The Soil Fungi

2 authors:

D. Lee Taylor
University of New Mexico
174 PUBLICATIONS **9,912** CITATIONS

Robert Sinsabaugh
University of New Mexico
245 PUBLICATIONS **19,113** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project Evolutionary Ecology of the Alder-Frankia Symbiosis View project

Project Extracellular enzyme activities (EEA) in several lakes within the McMurdo Dry Valleys, Antarctica View project

Chapter 4

The Soil Fungi: Occurrence, Phylogeny, and Ecology

D. Lee Taylor and Robert L. Sinsabaugh

Department of Biology, University of New Mexico, Albuquerque, NM, USA

Chapter Contents

I INTRODUCTION

There is now considerable circumstantial evidence that true fungi (Kingdom Eumycota) were instrumental in both the colonization of land by the ancestors of terrestrial plants (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 major evolutionary and ecological transitions illustrate why fungi play such important roles 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 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 profound influences 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 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. Supplementary online files provide definitions of some key terms, a primer on fungal systematics, and an example of the fungal life cycle.

II PHYLOGENY

A Definition of Eumycota

The *Fungi* (capitalized italic when used as a formal Linnean taxon) are recognized as a Kingdom (see online Supplemental Material Section I at http://booksite.elsevier.com/9780124159556 for a refresher on the taxonomic hierarchy of life). Although sometimes loosely referred to as *microbes*, fungi are eukaryotes and most are multicellular. A superkingdom of eukaryotes that includes fungi and animals is the *Opisthokonta*. The evolutionary lines that constitute the true fungi, or *Eumycota*, are all descended from a single common ancestor (i.e., constitute a monophyletic clade) within the *Opistokonta* (James et al., 2006; Steenkamp et al., 2006). There is now strong evidence that a small group of protists within the *Opisthokonta*, called the nuclearids, are the closest sister group to the *Eumycota* (Liu et al., 2009). Interestingly, nuclearids are phagotrophs (organisms lacking cell walls that engulf relatively large food items via phagocytosis), suggesting an important transition to osmotrophy (organisms that can only ingest small molecules that can move through pores in the cell wall) early in fungal evolution. Various molecular-clock estimates place the origin of the *Eumycota* from 600 million to > 1 billion years before the present (Berbee and Taylor, 1993; Heckman et al., 2001), but a robust estimate will require more reliable fossil calibration points (Berbee and Taylor, 2010).

A number of shared, derived traits ("synapomorphies" in phylogenetic terms) are characteristic of fungi (James et al., 2006; Stajich et al., 2009). Fungi depend on organic compounds for C, energy, and electrons, 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 a few parasitic lineages 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 today exist only in several early diverging lineages. 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).

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 at http://booksite.elsevier.com/9780124159556 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* (Fig. 4.1). In the more ancient fungal groups, the filaments in which the nuclei are housed do not contain cross-walls (septa), whereas in other groups, septa divide hyphal filaments into distinct cells. Although not representing any particular taxon, the features shown in
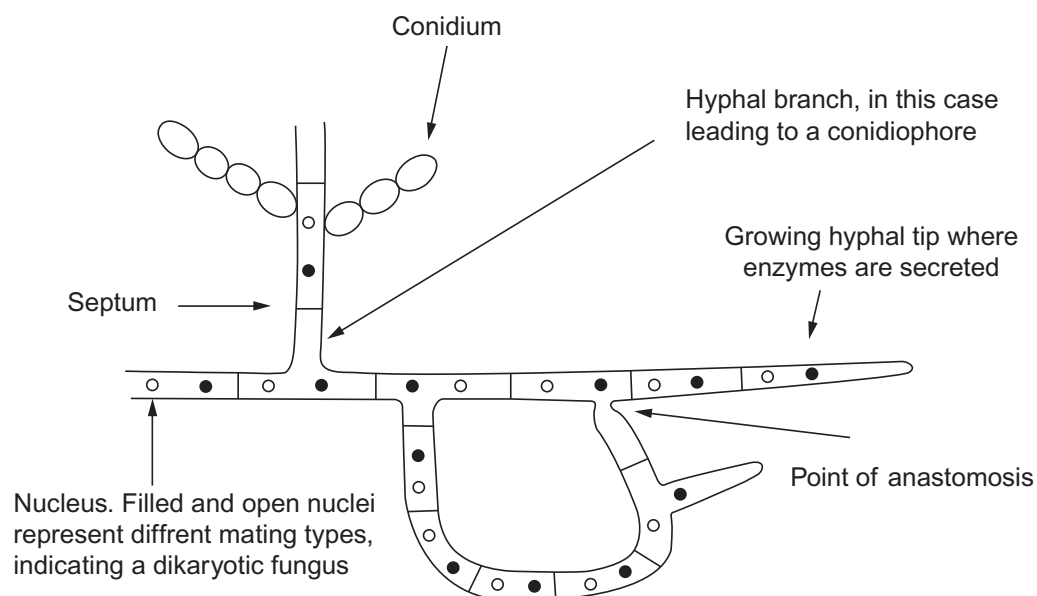
FIG. 4.1   Filamentous fungal growth form. Diagram depicts a mycelium growing from left to right.

Fig. 4.1 are characteristic of the *Dikarya*. Cross walls or septa separate individual cells (numbers of nuclei are usually variable in *Ascomycota*, but are more often fixed in *Basidiomycota*). As a mycelium grows, hyphae branch at regulated intervals in response to external and internal signals. 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 two most recently evolved phyla, the *Ascomycota* and *Basidiomycota*, nuclear division and apportionment to the cells comprising the hyphae is tightly regulated, whereas in groups without septa, nuclei flow freely through the entire mycelium (e.g., in phylum *Glomeromycota*).

Although the evolutionary cohesion of the *Eumycota* is widely accepted, some uncertainties and surprises with respect to membership have attracted attention in the last decade. There is mounting evidence that the *Microsporidia*, a lineage of highly specialized and reduced (unicellular, lacking mitochondria and chitin) animal parasites, fall within the *Eumycota* (Capella-Gutiérrez et al., 2012). The animal parasite *Pneumocystis* is now known to be a divergent fungus, probably falling within the *Ascomycota* (Edman et al., 1988; James et al., 2006). Molecular phylogenies confirm the long-held view that the *Oomycota*, which includes the filamentous plant pathogens *Pythium* and *Phytophthora*, belong to the superkingdom Stramenopiles (heterokonts), while the slime molds belong to the superkingdom *Amoebozoa*, both outside the *Opisthokonta*.

B   Present Phylogeny

Molecular systematics of the *Eumycota* are in the midst of radical revision (James et al., 2006; Liu et al., 2009; Floudas et al., 2012; see the special issue of Mycologia, 2006, volume 98, issue 6). About 20 years ago, a system of five fungal phyla achieved universal recognition based, in part, on initial rDNA phylogenies (Bruns et al., 1992). The five phyla were the *Chytridiomycota* (water molds), *Zygomycota* (bread molds), *Glomeromycota* (arbuscular mycorrhizal fungi), *Ascomycota* (cup fungi), and *Basidiomycota* (club fungi). Later multilocus, molecular analyses suggest that neither the *Zygomycota* nor the *Chytridiomycota* are monophyletic groups (O'Donnell et al., 2001). Several new phyla, subphyla, and unranked higher taxa have been proposed (Hibbett et al., 2007), including the *Blastocladiomycota* and *Neocalimastigomycota* (formerly members of *Chytridiomycota*), and the *Entomophthoromycotina*, *Kickxellomycotina*, *Mucoromycotina*, and *Zoopagomycotina* (formerly members of *Zygomycota*; Fig. 4.2). Even extremely data-rich phylogenomic analyses have yet to resolve with certainty relationships at the base of the fungal tree (Liu et al., 2009), so we can expect further rearrangements and optimization of high-order taxonomy in the years to come. See Fig. S4.1 and Table S4.1 in online Supplemental Material at http://booksite.elsevier.com/9780124159556 for help
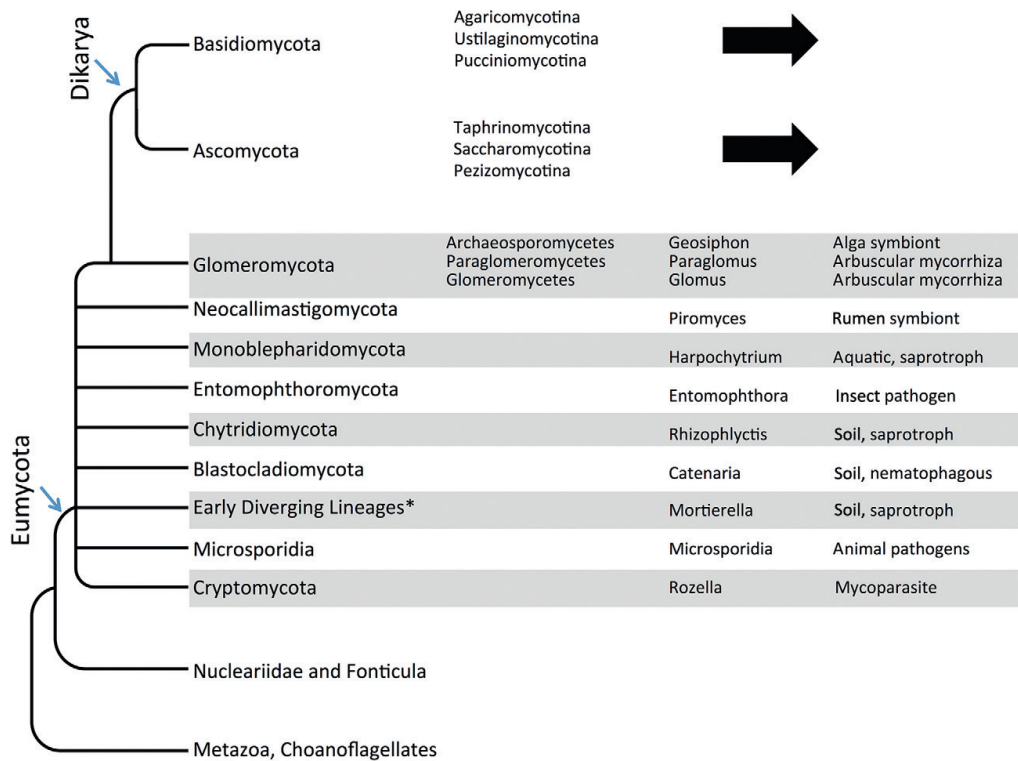
FIG. 4.2 Overview of fungal phylogeny. Currently recognized phyla and subphyla in the Kingdom Fungi. The *Metazoa* are an outgroup within the *Opisthokonta*, whereas the *Nucleariidae* are thought to be the closest relatives of the Fungi. Exemplar taxa and their ecological roles are provided on the right. *The Early Diverging Lineages include the *Kickxellomycotina*, *Mortierellomycotina*, *Mucoromycotina*, *Nephridiophagidae*, *Olpidiaceae*, and *Zoopagomycotina*. Information for phyla *Basidiomycota* and *Ascomyota* is provided in Figs. 4.3 and 4.4.

in making sense of some confusing terminology in fungal systematics. Good sources for the most up-to-date taxonomic hierarchy for the fungi include Index Fungorum (www.indexfungorum.org/), the Tree of Life (tolweb.org/Fungi/ 2377), and NCBI (www.ncbi.nlm.nih.gov/taxonomy).

Current understandings of the major evolutionary lines of fungi, along with a few exemplar taxa and their trophic niches, are presented in Figs. 4.2–4.4 (see also Hibbett et al., 2007; Stajich et al., 2009). Major evolutionary groups in soil include the chytrids, or the "water molds" generally viewed as aquatic organisms, many of which degrade pollen or algal biomass. However, as discussed in Section III.A, several orders, including the *Spizellomycetales* and *Rhizophlyctidales*, are found in diverse soils, taking on dominant roles in extreme, high elevations (Freeman et al., 2009). Phylogenetically diverse, filamentous species scattered among the early diverging fungal lineages are widespread in soils. Some are rapidly growing saprotrophs with a preference for labile C compounds; these include *Mortierella* (placed either within *Mortierellomycotina* or *Mucuromycotina*) and the bread molds *Rhizopus* and *Mucor* (*Mucuromycotina*). The phylum *Glomeromycota* encompasses all fungi that form arbuscular mycorrhizae, as well as the enigmatic, algal symbiont

Basidiomycota

Agaricomycotina	Agaricomycetes	Agaricus	Litter decomposer
		Coprinus	Litter decomposer
		Russula	Ectomycorrhizal
		Tomentella	Ectomycorrhizal
		Lacarria	Ectomycorrhizal
		Phanerochaete	White rot wood decay
		Postia	Brown rot wood decay
	Dacrymycetes	Dacrymyces	Brown rot wood decay
	Tremellomycetes	Cryptococcus	Soil yeast
Ustilaginomycotina	Exobasidiomycetes	Exobasidium	Plant pathogen
	Ustilaginomycetes	Ustilago	Smut, plant pathogen
Pucciniomycotina	Agaricostilbomycetes	Mycogloea	Yeast, mycoparasite
		Agaricostilbum	Yeast, plant pathogen
	Atractiellomycetes	Atractiella	
	Cystobasidiomycetes	Sporobolomyces	Yeast, phyllosphere
	Microbotryomycetes	Microbotryum	Plant pathogen
	Pucciniomycetes	Platygloea	Mycoparasite
		Melampsora	Rust, plant pathogen
		Septobasidium	Insect parasite

FIG. 4.3 Currently recognized subphyla and classes within the phylum *Basidiomycota*. 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.

Ascomycota

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

FIG. 4.4 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.

Geosiphon (Gehrig et al., 1996). There is some evidence that the *Glomeromycota* is basal to the *Dikarya*, but this is not yet certain. The subkingdom *Dikarya* is comprised of the most recent and derived "crown" phyla *Ascomycota* and *Basidiomycota*. 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) The *Taphrinomycotina*, which has recently gained support as monophyletic (Schoch et al., 2009), encompasses the fission yeasts (*Schizosaccharomyces*); the animal pathogen *Pneumocystis*; the unusual dimorphic (see definition in Section III of online Supplemental Material at http://booksite.elsevier.com/9780124159556) plant pathogen *Taphrina*; the root-associated, sporocarp-forming, filamentous genus *Neolecta*; and the newly erected class of filamentous soil fungi, the *Archaeorhizomyces* (see Section II. C). (2) The *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. (3) The third subphylum is the *Pezizomycotina*, which accounts for the greatest phylogenetic, species, and functional diversity within the *Ascomycota*. The vast majority of lichen-forming fungi fall within this lineage (there are a few basidiomycete lichens), as do a few ectomycorrhizal (EMF) taxa, all dark-septate endophyes (DSE), essentially all ericoid mycorrhizal (ERM) species, and a spectrum of pathogens and saprotrophs.

The diverse phylum *Basidiomycota* is also divided into three well-supported subphyla. The basal subphylum is the *Pucciniomycotina*, which includes all rust fungi, an economically important group of plant pathogens, as well as some yeasts that are common in soil, but relatively little 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 also frequently recovered from soils) and *Arcticomyces* (a cold-soil yeast). This subphylum appears to be more closely related to the *Agaricomycotina* than to the rusts (James et al., 2006). 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.

C Novel Lineages

Another important impetus for major taxonomic changes has been the discovery of novel lineages from environmental samples. A landmark paper described seasonal changes in soil fungal communities at the Niwot Ridge alpine research site in Colorado (Schadt et al., 2003). A considerable fraction of the community was comprised of taxa that appeared to fall within the *Ascomycota*, but were difficult to assign to any known class. Subsequent studies demonstrated that

these fungi occur in a wide range of habitats and geographic regions (Porter et al., 2008). Discovery of an isolate belonging to this lineage allowed the description of a new class of *Ascomycota*, the *Archaeorhizomycetes* (Rosling et al., 2011). Another deeply divergent lineage for which there is only one cultured representative, but evidence for wide occurrence in aquatic and soil habitats, is the *Cryptomycota* (Jones et al., 2011). This early-diverging lineage includes the mycoparasitic genus *Rozella*. The roles of other members of this group, which may comprise a significant fraction of the diversity of the *Eumycota*, remain to be elucidated. Additional deeply diverging lineages, some of which are weakly placed within the euchytrids, have been recovered in marine habitats (Nagano et al., 2010; Richards et al., 2012) and soils (Glass et al., 2013). It is likely that additional deep lineages will be added to the fungal tree in the coming years. Some of these lineages, such as *Archaeorhizomycetes*, likely play important roles in soils.

III OCCURRENCE

A Extremophiles, Distribution Across the Planet

Fungi are present and prominent in all soils. 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, including deep sea hydrothermal vents and sediments, subglacial sediments, ancient permafrost, sea ice, hot and cold deserts, salterns, and soils of the Dry Valleys of Antarctica (Cantrell et al., 2011). Surprisingly, fungi may be the most abundant eukaryotic members of some deep-sea sediments (Edgcomb et al., 2011). 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 by other vectors (Pearce et al., 2009; Bridge and Spooner, 2012). Phylogenetically diverse yeasts dominate the isolates obtained from many of these 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 (Connell et al., 2006; Bridge and Spooner, 2012; Buzzini et al., 2012). 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). Species of *Cryptococcus* are also very abundant in boreal and temperate soils. Ascomycotan yeasts, such as *Pichia*, *Debaromyces*, *Candida*, *Metschnikowia*, and *Aureobasidium pullulans* are also found in extremely cold and/or saline habitats (Gunde-Cimerman et al., 2003; Zalar et al., 2008; Cantrell and Baez-Félix, 2010; Butinar et al., 2011; Cantrell et al., 2011).

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); one isolate was reported to be metabolically active down to -35°C (Panikov and Sizova, 2007). A cold-soil dwelling member of this genus, *Geomyces destructans*, is the causal agent of white-nose syndrome, an epidemic that threatens numerous bat species in North America (Blehert et al., 2009; Lorch et al., 2011). 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, extreme drought tolerance, or can grow at pHs down to 0 (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). 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 earlier), 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). Humans encourage their growth through various composting methods. Mesophilic taxa initiate decomposition, causing the initial temperature to rise, but then cease to grow as temperatures surpass 40-45°C, at which point thermotolerant and thermophilic taxa germinate, grow, and drive the temperature of the heap toward their maximum growth temperatures of 50-60°C.

In the case of black yeasts, thermophiles, and lichens, there is no question of their activity and adaptation to extremes because 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 (Waldrop et al., 2008). It seems likely that some of the other extremophiles described, such as yeasts isolated from glacial habitats, are also "indigenous" taxa that are adapted to these extreme environments because they display tolerance to extreme conditions in the laboratory (Onofri et al., 2000; Gunde-Cimerman et al., 2003; Selbmann et al., 2005; Arenz and Blanchette, 2011; Butinar et al., 2011; Buzzini et al., 2012). Some cosmopolitan taxa detected in extreme environments, such as species of *Penicillium* and *Aspergillus*, may be present only as inactive spores.

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 (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).

To summarize, although no fungi match the extreme thermotolerance of *Archaea* and *Bacteria* from hot springs and hydrothermal vents, thermophilic fungi are among the most heat-tolerant eukaryotes. Furthermore, certain species equal or surpass any prokaryotes in cold tolerance and also occupy extreme habitats with respect to salt, desiccation, hydrostatic pressure, and pH. However, the most luxuriant fungal growth can be seen in moist, aerobic soils with large amounts of complex organic C.

B Biomass, Growth, and Abundance

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

Fungal biomass varies widely within and across biomes in relation to litter composition, root density, and nutrient availability. Fungi may comprise up to 20% of the mass of decomposing plant litter. In biomes dominated by EMF plants, extraradical mycelium 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), other 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).

Fungal mycelia generally grow radially as fractal networks in soil, wood, and litter (Fig. 4.1; Bolton and Boddy, 1993). Fungi alter hyphal development in response to environmental conditions to minimize cost-to-benefit ratios in terms of C or nutrient capture versus expenditure on growth. Very fine "feeder hyphae" are elaborated in resource-rich patches, whereas 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 (Boddy, 1999; Agerer, 2001; Donnelly et al., 2004).

IV BIODIVERSITY

A Estimates of Species Richness

The true diversity of the Eumycota is uncertain and controversial. There are roughly 100,000 described taxa (Kirk et al., 2008), which is thought to include many synonyms due to both duplicate descriptions and anamorph-teleomorph pairs (i.e., the tradition in mycology of giving separate names to asexual and sexual forms). New species are being described at a rapid rate, limited primarily by a dearth of fungal taxonomists rather than a lack of fungi in need of description (Blackwell, 2011; Hawksworth, 2012). A variety of approaches has been used to estimate how many species of fungi 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, 2002). This estimate was criticized as highly exaggerated by May (1991). A recent mathematical approach that used rates of species and higher taxonomic rank accumulation over time, as well as relationships between numbers of species and higher ranks from well-studied groups, to estimate numbers of species in less-well-studied groups yielded an estimate of 660,000 species of fungi (Mora et al., 2011). This is considered too low by many mycologists (Bass and Richards, 2011). Several recent molecular surveys of fungi in environmental samples have applied the fungus-to-plant ratio method and yielded estimates of 5-6 million species (O'Brien et al., 2005; Taylor et al., 2013); estimates based on thorough censuses from single plant species have yielded estimates as high as 10 million (Cannon, 1997). The fungus-to-plant ratio

estimates from molecular surveys are more likely to be within the correct order of magnitude, but will require further refinement as we learn more about how fungal specificity varies across biomes (Arnold et al., 2000; Berndt, 2012) and how plant and fungal geographic distributions scale to one another (Schmit et al., 2005; Schmit and Mueller, 2007; Tedersoo et al., 2009a, 2012).

B   Fungal Dispersal and Biogeography

Fungal biogeography and assembly of local communities are determined, in part, by dispersal. Fungi in soil 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, and so on; see Fig. 4.1 and Sections II and III in the online Supplemental Material at http://booksite. elsevier.com/9780124159556) 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 cannonball-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 as well as by many plant pathogenic fungi. 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 fungi colonizing individual pine "islands" in the midst of a "sea" of nonectomycorrhizal 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, many EMF taxa are shared between North America and Europe, suggesting that over longer timescales, rare dispersal events can eventually lead to very large geographic ranges.

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 (James et al., 1999; Taylor et al., 2006; Geml et al., 2008; Carlsen et al., 2011; Grubisha et al., 2012). 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 fungi 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 the arrival of these pathogens again underlines that cross-continental jumps are rare.

V   FUNGAL COMMUNITIES

A   Definition

In mainstream ecology, the term *community* refers to the set of sympatric, metabolically active organisms that interact or can potentially interact. We know 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. Fungi in soil vary at least four orders of magnitude in size. Single-celled yeasts may be 3-10 μm in diameter. In contrast, a single mycelial individual of the white rot, root pathogen *Armillaria mellea*, spanned 15 ha, with a predicted mass greater than 10,000 kg (Smith et al., 1992). In practice, we often define fungal communities in soil at plot scales similar to those often used in plant ecology. How well this scale agrees with "fungal community" as a theoretical construct remains to be determined. In some areas of mycology, more 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.

Fungal communities in soil can be extremely species rich and patchy at small spatial scales. For example, high throughput clone sequencing of fungi in cores collected approximately one m apart in a boreal forest site revealed in excess of 300 fungal taxa in 0.25 g soil (Fig. 4.5; M. G. Booth & D. L. Taylor, unpublished). Moreover, the dominant taxa in the first core were quite distinct from the dominant taxa in the second core (Fig. 4.6).

B   Abiotic Drivers

A variety of studies demonstrate that species composition within a sample, plot, or site can be influenced by an array of abiotic factors. Communities of EMF fungi from Northern Hemisphere temperate and boreal forests have been studied most extensively. A series of papers report sharp differences in fungal communities as a function of soil horizon (Taylor and Bruns, 1999; Dickie et al., 2002; Lindahl et al., 2006; Taylor et al., 2013). Soil pH, moisture content, and
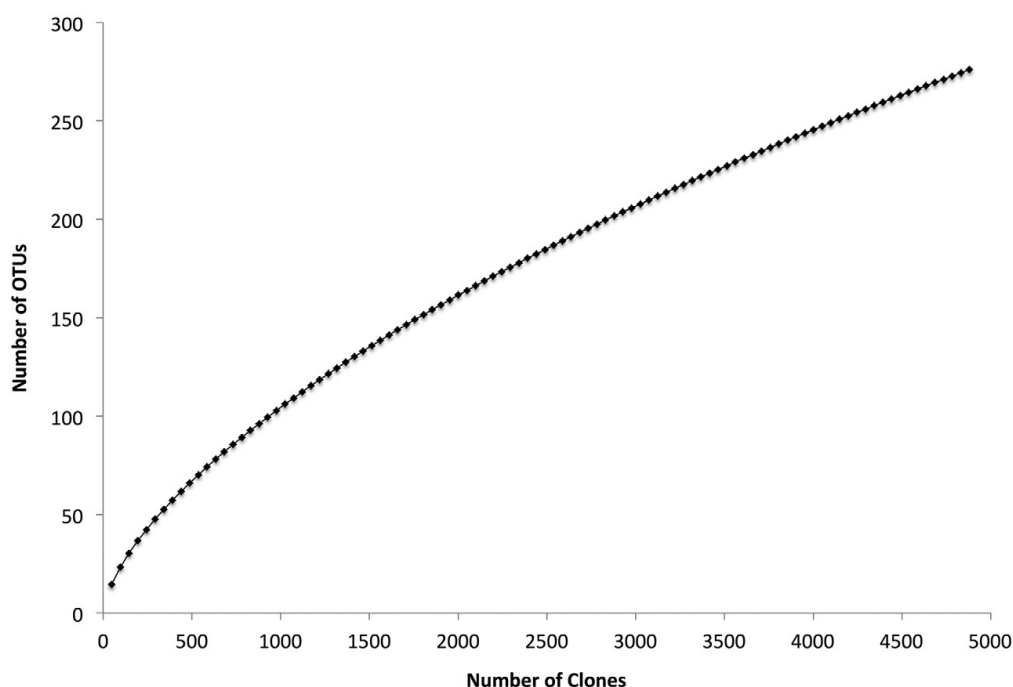
FIG. 4.5   Rarefaction curve for fungi in 0.25 g of soil. Rarefaction analysis showing the increase in number of observed OTUs (Mau Tau) with number of clone sequences resampled in Estimate 7.0 in a single ¼ g soil sample. Over 250 OTUs were recovered when ITS sequences were grouped at 97% identity; the rarefaction curve was not saturated, and the Chao I estimator was much higher, suggesting that many additional species were present. *M. G. Booth and D. L. Taylor, unpublished data.*
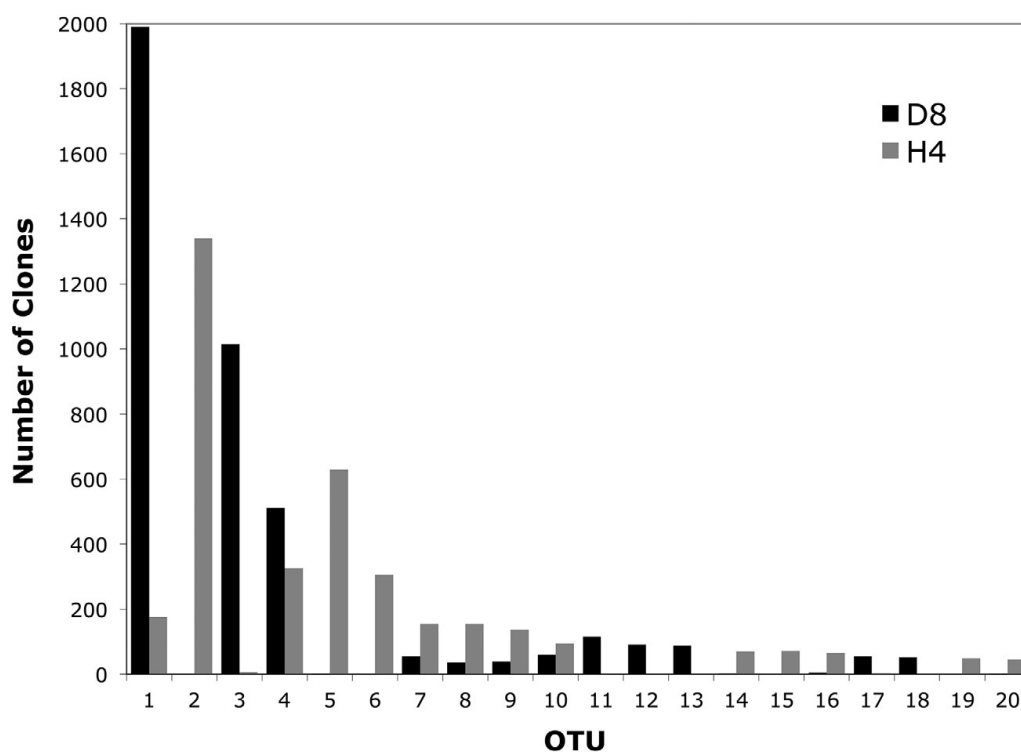
FIG. 4.6   Rank abundances of dominant fungi in adjacent cores. Numbers of clones (*Y* axis) belonging to dominant OTUs (*X* axis) documented in fungal ITS clone libraries generated from boreal forest soil samples collected ∼1 m apart. Most of the dominant operational taxonomic units (OTUs, roughly equivalent to species) occur preferentially or exclusively in only one of the two samples. *M. G. Booth and D. L. Taylor, unpublished data.*

nutrient levels (particularly N) are also correlated with community composition in soil (Taylor et al., 2000; Toljander et al., 2006; Cox et al., 2010), 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).

Even within guilds, fungal species vary considerably in their niche preferences, presumably due to competition and niche-partitioning over evolutionary time. 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) 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. 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 ERM fungi under acidic conditions (Smith and Read, 2008). Several recent papers have suggested that soil K and Ca levels are predictive of the composition of ectomycorrhizal (ECM) communities associated with *Alnus* species (Tedersoo et al., 2009b; Roy et al., 2013). In tandem, there is a great deal of interest in "bioweathering," the contribution of fungi and bacteria to the dissolution of minerals in rock (Taylor et al., 2009; see Chapter 16).

There is increasing evidence that soil fungal communities are influenced by climatic conditions on both geographic and temporal scales. Circumstantial evidence suggests that soil temperatures contribute to differences in fungal communities across latitude. For example, soil fungal communities were more strongly correlated with temperature than with latitude across the five bioclimactic subzones of the Arctic (I. Timling, D. A. Walker, & D. L. Taylor, unpublished). 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 much of belowground activity likely occurs at other times. For example, the aforementioned studies of midlatitude, high-elevation alpine sites at Niwot Ridge in Colorado showed that microbial (including fungal) biomass peaked in late winter under the snowpack (Schadt et al., 2003; Lipson and Schmidt, 2004). 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). Even in cold-dominated biomes, fungal communities in soil have been shown to shift predictably across seasons (Schadt et al., 2003; Taylor et al., 2010).

Seasonal climate variation could be considered a form of predictable disturbance. 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. EMF 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 (Stendell et al., 1999; Dahlberg et al., 2001; Smith et al., 2004). 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; Visser, 1995; Treseder et al., 2004; Taylor et al., 2010). The direct effects of fire versus the indirect effects mediated by vegetation changes are difficult to disentangle.

Disruption in the form of agricultural tillage has been shown to impact fungal communities (Helgason et al., 1998). It is likely that smaller-scale disturbances influence fungal communities, but fewer studies are available. In the Arctic, fungal communities in paired vegetated versus cryoturbated microsites ("frostboils") are distinct (I. Timling, D. A. Walker, & D. L. Taylor, unpublished), but again, effects of host plants versus direct effects of cryoturbation on fungi are uncertain.

C   Biotic Drivers

Most fungi consume living or dead plant material for their primary energy source, and a large fraction of fungi display some degree of specialization toward their living or dead plant substrates. Thus, plant community composition plays a dominant role in determining which fungi are present at a site. Historically, only the plant-to-fungus direction of influence has 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 have major impacts on plant community composition as well (van der Heijden et al., 1998a, b; Reynolds et al., 2003; Bever et al., 2010). Specific plant pathogens can dramatically reduce or eliminate particular host species, again altering plant community composition. Plant-soil feedbacks (Bever, 1994; Klironomos, 2002), often involving the buildup of host-specific pathogens in soil, can alter coexistence and competitive dynamics within plant communities.

It has been well documented that EMF fungi range from genus, 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 ECM fungi, but host-specialist fungi can be important players, for example in the reciprocally specific associations of alder (Miller et al., 1992). Although the several hundred species of AM fungi found in > 200,000 vascular plant species have been assumed to have low specificity, a more complicated picture is

emerging (see Chapter 11). Much like mycorrhizal fungi, decomposer fungi display a range of specialization toward their substrates. The genetic, physiological or ecological bases 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.

Competition among fungal species 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). Such "priority effects" have also been shown to occur for 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. 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 come from statistical analyses of patterns of co-occurrence and avoidance. In general, cooperating/synergistic species should co-occur more often than expected by chance, whereas antagonistic species should co-occur 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 co-occurrence 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 (Cooke and Rayner, 1984).

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 some fungal guilds 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 where no mature trees occur (e.g., "old-fields"), whereas 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 buildup 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). 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 wood itself, agree that *Basidiomycota*-dominated communities follow 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. Yet 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* often 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).

VI FUNCTIONS

A Introduction

Fungi mediate nearly every aspect of organic matter production, decomposition, and sequestration, with concomitant roles in the mineralization and cycling of N and P. Filamentous fungi support plant production through mycorrhizal associations that enhance the acquisition of water and nutrients (Chapter 11). Aboveground, ubiquitous fungal endophytes can confer 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 and, in arid and polar regions, the formation of biotic crusts that also mediate soil atmosphere exchanges, water infiltration, and stabilize surface

soils against erosion (Pointing and Belnap, 2012). As agents of organic matter decomposition, fungi mediate the creation and protection of soil organic matter (SOM), as well as its mineralization. Surface litter becomes SOM when the residue of humic material and microbial products reaches a threshold composition of 70% acid insoluble material (Berg and McClaugherty, 2003), at which point the cost of further degradation is not energetically favorable without additional inputs of more labile material (Moorhead et al., 2013). However, surface litter decomposition may not be the principal pathway of SOM formation in many ecosystems. Recent papers provide evidence that the growth and turnover of roots and their associated fungi is responsible for most soil C sequestration in forest soils (Wilson et al., 2009; Clemmensen et al., 2013).

Filamentous fungi promote macroaggregate formation by binding soil particles with hypha and producing 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).

B Nutrient Cycling

The most commonly measured characteristics of soil fungi are their biomass, elemental stoichiometry, growth rates and efficiencies, and activities of their extracellular enzymes (Sinsabaugh and Follstad Shah, 2011; Sinsabaugh et al., 2013; Wallander et al., 2013). These parameters define the size of fungal C and nutrient pools and rates of fungal-mediated biogeochemical reactions. Fungi must generate small, molecular mass, growth substrates by enzymatically degrading complex organic matter outside the cell. However, enzymes released to the environment by intent or as a result of cell lysis are beyond the control of that organism (Fig. 4.1). As a result, a substantial fraction of the enzymatic potential of soils is a legacy of enzymes that are spatially and temporally displaced from their origins (Burns et al., 2013). In some cases, particularly for oxidative enzymes, these enzymes catalyze degradation and condensation reactions secondary to their original function (Sinsabaugh, 2010).

1 Enzymes/Decomposition

It is becoming increasingly difficult to generalize about the enzymatic capabilities of higher fungal taxonomic categories. Most hydrolytic and oxidative capabilities are broadly distributed across taxonomic groups. As studies of fungal genomics advance, there is increasing emphasis on the expression and ecological purposes of these capabilities. Fungi are considered the principal degraders of plant cell wall material, especially during the early stages of decomposition when their filamentous growth form and their capacity to secrete a variety of glycosidases and oxidases allows them to ramify through the cellular structure of plant litter. The capacity to at least partially 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, which is facilitated by the synergistic expression of a variety of other polysaccharide-degrading enzymes. The ecological capacity of *Glomeromycota* to degrade cellulose and other cell wall polysaccharides appears more limited, but recent studies indicate greater capacity than once thought (Talbot et al., 2008; Kowalchuk, 2012).

Production of laccases and other phenol oxidases are also widely distributed among *Ascomycota*, *Basidiomycota*, and *Glomeromycota* (Baldrian, 2006). In some organisms, mainly saprotrophs, these enzymes function primarily in the degradation of lignin and other secondary compounds in plant cell walls, often indirectly through the production of 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). Mycorrhizal fungi appear to use the same strategy to mine N and P (Pritsch and Garbaye, 2011). 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. But once released into the environment through biomass turnover, these activities also contribute to the oxidative potential of soils, which catalyzes nonspecific condensation and degradation reactions that contribute to both the creation and loss of SOM (Burns et al., 2013).

Peroxidases, which have 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 diffusable 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).

The taxonomic distribution of extracellular enzymatic capacity is the basis for the traditional soft rot, brown rot, white rot ecological classification of decomposer fungi on the basis of the appearance of rotting wood. In enzymatic terms, these classifications refer to organisms that primarily attack cell wall polysaccharides, those that deploy lower redox potential laccases in addition to glycosidases, and those that deploy high redox potential laccase-mediated, or peroxidase systems capable of effectively depolymerizing lignin. Interestingly, recent phylogenomic studies suggest that the common ancestor of the *Agaricomycotina* (basidiomycete class containing all ECM, brown rot and white rot fungi) was capable of white rot. The evolution of brown rot appears to have occurred independently several times, in part through the loss of Mn-peroxidase genes.

ECM fungi were once thought to have little saprotrophic capability compared to wood and litter decay fungi. Some recent genomic data support this perspective (Martin et al., 2008). But there is growing evidence that at least some ECM fungi

can attack a wide range of organic polymers (Read and Perez-Moreno, 2003; Talbot et al., 2008; Pritsch and Garbaye, 2011), but these activities are likely under different environmental controls than those to which pure decomposer fungi respond. The key issue is that decomposer fungi are usually C-limited, while ECM fungi produce degradative enzymes to access and mobilize N and P (Talbot et al., 2008). Thus the cost-benefit ratios that drive the adaptive evolution of enzyme activities differ for ECM versus decomposer fungi.

2 Nitrogen

The potential to use chitin as an N source is widespread among fungi, largely because fungal cell walls include chitin and related compounds (Geisseler et al., 2010). In some studies, chitinase activity is used as an indicator of fungal biomass and metabolism. 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 much of their N from degradation of peptides (Hofmockel et al., 2010; Sinsabaugh and Follstad Shah, 2011). In contrast to their role in P acquisition, the role of AM fungi in N acquisition is poorly resolved (Veresoglou et al., 2012). The enzymatic capacity of ECM fungi to mine N from SOM has received more attention (Talbot et al., 2008; Pritsch and Garbaye, 2011). The role of fungi in the N cycle was once considered primarily assimilatory. That is, fungi assimilated inorganic N and N-containing organic molecules to support the production of new fungal biomass and supply plant hosts. Recent studies have shown that dissimilatory denitrification and codenitrification pathways are widespread among *Ascomycota* and are responsible for a large fraction of nitrous oxide efflux, especially in arid soils (Spott et al., 2011; Shoun et al., 2012).

Anthropogenic N deposition has been shown to decrease fungal diversity, biomass, and respiration (Knorr et al., 2005; Treseder, 2008). 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 (Sinsabaugh et al., 2002; Gallo et al., 2004). Nitrogen deposition also alters the economics of plant-fungal symbioses, which may also contribute to observed decreases in fungal biomass and activity. Another contributing factor may be the two- to three-fold difference in biomass C-to-N ratio of fungi (10-20) and bacteria (5-10), which might promote bacterial growth relative to fungi (Van Der Heijden et al., 2008; Strickland and Rousk, 2010) when N availability is high. A recent review noted a positive relationship between fungal dominance as indicated by qPCR and soil C-to-N ratios across biomes (Fierer et al., 2009).

3 Phosphorus

All soil microorganisms produce extracellular phosphatases. Consequently, phosphatase activities in soil are generally greater than any other measured enzymatic activity, making it difficult to resolve the contributions of individual

taxa to P mineralization. For fungi at least, it appears that most phosphatases released for extracellular P acquisition have acidic pH optima, whereas 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 (Plassard et al., 2011; Menezes-Blackburn et al., 2013). The abundance of these compounds has more to do with their recalcitrance to degradation than their rate of production. Phytate (inositol hexaphosphate) is crystalline; specific enzymes (phytases) are needed to hydrolyze the phosphate. *Ascomycota* are considered the best producers of phytase, but some *Glomeromycota* and *Basidomycota* also produce them (Plassard et al., 2011; Menezes-Blackburn et al., 2013). 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, whereas weathered acid soils may have high concentrations of iron and aluminum phosphates. Some fungi, particularly EMF *Basidiomycota*, solubilize phosphate from mineral sources using low molecular weight organic acids, such as oxalate (Courty et al., 2010; Plassard et al., 2011).

C 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*. 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 also produce nitroreductases and reductive dehalogenases that further contribute to the degradation of explosive residues and halogenated contaminants. Intracellularly, many fungi also 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. In natural systems, improving the bioremediation capabilities of ECM fungi is of particular interest because the C supply from host plants may support fungal growth into contaminated hotspots and stimulate cometabolic reactions.

VII FUNGUS-LIKE ORGANISMS AND SOIL FOOD WEBS

Fungi are linked to numerous other organisms in complex soil food webs. The spectrum of organisms that feed on or parasitize fungi in soil is extremely diverse, spanning viruses, bacteria, protists, insects, small mammals, and other fauna. Similarly, the spectrum of living organisms that are subject to attack by

fungi is equally diverse. Fungi that are placed into one guild designation often engage in other sorts of interactions, and the extent of these phenomena is poorly known. As with fungal linkages as mycorrhizae and decomposers, other food web linkages range from nonspecific to highly specific. Some of the most widespread trophic linkages of soil fungi appear to be related to N demand imparted by the high C:N ratios of plant materials that comprise the main energy source. A number of wood decay fungi obtain supplemental N by feeding on nematodes (Thorn and Barron, 1984; Barron, 2003). Some of these fungi are also able to prey on bacteria (Barron, 1988). Some of the best-known nematode-trapping fungi actively produce enzymes to degrade cellulose or lignocellulose, leading Barron (2003) to suggest that these fungi are primarily decomposers that have particularly dramatic adaptations for N supplementation. Mycorrhizal fungi also engage in various interactions that may seem unexpected given their guild designation. For example, some EMF fungi can supplement N by attacking living animals. such as collembolans (small wingless insects known as springtails; Klironomos and Hart, 2001). ECM *Tuber* species sometimes cause "brulés" or bare patches of surrounding herbaceous vegetation, perhaps by attacking these understory plants (Plattner and Hall, 1995). There are also numerous mycoparasitic fungi, some of which are closely related to EMF taxa. One example is *Gomphidius*, a member of the *Boletales* (*Basidiomycota*) that parasitizes an EMF genus of *Boletales*, *Suillus* (Olsson et al., 2000).

Fungal hyphae in soil are usually abundantly festooned with both extracellular and intracellular bacteria (Bonfante and Anca, 2009; Hoffman and Arnold, 2010). These bacterial communities are not the same as bacterial communities in bulk soil, and certain isolates have been shown to exert specific influences on the fungi. For example, "mycorrhizal helper bacteria" can strongly promote the formation of ectomycorrhizae by some ECM fungi (Garbaye, 1994; Frey-Klett et al., 2007). Bacteria on hyphal surfaces presumably benefit from fungal exudates just as rhizosphere bacteria benefit from root exudates. It is likely that many complex interactions between fungi, bacteria, and other organisms have important impacts on fungal function in soil, although only a few examples have been well studied to date.

Numerous insects are adapted to the consumption of fungal hyphae, either as mycelium in soil (e.g., mites and collembolans) or in the concentrated tissue of sporocarps (e.g., fungus gnats). Several studies have manipulated the presence of these grazers and have usually found strong impacts on competitive dominance among the fungi (Klironomos et al., 1992). In addition to insects, a diverse assemblage of soil protists, nematodes, earthworms, and small mammals consume fungi, often in a fungal species-specific fashion (Hanski, 1989; Jørgensen et al., 2005).

Although fungi and bacteria drive the bulk of primary litter decomposition in most soils, other small eukaryotes make important direct and indirect contributions to soil nutrient cycling. Several nonfungal protists act as primary

decomposers through the release of extracellular enzymes, just as do fungi (Adl and Gupta, 2006). Among these are various slime molds (*Amoebozoa*), which can be abundant in soil, and contribute to degradation of wood, bark, and dung. Similarly, some soil stramenopiles (Oomycetes), particularly in the *Saprolegniales*, participate in deconstruction of leaves, wood, dung, and animal remains.

However, nonfungal eukaryotes probably exert stronger effects through their roles as secondary decomposers, i.e., by consuming and reprocessing materials contained within the biomass of fungal and bacterial primary decomposers. Diverse protists grow in soil as naked amoebae, consuming bacteria, yeasts, and other small resources through either phagocytosis or osmotrophy. Important taxa of secondary saprotrophs include *Amoebozoa* (e.g., *Acanthamoebidae Flabellinea, Tubullinea, Mastigamoebidae, Eumycetozoa), Euglenozoa (Euglenida, Kinetoplastea), Heterobolosea (Acrasidae, Gruberellidae, Vahlkampfiidae), Cercozoa (Cercomonadidae, Silicofilosea),* and the *Ciliata* (Adl and Gupta, 2006). Species in these groups typically display marked substrate preferences and other fine-tuning to their soil environments (e.g., moisture gradients, seasonality). Naked amoebae are the most abundant protistan grazers in soil. Densities are greatest in the rhizosphere, up to 30 times greater than that of bulk soil (Bonkowski, 2004). Because the C-to-N ratio of protozoans is similar to that of their prey, grazing increases N mineralization rates, thereby promoting plant growth. Grazing intensity varies among taxa in relation to cell wall composition, cell size, and chemical signals. Gram-negative proteobacteria are more susceptible than G^+ bacteria. Grazing of mycorrhizal fungi reduces hyphal lengths and can alter fine root architecture. Last, soil protists also contribute to primary production. Specifically, the Chlorophyta and Charophyceae (green algae) can be abundant in the uppermost layers of soil, where sufficient light penetrates to allow photosynthesis (Hoffmann, 1989). Soil food webs may well be the most complex food webs on Earth, with fungi playing central roles as both specialized consumers and specific prey.

ACKNOWLEDGMENTS

REFERENCES

Adl, M., Gupta, V.S., 2006. Protists in soil ecology and forest nutrient cycling. Can. J. For. Res. 36, 1805–1817.

Agerer, R., 2001. Exploration types of ectomycorrhizae. Mycorrhiza 11, 107–114.

Arenz, B., Blanchette, R., 2011. Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross Sea Region and McMurdo Dry Valleys. Soil Biol. Biochem. 43, 308–315.

Arnold, A.E., Maynard, Z., Gilbert, G.S., Coley, P.D., Kursar, T.A., 2000. Are tropical fungal endophytes hyperdiverse? Ecol. Lett. 3, 267–274.

Baar, J., Horton, T., Kretzer, A., Bruns, T., 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. New Phytol. 143, 409–418.

Baldrian, P., 2006. Fungal laccases: occurrence and properties. FEMS Microbiol. Rev. 30, 215–242.

Barron, G., 1988. Microcolonies of bacteria as a nutrient source for lignicolous and other fungi. Can. J. Bot. 66, 2505–2510.

Barron, G.L., 2003. Predatory fungi, wood decay, and the carbon cycle. Biodiversity 4, 3–9.

Bass, D., Richards, T.A., 2011. Three reasons to re-evaluate fungal diversity "on Earth and in the ocean". Fungal Biol. Rev. 25, 159–164.

Berbee, M.L., Taylor, J.W., 1993. Dating the evolutionary radiations of the true fungi. Can. J. Bot. 71, 1114–1127.

Berbee, M.L., Taylor, J.W., 2010. Dating the molecular clock in fungi-how close are we? Fungal Biol. Rev. 24, 1–16.

Berg, B., McClaugherty, C., 2003. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration, first ed. Springer Verlag, Berlin.

Berndt, R., 2012. Species richness, taxonomy and peculiarities of the neotropical rust fungi: are they more diverse in the Neotropics? Biodivers. Conserv. 21, 2299–2322.

Bever, J.D., 1994. Feeback between plants and their soil communities in an old field community. Ecology 75, 1965–1977.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in microbial Interactions. Trends Ecol. Evol. 25, 468–478.

Blackwell, M., 2011. The fungi: 1, 2, 3. . . 5.1 million species? Am. J. Bot. 98, 426–438.

Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T., Darling, S.R., Gargas, A., Niver, R., et al., 2009. Bat white-nose syndrome: an emerging fungal pathogen? Science 323, 227.

Boddy, L., 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. Mycologia 91, 13–32.

Bolton, R.G., Boddy, L., 1993. Characterization of the spatial aspects of foraging mycelial cord systems using fractal geometry. Mycol. Res. 97, 762–768.

Bonfante, P., Anca, I.-A., 2009. Plants, mycorrhizal fungi, and bacteria: a network of interactions. Annu. Rev. Microbiol. 63, 363–383.

Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytol. 162, 617–631.

Bridge, P., Spooner, B., 2012. Non-lichenized Antarctic fungi: transient visitors or members of a cryptic ecosystem? Fungal Ecol. 5, 381–394.

Bruns, T.D., Vilgalys, R., Barns, S.M., Gonzalez, D., Hibbett, D.S., Lane, D.J., et al., 1992. Evolutionary relationships within the fungi: analyses of nuclear small subunit rRNA sequences. Mol. Phylogenet. Evol. 1, 231–241.

Burns, R., DeForest, J., Marxsen, J., Sinsabaugh, R., Stromberger, M., Wallenstein, M., Weintraub, M., Zoppini, A., 2013. Soil enzyme research: current knowledge and future directions. Soil Biol. Biochem. 58, 216–234.

Butinar, L., Strmole, T., Gunde-Cimerman, N., 2011. Relative incidence of ascomycetous yeasts in Arctic coastal environments. Microb. Ecol. 61, 832–843.

Buzzini, P., Branda, E., Goretti, M., Turchetti, B., 2012. Psychrophilic yeasts from worldwide glacial habitats: diversity, adaptation strategies and biotechnological potential. FEMS Microbiol. Ecol. 82, 217–241.

Cairney, J., Bastias, B., 2007. Influences of fire on forest soil fungal communities. Can. J. For. Res. 37, 207–215.

Cannon, P.F., 1997. Diversity of the Phyllachoraceae with special reference to the tropics. In: Hyde, K.D. (Ed.), Biodiversity of Tropical Microfungi. University Press, Hong Kong, pp. 255–278.

Cantrell, S.A., Baez-Félix, C., 2010. Fungal molecular diversity of a Puerto Rican subtropical hypersaline microbial mat. Fungal Ecol. 3, 402–405.

Cantrell, S.A., Dianese, J.C., Fell, J., Gunde-Cimerman, N., Zalar, P., 2011. Unusual fungal niches. Mycologia 103, 1161–1174.

Capella-Gutiérrez, S., Marcet-Houben, M., Gabaldón, T., 2012. Phylogenomics supports microsporidia as the earliest diverging clade of sequenced fungi. BMC Biol. 10, 47.

Carlsen, T., Engh, I.B., Decock, C., Rajchenberg, M., Kauserud, H., 2011. Multiple cryptic species with divergent substrate affinities in the *Serpula himantioides* species complex. Fungal Biol. 115, 54–61.

Chapela, I., Boddy, L., 1988. Fungal colonization of attached beech branches. I. Early stages of development of fungal communities. New Phytol. 110, 39–45.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618.

Connell, L., Redman, R., Craig, S., Rodriguez, R., 2006. Distribution and abundance of fungi in the soils of Taylor Valley, Antarctica. Soil Biol. Biochem. 38, 3083–3094.

Cooke, R.C., Rayner, A.D.M., 1984. Ecology of Saprophytic Fungi. Longman, London.

Courty, P.-E., Buée, M., Diedhiou, A.G., Frey-Klett, P., LeTacon, F., Rineau, F., 2010. The role of ectomycorrhizal communities in forest ecosystem processes: new perspectives and emerging concepts. Soil Biol. Biochem. 42, 679–698.

Cox, F., Barsoum, N., Lilleskov, E.A., Bidartondo, M.I., 2010. Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. Ecol. Lett. 13, 1103–1113.

Dahlberg, A., Schimmel, J., Taylor, A., Johannesson, H., 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biol. Conserv. 100, 151–161.

Deacon, J., Donaldson, S., Last, F., 1983. Sequences and interactions of mycorrhizal fungi on birch. Plant Soil 71, 257–262.

Dickie, I.A., Xu, B., Koide, R.T., 2002. Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytol. 156, 527–535.

Donnelly, D.P., Boddy, L., Leake, J.R., 2004. Development, persistence and regeneration of foraging ectomycorrhizal mycelial systems in soil microcosms. Mycorrhiza 14, 37–45.

Edgcomb, V.P., Beaudoin, D., Gast, R., Biddle, J.F., Teske, A., 2011. Marine subsurface eukaryotes: the fungal majority. Environ. Microbiol. 13, 172–183.

Edman, J.C., Kovacs, J.A., Masur, H., Santi, D.V., Elwood, H.J., Sogin, M.L., 1988. Ribosomal RNA sequence shows *Pneumocystis carinii* to be a member of the fungi. Nature 334, 519–522.

Feuerer, T., Hawksworth, D.L., 2007. Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. Biodivers. Conserv. 16, 85–98.

Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. Ecol. Lett. 12, 1238–1249.

Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R.A., Henrissat, B., Martínez, A.T., Otillar, R., Spatafora, J.W., Yadav, J.S., et al., 2012. The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science 336, 1715–1719.

Freeman, K., Martin, A., Karki, D., Lynch, R., Mitter, M., Meyer, A., Longcore, J., Simmons, D., Schmidt, S., 2009. Evidence that chytrids dominate fungal communities in high-elevation soils. Proc. Natl. Acad. Sci. U. S. A. 106, 18315–18320.

Frey-Klett, P., Garbaye, J., Tarkka, M., 2007. The mycorrhiza helper bacteria revisited. New Phytol. 176, 22–36.

Fukami, T., Dickie, I.A., Paula, Wilkie J., Paulus, B.C., Park, D., Roberts, A., Buchanan, P.K., Allen, R.B., 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol. Lett. 13, 675–684.

Galante, T.E., Horton, T.R., Swaney, D.P., 2011. 95% of basidiospores fall within 1 m of the cap: a field-and modeling-based study. Mycologia 103, 1175–1183.

Gallo, M., Amonette, R., Lauber, C., Sinsabaugh, R., Zak, D., 2004. Microbial community structure and oxidative enzyme activity in nitrogen-amended north temperate forest soils. Microb. Ecol. 48, 218–229.

Garbaye, J., 1994. Tansley review no. 76 helper bacteria: a new dimension to the mycorrhizal symbiosis. New Phytol. 128, 197–210.

Gehrig, H., Schüßler, A., Kluge, M., 1996. *Geosiphon pyriforme*, a fungus forming endocytobiosis with *Nostoc* (Cyanobacteria), is an ancestral member of the glomales: evidence by SSU rRNA analysis. J. Mol. Evol. 43, 71–81.

Geisseler, D., Horwath, W.R., Joergensen, R.G., Ludwig, B., 2010. Pathways of nitrogen utilization by soil microorganisms–a review. Soil Biol. Biochem. 42, 2058–2067.

Geml, J., Tulloss, R.E., Laursen, G.A., Sazanova, N.A., Taylor, D.L., 2008. Evidence for strong inter-and intracontinental phylogeographic structure in *Amanita muscaria*, a wind-dispersed ectomycorrhizal basidiomycete. Mol. Phylogenet. Evol. 48, 694–701.

Glass, D.J., Takebayashi, N., Olson, L.E., Taylor, D.L., 2013. Evaluation of the authenticity of a highly novel environmental sequence from boreal forest soil using ribosomal RNA secondary structure modeling. Mol. Phylogenet. Evol. 67, 234–245.

Gleason, F.H., Schmidt, S.K., Marano, A.V., 2010. Can zoosporic true fungi grow or survive in extreme or stressful environments? Extremophiles 14, 417–425.

Grubisha, L.C., Levsen, N., Olson, M.S., Taylor, D.L., 2012. Intercontinental divergence in the *Populus*-associated ectomycorrhizal fungus, *Tricholoma populinum*. New Phytol. 194, 548–560.

Gulis, V., Suberkropp, K., Rosemond, A.D., 2008. Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. Appl. Environ. Microbiol. 74, 1094–1101.

Gunde-Cimerman, N., Sonjak, S., Zalar, P., Frisvad, J.C., Diderichsen, B., Plemenitas, A., 2003. Extremophilic fungi in arctic ice: a relationship between adaptation to low temperature and water activity. Phys. Chem. Earth Parts A/B/C 28, 1273–1278.

Hanski, I., 1989. Fungivory: fungi, insects and ecology. In: Wilding, N., Collins, N.M., Hammond, P.M., Webber, J.F. (Eds.), Insect-Fungus Interactions. Academic Press, London, pp. 25–68.

Harms, H., Schlosser, D., Wick, L.Y., 2011. Untapped potential: exploiting fungi in bioremediation of hazardous chemicals. Nat. Rev. Microbiol. 9, 177–192.

Hawksworth, D.L., 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycol. Res. 95, 641–655.

Hawksworth, D.L., 2002. The magnitude of fungal diversity: the $1 \cdot 5$ million species estimate revisited. Mycol. Res. 105, 1422–1432.

Hawksworth, D., 2012. Global species numbers of fungi: are tropical studies and molecular approaches contributing to a more robust estimate? Biodivers. Conserv. 21, 2425–2433.

Heckman, D.S., Geiser, D.M., Eidell, B.R., Stauffer, R.L., Kardos, N.L., Hedges, S.B., 2001. Molecular evidence for the early colonization of land by fungi and plants. Science 293, 1129.

Helgason, T., Daniell, T., Husband, R., Fitter, A., Young, J., 1998. Ploughing up the wood-wide web? Nature 394, 431.

Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lucking, R., et al., 2007. A higher-level phylogenetic classification of the fungi. Mycol. Res. 111, 509–547.

Hobbie, E.A., Agerer, R., 2010. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. Plant Soil 327, 71–83.

Hoffman, M.T., Arnold, A.E., 2010. Diverse bacteria inhabit living hyphae of phylogenetically diverse fungal endophytes. Appl. Environ. Microbiol. 76, 4063–4075.

Hoffmann, L., 1989. Algae of terrestrial habitats. Bot. Rev. 55, 77–105.

Hofmockel, K.S., Fierer, N., Colman, B.P., Jackson, R.B., 2010. Amino acid abundance and proteolytic potential in North American soils. Oecologia 163, 1069–1078.

Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytol. 154, 791–795.

Högberg, M.N., Högberg, P., Myrold, D.D., 2007. Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? Oecologia 150, 590–601.

James, T.Y., Porter, D., Hamrick, J.L., Vilgalys, R., 1999. Evidence for limited intercontinental gene flow in the cosmopolitan mushroom, *Schizophyllum commune*. Evolution 53, 1665–1677.

James, T.Y., Kauff, F., Schoch, C.L., Matheny, P.B., Hofstetter, V., Cox, C.J., Celio, G., Gueidan, C., Fraker, E., Miadlikowska, J., et al., 2006. Reconstructing the early evolution of fungi using a six-gene phylogeny. Nature 443, 818–822.

Joergensen, R.G., Wichern, F., 2008. Quantitative assessment of the fungal contribution to microbial tissue in soil. Soil Biol. Biochem. 40, 2977–2991.

Jørgensen, H.B., Johansson, T., Canbäck, B., Hedlund, K., Tunlid, A., 2005. Selective foraging of fungi by collembolans in soil. Biol. Lett. 1, 243–246.

Jones, M.D., Forn, I., Gadelha, C., Egan, M.J., Bass, D., Massana, R., Richards, T.A., 2011. Discovery of novel intermediate forms redefines the fungal tree of life. Nature 474, 200–203.

Kennedy, P.G., Peay, K.G., Bruns, T.D., 2009. Root tip competition among ectomycorrhizal fungi: are priority effects a rule or an exception? Ecology 90, 2098–2107.

Kirk, P., Cannon, P., Minter, D., Stalpers, J., 2008. Ainsworth and Bisby's Dictionary of the Fungi, 10th ed. CABI, Wallingford.

Klironomos, J.N., 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417, 67–70.

Klironomos, J.N., Hart, M.M., 2001. Food-web dynamics: animal nitrogen swap for plant carbon. Nature 410, 651–652.

Klironomos, J.N., Widden, P., Deslandes, I., 1992. Feeding preferences of the collembolan *Folsomia candida* in relation to microfungal successions on decaying litter. Soil Biol. Biochem. 24, 685–692.

Knorr, M., Frey, S., Curtis, P., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.

Koide, R.T., Xu, B., Sharda, J., Lekberg, Y., Ostiguy, N., 2004. Evidence of species interactions within an ectomycorrhizal fungal community. New Phytol. 165, 305–316.

Kowalchuk, G.A., 2012. Bad news for soil carbon sequestration? Science 337, 1049–1050.

Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75, 5111.

Lilleskov, E., Fahey, T., Horton, T., Lovett, G., 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83, 104–115.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J., Finlay, R.D., 2006. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol. 173, 611–620.

Lipson, D., Schmidt, S., 2004. Seasonal changes in an alpine soil bacterial community in the Colorado Rocky Mountains. Appl. Environ. Microbiol. 70, 2867–2879.

Liu, Y., Steenkamp, E.T., Brinkmann, H., Forget, L., Philippe, H., Lang, B.F., 2009. Phylogenomic analyses predict sistergroup relationship of nucleariids and fungi and paraphyly of zygomycetes with significant support. BMC Evol. Biol. 9, 272.

Lorch, J.M., Meteyer, C.U., Behr, M.J., Boyles, J.G., Cryan, P.M., Hicks, A.C., Ballmann, A.E., Coleman, J.T.H., Redell, D.N., Reeder, D.A.M., et al., 2011. Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. Nature 480, 376–378.

Maheshwari, R., Bharadwaj, G., Bhat, M.K., 2000. Thermophilic fungi: their physiology and enzymes. Microbiol. Mol. Biol. Rev. 64, 461–488.

Martin, F., Aerts, A., Ahren, D., Brun, A., Danchin, E., Duchaussoy, F., Gibon, J., Kohler, A., Lindquist, E., Pereda, V., et al., 2008. The genome of Laccaria bicolor provides insights into mycorrhizal symbiosis. Nature 452, 88–92.

May, R.M., 1991. A fondness for fungi. Nature 352, 475–476.

Menezes-Blackburn, D., Jorquera, M.A., Greiner, R., Gianfreda, L., de la Luz Mora, M., 2013. Phytases and phytase-labile organic phosphorus in manures and soils. Crit. Rev. Environ. Sci. Technol. 43, 916–954.

Miller, S.L., Koo, C.D., Molina, R., 1992. Early colonization of red alder and Douglas fir by ectomycorrhizal fungi and *Frankia* in soils from the Oregon coast range. Mycorrhiza 2, 53–61.

Molina, R., Massicotte, H., Trappe, J.M., 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen, M.F. (Ed.), Mycorrhizal Functioning: an Integrative Plant-Fungal Process. Chapman & Hall, New York, pp. 357–423.

Moorhead, D.L., Lashermes, G., Sinsabaugh, R.L., Weintraub, M.N., 2013. Calculating co-metabolic costs of lignin decay and their impacts on carbon use efficiency. Soil Biol. Biochem. 66, 17–19.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., Worm, B., 2011. How many species are there on Earth and in the ocean? PLoS Biol. 9, e1001127.

Nagano, Y., Nagahama, T., Hatada, Y., Nunoura, T., Takami, H., Miyazaki, J., Takai, K., Horikoshi, K., 2010. Fungal diversity in deep-sea sediments-the presence of novel fungal groups. Fungal Ecol. 3, 316–325.

O'Brien, H., Parrent, J., Jackson, J., Moncalvo, J., Vilgalys, R., 2005. Fungal community analysis by large-scale sequencing of environmental samples. Appl. Environ. Microbiol. 71, 5544–5550.

O'Donnell, K., Lutzoni, F.M., Ward, T.J., Benny, G.L., 2001. Evolutionary relationships among mucoralean fungi (Zygomycota): evidence for family polyphyly on a large scale. Mycologia 93, 286–297.

Olsson, P.A., Münzenberger, B., Mahmood, S., Erland, S., 2000. Molecular and anatomical evidence for a three-way association between *Pinus sylvestris* and the ectomycorrhizal fungi *Suillus bovinus* and *Gomphidius roseus*. Mycol. Res. 104, 1372–1378.

Onofri, S., Fenice, M., Cicalini, A.R., Tosi, S., Magrino, A., Pagano, S., Selbmann, L., Zucconi, L., Vishniac, H.S., Ocampo-Friedmann, R., et al., 2000. Ecology and biology of microfungi from Antarctic rocks and soils. Ital. J. Zool. 67, 163–167.

Panikov, N.S., Sizova, M.V., 2007. Growth kinetics of microorganisms isolated from Alaskan soil and permafrost in solid media frozen down to -35°C. FEMS Microbiol. Ecol. 59, 500–512.

Pearce, D.A., Bridge, P.D., Hughes, K.A., Sattler, B., Psenner, R., Russell, N.J., 2009. Microorganisms in the atmosphere over Antarctica. FEMS Microbiol. Ecol. 69, 143–157.

Peay, K.G., Bruns, T.D., Kennedy, P.G., Bergemann, S.E., Garbelotto, M., 2007. A strong species-area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. Ecol. Lett. 10, 470–480.

Peay, K.G., Garbelotto, M., Bruns, T.D., 2010. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91, 3631–3640.

Peay, K.G., Schubert, M.G., Nguyen, N.H., Bruns, T.D., 2012. Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. Mol. Ecol. 21, 4122–4136.

Plassard, C., Louche, J., Ali, M.A., Duchemin, M., Legname, E., Cloutier-Hurteau, B., 2011. Diversity in phosphorus mobilisation and uptake in ectomycorrhizal fungi. Ann. For. Sci. 68, 33–43.

Plattner, I., Hall, I., 1995. Parasitism of non-host plants by the mycorrhizal fungus *Tuber melanosporum*. Mycol. Res. 99, 1367–1370.

Pointing, S.B., Belnap, J., 2012. Microbial colonization and controls in dryland systems. Nat. Rev. Microbiol. 10, 551–562.

Porras-Alfaro, A., Bayman, P., 2011. Hidden fungi, emergent properties: endophytes and microbiomes. Phytopathology 49, 291.

Porras-Alfaro, A., Herrera, J., Natvig, D.O., Lipinski, K., Sinsabaugh, R.L., 2011. Diversity and distribution of soil fungal communities in a semiarid grassland. Mycologia 103, 10–21.

Porter, T., Schadt, C., Rizvi, L., Martin, A., Schmidt, S., Scott-Denton, L., Vilgalys, R., Moncalvo, J., 2008. Widespread occurrence and phylogenetic placement of a soil clone group adds a prominent new branch to the fungal tree of life. Mol. Phylogenet. Evol. 46, 635–644.

Pritsch, K., Garbaye, J., 2011. Enzyme secretion by ECM fungi and exploitation of mineral nutrients from soil organic matter. Ann. For. Sci. 68, 25–32.

Rabinovich, M., Bolobova, A., Vasil'chenko, L., 2004. Fungal decomposition of natural aromatic structures and xenobiotics: a review. Appl. Biochem. Microbiol. 40, 1–17.

Read, D., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems-a journey towards relevance? New Phytol. 157, 475–492.

Reynolds, H.L., Packer, A., Bever, J.D., Clay, K., 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84, 2281–2291.

Richards, T.A., Jones, M.D., Leonard, G., Bass, D., 2012. Marine fungi: their ecology and molecular diversity. Ann. Rev. Mar. Sci. 4, 495–522.

Rosling, A., Cox, F., Cruz-Martinez, K., Ihrmark, K., Grelet, G.A., Lindahl, B.D., Menkis, A., James, T.Y., 2011. Archaeorhizomycetes: unearthing an ancient class of ubiquitous soil fungi. Science 333, 876–879.

Rousk, J., Baath, E., 2011. Growth of saprotrophic fungi and bacteria in soil. FEMS Microbiol. Ecol. 78, 17–30.

Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Appl. Environ. Microbiol. 75, 1589–1596.

Roy, M., Rochet, J., Manzi, S., Jargeat, P., Gryta, H., Moreau, P.-A., Gardes, M., 2013. What determines *Alnus*-associated ectomycorrhizal community diversity and specificity? A comparison of host and habitat effects at a regional scale. New Phytol. 198, 1228–1238.

Schadt, C.W., Martin, A.P., Lipson, D.A., Schmidt, S.K., 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301, 1359–1361.

Schmit, J.P., Mueller, G.M., 2007. An estimate of the lower limit of global fungal diversity. Biodivers. Conserv. 16, 99–111.

Schmit, J.P., Mueller, G.M., Leacock, P.R., Mata, J.L., Wu, Q., Huang, Y., 2005. Assessment of tree species richness as a surrogate for macrofungal species richness. Biol. Conserv. 121, 99–110.

Schoch, C.L., Sung, G.-H., López-Giráldez, F., Townsend, J.P., Miadlikowska, J., Hofstetter, V., Robbertse, B., Matheny, P.B., Kauff, F., Wang, Z., et al., 2009. The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Syst. Biol. 58, 224–239.

Selbmann, L., De Hoog, G.S., Mazzaglia, A., Friedmann, E.I., Onofri, S., 2005. Fungi at the edge of life: cryptoendolithic black fungi from Antarctic desert. Stud. Mycol. 51, 1–32.

Shoun, H., Fushinobu, S., Jiang, L., Kim, S.-W., Wakagi, T., 2012. Fungal denitrification and nitric oxide reductase cytochrome P450nor. Philos. Trans. R. Soc. B Biol. Sci. 367, 1186–1194.

Simon, L., Bousquet, J., Levesque, R.C., Lalonde, M., 1993. Origin and diversification of endomy-corrhizal fungi and coincidence with vascular land plants. Nature 363, 67–69.

Sinsabaugh, R.L., 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biol. Biochem. 42, 391–404.

Sinsabaugh, R.L., Follstad Shah, J.J., 2011. Ecoenzymatic stoichiometry of recalcitrant organic matter decomposition: the growth rate hypothesis in reverse. Biogeochemistry 102, 31–43.

Sinsabaugh, R., Carreiro, M., Repert, D., 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. Biogeochemistry 60, 1–24.

Sinsabaugh, R.L., Manzoni, S., Moorhead, D.L., Richter, A., 2013. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. Ecol. Lett. 16, 930–939.

Smith, S.E., Read, D., 2008. Mycorrhizal Symbiosis, third ed. Academic Press, Amsterdam.

Smith, M.L., Bruhn, J.N., Anderson, J.B., 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. Nature 356, 428–431.

Smith, J.E., McKay, D., Niwa, C.G., Thies, W.G., Brenner, G., Spatafora, J.W., 2004. Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. Can. J. For. Res. 34, 2477–2491.

Snajdr, J., Cajthaml, T., Valásková, V., Merhautová, V., Petránková, M., Spetz, P., Leppänen, K., Baldrian, P., 2011. Transformation of *Quercus petraea* litter: successive changes in litter chemistry are reflected in differential enzyme activity and changes in the microbial community composition. FEMS Microbiol. Ecol. 75, 291–303.

Spott, O., Russow, R., Stange, C.F., 2011. Formation of hybrid N_2O and hybrid N_2 due to codenitrification: first review of a barely considered process of microbially mediated N-nitrosation. Soil Biol. Biochem. 43, 1995–2011.

Stajich, J.E., Berbee, M.L., Blackwell, M., Hibbett, D.S., James, T.Y., Spatafora, J.W., Taylor, J.W., 2009. Primer–the fungi. Current Biol. 19, R840.

Starkey, R.L., Waksman, S.A., 1943. Fungi tolerant to extreme acidity and high concentrations of copper sulfate. J. Bacteriol. 45, 509–519.

Steenkamp, E.T., Wright, J., Baldauf, S.L., 2006. The protistan origins of animals and fungi. Mol. Biol. Evol. 23, 93–106.

Stendell, E., Horton, T., Bruns, T., 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycol. Res. 103, 1353–1359.

Sterflinger, K., Tesei, D., Zakharova, K., 2012. Fungi in hot and cold deserts with particular reference to microcolonial fungi. Fungal Ecol. 5, 453–462.

Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. Oecologia 85, 74–79.

Strickland, M.S., Rousk, J., 2010. Considering fungal: bacterial dominance in soils-methods, controls, and ecosystem implications. Soil Biol. Biochem. 42, 1385–1395.

Strong, P., Claus, H., 2011. Laccase: a review of its past and its future in bioremediation. Crit. Rev. Environ. Sci. Technol. 41, 373–434.

Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnestock, J., Romanovsky, V.E., 2005. Winter biological processes could help convert Arctic tundra to shrubland. Bioscience 55, 17–26.

Talbot, J., Allison, S., Treseder, K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. Funct. Ecol. 22, 955–963.

Taylor, D.L., Bruns, T.D., 1999. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. Mol. Ecol. 8, 1837–1850.

Taylor, A.F.S., Martin, F., Read, D.J., 2000. Fungal diversity in ectomycorrhizal communities of Norway spruce [*Picea abies* (L.) Karst.] and beech (*Fagus sylvatica* L.) along north-south transects in Europe. In: Schulze, E. (Ed.), Carbon and Nitrogen Cycling in European Forest Ecosystems. Springer Verlag, Heidelberg, pp. 343–365.

Taylor, J.W., Turner, E., Townsend, J.P., Dettman, J.R., Jacobson, D., 2006. Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. Philos. Trans. R. Soc. B Biol. Sci. 361, 1947–1963.

Taylor, L., Leake, J., Quirk, J., Hardy, K., Banwart, S., Beerling, D., 2009. Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. Geobiology 7, 171–191.

Taylor, D.L., Herriott, I.C., Stone, K.E., McFarland, J.W., Booth, M.G., Leigh, M.B., 2010. Structure and resilience of fungal communities in Alaskan boreal forest soils. Can. J. For. Res. 40, 1288–1301.

Taylor, D.L., Hollingsworth, T.N., McFarland, J., Lennon, N.J., Nusbaum, C., Ruess, R.W., 2013. A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. Ecol. Monogr. 84, 3–20.

Tedersoo, L., May, T.W., Smith, M.E., 2009a. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20, 217–263.

Tedersoo, L., Suvi, T., Jairus, T., Ostonen, I., Polme, S., 2009b. Revisiting ectomycorrhizal fungi of the genus *Alnus*: differential host specificity, diversity and determinants of the fungal community. New Phytol. 182, 727–735.

Tedersoo, L., Bahram, M., Toots, M., Diédhiou, A., Henkel, T., Kjøller, R., Morris, M., Nara, K., Nouhra, E., Peay, K., et al., 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. Mol. Ecol. 21, 4160–4170.

Thorn, R., Barron, G., 1984. Carnivorous mushrooms. Science 224, 76–78.

Toljander, J., Eberhardt, U., Toljander, Y., Paul, L., Taylor, A., 2006. Species composition of an ectomycorrhizal fungal community along a local nutrient gradient in a boreal forest. New Phytol. 170, 873–883.

Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecol. Lett. 11, 1111–1120.

Treseder, K., Mack, M., Cross, A., 2004. Relationships among fires, fungi, and soil dynamics in Alaskan Boreal Forests. Ecol. Appl. 14, 1826–1838.

Trum, F., Titeux, H., Cornelis, J.-T., Delvaux, B., 2011. Effects of manganese addition on carbon release from forest floor horizons. Can. J. For. Res. 41, 643–648.

Van der Heijden, M.G., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998a. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

Van der Heijden, M.G.A., Boiler, T., Wiemken, A., Sanders, I.R., 1998b. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79, 2082–2091.

Van Der Heijden, M.G., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310.

Veresoglou, S.D., Chen, B., Rillig, M.C., 2012. Arbuscular mycorrhiza and soil nitrogen cycling. Soil Biol. Biochem. 46, 53–62.

Visser, S., 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. 129, 389–401.

Vitt, D.H., 2007. Estimating moss and lichen ground layer net primary production in tundra, peat-lands, and forests. In: Fahey, T.J., Knapp, A.K. (Eds.), Principles and Standards for Measuring Primary Production. Oxford University Press, New York, pp. 82–105.

Waldrop, M., White, R., Douglas, T., 2008. Isolation and identification of cold-adapted fungi in the Fox Permafrost Tunnel, Alaska. Proc. Ninth Int. Conf. Permafrost 2, 1887–1891.

Wallander, H., Ekblad, A., Godbold, D., Johnson, D., Bahr, A., Baldrian, P., Bjork, R., Kieliszewska-Rokicka, B., Kjoller, R., Kraigher, H., et al., 2013. Evaluation of methods to estimate production, biomass and turnover of ectomycorrhizal mycelium in forests soils: a review. Soil Biol. Biochem. 57, 1034–1047.

Willis, A., Rodrigues, B., Harris, P., 2013. The ecology of arbuscular mycorrhizal fungi. Crit. Rev. Plant Sci. 32, 1–20.

Wilson, G.W., Rice, C.W., Rillig, M.C., Springer, A., Hartnett, D.C., 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecol. Lett. 12, 452–461.

Zalar, P., Gostincar, C., De Hoog, G., Ursic, V., Sudhadham, M., Gunde-Cimerman, N., 2008. Redefinition of *Aureobasidium pullulans* and its varieties. Stud. Mycol. 61, 21–38.