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Fungal Traits That Drive Ecosystem Dynamics on Land

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SUMMARY

Fungi contribute extensively to a wide range of ecosystem processes, including decomposition of organic carbon, deposition of recalcitrant carbon, and transformations of nitrogen and phosphorus. In this review, we discuss the current knowledge about physiological and morphological traits of fungi that directly influence these processes, and we describe the functional genes that encode these traits. In addition, we synthesize information from 157 whole fungal genomes in order to determine relationships among selected functional genes within fungal taxa. Ecosystem-related traits varied most at relatively coarse taxonomic levels. For example, we found that the maximum amount of variance for traits associated with carbon mineralization, nitrogen and phosphorus cycling, and stress tolerance could be explained at the levels of order to phylum. Moreover, suites of traits tended to co-occur within taxa. Specifically, the genetic capacities for traits that improve stress tolerance—β-glucan synthesis, trehalose production, and cold-induced RNA helicases—were positively related to one another, and they were more evident in yeasts. Traits that regulate the decomposition of complex organic matter—lignin peroxidases, cellobiohydrolases, and crystalline cellulases—were also positively related, but they were more strongly associated with free-living filamentous fungi. Altogether, these relationships provide evidence for two functional groups: stress tolerators, which may contribute to soil carbon accumulation via the production of recalcitrant compounds; and decomposers, which may reduce soil carbon stocks. It is possible that ecosystem functions, such as soil carbon storage, may be mediated by shifts in the fungal community between stress tolerators and decomposers in response to environmental changes, such as drought and warming.

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INTRODUCTION

Fungi can influence nearly every aspect of ecosystem function, especially processes that occur in soils (1). On the one hand, they can decompose organic material to obtain energy and nutrients (2). In doing so, they release CO_2 as a by-product. On the other hand, they can also produce their own organic compounds that form residues in soils that persist for years to decades (or longer); in this way, fungi contribute to soil carbon (C) storage (3–6). They also mediate the phosphorus (P) and nitrogen (N) cycles by releasing extracellular enzymes that convert organic P or N compounds to smaller products or mineral forms (7, 8). In fact, this enzymatic step often limits the rate at which N cycles between plants, microbes, and the soil (9). A subset of fungi (mycorrhizal fungi) form symbiotic associations with most plants, which ultimately increases rates of net primary productivity (10). Finally, fungi dominate many soil communities, representing an average of 55 to 89% of microbial biomass, depending on the biome (11, 12). Thus, their activities can have large-scale consequences for global biogeochemical cycles.

This diverse collection of ecosystem functions is paralleled by the taxonomic, physiological, and morphological diversity of fungi themselves. It is estimated that there are millions of fungal species worldwide (13–17). Yet, to date, we have described only a small portion of them (18, 19). Even fewer have been characterized ecologically, especially in natural settings. Nevertheless, it appears that there are at least a few major lifestyles among fungi that are reflected by suites of functional traits, which have important implications for ecosystem functioning. For instance, "classic" decomposer fungi are often described as free-living filamentous fungi that can degrade complex compounds, such as lignin, cellulose, and chitin (Fig. 1) (1). In contrast, yeasts (which are frequently single-celled) are considered to be specialized for simpler compounds, such as sugars (20). Last, mycorrhizal fungi form symbiotic relationships with plant roots and are generally thought to obtain most of their C from their host plants rather than from soil organic matter (21). Thus, these three groups of fungi are likely to elicit different consequences for C dynamics, based on their morphology and physiology. In other words, an ecosystem in which yeasts dominate might not necessarily be functionally equivalent to one in which free-living filamentous fungi are prevalent, even if fungal biomasses are equal.

If these morphologically classified groups of fungi vary in their responses to environmental conditions as well, they may generate feedbacks on ecosystem function (Fig. 2). For instance, yeasts are relatively rare in soils, except for more extreme or stressful environments, such as very cold, dry, saline, or acidic habitats (20, 22–24). Thus, if climate change exposes an ecosystem to stronger droughts (25), then perhaps the fungal community would shift toward yeasts, with a concomitant decline in the decomposition of recalcitrant soil C. However, this type of feedback depends on how strongly these and other traits are correlated with one another (26, 27). Are drought tolerance and specialization on simpler C compounds actually linked within individual fungal taxa, especially yeasts? Moreover, which specific physiological, morphological, or ecological traits confer drought tolerance, and will those traits likewise influence ecosystem functions in their own right?

To better predict ecosystem functions, researchers recently began developing models structured around microbial traits (e.g., see reference 28), and models with distinct functional groups of

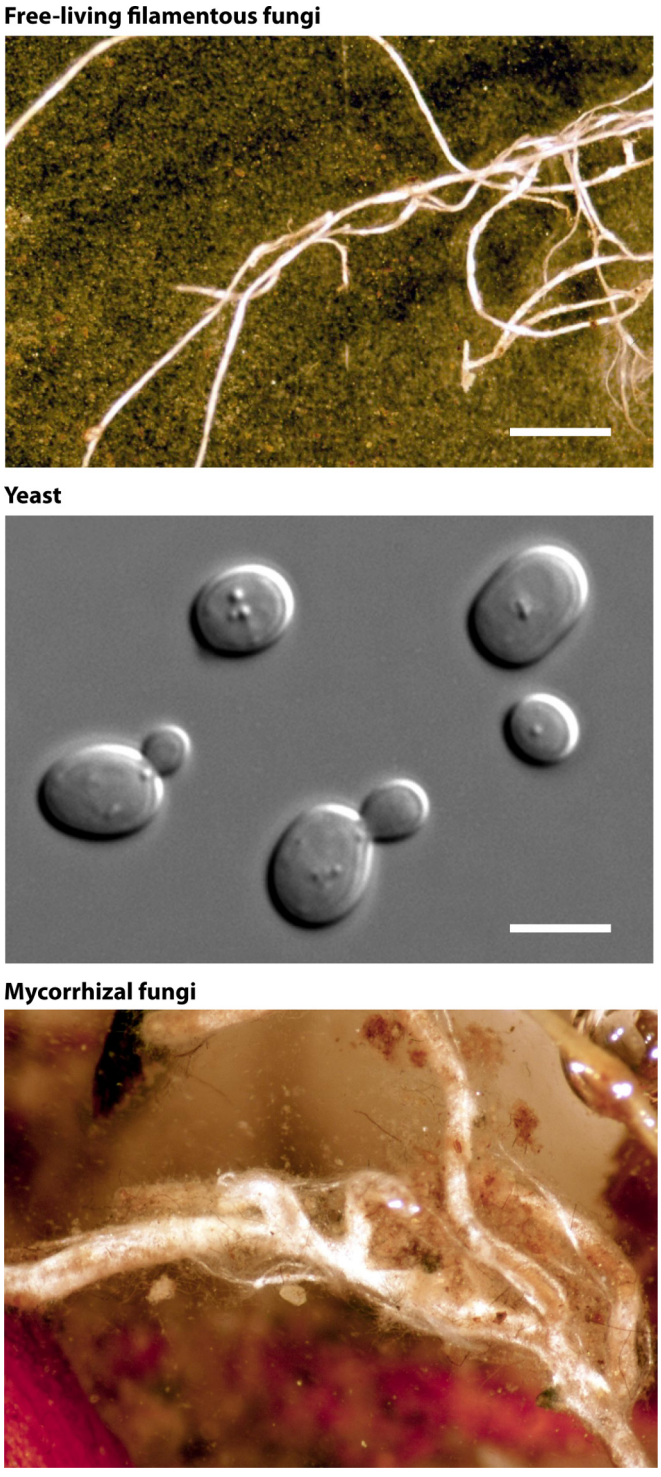

FIG 1 Examples of free-living filamentous fungi, yeasts, and mycorrhizal fungi. Depicted are rhizomorphs of a free-living filamentous fungus (top) (bar, 0.5 mm), cells of the model yeast *Saccharomyces cerevisiae* (middle) (bar, 5 μm), and a fine root tip colonized by an ectomycorrhizal fungus (bottom) (bar, 4 mm). (Middle photo from Wikipedia [user name Masur; http://en.wikipedia.org/wiki/Yeast#/media/File:S_cerevisiae_under_DIC_microscopy.jpg].)

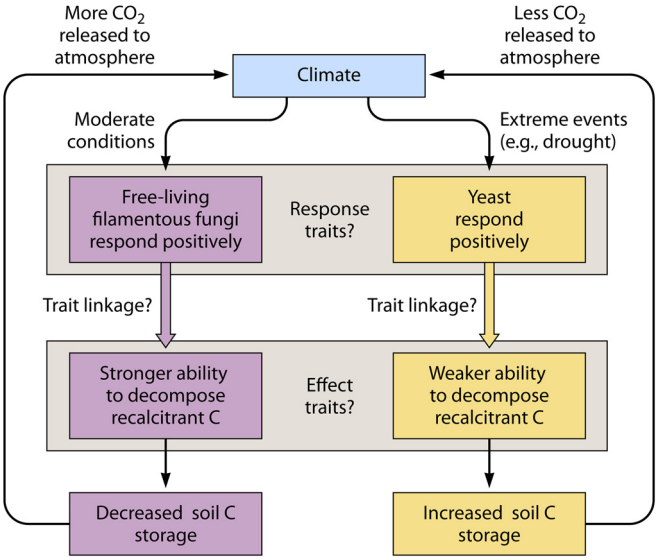

FIG 2 Hypothesized feedbacks on soil C storage associated with free-living filamentous fungi or yeasts. Yeasts tend to prevail under extreme conditions rather than moderate conditions, ostensibly because they possess one or more traits that confer stress tolerance ("response traits"). If these traits are linked to a relatively weak ability to decompose types of recalcitrant C ("effect traits"), then yeasts may contribute to a decline in CO_2 released into the atmosphere by the fungal community in regions exposed to extreme climate conditions. The specific response and effect traits that may be involved and the extent to which they are linked are addressed in this review.

microbes (e.g., see references 29–31). These models are capable of addressing ecosystem feedbacks from shifts in microbial communities and, in doing so, improve their accuracy (32–34). However, in order to parameterize them, we need better information regarding relationships among relevant traits within fungal taxa (for the trait-based models) and how these traits vary among broad groups of fungi (for the functional group models). In this review, we address this issue by asking three questions regarding ecosystem-relevant fungal traits. First, how are these traits distributed among taxa and broad morphological groups (i.e., free-living filamentous fungi, yeasts, and mycorrhizal fungi)? Second, what suites of traits tend to co-occur within fungi? And third, what are the implications for trait-mediated feedbacks on ecosystem functions?

LINKAGES AMONG TRAITS

We address linkages among traits because they can influence how ecosystems respond to environmental conditions. The conceptual framework of Lavorel and Garnier (35) distinguishes between "response" and "effect" traits of organisms and suggests that community composition can influence ecosystem responses to the environment if response and effect traits are linked within organisms. Response traits determine how organisms respond to environmental conditions, and effect traits determine how those organisms contribute to ecosystem dynamics. For example, if a certain response trait confers drought tolerance, then taxa with that trait will be selected for, and ultimately will comprise a larger portion of the fungal community, under dry conditions. If those taxa also carry a trait that alters soil C stocks—one that is not common among drought-sensitive taxa—then shifts in communities under drought conditions might lead to changes in soil C.

We might expect certain response and effect traits to covary within organisms owing to evolutionary, physiological, or thermodynamic trade-offs. In an evolutionary trade-off, for example, allocation of finite resources within organisms might require investment in one function, but at the expense of another function (36). For instance, in algae, adaptation to low nutrient availability is accompanied by a loss of defenses against predation (37). In terms of thermodynamic trade-offs, extracellular enzymes with the structural stability to withstand high temperatures may not perform as well under lower temperatures (38). Likewise, bacteria that are adapted to warmer temperatures can experience a loss of fitness at lower temperatures (39). Essentially, trade-offs can create linkages among traits and can form fundamental mechanisms through which changes in fungal communities can alter ecosystem function. They represent a theoretically predictable way that traits may be linked.

Alternatively, suites of traits can be selected simultaneously by a particular environmental condition if each is advantageous (40, 41). For instance, freshwater bacteria from resource-poor habitats tend to display relatively efficient resource use as well as predator avoidance, possibly because both traits are adaptive under these circumstances (40). Selection for "lifestyles" or "syndromes" such as this would elicit correlations between relevant traits.

Recently, Koide et al. (42) discussed the framework of Lavorel and Garnier (35) as it applies to mycorrhizal fungi. They emphasized that some fungal traits perform dual roles as response and effect traits; in these cases, mediation of ecosystem responses to the environment by fungal communities should be relatively straightforward to predict. For instance, mycorrhizal fungi with melanized cell walls tend to persist better under drought stress (43). In turn, melanized cell walls can be relatively resistant to decomposition (44–46). Thus, melanin may act as a mechanism for augmenting soil C storage (an effect) under drought conditions because fungi that produce it may become more common under dry conditions (a response). Because traits with dual roles may elicit clear ecosystem feedbacks, they are of particular interest in this review.

FUNGAL GROUPS

Suites of traits can frequently co-occur within groups of fungi that are broadly categorized as mycorrhizal fungi, free-living filamentous fungi, and yeasts. We can define these groups based on their gross morphology (Fig. 1). For example, mycorrhizal fungi can be characterized by the ability to form specialized structures (e.g., arbuscules, hyphal coils, and Hartig nets) that colonize plant roots (21). Free-living filamentous fungi are known for their rigid tubular hyphae (47) and lack of a symbiotic life stage (i.e., they are not mycorrhizal, pathogenic, endophytic, or lichen-forming). Yeasts reproduce asexually by budding or fission and display single-cell growth (48).

These morphologies coincide with some important ecological characteristics of each group. For the most part, mycorrhizal fungi form mutualistic relationships with plants; they receive C exudates directly from their plant hosts in exchange for N, P, and other soil nutrients. Free-living filamentous fungi can forage and translocate nutrients across microhabitats within the soil (49), so they have an advantage in acquiring resources that are spatially heterogeneous (50). Thus, they can "integrate" activities over larger environmental gradients than those of single-celled organisms, such as yeasts and bacteria. Yeasts vary widely in their eco-

logical functions, but they are particularly known for their tolerance of broad pH ranges, high osmotic pressure, high salinity (20), low water availability (22), and cold temperatures (23, 24). Many yeasts are capable of fermentation (20), and as a result, they are often found in habitats where sugar availability is high, such as nectar from flowers and sap from tree wounds (22). The single-cell morphology typical of yeasts has evolved multiple times, one of which is associated with a major evolutionary event within the phylum Ascomycota: the divergence of the subphylum Saccharomycotina (predominantly yeasts) and the subphylum Pezizomycotina (predominantly filamentous fungi) (51, 52). Altogether, these three morphological groups have such disparate ecological and nutritional requirements that few studies have directly compared ecosystem-related traits of all three under common conditions.

None of these morphological groups are monophyletic. The mycorrhizal habit is found in many of the major fungal lineages, including the Mucoromycotina, Glomeromycota, Ascomycota, and Basidiomycota (51). Free-living filamentous fungi occur throughout most of the fungal tree of life, although the most ancient fungal phyla are more typically endoparasites (53). Yeasts are found in subphyla of the Ascomycota (Taphrinomycotina and Saccharomycotina) and Basidiomycota (Pucciniomycotina, Agaricomycotina, and Ustilaginomycotina) (48). Because these groups are somewhat interspersed phylogenetically, it is possible to use phylogenetically independent contrasts (54, 55) to identify ecosystem-relevant traits that are consistently linked to gross morphology regardless of phylogenetic identity. For example, we can make a series of comparisons between phylogenetically related taxa that differ in gross morphology to identify other traits that are consistently associated with changes in gross morphology regardless of evolutionary history.

FUNGAL TRAITS RELATED TO ECOSYSTEM PROCESSES

In this review, we discuss fungal traits that are related to select, fundamental terrestrial ecosystem processes: the breakdown of organic C, transformations of N and P, and contributions to soil C storage. Fungi perform these processes as a by-product of their efforts to obtain C (i.e., decomposition) and acquire N and P (i.e., mineralization, depolymerization, and immobilization of nutrients). In addition, their capacity to withstand suboptimal conditions (i.e., stress tolerance) can mediate the extent to which these processes increase or decrease in response to changes in the environment. Moreover, certain stress tolerance traits, such as melanin or β1,3-glucan production, might directly contribute to soil C storage. For each process, we describe the costs and benefits to the fungus, the larger-scale consequences for ecosystem dynamics and global biogeochemistry, and known differences among fungal taxa in the ability to perform the process.

Decomposition

Breakdown of cellulose. Cellulose is a major component of plant cell walls and, accordingly, the most abundant biopolymer on land (56). It is essentially a chain of glucose units that can be used by fungi for energy. A portion of this consumed glucose is used for anabolic processes (growth), while the remainder is used for catabolic processes (respiration), which release CO_2 into the environment. First, though, fungi use extracellular cellulases to degrade cellulose into smaller compounds, such as cellobiose or glucose, which they can then take up across cell walls and metabolize (57, 58). Cellulases vary in their kinetics and mechanisms of catalysis. For example, endoglucanases are one type of cellulase that break cellulose into oligosaccharides that vary in length. Another type, cellobiohydrolases, release cellobiose or glucose from cellulose. Moreover, β-glucosidases hydrolyze cellobiose to glucose. In addition, the more recently described lytic polysaccharide monooxygenase (i.e., the auxiliary redox enzyme AA9) (59) can degrade relatively recalcitrant forms of cellulose, such as cellulose that is highly crystalline (60) or cross-linked with lignin or other cell wall constituents (61).

Many—but not all—fungi possess some capacity to break down cellulose (e.g., see references 62 and 63). Cellulose degraders are well represented among the Ascomycota and Basidiomycota (58), and the capacity to break down cellulose is especially strong in the class Agaricomycetes (64). In contrast, cellulose degraders are less common in the other phyla, with the exceptions of certain species of the genus *Mucor* in the Mucoromycotina (57) and of gut symbionts in the Neocallimastigomycota (65).

Breakdown of lignin. Fungi use extracellular peroxidases to oxidize lignin, ostensibly to obtain access to cellulose, N, and other nutrients that are physically or chemically protected by lignin in plant litter (63, 64, 66, 67). Because lignin is the second most common biopolymer on land (68), lignin degradation can have global consequences for C cycling (69). In addition, because lignin is often cross-linked with other compounds in plant litter, fragmentation of lignin by fungi can facilitate the decomposition of these other compounds and broadly accelerate litter turnover in ecosystems (70). Although some bacteria can break down lignin, this role is often thought to be dominated by fungi (68). In fungi, lignin degradation is conducted by high-oxidation-potential class II peroxidases, which are categorized as lignin peroxidases (LiP), manganese peroxidases (MnP), or versatile peroxidases (VPLs) (66, 71, 72). Only a fraction of fungal taxa possess genes encoding these enzymes, and they are largely restricted to the class Agaricomycetes within the Basidiomycota (63, 64).

Transformation of Phosphorus and Nitrogen

Phosphorus mineralization by extracellular phosphatases. Organic P represents one of the more common sources of P in soil (73, 74). In many soil organic P compounds, P is bound to C via an ester linkage (C—O—P) (75). Fungi can use extracellular phosphatases to cleave the ester bond, releasing phosphate for uptake (7). In this way, fungi contribute to mineralization of P in soils. The production of extracellular phosphatases has been documented broadly among arbuscular and ectomycorrhizal fungi (e.g., see references 76 to 79) and in model taxa, such as the free-living filamentous fungus *Neurospora crassa* (80, 81) and the yeast *Pichia pastoris* (82).

Depolymerization of nitrogen. (i) Extracellular chitinase. Chitin is produced within the cell walls of most fungi (83) and is also a primary component of arthropod exoskeletons. It consists of chains of *N*-acetylglucosamine and is one of the more abundant N-containing biopolymers in the biosphere (84). Fungi can use extracellular chitinases to break chitin into smaller polymers and, ultimately, glucosamine (84). They can then acquire and metabolize the glucosamine to meet demands for N or C (85). The depolymerization of relatively large N-containing polymers into oligomers or monomers, which are more readily taken up by microbes or plants, has been proposed as a rate-limiting step in the N cycle (9). Thus, the ability of fungal taxa to produce extracellu-

lar chitinases is a trait with particularly important consequences for ecosystem function. Extracellular chitinase production and the ability to grow on chitin as the sole N or C source in pure culture have been verified for a number of ectomycorrhizal, ericoid, and saprotrophic fungi (e.g., see references 86 to 90).

(ii) Extracellular protease and peptidase. About 20 to 40% of soil N is bound in various proteinaceous compounds (91–93), which fungi can depolymerize via extracellular proteases and peptidases. First, proteases, such as serine protease or metalloprotease, split long protein chains into shorter chains (94). Next, amino acids are released from these shorter chains by peptidases, such as glycine aminopeptidase and leucine aminopeptidase (7). Collectively, these enzymes produce small peptides and single amino acids, each of which can be taken up by fungi that possess the appropriate membrane transport proteins (95–98). Mycorrhizal fungi have received particular attention for their capacity to break down proteins as a source of N. In a recent review, Talbot and Treseder (99) reported that of 53 ericoid and ectomycorrhizal species examined, 46 possessed this trait.

Immobilization of nutrients by N and P transporters. In order to directly acquire N, P, and other nutrients from the environment, fungi can construct membrane transport proteins (i.e., transporters or permeases) to take up relatively small organic compounds, such as amino acids (96, 97, 100–103), or mineral nutrients, such as phosphate (104), ammonium (105), or nitrate (106). Fungi can also conduct endocytosis (107–112), which is another strategy for internalization of nutrients.

Even though fungi must take up N from the soil to maintain growth, they differ in their preferences for various forms of N (99, 113, 114). For instance, Lilleskov et al. (113) reported that fungal species dominating ecosystems with low N availability tended to prefer protein-derived N, and those inhabiting N-saturated systems targeted mineral N instead. Plett and Martin (115) have noted that amino acids, ammonium, and other N transporters are broadly upregulated in ectomycorrhizal tissues. Finally, nitrate transporter genes are known to be distributed widely throughout the fungal phylogeny, including in numerous Ascomycota and Basidiomycota genera (106).

As fungi internalize N and P, this activity results in microbial immobilization (2). In other words, the acquired nutrients are no longer readily available for other organisms, such as plants. This has important ecosystem-level consequences. For example, microbes immobilize 20 to 35% of organic P in soils (116–118). In contrast, microbially immobilized N represents about 2 to 5% of total soil N globally (119). Nitrogen will remain immobilized within fungi until their tissues senesce and are decomposed, until they are consumed by other organisms, or until they secrete the N as ammonium. Cycles of wetting and drying can alter each of these processes in the soil (120). The secretion of ammonium contributes to N mineralization, and it is expected to occur if fungi use acquired organic N as a source of energy or C instead of N (121, 122). In general, N mineralization is thought to be more prevalent in systems where soil N availability is high enough that fungal growth is not N limited (9).

Denitrification. In systems where O_2 is absent or minimal, certain fungi can denitrify nitrate or nitrite, resulting in the production of N_2O (123). Denitrification is important because N_2O is a particularly effective greenhouse gas and because denitrification is a pathway of N loss from ecosystems (2). Before the 1990s, fungi were not widely recognized as major contributors to denitrification in natural ecosystems (123–125). Nonetheless, terrestrial field studies have suggested that fungal denitrification can indeed represent a significant ecosystem flux (126–129). The distribution of this trait among fungal taxa has not been tested extensively, although Shoun et al. (123) screened 72 fungal genomes and found that 26% of them possessed homologues for at least one fungal denitrification gene.

Stress Tolerance

A number of traits can allow fungi to maintain activity under unusually dry, hot, or cold conditions; these include β1,3-glucan, trehalose, RNA helicase, melanin, and budding growth. We discuss each here because they can serve as "response" traits (35) that may direct shifts in fungal community composition in response to global change. In addition, β1,3-glucan and melanin might also influence ecosystem function directly (i.e., serve as effect traits), because they lead to the deposition of fungus-derived C in soil. This process is an important consideration, as microbial residues may contribute as much as 50% of organic C in soils (130).

β1,3-Glucan. Fungal cell walls provide protection from desiccation, freeze-thaw damage, and other environmental stresses (131, 132). Most fungal taxa construct cell walls with chitin (53); some can incorporate β1,3-glucan as well (133, 134). β1,3-Glucan is a carbohydrate that forms cross-linkages with chitin and other components (135), improving the strength and integrity of the cell wall (136). In fact, mutants of *Saccharomyces cerevisiae* that lack the ability to synthesize β1,3-glucan are about 5-fold more sensitive to drought stress than wild-type strains (137). β1,3-Glucan can constitute as much as 55% of the dry weight of the fungal cell wall (138). Moreover, it is highly polymerized, hydrophobic, and acid and alkali insoluble when cross-linked with chitin (138), which may make it relatively resistant to decomposition. Although few studies to date have assessed turnover rates or standing stocks of β1,3-glucan in soils, it is worth investigating as a potentially significant component of microbial residues within ecosystems (4). If it is such a component, the use of β1,3-glucan may be a mechanism that facilitates soil C storage in response to drought or other environmental stressors.

Trehalose. Trehalose is a compatible solute that improves stress tolerance in fungi via several potential mechanisms (139, 140). First, it is thought to substitute for water molecules in cell membranes, protecting them from desiccation and freezing damage (141–145). Second, trehalose may confer thermotolerance (146–148) by stabilizing proteins during heat shock (149). Third, it may act as a compatible osmolyte (150). Accordingly, a number of studies have documented increases in trehalose concentrations in fungi in response to environmental stress (139, 140, 145, 148). Trehalose concentrations can vary among fungi (145) and have been studied primarily in yeasts (e.g., see references 139 and 146).

Trehalose can represent a significant trade-off for fungi, because it requires C that could otherwise be allocated to growth or metabolism (120). It is a high-energy compound (139, 140), and it can represent as much as 20% of the fungal biomass (146). Indeed, Schimel et al. (120) estimated that the C cost of producing stress resistance compounds, such as trehalose, during a single drought event can reach as much as 6% of an ecosystem's annual net primary productivity.

RNA helicase. Under cold conditions, RNAs can form stable tertiary structures that render them nonfunctional and prevent translation (151). Certain cold-induced RNA helicases can un-

TABLE 1 Examples of ecosystem-relevant functional genes that have been verified experimentally in fungi

Fungal trait	Ecosystem function	Gene(s)	Domain[a]	Reference(s)
Decomposition traits				
β-Glucosidase	Breakdown of cellulose	*GH1-1*	IPR001360	272–274
Cellobiohydrolase	Breakdown of cellulose	*CBH1/cel7A* and *GH7* family	IPR001722	275–278
Lytic polysaccharide monooxygenase	Breakdown of cellulose	*AA9* family	IPR005103	60, 61, 279–281
Lignin peroxidase	Breakdown of lignin	*LIP*, *MNP*, *VPL*	IPR001621	66, 71, 72
Traits involved in transformation of P and N				
Extracellular phosphatase	P mineralization	*PHO3* in *Neurospora*	IPR000560	80, 81
Extracellular chitinase	N depolymerization	*GH18-5*	IPR001223	198–202
Phosphate transporter	P immobilization	*PHO4* in *Neurospora*	IPR001204	104, 282–284
Ammonium transporter	N immobilization	*AMT2*	IPR001905	105
Nitrate transporter	N immobilization	*NRT2*	IPR004737	106, 285, 286
Amino acid permease	N immobilization	*AAP1* and *GAP1*	IPR004762	96, 97, 100–103
Denitrification	Denitrification	*P450nor*, *NOR1*, and *nirK*	NA	123, 125, 287–289
Stress tolerance traits				
β1,3-Glucan synthase	C deposition	*FKS1*	GO:0000148	131, 132, 290, 291
Trehalase	C deposition	*NTH1*	GO:0005991	146
RNA helicase		*MRH4*	IPR014014	156, 157, 292, 293
Melanin	C deposition	*PKS1* in *Colletotrichum*	GO:0006582	294–297

[a] From the InterPro (www.ebi.ac.uk/interpro/) or Gene Ontology (geneontology.org/) database.

wind the RNAs or bind to them, which allows translation to proceed (152, 153). Fungi that carry these RNA helicases display improved cold tolerance (154–159) and can be more prevalent in colder environments (157). RNA helicase may form part of a generalized stress response (156, 160).

Melanin. Melanin is a condensed, randomly arrayed, aromatic pigment that is located in the cell wall or extracellular matrix of fungi (161–163). It broadly protects fungi from an array of environmental stresses, including extreme heat and cold, drought, UV radiation, high salinity, heavy metals, and anthropogenic pollutants (164–170). As a result, melanized fungi are often disproportionately represented in extreme environments, such as the Antarctic (171, 172). Many melanized fungi belong to the Dothideomycetes or Chaetothyriales within the Ascomycota (164, 173). They also include members of the yeast (e.g., see reference 174), mycorrhizal (e.g., see references 42 and 175), and free-living filamentous groups (e.g., see references 162 and 176).

Melanin resists decomposition, likely owing to its complex, aromatic structure (44). As a result, tissues of melanized fungi are particularly recalcitrant (46, 177, 178). Accordingly, it has been suggested that melanin contributes to C storage in soils (5), eventually accumulating as humic material (163, 177, 179). In consideration of these properties, Koide et al. (42) proposed melanin production as a fungal trait that may form a direct link between environmental stress and ecosystem function.

Budding growth. Budding growth forms, which are typical of yeasts, tend to allow better stress tolerance (180), perhaps because each cell is encased in a protective cell wall. In contrast, in many filamentous fungi, cells can be connected, allowing water and solutes to flow between them (47, 181). This connectivity can leave the cells more vulnerable to water loss (182). However, a trade-off of the budding growth form is that single-celled organisms must obtain resources from the microenvironment that immediately surrounds them. Their activities may slow or halt when one or more nutrients become limiting within this microsite (9).

In contrast, filamentous fungi do not have this restriction, since they can forage over relatively long distances—up to several meters for some species (50, 183, 184). As a result, decomposition is often faster when filamentous fungi translocate nutrients to meet their stoichiometric needs—such as transferring N from soil to maintain fungal growth on plant litter with high C:N ratios (185–190). In this sense, the filamentous growth form can indirectly augment C mineralization in ecosystems, via a mechanism that is not likely to occur with budding growth forms.

FUNCTIONAL GENES

Functional genes can indicate the genetic potential of fungal taxa to carry particular traits, and they are especially informative if their function has been verified empirically in mutant or transcription assays for at least one fungus (191–193). Of course, possession of a gene does not mean that the gene is expressed or translated (194–196). Nevertheless, gene identification is a useful tool for supplementing empirical measurements of traits of fungal taxa (197), which can be limited owing to logistical challenges, such as difficulties in generating laboratory cultures or measuring functions *in situ*. Moreover, we can use functional genes to document linkages among traits within whole genomes. Where possible, we have identified experimentally verified functional genes encoding ecosystem-related traits in fungi and have listed them in Table 1.

For some enzymes, additional care must be taken to ensure that the functional genes encode enzymes that are active in the appropriate sites. For example, fungi use chitinases internally to reorganize their own cell walls (198), and we would not consider this process to contribute to N depolymerization in soils. Nevertheless, the *GH18-5* gene has been verified as an extracellular chitinase gene, based on its sequence (198), mutation assays (199), the activity of the purified protein (200), and secretion of the protein into growth medium (201). Moreover, in *Trichoderma*, its transcription is induced by C and N starvation (198, 202). Altogether, the data indicate that it is a good candidate as a gene encoding a

standard extracellular chitinase used by fungi to acquire C or N, so we have listed it as such in Table 1. Likewise, only membrane transport proteins that internalize compounds from the environment are relevant for immobilization of nutrients, even though fungi use these proteins for intracellular transport as well. Thus, only functional genes for transporters that operate in the outer membrane are included in Table 1.

ANALYSIS OF ECOSYSTEM-RELATED TRAITS WITHIN WHOLE GENOMES

We have an unprecedented opportunity to examine how genes related to ecosystem function are linked within fungal taxa. The 1,000 Fungal Genomes Project (1000.fungalgenomes.org), in collaboration with the Fungal Genomics Program of the U.S. Department of Energy Joint Genome Institute, is a community effort to obtain, annotate, and share whole genomes of taxa representing the breadth of the fungal kingdom (203, 204). By June 2014, 157 whole annotated, published genomes were publicly available at the JGI MycoCosm web portal (205). They represented seven fungal phyla, with three subphyla each in the Basidiomycota and Ascomycota. For each of the whole genomes, we used the MycoCosm search tool to count numbers of genes identified as encoding a cellobiohydrolase ("cellulase GH7"), lytic polysaccharide monooxygenase ("cellulase AA9"), lignin peroxidase, amino acid permease, ammonium transporter, extracellular phosphatase, phosphate transporter, trehalase, RNA helicase, or β1,3-glucan synthase. For search terms, we used relevant domains from the InterPro (www.ebi.ac.uk/interpro) and Gene Ontogeny (geneontology.org) databases (Table 1). We omitted from our analyses any genes from Table 1 that were not assigned to InterPro or Gene Ontogeny domains (fungal denitrification genes) or that represented only a minority of the genes included in their respective domains (β-glucosidase gene *GH1-1*, extracellular chitinase gene *GH18-5*, nitrate transporter gene *NRT2*, and melanin gene *PKS1*).

Genome sizes varied widely among taxa, ranging from 1,831 genes in *Encephalitozoon romaleae* to 30,282 genes in *Rhizophagus* sp. To avoid spurious positive relationships owing to genome size, we standardized for genome size by calculating the frequency of genes in each genome (per 10,000 genes) that were represented by each function. Finally, to support our phylogenetic analyses, we downloaded the 2014 MycoCosm All-Fungi Species Tree, which was created based on clusters of conserved genes. We pruned the tree to remove any taxa not represented in our analyses.

Phylogenetic Distribution of Ecosystem-Related Traits

First, we analyzed the genomes to determine how the ecosystem-related traits were distributed among fungal taxa. Specifically, we wondered what level of taxonomic resolution would capture the greatest variation in a particular trait (akin to "ecological coherence" [206]). For instance, Floudas et al. (63) demonstrated that lignin peroxidase genes became common in the ancestors of the class Agaricomycetes but were relatively uncommon in other clades. Thus, if we wish to characterize the lignin-degrading capacity of a given fungal community, we should use a taxonomic resolution at the class level or finer. At the other end of the spectrum, Lennon et al. (207) found that preferences for soil moisture (i.e., optimum water potential) by fungi and bacteria varied most at the phylum level, which indicates that coarser-level distinctions among taxa are sufficient for this trait.

To address this question, we used Phylocom (54) to calculate the contribution index (CI) for each node within the fungal phylogeny. The CI is similar to a partitioning of the sum of squares in an analysis of variance, and it indicates the degree to which divergence at a particular node accounts for the total variation in a given trait across the entire phylogeny (208). Essentially, for a given trait, larger CIs indicate greater variation in that trait among the descendant taxa. We next determined the average CI for nodes at which phyla diverged, then subphyla, classes, and so on.

For nearly every trait that we examined, the average CIs tended to peak where subphyla or phyla diverged (Fig. 3). In other words, these ecosystem-related traits diverged relatively early in fungal evolutionary history, perhaps owing to broad selective advantages conferred by stress tolerance and nutrient acquisition. This indicates that for practical purposes, we can bin fungal taxa within subphyla and still expect to capture much of their variation in these particular traits (e.g., see Fig. 4). For instance, if one can identify a fungus to the subphylum level, one can make general predictions about its genetic capacity to construct trehalose or incorporate β1,3-glucan into its cell walls, even if the genome of that particular species remains unknown. This approach is also useful because the structures of functional group-based models would be much simpler if they could be based on relatively few subphyla rather than more diverse groups at a finer taxonomic resolution. Altogether, it is more tractable to isolate, characterize, or model representatives of each fungal subphylum than to do so for each of the millions of still-undescribed fungal species.

Lignin peroxidase was somewhat of an exception—the average CIs for this trait tended to peak at the order level (Fig. 3), especially where the orders Hymenochaetales and Corticiales diverge within the class Agaricomycetes. This finding is consistent with recent analyses of genomes of wood decay fungi, which noted that the class Agaricomycetes contains taxa that vary widely in their capacity to break down lignocellulose (63, 64, 204). Relatively recent evolutionary events may have influenced the radiation of lignin degradation in the Agaricomycetes. As Floudas et al. (63) suggested, the origin of lignin-degrading capabilities occurred during the Carboniferous period, when lignin-derived organic C was accumulating in the biosphere. It is likely that the prevalence of this compound selected for fungi that could degrade it to obtain lignin-protected C.

We should note that the phylogenetic distributions of functional genes involved in ecosystem function will likely change as additional whole fungal genomes are sequenced. For example, we may discover previously undescribed fungal clades that possess any number of these traits, and this might change the known taxonomic resolution of the traits accordingly. Most of the whole fungal genomes in our analyses were obtained from fungi that could be isolated in the laboratory. Although it is currently challenging to isolate most fungi, novel cultivation strategies are being developed, which may improve the taxonomic breadth of our culture collections (209, 210). In addition, genome sequencing of single cells or hypha may improve our ability to examine their traits in the near future (211–214).

The relatively coarse taxonomic resolution of ecosystem-related traits in fungi may not necessarily be mirrored in bacteria. In bacteria, phylogeny is sometimes correlated with functional traits (215) and habitat preferences (207, 216, 217), but not always (218). For bacteria, decomposition-related traits, such as cellulase production and organic C use, vary primarily at the species and

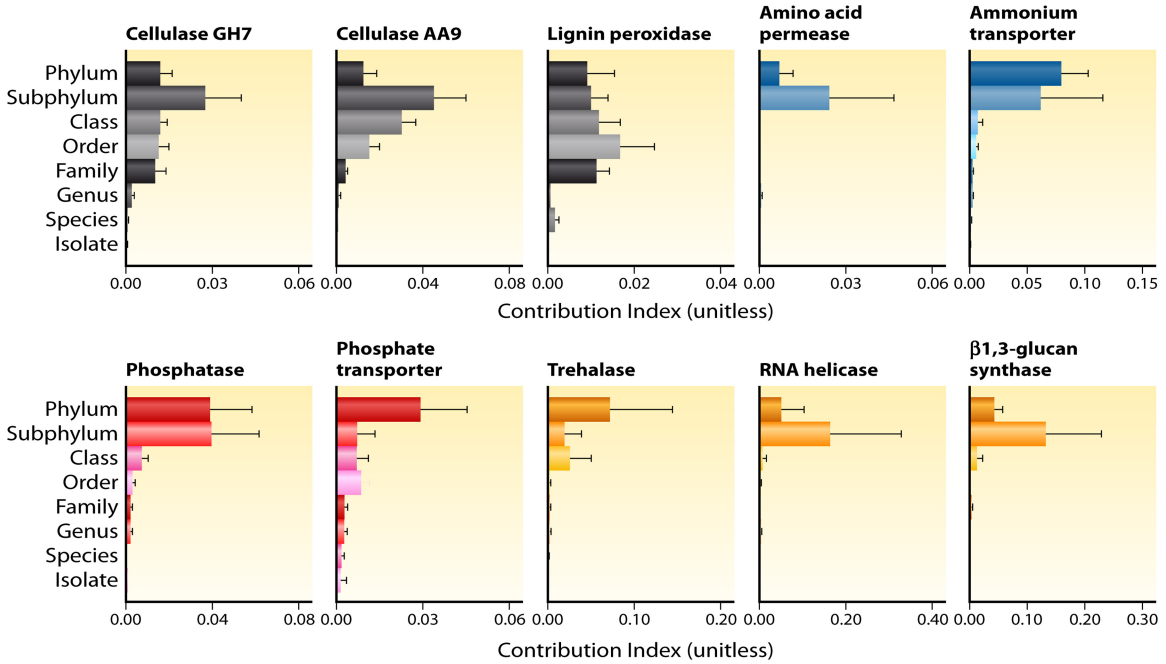

FIG 3 Variation in traits by taxonomic rank. The contribution index represents the proportion of trait variance across the entire phylogenetic tree that is attributable to the variance at a particular node. We categorized each node within the phylogenetic tree by the taxonomic rank of the clades that diverged from that node. For example, a node assigned to the "phylum" level represents a divergence between two phyla. Bars represent means + 1 standard error (SE) for nodes within each taxonomic rank. Each trait was assigned based on the frequency of relevant functional genes within each whole genome. Genomic data are from the 1,000 Fungal Genomes Project, obtained via the JGI MycoCosm Web portal (205).

subspecies levels (219, 220). Horizontal gene transfer is common within prokaryotes (221), and it may contribute to this pattern. Although horizontal gene transfer can also occur among fungi, it is believed to be less frequent (222–224).

Notably, the CIs of four traits were highest at the same node in the fungal phylogeny and occurred at the divergence between the subphyla Pezizomycotina and Saccharomycotina (within the Ascomycota). These traits included cellulase AA9, which was less prevalent in the Saccharomycotina than in the Pezizomycotina, and amino acid permease, ammonium transporter, and β1,3-glucan synthase, which were all more frequent in the Saccharomycotina (Fig. 4). Most taxa within the Saccharomycotina are yeasts, whereas the members of the Pezizomycotina include filamentous fungi as well as some yeasts (48). Differences between yeast and filamentous morphologies may have contributed to the trait variation observed at this node, which would suggest a linkage between gross morphology and functional traits.

Suites of Traits Associated with Broad Morphological Groups

To follow up on the possible influence of gross morphology, we tested for differences in ecosystem-related traits among yeasts, free-living filamentous fungi, and mycorrhizal fungi. The distributions of traits among these groups could be influenced simultaneously by their phylogenetic relatedness and by physiological/morphological trade-offs. For example, yeasts occur throughout the Dikarya but are most clustered within the Saccharomycotina (48). This means that if two yeast taxa possess similar complements of traits, it may simply be because they are likely to be closely related to one another, or it may be that selection for a single-cell morphology simultaneously selects for (or against) certain other traits (55). Thus, for each trait, we examined the variation among the three morphological groups, with and without the influence of phylogenetic relationships. First, we conducted a series of Kruskal-Wallis tests to check for significant differences in each trait among yeasts, free-living filamentous fungi, and mycorrhizal fungi; these differences may be influenced by phylogenetic relatedness. Second, we used Phylocom (54) to perform a series of phylogenetically independent contrasts for yeast versus nonyeast taxa, free-living filamentous fungi versus non-free-living filamentous fungi, and mycorrhizal fungi versus nonmycorrhizal fungi. At the time of writing, only three genomes of mycorrhizal fungi had been published, which limited our ability to analyze this functional group. Nonetheless, we present the mycorrhizal data to indicate preliminary trends.

We found that the three morphological groups exhibited distinct suites of traits independently of their phylogenetic relatedness (Fig. 5). Free-living filamentous fungi tended to be more genetically capable of breaking down lignin (independent contrast $P = 0.001$), cellobiose (GH7) ($P = 0.005$), and crystalline cellulose (AA9) ($P = 0.019$), and they possessed fewer trehalase genes ($P = 0.018$). They were not particularly distinct in other functional traits related to stress tolerance. On the other hand, yeasts were notable in their genetic capacity for traits that confer stress tolerance, such as trehalase (independent contrast $P = 0.006$), RNA helicase ($P = 0.024$), and β1,3-glucan synthase ($P = 0.018$). They also possessed higher gene frequencies for amino acid permeases ($P = 0.045$), ammonium transporters ($P = 0.027$), and extracellular phosphatases ($P = 0.012$) than did nonyeasts. However, they did not possess strong lignin- or cellulase-degrading capacities.

In essence, yeasts appeared to disproportionately possess traits

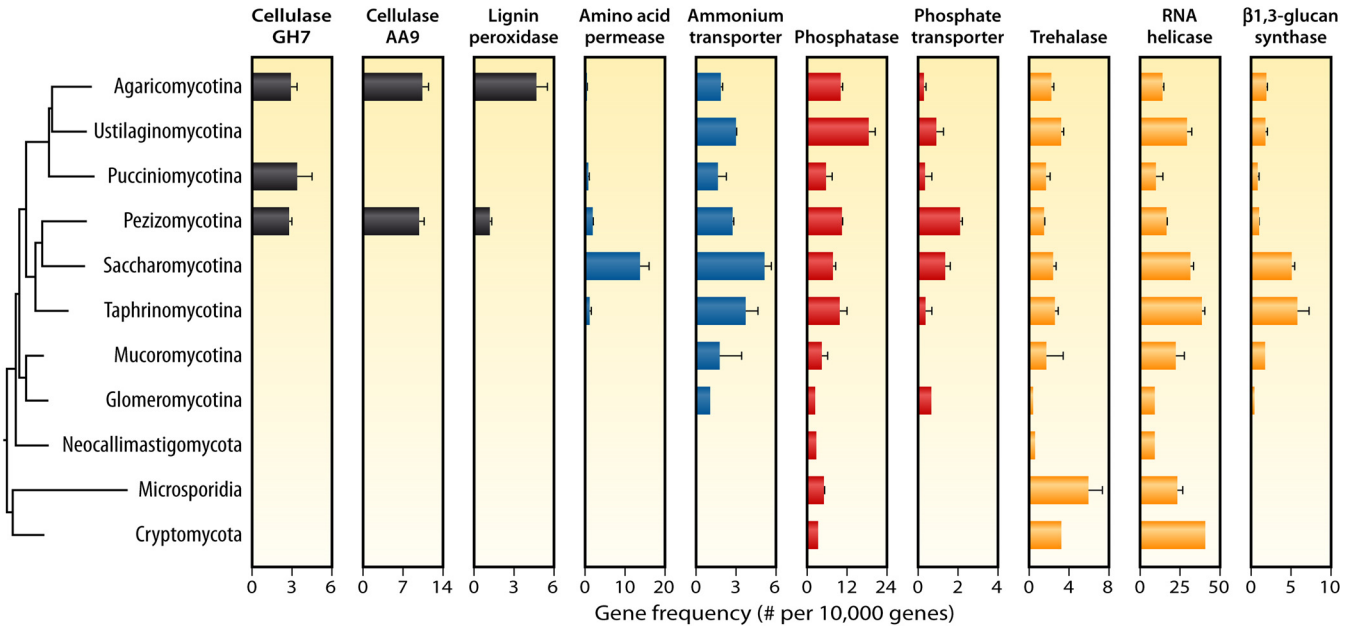

FIG 4 Distribution of ecosystem-related traits across fungal phyla (or subphyla, for Dikarya). Frequencies of functional genes were calculated for each whole genome by using MycoCosm to search for relevant InterPro and Gene Ontology domains (Table 1). Bars are means + 1 SE for each phylum/subphylum. Phylogeny is from the 2014 MycoCosm All-Fungi Species Tree.

associated with stress resistance and nutrient acquisition, but not necessarily decomposition; with free-living filamentous fungi, the reverse was true. These distinctions may represent life history strategies akin to the "stress tolerator" (for yeast) and "competitor" (for free-living filamentous fungi) strategies in the conceptual framework originally proposed by Grime (225) and later refined for microbes (26, 120, 226). In Grime's framework, competitors are characterized as species that can outcompete other species by more effectively exploiting available resources or by directly interfering with competitors. Recently, Crowther and colleagues (227) specifically addressed how this framework applies to fungi, especially with respect to drought tolerance versus combative ability. In fact, they reanalyzed data from a previously published study of fungal competition (228), and they found that strong competitors tended to display less tolerance for low water availability than did weaker competitors. In the case of fungi, the ability to deploy extracellular enzymes to acquire organic carbon that is unavailable to others—such as lignin-protected resources—may also confer competitive success (229). Filamentous growth can likewise be advantageous among fungi competing for wood colonization (50, 230–232).

Linkages among Ecosystem-Related Traits

Next, we addressed the question of which suites of traits tend to co-occur within fungi. We tested for positive or negative relationships between each pairwise combination of traits, and we were especially interested in relationship traits that met two criteria. First, they had to be significantly related independently of phylogenetic relationships (i.e., phylogenetically independent contrast [54]). Second, they also had to be significantly correlated in a standard correlation (i.e., Spearman ranked correlation on gene frequencies [233]). In this way, we could identify links between traits that are likely to be mechanism driven (indicated by a significant phylogenetically independent contrast) and, at the same time, broadly evident across known fungal taxa (indicated by a significant Spearman ranked correlation).

We found that several functional genes, especially genes that controlled similar processes, were positively related within fungal taxa (Fig. 6). For example, the traits related to stress tolerance were each positively related to one another. Others have noted that fungi exhibit a generalized stress response in which exposure to an environmental stressor initiates multiple physiological and biochemical changes that are relatively consistent regardless of the type of stress (e.g., heat, cold, or osmotic stress) (234). It is possible that environmental stress can simultaneously select for traits such as trehalase, RNA helicase, and β1,3-glucan synthase, because they confer stress tolerance via complementary mechanisms. Together, these suites of traits may form the "syndrome" or "lifestyle" of a stress tolerator (40, 41).

Traits related to decomposition—the genetic capacity to produce lignin peroxidase, cellulase AA9, and cellulase GH7—were likewise significantly positively related to one another. There may be selective advantages in the ability to target multiple types of organic compounds. For instance, a fungus that can use cellulose might possess a competitive advantage over other cellulose users if it can break down lignin as well (235). For example, it can release cellulose from its physical and chemical protections by lignin (70, 236) and then immediately break down and acquire the cellulose before "cheater" fungi can exploit it (237). In fact, fungi that can target lignin as well as cellulose often outcompete fungi that target cellulose alone (238, 239).

N- and P-acquisition traits were inconsistently linked with one another and with decomposition traits. If anything, nutrient acquisition was associated more strongly with stress tolerance traits, but not exclusively. For instance, both types of cellulases were positively associated with phosphate uptake. It is possible that stoichiometric constraints require acquisition of N and P to sup-

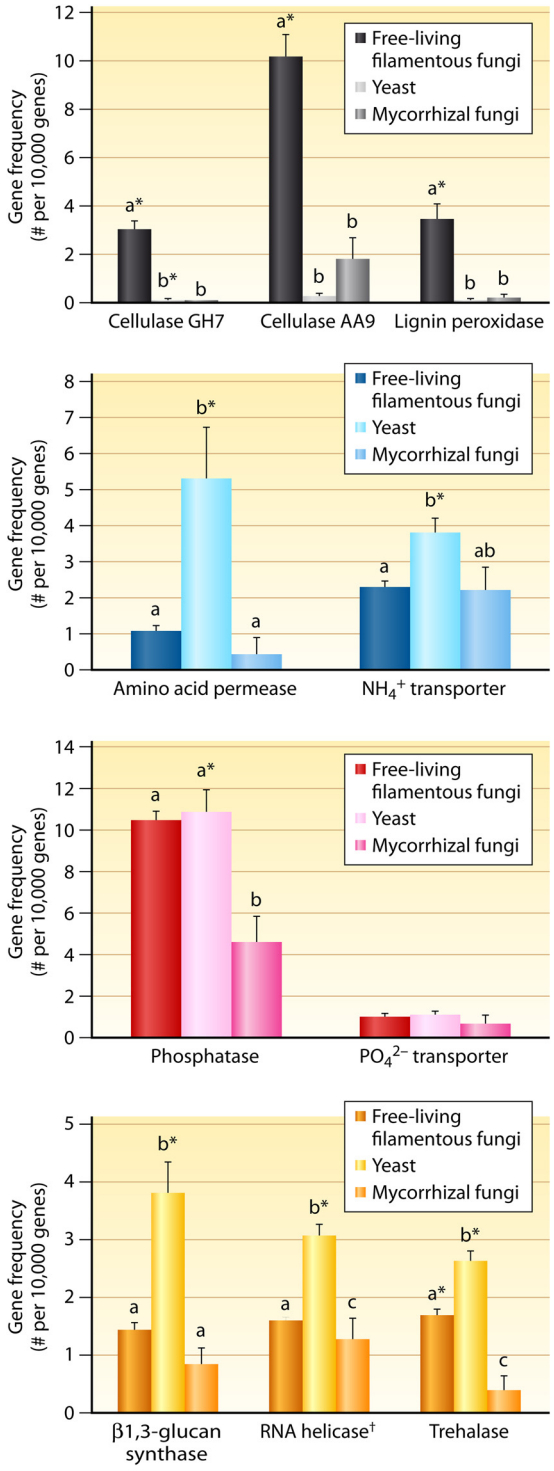

FIG 5 Ecosystem-related traits of free-living filamentous fungi, yeasts, and mycorrhizal fungi. Different letters indicate significant pairwise differences between morphological groups ($P < 0.05$), based on the Kolmogorov-Smirnov test. Asterisks indicate a significant phylogenetically independent contrast between members and nonmembers of the morphological group. †, for RNA helicase, gene frequency units are numbers per 1,000. Data are means + 1 SE.

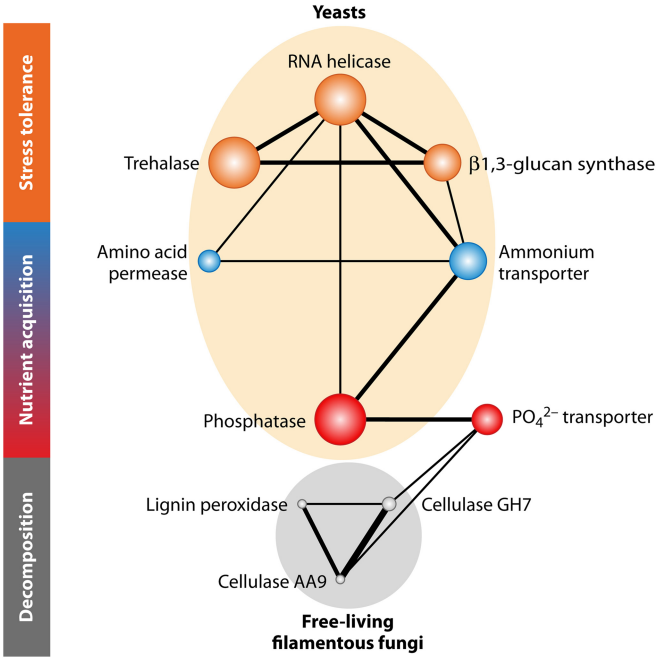

FIG 6 Relationships among traits and their associations with morphological groups of fungi. Symbols represent traits. Symbol size is proportional to the number of fungal phyla (or subphyla, for Dikarya) that possess the trait. Lines connect traits that are significantly positively related based on the following two criteria: (i) significance based on Spearman ranked correlations and (ii) significance based on phylogenetically independent contrasts. Line thickness is proportional to Spearman's ρ or phylogenetically independent contrast *r*, whichever is smaller; these values ranged between 0.2 and 0.47 (see Table S2 in the supplemental material). Ovals encompass traits that are significantly positively associated with yeasts or free-living filamentous fungi (Fig. 5).

port a broad range of fungal activities and that multiple nutrient sources and uptake mechanisms can be used to meet that need. For example, N can be acquired in inorganic or organic forms, and the relative abundances of these forms may determine which form is targeted in a given ecosystem, owing to physiological trade-offs (240).

Certain stress tolerance traits were negatively related to decomposition traits, but these relationships were only significant as standard correlations (see Table S2 in the supplemental material). Specifically, gene frequencies for RNA helicase were negatively correlated with those for cellulase GH7, cellulase AA9, and lignin peroxidase (Spearman correlation *P* value of <0.001 in each case). In addition, β1,3-glucan synthase and cellulase GH7 were negatively correlated, albeit only marginally significantly (Spearman correlation $P = 0.099$). However, none of these relationships were significant when phylogenetic identities were taken into account (independent contrast *P* value of >0.10 in each case). This inconsistency may be due to the limited phylogenetic distribution of the decomposer traits—they are evident in only a few subphyla. Thus, there was relatively little variation in contrasts of the decomposer traits, especially compared to contrasts of the stress tolerance traits. Altogether, we are cautious in how we interpret these relationships. It seems that fungal taxa that possessed these specific stress tolerance traits were less likely to perform cellulose or lignin breakdown, and vice versa. This information is useful for predicting ecosystem-level responses to environmental conditions. Nevertheless, we do not have strong evidence for an evolutionary or

physiological trade-off that drives this pattern, since it is not phylogenetically independent. Perhaps as more whole genomes within the Dikarya are sequenced, we will have a higher statistical power to detect phylogenetically independent relationships between stress tolerance and decomposer traits.

Environmentally Induced Shifts in Fungal Groups

Since fungal phyla and subphyla vary in their genetic capacity for stress tolerance (Fig. 4), we might expect their environmental distributions to covary accordingly, with stress tolerators occupying harsher climates. In a recent large-scale study, Treseder et al. (241) reported that ancient fungal phyla were relatively constrained to regions with higher precipitation levels, whereas younger phyla occurred in dry as well as wet ecosystems. The underlying physiological or morphological trait driving these differences in environmental preferences remained unknown. However, we found that the capacity to produce β1,3-glucan was linked to the preferred precipitation levels of fungi (Fig. 7). For example, the members of the Cryptomycota, the oldest phylum, did not possess any known β1,3-glucan synthase genes. Correspondingly, they preferred wetter habitats, with average precipitation rates of 4,000 mm year^{-1}. In contrast, the younger phyla/subphyla preferred drier sites, with the exception of the Glomeromycota, which contained the lowest frequency of β1,3-glucan synthase genes in this group. It is possible that the capacity to produce β1,3-glucan may be an important trait that allows fungi to tolerate drought stresses typical of ecosystems with low rainfall levels.

In a high-latitude boreal forest, Allison et al. (242) used greenhouses to simultaneously increase soil temperature and decrease soil moisture and then assessed changes in fungal community composition. In this ecosystem, ambient soil conditions are quite cold and dry, so the manipulations exacerbated drought while ameliorating temperature extremes (242). For the current study, we reanalyzed their community data and found that phyla/subphyla that responded most positively to warming and drying were those that carried higher frequencies of trehalase genes (Fig. 8). This response is consistent with our understanding of the role of trehalose in resistance to desiccation in fungi (120).

Likewise, Lennon et al. (207) recently reported that fungal taxa differed in preferred moisture availability under laboratory conditions. They assayed yeasts as well as free-living filamentous fungi. In a follow-up analysis of their published data, we observed that the yeasts displayed significantly lower optimum water potentials (i.e., greater drought tolerance) than those of free-living filamentous fungi (Fig. 9). Other researchers have found that yeasts are common in glacier ice in Antarctica and elsewhere, where water availability and temperature are extremely low (243, 244). These patterns are consistent with our findings of particularly high frequencies of genes related to stress tolerance in yeasts (Fig. 5).

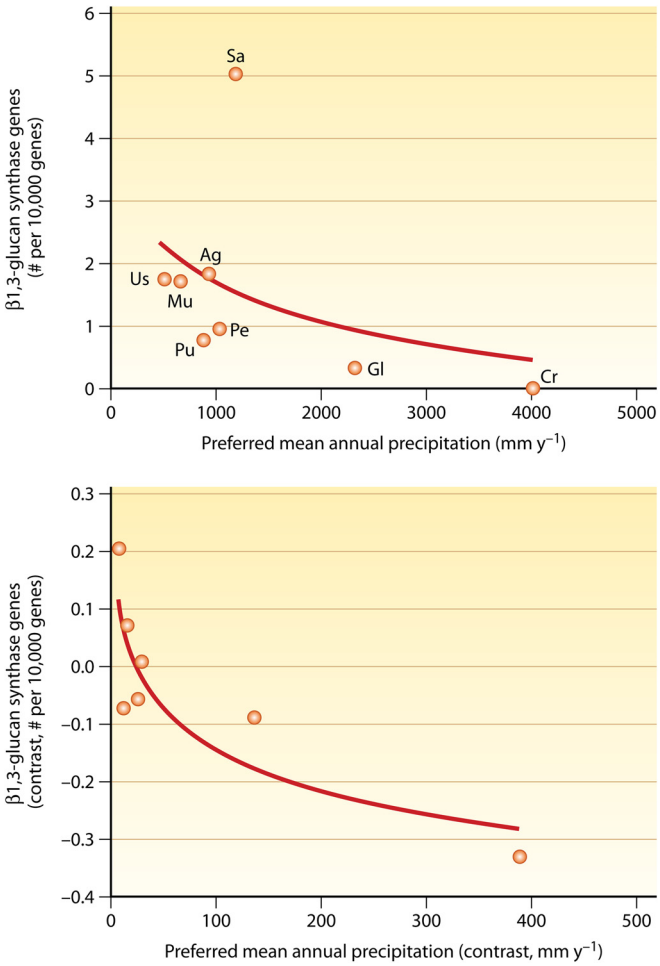

FIG 7 Relationship between preferred mean annual precipitation and frequency of β1,3-glucan synthase genes among fungal phyla (or subphyla, for Dikarya) (upper panel), with corresponding phylogenetically independent contrasts (lower panel). In the upper panel, symbols show the means for the fungal phyla/subphyla detected in a survey of soil fungi from North and South America. In the lower panel, symbols represent the contrast at each phylogenetic node (see Fig. 4 for the phylogenetic tree). Logarithmic lines show the best fit. "Preferred mean annual precipitation" is the average mean annual precipitation of all ecosystems in which a given taxon was detected in a survey of soils from North and South America; these data are from the work of Treseder et al. (241). The mean frequency of β1,3-glucan synthase genes for each phylum/subphylum was calculated as described in the legend to Fig. 4. Fungal phyla/subphyla that possessed higher frequencies of β1,3-glucan synthase genes were found in significantly drier ecosystems (phylogenetically independent contrast; $r = -0.813$; $P = 0.026$). Ag, Agaricomycotina; Cr, Cryptomycota; Gl, Glomeromycota; Mu, Mucoromycotina; Pe, Pezizomycotina; Pu, Pucciniomycotina; Sa, Saccharomycotina; Us, Ustilaginomycotina.

IMPLICATIONS

Altogether, our analyses indicate that ecosystem-related traits are unequally distributed among fungi, in a way that creates at least two distinct functional groups of fungi: stress tolerators (yeasts) and competitors (free-living filamentous fungi). Accordingly, our findings support the trade-off between these two fungal groups as theorized by Crowther and colleagues (227). These functional groups can form distinct feedbacks on ecosystem function owing to their possession of different response and effect traits. Specifically, drought or other extreme conditions can select for stress-tolerant fungi that might lead to soil C accumulation via their production of recalcitrant C residues derived from β1,3-glucan, for example (Fig. 2). In contrast, less stressful conditions may favor competitive fungi that more effectively decompose recalcitrant C compounds, such as lignin and cellulose. If these responses occur over a large scale, then global change-induced increases in extreme environmental conditions might lead to slower losses of soil C via shifts in the relative abundances of these functional groups. At the same time, in regions where environmental condi-

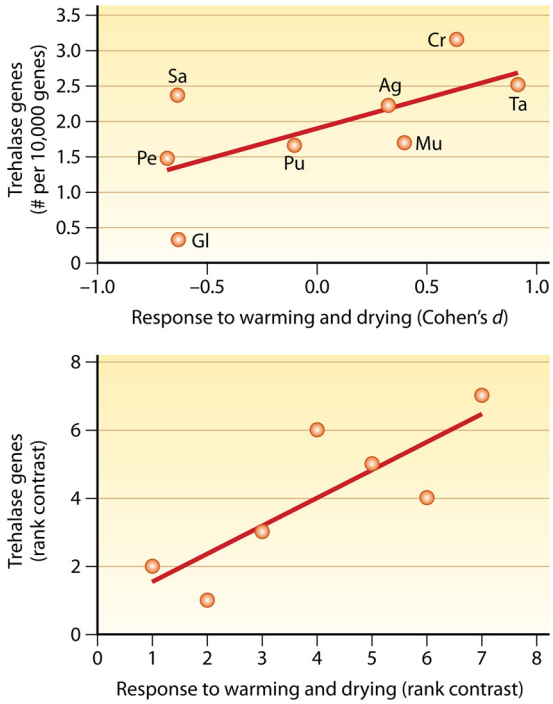

FIG 8 Relationship between frequency of trehalase genes and response to warming and drying among fungal phyla (or subphyla, for Dikarya) (upper panel), with associated phylogenetically independent contrasts (lower panel), detected in a climate manipulation experiment in an Alaskan boreal forest (242). In the upper panel, symbols represent means for the phyla/subphyla. In the lower panel, symbols represent the contrast at each phylogenetic node (see Fig. 4 for the phylogenetic tree); values were ranked to avoid an undue influence of outliers. Lines show the best fit. The mean frequency of trehalase genes for each phylum/subphylum was calculated as described in the legend to Fig. 4. The response to warming and drying of each fungal taxon was calculated as the Cohen's *d* effect size (298) and averaged within each phylum/subphylum. Cohen's *d* is the difference between the treatment mean and the control mean divided by the pooled standard deviation. Larger values of Cohen's *d* indicate stronger increases in relative abundance in response to warming and drying. Ag, Agaricomycotina; Cr, Cryptomycota; Gl, Glomeromycota; Mu, Mucoromycotina; Pe, Pezizomycotina; Pu, Pucciniomycotina; Sa, Saccharomycotina; Ta, Taphrinomycotina. Fungal phyla/subphyla with higher frequencies of trehalase genes became significantly more prevalent under warmer and drier conditions (phylogenetically independent contrast; $r = 0.821$; $P = 0.023$).

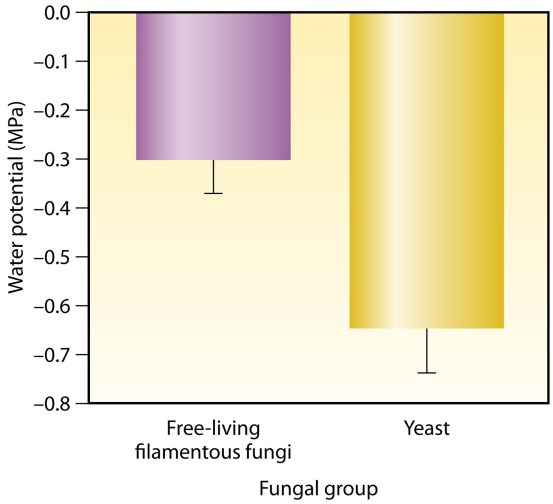

FIG 9 Difference in drought tolerance between free-living filamentous fungi and yeasts in a laboratory study by Lennon et al. (207). A more negative optimal water potential indicates greater drought tolerance. Bars show means and 1 SE. Yeasts were significantly more drought tolerant than were free-living filamentous fungi (Kruskal-Wallis test; $H = 53.5$; $P = 0.020$). The taxa representing free-living filamentous fungi were *Hypocrea* (2 isolates), *Mucor*, *Penicillium* (2 isolates), *Rhizopus*, *Schizophyllum*, *Trametes*, and *Umbelopsis*, and those representing yeasts were *Galactomyces*, *Geotrichum*, and *Trichosporon* (5 isolates).

tions become less extreme, we may observe increased losses of soil C. Essentially, this knowledge of the distribution of—and relationships between—fungal traits might improve our predictions of ecosystem function in response to global change.

Mycorrhizal fungi are an additional morphological (and ecological) group that was not positively related to any of the functional gene-based traits that we examined. To date, their defining characteristic—symbioses with plant roots—is not associated with known universal genes (245). In addition, only three published genomes of mycorrhizal fungi were available when we conducted our analyses, which limited our ability to detect phylogenetically independent differences between mycorrhizal fungi and other groups. Nevertheless, mycorrhizal fungi are common in many fungal communities and are globally distributed (246, 247). Their root-associated structures are also relatively easy to identify (248). Since their ecological functions have long been studied, we know that they typically improve plant growth (reviewed in reference 10) and net primary productivity. Although they can act as "decomposers in disguise" (reviewed in reference 249), their capacity for breakdown of complex organic C is relatively low (115, 250). In addition, ectomycorrhizal root tips and rhizomorphs can be long-lived and slow to decompose (45, 251–257), which can contribute to microbial immobilization of C, N, and P. Altogether, mycorrhizal fungi may augment soil C storage (30, 42, 255, 258, 259). Moreover, their abundance is influenced not only directly by climate and nutrient availability but also by the presence and activities of host plants (260–262). For instance, mycorrhizal fungi often decline upon exposure to anthropogenic N enrichment, ostensibly because host plants reduce their investment in mycorrhizal fungi when soil nutrients become less limiting to plant growth (reviewed in reference 263). These fungi merit consideration as a separate functional group with distinct responses to environmental conditions, even though they do not readily fit within the competitor/stress tolerator dichotomy.

Pathogenic fungi can also influence ecosystem processes by altering the function or population dynamics of other organisms (264). Nevertheless, these interactions are complex, and their ecosystem consequences depend upon traits of the target organisms as well as the pathogens. As such, a discussion of ecosystem-related traits of pathogenic fungi is beyond the scope of this review.

INTEGRATING FUNGAL TRAITS INTO ECOSYSTEM MODELS

Conventional ecosystem models do not contain many microbial details—most represent microbes as a single undifferentiated pool of biomass that uniformly transforms C, N, or P in response to environmental conditions (265). Thus, they are not necessarily structured in a way that facilitates the incorporation of fungal traits or functional groups (32). Instead, next-generation models with this capability were recently constructed (28-30, 266). One of the first was developed for ocean microbes by Follows et al. (266). Allison (28) used a similar approach for soils in his decomposition

model of enzymatic traits (DEMENT). In DEMENT, individual microbial taxa are represented, and they can be assigned suites of traits based on empirically derived relationships among traits (or theoretical trade-offs among traits) (28). Taxa then independently respond to environmental conditions, conduct ecosystem-relevant processes, and interact with one another based on their complements of traits. Relatively simple traits with known effects on ecosystem function—such as those we reviewed here—are most useful for these models. By integrating these activities, trait-informed models may better predict not only ecosystem function but also microbial community composition.

A number of approaches could be used to incorporate fungal traits into trait-based models such as DEMENT. First, we could model an ecosystem with highly diverse (i.e., hundreds to thousands) fungal species and assign traits to species based on observed relationships among traits (e.g., as in Fig. 6). In this case, the taxonomic identities of species need not be defined if we use trait relationships that are phylogenetically independent. Second, we could create a model ecosystem with known fungal subphyla (or phyla, orders, etc., as appropriate), each with its own set of traits as defined by representative genomes (e.g., as in Fig. 4). Third, we could simply use the three morphological groups (free-living filamentous fungi, yeasts, and mycorrhizal fungi) and their traits (e.g., as in Fig. 5). The best approach might vary by study, depending on the research question, the availability of trait information with which to parameterize the model, and the characterization of fungal communities for model validation. For instance, complements of functional genes derived from environmental metagenomics or metatranscriptomics could be used to test the predictive capability of the first modeling approach, taxonomic identities of communities the second, and microscopic assessments the third.

CONCLUSIONS

In the past few decades, we have learned a great deal about fungal traits that drive ecosystem functions. For instance, numerous empirical studies have established that fungal taxa are not functionally equivalent in their contributions to decomposition, nutrient transformations, and formation of fungal residues, nor do all fungi respond similarly to environmental stressors. Whole-genome sequences support these findings, since distributions of related functional genes vary among fungal phyla, subphyla, and so forth. Moreover, two distinct suites of ecosystem-related traits tend to occur within fungal taxa: the genetic capacity to decompose complex organic C versus the genetic capacity to tolerate environmental stress. Genes for N and P acquisition are more loosely distributed, perhaps because N and P can be obtained from diverse sources. Notably, free-living filamentous fungi are more likely to possess traits related to decomposition, whereas yeasts are more likely to possess traits related to stress tolerance. These distinctions are perhaps not surprising, given the documented tendency for yeasts to dominate extreme environments, such as Antarctic glaciers, and for free-living filamentous fungi to break down recalcitrant substrates, such as wood.

We found that by binning taxa within taxonomic groups (e.g., phyla/subphyla) or morphological groups (e.g., free-living filamentous fungi versus yeasts), we can identify traits that are related to previously published environmental responses of fungi. By taking this approach, we can broadly explore potential mechanisms influencing shifts in fungal community composition in response to environmental conditions, as well as potential effects on ecosystem function. Knowledge of the taxonomic resolution of relevant traits can also be useful for researchers who are analyzing sequence data for fungal communities. Historically, taxa have frequently been defined by binning at 97% sequence similarity (267, 268), but other delineations may coincide better with ecological functions of interest (269–271). Finally, our knowledge of fungal traits can be synthesized in next-generation ecosystem models to improve our predictions of ecosystem responses to global change. Altogether, this research area requires the integration of fungal taxonomy, microbial ecology, genomics, and ecosystem modeling. This is certainly a challenging endeavor, but one that we are increasingly capable of meeting—especially given the astounding rates of progress currently witnessed in each of these areas.

ACKNOWLEDGMENTS

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REFERENCES

1. **Dighton J.** 2003. Fungi in ecosystem processes, vol 17. Marcel Dekker, New York, NY.
2. **Chapin FS, Matson PA, Vitousek PM, Chapin MC.** 2011. Principles of terrestrial ecosystem ecology, 2nd ed. Springer, New York, NY.
3. **Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE.** 2011. Persistence of soil organic matter as an ecosystem property. Nature **478:**49–56. http://dx.doi.org/10.1038/nature10386.
4. **Kogel-Knabner I.** 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol Biochem **34:**139–162. http://dx.doi.org/10.1016/S0038-0717(01)00158-4.
5. **Six J, Frey SD, Thiet RK, Batten KM.** 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci Soc Am J **70:**555–569. http://dx.doi.org/10.2136/sssaj2004.0347.
6. **Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD.** 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science **339:**1615–1618. http://dx.doi.org/10.1126/science.1231923.
7. **Sinsabaugh RL.** 1994. Enzymatic analysis of microbial pattern and process. Biol Fertil Soils **17:**69–74. http://dx.doi.org/10.1007/BF00418675.
8. **Sinsabaugh RL, Antibus RK, Linkins AE, McClaugherty CA, Rayburn L, Repert D, Weiland T.** 1993. Wood decomposition—nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology **74:**1586–1593. http://dx.doi.org/10.2307/1940086.
9. **Schimel JP, Bennett J.** 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology **85:**591–602. http://dx.doi.org/10.1890/03-8002.
10. **Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umbanhowar J.** 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett **13:**394–407. http://dx.doi.org/10.1111/j.1461-0248.2009.01430.x.
11. **Waring BG, Averill C, Hawkes CV.** 2013. Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: insights from meta-analysis and theoretical models. Ecol Lett **16:**887–894. http://dx.doi.org/10.1111/ele.12125.
12. **Joergensen RG, Emmerling C.** 2006. Methods for evaluating human impact on soil microorganisms based on their activity, biomass, and

diversity in agricultural soils. J Plant Nutr Soil Sci **169:**295–309. http://dx.doi.org/10.1002/jpln.200521941.
13. **Taylor DL, Hollingsworth TN, McFarland J, Lennon NJ, Nusbaum C, Ruess RW.** 2013. A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. Ecol Monogr **84:** 3–20. http://dx.doi.org/10.1890/12-1693.1.
14. **Hawksworth DL.** 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycol Res **105:**1422–1432. http://dx.doi.org/10.1017/S0953756201004725.
15. **O'Brien HE, Parrent JL, Jackson JA, Moncalvo JM, Vilgalys R.** 2005. Fungal community analysis by large-scale sequencing of environmental samples. Appl Environ Microbiol **71:**5544–5550. http://dx.doi.org/10.1128/AEM.71.9.5544-5550.2005.
16. **Hawksworth DL.** 2012. Global species numbers of fungi: are tropical studies and molecular approaches contributing to a more robust estimate? Biodivers Conserv **21:**2425–2433. http://dx.doi.org/10.1007/s10531-012-0335-x.
17. **Blackwell M.** 2011. The fungi: 1, 2, 3. . .5.1 million species? Am J Bot **98:**426–438. http://dx.doi.org/10.3732/ajb.1000298.
18. **Kirk P, Cannon P, Minter D, Stalpers J.** 2008. Ainsworth and Bisby's dictionary of the fungi, 10th ed. CABI, Wallingford, United Kingdom.
19. **Hibbett DS, Ohman A, Glotzer D, Nuhn M, Kirk P, Nilsson RH.** 2011. Progress in molecular and morphological taxon discovery in fungi and options for formal classification of environmental sequences. Fungal Biol Rev **25:**38–47. http://dx.doi.org/10.1016/j.fbr.2011.01.001.
20. **Starmer WT, Lachance M.** 2011. Yeast ecology, p 65–83. *In* Kurtzman CP, Fell JW, Boekhout T (ed), The yeasts, a taxonomic study, vol 1. Elsevier, Amsterdam, Netherlands.
21. **Smith SE, Read DJ.** 2008. Mycorrhizal symbiosis, 3rd ed. Academic Press, San Diego, CA.
22. **Alexopoulos CJ, Mims CW, Blackwell M.** 1996. Introductory mycology, 4th ed. John Wiley & Sons, Inc, New York.
23. **Margesin R, Gander S, Zacke G, Gounot AM, Schinner F.** 2003. Hydrocarbon degradation and enzyme activities of cold-adapted bacteria and yeasts. Extremophiles **7:**451–458. http://dx.doi.org/10.1007/s00792-003-0347-2.
24. **Maggi O, Tosi S, Angelova M, Lagostina E, Fabbri AA, Pecoraro L, Altobelli E, Picco AM, Savino E, Branda E, Turchetti B, Zotti M, Vizzini A, Buzzini P.** 2012. Adaptation of fungi, including yeasts, to cold environments. Plant Biosyst **147:**247–258. http://dx.doi.org/10.1080/11263504.2012.753135.
25. **IPCC.** 2014. Climate change 2013: the physical science basis: Working Group I contribution to the fifth assessment report of the International Panel on Climate Change. Cambridge University Press, London, United Kingdom.
26. **Krause S, Le Roux X, Niklaus PA, Van Bodegom PM, Lennon JT, Bertilsson S, Grossart H-P, Philippot L, Bodelier PLE.** 2014. Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. Front Microbiol **5:**251. http://dx.doi.org/10.3389/fmicb.2014.00251.
27. **Schimel JP, Bennett J, Fierer N.** 2004. Microbial community composition and soil N cycling: is there really a connection? 2003 Annual Symposium: Soil Biodiversity and Function, vol 44. British Ecological Society, Lancaster, United Kingdom.
28. **Allison SD.** 2012. A trait-based approach for modelling microbial litter decomposition. Ecol Lett **15:**1058–1070. http://dx.doi.org/10.1111/j.1461-0248.2012.01807.x.
29. **Moorhead DL, Sinsabaugh RL.** 2006. A theoretical model of litter decay and microbial interaction. Ecol Monogr **76:**151–174. http://dx.doi.org/10.1890/0012-9615(2006)076[0151:ATMOLD]2.0.CO;2.
30. **Orwin KH, Kirschbaum MUF, St John MG, Dickie IA.** 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecol Lett **14:**493–502. http://dx.doi.org/10.1111/j.1461-0248.2011.01611.x.
31. **Wieder WR, Grandy AS, Kallenbach CM, Bonan GB.** 2014. Integrating microbial physiology and physio-chemical principles in soils with the microbial-mineral carbon stabilization (MIMICS) model. Biogeosciences **11:**3899–3917. http://dx.doi.org/10.5194/bg-11-3899-2014.
32. **Todd-Brown KEO, Hopkins FM, Kivlin SN, Talbot JM, Allison SD.** 2012. A framework for representing microbial decomposition in coupled climate models. Biogeochemistry **109:**19–33. http://dx.doi.org/10.1007/s10533-011-9635-6.
33. **Treseder KK, Balser TC, Bradford MA, Brodie EL, Dubinsky EA, Eviner VT, Hofmockel KS, Lennon JT, Levine UY, MacGregor BJ, Pett-Ridge J, Waldrop MP.** 2012. Integrating microbial ecology into ecosystem models: challenges and priorities. Biogeochemistry **109:**7–18. http://dx.doi.org/10.1007/s10533-011-9636-5.
34. **Wang G, Jagadamma S, Mayes MA, Schadt CW, Steinweg JM, Gu L, Post WM.** 2015. Microbial dormancy improves development and experimental validation of ecosystem model. ISME J **9:**226–237. http://dx.doi.org/10.1038/ismej.2014.120.
35. **Lavorel S, Garnier E.** 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol **16:**545–556. http://dx.doi.org/10.1046/j.1365-2435.2002.00664.x.
36. **Levins R.** 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.
37. **Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NG.** 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature **424:**303–306. http://dx.doi.org/10.1038/nature01767.
38. **Somero GN.** 1995. Proteins and temperature. Annu Rev Physiol **57:**43–68. http://dx.doi.org/10.1146/annurev.ph.57.030195.000355.
39. **Bennett AF, Lenski RE.** 2007. An experimental test of evolutionary trade-offs during temperature adaptation. Proc Natl Acad Sci U S A **104:**8649–8654. http://dx.doi.org/10.1073/pnas.0702117104.
40. **Livermore JA, Emrich SJ, Tan J, Jones SE.** 2014. Freshwater bacterial lifestyles inferred from comparative genomics. Environ Microbiol **16:** 746–758. http://dx.doi.org/10.1111/1462-2920.12199.
41. **Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D.** 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytol **167:**493–508. http://dx.doi.org/10.1111/j.1469-8137.2005.01428.x.
42. **Koide RT, Fernandez C, Malcolm G.** 2014. Determining place and process: functional traits of ectomycorrhizal fungi that affect both community structure and ecosystem function. New Phytol **201:**433–439. http://dx.doi.org/10.1111/nph.12538.
43. **Pigott CD.** 1982. Survival of mycorrhiza formed by *Cenococcum geophilum* FR in dry soils. New Phytol **92:**513–517. http://dx.doi.org/10.1111/j.1469-8137.1982.tb03409.x.
44. **Malik KA, Haider K.** 1982. Decomposition of ^{14}C-labeled melanoid fungal residues in marginally sodic soil. Soil Biol Biochem **14:**457–460. http://dx.doi.org/10.1016/0038-0717(82)90104-3.
45. **Fernandez CW, McCormack ML, Hill JM, Pritchard SG, Koide RT.** 2013. On the persistence of *Cenococcum geophilum* ectomycorrhizas and its implications for forest carbon and nutrient cycles. Soil Biol Biochem **65:**141–143. http://dx.doi.org/10.1016/j.soilbio.2013.05.022.
46. **Fernandez CW, Koide RT.** 2014. Initial melanin and nitrogen concentrations control the decomposition of ectomycorrhizal fungal litter. Soil Biol Biochem **77:**150–157. http://dx.doi.org/10.1016/j.soilbio.2014.06.026.
47. **Klein DA, Paschke MW.** 2004. Filamentous fungi: the indeterminate lifestyle and microbial ecology. Microb Ecol **47:**224–235. http://dx.doi.org/10.1007/s00248-003-1037-4.
48. **Kurtzman CP, Fell JW, Boekhout T.** 2011. Definition, classification, and nomenclature of yeasts, p 3–5. *In* Kurtzman CP, Fell JW, Boekhout T (ed), The yeasts, a taxonomic study, vol 1. Elsevier, Amsterdam, Netherlands.
49. **Cairney JWG.** 2005. Basidiomycete mycelia in forest soils: dimensions, dynamics and roles in nutrient distribution. Mycol Res **109:**7–20. http://dx.doi.org/10.1017/S0953756204001753.
50. **Boddy L.** 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. Mycologia **91:**13–32. http://dx.doi.org/10.2307/3761190.
51. **James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung GH, Johnson D, O'Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schussler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lucking R, Budel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R.** 2006. Reconstructing the early evolution

of Fungi using a six-gene phylogeny. Nature **443:**818–822. http://dx.doi.org/10.1038/nature05110.
52. **Stajich JE, Berbee ML, Blackwell M, Hibbett DS, James TY, Spatafora JW, Taylor JW.** 2009. The Fungi. Curr Biol **19:**R840–R845. http://dx.doi.org/10.1016/j.cub.2009.07.004.
53. **James TY, Pelin A, Bonen L, Ahrendt S, Sain D, Corradi N, Stajich JE.** 2013. Shared signatures of parasitism and phylogenomics unite Cryptomycota and Microsporidia. Curr Biol **23:**1548–1553. http://dx.doi.org/10.1016/j.cub.2013.06.057.
54. **Webb CO, Ackerly DD, Kembel SW.** 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics **24:**2098–2100. http://dx.doi.org/10.1093/bioinformatics/btn358.
55. **Webb CO, Ackerly DD, McPeek MA, Donoghue MJ.** 2002. Phylogenies and community ecology. Annu Rev Ecol Evol Syst **33:**475–505. http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150448.
56. **Klemm D, Heublein B, Fink H-P, Bohn A.** 2005. Cellulose: fascinating biopolymer and sustainable raw material. Angew Chem Int Ed Engl **36:**3358–3393. http://dx.doi.org/10.1002/anie.200460587.
57. **Lynd LR, Weimer PJ, van Zyl WH, Pretorius IS.** 2002. Microbial cellulose utilization: fundamentals and biotechnology. Microbiol Mol Biol Rev **66:**506–577. http://dx.doi.org/10.1128/MMBR.66.3.506-577.2002.
58. **Edwards IP, Upchurch RA, Zak DR.** 2008. Isolation of fungal cellobiohydrolase I genes from sporocarps and forest soils by PCR. Appl Environ Microbiol **74:**3481–3489. http://dx.doi.org/10.1128/AEM.02893-07.
59. **Levasseur A, Drula E, Lombard V, Coutinho PM, Henrissat B.** 2013. Expansion of the enzymatic repertoire of the CAZy database to integrate auxiliary redox enzymes. Biotechnol Biofuels **6:**41. http://dx.doi.org/10.1186/1754-6834-6-41.
60. **Langston JA, Shaghasi T, Abbate E, Xu F, Vlasenko E, Sweeney MD.** 2011. Oxidoreductive cellulose depolymerization by the enzymes cellobiose dehydrogenase and glycoside hydrolase 61. Appl Environ Microbiol **77:**7007–7015. http://dx.doi.org/10.1128/AEM.05815-11.
61. **Harris PV, Welner D, McFarland KC, Re E, Poulsen JCN, Brown K, Salbo R, Ding HS, Vlasenko E, Merino S, Xu F, Cherry J, Larsen S, Lo Leggio L.** 2010. Stimulation of lignocellulosic biomass hydrolysis by proteins of glycoside hydrolase family 61: structure and function of a large, enigmatic family. Biochemistry **49:**3305–3316. http://dx.doi.org/10.1021/bi100009p.
62. **Sasikala G, Gopal NO.** 2014. Evaluation and selection of native fungal isolates for cellulase enzyme production. Res J Biotechnol **9:**22–29.
63. **Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, Spatafora JW, Yadav JS, Aerts A, Benoit I, Boyd A, Carlson A, Copeland A, Coutinho PM, de Vries RP, Ferreira P, Findley K, Foster B, Gaskell J, Glotzer D, Górecki P, Heitman J, Hesse C, Hori C, Igarashi K, Jurgens JA, Kallen N, Kersten P, Kohler A, Kües U, Kumar TKA, Kuo A, LaButti K, Larrondo LF, Lindquist E, Ling A, Lombard V, Lucas S, Lundell T, Martin R, McLaughlin DJ, Morgenstern I, Morin E, Murat C, Nagy LG, Nolan M, Ohm RA, Patyshakuliyeva A, Rokas A, Ruiz-Dueñas FJ, Sabat G, Salamov A, Samejima M, Schmutz J, Slot JC, St John F, Stenlid J, Sun H, Sun S, Syed K, Tsang A, Wiebenga A, Young D, Pisabarro A, Eastwood DC, Martin F, Cullen D, Grigoriev IV, Hibbett DS.** 2012. The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. Science **336:**1715–1719. http://dx.doi.org/10.1126/science.1221748.
64. **Riley R, Salamov AA, Brown DW, Nagy LG, Floudas D, Held BW, Levasseur A, Lombard V, Morin E, Otillar R, Lindquist EA, Sun H, LaButti KM, Schmutz J, Jabbour D, Luo H, Baker SE, Pisabarro AG, Walton JD, Blanchette RA, Henrissat B, Martin F, Cullen D, Hibbett DS, Grigoriev IV.** 2014. Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. Proc Natl Acad Sci U S A **111:**9923–9928. http://dx.doi.org/10.1073/pnas.1400592111.
65. **Lee SS, Ha JK, Kang HS, McAllister TA, Cheng KJ.** 1997. Overview of energy metabolism, substrate utilization and fermentation characteristics of ruminal anaerobic fungi. Korean J Anim Nutr Feedstuffs **21:**295–314.
66. **Martínez ÁT, Ruiz-Dueñas FJ, Martínez MJ, del Río JC, Gutiérrez A.** 2009. Enzymatic delignification of plant cell wall: from nature to mill. Curr Opin Biotechnol **20:**348–357. http://dx.doi.org/10.1016/j.copbio.2009.05.002.
67. **Tien M, Kirk TK.** 1983. Lignin-degrading enzyme from the hymenomycete *Phanerochaete chrysosporium* burds. Science **221:**661–663. http://dx.doi.org/10.1126/science.221.4611.661.
68. **Bugg TDH, Ahmad M, Hardiman EM, Rahmanpour R.** 2011. Pathways for degradation of lignin in bacteria and fungi. Nat Prod Rep **28:**1883–1896. http://dx.doi.org/10.1039/c1np00042j.
69. **Schlesinger WH.** 1977. Carbon balance in terrestrial detritus. Annu Rev Ecol Evol Syst **8:**51–81. http://dx.doi.org/10.1146/annurev.es.08.110177.000411.
70. **Talbot JM, Treseder KK.** 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry-decay relationships. Ecology **9:**345–354. http://dx.doi.org/10.1890/11-0843.1.
71. **Tien M, Tu CPD.** 1987. Cloning and sequencing of a cDNA for a ligninase from *Phanerochaete chrysosporium*. Nature **326:**520–523. http://dx.doi.org/10.1038/326520a0.
72. **Ruiz-Dueñas FJ, Morales M, García E, Miki Y, Martínez MJ, Martínez AT.** 2009. Substrate oxidation sites in versatile peroxidase and other basidiomycete peroxidases. J Exp Bot **60:**441–452. http://dx.doi.org/10.1093/jxb/ern261.
73. **Walker TW, Syers JK.** 1976. Fate of phosphorus during pedogenesis. Geoderma **15:**1–19. http://dx.doi.org/10.1016/0016-7061(76)90066-5.
74. **Barrow NJ.** 1961. Phosphorus in soil organic matter. Soils Fertilizers **24:**169–173.
75. **McGill WB, Cole CV.** 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. Geoderma **26:**267–286. http://dx.doi.org/10.1016/0016-7061(81)90024-0.
76. **Gianinazzi S, Gianinazzi-Pearson V, Dexheimer J.** 1979. Enzymatic studies on the metabolism of vesicular-arbuscular mycorrhiza. III. Ultrastructural localisation of acid and alkaline phosphatase in onion roots infected by *Glomus*. New Phytol **82:**127–132.
77. **Ho I, Zak B.** 1979. Acid phosphatase activity of six ectomycorrhizal fungi. Can J Bot **57:**1203–1205. http://dx.doi.org/10.1139/b79-144.
78. **Dighton J.** 1983. Phosphatase production by mycorrhizal fungi. Plant Soil **71:**455–462. http://dx.doi.org/10.1007/BF02182686.
79. **Read DJ, Leake JR, Perez-Moreno J.** 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can J Bot **82:**1243–1263. http://dx.doi.org/10.1139/b04-123.
80. **Nelson RE, Lehman JF, Metzenberg RL.** 1976. Regulation of phosphate metabolism in *Neurospora crassa*: identification of the structural gene responsible for repressible acid phosphatase. Genetics **84:**183–192.
81. **Han SW, Nahas E, Rossi A.** 1987. Regulation of synthesis and secretion of acid and alkaline phosphatases in *Neurospora crassa*. Curr Genet **11:**521–527. http://dx.doi.org/10.1007/BF00384615.
82. **Payne WE, Gannon PM, Kaiser CA.** 1995. An inducible acid-phosphatase from the yeast *Pichia pastoris*—characterization of the gene and its product. Gene **163:**19–26. http://dx.doi.org/10.1016/0378-1119(95)00379-K.
83. **Rosenberger RF.** 1976. The cell wall, p 328–344. *In* Smith JE, Berry D (ed), The filamentous fungi, biosynthesis and metabolism, vol 2. Arnold, London, United Kingdom.
84. **Gooday GW.** 1990. The ecology of chitin degradation. Adv Microb Ecol **11:**387–430. http://dx.doi.org/10.1007/978-1-4684-7612-5_10.
85. **Allison SD, Gartner TB, Holland K, Weintraub M, Sinsabaugh RL.** 2007. Soil enzymes: linking proteomics and ecological processes, p 704–711. *In* Hurst CJ, Crawford RL, Garland JL, Lipson DA, Mills AL, Stetzenbach LD (ed), Manual of environmental microbiology, 3rd ed. ASM Press, Washington, DC.
86. **Bajwa R, Read DJ.** 1986. Utilization of mineral and amino N sources by the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* and by mycorrhizal and non-mycorrhizal seedlings of *Vaccinium*. Mycol Res **87:**269–277.
87. **Tzelepis GD, Melin P, Jensen DF, Stenlid J, Karlsson M.** 2012. Functional analysis of glycoside hydrolase family 18 and 20 genes in *Neurospora crassa*. Fungal Genet Biol **49:**717–730. http://dx.doi.org/10.1016/j.fgb.2012.06.013.
88. **Leake JR, Read DJ.** 1990. Chitin as a nitrogen source for mycorrhizal fungi. Mycol Res **94:**993–995. http://dx.doi.org/10.1016/S0953-7562(09)81318-X.
89. **Kerley SJ, Read DJ.** 1995. The biology of mycorrhiza in the Ericaceae. XVIII. Chitin degradation by *Hymenoscyphus ericae* and transfer of chitin-nitrogen to the host plant. New Phytol **131:**369–375.
90. **Read DJ, Perez-Moreno J.** 2003. Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytol **157:**475–492. http://dx.doi.org/10.1046/j.1469-8137.2003.00704.x.
91. **Schulten HR, Schnitzer M.** 1997. The chemistry of soil organic ni-

trogen: a review. Biol Fertil Soils **26:**1–15. http://dx.doi.org/10.1007/s003740050335.
92. **Jones DL, Shannon D, Murphy DV, Farrar J.** 2004. Role of dissolved organic nitrogen (DON) in soil N cycling in grassland soils. Soil Biol Biochem **36:**749–756. http://dx.doi.org/10.1016/j.soilbio.2004.01.003.
93. **Jones DL, Healey JR, Willett VB, Farrar JF, Hodge A.** 2005. Dissolved organic nitrogen uptake by plants—an important N uptake pathway? Soil Biol Biochem **37:**413–423. http://dx.doi.org/10.1016/j.soilbio.2004.08.008.
94. **Gottesman S.** 1996. Proteases and their targets in *Escherichia coli*. Annu Rev Genet **30:**465–506. http://dx.doi.org/10.1146/annurev.genet.30.1.465.
95. **Chalot M, Brun A, Botton B, Soderstrom B.** 1996. Kinetics, energetics and specificity of a general amino acid transporter from the ectomycorrhizal fungus *Paxillus involutus*. Microbiology **142:**1749–1756. http://dx.doi.org/10.1099/13500872-142-7-1749.
96. **Nehls U, Kleber R, Wiese J, Hampp R.** 1999. Isolation and characterization of a general amino acid permease from the ectomycorrhizal fungus *Amanita muscaria*. New Phytol **144:**343–349. http://dx.doi.org/10.1046/j.1469-8137.1999.00513.x.
97. **Wipf D, Benjdia M, Tegeder M, Frommer WB.** 2002. Characterization of a general amino acid permease from *Hebeloma cylindrosporum*. FEBS Lett **528:**119–124. http://dx.doi.org/10.1016/S0014-5793(02)03271-4.
98. **Abuzinadah RA, Read DJ.** 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. 1. Utilization of peptides and proteins by ectomycorrhizal fungi. New Phytol **103:**481–493.
99. **Talbot JM, Treseder KK.** 2010. Controls over mycorrhizal uptake of organic nitrogen. Pedobiologia **53:**169–179. http://dx.doi.org/10.1016/j.pedobi.2009.12.001.
100. **Gresham D, Usaite R, Germann SM, Lisby M, Botstein D, Regenberg B.** 2010. Adaptation to diverse nitrogen-limited environments by deletion or extrachromosomal element formation of the GAP1 locus. Proc Natl Acad Sci U S A **107:**18551–18556. http://dx.doi.org/10.1073/pnas.1014023107.
101. **Grenson M, Hou C, Crabeel M.** 1970. Multiplicity of amino acid permeases in *Saccharomyces cerevisiae*. IV. Evidence for a general amino acid permease. J Bacteriol **103:**770–777.
102. **Jauniaux J-C, Grenson M.** 1990. GAP1, the general amino acid permease gene of *Saccharomyces cerevisiae*. Eur J Biochem **190:**39–44. http://dx.doi.org/10.1111/j.1432-1033.1990.tb15542.x.
103. **Cappellazzo G, Lanfranco L, Fitz M, Wipf D, Bonfante P.** 2008. Characterization of an amino acid permease from the endomycorrhizal fungus *Glomus mosseae*. Plant Physiol **147:**429–437. http://dx.doi.org/10.1104/pp.108.117820.
104. **Versaw WK, Metzenberg RL.** 1995. Repressible cation-phosphate symporters in *Neurospora crassa*. Proc Natl Acad Sci U S A **92:**3884–3887. http://dx.doi.org/10.1073/pnas.92.9.3884.
105. **Mitsuzawa H.** 2006. Ammonium transporter genes in the fission yeast *Schizosaccharomyces pombe*: role in ammonium uptake and a morphological transition. Genes Cells **11:**1183–1195. http://dx.doi.org/10.1111/j.1365-2443.2006.01014.x.
106. **Slot JC, Hallstrom KN, Matheny PB, Hibbett DS.** 2007. Diversification of NRT2 and the origin of its fungal homolog. Mol Biol Evol **24:**1731–1743. http://dx.doi.org/10.1093/molbev/msm098.
107. **Read ND, Kalkman ER.** 2003. Does endocytosis occur in fungal hyphae? Fungal Genet Biol **39:**199–203. http://dx.doi.org/10.1016/S1087-1845(03)00045-8.
108. **Higuchi Y, Shoji JY, Arioka M, Kitamoto K.** 2009. Endocytosis is crucial for cell polarity and apical membrane recycling in the filamentous fungus *Aspergillus oryzae*. Eukaryot Cell **8:**37–46. http://dx.doi.org/10.1128/EC.00207-08.
109. **Penalva MA.** 2005. Tracing the endocytic pathway of *Aspergillus nidulans* with FM4-64. Fungal Genet Biol **42:**963–975. http://dx.doi.org/10.1016/j.fgb.2005.09.004.
110. **Dulic V, Egerton M, Elguindi I, Raths S, Singer B, Riezman H.** 1991. Yeast endocytosis assays. Methods Enzymol **194:**697–710. http://dx.doi.org/10.1016/0076-6879(91)94051-D.
111. **Geli MI, Riezman H.** 1998. Endocytic internalization in yeast and animal cells: similar and different. J Cell Sci **111:**1031–1037.
112. **Galletta BJ, Cooper JA.** 2009. Actin and endocytosis: mechanisms and phylogeny. Curr Opin Cell Biol **21:**20–27. http://dx.doi.org/10.1016/j.ceb.2009.01.006.
113. **Lilleskov EA, Hobbie EA, Fahey TJ.** 2002. Ectomycorrhizal fungal taxa differing in response to nitrogen deposition also differ in pure culture organic nitrogen use and natural abundance of nitrogen isotopes. New Phytol **154:**219–231. http://dx.doi.org/10.1046/j.1469-8137.2002.00367.x.
114. **Cairney JWG.** 1999. Intraspecific physiological variation: implications for understanding functional diversity in ectomycorrhizal fungi. Mycorrhiza **9:**125–135. http://dx.doi.org/10.1007/s005720050297.
115. **Plett JM, Martin F.** 2011. Blurred boundaries: lifestyle lessons from ectomycorrhizal fungal genomes. Trends Genet **27:**14–22. http://dx.doi.org/10.1016/j.tig.2010.10.005.
116. **Jonasson S, Michelsen A, Schmidt IK.** 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Appl Soil Ecol **11:**135–146. http://dx.doi.org/10.1016/S0929-1393(98)00145-0.
117. **Smith JL, Paul EA.** 1990. The significance of soil microbial biomass estimations, p 357–396. *In* Bollag J, Stotzky G (ed), Soil biochemistry. Marcel Dekker, New York, NY.
118. **Walbridge MR, Richardson CJ, Swank WT.** 1991. Vertical distribution of biological and geochemical phosphorus subcycles in two southern Appalachian forest soils. Biogeochemistry **13:**61–85.
119. **Wardle DA.** 1992. A comparative assessment of factors which influence microbial biomass, carbon, and nitrogen levels in soil. Biol Rev Camb Philos Soc **67:**321–358. http://dx.doi.org/10.1111/j.1469-185X.1992.tb00728.x.
120. **Schimel J, Balser TC, Wallenstein M.** 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology **88:**1386–1394. http://dx.doi.org/10.1890/06-0219.
121. **Rosswall T.** 1982. Microbiological regulation of the biogeochemical nitrogen cycle. Plant Soil **67:**15–34. http://dx.doi.org/10.1007/BF02182752.
122. **Schlesinger WH, Bernhardt ES.** 2013. Biogeochemistry: an analysis of global change, 3rd ed. Elsevier Science, Maryland Height, MO.
123. **Shoun H, Fushinobu S, Jiang L, Kim SW, Wakagi T.** 2012. Fungal denitrification and nitric oxide reductase cytochrome P450nor. Philos Trans R Soc B Biol Sci **367:**1186–1194. http://dx.doi.org/10.1098/rstb.2011.0335.
124. **Shoun H, Kim DH, Uchiyama H, Sugiyama J.** 1992. Denitrification by fungi. FEMS Microbiol Lett **94:**277–281. http://dx.doi.org/10.1111/j.1574-6968.1992.tb05331.x.
125. **Shoun H, Tanimoto T.** 1991. Denitrification by the fungus *Fusarium oxysporum* and involvement of cytochrome-P-450 in the respiratory nitrite reduction. J Biol Chem **266:**11078–11082.
126. **Marusenko Y, Huber DP, Hall SJ.** 2013. Fungi mediate nitrous oxide production but not ammonia oxidation in aridland soils of the southwestern US. Soil Biol Biochem **63:**24–36. http://dx.doi.org/10.1016/j.soilbio.2013.03.018.
127. **Wallenstein MD, Myrold DD, Firestone M, Voytek M.** 2006. Environmental controls on denitrifying communities and denitrification rates: insights from molecular methods. Ecol Appl **16:**2143–2152. http://dx.doi.org/10.1890/1051-0761(2006)016[2143:ECODCA]2.0.CO;2.
128. **Laughlin RJ, Stevens RJ.** 2002. Evidence for fungal dominance of denitrification and codenitrification in a grassland soil. Soil Sci Soc Am J **66:**1540–1548. http://dx.doi.org/10.2136/sssaj2002.1540.
129. **Herold MB, Baggs EM, Daniell TJ.** 2012. Fungal and bacterial denitrification are differently affected by long-term pH amendment and cultivation of arable soil. Soil Biol Biochem **54:**25–35. http://dx.doi.org/10.1016/j.soilbio.2012.04.031.
130. **Simpson AJ, Simpson MJ, Smith E, Kelleher BP.** 2007. Microbially derived inputs to soil organic matter: are current estimates too low? Environ Sci Technol **41:**8070–8076. http://dx.doi.org/10.1021/es071217x.
131. **Latgé J-P.** 2007. The cell wall: a carbohydrate armour for the fungal cell. Mol Microbiol **66:**279–290. http://dx.doi.org/10.1111/j.1365-2958.2007.05872.x.
132. **Bowman SM, Free SJ.** 2006. The structure and synthesis of the fungal cell wall. Bioessays **28:**799–808. http://dx.doi.org/10.1002/bies.20441.
133. **Latge J-P, Calderone R.** 2005. The fungal cell wall, p 73–104. *In* Kues U, Fischer R (ed), The Mycota. I. Growth, differentiation and sexuality. Springer-Verlag, Berlin, Germany.
134. **Xie XF, Lipke PN.** 2010. On the evolution of fungal and yeast cell walls. Yeast **27:**479–488. http://dx.doi.org/10.1002/yea.1787.
135. **Cabib E.** 2009. Two novel techniques for determination of polysaccharide cross-links show that Crh1p and Crh2p attach chitin to both beta(1-6)- and beta(1-3)glucan in the *Saccharomyces cerevisiae* cell wall. Eukaryot Cell **8:**1626–1636. http://dx.doi.org/10.1128/EC.00228-09.
136. **Kollar R, Reinhold BB, Petrakova E, Yeh HJC, Ashwell G, Drgonova**

J, Kapteyn JC, Klis FM, Cabib E. 1997. Architecture of the yeast cell wall—beta(1,6)-glucan interconnects mannoprotein, beta(1,3)-glucan, and chitin. J Biol Chem **272:**17762–17775. http://dx.doi.org/10.1074/jbc.272.28.17762.

137. **Shima J, Ando A, Takagi H.** 2008. Possible roles of vacuolar H+-ATPase and mitochondrial function in tolerance to air-drying stress revealed by genome-wide screening of *Saccharomyces cerevisiae* deletion strains. Yeast **25:**179–190. http://dx.doi.org/10.1002/yea.1577.
138. **Klis FM.** 1994. Cell wall assembly in yeast. Yeast **10:**851–869. http://dx.doi.org/10.1002/yea.320100702.
139. **Francois J, Parrou JL.** 2001. Reserve carbohydrates metabolism in the yeast *Saccharomyces cerevisiae*. FEMS Microbiol Rev **25:**125–145. http://dx.doi.org/10.1111/j.1574-6976.2001.tb00574.x.
140. **Estruch F.** 2000. Stress-controlled transcription factors, stress-induced genes and stress tolerance in budding yeast. FEMS Microbiol Rev **24:**469–486. http://dx.doi.org/10.1111/j.1574-6976.2000.tb00551.x.
141. **Crowe JH, Hoekstra FA, Crowe LM.** 1992. Anhydrobiosis. Annu Rev Physiol **54:**579–599. http://dx.doi.org/10.1146/annurev.ph.54.030192.003051.
142. **Yancey PH.** 2005. Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. J Exp Biol **208:**2819–2830. http://dx.doi.org/10.1242/jeb.01730.
143. **Diniz-Mendes L, Bernardes E, de Araujo PS, Panek AD, Paschoalin VMF.** 1999. Preservation of frozen yeast cells by trehalose. Biotechnol Bioeng **65:**572–578. http://dx.doi.org/10.1002/(SICI)1097-0290(19991205)65:5<572::AID-BIT10>3.0.CO;2-7.
144. **Kandror O, Bretschneider N, Kreydin E, Cavalieri D, Goldberg AL.** 2004. Yeast adapt to near-freezing temperatures by STRE/Msn2,4-dependent induction of trehalose synthesis and certain molecular chaperones. Mol Cell **13:**771–781. http://dx.doi.org/10.1016/S1097-2765(04)00148-0.
145. **Tibbett M, Sanders FE, Cairney JWG.** 2002. Low-temperature-induced changes in trehalose, mannitol and arabitol associated with enhanced tolerance to freezing in ectomycorrhizal basidiomycetes (*Hebeloma* spp.). Mycorrhiza **12:**249–255. http://dx.doi.org/10.1007/s00572-002-0183-8.
146. **Singer MA, Lindquist S.** 1998. Thermotolerance in *Saccharomyces cerevisiae*: the yin and yang of trehalose. Trends Biotechnol **16:**460–468. http://dx.doi.org/10.1016/S0167-7799(98)01251-7.
147. **Devirgilio C, Hottiger T, Dominguez J, Boller T, Wiemken A.** 1994. The role of trehalose synthesis for the acquisition of thermotolerance in yeast. 1. Genetic evidence that trehalose is a thermoprotectant. Eur J Biochem **219:**179–186.
148. **Deegenaars ML, Watson K.** 1998. Heat shock response in psychrophilic and psychrotrophic yeast from Antarctica. Extremophiles **2:**41–49. http://dx.doi.org/10.1007/s007920050041.
149. **Singer MA, Lindquist S.** 1998. Multiple effects of trehalose on protein folding *in vitro* and *in vivo*. Mol Cell **1:**639–648. http://dx.doi.org/10.1016/S1097-2765(00)80064-7.
150. **Hare PD, Cress WA, Van Staden J.** 1998. Dissecting the roles of osmolyte accumulation during stress. Plant Cell Environ **21:**535–553. http://dx.doi.org/10.1046/j.1365-3040.1998.00309.x.
151. **Owttrim GW.** 2006. RNA helicases and abiotic stress. Nucleic Acids Res **34:**3220–3230. http://dx.doi.org/10.1093/nar/gkl408.
152. **Jones PG, Mitta M, Kim Y, Jiang WN, Inouye M.** 1996. Cold shock induces a major ribosomal-associated protein that unwinds double-stranded RNA in *Escherichia coli*. Proc Natl Acad Sci U S A **93:**76–80. http://dx.doi.org/10.1073/pnas.93.1.76.
153. **Chamot D, Magee WC, Yu E, Owttrim GW.** 1999. A cold shock-induced cyanobacterial RNA helicase. J Bacteriol **181:**1728–1732.
154. **Lim J, Thomas T, Cavicchioli R.** 2000. Low temperature regulated DEAD-box RNA helicase from the Antarctic archaeon, *Methanococcoides burtonii*. J Mol Biol **297:**553–567. http://dx.doi.org/10.1006/jmbi.2000.3585.
155. **Markkula A, Lindstrom M, Johansson P, Bjorkroth J, Korkeala H.** 2012. Roles of four putative DEAD-box RNA helicase genes in growth of *Listeria monocytogenes* EGD-e under heat, pH, osmotic, ethanol, and oxidative stress conditions. Appl Environ Microbiol **78:**6875–6882. http://dx.doi.org/10.1128/AEM.01526-12.
156. **Schade B, Jansen G, Whiteway M, Entian KD, Thomas DY.** 2004. Cold adaptation in budding yeast. Mol Biol Cell **15:**5492–5502. http://dx.doi.org/10.1091/mbc.E04-03-0167.
157. **Ellison CE, Hall C, Kowbel D, Welch J, Brem RB, Glass NL, Taylor JW.** 2011. Population genomics and local adaptation in wild isolates of a model microbial eukaryote. Proc Natl Acad Sci U S A **108:**2831–2836. http://dx.doi.org/10.1073/pnas.1014971108.
158. **Strauss EJ, Guthrie C.** 1991. A cold-sensitive messenger RNA splicing mutant is a member of the RNA helicase gene family. Genes Dev **5:**629–641. http://dx.doi.org/10.1101/gad.5.4.629.
159. **Noble SM, Guthrie C.** 1996. Identification of novel genes required for yeast pre-mRNA splicing by means of cold-sensitive mutations. Genetics **143:**67–80.
160. **Gasch AP, Werner-Washburne M.** 2002. The genomics of yeast responses to environmental stress and starvation. Funct Integr Genomics **2:**181–192. http://dx.doi.org/10.1007/s10142-002-0058-2.
161. **Bell AA, Wheeler MH.** 1986. Biosynthesis and functions of fungal melanins. Annu Rev Phytopathol **24:**411–451. http://dx.doi.org/10.1146/annurev.py.24.090186.002211.
162. **Free SJ.** 2013. Fungal cell wall organization and biosynthesis. Adv Genet **81:**33–82. http://dx.doi.org/10.1016/B978-0-12-407677-8.00002-6.
163. **Butler MJ, Day AW.** 1998. Fungal melanins: a review. Can J Microbiol **44:**1115–1136. http://dx.doi.org/10.1139/w98-119.
164. **Gessler NN, Egorova AS, Belozerskaya TA.** 2014. Melanin pigments of fungi under extreme environmental conditions. Appl Biochem Microbiol **50:**105–113. http://dx.doi.org/10.1134/S0003683814020094.
165. **Gorbushina AA, Kotlova ER, Sherstneva OA.** 2008. Cellular responses of microcolonial rock fungi to long-term desiccation and subsequent rehydration. Stud Mycol **61:**91–97. http://dx.doi.org/10.3114/sim.2008.61.09.
166. **Sterflinger K, Tesei D, Zakharova K.** 2012. Fungi in hot and cold deserts with particular reference to microcolonial fungi. Fungal Ecol **5:**453–462. http://dx.doi.org/10.1016/j.funeco.2011.12.007.
167. **Selbmann L, Isola D, Zucconi L, Onofri S.** 2011. Resistance to UV-B induced DNA damage in extreme-tolerant cryptoendolithic Antarctic fungi: detection by PCR assays. Fungal Biol **115:**937–944. http://dx.doi.org/10.1016/j.funbio.2011.02.016.
168. **Gunde-Cimermana N, Zalar P, de Hoog S, Plemenitas A.** 2000. Hypersaline waters in salterns—natural ecological niches for halophilic black yeasts. FEMS Microbiol Ecol **32:**235–240. http://dx.doi.org/10.1111/j.1574-6941.2000.tb00716.x.
169. **Kul'ko AB, Marfenina OE.** 1998. Species composition of microscopic fungi in urban snow cover. Microbiology **67:**470–472.
170. **Marfenina OE, Kul'ko AB, Ivanova AE, Sogonov MV.** 2002. The microfungal communities in the urban outdoor environment. Mikol Fitopatol **36:**22–32.
171. **Vlasov DY, Gorbunov GA, Krylenkov VA, Lukin VV, Safronova EV, Senkevich YI.** 2006. Micromycetes from the polar stations area in western Antarctica. Mikol Fitopatol **40:**202–211.
172. **Onofri S, Seltimann L, de Hoog GS, Grube M, Barreca D, Ruisi S, Zucconi L.** 2007. Evolution and adaptation of fungi at boundaries of life. Adv Space Res **40:**1657–1664. http://dx.doi.org/10.1016/j.asr.2007.06.004.
173. **de Hoog GS.** 2014. Ecology and phylogeny of black yeast-like fungi: diversity in unexplored habitats. Fungal Divers **65:**1–2. http://dx.doi.org/10.1007/s13225-014-0284-7.
174. **Gunde-Cimerman N, Grube M, de Hoog GS.** 2011. The emerging potential of melanized fungi: black yeast between beauty and the beast. Fungal Biol **115:**935–936. http://dx.doi.org/10.1016/j.funbio.2011.05.003.
175. **Zarivi O, Bonfigli A, Colafarina S, Aimola P, Ragnelli AM, Pacioni G, Miranda M.** 2011. Tyrosinase expression during black truffle development: from free living mycelium to ripe fruit body. Phytochemistry **72:**2317–2324. http://dx.doi.org/10.1016/j.phytochem.2011.08.025.
176. **Kroken S, Glass NL, Taylor JW, Yoder OC, Turgeon BG.** 2003. Phylogenomic analysis of type I polyketide synthase genes in pathogenic and saprobic ascomycetes. Proc Natl Acad Sci U S A **100:**15670–15675. http://dx.doi.org/10.1073/pnas.2532165100.
177. **Linhares LF, Martin JP.** 1978. Decomposition in soil of humic acid-type polymers (melanins) of *Eurotium echinulatum*, *Aspergillus glaucus* sp and other fungi. Soil Sci Soc Am J **42:**738–743. http://dx.doi.org/10.2136/sssaj1978.03615995004200050016x.
178. **Martin JP, Haider K.** 1986. Influence of mineral colloids on turnover rates of soil organic carbon, p 283–304. *In* Huang PM, Shnitzer M (ed), Interactions of soil minerals with natural organics and microbes. SSSA special publication no. 17. SSSA, Madison, WI.
179. **Saiz-Jimenez C.** 1994. Analytical pyrolysis of humic substances: pitfalls,

limitations, and possible solutions. Environ Sci Technol **28:**1773–1780. http://dx.doi.org/10.1021/es00060a005.
180. **Whiteway M, Bachewich C.** 2007. Morphogenesis in *Candida albicans*. Annu Rev Microbiol **61:**529–553. http://dx.doi.org/10.1146/annurev.micro.61.080706.093341.
181. **Cairney JWG.** 1992. Translocation of solutes in ectomycorrhizal and saprotrophic rhizomorphs. Mycol Res **96:**135–141. http://dx.doi.org/10.1016/S0953-7562(09)80928-3.
182. **Beck J, Echtenacher B, Ebel F.** 2013. Woronin bodies, their impact on stress resistance and virulence of the pathogenic mould *Aspergillus fumigatus* and their anchoring at the septal pore of filamentous Ascomycota. Mol Microbiol **89:**857–871. http://dx.doi.org/10.1111/mmi.12316.
183. **Smith ML, Bruhn JN, Anderson JB.** 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. Nature **356:**428–431. http://dx.doi.org/10.1038/356428a0.
184. **Legrand P, Ghahari S, Guillaumin JJ.** 1996. Occurrence of genets of *Armillaria* spp in four mountain forests in central France: the colonization strategy of *Armillaria ostoyae*. New Phytol **133:**321–332. http://dx.doi.org/10.1111/j.1469-8137.1996.tb01899.x.
185. **Frey SD, Six J, Elliott ET.** 2003. Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil-litter interface. Soil Biol Biochem **35:**1001–1004. http://dx.doi.org/10.1016/S0038-0717(03)00155-X.
186. **Gartner TB, Cardon ZG.** 2004. Decomposition dynamics in mixed-species leaf litter. Oikos **104:**230–246. http://dx.doi.org/10.1111/j.0030-1299.2004.12738.x.
187. **Li A, Fahey TJ.** 2013. Nitrogen translocation to fresh litter in northern hardwood forest. Ecosystems **16:**521–528. http://dx.doi.org/10.1007/s10021-012-9627-y.
188. **Berglund SL, Agren GI, Ekblad A.** 2013. Carbon and nitrogen transfer in leaf litter mixtures. Soil Biol Biochem **57:**341–348. http://dx.doi.org/10.1016/j.soilbio.2012.09.015.
189. **Chigineva NI, Aleksandrova AV, Marhan S, Kandeler E, Tiunov AV.** 2011. The importance of mycelial connection at the soil-litter interface for nutrient translocation, enzyme activity and litter decomposition. Appl Soil Ecol **51:**35–41. http://dx.doi.org/10.1016/j.apsoil.2011.08.009.
190. **Boddy L, Watkinson SC.** 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Can J Bot **73:**S1377–S1383.
191. **Grigoriev IV, Martinez DA, Salamov AA.** 2006. Fungal genomic annotation. Appl Microbiol Biotechnol **6:**123–142.
192. **Haas BJ, Zeng Q, Pearson MD, Cuomo CA, Wortman JR.** 2011. Approaches to fungal genome annotation. Mycology **2:**118–141. http://dx.doi.org/10.1080/21501203.2011.606851.
193. **Dutilh BE, Backus L, Edwards RA, Wels M, Bayjanov JR, van Hijum SAFT.** 2013. Explaining microbial phenotypes on a genomic scale: GWAS for microbes. Brief Funct Genomics **12:**366–380. http://dx.doi.org/10.1093/bfgp/elt008.
194. **Pradet-Balade B, Boulmé F, Beug H, Müllner EW, Garcia-Sanz JA.** 2001. Translation control: bridging the gap between genomics and proteomics? Trends Biochem Sci **26:**225–229. http://dx.doi.org/10.1016/S0968-0004(00)01776-X.
195. **Wilmes P, Bond PL.** 2006. Metaproteomics: studying functional gene expression in microbial ecosystems. Trends Microbiol **14:**92–97. http://dx.doi.org/10.1016/j.tim.2005.12.006.
196. **Myrold DD, Zeglin LH, Jansson JK.** 2014. The potential of metagenomic approaches for understanding soil microbial processes. Soil Sci Soc Am J **78:**3–10. http://dx.doi.org/10.2136/sssaj2013.07.0287dgs.
197. **Myrold DD, Nannipieri P.** 2014. Classical techniques versus omics approaches, p 179–187. *In* Nannipieri P, Pietramellara G, Renella G (ed), Omics in soil science. Caister Academic Press, Hethersett, United Kingdom.
198. **Seidl V, Huemer B, Seiboth B, Kubicek CP.** 2005. A complete survey of *Trichoderma* chitinases reveals three distinct subgroups of family 18 chitinases. FEBS J **272:**5923–5939. http://dx.doi.org/10.1111/j.1742-4658.2005.04994.x.
199. **Woo SL, Donzelli B, Scala F, Mach R, Harman GE, Kubicek CP, Del Sorbo G, Lorito M.** 1999. Disruption of the ech42 (endochitinase-encoding) gene affects biocontrol activity in *Trichoderma harzianum* P1. Mol Plant Microbe Interact **12:**419–429. http://dx.doi.org/10.1094/MPMI.1999.12.5.419.
200. **Delacruz J, Hidalgogallego A, Lora JM, Benitez T, Pintortoro JA, Llobell A.** 1992. Isolation and characterization of three chitinases from *Trichoderma harzianum*. Eur J Biochem **206:**859–867. http://dx.doi.org/10.1111/j.1432-1033.1992.tb16994.x.
201. **Garcia I, Lora JM, Delacruz J, Benitez T, Llobell A, Pintortoro JA.** 1994. Cloning and characterization of a chitinase (CHIT42) cDNA from the mycoparasitic fungus *Trichoderma harzianum*. Curr Genet **27:**83–89. http://dx.doi.org/10.1007/BF00326583.
202. **Donzelli BGG, Harman GE.** 2001. Interaction of ammonium, glucose, and chitin regulates the expression of cell wall-degrading enzymes in *Trichoderma atroviride* strain P1. Appl Environ Microbiol **67:**5643–5647. http://dx.doi.org/10.1128/AEM.67.12.5643-5647.2001.
203. **Grigoriev IV, Cullen D, Goodwin SB, Hibbett D, Jeffries TW, Kubicek CP, Kuske C, Magnuson JK, Martin F, Spatafora JW, Tsang A, Baker SE.** 2011. Fueling the future with fungal genomics. Mycology **2:**192–209. http://dx.doi.org/10.1080/21501203.2011.584577.
204. **Ohm RA, Riley R, Salamov A, Min B, Choi I-G, Grigoriev IV.** 2014. Genomics of wood-degrading fungi. Fungal Genet Biol **72:**82–90. http://dx.doi.org/10.1016/j.fgb.2014.05.001.
205. **Grigoriev IV, Nikitin R, Haridas S, Kuo A, Ohm R, Otillar R, Riley R, Salamov A, Zhao X, Korzeniewski F, Smirnova T, Nordberg H, Dubchak I, Shabalov I.** 2014. MycoCosm portal: gearing up for 1000 fungal genomes. Nucleic Acids Res **42:**D699–D704. http://dx.doi.org/10.1093/nar/gkt1183.
206. **Philippot L, Andersson SGE, Battin TJ, Prosser JI, Schimel JP, Whitman WB, Hallin S.** 2010. The ecological coherence of high bacterial taxonomic ranks. Nat Rev Microbiol **8:**523–529. http://dx.doi.org/10.1038/nrmicro2367.
207. **Lennon JT, Aanderud ZT, Lehmkuhl BK, Schoolmaster DR.** 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. Ecology **93:**1867–1879. http://dx.doi.org/10.1890/11-1745.1.
208. **Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M.** 2005. A brief history of seed size. Science **307:**576–580. http://dx.doi.org/10.1126/science.1104863.
209. **Vartoukian SR, Palmer RM, Wade WG.** 2010. Strategies for culture of 'unculturable' bacteria. FEMS Microbiol Lett **309:**1–7. http://dx.doi.org/10.1111/j.1574-6968.2010.02000.x.
210. **Ferrari BC, Zhang C, van Dorst J.** 2011. Recovering greater fungal diversity from pristine and diesel fuel contaminated sub-Antarctic soil through cultivation using both a high and a low nutrient media approach. Front Microbiol **2:**217. http://dx.doi.org/10.3389/fmicb.2011.00217.
211. **Zhang L, Cui XF, Schmitt K, Hubert R, Navidi W, Arnheim N.** 1992. Whole genome amplification from a single cell—implications for genetic analysis. Proc Natl Acad Sci U S A **89:**5847–5851. http://dx.doi.org/10.1073/pnas.89.13.5847.
212. **Foster SJ, Monahan BJ.** 2005. Whole genome amplification from filamentous fungi using Phi29-mediated multiple displacement amplification. Fungal Genet Biol **42:**367–375. http://dx.doi.org/10.1016/j.fgb.2005.01.013.
213. **Binga EK, Lasken RS, Neufeld JD.** 2008. Something from (almost) nothing: the impact of multiple displacement amplification on microbial ecology. ISME J **2:**233–241. http://dx.doi.org/10.1038/ismej.2008.10.
214. **Blainey PC.** 2013. The future is now: single-cell genomics of bacteria and archaea. FEMS Microbiol Rev **37:**407–427. http://dx.doi.org/10.1111/1574-6976.12015.
215. **Fierer N, Bradford MA, Jackson RB.** 2007. Toward an ecological classification of soil bacteria. Ecology **88:**1354–1364. http://dx.doi.org/10.1890/05-1839.
216. **von Mering C, Hugenholtz P, Raes J, Tringe SG, Doerks T, Jensen LJ, Ward N, Bork P.** 2007. Quantitative phylogenetic assessment of microbial communities in diverse environments. Science **315:**1126–1130. http://dx.doi.org/10.1126/science.1133420.
217. **Philippot L, Bru D, Saby NPA, Cuhel J, Arrouays D, Simek M, Hallin S.** 2009. Spatial patterns of bacterial taxa in nature reflect ecological traits of deep branches of the 16S rRNA bacterial tree. Environ Microbiol **11:**3096–3104. http://dx.doi.org/10.1111/j.1462-2920.2009.02014.x.
218. **Salles JF, Le Roux X, Poly F.** 2012. Relating phylogenetic and functional diversity among denitrifiers and quantifying their capacity to predict community functioning. Front Microbiol **3:**209. http://dx.doi.org/10.3389/fmicb.2012.00209.
219. **Martiny AC, Treseder K, Pusch G.** 2013. Phylogenetic conservatism of functional traits in microorganisms. ISME J **7:**830–838. http://dx.doi.org/10.1038/ismej.2012.160.
220. **Zimmerman AE, Martiny AC, Allison SD.** 2013. Microdiversity of extracellular enzyme genes among sequenced prokaryotic genomes. ISME J **7:**1187–1199. http://dx.doi.org/10.1038/ismej.2012.176.

221. **Polz MF, Alm EJ, Hanage WP.** 2013. Horizontal gene transfer and the evolution of bacterial and archaeal population structure. Trends Genet **29:**170–175. http://dx.doi.org/10.1016/j.tig.2012.12.006.
222. **Rosewich UL, Kistler HC.** 2000. Role of horizontal gene transfer in the evolution of fungi. Annu Rev Phytopathol **38:**325–363. http://dx.doi.org/10.1146/annurev.phyto.38.1.325.
223. **Leonard G, Richards TA.** 2012. Genome-scale comparative analysis of gene fusions, gene fissions, and the fungal tree of life. Proc Natl Acad Sci U S A **109:**21402–21407. http://dx.doi.org/10.1073/pnas.1210909110.
224. **Andersson JO.** 2005. Lateral gene transfer in eukaryotes. Cell Mol Life Sci **62:**1182–1197. http://dx.doi.org/10.1007/s00018-005-4539-z.
225. **Grime JP.** 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat **111:**1169–1194. http://dx.doi.org/10.1086/283244.
226. **Ho A, Kerckhof FM, Luke C, Reim A, Krause S, Boon N, Bodelier PLE.** 2013. Conceptualizing functional traits and ecological characteristics of methane-oxidizing bacteria as life strategies. Environ Microbiol Rep **5:**335–345. http://dx.doi.org/10.1111/j.1758-2229.2012.00370.x.
227. **Crowther TW, Maynard DS, Crowther TR, Peccia J, Smith JR, Bradford MA.** 2014. Untangling the fungal niche: a trait-based approach. Front Microbiol **5:**579. http://dx.doi.org/10.3389/fmicb.2014.00579.
228. **Magan N, Lacey J.** 1984. Effect of water activity, temperature and substrate on interactions between field and storage fungi. Mycol Res **82:**83–93.
229. **Boddy L.** 2000. Interspecific combative interactions between wood-decaying basidiomycetes. FEMS Microbiol Ecol **31:**185–194. http://dx.doi.org/10.1111/j.1574-6941.2000.tb00683.x.
230. **Holmer L, Stenlid J.** 1993. The importance of inoculum size for the competitive ability of wood decomposing fungi. FEMS Microbiol Ecol **12:**169–176. http://dx.doi.org/10.1111/j.1574-6941.1993.tb00029.x.
231. **Holmer L, Stenlid J.** 1997. Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. Oikos **79:**77–84. http://dx.doi.org/10.2307/3546092.
232. **Boddy L.** 1993. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. Mycol Res **97:**641–655. http://dx.doi.org/10.1016/S0953-7562(09)80141-X.
233. **SPSS.** 2009. Systat 13, version 13.00.05. Systat Software, Inc, San Jose, CA.
234. **Zakrzewska A, van Eikenhorst G, Burggraaff JEC, Vis DJ, Hoefsloot H, Delneri D, Oliver SG, Brul S, Smits GJ.** 2011. Genome-wide analysis of yeast stress survival and tolerance acquisition to analyze the central trade-off between growth rate and cellular robustness. Mol Biol Cell **22:**4435–4446. http://dx.doi.org/10.1091/mbc.E10-08-0721.
235. **Kirk TK, Farrell RL.** 1987. Enzymatic "combustion": the microbial degradation of lignin. Annu Rev Microbiol **41:**465–501.
236. **Talbot JM, Yelle DJ, Nowick J, Treseder KK.** 2012. Litter decay rates are determined by lignin chemistry. Biogeochemistry **108:**279–295. http://dx.doi.org/10.1007/s10533-011-9599-6.
237. **Allison SD.** 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. Ecol Lett **8:**626–635. http://dx.doi.org/10.1111/j.1461-0248.2005.00756.x.
238. **Song ZW, Vail A, Sadowsky MJ, Schilling JS.** 2012. Competition between two wood-degrading fungi with distinct influences on residues. FEMS Microbiol Ecol **79:**109–117. http://dx.doi.org/10.1111/j.1574-6941.2011.01201.x.
239. **Arfi Y, Levasseur A, Record E.** 2013. Differential gene expression in *Pycnoporus coccineus* during interspecific mycelial interactions with different competitors. Appl Environ Microbiol **79:**6626–6636. http://dx.doi.org/10.1128/AEM.02316-13.
240. **Treseder KK, Kivlin SN, Hawkes CV.** 2011. Evolutionary trade-offs among decomposers determine responses to nitrogen enrichment. Ecol Lett **14:**933–938. http://dx.doi.org/10.1111/j.1461-0248.2011.01650.x.
241. **Treseder KK, Maltz MR, Hawkins BA, Fierer N, Stajich JE, McGuire KL.** 2014. Evolutionary histories of soil fungi are reflected in their large-scale biogeography. Ecol Lett **17:**1086–1093. http://dx.doi.org/10.1111/ele.12311.
242. **Allison SD, McGuire KL, Treseder KK.** 2010. Resistance of microbial and soil properties to warming treatment seven years after boreal fire. Soil Biol Biochem **42:**1872–1878. http://dx.doi.org/10.1016/j.soilbio.2010.07.011.
243. **Gunde-Cimerman N, Sonjak S, Zalar P, Frisvad JC, Diderichsen B, Plemenitas A.** 2003. Extremophilic fungi in arctic ice: a relationship between adaptation to low temperature and water activity. Phys Chem Earth **28:**1273–1278. http://dx.doi.org/10.1016/j.pce.2003.08.056.
244. **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. http://dx.doi.org/10.1111/j.1574-6941.2012.01348.x.
245. **Kuo A, Kohler A, Martin FM, Grigoriev IV.** 2014. Expanding genomics of mycorrhizal symbiosis. Front Microbiol **5:**582. http://dx.doi.org/10.3389/fmicb.2014.00582.
246. **Tedersoo L, May TW, Smith ME.** 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza **20:**217–263. http://dx.doi.org/10.1007/s00572-009-0274-x.
247. **Kivlin SN, Hawkes CV, Treseder KK.** 2011. Global diversity and distribution of arbuscular mycorrhizal fungi. Soil Biol Biochem **43:**2294–2303. http://dx.doi.org/10.1016/j.soilbio.2011.07.012.
248. **Brundrett M, Bougher M, Dell B, Grove T, Malajczuk N.** 1996. Working with mycorrhizas in forestry and agriculture. ACIAR, Canberra, Australia.
249. **Talbot JM, Allison SD, Treseder KK.** 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. Funct Ecol **22:**955–963. http://dx.doi.org/10.1111/j.1365-2435.2008.01402.x.
250. **Lindahl BD, Tunlid A.** 2015. Ectomycorrhizal fungi—potential organic matter decomposers, yet not saprotrophs. New Phytol **205:**1443–1447. http://dx.doi.org/10.1111/nph.13201.
251. **Treseder KK, Allen MF, Ruess RW, Pregitzer KS, Hendrick RL.** 2005. Lifespans of fungal rhizomorphs under nitrogen fertilization in a pinyon-juniper woodland. Plant Soil **270:**249–255. http://dx.doi.org/10.1007/s11104-004-1559-7.
252. **Pritchard SG, Strand AE, McCormack ML, Davis MA, Oren R.** 2008. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. Glob Chang Biol **14:**1252–1264. http://dx.doi.org/10.1111/j.1365-2486.2008.01567.x.
253. **Vargas R, Allen MF.** 2008. Dynamics of fine root, fungal rhizomorphs, and soil respiration in a mixed temperate forest: integrating sensors and observations. Vadose Zone J **7:**1055–1064. http://dx.doi.org/10.2136/vzj2007.0138.
254. **Allen MF, Kitajima K.** 2013. *In situ* high-frequency observations of mycorrhizas. New Phytol **200:**222–228. http://dx.doi.org/10.1111/nph.12363.
255. **Ekblad A, Wallander H, Godbold DL, Cruz C, Johnson D, Baldrian P, Bjork RG, Epron D, Kieliszewska-Rokicka B, Kjoller R, Kraigher H, Matzner E, Neumann J, Plassard C.** 2013. The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. Plant Soil **366:**1–27. http://dx.doi.org/10.1007/s11104-013-1630-3.
256. **Koide RT, Malcolm GM.** 2009. N concentration controls decomposition rates of different strains of ectomycorrhizal fungi. Fungal Ecol **2:**197–202. http://dx.doi.org/10.1016/j.funeco.2009.06.001.
257. **Langley JA, Chapman SK, Hungate BA.** 2006. Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. Ecol Lett **9:**955–959. http://dx.doi.org/10.1111/j.1461-0248.2006.00948.x.
258. **Cairney JWG.** 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. Soil Biol Biochem **47:**198–208. http://dx.doi.org/10.1016/j.soilbio.2011.12.029.
259. **Mohan JE, Cowden CC, Baas P, Dawadi A, Frankson PT, Helmick K, Hughes E, Khan S, Lang A, Machmuller M, Taylor M, Witt CA.** 2014. Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. Fungal Ecol **10:**3–19. http://dx.doi.org/10.1016/j.funeco.2014.01.005.
260. **Read DJ.** 1991. Mycorrhizas in ecosystems. Experientia **47:**376–391. http://dx.doi.org/10.1007/BF01972080.
261. **Read DJ.** 1991. Mycorrhizas in ecosystems—Nature's response to the "law of the minimum," p 101–130. *In* Hawksworth DL (ed), Frontiers in mycology. CAB International, Regensburg, Germany.
262. **Treseder KK, Cross A.** 2006. Global distributions of arbuscular mycorrhizal fungi. Ecosystems **9:**305–316. http://dx.doi.org/10.1007/s10021-005-0110-x.
263. **Treseder KK.** 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol **164:**347–355. http://dx.doi.org/10.1111/j.1469-8137.2004.01159.x.
264. **van der Heijden MGA, Bardgett RD, van Straalen NM.** 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett **11:**296–310. http://dx.doi.org/10.1111/j.1461-0248.2007.01139.x.

265. **McGuire KL, Treseder KK.** 2010. Microbial communities and their relevance for ecosystem models: decomposition as a case study. Soil Biol Biochem **42:**529–535. http://dx.doi.org/10.1016/j.soilbio.2009.11.016.
266. **Follows MJ, Dutkiewicz S, Grant S, Chisholm SW.** 2007. Emergent biogeography of microbial communities in a model ocean. Science **315:** 1843–1846. http://dx.doi.org/10.1126/science.1138544.
267. **Stackebrandt E, Goebel BM.** 1994. A place for DNA-DNA reassociation and 16S ribosomal-RNA sequence analysis in the present species definition in bacteriology. Int J Syst Bacteriol **44:**846–849. http://dx.doi.org/10.1099/00207713-44-4-846.
268. **Das S, Dash HR, Mangwani N, Chakraborty J, Kumari S.** 2014. Understanding molecular identification and polyphasic taxonomic approaches for genetic relatedness and phylogenetic relationships of microorganisms. J Microbiol Methods **103:**80–100. http://dx.doi.org/10.1016/j.mimet.2014.05.013.
269. **Powell JR, Sikes BA.** 2014. Method or madness: does OTU delineation bias our perceptions of fungal ecology? New Phytol **202:**1095–1097. http://dx.doi.org/10.1111/nph.12823.
270. **Powell JR, Monaghan MT, Opik M, Rillig MC.** 2011. Evolutionary criteria outperform operational approaches in producing ecologically relevant fungal species inventories. Mol Ecol **20:**655–666. http://dx.doi.org/10.1111/j.1365-294X.2010.04964.x.
271. **Nilsson RH, Kristiansson E, Ryberg M, Hallenberg N, Larsson KH.** 2008. Intraspecific ITS variability in the kingdom Fungi as expressed in the International Sequence Databases and its implications for molecular species identification. Evol Bioinform **4:**193–201.
272. **Znameroski EA, Coradetti ST, Roche CM, Tsai JC, Iavarone AT, Cate JHD, Glass NL.** 2012. Induction of lignocellulose-degrading enzymes in *Neurospora crassa* by cellodextrins. Proc Natl Acad Sci U S A **109:**6012–6017. http://dx.doi.org/10.1073/pnas.1118440109.
273. **Tian C, Beeson WT, Iavarone AT, Sun J, Marletta MA, Cate JHD, Glass NL.** 2009. Systems analysis of plant cell wall degradation by the model filamentous fungus *Neurospora crassa*. Proc Natl Acad Sci U S A **106:**22157–22162. http://dx.doi.org/10.1073/pnas.0906810106.
274. **Eriksen DT, Hsieh PCH, Lynn P, Zhao HM.** 2013. Directed evolution of a cellobiose utilization pathway in *Saccharomyces cerevisiae* by simultaneously engineering multiple proteins. Microb Cell Fact **12:**61. http://dx.doi.org/10.1186/1475-2859-12-61.
275. **Ilmen M, Saloheimo A, Onnela ML, Penttila ME.** 1997. Regulation of cellulase gene expression in the filamentous fungus *Trichoderma reesei*. Appl Environ Microbiol **63:**1298–1306.
276. **Shoemaker S, Schweickart V, Ladner M, Gelfand D, Kwok S, Myambo K, Innis M.** 1983. Molecular cloning of exo-cellobiohydrolase I from *Trichoderma reesei* strain L27. Nat Biotechnol **1:**691–696. http://dx.doi.org/10.1038/nbt1083-691.
277. **Teeri T, Salovuori I, Knowles J.** 1983. The molecular cloning of the major cellulase gene from *Trichoderma reesei*. Nat Biotechnol **1:**696–699. http://dx.doi.org/10.1038/nbt1083-696.
278. **Kumar R, Singh S, Singh OV.** 2008. Bioconversion of lignocellulosic biomass: biochemical and molecular perspectives. J Ind Microbiol Biotechnol **35:**377–391. http://dx.doi.org/10.1007/s10295-008-0327-8.
279. **Karlsson J, Saloheimo M, Siika-aho M, Tenkanen M, Penttilä M, Tjerneld F.** 2001. Homologous expression and characterization of Cel61A (EG IV) of *Trichoderma reesei*. Eur J Biochem **268:**6498–6507. http://dx.doi.org/10.1046/j.0014-2956.2001.02605.x.
280. **Hori C, Igarashi K, Katayama A, Samejima M.** 2011. Effects of xylan and starch on secretome of the basidiomycete *Phanerochaete chrysosporium* grown on cellulose. FEMS Microbiol Lett **321:**14–23. http://dx.doi.org/10.1111/j.1574-6968.2011.02307.x.
281. **Berka RM, Grigoriev IV, Otillar R, Salamov A, Grimwood J, Reid I, Ishmael N, John T, Darmond C, Moisan M-C, Henrissat B, Coutinho PM, Lombard V, Natvig DO, Lindquist E, Schmutz J, Lucas S, Harris P, Powlowski J, Bellemare A, Taylor D, Butler G, de Vries RP, Allijn IE, van den Brink J, Ushinsky S, Storms R, Powell AJ, Paulsen IT, Elbourne LDH, Baker SE, Magnuson J, LaBoissiere S, Clutterbuck AJ, Martinez D, Wogulis M, de Leon AL, Rey MW, Tsang A.** 2011. Comparative genomic analysis of the thermophilic biomass-degrading fungi *Myceliophthora thermophila* and *Thielavia terrestris*. Nat Biotechnol **29:**922–927. http://dx.doi.org/10.1038/nbt.1976.
282. **Bowman BJ, Allen KE, Slayman CW.** 1983. Vanadate-resistant mutants of *Neurospora crassa* are deficient in a high-affinity phosphate transport system. J Bacteriol **153:**292–296.
283. **Sengottaiyan P, Ruiz-Pavon L, Persson BL.** 2013. Functional expression, purification and reconstitution of the recombinant phosphate transporter Pho89 of *Saccharomyces cerevisiae*. FEBS J **280:**965–975. http://dx.doi.org/10.1111/febs.12090.
284. **Persson BL, Petersson J, Fristedt U, Weinander R, Berhe A, Pattison J.** 1999. Phosphate permeases of *Saccharomyces cerevisiae*: structure, function and regulation. Biochim Biophys Acta Rev Biomembr **1422:** 255–272. http://dx.doi.org/10.1016/S0304-4157(99)00010-6.
285. **Rekangalt D, Pepin R, Verner MC, Debaud JC, Marmeisse R, Fraissinet-Tachet L.** 2009. Expression of the nitrate transporter nrt2 gene from the symbiotic basidiomycete *Hebeloma cylindrosporum* is affected by host plant and carbon sources. Mycorrhiza **19:**143–148. http://dx.doi.org/10.1007/s00572-008-0221-2.
286. **Jargeat P, Rekangalt D, Verner M-C, Gay G, Debaud J-C, Marmeisse R, Fraissinet-Tachet L.** 2003. Characterisation and expression analysis of a nitrate transporter and nitrite reductase genes, two members of a gene cluster for nitrate assimilation from the symbiotic basidiomycete *Hebeloma cylindrosporum*. Curr Genet **43:**199–205. http://dx.doi.org/10.1007/s00294-003-0387-2.
287. **Zhang L, Takaya N, Kitazume T, Kondo T, Shoun H.** 2001. Purification and cDNA cloning of nitric oxide reductase cytochrome P450nor (CYP55A4) from *Trichosporon cutaneum*. Eur J Biochem **268:**3198–3204. http://dx.doi.org/10.1046/j.1432-1327.2001.02206.x.
288. **Zhang L, Shoun H.** 2008. Purification and functional analysis of fungal nitric oxide reductase cytochrome P450nor, p 117–133. *In* Poole RK (ed), Globins and other nitric oxide-reactive proteins, part B, vol 437. Elsevier Academic Press Inc, San Diego, CA.
289. **Chao LY, Rine J, Marletta MA.** 2008. Spectroscopic and kinetic studies of Nor1, a cytochrome P450 nitric oxide reductase from the fungal pathogen *Histoplasma capsulatum*. Arch Biochem Biophys **480:**132–137. http://dx.doi.org/10.1016/j.abb.2008.09.001.
290. **Mazur P, Morin N, Baginsky W, el-Sherbeini M, Clemas JA, Nielsen JB, Foor F.** 1995. Differential expression and function of two homologous subunits of yeast 1,3-beta-D-glucan synthase. Mol Cell Biol **15:** 5671–5681.
291. **Levin DE.** 2011. Regulation of cell wall biogenesis in *Saccharomyces cerevisiae*: the cell wall integrity signaling pathway. Genetics **189:**1145–1175. http://dx.doi.org/10.1534/genetics.111.128264.
292. **Schmidt U, Lehmann K, Stahl U.** 2002. A novel mitochondrial DEAD box protein (Mrh4) required for maintenance of mtDNA in *Saccharomyces cerevisiae*. FEMS Yeast Res **2:**267–276. http://dx.doi.org/10.1016/S1567-1356(02)00109-5.
293. **Shiratori A, Shibata T, Arisawa M, Hanaoka F, Murakami Y, Eki T.** 1999. Systematic identification, classification, and characterization of the open reading frames which encode novel helicase-related proteins in *Saccharomyces cerevisiae* by gene disruption and northern analysis. Yeast **15:**219–253. http://dx.doi.org/10.1002/(SICI)1097-0061(199902)15:3<219::AID-YEA349>3.0.CO;2-3.
294. **Pihet M, Vandeputte P, Tronchin G, Renier G, Saulnier P, Georgeault S, Mallet R, Chabasse D, Symoens F, Bouchara J-P.** 2009. Melanin is an essential component for the integrity of the cell wall of *Aspergillus fumigatus* conidia. BMC Microbiol **9:**177. http://dx.doi.org/10.1186/1471-2180-9-177.
295. **Feng B, Wang X, Hauser M, Kaufmann S, Jentsch S, Haase G, Becker JM, Szaniszlo PJ.** 2001. Molecular cloning and characterization of Wd-PKS1, a gene involved in dihydroxynaphthalene melanin biosynthesis and virulence in *Wangiella* (*Exophiala*) *dermatitidis*. Infect Immun **69:** 1781–1794. http://dx.doi.org/10.1128/IAI.69.3.1781-1794.2001.
296. **Takano Y, Kubo Y, Shimizu K, Mise K, Okuno T, Furusawa I.** 1995. Structural analysis of PKS1, a polyketide synthase gene involved in melanin biosynthesis in *Colletotrichum lagenarium*. Mol Gen Genet **249:**162–167. http://dx.doi.org/10.1007/BF00290362.
297. **Takano Y, Kubo Y, Kawamura C, Tsuge T, Furusawa I.** 1997. The *Alternaria alternata* melanin biosynthesis gene restores appressorial melanization and penetration of cellulose membranes in the melanin-deficient albino mutant of *Colletotrichum lagenarium*. Fungal Genet Biol **21:**131–140. http://dx.doi.org/10.1006/fgbi.1997.0963.
298. **McGuire KL, Bent E, Borneman J, Majumder A, Allison SD, Treseder KK.** 2010. Functional diversity in resource use by fungi. Ecology **91:** 2324–2332. http://dx.doi.org/10.1890/09-0654.1.