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State of the World's Fungi 2018

9. Climate change: Fungal responses and effects

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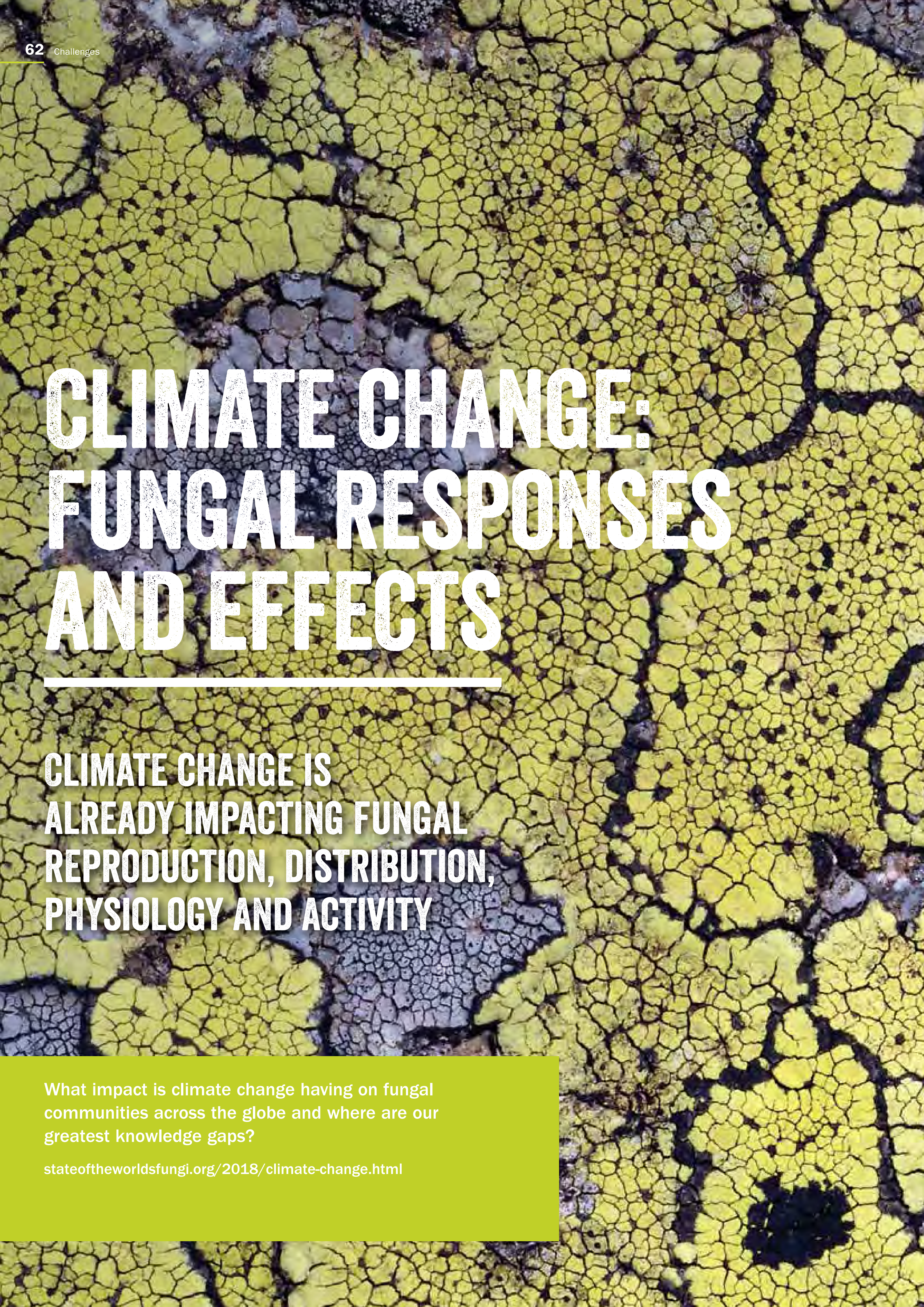


CLIMATE CHANGE: FUNGAL RESPONSES AND EFFECTS

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

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

stateoftheworldsfungi.org/2018/climate-change.html

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

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

THE IMPACTS OF CLIMATE CHANGE

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

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

FIGURE 1: QUESTIONS AND KNOWLEDGE GAPS

KEY UNRESOLVED QUESTIONS:

What is the relative importance of fungal adaptation, migration and acclimatisation?

How does climate change affect the yield of fungal spore-bearing structures?

How does climate change affect fungal growth and activity?

How do fungi mediate ecosystem responses to climate change?

How do changes in the phenology of spore-bearing structure production reflect changes in activity, abundance, biomass and distribution?

Can fungi track climate space shifts?

KEY INFORMATION GAPS:

Long-term data

Large-scale data

Data from tropical, subtropical and warm temperate ecosystems

Experimental data from fungi associated with trees, rather than seedlings

Fungal response and effect traits

Data from multiple simultaneous drivers of change (nitrogen deposition, carbon dioxide, ozone, UV, temperature, drought, fire)

OBSERVING HOW FUNGI RESPOND

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

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

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

MYCORRHIZAL INTERACTIONS AND FEEDBACK

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

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

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

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

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

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

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

BOX 3: MODELLING CLIMATE CHANGE EFFECTS ON LICHENS

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

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

THICK-WALLED SPORES

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

DROUGHT TEMPERATURE FIRE

MELANISATION

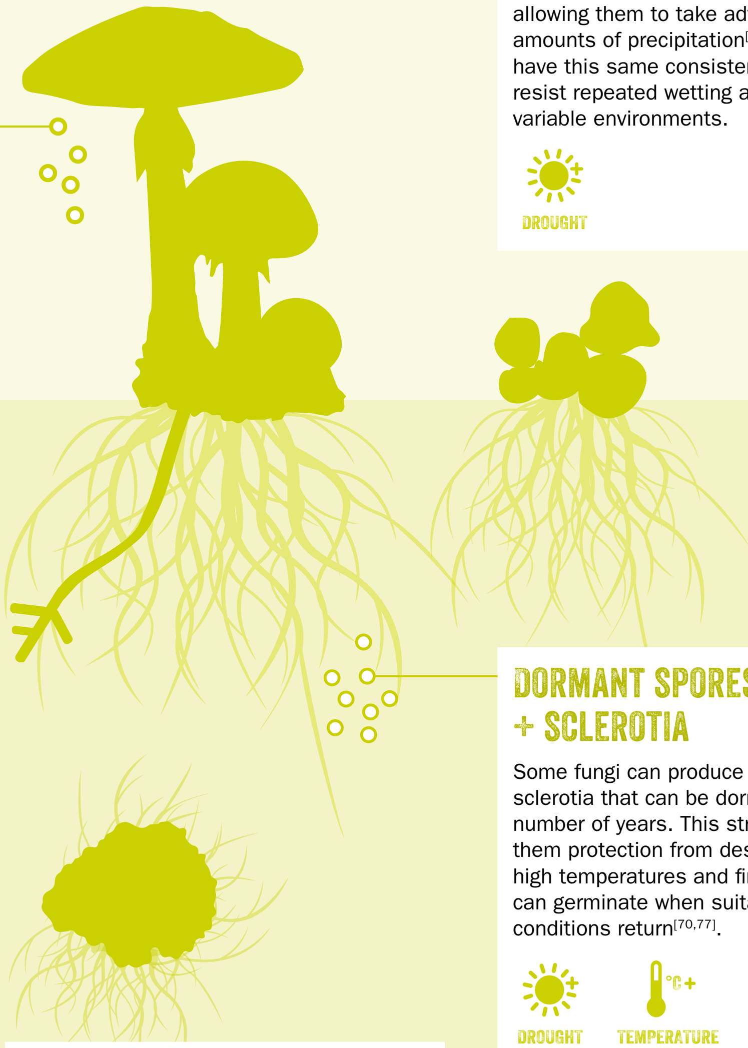
Melanin is a complex pigment found in some fungi. It can provide resistance to desiccation, high temperatures and UV radiation[71]. It also provides strength, allowing hyphae to penetrate deeper into the soil to access water and to transport water over larger distances without leaks[70,71].

DROUGHT TEMPERATURE

RHIZOMORPHS

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

DROUGHT



JELLY FUNGI

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

DROUGHT

DORMANT SPORES + SCLEROTIA

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

DROUGHT TEMPERATURE FIRE

TRUFFLES AND FALSE TRUFFLES

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

DROUGHT TEMPERATURE FIRE

FUNGAL PESTS AND PATHOGENS

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

THE CASE OF LICHENS

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

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

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

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