Chapter 4

Fungi in soil: a rich community with diverse functions

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Chapter outline

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4.1 Introduction

While plants dominate global and terrestrial biomass, fungi likely rank second only to plants in terrestrial biomes and constitute the major fraction of biomass in soil (Bar-On et al., 2018). From an evolutionary perspective, there is now considerable circumstantial evidence that fungi were instrumental in both the colonization of land by the ancestors of terrestrial plants (Pirozynski and Malloch, 1975; Simon et al., 1993) and the termination of carbon (C) deposition into geological reserves (i.e., fossil fuels, Floudas et al., 2012). The traits that underlie these features illustrate why fungi play such an important role in soils. Most fungi interact intimately with both living and dead organisms, especially plants. The mycorrhizal symbiosis with plant roots is thought to have permitted aquatic plants to transition into the challenging terrestrial habitat. Mycorrhizal and other fungal interactions with living plants (pathogens, endophytes) may be highly specific or generalized, with outcomes that vary among taxa but influence the structure and function of plant communities. Fungi have a profound influence on biogeochemical cycles through their growth habits, which include external digestion of food resources using a powerful arsenal of degradative enzymes and secondary metabolism. It was the innovation and diversification of polyphenolic-degrading enzyme machinery among the white-rot basidiomycete fungi that may have halted the accumulation of undecayed plant materials during the carboniferous (Floudas et al., 2012). The filamentous habit common to the majority of soil-dwelling fungi allows them to bridge gaps between pockets of soil water and nutrients, force their way into substrates such as decaying wood, and redistribute C, minerals, and water through the soil. Filamentous growth may underlie the abilities of some fungi to withstand soil water deficits and cold temperatures that are beyond the tolerance of bacteria and archaea. Fungi constitute large fractions of living and dead soil biomass, particularly in forested habitats. Their growth and production of cell wall materials lead to the creation and stabilization of soil aggregates, which are key elements of soil structure. Rates of production and turnover of fungal biomass have important consequences for C cycling and long-term sequestration in soil. In this chapter we summarize recent advances in our understandings of the phylogeny, biodiversity, and ecology of fungi of relevance to their diverse roles in soil environments. Of particular note is the accumulation of massive phylogenomic datasets that provide new insights into deep-level relationships and early evolution of the fungal kingdom, as well as key changes in gene repertoires across lineages and time. In addition, new insights have been acquired into how fungal communities assemble and how these processes impact ecosystem function, such as soil C storage.

4.2 Diversity and evolutionary relationships of the true fungi

4.2.1 The origin of fungi

The fungi are recognized as a kingdom (see online Supplemental material Section S4.1 for a refresher on the taxonomic hierarchy of life). Although sometimes loosely referred to as microbes, fungi are eukaryotes and most are multicellular. The superkingdom of eukaryotes that includes fungi and animals is the Opisthokonta. The common ancestor of all Opisthokonta was almost certainly a heterotrophic, single-celled, phagotrophic protist (Berbee et al., 2020). While the relationships of the earliest branches of the eukaryotes remain to be resolved with certainty, it is clear that the Opisthokonta dates back to the early origins of eukaryotes some $\sim$1.6 billion years ago (Cerón-Romero et al., 2022). This superkingdom has been further subdivided into two groups: the Holozoa (animal lineage) and Holomycota (fungal lineage).

There is now strong evidence that a small group of protists within the Opisthokonta, including Nucleria and the cellular slime mold Fonticula, are the closest sister group to the true fungi, or Eumycota (Liu et al., 2009; Steenkamp et al., 2006). There is also support for monophylly of the Eumycota (James et al., 2006; Li et al., 2021), although relationships among basal lineages near the divergence between nucleārids and fungi are not yet certain.

About 30 years ago, a system of five fungal phyla achieved universal recognition based, in part, on initial rDNA phylogenies (Bruns et al., 1991). The five phyla were the Chytridiomycota (water molds), Zygomycota (bread molds), Glomeromycota (arbuscular mycorrhizal fungi [AMF]), *Ascomycota* (cup fungi), and Basidiomycota (club fungi). Later multilocus, molecular analyses suggested that neither the Zygomycota nor the Chytridiomycota is a monophyletic group (James et al., 2006; Liu et al., 2009; O'Donnell et al., 2001), although there remains uncertainty concerning the Zygomycota (Li et al., 2021; Spatafora et al., 2016). Furthermore, this five-phylum system ignored diverse taxa now known to be basal fungi, including Rozella. Current taxonomic ranks and best estimates of deep branch orders are in flux, but consensus for several key points is growing. Recent phylogenomic studies and related taxonomic revisions recognize 12 to 20 phylum-level lineages organized into a few subkingdom supergroups (James et al., 2020; Li et al., 2021; Voigt et al., 2021). Most recognize a constellation of obscure, ancient, mostly parasitic phyla within the supergroup Opisthosporidia, including Rozella, Microsporidia, and Aphelids. A second supergroup of basal fungi is sometimes named the Chytridiomyceta and includes the Chytridiomycota, Monoblepharidomycota, and Neocallimastigomycota, which are all flagellated and single to few-celled. Additionally, nonflagellated ancient lineages are currently recognized as discrete phyla that are not lumped within the preceding two supergroups and include the Mucoromycota, Zoopagomycota, and Dikarya. As described further below, only the Chytridiomycota and Mucoromycota are known to have prominent roles in soil among these early branching lineages. A third, more recently evolved supergroup is the Dikarya, which includes the majority of important soil fungi belonging to the phyla Entorrhizomycota, Ascomycota, and Basidiomycota. Molecular phylogenies confirm the long-held view that the Oomycota, which includes the important filamentous plant pathogens *Pythium* and *Phytophthora*, belong to the superkingdom Stramenopiles (heterokonts), while most slime molds (i.e., except *Fonticula*) belong to the superkingdom Amoebozoa, both outside the Opisthokonta. Even extremely data-rich phylogenomic analyses have yet to resolve with certainty the relationships at the base of the fungal tree (James et al., 2020; Li et al., 2021), so we can expect further rearrangements and optimization of high-order taxonomy in the years to come. Current understandings of the major evolutionary lines of fungi, along with a few exemplar taxa and their trophic niches, are presented in Figs. 4.1–4.3. (See Fig. S4.1 and Table S4.1 in online Supplemental material for help in making sense of some confusing terminology in fungal systematics.) Good sources for the most up-to-date taxonomic hierarchy for the fungi include Wijayawardene et al. (2020) and Index Fungorum (www.indexfungorum.org).

A number of shared, derived traits are characteristic of fungi, although no single unique trait is shared by all fungi (James et al., 2006, 2020; Stajich et al., 2009). Fungi depend on organic compounds for C, energy, and electrons, with most species taking up these resources via osmotrophy. Although many fungi can fix CO_2 using enzymes of central anabolic cycles (e.g., pyruvate carboxylase), they are considered heterotrophs in a broad sense. Chitin, a polymer of N-acetylglucosamine, is a feature of the cell wall matrix of most fungi, although quite a few parasitic lineages, especially within the Apistophelida, have life stages that lack cell walls (e.g., *Rozella*), and some groups have little or no chitin in their walls (e.g., ascomycete yeasts). The ancestral state for the true fungi includes a mobile, flagellated meiospore (zoospore) stage; flagella appear to have been lost several times through the evolution of the fungi and

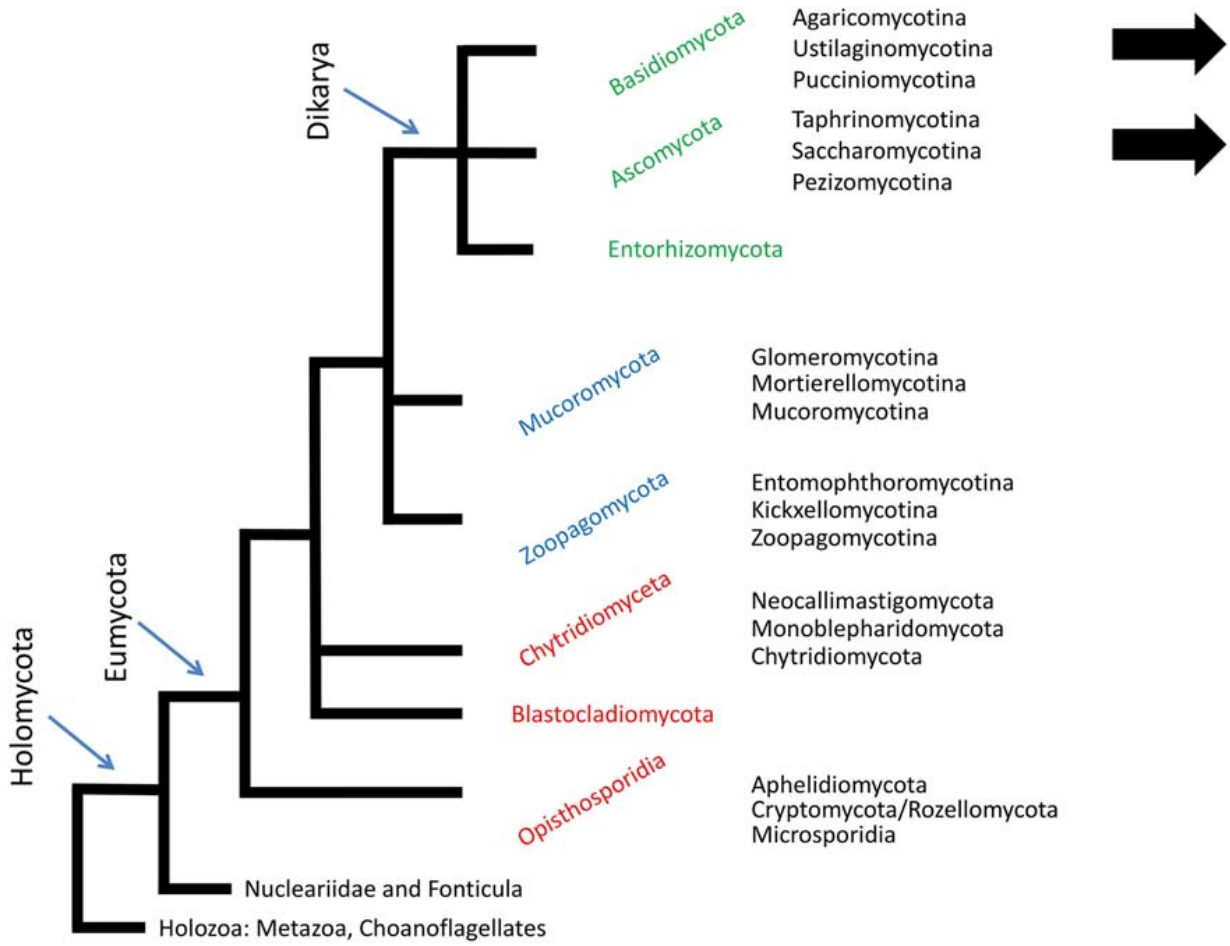

FIGURE 4.1 Overview of fungal phylogeny. Currently recognized phyla and subphyla in the kingdom fungi (Eumycota). The Holozoa are an outgroup within the Opisthokonta, while the Nucleariidae are thought to be the closest relatives of the fungi. Exemplar taxa and their ecological roles are provided on the right.

today exist only in several early diverging lineages, most prominently within the Chytridiomyceta (James et al., 2020). It is now clear that the oldest lineages of fungi were aquatic. Most fungi also use the sugar trehalose as an energy store, display apical growth, and have spindle-pole bodies rather than centrioles (with the exception of ancient, flagellated lineages). While fungi have a very long history of intimate association with land plants and their green-algal ancestors, the most ancient lineages of the Apistophelida lack the unique enzymes, such as pectinases, that are suited to attacking plant cell walls (Berbee et al., 2020). Hence the common ancestor of the Eumycota was likely not plant associated. These patterns are logical given that the origin of Eumycota has been estimated at about 1.3 billion years based on several sophisticated molecular clock studies (James et al., 2020). This origin predates the evolution of pectin-cellulosic walls in the charophycean algal ancestors of land plants (Viridiplantae). The common ancestor of all fungi, and indeed all Opistokonts, was likely a swimming, flagellated, single-celled, phagotrophic protist (Berbee et al., 2020). Indeed, nuclearids are phagotrophs (organisms lacking cell

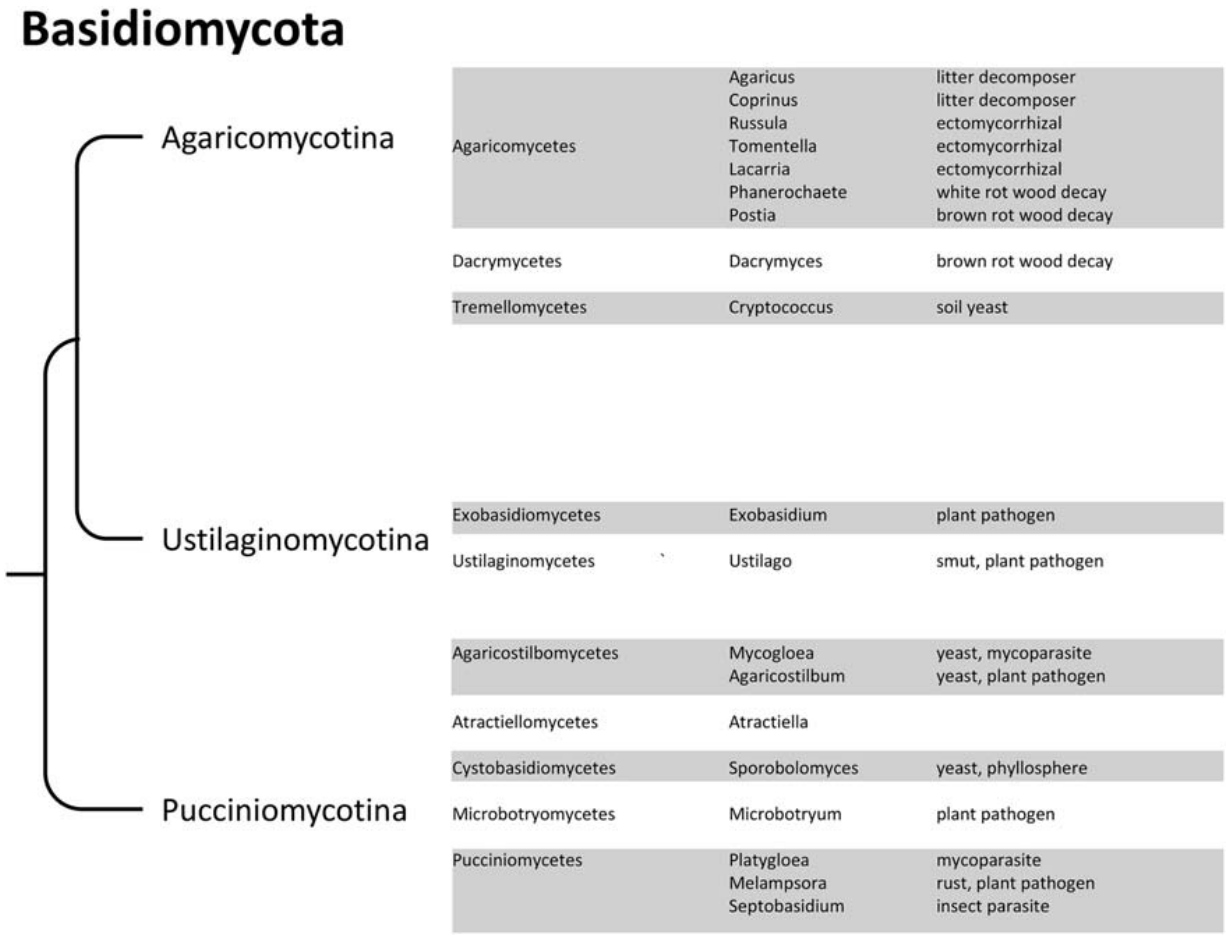

FIGURE 4.2 Currently recognized subphyla and classes within the phylum Basidiomcota. Several subphyla and classes that contain only a few, rarely encountered species are not shown. Exemplar taxa and their ecological roles are provided on the right.

walls that engulf relatively large food items via phagocytosis). Some extant members of Opisthophelida/Opisthosporidia still exhibit phagotrophy (i.e., uptake of food particles via encasement and engulfment of membrane-bound spheres). In contrast, in the next more recently evolved cluster of ancient fungal lineages, the "chytrids" (Blastocladiomycota and Chytriomyceta, Fig. 4.1), we see a sharp transition to osmotrophy (i.e., the direct uptake of very small molecules such as sugars and amino acids through the cell wall and into the cytoplasm via transporters). Osmotrophy requires that an organism grow into its food and digest external resources into sufficiently small molecules outside its cells and is the only option available for organisms with stiff cell walls that therefore cannot use phagotrophy.

4.2.2 Major lineages in soil

The most abundant and diverse fungal phyla in the majority of soils belong to the more recently evolved Ascomycota and Basidiomycota. However, a number of taxa from older lineages, particularly the

Pezizomycetes	Tuber (truffle) Wilcoxina	ECM ectendomycorrhizal
Sordariomycetes	Chaetomium Trichoderma	soil, thermophilic saprotroph soil, saprotroph, mycoparasite
Leotiomycetes	Geomyces Meliniomyces	soil, saprotroph, psychrophile ERM
Dothideomycetes	Cenococcum Cryomyces	ECM soil, psychrophilic black yeast
Eurotiomycetes	Phialophora Aspergillus	DSE seed pathogen, many other niches
Lecanoromycetes	Lobaria	lichen
Geoglossomycetes	Geoglossum (earth tongues)	soil, saprotroph?
Lichinomycetes	Peltula	lichen
Orbiliomycetes	Arthrobotrys	soil, nematophagous saprotrophs
	Saccharomyces	yeast, saprotroph
Archaeorhizomycetes	Archaeorhizomyces	soil, plant associated?
Neolectomycetes	Neolecta	soil, plant associated?
Pneumocystidomycetes	Pneumocystis	animal pathogen
Schizosaccharomycetes	Schizosaccharomyces	yeast, saprotroph
Taphrinomycetes	Taphrina	yeast, plant pathogen

FIGURE 4.3 Currently recognized subphyla and classes within the phylum Ascomycota. Several subphyla and classes that contain only a few, rarely encountered species are not shown. Exemplar taxa and their ecological roles are provided on the right.

Mucoromycotina and Mortierellomycotina, are also abundant in many soils. Even members of the ancient Chytridiomycota are often recovered in soil metabarcoding studies (Taylor et al., 2014; Tedersoo et al., 2014), though at low abundances. As discussed in the next section, whether these low abundances may be due in part to negative biases of current primer sets is yet to be determined. The trophic roles of chytrids are poorly understood, although it has been suggested that they may decompose allochthonous plant materials in some unvegetated high-elevation soils where they comprise a higher fraction of the fungal community than in less extreme environments (Freeman et al., 2009; Schmidt et al., 2012).

Many taxa of zygospore-forming fungi belonging to the Mortierellomycotina and Mucoromycotina are found primarily in soil. Some are clearly decomposers, with apparent preferences for labile C sources (e.g., members of the cosmopolitan soil genus *Mortierella*). However, in the last decade a diverse array of *Mucoromycotina* related to *Endogone* have been documented forming arbuscular mycorrhizal (AM)−like coils within roots based on combined molecular diagnostics and detailed microscopy (Bidartondo et al., 2011; Field et al., 2015; Humphreys et al., 2010). The first records came

from some of the oldest living lineages of nonvascular plants and led to the hypothesis that relatives of these fungi, which were thought to be older than true AMF of the Glomeromycotina, may have been the symbionts that aided plants in colonizing land rather than AMF. In support of this hypothesis these fungi exchange P and N in return for C, demonstrating a true mutualistic mycorrhizal role (Field et al., 2015). On the other hand, these fungi often cooccur with AMF in nonvascular plants (Field et al., 2016) and have more recently been found in vascular and even flowering plants (Albornoz et al., 2020). Furthermore, very recent phylogenomic studies suggest that the Glomeromycotina is not sister to the Dikarya and, instead, is likely affiliated with the Mucoromycota (Li et al., 2021; Spatafora et al., 2016). Hence mycorrhizal Mucoromycotina may or may not predate AM Glomeromycotina. The class Glomeromycotina encompasses all fungi that form true arbuscular mycorrhizae, as well as the enigmatic, algal symbiont Geosiphon (Gehrig et al., 1996).

The subkingdom Dikarya is comprised of the most recent and derived "crown" phyla Ascomycota and Basidiomycota. A recent surprise has been the proposed addition of a new phylum, the Entorrhizomycota, to the Dikarya (Bauer et al., 2015). This new phylum is comprised of just a few species of filamentous root pathogens. These fungi share more cellular and ultrastructural features with Basidiomycota, including dikaryotic vegetative cells, tripartite septa, spindle-pole-body structure, and meiospores formed in tetrads. Yet current multigene phylogenies place them basal to Ascomycota + Basidiomycota (Riess et al., 2019). However, no full Entorrhizomycota genomes are yet available, and the placement of this phylum relative to the Ascomycota and *Basidiomycota* remains uncertain.

The Ascomycota constitute the most species-rich fungal phylum, accounting for roughly 75% of described fungal species. These species fall into three subphyla, as follows: (1) Taphrinomycotina, which encompasses the fission yeasts (Schizosaccharomyces), the animal pathogen Pneumocystis, the unusual dimorphic plant pathogen *Taphrina*, the root-associated, sporocarp-forming, filamentous genus *Neolecta*, and the newly erected class of filamentous soil fungi, the Archaeorhizomyces; (2) Saccharomycotina include the budding yeasts, such as *Saccharomyces*, *Debaromyces*, *Pichia*, *Candida*, and others, many of which are found in soils, presumably decomposing labile organic materials both aerobically and anaerobically; and (3) Pezizomycotina which accounts for the greatest phylogenetic, species, and functional diversity within the Ascomycota. The majority of lichen-forming fungi fall within this lineage (there are a few basidiomycete lichens), as do a few ectomycorrhizal fungal (EMF) taxa, all dark-septate endophytes (DSE), essentially all ericoid-mycorrhizal (ERM) species, and a wide spectrum of endophytes, pathogens, and saprotrophs. Recent phylogenomic studies support each of these subphyla as monophyletic and suggest that the Sacharomycotina and Pezizomycotina are sister groups (Shen et al., 2020).

The diverse phylum Basidiomycota is also divided into three well-supported subphyla. The branching order of these subphyla, which likely radiated in a short period of time, remains unresolved even using advanced phylogenomic data and methods (Li et al., 2021). The subphylum Pucciniomycotina includes all rust fungi, an economically important group of plant pathogens, as well as some yeasts that are common in soil, yet rarely studied, such as *Sporobolomyces* and Leucosporidium. The second subphylum, Ustilaginomycotina, is also predominantly comprised of plant pathogens, the smuts. Similar to the rusts, the Ustilagomycotina includes several yeasts, such as *Malassezia* (a skin pathogen that is frequently recovered from soils) and *Arcticomyces* (a cold-soil yeast). The Agaricomycotina includes the vast majority of filamentous Basidiomycota, including all mushroom-forming taxa. These encompass nearly every conceivable soil niche (except thermophiles and psychrophiles), accounting for all brown rot and white rot fungi, as well as most EMF taxa.

4.2.3 Extremophiles and novel lineages

While fungi do not equal the extremes of heat, salinity, acidity, or UV tolerance of the most extremophilic of the prokaryotes, certain fungal taxa surpass most other eukaryotes in tolerance to these and other extreme conditions, including cold and aridity. Fungi are found in essentially all biomes and habitats, both terrestrial and aquatic. Some of these habitats are extreme, such as soils in the Dry Valleys of Antarctica, on Arctic glaciers, and in high molarity salterns. A key question is the extent to which these taxa are active in these hostile environments as opposed to surviving in highly resistant, dormant spore stages following introduction by wind or other vectors (Bridge and Spooner, 2012; Pearce et al., 2009). Nonetheless, there is clear evidence that some of these extreme environment fungi are indeed active in these habitats. Phylogenetically diverse yeasts dominate the isolates obtained from many extreme habitats. For example, species of the dimorphic basidiomycete yeast *Cryptococcus* can be dominant in glacial habitats, permafrost, marine sediments, and unvegetated Antarctic Dry Valley soils (Bridge and Spooner, 2012; Buzzini et al., 2012; Connell et al., 2006). In the marine study these yeasts were detected by culture-independent DNA and RNA methods, the latter strongly suggesting in situ metabolic activity (Edgcomb et al., 2011). Ascomycota yeasts, such as *Pichia*, *Debaromyces*, *Candida*, *Metschnikowia*, and *Aureobasidium pullulans*, are also found in extremely cold and/or saline habitats (Butinar et al., 2011; Cantrell and Baez-Félix, 2010; Cantrell et al., 2011; Gunde-Cimerman et al., 2003; Zalar et al., 2008). The so-called "meristematic," "microcolonial," or "black yeasts" are distributed among several lineages of Sordariomycetes, Eurotiomycetes, and Dothideomycetes (Onofri et al., 2000; Selbmann et al., 2005; Sterflinger et al., 2012) and commonly occur in extreme habitats; e.g., in canyon walls of the Antarctic Dry Valleys. Some species grow on or within rocks (endolithic) in both hot and cold deserts and at high elevations. Some members of this group display moderate halotolerance and extreme drought tolerance or can grow at pHs down to zero (Starkey and Waksman, 1943). Convergent evolution of strong melanization, slow growth, isodiametric meristematic cells (i.e., cells that can reinitiate growth when dislodged from the colony), and other putative stress-related features is seen among the black yeasts (Selbmann et al., 2005; Sterflinger et al., 2012). Several filamentous Ascomycota are also noteworthy extremophiles. Species of *Geomyces* (*Leotiomycetes*; now placed in teleomorph *Pseudogymnoascus*) have been recorded from marine habitats as well as cold soils (Arenz and Blanchette, 2011; Bridge and Spooner, 2012; Richards et al., 2012; Waldrop et al., 2008). One isolate was reported to be metabolically active down to −35°C (Panikov and Sizova, 2007).

Lichens are also formed predominantly by filamentous taxa of Ascomycota and are found across the array of extreme hot, cold, dry, and saline environments (discussed above), often playing the role of chief primary producer by virtue of photosynthetic activities of their cyanobacterial or algal photobionts (Vitt, 2007). Lichens are also important and widespread in less extreme terrestrial habitats (Feuerer and Hawksworth, 2007). These same classes of Ascomycota include species with the highest heat tolerance seen in the Eukaryota. Thermophilic and thermotolerant fungi share several key convergent traits. Their spores usually do not germinate below temperatures of 45°C, even though the mycelium can grow at lower temperatures (Maheshwari et al., 2000). These fungi, which belong to several orders within the Ascomycota (Sordariales, Eurotiales, Onygenales), one of which is within the early diverging lineages (*Mucorales*), have been recovered from diverse soils in both hot and cold regions. Within the Ascomycota, closely related species may be mesophiles and thermophiles, although many members of the Chaetomiaceae (Sordariales) are thermophilic. The primary niches of thermophiles are concentrated

aggregations of moist, well-oxygenated organic material that self-heat due to intensive respiration during decomposition (Maheshwari et al., 2000).

In the case of black yeasts, thermophiles, and lichens, there is no question of their activity and adaptation to extremes since they can be observed actively growing under these extreme conditions. This is also true of some of the cold-tolerant taxa, such as Geomyces, which can be observed growing in a dense mat across permanently frozen ice lenses in the Fox Permafrost Tunnel near Fairbanks, Alaska, United States (Waldrop et al., 2008). It seems likely that some of the other extremophiles described above, such as yeasts isolated from glacial habitats, are also indigenous taxa that are adapted to these extreme environments since they display tolerance to extreme conditions in the laboratory (Arenz and Blanchette, 2011; Butinar et al., 2011; Buzzini et al., 2012; Gunde-Cimerman et al., 2003; Onofri et al., 2000; Selbmann et al., 2005). Some cosmopolitan taxa detected in extreme environments, such as species of *Penicillium* and *Aspergillus*, may be present only as inactive spores. A recent study used RNA-based metabarcoding to isolate the putatively active fraction of the fungal community and compared it to the total community, derived from standard DNA metabarcoding in high-latitude cold soils (Cox et al., 2019). Differences between the RNA and DNA profiles revealed overrepresentation of endemic taxa, particularly chytrids, in the active community and overrepresentation of cosmopolitan, wind-dispersed Ascomycota in the DNA community, supporting the hypothesis that some of these cosmopolitan taxa do not actually grow under extreme conditions (Cox et al., 2019).

Although members of the Dikarya dominate records for extremophilic fungi, members of the early diverging fungal lineages have been reported from marine habitats using culture-independent methods (Comeau et al., 2016; Richards et al., 2012). Culture-independent approaches have also revealed a preponderance of chytrid lineages in soils at globally distributed, high-elevation sites that are above the vegetated zone (Freeman et al., 2009; Gleason et al., 2010). It has been proposed that these fungi may derive nutrients from algae and/or pollen transported by wind from distant locations; their presence in marine habitats might also be due to trophic linkages with algae (Richards et al., 2012).

4.2.4 Fungal structure and growth

The body of a fungal individual may contain one type of nucleus with only a single set of chromosomes — a haploid growth form. Alternatively, the cells of two different haploid individuals may fuse (plasmogamy). In most fungi this fusion occurs only immediately before nuclear fusion (karyogamy) and meiosis (see Fig. S4.1 in online Supplemental material for an exemplar fungal life cycle). However, in some fungi there is a brief (phylum Ascomycota) or prolonged (phylum Basidiomycota) stage in which the two different nuclei multiply in a synchronized fashion; this phase of the life cycle is termed dikaryotic. While not representing any particular taxon, the features shown in Fig. 4.4 are characteristic of the Dikarya. As a mycelium grows, hyphae branch at regulated intervals in response to external and internal signals (Fig 4.5a). In many fungi cytoplasm is retracted from older parts of the mycelium, leaving walled-off empty cells. The newly formed thin and soft hyphal tip extends due to turgor pressure. The growing tip is the area of most active enzyme secretion and nutrient uptake. In the more ancient fungal groups the filaments in which the nuclei are housed do not contain cross-walls (septa), while in other groups septa divide hyphal filaments into distinct cells (Fig 4.5b). Cross walls or septa separate individual cells (numbers of nuclei are usually variable in Ascomycota but are more often fixed in Basidiomycota). In the two most recently evolved phyla the Ascomycota and Basidiomycota, nuclear division, and

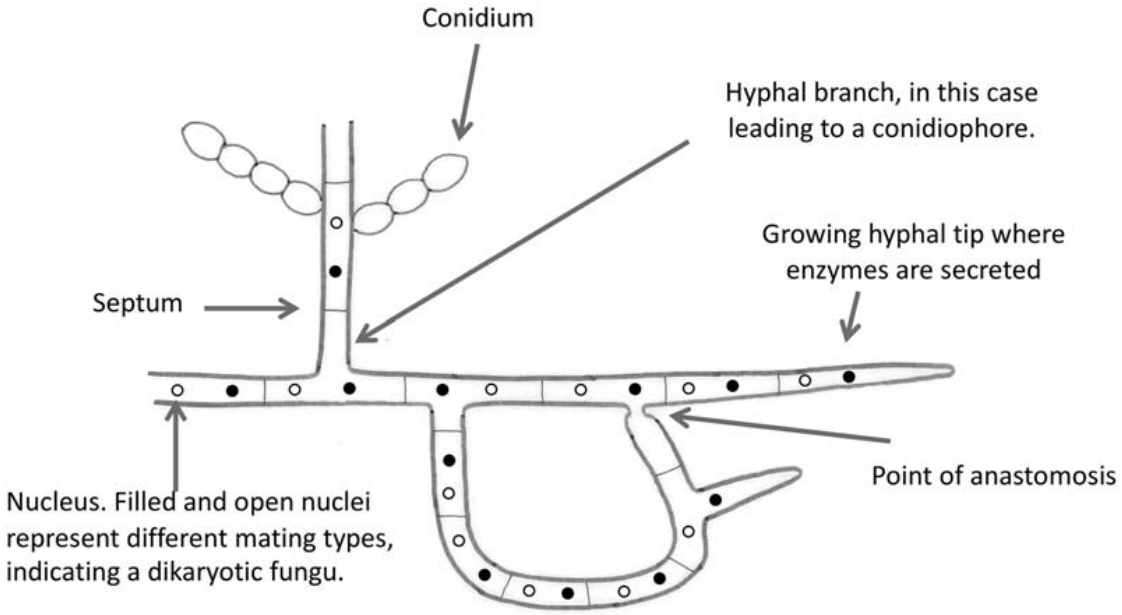

FIGURE 4.4 Filamentous fungal growth form typical of fungi in soil. Cartoon depicts a mycelium growing from left to right.

apportionment to the cells comprising the hyphae are tightly regulated (see Fig. 4.5b, c, d), while in groups without septa nuclei flow freely through the entire mycelium (e.g., in phylum Glomeromycota).

Fungal mycelia generally grow radially as fractal networks in soil, wood, and litter (Bolton and Boddy, 1993). Fungi alter hyphal development in response to environmental conditions to minimize cost:benefit ratios in terms of C or nutrient capture versus expenditure on growth. Very fine feeder hyphae are elaborated in resource-rich patches, while nutrient-poor areas are less densely colonized by hyphae specialized for efficient searching and nutrient transport. The transport hyphae may aggregate into tightly woven bundles called cords, strands, or rhizomorphs depending on their developmental structure. All these aggregations provide larger diameter transport tubes. However, species vary considerably in hyphal growth patterns, the size and structure of transport networks, and the resulting foraging strategies (Agerer, 2001; Boddy, 1999; Donnelly et al., 2004).

4.3 Diversity and biogeography

Fungi generally dominate microbial biomass and activity (i.e., respiration) in soil organic horizons, particularly in forests (Joergensen and Wichern, 2008). Bacterial:fungal ratios tend to be lower in acidic, low-nutrient soils with recalcitrant litter and high C:N ratios (Fierer et al., 2009), while bacteria are increasingly prominent in high−N and P, saline, alkaline, and anaerobic (waterlogged) soils (Joergensen and Wichern, 2008).

Fungal biomass varies widely within and across biomes in relation to plant litter composition, root density, and nutrient availability. Fungi may comprise up to 20% of the mass of decomposing plant litter.

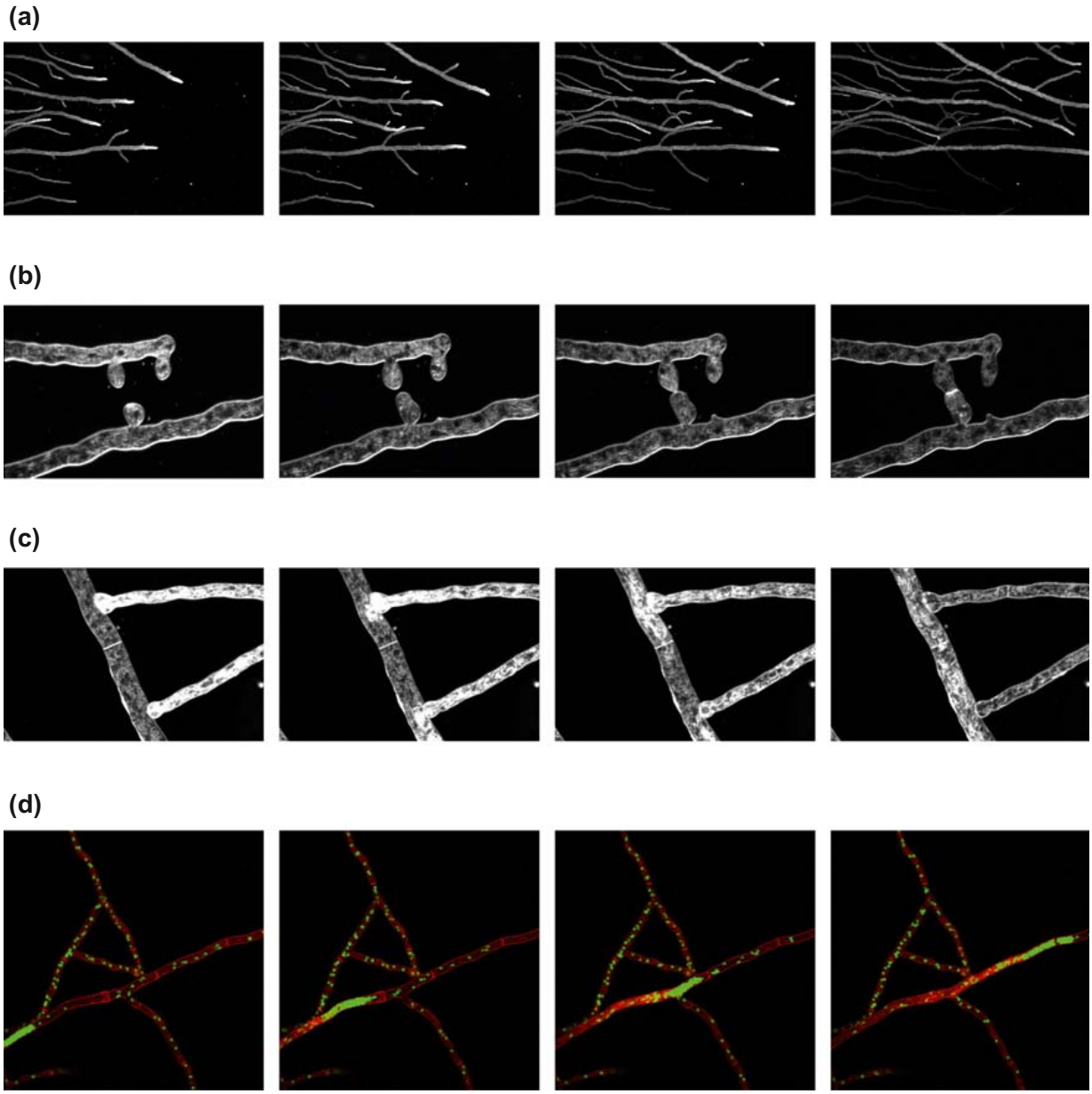

FIGURE 4.5 **Mycelial structure and growth.** (a) Time series showing tip growth and branching as mycelium spreads across substrate. Left image is the earliest in the series. *(Images courtesy of Patrick Hickey.)* (b) Time series showing anastomosis (fusion) of hyphal branches followed by septum formation. *(Images courtesy of Patrick Hickey.)* (c) Time series showing mixing of cytoplasmic contents following anastomosis. *(Images courtesy of Patrick Hickey.)* (d) Time series showing migration of cytoplasm and nuclei through septa. *(Images courtesy of Patrick Hickey.)*

In biomes dominated by ectomycorrhizal plants extraradical mycelia may comprise 30% of the microbial biomass and 80% of the fungal biomass (Högberg and Högberg, 2002). Although fungal abundance and ratios of fungal to bacterial biomass tend to increase as soil pH decreases (Högberg et al., 2007; Joergensen and Wichern, 2008; Rousk et al., 2009), studies suggest that fungal distributions are more influenced by N and P availability than pH per se (Fierer et al., 2009; Lauber et al., 2009). Estimates of fungal biomass turnover in soils are on the order of months (i.e., 130−150 days; Rousk and Baath, 2011), which is comparable to studies of fungal growth rates on submerged litter (e.g., Gulis et al., 2008).

Fungi are present in all soils and are a prominent biological component of most. At broad phylogenetic scales, the aphorism "everything is everywhere" does seem to apply to fungi: beyond soils, they are also found in nearly every other habitat on Earth. High-throughput sequencing (HTS) is providing remarkable new insights into the local to global distribution of fungal species (Bahram et al., 2018; Talbot et al., 2014; Taylor et al., 2014; Tedersoo et al., 2014, 2021). However, a consensus as to whether endemism or global distribution accounts for the larger fraction of species in typical communities remains elusive. What we do know with certainty is that some species occur over only a limited range, from regional to continental, while other species are clearly able to disperse across the globe. Patterns with respect to distribution ranges and species diversity across latitudes and functional guilds are also beginning to emerge.

4.3.1 Estimates of species richness

The true diversity of the Eumycota is uncertain and controversial. To date, there are roughly 148,000 described taxa (Index Fungorum). New species are being described at a rapid rate (Cheek et al., 2020), limited primarily by a dearth of fungal taxonomists rather than a lack of fungi in need of description (Blackwell, 2011; Hawksworth, 2012). Mycologists widely acknowledge that the true number of species on Earth vastly exceeds the number that has been described (Bass and Richards, 2011). A variety of approaches have been used to estimate how many species of fungi may exist. The approach that has received the most attention has been to census both plants and fungi at focal sites within a region to derive species ratios of fungal to plant taxa. These regional ratios are then multiplied by the estimated numbers of plants on Earth to arrive at an estimate for fungal richness. Hawksworth compiled data from well-studied sites in the United Kingdom and obtained a ratio of six fungi per vascular plant species, giving rise to a widely cited global estimate of 1.5 million fungi (Hawksworth, 1991). Updates by Hawksworth have raised the estimate to 2.2 to 3.8 million (Hawksworth and Lücking, 2017). Several molecular surveys of fungi in soil have applied the fungus:plant ratio method and yielded estimates of 5 to 6 million species (O'Brien et al., 2005; Taylor et al., 2014). Estimates based on thorough censuses from single plant species have yielded estimates as high as 10 million (Cannon, 1997). However, there is also evidence that fungus:plant ratios vary geographically and with latitude and are lower in the tropics (Tedersoo et al., 2014). Hence fungus:plant ratios may not be the best path to accurately estimate fungal diversity. It is also important to note that soil-based estimates largely overlook aquatic fungi, insect pathogens, gut symbionts, and many others (Blackwell, 2011). PCR-based surveys also likely overlook divergent taxa due to primer biases. Thus we can confidently state that estimates of total fungal species diversity on Earth of 2 to 3 million are likely to fall well below the true number but also that an immense amount of additional work will be required to approach a reliable tally.

4.3.2 Fungal dispersal and biogeography

Fungal biogeography and assembly of local communities are determined, in part, by dispersal. Fungi in soils disperse, albeit slowly, through growth of their mycelial networks. They disperse more rapidly and over larger distances through movement of various propagules. A hallmark of fungi is the production of propagules in the forms of meiotic or mitotic single-celled resting structures (zygospores, ascospores, basidiospores, conidia, etc.) (see Fig. S4.1 and Section 4.2.4) capable of surviving harsh conditions and dispersing great distances by air. Thick-walled vegetative cells (e.g., monilioid cells) or aggregations of such cells, such as the canon ball—like sclerotia formed by Cenococcum and *Thanatephorus*, can also be important propagules. Meiotic basidiospores are very small and are released into the air by fungi that form mushrooms and by other plant pathogenic fungi such as rusts and smuts. However, studies of mushrooms have shown that, much like plant seeds, the vast majority of basidiospores fall to the ground within centimeters of the fruiting body (Galante et al., 2011). Studies of EMF colonizing individual pine islands amid a sea of non-EMF plants have shown that distance to forest edge and airborne dispersal capabilities of spores of different fungi have strong effects on potential and actual colonization (Peay et al., 2007, 2010, 2012). On the other hand, recent molecular surveys and meta-analyses have shown that a core set of Ascomycota are both dominant in many soils and have global species distributions (Egidi et al., 2019; Větrovský et al., 2019). These were DNA-based whole-soil surveys, so the degree to which the incidence of these global taxa can be attributed to inactive spores or relic DNA (Carini et al., 2017) versus active mycelium is an open question (Cox et al., 2019).

A single taxon defined by traditional morphological and anatomical characters may encompass two or more subgroups that are distinct when phylogenetic or biological species concepts are applied; these are cryptic species. Cryptic species nested within traditional taxonomic species often have much narrower geographic distributions. Molecular studies are revealing cryptic species within widespread species complexes in a number of EMF and decomposer fungi (Aldrovandi et al., 2015; Carlsen et al., 2011; Feng et al., 2016; Geml et al., 2008; Grubisha et al., 2012; Haight et al., 2016; James et al., 1999; Taylor et al., 2006). Some of these studies also reveal finer host-specificity than previously recognized. It seems reasonable to expect that the capacity for aerial dispersal interacts with host and habitat specificity to influence the patterns of successful dispersal that are observed in nature. In contrast to EMF and decomposers, plant pathogens are notorious for very wide dispersal capabilities. However, this perspective may be driven in part by our alarm at the devastation that can ensue when a rare dispersal event (often human-mediated) carries a virulent pathogen to a novel, susceptible host. Native elms and chestnut trees were effectively lost to North America due to the introduction of virulent Dutch elm disease (*Ophiostoma novo-ulmi*), possibly from Asia, and chestnut blight (*Cryphonectria parasitica*) from Japan. However, the survival of these trees for millennia before arrival of these pathogens again underlines that cross-continental jumps are rare.

4.4 Fungal communities

In mainstream ecology the term "community" refers to the set of sympatric, metabolically active organisms that either interact or can potentially interact (Krebs, 1978). We know relatively little about when, where, and how fungi interact with other organisms in soil, aside from conspicuous manifestations, such as mycorrhizal colonization of plant roots or nematode-trapping fungi, and a few recent discoveries of fungal-bacteria interactions (Deveau et al., 2018; Romaní et al., 2006). Fungi in soil vary

at least four orders of magnitude in size. Single-celled yeasts may be 3 to 10 μm in diameter. In contrast, a single mycelial individual of the white-rot, root pathogen *Armillaria gallica* spans >37 hectares with a predicted mass greater than 400,000 kg (Anderson et al., 2018; Smith et al., 1992). In some areas of mycology careful attention has been paid to the spatial definition of community. In particular, researchers studying wood, litter, and dung decay have recognized that fungal species must colonize, grow, and reproduce within the confines of a particular substrate, leading to the designation of unit communities (Cooke and Rayner, 1984). For example, the fungi that occupy a single, isolated leaf might constitute a unit community. The application of the unit community perspective to soil is difficult due to the complex distribution of resources and lack of distinct spatial boundaries. From a practical perspective, soil fungal communities are usually sampled at the plot scale (e.g., 5−50 m diameter), which is defensible in terms of the potential for filamentous individuals to interact, given the size range of sizes of fungal genets.

4.4.1 Abiotic drivers

Like all terrestrial organisms, the distributions and abundances of fungal species are influenced by history (e.g., dispersal, plate tectonics), climate, and numerous environmental factors, especially edaphic factors. There is increasing evidence that soil fungal communities are influenced by climatic conditions on both geographic and temporal scales. For example, the correlation of soil fungal communities is stronger with temperature than with latitude across the five bioclimatic subzones of the Arctic (Timling et al., 2014). Moisture, measured as mean annual precipitation (MAP), was one of the strongest predictors of community composition in the global soil studies by Tedersoo and colleagues (Bahram et al., 2018; Tedersoo et al., 2014, 2021). In communities of EMF, climate explained 58% of the variance in richness and 41% in community composition in 68 sites across North America (Steidinger et al., 2020). In concert with patterns of fungal species composition, climate and pH appear to be the major drivers of the relative dominance of EMF versus AMF or nonmycorrhizal symbioses in forests worldwide (GFBI consortium et al., 2019). Ectomycorrhizal symbioses increase in dominance with distance from the equator in a pattern that aligns with decreasing decomposition coefficient (an index based on moisture and temperature). A recent meta-analysis of fungal communities in soil globally supports the preeminence of climate as a driver (Větrovský et al., 2019). However, the relative importance of temperature versus moisture and how these factors influence the physiology and performance of different fungi remain outstanding questions. Moreover, the degree to which climate influences fungal communities directly or indirectly via differences in vegetation remains to be elucidated.

Most studies have undertaken sampling in the summer at higher latitudes or the equivalent at peak growing season (e.g., wet season) in tropical latitudes, yet most belowground activity likely occurs at other times. For example, midlatitude, high-elevation alpine sites at Niwot Ridge in Colorado showed that microbial (including fungal) biomass peaked in late winter under the snowpack (Lipson and Schmidt, 2004; Schadt, 2003). Enzyme activities also peaked in winter following leaf-drop in a deciduous forest, with saprotrophs increasing in biomass through the winter (Voříšková et al., 2014). Given that up to 10 months of the year are snow covered in boreal, Arctic, and Antarctic regions, activity under snow could strongly influence annual biogeochemical fluxes (Sturm et al., 2005). In temperate biomes (Averill et al., 2019; Voříšková et al., 2014), and even in cold-dominated boreal and alpine biomes, fungal communities in soil have been shown to shift predictably across seasons (Schadt, 2003; Taylor et al., 2010).

Other more extreme and less predictable disturbances also perturb the biomass and composition of fungal communities in soil. The disturbance that has received the greatest attention is fire. Ectomycorrhizal communities are strongly impacted by fire as a consequence of direct heat injury and consumption of fungal biomass, as well as death or injury to host plants, loss of organic matter, and changes in soil chemistry (e.g., transient increases in N availability, higher pH). Studies showing mild effects of fire have usually been conducted in habitats with frequent low-severity burns that do not kill the host trees (Dahlberg et al., 2001; Smith et al., 2004; Stendell et al., 1999). Where hotter, stand-replacing fires occur, impacts on ECM fungi are stronger (Baar et al., 1999; Cairney and Bastias, 2007). In general, fire reduces fungal diversity and preferentially removes those taxa that have strong preferences for the litter layer. When mycorrhizal hosts are killed, vegetation succession is reset and suites of so-called early-stage fungi are the dominant colonizers (see next section; Taylor et al., 2010; Treseder et al., 2004; Visser, 1995). There are also a number of soil fungi that respond positively to fire, the so-called pyrophilous fungi (Glassman et al., 2016; Hughes et al., 2020). Most of these appear to be saprotrophic taxa that benefit from new substrates and possibly reduced competition from established mycorrhizal and decomposer taxa.

Other well-studied abiotic disturbances include land management, both forest and agricultural, as well as pollution. For example, agricultural tillage strongly reduces the diversity of AMF (Helgason et al., 1998). Heavy metal contamination (Colpaert and van Assche, 1987; Op De Beeck et al., 2015) and nitrogen (N) deposition (Lilleskov et al., 2002; van der Linde et al., 2018) also reduce diversity and reshape fungal communities. Disturbances that occur at smaller spatial scales also impact fungal communities. For example, fungal communities in paired vegetated versus cryoturbated microsites (frost boils) in the Arctic are highly distinct (Timling et al., 2014). At the micrometer scale of hyphae and mycelia, soil fungi face constant impacts ranging from fresh litter inputs to dying roots to fluctuation in moisture to grazing by soil fauna such as collembolans.

At local to global scales, soil fungi respond to environmental gradients in factors such as pH and moisture (Bahram et al., 2018; Tedersoo et al., 2014). A series of papers report sharp differences in fungal communities as a function of soil horizon (Bahram et al., 2015; Dickie et al., 2002; Taylor and Bruns, 1999; Taylor et al., 2014). Soil pH, moisture content, and nutrient levels (particularly N) are also correlated with community composition in soil (Cox et al., 2010; Taylor et al., 2000; Toljander et al., 2006; van der Linde et al., 2018) but are relatively weak drivers compared to soil horizon, except in cases of extreme gradients such as gaseous ammonia pollution from a fertilizer plant (Lilleskov et al., 2002). On the other hand, at regional to continental scales, geographic distance was shown to play a larger role than edaphic factors or horizon in structuring soil fungi in North American coniferous forests (Talbot et al., 2014).

Not surprisingly, edaphic factors are strongly correlated with the composition of both mycorrhizal and saprotrophic fungal communities. Among EMF, there is evidence that mycelial exploration type (i.e., hyphal growth and foraging patterns; Agerer, 2001) may be related to strategies for N acquisition from different sources (Hobbie and Agerer, 2010; Taylor et al., 2000). Taylor et al. (2000) found higher capacities for growth on media containing only organic N sources among fungal isolates from the pristine end of an N-deposition gradient across Europe compared with those from the polluted end of the gradient where mineral N is more available. Corresponding to the aforementioned pattern, EMF taxa that produce potent peroxidases increase in abundance with latitude and declining soil mineral N availability (Argiroff et al., 2022). Less attention has been paid to how pH or moisture may underlie habitat preferences other than the well-known high levels of enzyme activity, and resulting competitive dominance, exhibited by

ericoid mycorrhizal fungi under acidic conditions (Read, 1991; Read and Perez-Moreno, 2003). Several papers have suggested that soil K and Ca levels are predictive of the composition of EMF communities associated with *Alnus* species (Roy et al., 2013; Tedersoo et al., 2009). The physiological traits that underlie preferences of soil fungi for particular abiotic conditions are mostly unknown, although soil C:N ratios, decomposition rates, and host mycorrhizal type appear to exert selection that alters the relative roles of mycorrhizal versus saprotrophic fungi in the liberation of macronutrients from soil organic matter (SOM) (Argiroff et al., 2022; Bahram et al., 2018; GFBI consortium et al., 2019; Kyaschenko et al., 2017; Mayer et al., 2021).

4.4.2 Biotic drivers

Vegetation is the most important biotic factor that influences the composition of fungal communities in soil. Most fungi consume living or dead plant material for their primary energy source, with a large fraction of fungi displaying some degree of specialization toward living or dead tissue of particular plant lineages or functional groups. Thus plant community composition plays a critical role in determining which soil fungi are present at a site. It has been well-documented that EMF range from genus-specific, or even species-specific, to quite generalist, associating with both angiosperms and gymnosperms (Molina et al., 1992). Broader associations appear to be the norm in EMF, but host-specialist fungi can be important players, such as in the reciprocally specific associations of alder (Kennedy et al., 2011; Roy et al., 2013). While the several hundred species of AMF found in >200,000 vascular plant species have been assumed to have low specificity, a more complicated picture is emerging. Much like mycorrhizal fungi, decomposer fungi display a range of specialization toward their substrates. The genetic, physiological, or ecological basis for such specialization are not known in most cases. Certain white and brown rot wood decay fungi are found on wide arrays of both angiosperm and gymnosperm hosts. Yet many fungi in these guilds favor either angiosperms or gymnosperms and may even prefer families or genera within these lineages.

Historically, only the plant-to-fungus direction of influence received much recognition. However, there is increasing evidence that these influences are reciprocal: the spectrum of species present, i.e., the plant microbiome, and their relative abundances can also have major impacts on plant community composition (Rúa et al., 2016; van der Heijden et al., 1998). Specific plant pathogens can dramatically reduce or eliminate particular host species, altering plant community composition (Packer and Clay, 2000; Reynolds et al., 2003). Plant-soil-feedbacks (Bever, 2003, 1994; Kulmatiski et al., 2008), which often involve the buildup of host-specific pathogens in soil, can alter coexistence and competitive dynamics within plant communities.

Competition among fungal species also plays an important role in structuring communities. Studies have demonstrated that the arrival order of ECM species can shift competitive dominance in colonization of seedling root systems (Kennedy et al., 2009). These priority effects have been shown to occur for fungal decomposer communities in wood (Fukami et al., 2010). In this latter example the order of species arrivals also affected the progress of decay, suggesting that competition and community assembly may have ecosystem consequences (see also Argiroff et al., 2022; Kyaschenko et al., 2017). These interactions likely involve indirect exploitative competition for resources as well as various forms of direct interference competition. Further evidence for competition in soil fungi comes from statistical analyses of patterns of cooccurrence and avoidance. In general, cooperating/synergistic species should cooccur more often than expected by chance, while antagonistic species should cooccur less often than

expected by chance; the latter situation is called a "checkerboard" pattern (Stone and Roberts, 1990). In a study of pine ECM communities avoidance patterns suggestive of competition were more common than were cooccurrence patterns (Koide et al., 2004). Wood decay fungi are well-known for overt signs of competitive interactions, as many use combative strategies, including production of bioactive compounds as well as direct invasion and lysis of opposing hyphae (Boddy, 2006; Cooke and Rayner, 1984).

Soil fungal communities undergo succession, likely driven by a combination of species interactions and changing resource/environmental conditions, analogous to patterns known from prokaryotes and plants. Patterns of succession are complicated in soil fungal communities due to the wide range of relevant spatial and temporal scales. In vegetated ecosystems succession of EMF occurs in tandem with plant succession. These observations led to the classification of early-stage and late-stage EMF taxa (Deacon et al., 1983). Early-stage species are the first to colonize young tree seedlings in habitats with no mature trees (e.g., old-fields), while late-stage species are typical of mature forests. These changes in fungal communities may be driven by changes in the C-provisioning capacity of trees as they grow (late-stage fungi tend to produce larger mycelial mats and may have larger C demands) or due to changes in the soil environment, particularly the build-up of a well-decomposed organic horizon (late-stage fungi appear to have a greater capacity to degrade complex organic polymers). Studies of fungal communities in soil beyond only ECM taxa also demonstrate strong shifts in composition in concert with plant successional stage (Taylor et al., 2010).

A microhabitat in which fungal succession has been well studied is coarse woody debris. As with EMF communities, wood-decomposer fungi are territorial, usually occupying contiguous patches of substrate to the exclusion of other species. A series of studies have demonstrated that the first colonists of wood are present at low levels in the living tree and grow actively once the dead wood has dried beyond a certain threshold (Chapela and Boddy, 1988; Parfitt et al., 2010). These fungi are primarily soft rot members of the Ascomycota, such as *Xylaria*. These taxa are quickly followed by white and brown rot fungi in the Basidiomycota. Observations of fruit body formation over time on downed logs, as well as direct molecular analyses of the wood itself, agree that Basidiomycota-dominated communities follow a predictable series of species appearance and disappearance. Carbohydrate and phenolic composition, as well as C:N:P ratios, change significantly as decomposition progresses, which likely provides a basis for niche-differentiation and successional patterns among decomposers. However, chemical composition does not entirely explain the successional patterns. For example, certain wood-rot Basidiomycota follower species seem to occur only when another species of Basidiomycota has previously colonized the log. Whether these patterns arise from direct species interactions or from changes in the chemical environment imparted by the primary species (i.e., facilitation in the sense of classical succession theory) is unknown.

Successional patterns in leaf litter are similar but faster than in wood. The earliest colonizers are often found within the attached, senescent leaves as endophytes, primarily Sordariomycetes and Dothideomycetes (Ascomycota) (Snajdr et al., 2011). R-selected sugar fungi that are not present as endophytes, such as *Mortierella*, may also play important roles in the earliest stages of decay when labile carbohydrates are readily available. Once litter is exposed to the moist forest floor, rhizomorph and cord-forming Basidiomycota can aggressively colonize leaves. However, in arid lands it appears that various drought-tolerant, melanized Ascomycota predominate over Basidiomycota as both plant symbionts and decomposers (Porras-Alfaro et al., 2011).

4.5 Fungal traits

Trait-based perspectives have been extremely important in plant and animal ecology (Chapin et al., 1996; Grime, 1974, 1977). Considerable effort has been put into building trait databases for plants and animals (Kattge et al., 2011). Efforts to apply similar perspectives to microbial ecology have gained momentum (Aguilar-Trigueros et al., 2015; Crowther et al., 2014; Lajoie and Kembel, 2019; Lustenhouwer et al., 2020; Romero-Olivares et al., 2021; Zanne et al., 2020a, 2020b). The trait-based perspective seeks to link specific phenotypic characteristics of an organism to its performance (fitness) in a particular environment. Through assembling data on numerous traits across species and environments, ecologists seek to discern tradeoffs between trait values and combinations of traits (strategies) that perform well under the specific conditions. This perspective can improve mechanistic understandings of fundamental ecological processes, such as community assembly, and can also improve capacity to predict future community composition and function (Lajoie and Kembel, 2019; Zanne et al., 2020a), such as under climate change.

Efforts to build trait databases are underway for fungi (Nguyen et al., 2016; Põlme et al., 2020; Zanne et al., 2020b), particularly soil fungi, although there are considerable challenges. In introductory biology textbooks fungi are often divided between parasites, decomposers, and mutualistic symbionts. These coarse trophic categories can then be further divided into numerous guilds, such as AMF versus EMF symbiotic fungi. Distinguishing systems that are dominated by one mycorrhizal type versus another provide valuable predictive power with respect to key soil processes such as C storage, decomposition rates, and productivity (Bennett et al., 2017; Clemmensen et al., 2013; Read, 1991). At the same time, variation in ecological strategies among fungal species belonging to a single guild can be immense. This is well illustrated by recent advances in our understandings of fungal wood decay brought by genomics and biochemical techniques (Eastwood et al., 2011; Riley et al., 2014).

4.5.1 Structural traits

Broad categories of traits of interest in ecology span morphology to biochemistry to genes. For soil fungi, mycelial growth traits (described above) vary widely among taxa and in response to internal and external stimuli. Because fungi must grow to both find and digest their food, mycelial traits are clearly essential to their fitness and ecosystem functions. Among the key traits are hyphal diameters, growth rates, and branching and anastomosis frequencies (Fricker et al., 2017). How individuals alter these traits in response to environmental stimuli such as resource distribution and abundance and the presence of competitors will likely contribute insights into fundamental ecological strategies of fungi. Unfortunately, fitness of filamentous fungi is extremely difficult to measure (Pringle and Taylor, 2002), particularly in natural settings like soil, where distinguishing the boundaries of a single, physiologically integrated individual is nigh to impossible. However, the imprint of natural selection as well as developmental and genetic constraints can be inferred through study of trait combinations that do and do not occur in extant species. We thus expect tradeoffs in trait expression due to resource limitation. For example, Lehman et al. (2019) studied a range of mycelial traits in phylogenetically diverse isolates from the same habitat and uncovered correlations between long internodes (distance between branches) and wide hyphae. Mycelial network architecture was most complex in members of the *Mucoromycotina*, but trait values varied widely, even among closely related taxa.

The morphology of fungal reproductive structures is obviously of great importance to dispersal and fitness. With respect to sexual structures in the *Dikarya*, there are clear tradeoffs between above- and

belowground fruiting strategies. Mushrooms have little capacity to restrict water loss (Lilleskov et al., 2009), which explains why aboveground (epigeous) mushrooms are seen nearly exclusively in moist habitats or seasons. In semiarid to arid environments taxa that rely on epigeous fruiting are largely replaced by taxa that fruit belowground. This includes taxa with resupinate (stalkless, mat-like crusts) or gastroid (sealed, semispherical) sexual structures. These taxa rely less on wind for dispersal and many have evolved to attract animal vectors such as mites (Lilleskov and Bruns, 2005) and small mammals (Fogel and Trappe, 1978). Most famous among these are the highly sought edible truffles, which are gastroid fruitbodies produced by ectomycorrhizal Ascomycota in the genus *Tuber*. Not surprisingly, belowground fruiters have much shorter average dispersal distances than their epigeous counterparts (Kivlin et al., 2014; Kjøller and Bruns, 2003), illustrating a key tradeoff.

There is recent evidence showing that Ascomycota with forcibly ejected ascospores are precisely apportioned to minimize drag (Roper et al., 2008), which aids spores in escaping the zone of still air immediately adjacent to the sporocarp. That simultaneous ejection of ascospores across the surface further increases dispersal by creating a small wind current (Roper et al., 2010). Asexual spores are also key components to the dispersal and survival of some fungi. Conidia are small (one- to few-celled) haploid, asexual spores produced by many Dikarya. These spores are often dispersed by wind but also by water (aquatic hyphomycetes) or insects. Spores play critical roles in surviving disturbances or harsh conditions, not just in dispersal. Emphasizing their role in survival, durable resting (metabolically inactive) structures of soil fungi have sometimes been called resistant propagules. In addition to sexual spores and conidia, resistant propagules include thick-walled, inflated hyphal segments called chlamydospores as well as aggregations of cells in highly protected, tough structures called sclerotia. Sclerotia are seen in many plant-pathogenic fungi and serve various roles, such as overwintering in soil while awaiting the next generation of host plants. The diverse structures that soil fungi use to disperse and withstand harsh conditions are clearly key traits with respect to understanding the movement and population dynamics of fungi. Improved knowledge of these traits should aid in applying fundamental ecological theory to soil fungi. For example, do competition-colonization tradeoffs help explain distinct fungal strategies and community assembly (Smith et al., 2018)? Are there tradeoffs in spore size versus number, as well known for seeds in vascular plants (Zanne et al., 2020a)?

4.5.2 Elemental stoichiometry

Considerable work in animal macroecology has focused on scaling laws in relation to body size and metabolism (Brown, 1995). From a theoretical point of view, such principles should apply equally to fungi and animals. Unfortunately, taking the necessary measurements is impractical for most fungi, in part due to difficulties in measuring body size. However, a related body of theory holds more promise in fungi, namely ecological stoichiometry, which relates tissue elemental ratios to nutrient acquisition (Sterner and Elser, 2017). In general, fungi have higher tissue N contents and lower C:N ratios than the plant tissues from which most obtain their nutrition due to the higher N content of chitin as compared to cellulose. However, studies of C:N:P contents and ratios in terrestrial fungi have revealed wide variation (Lodge, 1987; Zhang and Elser, 2017), making it difficult to infer ecological strategies from stoichiometric traits of soil fungi. A recent analysis of saprotrophic versus EMF mushrooms growing in the same habitats across steep soil N and P gradients did reveal some strong guild-level patterns despite considerable variation among species within a guild (Kranabetter et al., 2019). More specifically, EMF had consistently lower N and P contents than saprotrophs, where nutrient contents were strongly correlated

with their availability in soil. One inference was that mycorrhizal fungi have lower N and P because they provide any excess to their hosts, while saprotrophs may benefit from accumulating these resources. Variation in nutrient contents within guilds may point the way toward elucidating further axes of niche partitioning. The same can be said of stable isotope ratios, which differ predictably between EMF and saprotrophic taxa (Hobbie et al., 2001). *Laccaria bicolor* is an ectomycorrhizal fungus that often displays an unusual ^{15}N natural abundance, likely because it supplements its N supply by killing and consuming soil collembola (Klironomos and Hart, 2001).

4.5.3 Genes and enzymes

One of the most important categories of trait variation in soil fungi from the perspective of ecosystem function and nutrient cycling is the production of extracellular enzymes. All osmotrophic fungi produce some extracellular enzymes to break down extracellular molecules into subunits that can be absorbed. However, the range of enzymes produced, and likely the controls over production, vary widely across fungal guilds and taxa. Some fungi, such as AMF, have limited arrays of hydrolytic and oxidative enzymes. At the other extreme, white-rot fungi in the Basidiomycota express complex batteries of enzymes, including polyphenol peroxidases, that allow them to attack recalcitrant, lignocellulosic polymers from woody plants. Analyses of enzyme potentials from soil have been widely used to interrogate the functional potentials of soils under various conditions (Sinsabaugh et al., 2002; Sinsabaugh, 2010; Snajdr et al., 2011; Talbot et al., 2013, 2015; Talbot and Treseder, 2012). In such analyses the activities of the entire microbial community are summed, providing little insight into trait variation among taxa. However, studies of pure cultures and single-fungus, ectomycorrhizal root tips have provided valuable information about the enzymatic activities of specific saprotrophic and mycorrhizal fungi (Courty et al., 2005; Kirk and Cullen, 1998; Rineau and Courty, 2011; Ruess et al., 2019).

An exciting extension of physiological and biochemical assays has been the acceleration of genome and transcriptome sequencing across diverse fungal lineages (Grigoriev et al., 2014). Together with biochemical studies, accumulating genomes suggest that hard and fast distinctions between mycorrhizal fungi and decomposers, as well as decomposer categories within wood decay fungi (white vs. brown vs. soft rotters), do not hold up. Some mycorrhizal fungi retain oxidative genes inherited from the common ancestor of the Agaricomycotina (Floudas et al., 2012), presumably as a mechanism for obtaining N to trade to their host trees (Bödeker et al., 2014), while white and brown rot fungi display a wide spectrum of hydrolytic and oxidative gene contents (Eastwood et al., 2011; Riley et al., 2014).

4.6 Ecosystem functions

Soil fungi regulate the cycling of C, N, and other elements in ecosystems through their activities as decomposers, pathogens, endophytes, and mutualists of other organisms. Filamentous fungi support plant production through mycorrhizal associations that enhance the acquisition of water and nutrients, while fungal endophytes of plant roots can confer plant resistance to thermal and drought stress and reduce herbivory (Porras-Alfaro and Bayman, 2011). Fungi also support C and N fixation by algae and cyanobacteria through lichen associations (Liu et al., 2021) and in arid and polar regions, the formation of biotic crusts. Biotic crusts mediate soil-atmosphere exchange of greenhouse gases (such as CO_2), as well as water infiltration and stabilization of surface soils against erosion (Pointing and Belnap, 2012).

Fungi mediate nearly every aspect of organic matter production, decomposition, and sequestration in soil. As major drivers of surface organic matter (i.e., plant litter) decomposition, fungi mediate the creation of SOM, as well as the balance between its sequestration in aggregates or mineral-associated particles and its mineralization into CO_2. From a microbial perspective, SOM can be defined as the point at which the cost of further decomposition is not energetically favorable without additional inputs of more labile material (Moorhead et al., 2013). SOM can develop from the decay of surface leaf and stem litter or from the growth and turnover of roots, their associated fungi, and other microorganisms (Clemmensen et al., 2013; Wilson et al., 2009). Fungi can also protect SOM from decomposition through both chemical and physical means. Filamentous fungi promote formation of large macroaggregates in soil by binding soil particles with hypha and produce cell wall materials that act as adhesives (Willis et al., 2013). Aggregate formation promotes soil C sequestration by providing physical protection from decomposers and their degradative enzymes (Wilson et al., 2009). Paradoxically, fungi are also major decomposers of SOM on land, generating a large fraction of extracellular enzyme activity in soil (Fernandes et al., 2022; López-Mondéjar, 2020). In the process they release large amounts of major growth-supporting elements from dead organic matter (Joergensen and Wichern, 2008).

4.6.1 Carbon and nutrient cycling

Soil fungi control the cycling of C and other nutrients (primarily N and P) through both exchange with plants (Averill et al., 2019) and their biochemical interactions with SOM. Root symbionts (e.g., mycorrhizal fungi), endophytes, and epiphytes can promote plant growth by providing nutrients like N and P in exchange for C, and by ameliorating abiotic stressors, such as high salinity, temperature extremes, drought, and metal toxicity (Hashem et al., 2018). Root-associated fungi can act as biopesticides that deter microbial and insect pathogens of roots (Müller and Ruppel, 2014; Rodriguez et al., 2009). Mycorrhizal fungi often serve as conduits of plant C to soil, providing photosynthate to other free-living members of the soil microbiome (e.g., saprotrophs) (Gorka et al., 2019). By contrast, saprotrophic fungi feed on plant litter and microbial necromass as their main source of C. Saprotrophic, mycorrhizal, and all other aerobic soil fungi release a portion of their acquired C into the atmosphere as CO_2 and recycle the rest into fungal molecules in biomass and exudates. This process feeds nearby fungi and other organisms in soil. In some northern forest ecosystems the majority of soil organic C may be sequestered within fungal biomass (Clemmensen et al., 2013) due to chemical and physical protection of fungal molecules from decomposition (Fernandez and Koide, 2014).

One of the greatest impacts of soil fungi on the Earth system is through regulating the balance between C sequestration in the biosphere and C release into the atmosphere as CO_2. Root-associated fungi can consume up to 20% of plant C, with additional C consumed by fungal pathogens and parasites. Through the process of decomposition, saprotrophic fungi are responsible for releasing up to 36 Pg C from soils into the atmosphere as CO_2 annually, while root-associated fungi are estimated to release an additional 1.3 to 5.4 Pg C as CO_2 (Dighton and White, 2017). Through these processes, fungi are second only to plants in directly cycling and sequestering C in most terrestrial ecosystems. However, fungi also indirectly influence plant C cycling through their activities in nutrient cycling and disease.

4.6.1.1 Nutrient exchange with plants

Soil fungi facilitate uptake of N, P, other elements, and water by plant roots either by direct association and exchange (e.g., mycorrhizal fungi) or by decomposing and mineralizing nutrients from SOM for root

uptake (Schimel and Bennett, 2004). Both strategies are widespread; over 90% of plant families, comprising approximately 250,000 plant species, engage in mycorrhizal symbioses. An estimated 50,000 species of fungi are mycorrhizal (van der Heijden et al., 2015), with the vast majority of the remaining 3.5 million fungal species having saprotrophic capabilities. Both mycorrhizal and saprotrophic functional groups have positive effects on plant nutrition, photosynthesis rates, and biomass accumulation. Mycorrhizal fungi can trigger stress resistance metabolism in plants such that they are capable of living in extreme — and otherwise deadly — environmental conditions (Bunn et al., 2009). Mycorrhizal fungi are even known to connect plants within a community (GFBI consortium et al., 2019) allowing the movement of nutrients between coexisting plants (Gorzelak et al., 2015). However, the rate of C and nutrient exchange between plants and soil fungi depends on environmental conditions, the identity of the fungus (Kiers et al., 2011), with the molecular controls over the metabolic exchange between fungi and plants just beginning to be revealed (Liao et al., 2014).

Mycorrhizal fungi can provide up to 80% of plant N and 90% of plant P (van der Heijden et al., 2015). Nevertheless, careful experiments with isotopic tracers in the AM symbiosis have established that the identity of the fungus, including both its taxonomy and nutrient delivery traits, can determine the amount of nutrients and C exchanged between soil and plants. Multiple studies have shown that plants can preferentially allocate more C to roots associated with a fungus delivering more P to the plant (Ji and Bever, 2016) and that conversely, C allocation can trigger N and P transfer from fungus to host plant (Fellbaum et al., 2012). Because nutrient uptake and transfer from AMF to plant hosts can increase foliar P and deplete soil P pools (van der Heijden et al., 1998), higher rates of C and nutrient exchange among strong plant-fungal mutualists could drive faster rates of soil nutrient cycling and plant productivity at the ecosystem level. Preferential plant C allocation to nutrient-generous AMF is predicted as part of biological market theory, in which plants and fungi can discriminate resource transfer between partners depending on the rate of transfer. Similar activities among EMF and their plant hosts have recently been revealed (Bogar et al., 2019). Nevertheless, resource exchange in mycorrhizal symbiosis does not always follow predictions from this theory, especially in the case of mycoheterotrophic plants or when plant health is compromised and mycorrhizal fungi turn parasitic (Walder and van der Heijden, 2015).

Despite the commonality of mycorrhizal symbioses in nature, C and nutrient exchange between the plant and fungal partners appears to be extremely chemical specific. In EMF-pine associations C is transferred to the fungus primarily as sugar alcohols (e.g., mannitol). Compatibility between plant and fungus — and therefore, the ability to develop mycorrhizal cellular structures and exchange molecules in the root — seems to be controlled by secreted proteases (Tang et al., 2021), which are small secreted proteins that have molecular properties similar to proteins associated with fungal virulence (Liao et al., 2014, 2016). It is still unclear how these molecular processes vary across fungal and plant taxa.

4.6.1.2 Enzymes and the decomposition of biopolymers

To fuel their growth, fungi must generate small molecular weight molecules (i.e., substrates) by enzymatically degrading complex organic matter (i.e., biopolymers) outside their cells. Enzymes released into the environment to acquire nutrients, or as a result of cell lysis, can be beyond the control of that organism (Fig. 4.1) such that a substantial fraction of biogeochemical cycling in soils is a legacy of fungal enzymes that are spatially and temporally displaced from their origins (Burns et al., 2013). However, some fungi secrete extracellular enzymes within mucopolysaccharides that are reabsorbed after the decomposition of organic matter. This strategy could allow fungi to reuse or reduce the loss of C and N used to construct

extracellular enzymes and might also allow fungi to control the decomposition process and soil biogeochemical cycling more carefully than previously thought.

Fungi are considered principal degraders of plant cell wall material, especially during the early stages of litter decomposition in soil when their filamentous growth form and their capacity to secrete a variety of enzymes (primarily glycosidases and oxidases) allows them to bore through the cellular structure of plant litter. The capacity to partially or wholly degrade cellulose, especially after it has been decrystallized, is widespread in fungi, including basal lineages. Ascomycota and Basidiomycota have the widest genetic and ecological capacity for cell wall decomposition, which is facilitated by the synergistic expression of a variety of other polysaccharide-degrading enzymes. The ecological capacity of the Glomeromycota to degrade cellulose and other cell wall polysaccharides appears more limited, but several studies indicate greater capacity than once thought (Kowalchuk, 2012; Talbot et al., 2008).

Production of laccases and other phenol oxidases is also widely distributed among Ascomycota, Basidiomycota, and Glomeromycota (Baldrian, 2006). In some organisms, mainly saprotrophs, these enzymes primarily degrade lignin and other secondary metabolites in plant cell walls, often indirectly by producing small reactive oxidants known as redox mediators (Rabinovich et al., 2004). Other saprotrophs oxidatively degrade SOM to obtain chemically protected C, N, and P (Burns et al., 2013). In many taxa a large but indeterminate portion of oxidative activity is related to morphogenesis (e.g., melanin production), detoxification, and oxidative stress (Baldrian, 2006; Sinsabaugh, 2010) rather than nutrient acquisition. However, once released into the environment through biomass turnover, these activities also contribute to the oxidative potential of soils, which catalyzes nonspecific degradation reactions that contribute to the loss of SOM (Burns et al., 2013) as well as condensation reactions that can reform SOM (Sinsabaugh, 2010).

Peroxidases, with greater oxidative potential than laccases, are produced by some members of the Ascomycota and Basidiomycota. The most widely distributed enzyme, Mn peroxidase, acts indirectly on organic compounds by generating diffusible Mn^{+3}. The contribution of Mn peroxidase to soil C dynamics is highlighted by manipulation studies showing that Mn availability can limit the decomposition of plant litter (Trum et al., 2011). Some Basidiomycota, principally wood-rotting fungi, produce lignin peroxidase, which directly oxidizes aromatic rings (Rabinovich et al., 2004).

While most hydrolytic and oxidative enzymes are broadly distributed across taxonomic groups, functional groups of fungi (i.e., fungi that have different primary C sources) have unique enzyme profiles (Zanne et al., 2020a). For example, the distribution of extracellular enzymatic capacity is the basis for the traditional soft rot/brown rot/white rot ecological classification of wood rot decomposer fungi. In enzymatic terms these classifications refer to organisms that primarily attack cell wall polysaccharides (soft rot), those that deploy lower redox potential laccases in addition to glycosidases (brown rot), and those that deploy high redox potential laccase-mediated or peroxidase systems capable of effectively depolymerizing lignin (white rot). Interestingly, recent phylogenomic studies suggest that the common ancestor of the Agaricomycotina (basidiomycete class containing all EMF, brown rot, and white rot fungi) was capable of white rot such that fungi in all these functional groups retain some capacity for recalcitrant SOM breakdown (Bödeker et al., 2009, 2016; Lindahl and Tunlid, 2015). The evolution of brown rot appears to have occurred independently several times, in part through the loss of Mn-peroxidase genes.

EMF were once thought to have little saprotrophic capability compared to wood and litter decay fungi, but there is growing evidence that at least some EMF can attack a wide range of organic compounds (Pritsch and Garbaye, 2011; Read and Perez-Moreno, 2003; Talbot et al., 2013) such that these EMF are now considered a class of decomposers (Lindahl and Tunlid, 2015). EMF extracellular enzymes seem

largely targeted toward N-acquisition based both on actual activity (Talbot and Treseder, 2010) and on genomic sequence data (Martin et al., 2008; Zak et al., 2019). However, some EMF have retained the capacity to generate oxidative enzymes (such as peroxidases) and Fenton chemistry, which can depolymerize lignin, cellulose, and hemicellulose (Bödeker et al., 2016; Lindahl and Tunlid, 2015; Nicolás et al., 2019; Op De Beeck et al., 2015; Rineau et al., 2013; Shah et al., 2016), suggesting that the ability to decompose litter C to some extent may be common among EMF. For example, the relative abundance of *Cortinarus acutus*, an EMF species capable of producing Mn peroxidases, was linked to a 33% decrease in C stocks in the organic soil horizon of a Swedish boreal forest (Lindahl et al., 2021). Nevertheless, the selective pressures that drive the adaptive evolution of enzyme activities likely differ for EMF versus saprotrophic fungi such that enzyme activities generated by EMF may be under different environmental controls (e.g., plant physiology) than those of free-living saprotrophs.

4.6.1.3 Soil nitrogen cycling

Soil fungi are involved in many key steps of the soil N cycle. While no fungi have been discovered that conduct N fixation, fungi are adept at decomposing and taking up N-rich molecules from soil, potentially because decomposition and symbiosis with plants require large nutrient (e.g., N, P) investment by the fungus. The potential to use chitin as an N source is widespread among fungi (Geisseler et al., 2010), potentially because fungi also decompose chitin internally during the process of hyphal extension (Gooday et al., 1986). However, proteins and their degradation products are the largest source of organic N in soils and it is likely that most saprotrophic and biotrophic fungi obtain the majority of their N from degradation of peptides in soil (Hofmockel et al., 2010; Sinsabaugh and Shah, 2011). In contrast to their role in P acquisition, the role of AMF in N acquisition is poorly resolved (Veresoglou et al., 2012). The enzymatic capacity of EMF to mine N from SOM has received more attention (Pritsch and Garbaye, 2011; Talbot et al., 2008). The role of fungi in the N cycle was once considered primarily assimilatory, where fungi assimilated inorganic N and N-containing organic molecules to support the production of new fungal biomass and supply plant hosts. However, recent studies have shown that denitrification pathways are widespread among *Ascomycota* and are responsible for a large fraction of nitrous oxide efflux, especially in arid soils (Shoun et al., 2012; Spott et al., 2011).

While fungi often mine soil for N, anthropogenic N deposition and addition has been shown to decrease fungal diversity, biomass, and respiration in soil (Knorr et al., 2005; Saiya-Cork et al., 2002; Treseder, 2008) for multiple potential reasons. Increased N deposition is associated with decreases in laccase and peroxidase activities in litter and soil, leading to slower decomposition and increased soil C sequestration (Gallo et al., 2004; Sinsabaugh et al., 2002). Nitrogen deposition also reduces the need for plants to engage in mycorrhizal symbiosis such that mycorrhizal fungi often decline in abundance with N deposition (Treseder, 2004), which may contribute to observed decreases in overall fungal biomass and activity in soil. Another contributing factor may be the difference in biomass C:N ratio of fungi and bacteria, where high N levels might promote bacterial growth relative to fungi (Strickland and Rousk, 2010; Van Der Heijden et al., 2008). Fungi can have extremely wide-ranging C:N:P ratios that can vary with both environmental conditions and across lineages (Zhang and Elser, 2017). Nevertheless, many fungal species have high C:N ratios (in the range of 13−60) (Strickland and Rousk, 2010) that exceed C:N ratios in biomass of bacteria (Danger et al., 2016). One review noted a positive relationship between fungal dominance (as indicated by qPCR) and soil C:N ratios across biomes (Fierer et al., 2009). Nitrogen deposition is typically composed of nitrate, ammonium, and organic N (Holland et al., 1999). There is

evidence that these molecules may also suppress fungal activity in soil through various mechanisms (Fog, 1988).

Despite the suppressive effect of N deposition on fungal growth and activity, soil fungi also have the capability to process nitrate into more reduced N forms that can be exported from soil systems as greenhouse gas. Nitrate reduction has historically been considered specific to prokaryotes in soil, yet nitrate reduction was reported in eukaryotes as early as the 1980s (Finlay et al., 1983) and nitrous oxide production was reported in soil fungi during the 1990s (Shoun and Tanimoto, 1991). The ability of fungi to reduce nitrite often occurs under anoxic (or less oxic) conditions and may be performed through the mitochondria. However, there is some suggestion that fungi have acquired the ability to reduce nitric oxide (NO) to nitrous oxide (N_2O) through horizontal gene transfer (Kamp et al., 2015). Forty-three percent of the over 380 soil fungal isolates tested have been observed to produce measurable amounts of N_2O in culture (Jirout, 2015; Mothapo et al., 2013; Takaya, 2002). These strains represent a diversity of lineages in the Ascomycota, Basidiomycota, and Zygomycota. Species that release N_2O also encompass a diversity of functional types, including EMF, plant pathogens, and saprotrophic fungi (Kamp et al., 2015). Studies using selective inhibition of fungi in soil have shown that fungi can contribute 10% to 89% of N_2O emissions from soil, with the highest contributions under moderately reducing to weakly oxidizing conditions, such as under intense cattle farming (Jirout, 2015).

4.6.1.4 Soil phosphorus cycling

Extracellular phosphatase production is common in soil fungi, indicating that many taxa are capable of releasing phosphate from organic P sources. For fungi, it appears that most phosphatases released for extracellular P acquisition have acidic pH optima, while those intended for intracellular reactions have optima at neutral to alkaline pH (Plassard et al., 2011). Inositol phosphates, produced mostly as P storage products by plants, account for half of soil organic P (Menezes-Blackburn et al., 2013; Plassard et al., 2011). The abundance of these compounds has more to do with their resistance to degradation than with their rate of production. Phytate (inositol hexaphosphate) is crystalline such that specific enzymes (phytases) are needed to hydrolyze the phosphate. Ascomycota are considered the best producers of phytase, but some Glomeromycota and Basidiomycota also produce them (Menezes-Blackburn et al., 2013; Plassard et al., 2011). Like all extracellular phosphatases, enzyme expression is induced by P deficiency.

Mineral phosphate is also important to fungi and plants. In alkaline soil calcium phosphates may be abundant, while weathered acid soils may have high concentrations of iron and aluminum phosphates. Some fungi, particularly ectomycorrhizal Basidiomycota, solubilize phosphate from mineral sources using low-molecular-weight organic acids, such as oxalate (Courty et al., 2010; Plassard et al., 2011).

4.6.1.5 Soil carbon cycling

Soil fungi release C from the biosphere through plant litter C and SOM decomposition and respiration of CO_2, but they also sequester CO_2 by producing recalcitrant C molecules that can be stored in soil (King, 2011) or by recycling nutrients to promote growth of other organisms, including plants, invertebrates, and animals. Fungi are responsible for 27% to 95% of CO_2 respiration from soils across ecosystems, averaging 60% (+/− 9−12%) of total respiration from aerobic soils based on selective inhibition (Joergensen and Wichern, 2008). Somewhat paradoxically, however, the more active fungi are in SOM decomposition, the more capacity they have for sequestering C in soil. Across soil types, fungal biomass contributes 68%

to 76% microbial C on average in soils, with the highest contribution in leaf litter layers (Joergensen and Wichern, 2008). Fungal necromass can decompose more slowly than bacterial necromass (Joergensen and Wichern, 2008; Strickland and Rousk, 2010), in part because fungal molecules like melanin (and other hydrophobic compounds) may decompose slowly (Fernandez and Kennedy, 2016). Hydrophobins play important roles in the hydrophobicity of spores and other cell surfaces in fungi (King, 2011), so they may also contribute to slow turnover of fungal biomass in soil.

Different species and functional groups of soil fungi will contribute to stable soil C stocks in different biomes. In boreal forests much of the C stabilized to decomposition (i.e., over 100 years old) can be attributed to mycelium of EMF (Clemmensen et al., 2013), which are the major fungal symbionts of the dominant vegetation of the region (Read et al., 2004). In systems dominated by AMF, such as temperate grasslands, savannah, and some tropical forests (Treseder and Cross, 2006), stable soil C in aggregates may develop from AMF-derived C compounds like glomalin, a heat-shock protein (Rillig and Steinberg, 2002; Rillig et al., 2010; Wright and Upadhyaya, 1996). Some functional traits related to C sequestration potential may vary more across taxa or lineage than across functional groups of fungi. For example, members of the Glomeraceae can produce less extraradical mycelium than taxa within the Gigasporaceae (Maherali and Klironomos, 2007). Glomalin production varies among AMF taxa (Treseder and Turner, 2007).

Fungi can also contribute to the release of other greenhouse gases, such as methane. Microbial production of methane in soils is mainly conducted by prokaryotes (methanogenic archaea), yet the presence of fungi can increase methane yields from methanogenic archaea (Beckmann et al., 2011). Fungi have also been reported to release methane during aerobic respiration (Lenhart et al., 2012) through the activity of mitochondria. These activities indicate that fungal metabolism in soil could be an important component of nutrient loss from ecosystems via greenhouse gas emissions beyond CO_2.

4.6.2 Bioremediation

The filamentous growth habit and enzymatic versatility of fungi can also be adapted to treat waste streams and remediate soils contaminated with organic pollutants or toxic metals (Harms et al., 2011; Strong and Claus, 2011). The most effective pollutant remediators belong to the phyla Ascomycota and Basidiomycota and include many EMF species. Most of this capacity is related to the production of a broad spectrum of extracellular laccases and peroxidases with varying redox potentials, pH optima, and substrate specificity that oxidatively modify or degrade aliphatic and aromatic pollutants, including halogenated compounds. In addition, some fungi produce nitroreductases and reductive dehalogenases that further contribute to the degradation of explosive residues and halogenated contaminants. Intracellularly, many fungi have cytochrome P450 oxidoreductases that can mitigate the toxicity of a broad range of compounds. The toxicity of metal contaminants can be mitigated by translocation and sequestration in chemically inaccessible complexes. Improving the bioremediation capabilities of EMF is of particular interest because the C supply from host plants may support fungal growth into contaminated hotspots and stimulate cometabolic reactions (Policelli et al., 2020).

4.7 Soil fungi and global change

Soil fungi are affected by global change — including changes in climate and other environmental conditions over the longer-term — but also feedback to some of these changes through their biogeochemical

cycling activities as pathogens, mutualists of other organisms, and free-living decomposers (saprotrophs). Fungi can be affected directly by a shift in their abiotic environment, or indirectly through climate change impacts on their biotic resource pools or on other members of the soil microbial community with which they interact. Any climate changes that alter resource availability will not only alter total fungal activity in the environment but also affect species composition due to varying resource preferences and competitive abilities among fungal species (Hawkes and Keitt, 2015). Fungal communities also change because of the dependence of fungal species on the presence and activity of others, e.g., through processes such as cross-feeding, cheating, and commensalism. One of the strongest indirect impacts of climate change on fungal communities could be through the effect on bacterial communities, which can act as population controllers of soil fungi (Romaní et al., 2006). These direct and indirect impacts of global change on soil fungal communities can often be related to the tolerance of specific species to new environmental conditions (e.g., response traits). The feedback of these community changes to ecosystem biogeochemistry is a result of the emergent biogeochemical functions of the new fungal community, which can be shaped by its most active members.

Experiments have applied global change manipulations to soils in the field and in the laboratory that are regularly applied at a level comparable to the effects that have been observed over the past decades or that are expected to occur over the next century. Most of these manipulative experiments apply changes almost immediately, simulating an event even more extreme than the most extreme weather documented in the last century. These manipulations often reveal where the boundaries of species niches and survivability lie in the face of future worst-case global change scenarios, rather than the response to gradual, chronic, longer-term global changes.

4.7.1 Climate change effects on soil fungi

One of the most dramatic and widespread human-induced changes in Earth's condition has been rising air temperatures due to increased greenhouse gas emissions. Climate warming affects many other aspects of climate, including precipitation regimes, surface humidity, and extreme temperature events, as well as the amount of snow and ice on land. These cascading effects of warming often have larger impacts on soil fungi than climate warming alone, yet fungi do not have a uniformly negative response to each of these individual and interacting factors.

4.7.1.1 Elevated CO_2

Elevated levels of atmospheric CO_2 have overall positive effects on growth and C acquisition of soil fungi, yet seem to be strongest for plant root associates. Recent meta-analyses of field-based elevated CO_2 experiments show that increasing atmospheric CO_2 (100−500 ppm above ambient) tends to increase both fungal biomass and richness of fungal communities (Zhou et al., 2020) in soil, although the trends are not significant. By contrast, elevated CO_2 consistently increases the biomass of mycorrhizal fungi in soil. Ectomycorrhizal fungi increase biomass by 19% and AMF increase biomass by 84% under elevated CO_2 (Garcia et al., 2008; Treseder, 2004). These results suggest that most CO_2 effects on fungi may be indirect, through changes in plant growth, and by inducing plant C allocation belowground into the rhizosphere where root symbionts presumably have first access to the supplied C. A recent meta-analysis documented that under elevated CO_2, ectomycorrhizal forests increase C in plant biomass but reduce C in soils. Alternatively, AM grasslands show an increase in C inputs, particularly to the more stable, difficult-to-decompose, mineral-associated organic matter (MAOM) (Terrer et al., 2021). The authors hypothesize

that these trends result from EMF more efficiently, leveraging plant C to mine soil for N, which accelerates soil C losses but increases photosynthetic capacity of the host plant. Variations in AMF responses to CO_2 enrichment have been observed to depend on both plant and fungal species, perhaps due to fundamentally different C exchange relationships between mutualistic mycorrhizal fungi and their hosts (Johnson et al., 2005).

4.7.1.2 Temperature changes

Fungal physiology is sensitive to temperature in a way that can impact growth and nutrient-cycling activity of individual fungi. Fungal metabolism increases with temperature as enzyme-catalyzed reaction rates increase (Allison et al., 2018; Gasch et al., 2000; Mohsenzadeh et al., 1998), up to an optimum temperature which, for most fungi, is just under 30°C (Kerry, 1990). Beyond this optimum, metabolic activity decreases due to biochemical phenomena such as protein denaturation (Boddy et al., 2014). Both yeasts and filamentous fungi can acclimate to warming by reducing C use efficiency (CUE), which increases the amount of CO_2 respired per unit C uptake (Allison et al., 2018; Bradford and Crowther, 2013). Recent studies have also revealed that fungi can evolve in response to repeat warming events, increasing respiration rates and reproduction (Romero-Olivares et al., 2015), and labile C consumption through beta-glucosidase activity (Finestone et al., 2022), while reducing the ability to decompose recalcitrant substrates in soil, such as aromatic organic matter (Anthony et al., 2021). These observations suggest that fungi could feed back to climate change by increasing soil respiration, at least initially; however, this impact could be offset by increased soil C storage if fungi fail to recover the ability to degrade older, more recalcitrant SOM.

At the community level, warming can decrease total fungal abundance in soil (DeAngelis et al., 2015; Morrison et al., 2019), yet the effects are often small, potentially because warming effects can vary based on initial soil temperature and moisture regimes. Warming tends to reduce the abundance of fungi and lichen in soils that are dry due to habitat type (Allison and Treseder, 2008; Ferrenberg et al., 2015) or long-term warming (DeAngelis et al., 2015). This is true especially when temperatures are reaching the limit for growth (Bárcenas-Moreno et al., 2009) but can also occur in dry habitats with small increases in temperature (e.g., +0.5°C). High summer temperatures are associated with low yields of *T. melanosporum* fruit bodies (i.e., truffles) and reduced soil moisture availability (Boddy et al., 2014). Based on these observations, one study projected decreased truffle yields across most of the Mediterranean Basin based on the expected increasing temperatures and decreasing precipitation in the coming decades (Büntgen et al., 2012). By contrast, warming can increase fungal abundance in soils that have sufficient moisture, such as tundra soils. A meta-analysis by Chen et al. (2015) found that warming significantly increased fungal abundances in tundra soils and histosols, rising 9.5% and 31% above control soils, respectively. Both soils experience low mean annual temperatures (−2.4°C for tundra and 3.1°C for histosols) and store large amounts of C for fungi that can be metabolized quickly to generate biomass. This indicates that fungi in historically cold soils show higher sensitivity to warming, which is possibly contingent on resource availability.

Warming also appears to select for certain lineages or groups of fungi, reshaping community composition and, potentially, its functional capabilities. Warming generally increases fungal diversity across ecosystems, with the greatest effects in forests (Zhou et al., 2020). In their global meta-analysis Gang et al. (Gang et al., 2019) found that biomass of saprotrophic fungi increased with experimental warming, while that of AMF (based on PLFA) showed no significant change. A recent publication in a

northern hardwood forest found an increase in brown rot fungi and plant pathogenic fungi in soil, a response that correlated with an increase in peroxidase activity in soil and a decrease in plant photosynthetic rate, respectively (Garcia et al., 2020). This shift in fungal functional groups was driven by changes in the relative abundance of dominant fungal genera; changes in AMF were associated with changes in the dominant genus *Glomus*. Changes in the relative abundance of brown rot fungi in soil with warming were driven by increases in the dominant brown rot genera *Cerinosterus* and *Amylocystis*. Another recent study in a different northern hardwood forest found that community composition of saprotrophic and AMF shifted with ~10 years of continuous soil warming (Anthony et al., 2021). Heated plots were hyperdominated by certain fungi (e.g., *Russula* species and *Mortierella gemmifera*), which showed a 10-fold increase in heated soil, while several other warming-sensitive taxa declined in heated plots.

Fungi that survive and thrive in warmed soils seem to reallocate resources away from biomass accumulation and towards maintenance of metabolic rate (i.e., rate-yield trade-off), potentially contributing to the often observed increase in soil C losses with warming. Recent -omics studies show that soil fungi under 10 years of continuous soil warming have greater rRNA gene copy numbers without a parallel increase in biomass production (Anthony et al., 2021) and express more genes for cell metabolic maintenance than for carbohydrate decomposition control soils (Romero-Olivares et al., 2019). Similarly, it was recently reported that under longer-term warming, eukaryotic genes coding for CAZymes are lower under long-term warming than control soils (Pold et al., 2016). The accumulation of examples where fungi trade off growth for metabolic rate under warming suggests that soil fungi invest in metabolic maintenance to ensure survival under the stress of increased temperatures (Bennett and Lenski, 2007). Under warming-only experiments, soil fungi appear to evolve to trade off growth for activity of oxidative enzymes that decompose more recalcitrant C substrates, such as those in soil humus (Pold et al., 2015, 2016). Interestingly, a recent study found that in heated soils, there was a lower negative cooccurrence and higher positive cooccurrence among fungal community members compared to unheated plots (Anthony et al., 2021), suggesting that warming leads to selection for soil fungi that either collaborate more than fungi under cooler temperatures or share similar environmental preferences.

Paradoxically, climate warming can generate colder soils in some regions, forcing soil fungi to contend with the stress of a wider range in annual soil temperatures. Rising air temperatures increase soil temperatures during the growing season but also decrease the fraction of precipitation occurring as snow in winter in northern latitudes, which decreases snowpack formation, increases snowmelt, and increases the frequency of soil freeze/thaw events (Campbell et al., 2010). This counterintuitive effect of climate change — warmer soils in the growing season but colder soils in winter — has unusual effects on soil fungi that we are just beginning to understand. Soil freeze/thaw cycles may exert particularly strong selection for taxa that can survive extreme fluctuations in temperature, moisture, and physical structure (Ostroumov and Siegert, 1996), as well as changes in plant C availability belowground due to root damage (Sanders-DeMott et al., 2018). Fungi originating from polar climates, for example, have developed mechanisms to survive extreme conditions, including higher concentrations of sugars, alcohols, lipids and fatty acids, or antifreeze proteins in their cells compared to their mesophilic relatives (Robinson, 2001). There is new evidence that soil fungi can rapidly evolve in response to freeze/thaw cycles, potentially shaping forest biogeochemical cycling over the longer term. Common-garden experiments with fungal cultures have shown that soil fungi evolved under the combined impact of soil warming during the growing season and increased frequency of freeze/thaw cycles in winter to have inherently higher cellulase activity but lower acid phosphatase activity than fungi that are evolving under warming alone (Finestone et al., 2022).

Repeated soil freeze/thaw cycles may exacerbate soil C losses under these conditions as severely stressed microbial cells are more easily decomposed in soils than unstressed cells (Crowther et al., 2015). By contrast, consistently lower acid phosphatase activities of soil communities, both initially (Sorensen et al., 2018) and over the longer term (Finestone et al., 2022), suggest a decoupling of C and P decomposition from SOM by fungi that would not occur with warming alone.

4.7.1.3 Precipitation changes

Changes in precipitation can affect fungal biomass and community composition through their effects on soil moisture. Fungi are generally considered more resistant to desiccation than bacteria (de Vries et al., 2012) but less resilient in the face of desiccation as they grow slower in soils compared to bacteria. Nevertheless, global meta-analyses have shown that soil fungal biomass can respond positively to precipitation (Blankinship et al., 2011) and reduced soil moisture (i.e., drought) can severely reduce the abundance of fungi in laboratory-based experiments (Waring and Hawkes, 2015). Both temperature and moisture impact fungal physiology. Under moisture stress, some fungi produce trehalose, which protects fungal cell membranes from desiccation, freezing, and heat shock (Treseder and Lennon, 2015). This trait is commonly found among fungi in the Arctic (Gunde-Cimerman et al., 2003), where water availability is low, as in xerotolerant lichenicolous fungi (Mittermeier et al., 2015). Interestingly, recent work shows that soil fungal diversity responds negatively to increased soil moisture, declining with increased precipitation (Zhou et al., 2020). In addition, fluctuating water potential of soil can cause turnover in fungal community composition (Kaisermann et al., 2015), indicating selection against many species by rainfall or drought. In soils that were experimentally dried and warmed in an Alaskan boreal forest, soil fungi orders known to house lichenized, corticioid, melanized, high-sporulating, endophytic, pathogenic, and xerotolerant fungi were significantly more abundant in the warmed treatment compared to controls (Romero-Olivares et al., 2019).

Similar to warming effects, moisture effects on soil fungi depend on initial environmental conditions. One study found that fungi in tropical soils that experience historical drought are more tolerant of future extreme drought conditions (Waring and Hawkes, 2015). By contrast, fungal communities in soils that are seasonally dry often have negative responses to precipitation, i.e., reductions in biodiversity and total biomass of fungi (Hawkes et al., 2011). These effects are thought to occur when the new environment falls outside the range of conditions previously experienced (Hawkes and Keitt, 2015), because taxa may have evolved a particular range of niche optima best suited to the initial environment. Modeling experiments show that a greater range of niche optima in diverse communities leads to a greater chance of these species showing resiliency to environmental change (Hawkes and Keitt, 2015). Fungal communities under fluctuating precipitation regimes may therefore have a diversity of taxa with specific physiologies (specialists) to tolerate a wider range of moisture conditions.

Certain functional guilds tolerate drought more than others. In contrast to saprotrophs, mycorrhizal fungi can receive water from the host tree through hydraulic lift (nocturnal water transfer from the tree to the associated mycorrhizal symbiont) (Querejeta et al., 2003) and transfer this water to their sporocarps (Lilleskov et al., 2009). In addition, root-associated fungal symbionts often respond to soil drying through increased root colonization (Rudgers et al., 2014; Talbot et al., 2008). This may be driven by increased nutrient limitation of plants due to low nutrient diffusion rates in dry soil or by the need for plants to reduce water losses through root systems (Finlay et al., 2008). AMF can down-regulate transcription of genes coding for aquaporins in plant roots, which may serve as a mechanism for both water-conservation and tolerance of salt-stress (Finlay et al., 2008). Fungal endophytes also confer drought tolerance to many plant species (Kivlin et al., 2013), with endophyte colonization of roots observed to increase under

experimental warming that inadvertently dries soils (Rudgers et al., 2014). By contrast, EMF showed greater variability in their response to drought (Talbot et al., 2008).

In addition to a functional guild effect, there appears to be a phylogenetic signal to fungal drought responses. Melanin may be an adaptive response to prevent cells from desiccation (Horikoshi et al., 2010). Generally, more derived fungi are more resilient to changes in water availability as they have drought-resistant biochemistry (e.g., melanized spores) that basal lineages lack (Treseder et al., 2014). Older phyla of soil fungi dominate soils of low-latitude, high-moisture ecosystems (Treseder et al., 2014), potentially due to their zoospore stage of development that requires high-moisture conditions. Indeed, basal lineages like the *Chytridiomycota* drop out in drought experiments in the field (Waring and Hawkes, 2015). These traits may constrain the phylogenetic distribution of taxa around the globe, such that ranges of entire fungal clades could be determined by precipitation regimes.

4.7.2 Other global change effects on soil fungi

Global changes beyond climate change — including pollution, fire frequency and severity, vegetation shifts, and species introductions — often have more pronounced immediate impacts on soil fungi and their function than climate changes per se.

4.7.2.1 Fire

Soil fungal abundances are reduced under fire (Holden et al., 2013) regardless of fire severity or habitat type; however, certain lineages recover quickly suggesting an adaptive response to the disturbance created by fire. *Pyronema* sp. and several EMF species are known to be fire-adapted, but their postfire recovery depends on the intensity and frequency of fire (Dove and Hart, 2017; Glassman et al., 2016). These EMF may be able to capitalize on the N (ammonium) that increases in soil after fire (Wan et al., 2001) and transfer it to their hosts (Claridge et al., 2009). Postfire fungal communities can establish from fire-adapted propagules present in the soil, dispersal from adjacent areas, or propagules present in less affected areas, such as deeper soil horizons (Policelli et al., 2020).

4.7.2.2 Plant community change

While soil fungal abundances are reduced under plant harvest disturbance, such as clearcutting forest (Jones et al., 2003) in tropical forests (Holden and Treseder, 2013), shifts in plant community composition can impact fungal abundance, community composition, and activity belowground. Nonnative plant invasions are increasing worldwide (Seebens et al., 2018) and can impact soil fungi through shifts in plant chemistry (often conserved at the family level), the plant microbiome, or other species- and community-specific plant traits. For example, invasions by EMF-associating trees are associated with coinvasion by their EMF symbionts such that nonnative EMF have been introduced to many countries in the Southern Hemisphere (Policelli et al., 2019; Pringle et al., 2009; Vellinga et al., 2009). In eastern North America invasion by garlic mustard shifts belowground fungal communities over the longer term (Lankau, 2011) due to the nonmycorrhizal status of garlic mustard and the production of secondary metabolites (glucosinolates) that can be toxic to fungi (Rodgers et al., 2008; Stinson et al., 2006). Garlic mustard appears to target mycorrhizal fungi, shifting the soil fungal community toward dominance by saprotrophic and plant pathogenic fungi (Anthony et al., 2017). In some cases plant invasion effects are exacerbated by other concomitant abiotic stressors. A recent study found that fungi dominant in warmed soils were

sensitive to invasion, whereas fungi dominant in control soils were less responsive (Anthony et al., 2020). The authors also found a positive correlation between fungal community response to invasion and mean annual temperature, over a temperature gradient of 4°C, providing additional support for the idea that warming increases the invasibility of soil fungal communities.

4.7.2.3 Pollution

Organic and inorganic toxins can impact community composition of soil fungi. One major pollutant of interest has been N, with an increase in availability to soil fungi (and other soil organisms) since the mid-20th century, primarily through the application of N-based fertilizer to agricultural lands (Galloway et al., 2008). Of all the global change factors applied to soil, N appears to be the most consistent in its impact on fungi. Across ecosystems, N reduces fungal biomass and diversity in soil (Zhou et al., 2020). The strength of the effect can vary, with strongest impacts on historically low-N soil and weakest impacts on historically polluted, high-N ground (Cox et al., 2010). One hypothesis is that N effects can largely be explained by pH shifts, because increased ammonium deposition can promote the process of nitrification by bacteria, which decreases soil pH (Averill and Waring, 2018). While many soil fungi thrive at low pH (<5), it has been observed that N addition tends to acidify soil across experiments. This reduction in pH is correlated with a reduction in soil fungal diversity (Zhou et al., 2020). Similar to other global change factors, N addition to soil selects for specific taxa, particularly more nitrophilic taxa that show lower levels of hyphal production and N-acquiring enzyme activities (i.e., extracellular peptidases and proteases; van der Linde et al., 2018). These types of shifts in fungal communities, combined with overall declines in fungal abundance, under N fertilization may be associated with decreases in decomposition and soil C accumulation (Frey et al., 2014).

Other soil contaminants can have strong effects on fungal communities belowground. While organic contaminants can be degraded, metals need to be physically removed or immobilized (Policelli et al., 2020). Some EMF species can be negatively affected by high levels of heavy metals, reducing the number of sporocarps produced as heavy metal concentrations in soil increase (Rühling and Söderström, 1990). However, several common EMF species — including *Amanita*, *Paxillus*, *Pisolithus*, *Scleroderma*, *Suillus*, and *Rhizopogon* — accumulate high metal concentrations in the extramatrical mycelium (Khan et al., 2000). In these cases EMF can reduce metal toxicity to their host plants (Wilkins, 1991).

Tropospheric ozone (O_3), which absorbs UV radiation, has negative chemical effects on organisms, including fungi. Ozone tends to reduce conidia germination, increase rates of hyphae death, and promote production of reactive oxygen species (ROS) that damage fungal tissues (Savi and Scussel, 2014). Total fungal biomass (Bao et al., 2015) and fungal/bacterial ratios in soil can decline under elevated O_3 (Li et al., 2015). However, effects of O_3 on fungal communities in the field can be delayed (Cotton et al., 2015), potentially when O_3 affects fungi indirectly through damaging plants. For example, colonization of tomato by the AMF *Glomus fasciculatum* was reduced after only nine weeks of exposure to elevated O_3 (McCool and Menge, 1984) and microbial communities of meadow mesocosms were unaffected by elevated O_3 after 2 months, showing response after 2 years (Kanerva et al., 2008).

4.7.3 Effects of multiple interacting global changes

Global change is caused by various factors (Aber et al., 2001). Nevertheless, the impact of multiple global change stressors on microbial communities is seldom tested — only 20% of studies have examined more than one factor, and only 1% have examined more than two factors (Rillig et al., 2019). One interesting

study on soil fungi in laboratory microcosms examined the effects of an increasing number of global change factors in combination, including temperature, drought, resource availability, chemical toxicants, and microplastics (Rillig et al., 2019). When exposed to multiple factors at once, soil fungal communities showed a decrease in diversity and an increase in similarity (regardless of the global change factor) and were primarily composed of generalist stress-tolerant fungi while losing Basidiomycota. These soils experienced water repellency at an increased level relative to single-factor global changes and far greater than the effect predicted from a purely additive response of each change. Soils with multiple global change manipulations also exhibited severely reduced CO_2 flux. However, the type of global change factor was a better predictor of soil fungal function and community composition than the number of manipulations alone. Long-term soil warming in combination with nonnative plant invasion significantly increased relative abundances of saprotrophic fungi and fungal genes encoding for hydrolytic enzymes (Anthony et al., 2020), suggesting that the stress of multiple interacting global changes on certain fungal functions, such as plant C decomposition, can be remediated by sufficient C substrate supply.

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Supplemental material

S4.1 A primer on fungal systematics

While kingdoms were long recognized as the most encompassing categories in the taxonomic hierarchy of life, the landmark work of Karl Woese, showing that two groups of prokaryotes (microbial organisms without nuclei) were equally divergent from one another as from eukaryotes (single-celled and

multicellular organisms with nuclei and additional organelles), led to the establishment of domain as the deepest division (Woese and Fox 1977). There are three domains: the prokaryotic domains of archaea and bacteria, and the *Eukaryota*. Thus the formal Linnaean hierarchy proceeds as follows: domain, kingdom, phylum (= division for animalia), class, order, family, genus, and species. However, this limited set of rankings does not allow recognition of all important groupings; hence informal rankings above (e.g., "superkingdom") and below (e.g., "subphylum") these formal levels are often used in systematics. Exemplar taxonomic classifications downloaded from the NCBI taxonomy pages (www.ncbi.nlm.nih.gov/taxonomy) for two soil-dwelling fungi are shown in Table S4.1. The ranks at the top are the broadest and proceed through successively narrower groupings until reaching the species. Notice that several unranked taxonomic groupings have been used for these fungi due to insufficient resolution provided by the traditional Linnaean levels alone.

Bacteria and archaea are subject to the International Code of Nomenclature of Bacteria (ICNB; www.the-icsp.org/), while formal taxonomy in the kingdom fungi falls under the International Code of Nomenclature (ICN) for algae, fungi, and plants (www.iapt-taxon.org/nomen/main.php). Molecular, physiological, and ultrastructural data are increasingly useful in efforts to ascertain the boundaries of species and higher taxonomic ranks, but technical descriptions of the morphology of reproductive structures are still required to name (or rename) a fungal taxon. In most cases these descriptions relate to structures produced in the sexual phase of the fungal lifecycle in which meiosis occurs (see Section II),

TABLE S4.1 Two Examples of Formal Fungal Classification

Taxonomic Rank	Classification for *Tuber melanosporum*	Classification for *Agaricus bisporus*
Superkingdom	*Eukaryota*	*Eukaryota*
Unranked	*Opisthokonta*	*Opisthokonta*
Kingdom	Fungi (=*Eumycota*)	Fungi (=*Eumycota*)
Subkingdom	*Dikarya*	*Dikarya*
Phylum	*Ascomycota*	*Basidiomycota*
Unranked	*Saccharomyceta*	
Subphylum	*Pezizomycotina*	*Agaricomycotina*
Class	*Pezizomycetes*	*Agaricomycetes*
Subclass		*Agaricomycetidae*
Order	*Pezizales*	*Agaricales*
Family	*Tuberaceae*	*Agaricaceae*
Genus	*Tuber*	*Agaricus*
Species	*Tuber melanosporum*	*Agaricus bisporus*
Common name	Perigord truffle	Button mushroom

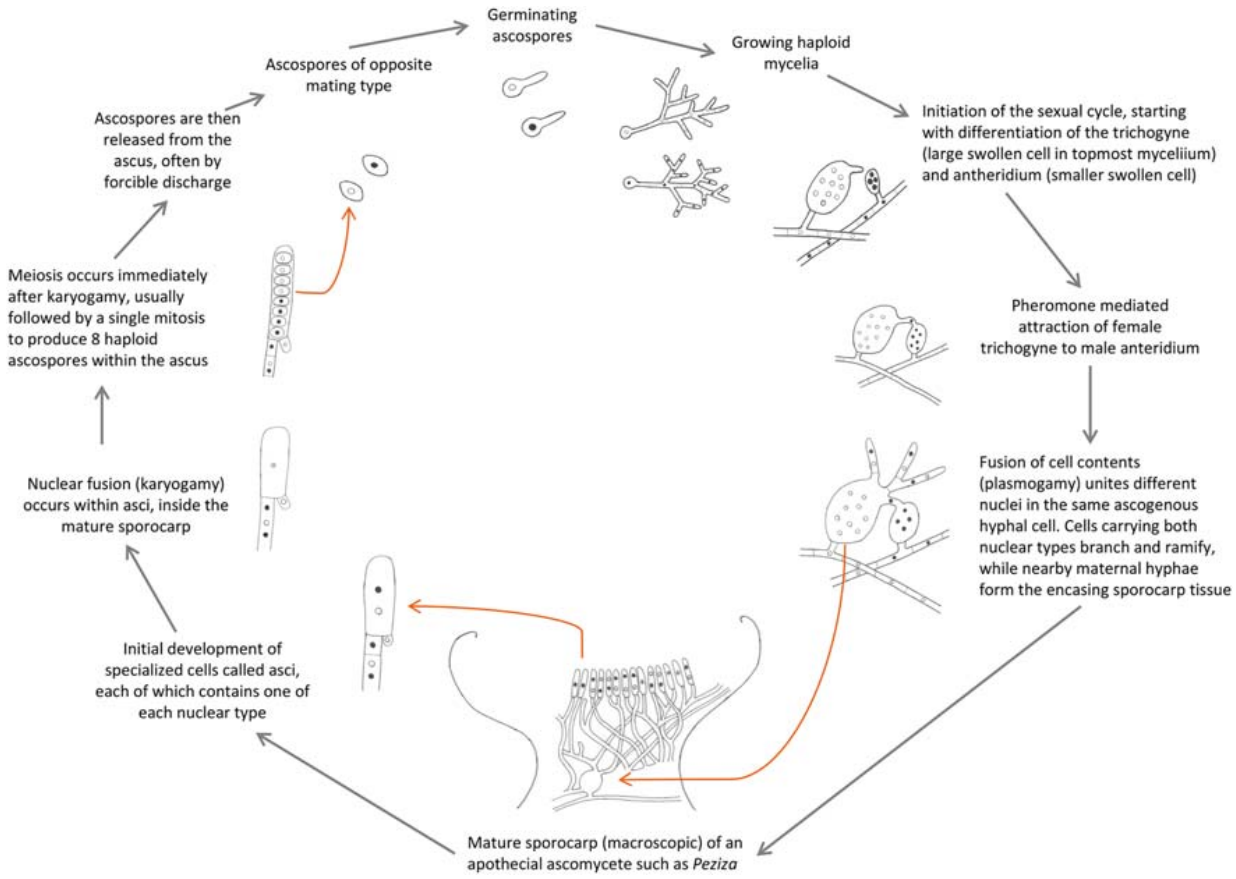

FIGURE S4.1 A typical life cycle for a fungus in the *Ascomycota*.

such as mushrooms of the *Agaricomycetes* or morels of the *Ascomycota*. Species names based on a sexual sporocarp are called teleomorphs. If a fungus produces asexual reproductive structures (e.g., conidia and conidiophores, Fig. S4.1) and no sexual structures are known for this species, the Latin species description may be based upon these asexual forms; in this case the species name is called the anamorph. Many fungi have been named based on sexual sporocarps collected in the wild without any accompanying pure culture isolate. Many other fungi have been named based on isolates brought into pure culture. Often these isolates produce asexual reproductive forms readily in culture but rarely or never produce sexual structures (e.g., molds of the *Ascomycota*). As a consequence of these two strategies for naming new fungi, a number of species had both a teleomorphic and an anamorphic name attached to them. The connections between teleomorphs and anamorphs are slowly being discovered over time as more sterile fungi are induced to produce sexual structures in culture and molecular diagnostics are brought to bear. Furthermore, the sexual reproductive structures are historically the basis upon which fungi are placed in higher taxonomic ranks, e.g., class *Agaricomycetes* or phylum *Basidiomycota*. Hence, the asexual fungi known only by their anamorphs were traditionally placed in an artificial class, the *Deuteromycetes*. It turns out that most members of the *Deuteromycetes* belong to the *Ascomycota* in terms of their shared evolutionary history; however, there are some anamorphic names spread among the other fungal phyla

(e.g., *Rhizoctonia*, a widespread soil fungus in the *Basidiomycota*). These aspects of fungal systematics have caused great confusion for biologists from other disciplines seeking to use or interpret fungal names. Recently, a movement under the banner "one fungus, one name" was successful in their lobbying to abolish the two-name, anamorph-teleomorph system (Taylor, 2011). Every fungus will now have only one formally recognized name. In addition, nonphylogenetic classifications, such as Deuteromycetes, are no longer recognized. These changes will help make fungal systematics more digestible for ecologists, soil scientists, evolutionary biologists, and others. However, some familiarity with these outdated terms may be helpful, since they will be widely encountered in the literature. Some additional terms that are fading from use are hyphomycete, which is a synonym for Deuteromycetes, and microfungi, which refers to fungi that only produce very small sexual or asexual reproductive structures, i.e., filamentous soil fungi other than mushroom-forming *Basidiomycota*. Microfungi are mostly members of the *Ascomycota*; the term encompasses common soil molds, such as *Trichoderma*, *Aspergillus*, and *Penicillium*.

S4.2 Fungal life cycles

In general, fungi spend the majority of their life cycle in a haploid state. Haploid spores produced by meiosis or mitosis disperse. If conditions are conducive, the spore will then germinate and a hypha will begin to grow (unless the fungus is a yeast). A fungal body or thallus develops through progressive growth and branching of this original hypha (Figs. 4.5 and S4.1). In many fungi asexual reproduction by mitotic production of conidia or other mitospores can occur at any time during growth of the mycelium (usually triggered by specific growth conditions). For sexual reproduction to occur, karyogamy to generate a transient diploid stage must take place. Most fungi are heterothallic, meaning they cannot mate with themselves but must instead mate with a different individual of an opposing mating type. When a haploid hypha encounters a hypha or conidium of another individual of the same species, but different mating type, it may engage in a series of steps leading to sexual reproduction. In brief, the cytoplasms fuse by anastomosis — a process called plasmogamy. This places the two different nuclei within the same cell (see Fig. S4.1). Next, a complex developmental process unfolds, often involving synchronized mitotic replication of the two nuclei within the developing sporocarp. Finally, the two different nuclei fuse (karyogamy) within a specialized reproductive cell (e.g., the ascus in *Ascomycota* and the basidium in *Basidiomycota*), followed by meiosis and production of haploid spores. There are exceptions to immediate meiosis; for example, the zygospore in members of the former *Zygomycota* remains diploid until this resting spore is triggered to germinate. The exception to dominance of the haploid stage occurs in the *Basidiomycota*, in which mycelia are more likely to be dikaryotic. Here, the difference is that compatible hyphae of opposing mating types anastomose early in the life cycle, rather than late in the life cycle immediately before sexual reproduction. However, as with other fungi, these nuclei do not fuse until immediately before meiosis. Hence cells of the vegetative hyphae of most *Basidiomycota* contain pairs of unfused haploid nuclei from the two parents, a situation that is termed “dikaryotic” (Fig. S4.1). Many basidiomycete fungi have bumps (actually a small hyphal loop) over the septa that separate cells called clamp connections. Clamp connections maintain exactly one nucleus of each type per cell. A third exception to the life cycle patterns described above concerns so-called homothallic species. These are species that do not require nuclei to have opposing mating types and so are able to mate with themselves and undergo sexual reproduction.

S4.3 Glossary of terms

Term	Definition
-ales	Ending for taxa at the ordinal level.
-cetes	Ending for taxa at the class level.
-eae	Ending for taxa at the familial level.
-ota	Ending for taxa at the phylum level.
-otina	Ending for taxa at the subphylum level.
anamorph	The asexual phase of the life cycle of a fungus. Can also refer to the Latin name for a fungal species based on a description of the asexual stage; e.g., anamorph = *Fusarium moniliforme*, teleomorph = *Gibberella fujikuroi*.
anastomosis	The fusion of two fungal hyphae to form a unified cytoplasm. Occurs often within the mycelium of a single fungal individual; can sometimes occur among different genotypes within a species.
ascocarp	A conglomeration of asci and surrounding tissue forming the sexual reproductive structure of fungi in the *Ascomycota*.
ascospore	A single-celled haploid spore produced by meiosis within an ascus of a fungus in the *Ascomycota*.
ascus (singular), asci (plural)	A specialized sack-shaped reproductive cell of fungi in the *Ascomycota* in which meiosis occurs and ascospores are produced.
basal fungal lineages = early-diverging fungal lineages	Refers to major evolutionary lineages at the class to phylum level toward the base of the fungal tree of life. Most of these lineages were once placed within either the *Chytridiomycota* or the *Zygomycota* but now stand on their own due to the polyphyly of the aforementioned phyla. Relationships among these lineages remain to be resolved.
basidiocarp	A conglomeration of basidia and surrounding tissue forming the sexual reproductive structure of fungi in the *Ascomycota*.
basidiospore	A single-celled haploid spore produced by meiosis within a basidium of a fungus in the *Basidiomycota*.
basidium (singular), basidia (plural)	A specialized club-shaped reproductive cell of fungi in the *Basidiomycota* in which meiosis occurs and basidiospores are produced.
black yeasts = microcolonial yeasts = meristematic yeasts	A polyphyletic assemblage
brown rot	A type of wood decay in which lignin is only partially depolymerized and its C is not consumed. The cellulose and hemicellulose are attacked using hydrogen peroxide and the cellulosic C is mostly consumed. This type of decay leaves behind blocky brown material. Carried out by a spectrum of fungi in the *Basidiomycota*.

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Term	Definition
clamp connection	A hump-shaped outgrowth forming a channel from one cell to the next, bypassing a septum; found only in some species of *Basidiomycota*.
codenitrification	A process in which additional amines react with intermediates in normal denitrification, resulting in N-N compounds with each N atom coming from a different source. This process can alter the dynamics of N turnover and loss from soil systems but is poorly understood or quantified.
conidium (singular), conidia (plural)	A single-celled dispersal unit produced mitotically (i.e., not a sexual product).
cryptic species	A situation in which multiple phylogenetic or biological species occur within a single morphologically demarcated species.
Deuteromycete (= Fungi Imperfecti)	An outdated taxonomic term to encompass asexual, anamorphic fungal species of uncertain evolutionary affiliation.
dikaryon	A fungal individual that contains two types of haploid nuclei, one from each parent.
dimorphic	A fungus that is able to switch between a single-celled yeast growth form and a multicellular filamentous growth form.
dissimilatory denitrification	The reduction of nitrate or nitrite to gaseous forms (N_2O, N_2), resulting in loss of N back to the atmosphere. Nitrate is used in place of oxygen as the electron acceptor to carry out respiration.
DSE	Dark septate endophyte; melanized fungi growing inside of roots, may also extend beyond the root and may be mildly beneficial or mildly harmful to the plant.
extracellular enzyme	An enzyme that is targeted for export across the cell membrane and cell wall so that it can function outside the cytoplasm; often involved in degradation of organic polymers, such as starch, cellulose, proteins, or lignin.
glomalin	A complex glycoprotein compound found in soil thought to be secreted by arbuscular mycorrhizal fungi. Glomalin contributes to aggregate formation and soil stabilization.
glycosidase = glycosyl hydrolase	A hydrolytic enzyme that contributes to depolymerization of sugar polymers, such as cellulose and chitin. This is a very large group containing many families of enzymes; in fungi many are secreted (i.e., extracellular). This class includes xylanases, chitinases, beta-glucosidases, cellobiohydrolases, and endo-glucanases, among others.
heterothallic	A species of fungus that requires the joining of nuclei from different mating types for sexual reproduction.

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Term	Definition
homothallic	A species of fungus identical nuclei (i.e., not from different mating types) can fuse and undergo sexual reproduction.
hypha (singular), hyphae (plural)	An individual filament or thread formed of tube-like cells attached end to end; hyphae are the basic building blocks of all multicellular fungal structures, such as mushrooms.
hyphomycete (= soil microfungi)	An umbrella term for asexual filamentous fungi in soils, particularly ascomycetous molds.
karyogamy	The fusion of two different haploid nuclei from compatible mating types to form the diploid stage; followed immediately by meiosis in the vast majority of fungi.
laccase	Copper-containing oxidative enzymes that may function inside the cytoplasm as part of various developmental processes or may be secreted to attack polyphenolics, such as lignin.
mold (= mould)	An evolutionarily heterogeneous group of fast-growing fungi that rapidly produce masses of asexual spores soon after colonizing a high-energy substrate, such as bread, fruit, or dung.
monophyletic	A group that encompasses all taxa descended from a single common ancestor; synonymous with natural evolutionary group and clade.
mycelium	A constellation of interconnected hyphae belonging to a single fungal individual.
mycoparasite	A fungus that preys upon (i.e., infects) other living fungi.
phosphatase	A hydrolytic enzyme that cleaves phosphoric acid monoesters to release phosphate. Secreted by many fungi to aid in P scavenging.
phytase	A type of phosphatase that cleaves phosphate groups from phytic acid.
plasmogamy	The fusion of cytoplasmic material by the joining of the cell walls of two compatible fungal individuals; usually precedes karyogamy and meiosis.
polyphyletic	An assemblage of taxa that does not include all descendants from a single common ancestor; rather, taxa derived from different common ancestors are placed in the same grouping, such as yeasts.
psychrophile	Cold-loving organisms that can grow below 5°C with a maximum growth rate below 20°C.
psychrotolerant	Cold-tolerant organisms that can grow below 5°C with a maximum growth rate above 20°C.

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Term	Definition
rhizomorph	A developmentally complex tube structure formed through the coordinated growth or a large number of hyphae. Similar to cords but includes a cap that resembles a root cap rather than a diffuse mycelial front. Most common in *Basidiomycota*.
rust	Common name for plant pathogens of the order *Pucciniales*, *Basidiomycota*. Rusts typically have complex life cycles that may include five different spore stages and alternation between two unrelated host species. The common name comes from the typical orange-brown color of the telial spore stage.
sclerotium (singular), sclerotia (plural)	A conglomeration of thick-walled, resistant cells produced by mitosis.
septum (singular), septa (plural)	Cell wall material laid down within a hypha to divide the filament into discrete cells; has a septal pore in the middle that controls movement of structures, such as nuclei from cell to cell.
smut	Common name for a class of fungi in the *Basidiomycota*, most of which are plant pathogens. The life cycles of smuts are not as complex as those of rusts, with completion of the life cycle usually requiring only one host. The common name comes from the gray-black, moldy teliospore stage produced within the flowering tissue of hosts, such as maize (corn).
soft rot	A type of wood decay in which lignin is only partially depolymerized and its C is not consumed. Hyphae secrete cellulase leading to microcavities in the wood. Carried out primarily by members of the *Ascomycota*.
sporocarp	A conglomeration of fungal cells in which meiosis occurs and from which spores are released, e.g., a mushroom. Analogous to a plant flower.
strand = cord	An aggregation of hyphae into a larger-diameter, tube-like transport structure. Similar to rhizomorphs but with a diffuse mycelial front. Most common in *Basidiomycota*.
teleomorph	The sexual phase of the life cycle of a fungus. Can also refer to the Latin name for a fungal species based on a description of the sexual stage, e.g., teleomorph = *Talaromyces spiculisporus*, anamorph = *Penicillium lehmanii*.
thermophile	Heat-loving organisms that can grow at 45–60°C.
truffle	Species of fungi that produce macroscopic sexual sporocarps belowground. Divided into the true truffles (e.g., *Tuber*) that belong to the *Ascomycota* and the false truffles that belong to other phyla, especially the *Basidiomycota*.

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Term	Definition
white rot	A type of wood decay in which lignin is completely broken down and its C is consumed. This type of decay leaves behind a stringy/powdery white residue primarily composed of crystalline cellulose. Carried out by a limited number of species in the *Basidiomycota*.
yeast	Any fungus with cells that separate after budding (e.g., *Saccharomyces*) or splitting (e.g., *Schizosaccharomyces*); note that the term does not describe a phylogenetically united group of fungi.
zygospore	A single-celled diploid resting spore resulting from fusion of compatible nuclei of opposite mating types that is produced within a Zygosporangium; characteristic of fungi that were once placed in the *Zygomycota*. Meiosis occurs when the zygospore is triggered to germinate.

See also:
www.mushroomexpert.com/glossary.html
botit.botany.wisc.edu/toms_fungi/

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