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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

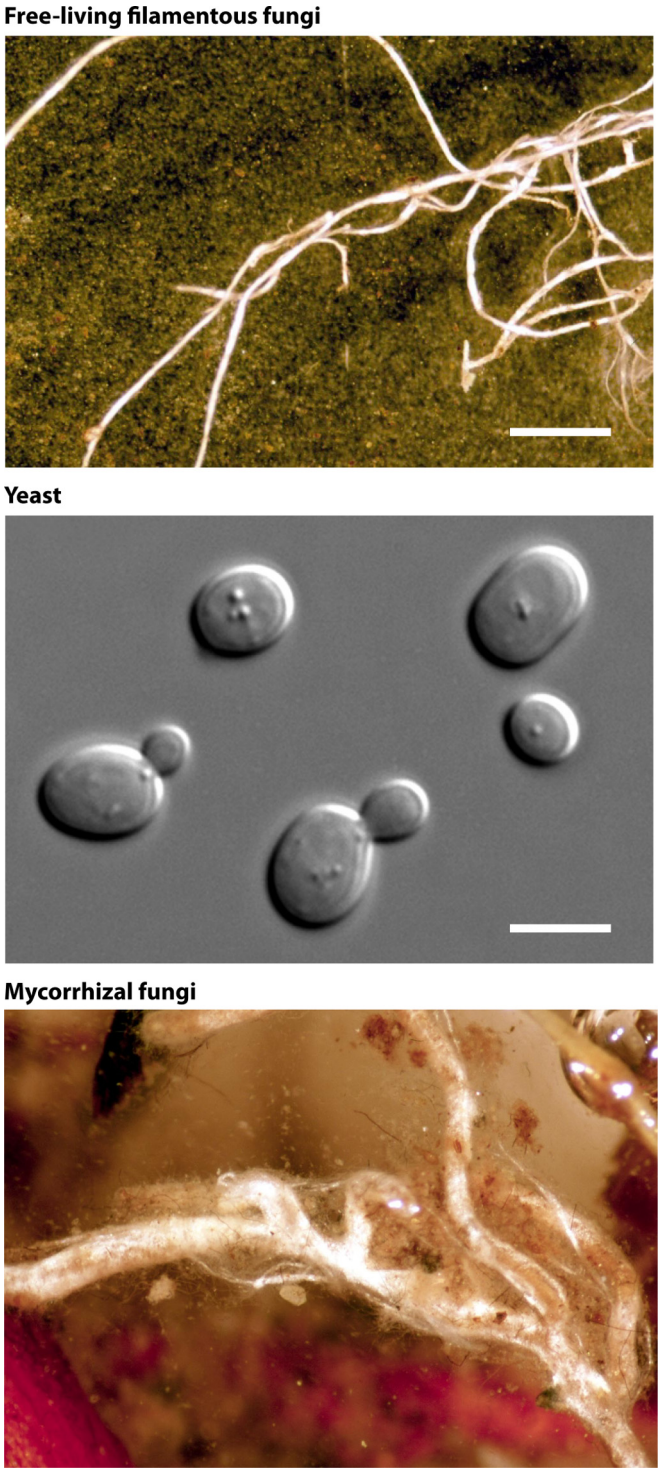

FIG 1 Examples of free-living filamentous fungi, yeasts, and mycorrhizal fungi. Depicted are rhizomorphs of a free-living filamentous fungus (top) (bar, 0.5 mm), cells of the model yeast *Saccharomyces cerevisiae* (middle) (bar, 5 μm), and a fine root tip colonized by an ectomycorrhizal fungus (bottom)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

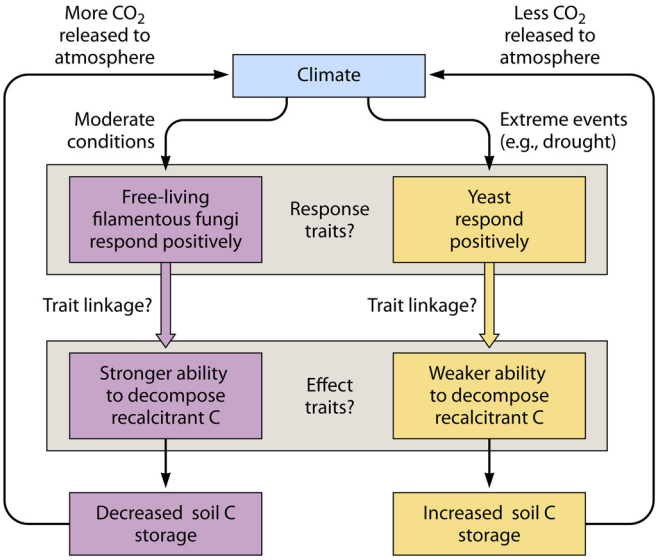

FIG 2 Hypothesized feedbacks on soil C storage associated with free-living filamentous fungi or yeasts. Yeasts tend to prevail under extreme conditions rather than moderate conditions, ostensibly because they possess one or more traits that confer stress tolerance ("response traits"). If these traits 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

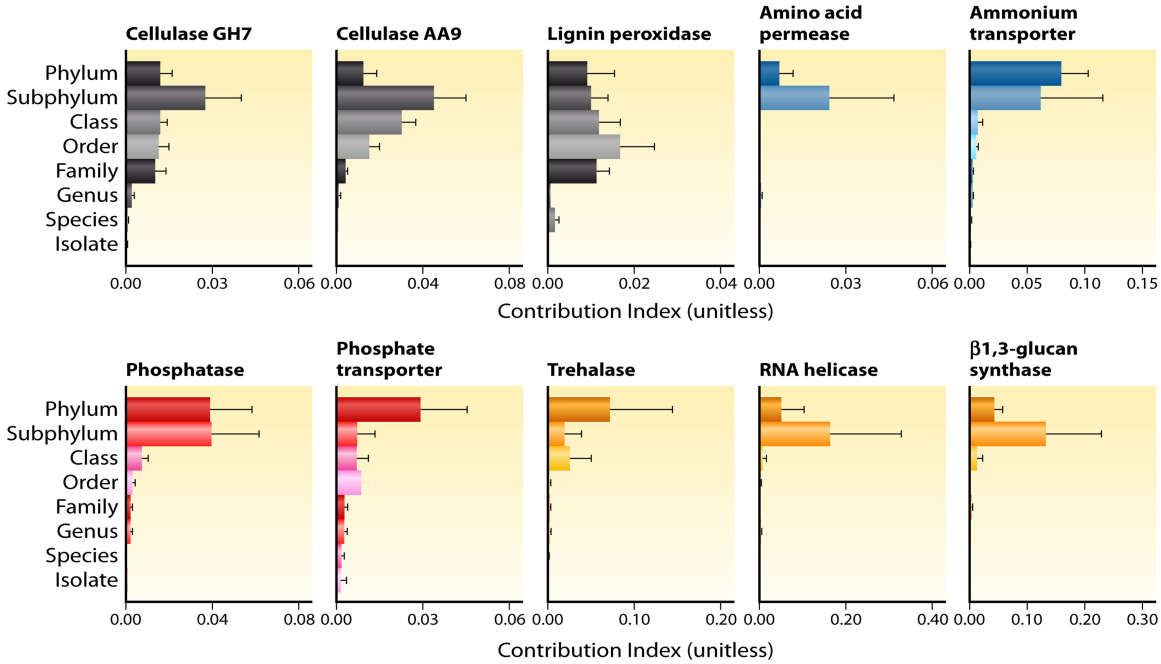

FIG 3 Variation in traits by taxonomic rank. The contribution index represents the proportion of trait variance across the entire phylogenetic tree that is attributable to the variance at a particular node. We categorized each node within the phylogenetic tree by the taxonomic rank of the clades that 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

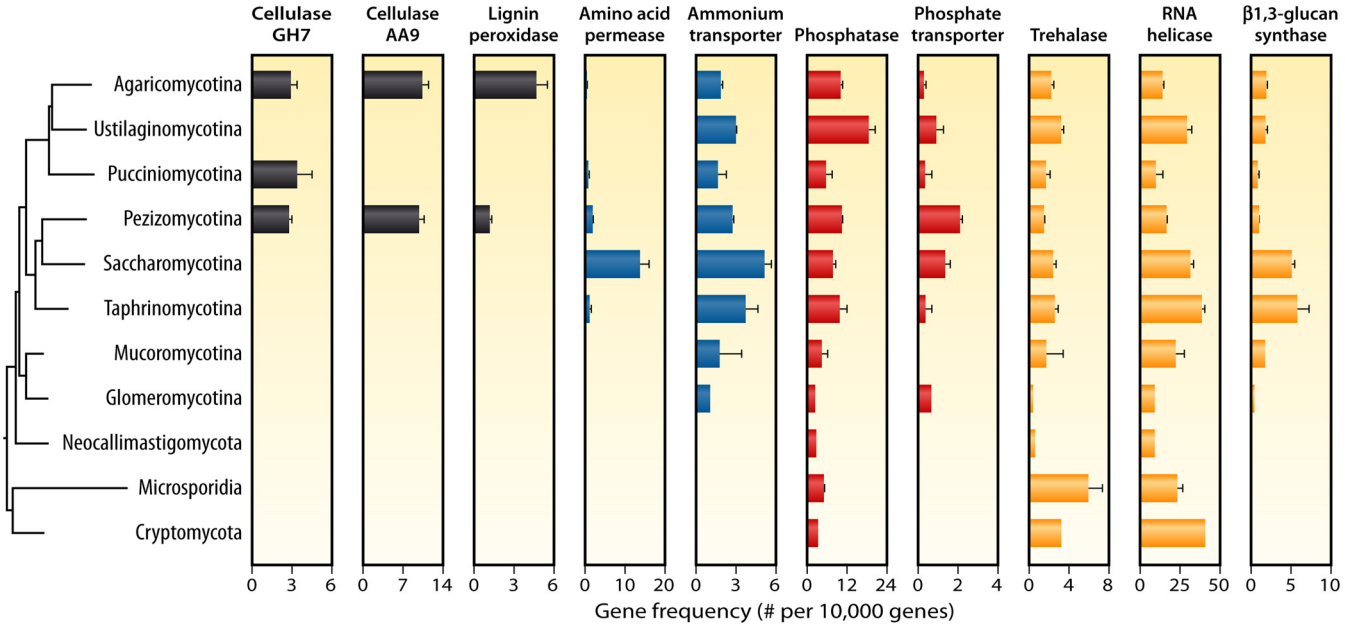

FIG 4 Distribution of ecosystem-related traits across fungal phyla (or subphyla, for Dikarya). Frequencies of functional genes were calculated for each whole genome by using MycoCosm to search for relevant InterPro and Gene Ontology domains (Table 1). Bars are means + 1 SE for each phylum/subphylum.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

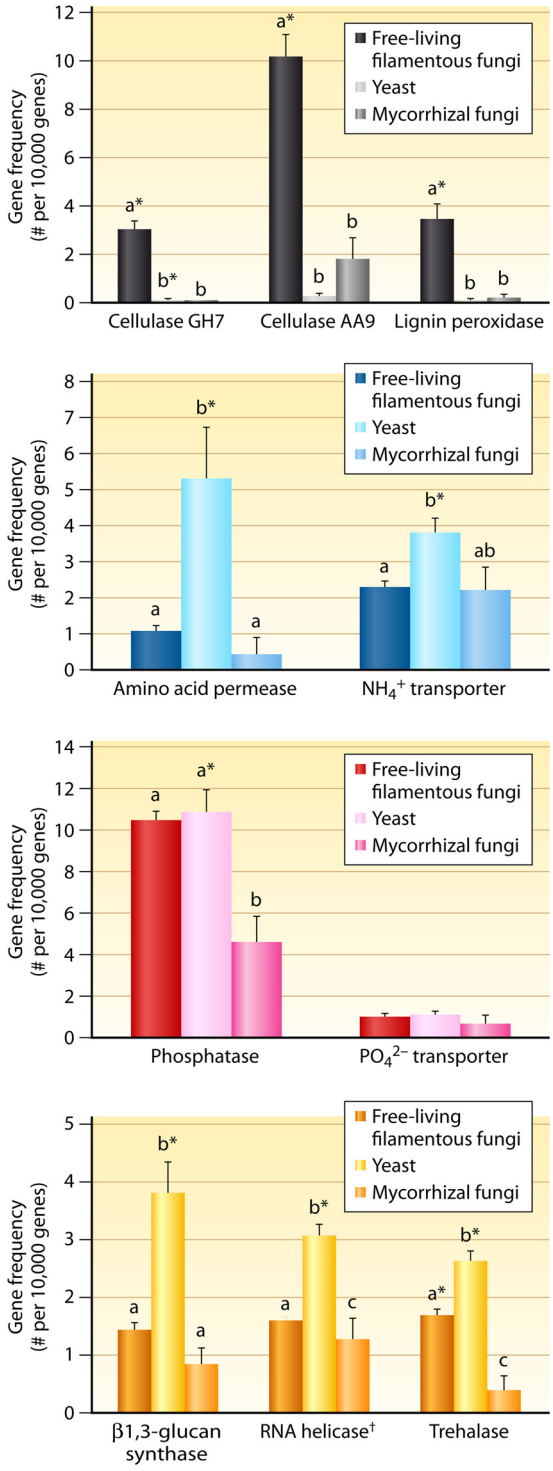

FIG 5 Ecosystem-related traits of free-living filamentous fungi, yeasts, and mycorrhizal fungi. Different letters indicate significant pairwise differences between morphological groups ($P < 0.05$), based on the Kolmogorov-Smirnov test. Asterisks indicate a significant phylogenetically independent contrast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

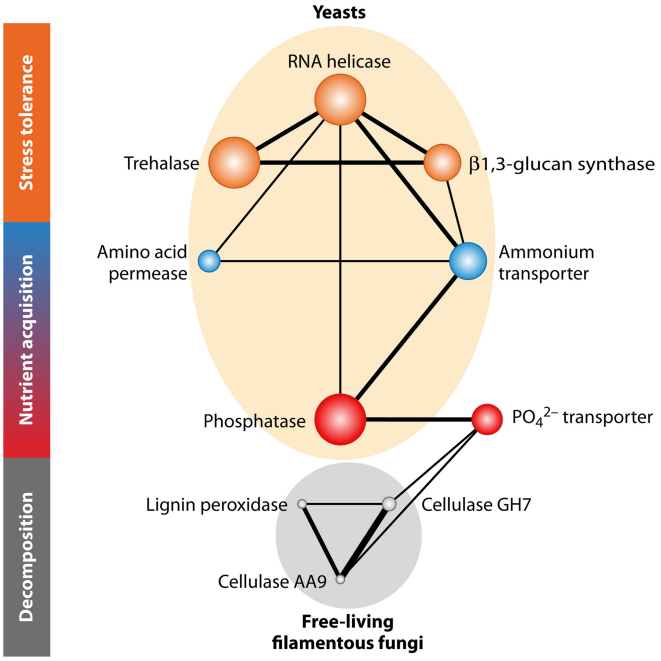

FIG 6 Relationships among traits and their associations with morphological groups of fungi. Symbols represent traits. Symbol size is proportional to the number of fungal phyla (or subphyla, for Dikarya) that possess the trait. Lines connect traits that are significantly positively related based on the 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).

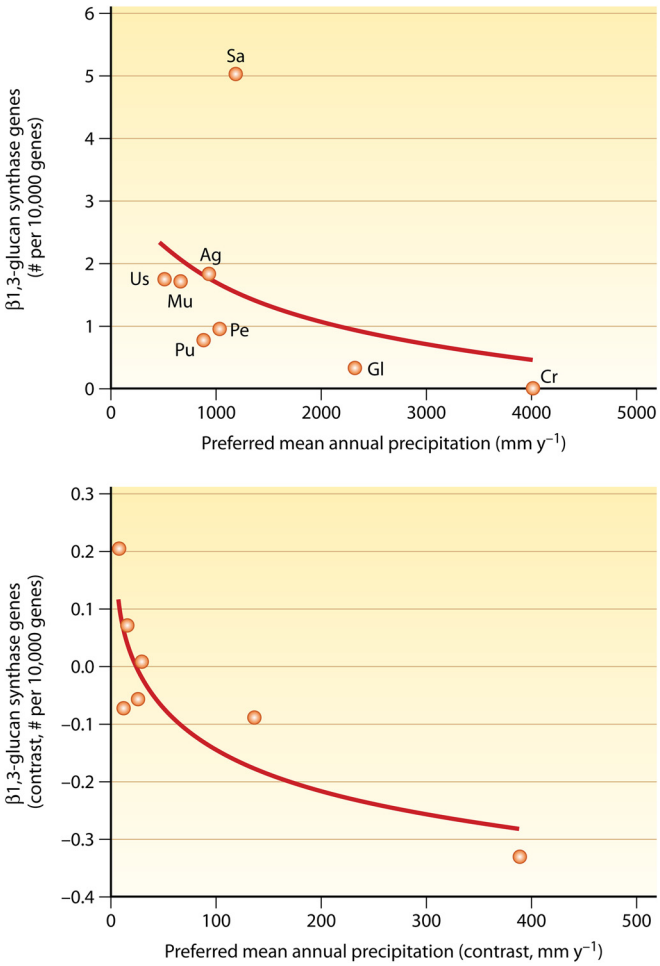

FIG 7 Relationship between preferred mean annual precipitation and frequency of β1,3-glucan synthase genes among fungal phyla (or subphyla, for Dikarya) (upper panel), with corresponding phylogenetically independent contrasts (lower panel). In the upper panel, symbols show the means for the fungal phyla/subphyla 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-

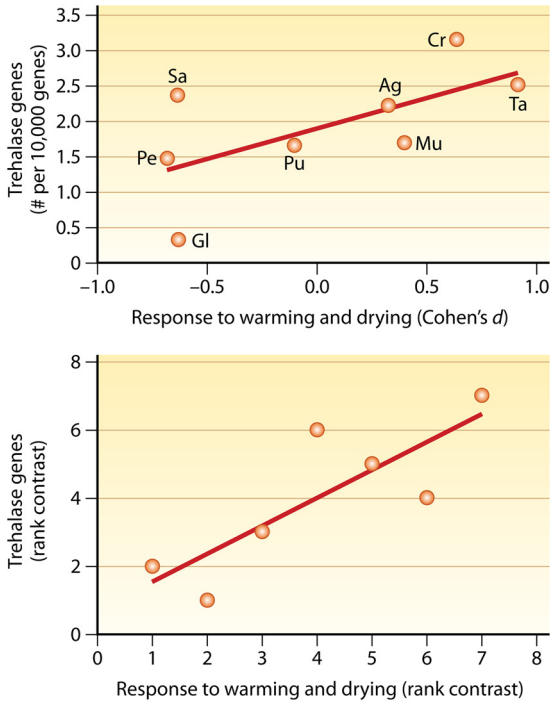

FIG 8 Relationship between frequency of trehalase genes and response to warming and drying among fungal phyla (or subphyla, for Dikarya) (upper panel), with associated phylogenetically independent contrasts (lower panel), detected in a climate manipulation experiment in an Alaskan boreal forest (242). 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; $r = 0.821$; $P = 0.023$).

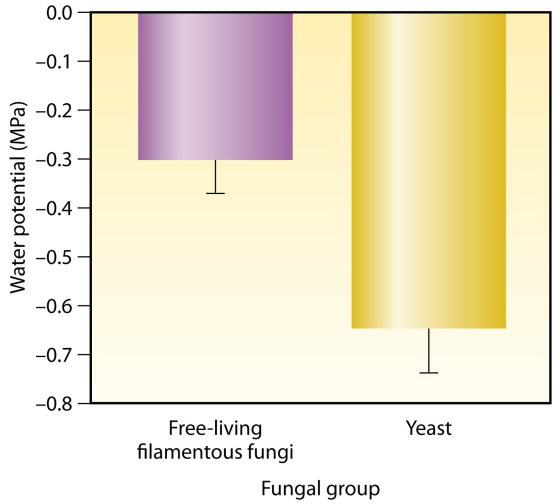

FIG 9 Difference in drought tolerance between free-living filamentous fungi and yeasts in a laboratory study by Lennon et al. (207). A more negative optimal water potential indicates greater drought tolerance. Bars show means and 1 SE. Yeasts were significantly more drought tolerant than were free-living 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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