen cover and diversity are stable at 1000–1400 m above sea level, but at higher altitudes dominant lichen species have changed, and lichen cover has increased.

Lichen community composition in most regions of the globe, including the temperate zone, is changing in response to changing climate. In The Netherlands, long-term monitoring indicates that species typical of cold environments are decreasing or have recently disappeared, while warm temperate species have increased. In Western Europe, patterns of species change depending on habitat: many terricolous species are declining, whereas many epiphytic species are increasing. Interestingly, species increasing most rapidly in forests are from different genera, but all contain *Trentepohlia* algae as photobiont. Potential changes in lichen distribution have been elegantly demonstrated for Britain, where the bioclimatic envelope in which different species can grow was modelled using different climate change scenarios. Even using climatic scenarios based on low greenhouse gas emissions, considerable changes in distributions of species are predicted ([Figure 11.7](#)). This type of predictive approach can be used as a valuable tool in developing conservation strategy.

Changing Patterns of Plant Disease

Climate change, particularly elevated temperature and CO₂, and amount and patterns of precipitation, with consequent changes in air and soil humidity, are having or will have major effects on plant disease. Almost all research concerns diseases of plants of agricultural importance, because of the impact on food security. As with mutualistic symbioses, one consequence of climate change is the poleward shift of agro-climatic zones, and the concomitant expansion of the geographic range of pathogens to higher latitudes. Both host and pathogen biology, including life cycles, are affected by changing climate, and it is the interactions between the two that will determine how patterns of disease will alter. Not surprisingly, therefore, effects vary between different host-pathogen combinations ([Table 11.1](#)), and between different host and pathogen strains. Also, even for the same host-pathogen combination, effects of changing one or a few climate variables are not always the same if another variable changes slightly, hence effects vary amongst and between growing regions. Climate change can also have indirect effects on plant disease; for example, by prompting man to change cropping strategies, such as planting new varieties better adapted to heat stress during flowering. Planting 'Mediterranean-type' wheat varieties has been suggested for the UK, as they typically flower 2 weeks earlier than the cultivars currently used. This may have unexpected consequences for diseases to which the plants are susceptible during flowering, such as fusarium head blight (FHB). Changes in cultivation practice, such as including new crops in crop rotations, may provide additional hosts for pathogens.

Temperature is the single most significant environmental variable affecting spread and development of fungal pathogens. Elevated precipitation and humidity are important for spore production, release, germination and infection for most fungal pathogens, apart from those adapted to hot dry conditions (e.g. *Ustilago* species, pp. 16–18). Though average temperature and moisture values are often used in studies and predictive modelling, single extreme maximum and minimum values can be much more important.

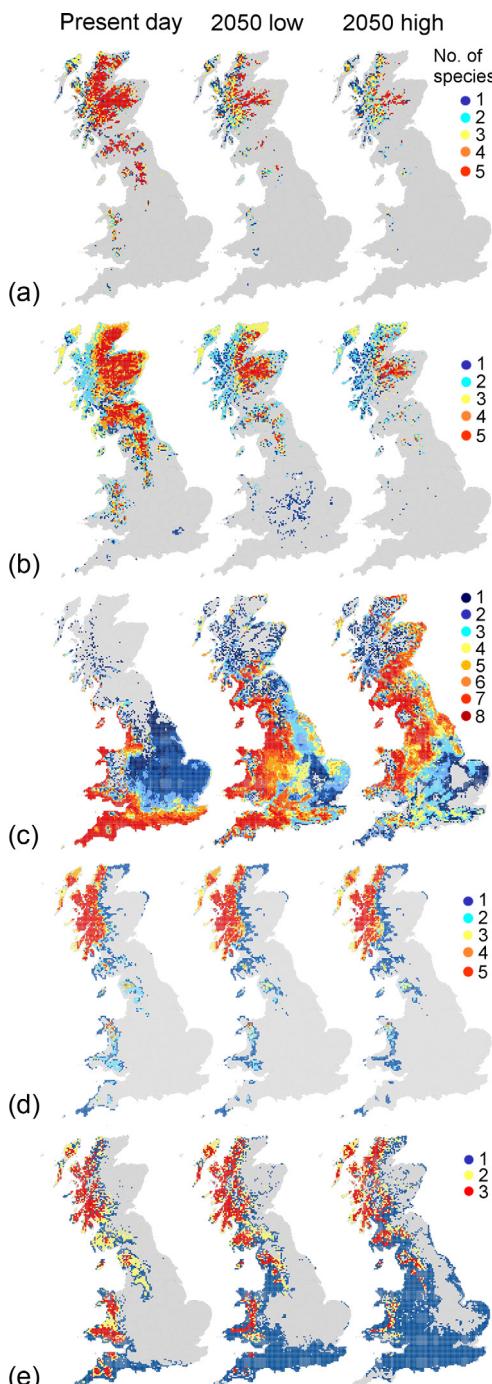


FIGURE 11.7 Predictive modelling is an extremely useful tool for revealing possible impacts of climate change on species distributions. A modelling approach used information on the bioclimatic growth envelope of 26 species of lichens whose distributions are well defined within Britain. Even using climatic data for a low greenhouse gas scenario resulted in modelled bioclimatic growth envelopes for 2050 that are very different from those now. The lichen species were considered separately under five biogeographic groups: (a) northern-montane; (b) northern-Boreal; (c) southern-widespread; (d) oceanic-northern; and (e) oceanic-widespread. Source: Modified from: Ellis *et al.* (2007).

TABLE 11.1 Climate Change Effects on Disease of Major Energy Food Crops

Crop		Examples of major diseases	Pathogen mode of nutrition	Main weather factors affecting epidemics	Climate change effects (actual or predicted)
Wheat	The most important source of carbohydrate, providing 20% of the calorie intake of the global population. Cultivated worldwide, 10 main producing regions: China, India, USA, Russia, France, Canada, Australia, Germany, Pakistan, Turkey.	Rust: <i>Puccinia striiformis</i> f. sp. <i>tritici</i> (Pst)	Biotrophic	Moisture, temperature, wind	Elevated temperature may decrease development and survival in some wheat-growing regions, but most reports of increase with rising temperature. New Pst strains, better adapted to higher temperatures, now dominate in south central United States
	In the United States, a projected decrease in production of 25–44% under slowest warming, and 60–79% decrease under most rapid warming	Fusarium head blight (FHB) and crown rot (CR): <i>Fusarium</i> and <i>Microdochium</i> spp.	Necrotrophic	FHB favoured by warm wet weather at flowering. CR when there is drought post-flowering	The species responsible for disease change depending on temperature
		Crown rot: <i>Fusarium pseudograminearum</i>	Necrotrophic	–	Prevalent in Australia in southern regions, where there has been drought since 2000. Under elevated CO ₂ (825 ppm) fungal biomass increased in wheat stems
Rice	Staple food crop of the world, mainly produced in Asia and Brazil, with demand increasing. Rising sea levels, changing patterns of rainfall and elevated temperatures will lead to major alterations in land and water resources for rice production	Spot blotch: <i>Cochliobolus sativus</i>	Necrotrophic	–	Increased in South Asia with higher night time temperatures
		Rice blast: <i>Magnaporthe grisea/oryzae</i> complex	Biotrophic	Temperature	Severity predicted to increase. In cool subtropics of Japan and northern China epidemic severity is predicted to increase, but in warm/cool subtropics fewer epidemics are predicted following warming. Elevated temperature can increase effectiveness of some genes, e.g. <i>Xa7</i> (most effective against <i>Xanthomonas oryzae</i> pv. <i>oryzae</i>) With elevated CO ₂ leaf blast severity increased
		Sheath blight: <i>Rhizoctonia solani</i>	Necrotrophic	–	With elevated CO ₂ there were more diseased plants, but lesion size was unaltered

Barley	Less produced than for other cereals; mainly Europe	Powdery mildew: <i>Blumeria graminis</i>	Biotrophic	-	Decrease at elevated CO ₂
		Smut: <i>Ustilago hordei</i>	Biotrophic	-	Decrease at elevated CO ₂
Maize	Particularly produced in the Americas	Smut: <i>Ustilago maydis</i>	Biotrophic	-	Inhibited at elevated CO ₂
Soybean	A major crop and now rapidly expanding, as an important source of protein as well as carbohydrate. Four main producers: Argentina, Brazil, China and USA	Downy mildew: <i>Peronospora manshurica</i>	Biotrophic	-	Elevated CO ₂ alone or with O ₃ reduced severity by 39–66%
		Brown spot: <i>Septoria glycines</i>	Necrotrophic	-	Elevated CO ₂ alone or with O ₃ caused a small increase, occasionally
		Sudden death syndrome (SDS): <i>Fusarium virguliforme</i>	Necrotrophic	-	Elevated CO ₂ and O ₃ had no effect
		Asian soybean rust (ASR): <i>Phakopsora pachyrhizi</i>		-	This extremely aggressive pathogen has rapidly spread, since 2000, from Asia to Africa to South America, and was introduced to 8 US states by hurricane Ivan
Potato	Grown worldwide, but more now grown in developing than industrialised countries. China is the main grower, with over 20% global production. 18–32% predicted decrease with climate change. Elevated temperature will lead to change in planting time and location of growing regions, and longer growing seasons	Late blight: <i>Phytophthora infestans</i> (Oomycota)	Necrotrophic	-	In Canada: predicted increase in duration of epidemics and levels of inoculum, but decrease in disease progression In Finland: 17 fold more outbreaks in 1998–2002 than in 1933–1962 and 1983–1997 due to more conducive conditions; 2–4 week earlier start to outbreaks; 10°C rise predicted to extend the infection period.
		<i>Verticillium</i> spp.	Necrotrophic	-	In Canada: predicted to increase due to elevated temperature

Data from Luck et al. (2011).

Temperature and water regime affect differently the various stages of the fungal pathogen life cycle, including spore production, survival, germination, mycelial growth, and disease progress. Hence, the timing of these weather events in relation to different stages of the fungus lifecycle is important. Mild, damp winters, for example, increase survival of pathogens that overwinter on infected seed or crop debris. In contrast, warmer, drier summers tend to reduce incidence of pathogenesis.

Most pathogens are active over a wide range of temperatures, but the extent of the time under optimum conditions may extend or narrow, and the infection window may alter. The relative importance of different spore types in infection and survival between crops may change. For example, *Leptosphaeria maculans* (=*Phoma lingam*) – the cause of blackleg and stem canker of oilseed rape (*Brassica napus*) – produces ascospores and conidia; conidia require higher temperatures for germination, so their importance in the disease cycle is predicted to increase with climate warming in Northern Germany. Temperature may also influence which species are actually dominant causes of particular disease types. FHB of small grain cereals is caused by a complex of many different species of *Fusarium* and *Microdochium* (Figure 11.8). *Fusarium graminearum* has temperature optima for growth at 24–28 °C, and predominates in regions having relatively hot summers, such as Australia, North America, and parts of continental Europe, whereas *Fusarium culmorum*, with lower optima for growth (20–25 °C), is found in cooler maritime areas such as northwest Europe. In northern Europe, there has recently been a shift from *Fusarium culmorum* to *Fusarium graminearum*. In maize, *Fusarium graminearum* was the predominant species but with warmer temperatures this has shifted to *Fusarium proliferatum*, *Fusarium subglutinans*, and *Fusarium verticillioides*.

Development of FHB is related to temperature during the 6 weeks prior to flowering, and also to rainfall during flowering, as high humidity promotes sporulation. Not only is there greater infection from spores during warm (15–30 °C), wet weather but also mycelia spread to more florets. Modelling predicts that under climate change scenarios, rainfall will be considerably reduced at the current flowering time suggesting that FHB would be decreased; however, UK flowering is predicted to occur 2 weeks earlier when there will still be high rainfall, hence no predicted reduction, and even a slight increase, in FHB. This earlier and more rapid development will occur in many crop plants in existing production regions. Clearly, interactions between host, pathogen, and climate are extremely complex, and different effects will be expected in different locations. Modelling suggests that FHB will increase in the UK (Figure 11.8), though studies in other areas such as Ontario suggest no increase (Table 11.1).

Elevated atmospheric CO₂ has been reported to increase growth and fecundity of some fungal pathogens, but to cause decrease in pathogenesis of others (Table 11.1). It also indirectly affects fungal pathogens by affecting plant growth. Plant yield increases by over 15% as a result of the ‘fertiliser’ effect. Increase in the thickness of the epidermis and of leaf waxes under elevated CO₂ results in increased resistance to some pathogens. As with elevated temperature, increased rate of photosynthesis as a result of increased CO₂ may lead to earlier growth flushes, which may affect pathogen colonisation. More luxuriant canopy will develop with associated different microenvironment for pathogen development. The larger aerial biomass and increased biomass of crop debris could lead to larger reservoirs of pathogens.

Currently, there are major gaps in our understanding of how plant diseases will be influenced by climate change, with a lack of information in the field and at cellular and genomic level. Since several interacting factors influence disease outcome, modelling is an important

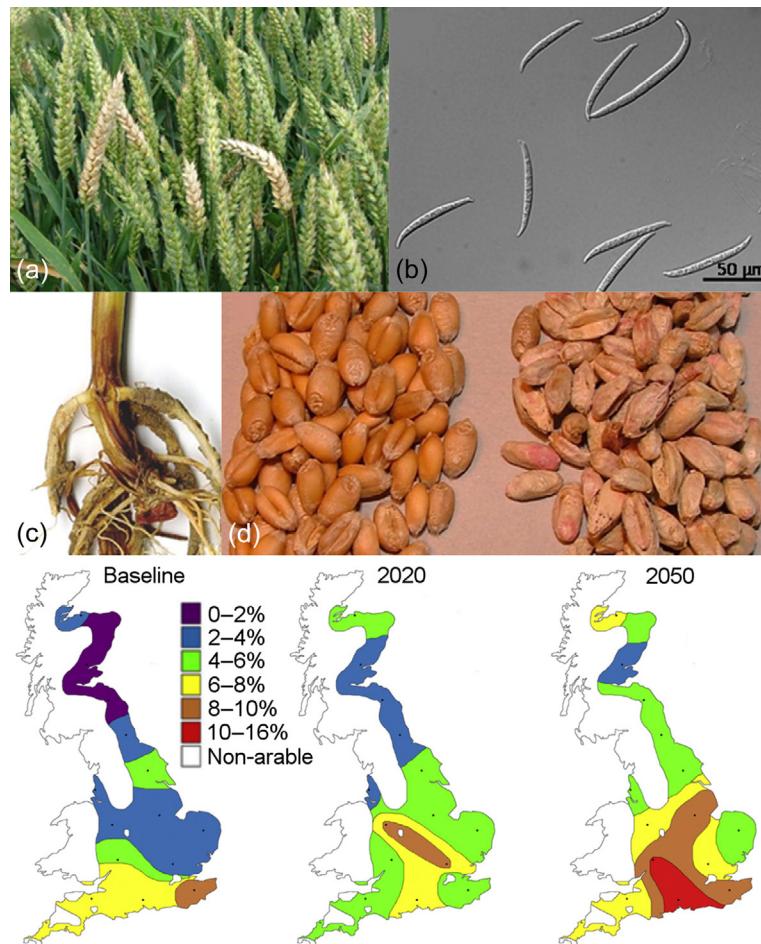


FIGURE 11.8 Fusarium head blight, also known as fusarium ear blight or scab, is a serious disease of cereals, caused by many different species of *Fusarium* and *Microdochium*. (a) Fusarium ear blight in winter wheat crop; (b) Macroconidia of *Fusarium graminearum*; (c) fusarium foot rot; (d) healthy harvested grain (left) and *Fusarium* infected grain (right). Models can be used to predict disease outbreaks in the short term, and changing patterns of incidence in the longer term. The maps show the predicted current incidence (% plants affected) of fusarium head blight disease in Great Britain, by a model that combined crop growth with a weather-based disease model using simulated future climate data. The baseline scenario prediction used weather from 1960 to 1990, and the maps for 2020 and 2050 both used a high emission scenario. Source: West, J.S., Holdgate, S., Townsend, J.A., Edwards, S.G., Jennings, P., Fitt, B.D.L., 2011. Impacts of changing climate and agronomic factors on fusarium ear blight of wheat in the UK. *Fungal Ecol.* 5, 53–61. Maps adapted from: Madgwick, J.W., West, J.S., White, R.P., Semenov, M.A., Townsend, J.A., Turner, J.A., Fitt, B.D.L., 2011. Impacts of climate change on wheat anthesis and fusarium ear blight in the UK. *Eur. J. Plant Pathol.* 130, 117–131.

predictive approach (Figure 11.8). Little consideration has yet been given to strategies for managing disease under a changing climate, but this is extremely important for long-term planning. It takes, for example, at least 10 years to develop annual crop varieties resistant to any particular disease. Clearly, much remains to be done to safeguard the food supply of the planet's human population.

Changing Patterns of Animal Disease

As with diseases of plants, climate change affects the biology of both the pathogen and the host, including distribution, survival, rate of growth/development, and extent and timing of reproduction. Perhaps the most widely reported fungal disease of animals in relation to climate change is the chytridiomycosis of amphibians caused by *Batrachochytrium dendrobatidis* (Bd) (pp. 311–312). The biology of Bd is clearly affected by temperature; growth in the lab is optimal between 17 and 25 °C, so rising environmental temperatures in montane environments are likely to result in increased growth of the pathogen. Interestingly, however, while at these temperatures infectious zoospores of Bd encyst and develop into zoosporangia more rapidly than at lower temperatures, more zoospores per sporangium are produced at 7–10 °C, and these remain infectious for longer. Life-history tradeoffs, therefore, mean that Bd maintains high fitness over a wide range of temperatures.

Changes in climatic temperature are widely thought to be a major driver in host/pathogen dynamics, but the situation is more complicated and effects of temperature are often confounded with other factors. Increasing mean and minimum temperatures are associated with increased disease incidence. With some hosts, though not with others, experimentally altering environmental temperature affects expression of host immune response, maintenance of infection and host survival. The common toad, *Bufo bufo*, which inhabits temperate regions of the Old World, has shifted its breeding phenology in response to warmer winters; the overwintering period is shorter and the post-hibernation body condition of females is poorer, as is reproductive investment and survival. Higher overwintering temperature increases the chance of infection by Bd. However, once established, the proliferation of Bd in toadlets is better in colder winters, and overall, the survival of overwintering toadlets is related to factors other than winter temperature and infectious disease. Temperature variability also seems sometimes to be a driver of amphibian decline; the El Nino climatic events result in regional temperature variability which may reduce amphibian defences against pathogens, causing widespread losses in the genus *Atelopus*.

The distribution and incidence of fungal diseases of humans (pp. 293–310) is also likely to change along with changing climate. Valley fever, caused by *Coccidioides* spp. (Ascomycota; pp. 303–305), which occurs in very dry regions of western North America, is more prevalent 1 or 2 years after an abnormal increase in rainfall, following prolonged drought, associated with El Nino. Regional warming, changes in the rain season and increasing frequency of extreme weather events, as a result of climate change, are likely to alter the distribution of the disease and to increase the risk of infection. Less obviously, fungi may affect hosts differently when they have grown outside the host under different abiotic conditions. *Aspergillus fumigatus*, which grows saprophytically but is also an opportunistic mammal pathogen and an airborne allergen (Chapter 9), expresses genes encoding for major allergens more highly at 17 °C than at 32 °C, resulting in a 12-fold difference in allergenicity per spore. Atmospheric CO₂ concentrations also affect allergenicity of spores: spores of *Aspergillus fumigatus* produced under ambient CO₂ (392 ppm) have over 8 times the allergenicity of those produced under preindustrial (280 ppm) conditions, as reflected by the allergic protein Asp f1. Extremely elevated CO₂ (560 ppm), however, reduces spore allergenicity.

Extinctions Due to Climate Change

Some habitats and the fungi within them are clearly threatened by global warming, including arctic and alpine, mangrove swamps, coastal areas, and coral reefs. As climate warms, fungi inhabiting the coldest areas, for example, will find their niches moving progressively poleward and higher up mountains until their habitats disappear and the fungi are replaced by fungi more competitive in the slightly warmer environments. The ascomycete cup fungus, *Lachnellula pini*, causes a canker disease of Scots pine in Scandinavia. It is restricted to the far north and mountainous areas with low January temperatures, and is apparently dependent on snow damage of trees for infection. This species is likely to be threatened as snow damage decreases. It also raises an interesting moral and political dilemma that fungi that are viewed as harmful to our crops will enter our lists of endangered species. Indeed, there is a Red List for rust fungi in Wales, UK.

LAND USE CHANGE

Since the human lifestyle changed from hunter-gatherer to farming, the vegetation landscape of much of the planet has changed from continuous forest cover at ca. 4000 BP to vast swathes of arable land and grassland as grazing pasture. Though forests have been lost, a need for wood remains, and so man plants and manages forests to provide the types of timber required. In grassland, arable land and plantation forests, productive and pathogen-resistant species and varieties are commonly selected and often grown as a monoculture. Further, mineral nutrient fertilisers, pesticides, and herbicides are applied to enhance yield. Habitat has been lost, and all of these management practices dramatically alter the microbial communities and activities within these ecosystems. As seen in some of the examples that follow, intensification of agricultural practices can sometimes result in less diverse fungal communities. These may be less able to adapt to other global change factors, particularly climate. Maintenance of biodiversity provides an 'insurance effect' with respect to ecosystem functioning, as a more diverse community is more likely to contain some species able to adapt to change, which is a good argument for conservation (pp. 391–398).

Grasslands

Grasslands cover about 20% of Earth's land surface, usually where there is low or seasonal rainfall (250–1500 mm/year). Grasslands are found at a range of latitudes and altitudes, e.g. tropical east African savannah to temperate steppes, prairies and pampas, montane alpine meadows, and Andean Páramo, often merging into tundra and heathland. The grassland habitat type reached its maximum extent in Europe between the fifteenth and twentieth centuries. Since then, dry mesic grassland has been converted to arable crops, conifer plantations and scrubland, and in many countries grassland areas have decreased by more than 90%, though even in Europe there are still some countries with significant areas of semi-natural grassland (e.g. The Faeroe Isles, Norway, Romania, Scotland and Wales). Most grasslands are semi-natural, grazing preventing succession to scrubland and woodland. Most dry

grasslands are nutrient poor, because grazers remove nitrogen and phosphorus, and have often been 'improved' by addition of fertiliser and sowing with a few fast growing grasses.

Grasslands are very different ecosystems to forest and woodland. In grasslands, litter components input to soil are smaller, and contain less lignin and fungitoxic compounds. Mammalian herbivores eat 40–70% of above ground NPP in grasslands, hence a large amount of material enters the soil in a comminuted, partially digested form as dung. A high proportion of plant biomass is underground, especially when grazing pressure is high and regular grazing results in a high root turnover and large input of dead organic matter to soil. It comes as no surprise then that grasslands and woodlands have very different communities of fungi. In 'unimproved' dry grassland with long continuity in Europe, characteristic fungi include the waxcaps (*Hygrocybe* and *Camarophyllus* species), and pink gills (*Entoloma* spp.), some club fungi (*Clavaria*, *Clavulinopsis*, *Ramariopsis*), and earth tongues (*Geoglossum*, *Microglossum*, *Trichoglossum*). In several countries, the number of waxcap species has been suggested as a good indicator of valuable 'unimproved' grassland sites: 1–3 of limited importance; 4–8 of local importance; 9–16 of regional importance; 17–21 of national importance; and ≥22 of international importance. The exact habitat and nutritional requirements of most grassland fungi is unknown, but it is generally accepted that some species seem to occur in grasslands with long continuity (e.g. *Entoloma anatinum*, *Entoloma longistriatum*, *Entoloma mougeotii*, *Hygrocybe intermedia*, *Hygrocybe citrinovirens*, *Hygrocybe ovina*, *Hygrocybe aurantiosplendens*, and *Hygrocybe ingrate*), whereas some rare species (e.g. *Entoloma formosum*, *Entoloma hispidulum*, *Entoloma xanthochroum*, *Hygrocybe subpapillata*, *Hygrocybe glutinipes*, *Hygrocybe vittellina*, and *Hygrocybe spadicea*) are found in grasslands with long and shorter continuity. A more broadly applicable indicator system than that based only on *Hygrocybe* species, assigns a different point score to each grassland species, so that the value of a locality is calculated by summing the value assigned to each of the species found there. Many other groups are also found in dry grasslands, both 'improved' and 'unimproved' and other habitats too, including species of *Agaricus*, *Galerina*, and *Macrolepiota*, and also puff balls.

Not only are there major differences in the communities of fungi that produce macroscopic fruit bodies but also in microfungi, depending on vegetation type and management intensity. Considering yeasts as an example, while forests harbour predominantly basidiomycete yeasts (e.g. *Cryptococcus terricola* and *Trichosporon porosum*), those of grasslands are largely ascomycetous (e.g. *Schwanniomyces castelli*). The proportion of ascomycetes in grasslands increases with management intensity, but community composition also changes, *Schwanniomyces castelli*, for example, decreasing and *Barnettozyma californica* increasing. These changes reflect the fact that land management, grazing, and application of fertilisers alter the soil nutrient status, providing readily assimilable carbon and mineral nutrient sources.

Arable and Plantation Forests

In the developed world, though land use is always changing, agricultural land has been established for a long time. In the developing world, however, there is a very high rate of conversion from forest to cultivated land, often with monoculture of crops. As well as loss of biodiversity of macrobiota and loss of soil quality, there are changes in the microbial communities. As an example, in Central Mexico, forest is being converted to avocado (*Persea americana*) plantations and to fields of maize (*Zea mays*). In a study comparing the arbuscular

mycorrhizal fungal (AMF) communities in all three vegetation types, it was found that AMF species diversity was only slightly less in avocado plantations than in forest, despite the use of copper-based fungicides and fertilisers in the former, perhaps reflecting a similar microclimate and the presence of many similar herbaceous plants which provide additional hosts for AMF. In maize fields, however, there were 50% less AMF species, probably due to lack of other herbaceous plants, no irrigation or canopy, low soil organic matter, and low available phosphorus. There were more AMF species unique to forest than to avocado plantations, and more unique to avocado than to maize, highlighting the importance of preserving forests. The geographical region in which the vegetation types were found had a major impact on the AMF communities, suggesting that climate change may have a bigger effect on AMF communities than changes in land use.

POLLUTION, PESTICIDES, FERTILISERS, NUTRIENT DISTRIBUTION, AND RECYCLING

Pollutants can arrive by air, water, or directly deposited by man. There are three main classes of air pollutants: (1) primary pollutants that remain in the same form as they were emitted (e.g. SO_2 , NO_x , and fluoride compounds); (2) secondary pollutants formed by the primary pollutants in the atmosphere (e.g. ozone (O_3), peroxyacetyl nitrate, nitric (HNO_3), and sulphuric (H_2SO_4) acids); and (3) other compounds – pesticides, industrial organic compounds, metals, metalloids, and radionuclides.

Fungal hyphae feed by absorption (Chapters 2 and 5), and can accumulate both micronutrient and non-nutrient elements. Lichen thalli, in contrast, can also accumulate absorbed nutrients, non-nutrients and other particles that land on their surface both as dry deposition and deposited in precipitation. Very high element concentrations tend to result from entrapment of particles, which can accumulate in large intercellular medullary spaces. These particles can range in size from microscopic aerosols ($<1\text{ }\mu\text{m}$) to macroscopic dust ($>1\text{ mm}$). Lichens and other fungi vary in their sensitivity to pollutants, pesticides, and fertilisers, resulting in changes in communities, including species loss. Differences in sensitivity, ability to accumulate, and the perennial nature of lichens and some macrofungi make them useful monitors of pollutants and other elemental deposits.

Lichens and Air Pollution

Large scale pollution, especially from SO_2 and NO_x , resulting from the burning of fossil fuels started in the industrial revolution during the late eighteenth century. Since then the lichen biota of almost all of Europe has undergone considerable change. These effects are well illustrated by the classic study of Hawksworth and Rose on the distribution of lichen communities in Britain in relation to atmospheric SO_2 (Figure 11.9 and Table 11.2). The lichen communities around industrial conurbations became depauperate, with only very resistant species present, while less polluted areas had more species rich communities. These atmospheric pollutants declined following targeted emission controls, and pollution-sensitive lichen species have begun to recolonise areas from which they had become extinct. Habitats seem to become suitable for lichens relatively soon (10–100 year) after removal of SO_2 deposition and

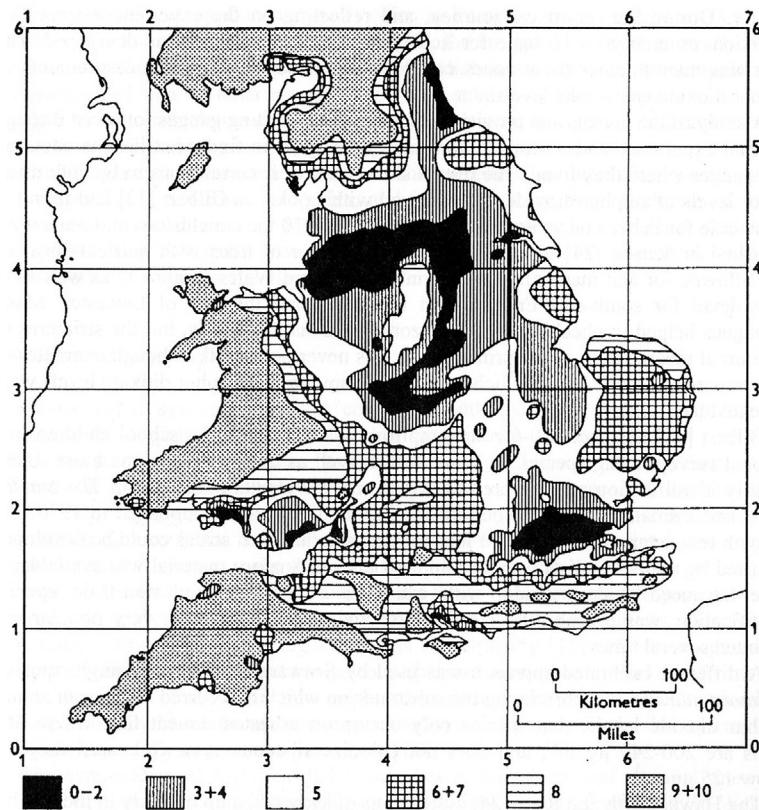


FIGURE 11.9 Lichen communities are dramatically affected by airborne pollutants. Shown here are zones of lichens in England and Wales in the late 1960s. The communities are highly correlated with atmospheric SO₂ concentration. Typical lichens found in each zone are indicated in Table 11.2. The key beneath the map indicates the zone number, and corresponds to zone numbers in the table. Notice the restricted lichen biota around the industrial conurbations of London, the midlands and south Wales, and the diverse biota including sensitive lichens in the nonindustrial south west, west Wales and northern UK. Source: Hawksworth, D.L., Hill, D.J., 1984. *The Lichen-Forming Fungi*. Blackie, Glasgow.

accompanying acidity. However, unfortunately, the decline in atmospheric SO₂ has been accompanied by an increase in N-pollution from intensive agriculture, and not just in Europe but also in biodiversity hotspots, including Southeast Asia, Central America, and India. Lichen community composition changes in response to even small increases in nitrogen deposition. In the Pacific Northwest of the USA, in polluted areas, sensitive species (e.g. *Alectoria sarmentosa*, *Bryoria fuscescens*, *Sphaerophorus globosus*, *Usnea filipendula*) and N-fixing cyanolichens (e.g. *Lobaria oregana*) have declined or disappeared, while nitrophilous species (e.g. *Xanthoria polycarpa*, *Physcia adscendens*, and *Candelaria concolor*) are common.

Since lichens are long-lived and able to bioaccumulate atmospheric deposits, their thalli are valuable archives, providing useful tools for monitoring changes in atmospheric pollutants. The residence times of pollutants and nutrients within thalli vary among elements. Macronutrients (e.g. N, P, K, Ca, Mg, S) are relatively mobile and easily leached, so that

TABLE 11.2 Relationship between lichens and SO₂ pollution in England and Wales in the late 1960s, on deciduous trees, particularly *Fraxinus* and *Quercus*, with moderately acidic, rough bark.

Zone	Not eutrophicated: nitrogen-loving communities have not developed	Eutrophicated: nitrogen-loving communities have developed	Mean winter SO ₂ (mg m ⁻³)
0	Lichens absent	Lichens absent	?
1	<i>Desmococcus viridis</i> at trunk base	<i>Desmococcus viridis</i> extends up trunk	about 170
2	<i>Desmococcus viridis</i> extends up trunk; <i>Lecanora conizaeoides</i> at trunk base	<i>Lecanora conizaeoides</i> abundant; <i>Lecanora expallens</i> occasionally on base of trunk	about 150
3	<i>Lecanora conizaeoides</i> extends up trunk; <i>Lepraria incana</i> frequent at trunk base	<i>Lecanora expallens</i> and <i>Buellia punctata</i> abundant; <i>Buellia canescens</i> sometimes present	about 125
4	<i>Hypogymnia physodes</i> and/or <i>Parmelia saxatilis</i> and/or <i>Parmelia sulcata</i> at trunk base; <i>Chaenotheca ferruginea</i> , <i>Hypocenomyce scalaris</i> and <i>Lecanora expallens</i> often present	<i>Buellia canescens</i> common; <i>adscendens</i> , <i>Physcia tribacia</i> (south facing) and <i>Xanthoria parietina</i> sometimes present.	about 70
5	<i>Hypogymnia physodes</i> or <i>Parmelia saxatilis</i> extends up trunk; <i>Lecanora chlarotera</i> , <i>Parmelia glabratula</i> , <i>Parmelia subrudecta</i> or <i>Parmeliopsis ambigua</i> present; <i>Calicium viride</i> , <i>Chrysotrichia candelaris</i> and <i>Pertusaria amara</i> may occur; <i>Ramalina farinacea</i> and <i>Evernia prunastri</i> may be present but usually only at trunk base; <i>Platismatia glauca</i> may be present on horizontal branches	<i>Buellia canescens</i> and <i>Xanthoria parietina</i> common; <i>Buellia alboatra</i> , <i>Haematomma coccineum</i> , <i>Opegrapha varia</i> , <i>Opegrapha vulgata</i> , <i>Parmelia acetabulum</i> (in East), <i>Physconia grisea</i> , <i>Physconia farrea</i> , <i>Physcia orbicularis</i> , <i>Physcia tenella</i> , <i>Ramalina farinacea</i> , <i>Schismatomimma decolorans</i> , <i>Xanthoria candelaria</i> sometimes present	about 60
6	<i>Parmelia caperata</i> present at least on the base; rich in species of <i>Pertusaria</i> (e.g. <i>Pertusaria albescens</i> , <i>Pertusaria hymenea</i>) and <i>Parmelia Graphis elegans</i> appearing; <i>Pseudevernia furfuracea</i> and <i>Bryoria fuscescens</i> present in upland areas	<i>Physcia orbicularis</i> , <i>Physconia grisea</i> , <i>Opegrapha varia</i> and <i>Opegrapha volgata</i> abundant; <i>Arthopyrenia alba</i> , <i>Caloplaca luteoalba</i> , <i>Lecania cyrtella</i> , <i>Pertusaria albescens</i> , <i>Physconia pulverulenta</i> , <i>Physciopsis adglutinata</i> , <i>Xanthoria polycarpa</i> sometimes present.	about 50
7	<i>Parmelia caperata</i> , <i>Parmelia revoluta</i> (except in North east), <i>Parmelia tiliacea</i> , <i>Parmelia exasperatula</i> (in North) extend up the trunk; <i>Pertusaria hemisphaerica</i> , <i>Rinodina roboris</i> , <i>Usnea subfloridana</i> (in South) and <i>Arthonia impolita</i> (in East) appear	<i>Anaptychia ciliaris</i> , <i>Arthopyrenia biformis</i> , <i>Bacidia rubella</i> , <i>Candelaria concolor</i> , <i>Physcia aipolia</i> sometimes present	about 40
8	<i>Usnea ceratina</i> , <i>Parmelia perlata</i> or <i>Parmelia reticulata</i> (South and West) appear; <i>Rinodina roboris</i> extends up the trunk (in South); <i>Normandina pulchella</i> and <i>U. rubicunda</i> (in South) usually present	<i>Physcia aipolia</i> abundant; <i>Anaptychia ciliaris</i> occurs with apothecia; <i>Desmaziera evernioides</i> , <i>Gyalecta flotowii</i> , <i>Parmelia perlata</i> , <i>Parmelia reticulata</i> (in south and west) <i>Ramalina obtusata</i> and <i>Ramalina pollinaria</i> sometimes present.	about 35
9	<i>Dimerella lutea</i> , <i>Lobaria pulmonaria</i> , <i>Lobaria amplissima</i> , <i>Pachyphiale cornea</i> , or <i>Usnea florida</i> present; if these are absent crustose flora well developed with often more than 25 species on larger well lit trees	<i>Caloplaca aurantiaca</i> , <i>Caloplaca cerina</i> , <i>Physcia leptalea</i> , <i>Ramalina calicaris</i> , <i>Ramalina fraxinea</i> , <i>Ramalina subfarinacea</i> sometimes present	<30
10	<i>Lobaria amplissima</i> , <i>Lobaria scrobiculata</i> , <i>Pannaria spp.</i> , <i>Sticta limbata</i> , <i>Teloschistes flavicans</i> , <i>Usnea articulate</i> or <i>Usnea filipendula</i> present and locally abundant.	<i>Caloplaca aurantiaca</i> , <i>C. cerina</i> , <i>Physcia leptalea</i> , <i>Ramalina calicaris</i> , <i>Ramalina fraxinea</i> , <i>Ramalina subfarinacea</i> sometimes present	'unpolluted'

Modified from 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. Hawksworth, D.L., Hill, D.J., 1984. *The Lichen-Forming Fungi*. Blackie, Glasgow.

measurable changes can be detected over weeks or months. Total nitrogen in thalli of *Cladonia portentosa* ranged from 7 to 13 mg/g in low to high nitrogen deposition sites across the UK. Some environments are naturally rich in nitrogen (e.g. bird perching stones). Up to 3% of thallus dry weight was N in *Xanthomendoza borealis* (a *Xanthoria*-like species) close to a penguin roosting site in Antarctica. In lichens near industrialised areas in the 1960s and 1970s, 1000 µg/g or more of sulphur was commonly found in thalli near pollution sources, which compares with 300 µg/g or less in green algal lichens in clean sites.

Toxic metals (e.g. cadmium, lead, and zinc) are more tightly bound within lichen thalli and hence more slowly released. The use of lichens as monitors of heavy metals is nicely shown by a study in which freshly collected samples and herbarium specimens, from a site within 15 km of the centre of Washington, DC, from 1907 to 1992 were analysed for lead. Lead content peaked in 1970 and then declined with the advent of catalytic converters in cars, despite the increase in road traffic.

Lichens also accumulate radionuclides, and have been used to monitor fallout from nuclear bomb testing and following the Chernobyl power station accident. This accumulation of radionuclides was a particular problem in arctic tundra, where lichens dominate the vegetation, and are the main food source of caribou/reindeer (*Rangifer tarandus*) (See also p. 233). The radionuclides accumulated in the *Cladonia* lichens and, therefore, accumulated in wild and domestic herds and ultimately in the North American Inuit and Scandinavian Sàmi people that use them as a major food source.

From the forgoing it is clear that lichens can be used for monitoring environmental pollution in several different ways: (1) community surveys as done by Hawksworth and Rose (Figure 11.9); (2) analysing pollutant content of resident lichens, including those collected historically; and (3) transplanting lichens, attached to twigs, rocks, etc., especially into areas where there are no suitable indigenous lichens. Transplanting also has the advantage that procedures can be standardised.

Metal and Radionuclide Pollution Effects on Saprotrophic and Mycorrhizal Fungi

Non-lichenised fungi accumulate pollutants, pesticides, etc., by absorption through hyphae, and elevated levels in mycelium are mirrored in the fruit bodies of macrofungi. It is the fruit bodies that have usually been analysed. The ability to accumulate metals varies widely between taxa, but can be considerable in species growing on polluted sites (Table 11.3). Generally, concentrations of cadmium, lead, mercury, and zinc, for example, are higher in fruit bodies from urban and industrialised regions than from rural areas. So, fruit bodies could be used as bioindicators of soils polluted by these and other metals. There are two sorts of bioindicators: (1) reaction indicators – individual species or communities that are sensitive or tolerant and respectively decline/disappear or increase on polluted sites; and (2) accumulation indicators that are analysed for the pollutant. Some mycorrhizal basidiomycetes are particularly tolerant of heavy metals, including *Amanita muscaria*, *Laccaria laccata*, and several *Boletus* species, while some *Russula* species are sensitive. There is no simple positive relationship between fruit body content and soil content of cadmium, lead and mercury but some species have been proposed as bioindicators based on metal analyses. For example: species of *Agaricus* and *Mycena pura* for mercury and cadmium; *Amanita rubescens*, *Amanita*

TABLE 11.3 Examples of Heavy Metal Accumulation in Saprotrrophic and Ectomycorrhizal Basidiomycetes Growing on Metal Polluted Sites

Metal	Species	Nutritional mode	Fruit body or rhizomorph	Concentrations (mg/kg dry wt)	Comments
Aluminium Al	<i>Armillaria</i> spp.	Saprotrroph	Rhizomorph	3440	
Antimony	<i>Chalciporus piperatus</i>	Mycorrhizal	Fruit body	Maximum 1423	
Arsenic As			Fruit body	100-200	
Cadmium Cd	<i>Laccaria amethystina</i>	Mycorrhizal	Fruit body	Average 5, maximum 40	
Copper Cu	<i>Amanita muscaria</i>	Mycorrhizal	Fruit body	93	
Copper Cu	<i>Armillaria</i> spp.	Saprotrroph	Rhizomorph	15	
Gold Au	<i>Boletus edulis</i>	Mycorrhizal	Fruit body	Maximum 235 ng/g	in nongold sites 10 ng/g
Gold Au	<i>Langemannia gigantea</i>	Saprotrroph	Fruit body	160 ng/g	in nongold sites 10 ng/g
Lead Pb	<i>Armillaria</i> spp.	Saprotrroph	Rhizomorph	680	
Lead Pb	<i>Hypholoma fasciculare</i>	Saprotrroph	Fruit body	7	
Silver ¹¹⁰ Ag	<i>Agaricus bisporus</i>	Saprotrroph	Fruit body	Maximum 167	Concentration factor up to 40
Manganese Mn	<i>Polyporus squamosus</i>	Saprotrroph	Fruit body	Mean 138	
Mercury ²⁰³ Hg	<i>Agaricus bisporus</i>	Saprotrroph	Fruit body	Maximum 75	Concentration factor up to 3.7
Mercury Hg	<i>Hydnnum repandum</i>	Mycorrhizal	Fruit body	1	
Zinc Zn	<i>Armillaria</i> spp.	Saprotrroph	Rhizomorph	1930	
Zinc Zn	<i>Polyporus squamosus</i>	Saprotrroph	Fruit body	Mean 200	

Examples of highest accumulating species given unless otherwise indicated.

Source: [Gadd \(2007\)](#).

strobiliformis, *Coprinus comatus*, *Lycoperdon perlatum*, and *Marasmius oreades* for mercury; and *Agaricus* sp. and *Lycoperdon* sp. for lead, zinc, and copper. Non-lichenised fungi also accumulate radionuclides; the mycorrhizal *Hebeloma cylindrosporum* has particularly high transfer factors for uranium and thorium, which might make it a good bioindicator of radioactive content of soil. *Hebeloma cylindrosporum* and the saprotrophic *Lycoperdon perlatum* have been suggested as bioindicators for ²³⁹Pu, ²⁴⁰Pu, and ²⁴¹Am.

Aquatic fungi can also face elevated levels of metals, if streams run through rock, are fed by soils rich in a particular element, and most particularly as a result of mining activity. Effluent from coal, copper, gold, zinc, and uranium mining has negative effects on fungal species richness, biomass, leaf decomposition rates, and spore production. At relatively low pollution levels, though diversity is strongly affected, biomass, growth and decomposition activity are affected relatively little, implying some compensation by tolerant species or strains.

Nitrogen Enrichment Effects on Saprotrrophic and Mycorrhizal Fungi, and Nutrient Cycling

Though dinitrogen (N_2) makes up over 70% of Earth's atmosphere, it cannot be used directly by plants. Plants can only obtain nitrogen as nitrate (NO_3^-) or ammonium (NH_4^+) ions, directly from soil solution, from nitrogen-fixing bacteria in the case of legumes, and via mycorrhizal associations for over 90% of plants (Chapter 7). Nitrogen is often limiting for plant growth, so man adds fertilisers (N, P, K) to agricultural ecosystems, from natural sources and fixed industrially. Burning fossil fuels releases vast quantities of nitrogenous oxides and other compounds; nitrous oxide (N_2O) in the atmosphere has rapidly increased since the 1940s and is now about 310 ppm compared with 285 ppm from preindustrial times, as revealed by analysis of air bubbles in glacier ice. As a result of all of these inputs, nitrogen deposition has increased by 3–5 times. This nitrogen pollution affects fungal species diversity, abundance and activity, and hence also ecosystem functioning.

N-pollutant effects on mycorrhizal fungi are evident. Though mycorrhizal abundance is increasing as a result of climate change (see previous section), N-pollution has opposite effects with an average 15% decline in mycorrhizal biomass (AM 25%, ECM 5%). The diversity and richness of ECM fungi also declines in coniferous forests and to a lesser extent in deciduous forests, as shown by studies along nitrogen deposition gradients, natural fertility gradients and experiments adding N-fertiliser, based on root tips, soil hyphae and fruit body studies. Sensitivity varies between species and genera. Species of *Cortinarius*, *Piloderma*, *Suillus*, and *Tricholoma* respond negatively to elevated N, while *Paxillus involutus* and species of *Laccaria*, *Lactarius*, and *Thelephora*, which tend to be early successional species, increase. Sporocarp declines in the genera *Cantharellus*, *Cortinarius*, *Suillus* and *Tricholoma*, first noticed in Europe in the 1980s, have now largely been backed up by soil and root tip studies there and elsewhere. Further, some species, for example stipitate hydnoids (*Bankera*, *Hydnellum*, *Phellodon*, and *Sarcodon*), are now endangered as a result of nitrogen increase (see p. 367). Mycorrhizal fungi do not all respond to elevated nitrogen in the same way, depending on functional traits. Species with medium distance fringe category exploration types (p. 217) (e.g. species of *Cortinarius*, *Piloderma*, and *Tricholoma*) have declined dramatically in response to elevated nitrogen. This exploration type is characterised by dense proliferation of hyphae into loose undifferentiated aggregations (cords) that ramify around and within patches of organic matter. In contrast, short distance exploration types are favoured under elevated N.

Because of effects on ECM fungi, nutrient cycling in polluted forest ecosystems is altered (Figure 11.10). In non-polluted ecosystems, ECM not only sequester inorganic nitrogen from soil solution but also short-circuit the N cycle by utilising organic N, as a result of their abilities as decomposers. This restricts the supply of N in soil available to soil microorganisms and to non-ECM plants, suppressing arbuscular mycorrhizal herbs and some tree saplings whose AM partners are less effective at obtaining organic N. Since little N is available in soil solution, little N is lost through leaching of ammonium and nitrate, and through denitrification. In N-polluted ecosystems, however, the situation is very different as there is a decline in ECM fungi: organic and inorganic (ammonium and nitrate) N pools are much larger resulting in losses through leaching; utilisation of organic N by ECM is reduced; and use of inorganic N increases.

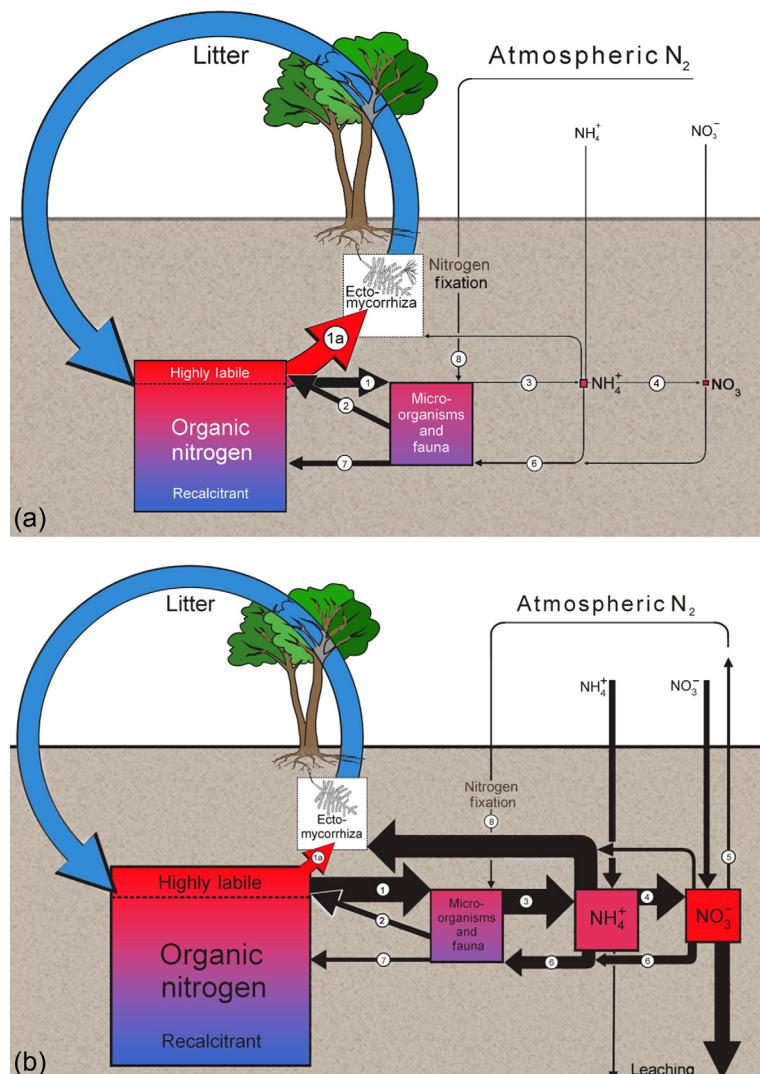


FIGURE 11.10 The nitrogen cycle in unpolluted, N-limited, forest ecosystems with ectomycorrhizal (ECM) trees (a) is very different from in N-polluted forests. In N-polluted forests, trees obtain organic nitrogen directly from dead organic matter through the activities of their fungal partners (pathway 1a; largest arrow), short-circuiting the microbial mineralization pathways (pathways 3 and 4). The main microbially driven pathways are: (1) fungal depolymerisation and assimilation of organic N, (2) release of nutrients from dead microbes, (3) mineralisation (ammonification), (4) nitrification, (6) microbial immobilisation, (7) humus formation, and (8) nitrogen fixation. (b) In N-polluted forests dominated by ectomycorrhizal trees, organic and inorganic (ammonium and nitrate) N pools are much larger, utilisation of organic N by ECM is reduced, and use of inorganic N increases. Rates of mineralization, nitrification and ensuing N losses through nitrate leaching and denitrification, all increase. Source: Leake, J.R., Johnson, D., Donnelly, D.P., Muckle, G., Boddy, L., Read, D.J., 2004. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agro-ecosystem functioning. *Can. J. Bot.* 82, 1016-1045.

N deposition affects saprotrophic fungi too. This is important because changes in decomposition rates will affect net carbon sequestration in ecosystems. Because organic matter with a low C:N ratio decomposes more rapidly than that with a high C:N ratio, decomposition is thought to be N-limited. Effects of increased nitrogen seem to be quite variable depending on sites, though leaf litter decomposition often increases along increasing N-deposition gradients in both terrestrial and aquatic ecosystems. However, additional N suppresses basidiomycete decomposition of lignin-rich organic matter, due to inhibition of the lignolytic enzymes, which contrasts with an increase in cellulose activity.

Eutrophication of freshwater ecosystems, caused by run-off from fertilised soil and from domestic effluents, affects aquatic fungal activity and community composition. Variable effects have sometimes been reported, but increased nitrates and phosphates usually increase fungal growth, spore production, and litter decomposition, though fungal diversity tends to decrease. Reports of negative effects are probably not due to increase in nutrients per se, but to accompanying inorganic pollutants, deposition of fine sediments, and changes in activity of competitive microbes.

MOVEMENT OF BIOTA

Fungi can invade new areas by wind, water, and animal dispersal of spores. Sometimes movement can be rapid and widespread, even global, particularly as a result of man's activities. There are numerous examples of both plant and animal pathogens spread by man (Chapters 8 and 9). To give two examples: Bd, the chytrid pathogen of amphibians (pp. 311–312), has probably been spread across the globe by man's trade in amphibians. There is clear evidence, from whole genome-amplification quantitative polymerase chain reaction (PCR), that the IUCN (International Union for Conservation of Nature) red-listed (pp. 392–394) Mallorcan midwife toad (*Alytes muletensis*) was infected by Bd when the endangered frog *Xenopus gilli* was brought into breeding facilities in Mallorca from Western Cape, South Africa. Dutch elm disease, (pp. 274–275) caused by several species of *Ophiostoma*, though spread locally via carriage by bark beetles in the genus *Scolytus*, was first noticed in Europe in 1910, but the species had relatively mild effects. In about 1967, however, the extremely virulent *Ophiostoma novo-ulmi* was transported to the UK in Rock elm (*Ulmus thomasii*) from North America, and by the early 1980s *Ophiostoma novo-ulmi* had almost completely eradicated English elm (*Ulmus glabra*) as mature trees in Southern Britain, though English elm still survives in hedgerows from suckers (root sprouts). Introduction of pathogens into new biogeographic zones is increasingly occurring, and as a tree pathologist once described it, every introduced pathogen is an open-ended experiment in evolution. Host/environment clones evolve where there are isolating mechanisms, and this leads to emergence of new species (pp. 135–137).

It is not only pathogenic fungi that invade new areas – though they are most obvious because of their dramatic effects on hosts, but also mutualistic fungi including mycorrhizas. Ectomycorrhizas have been frequently introduced to new locations along with their hosts. Though they may not always spread, being restricted to a few locations and their original hosts, there are examples of mycorrhizal fungi that become invasive, the best documented example probably being the death cap *Amanita phalloides*. It is native to Europe and North Africa, has been reported in Asia and definitely introduced to southern Africa, Australia,

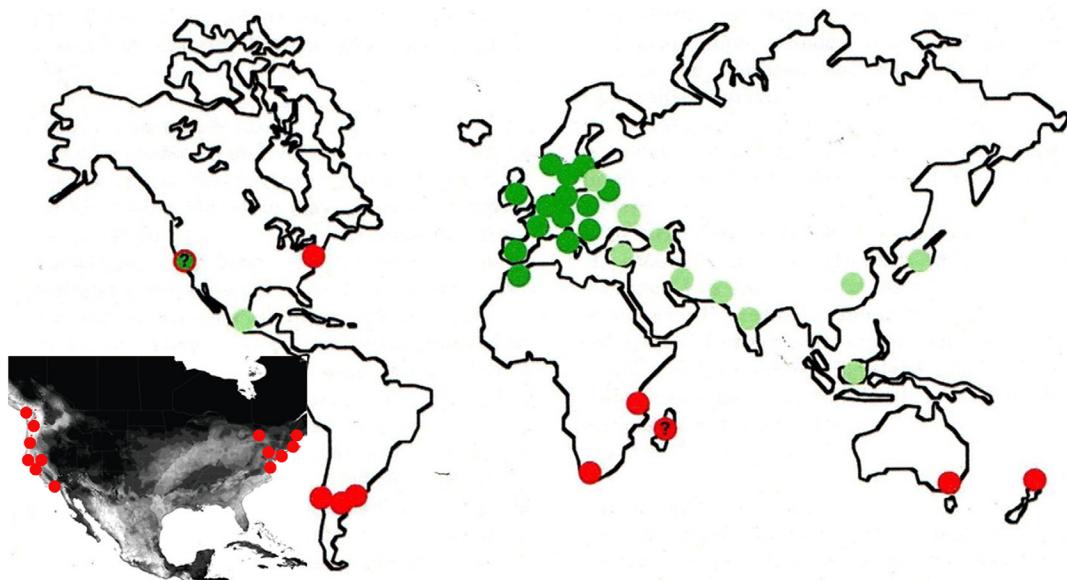


FIGURE 11.11 Current biogeography of the ectomycorrhizal death cap *Amanita phalloides*. Green (dark grey in the print version) dots indicate locations where the fungus is known to be native. Pale green (light grey in the print version) dots are places where the fungus has been reported but the description does not match the current concept of the species. Red (black in the print version) dots indicate where the species has been introduced. Dots with a question mark are places where the fungus is definitely found and has probably been introduced, but this is uncertain. From: Pringle, A., Vellinga, E.C., 2006. Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides*. *Biol. Invas.* 8, 1131–1144. The inset shows the known occurrences of *A. phalloides* (red (grey in the print version) dots), and the shading indicates the probability of occurrence: white 50–100% to dark shading <1%. Source: Wolfe B.E., Richard, F., Cross, H.B., Pringle, A., 2010. Distribution and abundance of the introduced ectomycorrhizal fungus, *Amanita phalloides*, in North America. *New Phytologist* 185, pp. 803–816.

New Zealand, South America, and the United States (Figure 11.11). From its native Europe, it was introduced to North America's east and west coasts, but the distribution and abundance on these coasts are different. It has a large range on the west coast (Figure 11.11 inset), and in California it is common in native forests where it is sometimes the dominant ECM species, but on the east coast it is most common in plantations of native and nonnative trees, and has a smaller range; temperature is probably the major factor affecting its distribution.

FUNGAL CONSERVATION

The loss of biodiversity is a pressing crisis across the globe. As with plants and animals, many fungal populations most likely have and are experiencing large declines due to destruction, fragmentation, and loss of habitat, pollution, invasive species, climate change and other human impacts. Again, as with plants and animals, mass extinctions of fungi are likely to occur, but when they do many will be unrecorded, as so many species are still unknown (Chapter 1). Six species of ascomycetes new to science were found associated with the living

leaves of *Coussapoa floccosa*, a red listed Brazilian tree, until recently thought to be extinct in the wild. When plants become extinct, fungi that are specific to them also become extinct. Large population declines of some of the larger fungi were first shown beyond doubt in The Netherlands in the 1970s, by comparing annual records from the same sites. The decline can also be seen in records of the amounts of locally collected wild mushrooms on sale in the markets of some European towns. For example, in Saarbrucken (Germany) in the mid-1950s, annual sales of fruit bodies of the chanterelle (*Cantharellus cibarius*), a mycorrhizal fungus, were 6–8 tonnes, but had decreased to about 2% of this by the mid-1970s. Since then evidence has accumulated for the decline of many species to critical levels in many countries.

Though loss of diversity is a problem at least as large for fungi as for plants and animals, fungi are not a high profile group in most of the world, a notable exception being in Fennoscandia. Further, fungi are not explicitly mentioned in the Bern Convention and most people are unaware of their significance and decline. A first step towards halting this loss is to determine which species are threatened, and then to determine and implement appropriate conservation measures. The most widely used scheme for assessing and documenting the current status of biodiversity is the IUCN red-listing system.

Fungus Red Lists

It is important to present the biodiversity status of all organisms with one voice, so that the public and decision-makers can easily understand the situation. The IUCN red-listing system allows comparisons to be made between species from different taxonomic groups and in different regions, and it is increasingly being used to set national, regional, and global priorities for conservation action. Around 15,000 fungal species have been evaluated at the national level, though not all Red Lists fully meet the IUCN criteria. As with several groups of animals and plants, it is challenging to apply the IUCN criteria to fungi. With fungi this is because, for most of the time, they are hidden from sight, revealing themselves only occasionally as fruit bodies. Many of the macrofungi fruit annually, but irregularly, depending on weather and many other factors, and there is low correlation between the presence of fruit bodies and the presence and extent of mycelium. Difficulties in applying the IUCN criteria stem from difficulties in defining mature individuals, generation length, location, and uncertainty of how absence data should be handled (because absence of fruit bodies does not necessarily imply absence of a fungus).

There are nine IUCN Red List categories ([Table 11.4](#)). To assess the conservation status of a species (i.e. to determine to which Red List category a species belongs) the following data are necessary: (1) its geographic distribution; (2) an estimate of its population size; and (3) how geographic distribution and population size are changing over time. However, species with very small population sizes can be red-listed ([Table 11.5](#) criterion D) even if there is no evidence that a population is in decline or will decline. The assessment aims to give a likely estimate of the total population and, if possible, also the population trend. The yet unrecorded number of localities or individuals always needs to be considered, and factors such as whether a species is conspicuous or inconspicuous, and how much it has been looked for, etc., must be taken into account.

For red listing, the size of a population is the number of mature individuals, defined by the [IUCN Standards and Petitions Subcommittee \(2010\)](#) as ‘individuals known, estimated or

TABLE 11.4 The IUCN Red List Categories Applied for Fungi

A species is	When
Extinct (EX) or Regionally extinct (RE)	The species has previously been resident and there is no reasonable doubt that the last individual has died. Due to the cryptic nature of fungi, RE should be used only if exhaustive surveys during an adequate time period have failed to record an individual. Extinct (EX) refers to the global scale and RE to any lower geographical scale
Critically endangered (CR)	The best available evidence indicates that it meets any of the criteria A ^a to E for CR, and it therefore faces an extremely high risk of regional extinction
Endangered (EN)	The best available evidence indicates that it meets any of the criteria A ^a to E for EN, and it therefore faces a very high risk of regional extinction
Vulnerable (VU)	The best available evidence indicates that it meets any of the criteria A ^a to E for VU, and it therefore faces a high risk of regional extinction
Near threatened (NT)	It has been evaluated against the criteria and does not qualify for CR, EN, or VU, but is likely to qualify for a threatened category in the near future
Least concern (LC)	The species has been evaluated against the criteria and does not qualify for CR, EN, VU, or NT. Species in this category are normally widespread and abundant
Data deficient (DD)	There is inadequate information to make assessment of the species risk of extinction based on its distribution and population status. DD is not a threat category and species designated DD are rarely targets for conservation action
Not applicable (NA)	The taxon is not native to the region or of lower taxonomic rank than considered eligible for red-listing within the region. This category is not used at the global level
Not evaluated (NE)	The species has not yet been evaluated against the criteria

^aSee Table 11.5.

Modified from: Dahlberg and Mueller (2011).

inferred to be capable of reproduction'. The concept of a fungal individual is complex (pp. 100–101), and the IUCN unit of red-listing is the ramet (p. 100) rather than the genet (p. 100). Unfortunately, there is little information on the number and dynamics of mycelial ramets in nature, and it would be extremely hard and costly to collect data on the number of mycelial ramets in large geographical areas over many years. For practical purposes, the concept of a functional individual is used, which is based on numbers of fruit bodies. For purposes of red-listing, a functional individual of a wood-inhabiting fungus is defined as all conspecific fruit bodies on an individual tree, log, twig, etc., and for fungi found on the ground as all conspecific fruit bodies within a diameter of 10 m. Since functional individuals on the ground are likely to be fragmented into several ramets, for IUCN purposes each functional individual can be considered to correspond with 10 mature individuals (ramets) if fruit bodies on the ground occur as scattered gregarious patches, and two individuals if fruit bodies occur solitary. On a log, a few aggregated fruit bodies are counted as two mature individuals, but when widely scattered they can be counted as 5–10. This approach will usually underestimate the number of mature individuals, so it will provide a conservative, but realistic, indication of species of conservation concern.

To determine if populations are declining, the IUCN evaluates changes in population size not over years but over numbers of generations, for equivalence between different organisms.

Length of a generation is defined as the average age of the parents of the current cohort. This has not been estimated for any species of fungi (nor for most plants and animals), but must be greater than the age at first fruiting and less than the age at final fruiting. It will vary considerably between fungi with different ecological strategies. For example: mycelia growing in small, discrete, rapidly decomposing substrata (e.g. dung) have shorter generation times than do wood decay fungi; mycelia growing through continuous substrata such as soil and leaf litter layers are able to persist longer than mycelia growing in discrete, resource-limited patches such as twigs and logs; ruderal fungi colonising freshly felled sapwood have shorter generation times than heartrot fungi. The time frame for evaluations of population size vary between different IUCN criteria (Table 11.5): for criterion A, it is 3 generations or 10 years, whichever is longer; for criterion C, it is 1–3 generations. Different operational times for assessment of population change have been proposed for fungi in different habitats and having different life strategies (Table 11.6).

Conservation Measures, Future Needs, and Prospects

Since the causes of fungal species decline are destruction, fragmentation, and loss of habitat, pollution, invasive species, climate change and other human impacts, remedying these should halt decline. Indeed, strict controls on SO₂ emissions have seen the return of sensitive lichen species to industrialised areas, as mentioned earlier (p. 383). A decrease in nitrogen pollution in The Netherlands is heralding a slight increase in the rare stipitate hydnoids, though there has been no similar increase in the UK. In hay meadows, management that

TABLE 11.5 The Main Criteria (A–D) for IUCN Red Listing

IUCN criteria code	Criteria	Summary criteria
A	Severe population reduction	Reduction
B	Small geographic range (and reduction and fragmentation)	Reduction; few individuals
C	Small population (and reduction)	Reduction; few individuals
D	Very small or restricted population	Few individuals
E	Quantitative analysis	

TABLE 11.6 Operational Estimates of the Time Over Which Population Changes Should be Assessed for Fungi in Different Habitats

Habitat/ecological role	Assessment period
Ephemeral, short-lived substrata, e.g. dung	10 year, the minimum assessment period for IUCN
Wood	20–50 year (=3 generations) depending on decay rate. <i>Quercus</i> and <i>Pinus</i> , 50 year; <i>Picea</i> and <i>Fagus</i> , 30 year; <i>Betula</i> , <i>Alnus</i> , and <i>Populus</i> , 20 year
Ecomycorrhizal fungi	50 year (=3 generations)
Soil and litter inhabiting fungi	20–50 year (=3 generations)

involves cutting followed by maintenance of a short sward increases fruiting of grassland fungi, including rare waxcaps, though whether this reflects increase in presence of mycelia is not known. There was rapid recovery of lichens in overexploited reindeer winter grazing pastures in northern Norway when protective fencing was erected. Clearly, most causes of decline will be halted very slowly, so measures need to be taken to protect declining or rare and endangered species, including: red-listing; protection by law; responsible harvesting; formation of reserves; habitat management; action programmes; and research.

Rare and endangered fungi are protected by law in some countries, including 14 European countries, but the amount of species protected and the extent of that protection is variable, ranging from four species in the UK to over 300 species in Croatia. Usually, picking or destroying protected species is prohibited. While there is little or no evidence that removing fruit bodies results in a reduced yield of fruit bodies, at least for the more common fungi, there are certainly negative effects of habitat destruction, trampling and raking to reveal fruit bodies. Currently, there is only one basidiomycete on the International IUCN Red List – *Pleurotus nebrodensis* categorised as Critically Endangered ([Table 11.4](#)), and three lichens – *Cladonia perforata* (endangered), *Erioderma pedicellatum* (critically endangered), and *Gymnopholus lichenifer* (vulnerable). Known only from an area of less than 100 km² in limestone mountain meadows in Sicily, *Pleurotus nebrodensis* populations are becoming fragmented by road building and other developments, and it is overpicked as it is a desirable edible species. It has no legal protection, but is easily cultivated and is now grown commercially which will hopefully relieve pressure from wild populations. Another example of overpicking as a threat to a fungus is the ascomycete *Ophiocordyceps sinensis*, which parasitizes and kills Lepidoptera ([Figure 11.15k](#)). It is highly prized as an aphrodisiac and Chinese medicinal treatment for various ailments, and fetched a price of US \$18,000/kg with annual sales of around 100 tonnes in Tibet in 2008, and an estimated US \$20 million in the black economy of Bhutan in the early 2000s. This over-collecting, which is largely beyond the law and is the fungal equivalent of poaching, is not sustainable. However, again the fungus can be grown in culture, and commercial cultivation may save its wild populations.

An overarching principle should be to protect and manage biodiversity in general, and to focus on certain plants, animals, or fungi when appropriate. Fungi, however, in common with some plant and animal species, often suffer from not being considered by the public as charismatic. Useful general principles are laid out in [Table 11.7](#). Conservation of habitats likely to be important for fungi is usually likely to be implemented by non-mycologists whose foremost interest is often other organisms; a forerunner has been the integration of mycological considerations with forest management in Fennoscandia since the mid-1980s. In The Netherlands, common activities in urban planning, land management, etc., are classified as favourable or unfavourable to fungi. These approaches have a general benefit, though some fungal species will require specific and detailed management guidelines. Six European countries have species action programmes (SAP) for threatened fungal species. There are SAPs for 19 nonlichenised species in Estonia, 10–15 in Finland, 27 in Sweden, 150 in Switzerland and 77 in the UK. Conservation science has been described above, but when legalities and money are involved then conservation becomes political. Conservation has a greater political impact if species are red-listed at a continental or global scale. Thirty three threatened macrofungi were proposed for inclusion in the Bern Convention in 2001, but political difficulties prevented their adoption. There is not even an official European fungal Red List, though all

TABLE 11.7 Principles and considerations for conservation and management of fungi

Principle	Justification	Management Considerations
Maintain habitat diversity at landscape scales	Fungal species have evolved within a shifting mosaic of plant communities, and periodic disturbances across broad landscapes over millennia	<ul style="list-style-type: none"> • Protect and restore disappearing habitat (e.g. old-growth forests, 'unimproved' grassland) • Maintain a diversity of forest successional stages • Ensure that habitat patches are located sufficiently closely to allow for fungal dispersal and population establishment
Maintain habitat diversity	Fungal species often reside in unique niches and respond to myriad microhabitat conditions	<ul style="list-style-type: none"> • Maintain or develop habitat diversity within ecosystems (e.g., diverse plant composition, retain coarse woody debris in forests, continue grazing and refrain from fertilisation of old grasslands)
Maintain host diversity	Many ectomycorrhizal and saprotrophic fungi associate with specific host plants	<ul style="list-style-type: none"> • Plant mixtures of plants that resemble natural assemblages • In forests, diversify the understory vegetation which acts as hosts or create unique microhabitat
Maintain soil health	Most soil fungi are aerobic and utilise diverse organic and mineral resources.	<ul style="list-style-type: none"> • Avoid soil compaction and hot surface fires that destroy soil structure • Avoid removal of the forest floor litter layer and minimise disturbance • Maintain natural levels of soil organic matter • Reduce nitrogen inputs to soil from emissions and fertiliser application
In forests, maintain legacy trees and limit size of timber harvest units	When all tree hosts are removed (e.g. clearcuts), fungal populations are reduced and slow to recover compared to forest thinnings or partial cuts	<ul style="list-style-type: none"> • Retain some living trees in felled areas to maintain variety of age structure and live mycorrhizal populations on roots • Avoid large clearcuts; adopt thinning approaches or aggregate uncut trees to create reservoirs of fungal diversity and allow fungal dispersal into disturbed areas • Maintain refuge understory plants that may act as mycorrhizal hosts or create microhabitat within the future forest • Plant seedlings soon after harvest while there is residual fungal inoculum in the soil
Protect known locations of rare fungi and fungal diversity hot spots	Repeated inventorying of fungi has revealed locations of rare species and areas where fungal richness remains high (e.g. parks or reserves)	<ul style="list-style-type: none"> • Protect known sites of rare species by minimising disturbance and maintaining critical habitat elements • Identify fungal diversity hotspots and work with responsible managers to protect these areas or designate them as fungal reserves
Other activities essential for fungal conservation:		
Monitor fungal populations	Data collection spanning several years is needed to detect trends in fungal populations	<ul style="list-style-type: none"> • Establish permanent monitoring locations for targeted species or fungal communities • Include fungal monitoring within long-term biodiversity monitoring programmes • Include citizen scientists in the design and implementation of fungal monitoring programmes

TABLE 11.7 Principles and considerations for conservation and management of fungi—cont'd

Principle	Justification	Management Considerations
Develop partnerships with the public, other scientists and resource managers	Species conservation is a complex and expensive undertaking. Mycologists should take advantage of other ongoing biodiversity monitoring and conservation programmes	<ul style="list-style-type: none"> • Educate the public and resource managers as to the importance of fungi, and principles for their conservation • Integrate fungal conservation goals within ongoing multitaxa conservation programmes • Work directly with resource managers to include fungi in management programmes

Conservation efforts can concentrate on maintaining the species currently present at particular sites, focus on what species we want to have, or a combination of both.

Modified from: Molina et al. (2011).

Red Lists from European countries have been compiled, and 1644 species suggested for a European Red List, though these still need to be evaluated. The major challenges for fungal conservation are to: (1) raise both public and political awareness; (2) integrate fungi into national, continental and global conservation strategies for plants and animals; and (3) perform the science that will provide understanding of why each species is declining or rare, and how to counteract declines. Protection is not the only answer, rather we need to manage habitats and substrata to create appropriate conditions in time and space for the diversity of fungi we want to have in the long term.

Rare and Endangered Species – Case Studies

To determine if a species is rare and endangered, or common but declining, and to determine its conservation needs, it is essential to be able to distinguish one species from another, and to understand its ecology, particularly the biotic and abiotic factors involved in its reproductive success and decline. This is illustrated by case studies of two groups of endangered basidiomycetes in Europe: (1) saprotrophic *Hericium* species and (2) ECM stipitate hydnoids.

Hericium cirrhatum, *Hericium coralloides*, and *Hericium erinaceus* (Figure 11.5) are on the Red List of several European countries, and *Hericium erinaceus* was one of the species proposed for inclusion in the Bern Convention, though it is common in Japan and North America, and easily cultivated. All three are saprotrophs on wood of angiosperm trees, especially *Fagaceae*. They fruit prolifically in culture in the lab, perhaps indicating that the few fruit bodies seen in the field is a true indication of lack of mycelial individuals, though the fungi may be trapped in central regions of wood with no access to the surface for production of fruit bodies. When fruit bodies are formed, they are large and sporulation is prolific, though germination on agar is poor. Following germination in nature, it is suspected that the fungus may exist in the homokaryotic state (p. 113) for a prolonged time, due to low frequency of contact between mating compatible partners. This is a major difficulty faced by all rare fungi. Both homokaryotic and heterokaryotic mycelia grow rapidly and are combative against other wood decay fungi, so this is unlikely to be the cause of their rarity in Europe, but poor germination and infrequent establishment may be. They have been detected latently present within functional sapwood, but gaining entry to trees and encountering appropriate conditions to develop overtly may be limiting factors.

The decline of stipitate hydnoids, an informal grouping of basidiomycetes whose fruit bodies have a stalk and cap with spore-producing spines (*Bankera*, *Hydnellum*, *Phellodon*, and *Sarcodon*), has been alluded to on several occasions earlier in this chapter. They are ECM partners with a range of woody angiosperms and gymnosperms, especially within *Fagaceae* and *Pinaceae*, though the suites of fungal species are associated with each differ. Typically they fruit on sparsely vegetated soil with low nitrogen and organic matter content, and sloping ground (e.g. animal burrows, hillsides, glacial moraines, ditches, and the margins of tracks and roads). They are well represented in Red Lists of Europe, and *Sarcodon fuligineoviolaceus* was proposed for inclusion in the Bern Convention. There are two main difficulties when studying them: (1) it is not currently possible to culture them on artificial media and (2) distinguishing one species from another. The fruit bodies of some species are very similar to others, yet it is essential to be able discriminate one from another, as even closely related taxa can have different nutritional modes and lifestyles. DNA sequencing, together with morphological analysis, has now made this possible. Also, use of PCR primers, specific to different species, on DNA and RNA extracted directly from soil, have revealed that mycelium is present in soil where the fungus has fruited previously, even though there has been no evidence of fruit bodies for 5 or more years. It is obviously much harder to unravel the ecophysiology of fungi, such as the stipitate hydnoids, that grow in intimate association with a living host, making culturing difficult or impossible, but molecular sequencing will allow researchers to ascribe host to fungal species by analysis of root tips, as well as detection in soil.

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