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LETTER

Evolutionary histories of soil fungi are reflected in their large-scale biogeography

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Abstract

Although fungal communities are known to vary along latitudinal gradients, mechanisms underlying this pattern are not well-understood. We used high-throughput sequencing to examine the large-scale distributions of soil fungi and their relation to evolutionary history. We tested the Tropical Conservatism Hypothesis, which predicts that ancestral fungal groups should be more restricted to tropical latitudes and conditions than would more recently derived groups. We found support for this hypothesis in that older phyla preferred significantly lower latitudes and warmer, wetter conditions than did younger phyla. Moreover, preferences for higher latitudes and lower precipitation levels were significantly phylogenetically conserved among the six younger phyla, possibly because the older phyla possess a zoospore stage that is vulnerable to drought, whereas the younger phyla retain protective cell walls throughout their life cycle. Our study provides novel evidence that the Tropical Conservatism Hypothesis applies to microbes as well as plants and animals.

Keywords

Latitude, phylum, precipitation, regular septa, snowball earth events, soil, temperature, traits, zoospore.

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INTRODUCTION

Numerous studies have reported shifts in fungal community composition by latitude, temperature, and precipitation (Arnold & Lutzoni 2007; Tedersoo *et al.* 2010, 2012; Kivlin *et al.* 2011; Sun *et al.* 2012; Öpik *et al.* 2013). Such spatial shifts are expected to contain phylogenetic patterns if we assume that the evolution of key morphological or physiological traits of fungal taxa determines their response to temperature and precipitation. These traits include possession of cell walls or the presence of regular septa. In turn, these traits could constrain the geographic distribution of fungal taxa. Nevertheless, the relationships between the evolutionary history of soil fungi and their biogeographical patterns remain largely unknown, especially at very large scales.

For many terrestrial plants and animals, younger taxa tend to reside at higher latitudes (Hillebrand 2004; Weir & Schluter 2007; Buckley *et al.* 2010; Hawkins *et al.* 2012; Romdal *et al.* 2013). The Tropical Conservatism Hypothesis (TCH) represents one potential explanation for this pattern (e.g., Wiens & Donoghue 2004), whereby older groups that evolved under warmer, wetter conditions are constrained by phylogenetic niche conservatism, making it difficult for them to evolve the necessary physiological traits that allow them to proliferate under cooler, drier climates. Thus, older groups (and their traits) are more likely to be restricted to lower latitudes, whereas younger groups can reside at higher latitudes. It is unknown, however, whether these patterns apply to fungi.

Here, we test predictions of TCH as they may apply to a group of organisms much older than those normally considered. The Earth's paleoclimate was relatively warm and wet during the earliest evolution of ancestral fungi, whereas severe ice ages (Evans *et al.* 1997; Kopp *et al.* 2005; Smith 2009) and drought (Algeo & Scheckler 1998) occurred later in their evolutionary history. We hypothesized that younger fungal phyla should be more likely to reside in soils of higher latitudes, with older lineages having evolved traits that provide maximal fitness under warm and wet conditions. We also explored the distributions of potential traits that could account for the spatial structure of lineage ages.

We are focusing on the biogeography of soil fungi at the phylum level, because we are examining evolutionary histories over very long time periods that correspond to divergence at this broad taxonomic level. The divergence of fungal phyla coincided with key evolutionary events, some of which could have conferred greater tolerance to stressful environmental conditions. For example, the ancestral phyla Cryptomycota, Chytridiomycota, and Blastocladiomycota each reproduce via zoospores, which do not have cell walls; the zoospore form was lost from younger phyla (Liu *et al.* 2006; Stajich *et al.* 2009; James *et al.* 2013). This event may have coincided with the onset of extreme cold periods during the Neoproterozoic (Evans *et al.* 1997; Smith 2009). It is well-documented that fungal cell walls protect the interior from damage caused by freezing, desiccation, and osmotic stresses (reviewed in Latgé 2007). Some zoosporic fungi can produce resting or resistant spores

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that allow them to become dormant during stressful conditions, but they nevertheless form zoospores upon germination (Olson 1973). Thus, their active phases may be relatively limited under stressful conditions.

Differentiated tissues with regular septa are thought to have evolved in the two youngest phyla (Ascomycota and Basidiomycota, also known as the Dikarya) during the Devonian (Stajich *et al.* 2009; Kumar *et al.* 2012; Healy *et al.* 2013). In this period, much of the Earth's land mass was located in the naturally arid zone near the Tropic of Capricorn (Algeo & Scheckler 1998), so land-based fungi should have been exposed to dry conditions. Regular septa of the Dikarya include central pores that can be plugged by specialized organelles, and together they form a regulatory structure that improves water conservation under dry conditions and reduces leakage that might occur from freeze-thaw ruptures (Maruyama *et al.* 2005; Beck *et al.* 2013). In comparison, regular septa like these are rare within older phyla and are known to occur in only a few groups within the Kickxellomycotina (Tretter *et al.* 2013). Altogether, the elimination of the zoospore stage and the evolution of regular septa might each contribute to the latitudinal distributions of fungal phyla.

To test our hypothesis, we mapped the distributions of fungal taxa in soils collected from local communities across the Western Hemisphere. For each taxon, we calculated the average latitudinal distance from the equator (i.e., higher versus lower latitudes), mean annual temperature, and mean annual precipitation for sites in which the taxon was detected. These were considered the environmental conditions 'preferred' by each taxon, akin to niche space. Finally, we related these preferred environments to phylum age and phylum-level traits.

MATERIALS AND METHODS

Study sites

We assayed soils from 47 sites in North and South America. This number of sites was smaller than some other large-scale analyses (e.g., Lauber *et al.* 2009). Nevertheless, the sites represented a wide range in latitude (28 °S to 69 °N), mean annual temperature (−9.3 to 25.0 °C) and mean annual precipitation (150 to 5000 mm year^{−1}) (Table S1), which allowed us to test relationships with each parameter. For these sites, mean annual temperature and precipitation were relatively high near the equator and then declined substantially at higher latitudes (Fig. S1). Moreover, mean annual temperature and precipitation were positively associated across sites (Fig. S2). Sites with lower precipitation rates also experienced greater drought (i.e., soil moisture deficit, Fig. S2). In addition, 18 of the sites were dominated by at least one ectomycorrhizal (ECM) host plant (Table S1). These sites tended to differ from the others in terms of distance from the equator (ECM: 42 ± 3° latitude, non-ECM: 33 ± 2° latitude, mean ± SE) and temperature (ECM: 6.0 ± 1.9 °C, non-ECM: 14.6 ± 1.5 °C), but not necessarily precipitation (ECM: 709 ± 274 mm year^{−1}, non-ECM: 1252 ± 216 mm year^{−1}). The top 5 cm of mineral soil was composited from 5 to 10 locations within a given site, near the peak plant growing

season. These soil samples were identical to a subset of those reported in Fierer & Jackson (2006).

DNA sequencing and analysis

DNA was extracted from 5 to 10 g dry weight of each soil sample as described in Lauber *et al.* (2009). We used universal fungal primers of Borneman & Hartin (2000) modified for barcoded pyrosequencing to amplify a ~ 422 bp region of the 18S rRNA gene as in McGuire *et al.* (2012). This region extends from nucleotide 817 to 1196 of the 18S sequence of *Saccharomyces cerevisiae* and includes the V4 (partial) and V5 variable regions (Borneman & Hartin 2000). This primer set has previously been used to successfully amplify Cryptomycota, Blastocladiomycota, Chytridiomycota, Zygomycota, Mucoromycotina, Glomeromycota, Ascomycota, and Basidiomycota (Borneman & Hartin 2000; Nagahama *et al.* 2011). Cryptomycota are classified as fungi (Jones *et al.* 2011a,b; Capella-Gutierrez *et al.* 2012; James *et al.* 2013). We obtained 52 906 fungal sequences, representing 910 to 1699 sequences per sample. The Quantitative Insights Into Microbial Ecology (QIIME) pipeline was then used to process sequences (Caporaso *et al.* 2010). Sequences were quality checked, aligned, and grouped into phylotypes (hereafter, 'taxa') at a 97% sequence similarity cut-off. This cut-off corresponds to approximately the family level for this DNA region (Anderson *et al.* 2003). One representative sequence from each taxon was chosen. Each representative sequence was identified to phylum by BLAST comparison against all non-environmental fungal sequences in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). We double-checked our identifications by manually performing BLAST comparisons with curated sequences produced by the Assembling the Fungal Tree of Life (AFTOL) project (James *et al.* 2006). We randomly selected 910 sequences per sample to control for differences in sequence number among samples.

Altogether, 516 fungal taxa were identified to phylum, and collectively they represented nine phyla (Table S2). A representative sequence of each taxon has been submitted to GenBank under the BioProject Accession PRJNA237127. One hundred seventeen of these taxa matched (≥ 97% identity) a sequence from an AFTOL or other vouchered specimen, so they could be identified at a higher taxonomic resolution (Table S2). For each taxon, we determined the average (i.e., 'preferred') distance from the equator, mean annual temperature and mean annual precipitation of the sites in which it was observed. Distance from the equator was computed as degrees latitude north or south, so that greater distance indicates higher latitudes, regardless of hemisphere. Note that we did not weight these preferences by relative abundance of the taxon in each site; to be conservative, preferences were calculated solely based on presence/absence data. Moreover, none of the data was normally distributed, so we performed all statistical analyses on ranked data or with nonparametric tests. Systat 13 (Version 13.00.05, Chicago, IL, USA) was used for all non-phylogenetic tests, and differences were considered significant when $P < 0.05$.

First, we tested whether phyla differed from one another in environmental preferences with a series of Kruskal–Wallis

tests (analogous to a nonparametric one way analysis of variance, Sokal & Rohlf 1995). We used phylum identity as the independent variable and each environmental preference, in turn, as a dependent variable. Units of observation were individual taxa. In each case, a Kolmogorov–Smirnov test for pairwise differences was applied *post hoc* (Sokal & Rohlf 1995).

Second, we quantified relationships between phylum age and environmental preferences. We conducted a mixed hierarchical regression between phylum age (independent variable) and preferred distance from equator (dependent variable). A mixed hierarchical regression is essentially a linear regression that allowed us to nest taxa within phyla (Raudenbush 1993). This approach takes into account the fact that taxa were related within phyla. In other words, phyla—but not taxa within phyla—were considered to be independent. Moreover, we used a mixed hierarchical regression because our data were not distributed equally among phyla, and this test is not sensitive to unequal distributions (Raudenbush 1993). For phylum age, we used rankings of basal ages from Stajich *et al.* (2009), which are based on calibrations from Taylor & Berbee (2006) and the AFTOL phylogenetic tree (James *et al.* 2006). Taxa represented data points that were nested within phylum; phylum was the unit of analysis. A significant negative relationship between preferred distance from equator and phylum age would be consistent with our hypothesis. Similar mixed hierarchical regressions were then performed, with preferred mean annual temperature or preferred mean annual precipitation as the dependent variables. Significant relationships between phylum age and these environmental conditions would aid the interpretation of any latitudinal patterns.

Third, we performed phylogenetic independent contrasts between phylum age and environmental preferences as an additional test of our hypothesis. For these analyses, we used the phylogeny of James *et al.* (2006), which includes the 18S rDNA region as well as five other genes to better-resolve early evolutionary events. We pruned the phylogeny so that it included one representative of each of the nine phyla from our study. We applied the Phylocom 4.2 AOT algorithm (Webb *et al.* 2008) to conduct a set of phylogenetic independent contrasts between the basal age of each phylum (from Stajich *et al.* 2009) and each environmental preference. Proportional branch lengths were used. Units of observation were phyla. Thus, for each phylum, we used the mean preferred distance from equator, temperature, or precipitation for all taxa within that phylum.

Fourth, we examined morphological or physiological traits that might have influenced environmental preferences. We did so by performing a series of comparisons among dichotomous traits that differed at the phylum level. The traits were presence vs. absence of a zoospore stage, and presence vs. absence of regular septa in hyphae. For each trait, we used the Phylocom 4.2 AOT algorithm (Webb *et al.* 2008) to check for significant phylogenetic conservation of each environmental preference within the relevant clade. Specifically, we tested whether the clade representing phyla without a zoospore stage (Entomophthoromycota, Mucoromycotina, Zygomycota, Glomeromycota, Ascomycota, and Basidiomycota) displayed phylogenetic conservation of greater preferred distance from the equator,

lower temperature, and less precipitation. We next tested whether environmental preferences were conserved within the clade representing phyla with regular septa (Ascomycota and Basidiomycota). For both tests of phylogenetic conservation, phylum was the unit of analysis; for each phylum, we used the mean preferred distance from equator, temperature, or precipitation for all taxa within that phylum.

RESULTS

The fungal phyla differed significantly in preferred distance from equator (Kruskal–Wallis $H = 47.9$, $n = 516$, $P < 0.001$), temperature ($H = 41.0$, $n = 516$, $P < 0.001$), and precipitation ($H = 30.4$, $n = 516$, $P < 0.001$, Table S3). Moreover, younger phyla preferred significantly higher latitudes (Fig. 1, $z = -3.31$, $P = 0.001$) and cooler temperatures ($z = 3.26$, $P = 0.001$). There was also a significant relationship between phylum age and preferred precipitation, but with greater scatter ($z = 4.60$, $P < 0.001$). Cryptomycota exhibited preferences for particularly low latitudes, warm temperatures and high precipitation rates, yet relationships between phylum age and each environmental preference remained significant even when Cryptomycota was omitted (distance from equator: $P = 0.003$, temperature: $P = 0.005$, precipitation: $P < 0.001$). Phylogenetic independent contrasts likewise indicated significant relationships between phylum age and preference for distance from equator (Fig. 2, $r_{IC} = -0.89$, $P = 0.009$), temperature ($r_{IC} = 0.85$, $P = 0.016$) and precipitation rate ($r_{IC} = 0.81$, $P = 0.026$). The decreases in preferred distance from the equator with phylum age are expected under the Tropical Conservatism Hypothesis, as are the significant positive relationships between phylum age and preferred temperatures and precipitation rates, if niche conservatism among fungi is strong enough to be manifested at the phylum rank.

In terms of traits, phyla that lacked zoospores were associated with significantly higher latitudes (Fig. 3, $P = 0.033$), marginally significantly cooler temperatures ($P = 0.064$), and significantly lower precipitation ($P = 0.023$), based on tests for phylogenetic conservation. In contrast, the formation of regular septa was not significantly related to preferred distance from the equator (Fig. S3, $P = 0.256$), temperature ($P = 0.248$), or precipitation ($P = 0.367$). Thus, of the two traits we examined, the evolutionary event associated with the loss of the zoospore stage was more strongly related to environmental preferences at the phylum level.

DISCUSSION

Overall, the age of fungal phyla was related to their biogeographic distributions in soils of North and South America as we had hypothesized. In general, older fungal phyla tended to reside in soils of lower latitudes than did younger phyla (Figs 1 and 2). These preferences may have been tied to the ability of taxa to tolerate cooler and drier conditions, as younger phyla were also found in ecosystems with lower temperatures and precipitation rates (Figs 1 and 2). Together, these patterns are consistent with the idea of niche conservatism—ancestral phyla that originated under warmer and wetter conditions may lack the traits that would allow

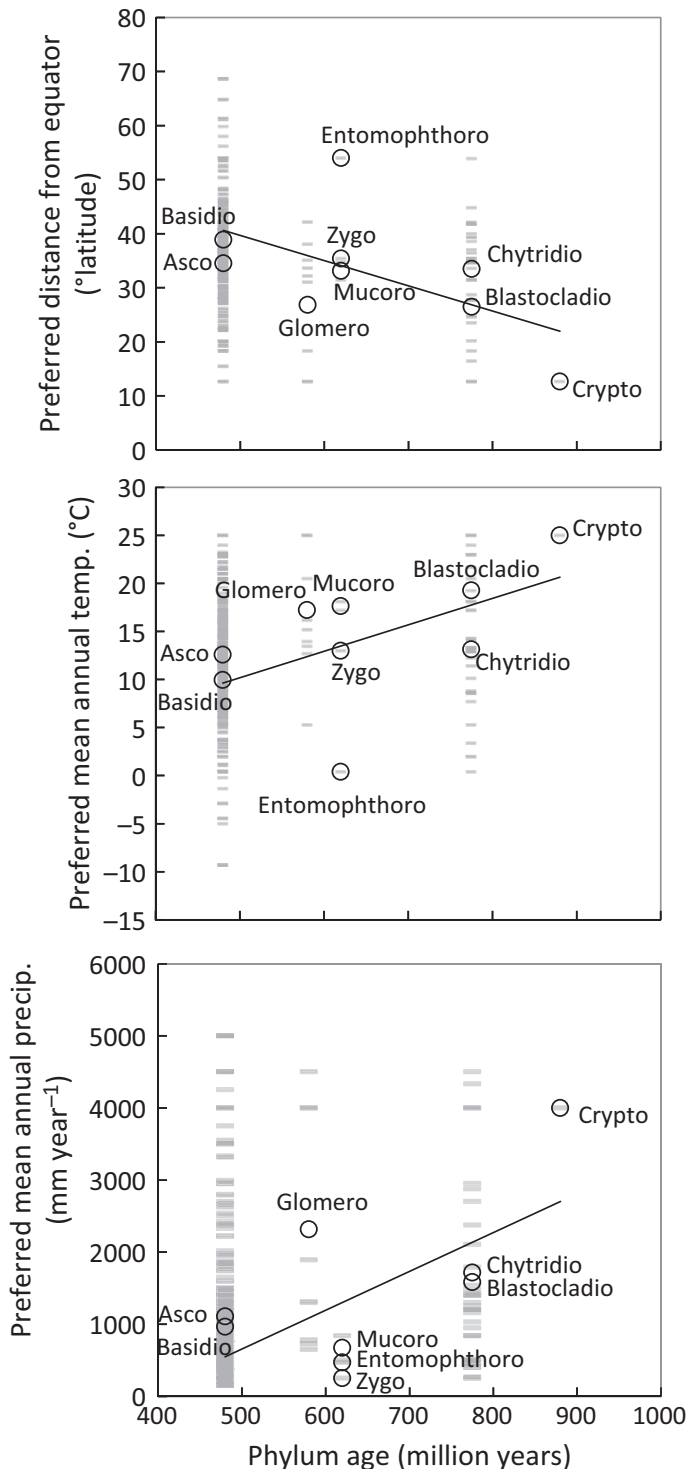


Figure 1 Relationships between phylum age (from Stajich *et al.* 2009) and preferred distance from equator, preferred temperature and preferred precipitation. Younger phyla were generally observed at higher latitudes ($P = 0.001$), cooler temperatures ($P = 0.001$) and drier sites ($P < 0.001$). Circles represent means of each phylum and are labelled with phylum name (suffix '-mycota' or '-mycotina'). Grey dashes represent individual taxa. Lines are best-fit.

them to tolerate the cooler and drier conditions more typical of higher latitudes. Younger phyla could have evolved a trait (or suite of traits) that conferred cold and drought resistance,

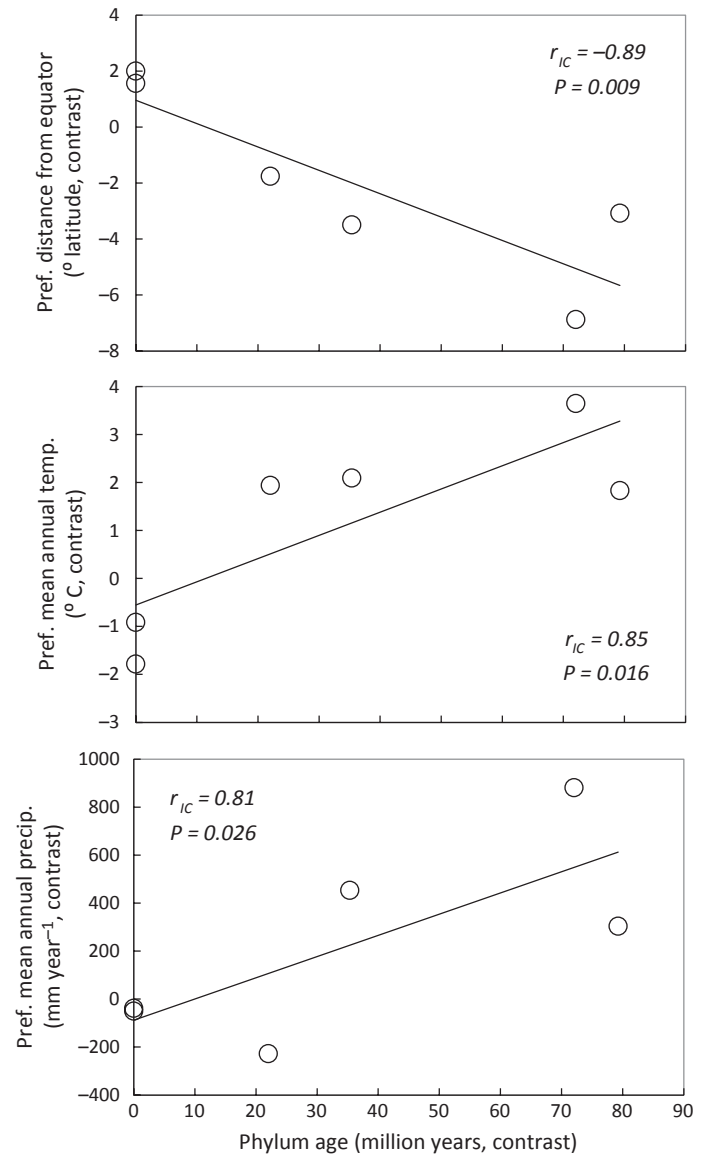


Figure 2 Phylogenetic-independent contrasts between phylum age and preferred environmental characteristics. Symbols represent contrasts at each phylogenetic node (see Fig. 3 for phylogenetic tree). For preferred distance from equator, more negative latitudes represent more southern distributions. Lines are best-fit.

allowing them to colonize higher latitudes unavailable to older phyla. The loss of the zoospore stage is one possible candidate, especially regarding tolerance of drier conditions (Fig. 3). In this way, the evolutionary histories of fungal taxa appears to have influenced their distributions across latitudes at large scales.

The latitudinal gradient in evolutionary age of taxa is common, and has been documented in numerous plant and animal groups (e.g., Buckley *et al.* 2010; Hawkins *et al.* 2012; Romdal *et al.* 2013). Moreover, some of these studies have also found evidence for temperature and precipitation rates as underlying factors (Hawkins *et al.* 2012; Romdal *et al.* 2013). Our study suggests that these patterns can apply to microbes as well. As with plant and animals, there was overlap in

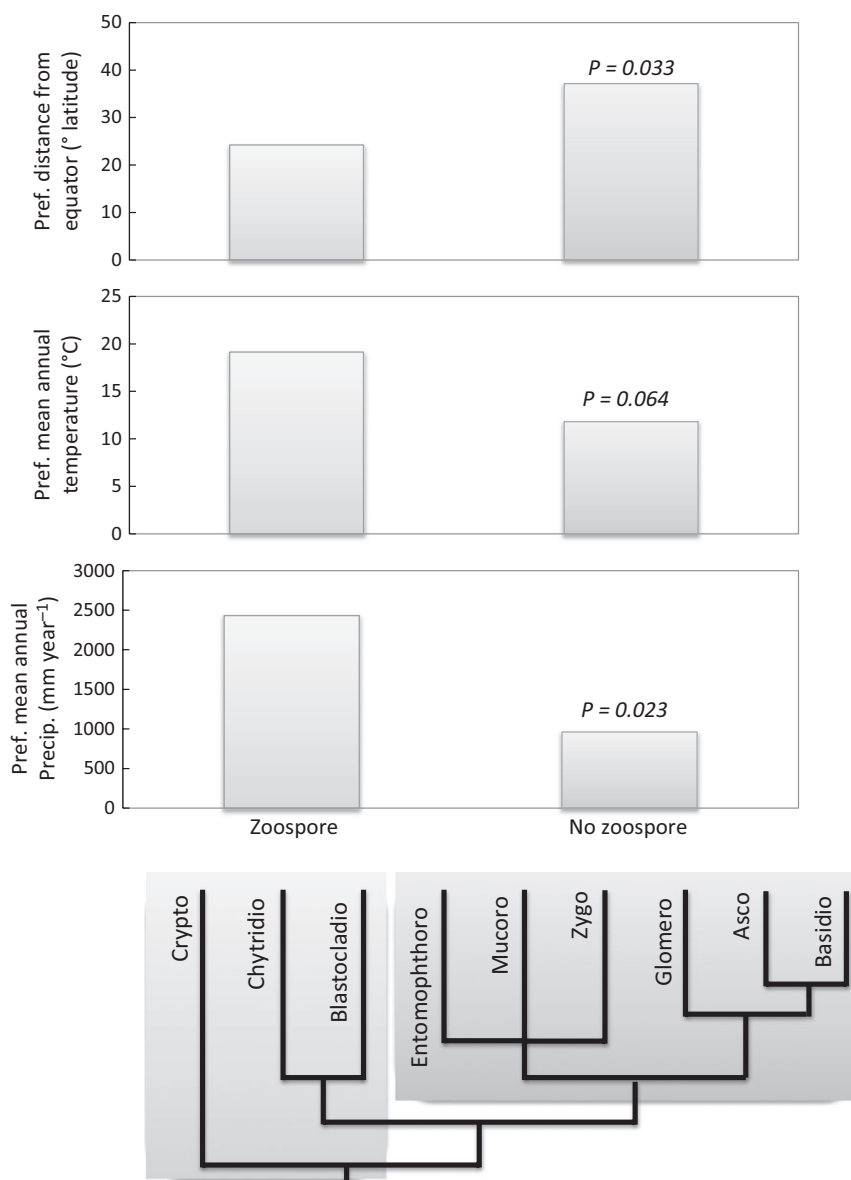


Figure 3 Environmental preferences of fungal phyla with and without the zoospore stage. Phyla lacking a zoospore stage (Entomophthoromycota, Mucoromycotina, Zygomycota, Glomeromycota, Ascomycota, and Basidiomycota) displayed significant phylogenetic conservatism in their preferences for higher latitudes and lower precipitation levels, and marginally significant phylogenetic conservatism in preference for lower temperatures. Bars are means of phyla. Phylogenetic relationships among fungal phyla (suffix '-mycota' or '-mycotina') are as reported in James *et al.* (2006) and Stajich *et al.* (2009).

latitudinal distributions of old vs. young fungal groups. For instance, the younger fungal phyla were well-represented in soils throughout the latitudinal gradient (Fig. 1). This result is consistent with others who have recorded ECM fungi (Ascomycota and Basidiomycota) within the tropics as well as higher latitudes (e.g., Buyck *et al.* 1996; Tedersoo *et al.* 2012). In contrast, although some taxa from older phyla were found in the higher latitudes, in general the older phyla were better-represented in the lower latitudes (Fig 1). In other words, the relative constraint of older phyla to the lower latitudes seems to be the main driver of differences in latitudinal distributions among phyla.

We found that the lack of a zoospore stage was more strongly related to preferences for drier conditions than for

colder temperatures (Fig. 3), so water availability may be a particularly important constraint for zoosporic phyla. Zoospores of the three ancestral phyla (Cryptomycota, Chytridiomycota, and Blastocladiomycota) lack cell walls, so they are relatively vulnerable to osmotic shock (Gleason *et al.* 2010; James *et al.* 2013). Among our samples, the oldest phylum, Cryptomycota, displayed a notable preference for high precipitation rates (Fig. 1). Likewise, in a survey of diverse environmental samples, Jones *et al.* (2011a) found Cryptomycota-related sequences primarily (though not exclusively) in aquatic samples as well as water-saturated sediments and soils. An additional consideration is that many zoospores use flagella to disperse through water (Liu *et al.* 2006), which could also influence their biogeography. In contrast, many

Ascomycetes and Basidiomycetes discharge spores into the air for wind transport (Ingold 1953), so they may not be as dependent on standing water for dispersal.

The Dikarya are capable of producing regular septa with central pores that can be closed to prevent leakage; fungi with these structures are more stress-tolerant (Beck *et al.* 2013). In addition, numerous members of the Dikarya form ECM relationships with specific host plants (e.g., Tedersoo *et al.* 2010, 2012). This latter trait could also have influenced somewhat the environmental preferences of Dikarya (Tedersoo *et al.* 2010), as the study sites dominated by ECM host plants tended to occupy higher latitudes and colder habitats (Table S1). However, environmental preferences of the Dikarya were not significantly phylogenetically conserved in any case: not for distance from the equator, temperature, nor precipitation level (Fig. S3). Thus, we found no evidence that the possession of regular septa by the youngest phyla, or their associations with ECM host plants, noticeably influenced their biogeographical distributions in this study. We note that regular-like septa can also be produced by taxa of the Kickxellales and Harpellales within Kickxellomycotina, which is older than the Dikarya (Tretter *et al.* 2013). Nevertheless, no members of these groups were detected in our samples. They often reside within insect guts (Tretter *et al.* 2013), and their large-scale distributions in soil remain relatively unexamined.

The loss of the zoospore stage was, in general, more strongly related to shifts in environmental preferences than was the development of regular septa. A number of additional physiological and morphological traits distinguish the Cryptomycota, Chytridiomycota, and Blastocladiomycota clades from those that evolved later (e.g., James *et al.* 2006, 2013; Kumar *et al.* 2011), and these traits might each have elicited differences in environmental preferences. The loss of zoospores is just one possible mechanism. In studies that have used culture-independent techniques to characterize fungal community composition in high latitudes, fungi of the Cryptomycota, Chytridiomycota, and Blastocladiomycota are often much rarer than those of the Dikarya (e.g., Deslippe *et al.* 2012; Taylor *et al.* 2013). The environmental conditions found at higher latitudes might either directly inhibit activities of older phyla, or might provide a competitive advantage to younger phyla.

The absolute age of fungal phyla is an area of active research, and only broad estimates exist for the oldest clades (Taylor & Berbee 2006). Currently, the divergence of younger phyla from the Cryptomycota, Chytridiomycota, and Blastocladiomycota clades—and the loss of the zoospore stage—is thought to have occurred during the Neoproterozoic, approximately 600 to 800 Ma (Stajich *et al.* 2009). During this time span, multiple ‘Snowball Earth’ events occurred (Evans *et al.* 1997; Smith 2009). Snowball Earths were extreme ice ages, when mean annual temperatures were below freezing even at the equator (Hyde *et al.* 2000). Widespread glaciation was rare before this period, with the exception of a Snowball Earth event in the Paleoproterozoic (Evans *et al.* 1997; Kopp *et al.* 2005) when fungi had not yet evolved (Taylor & Berbee 2006). Thus, the Neoproterozoic Snowball Earths might have subjected ancestral fungi to sustained cold periods that were unprecedented in their evolutionary history. We tentatively propose that the novel environmental conditions selected for

new clades that possessed protective cell walls throughout their lifespan.

Latitudinal shifts in fungal diversity and community composition have previously been documented over smaller scales and for specific fungal groups. For example, the species richness of ectomycorrhizal fungi peaks in higher latitudes and at lower precipitation levels (Tedersoo *et al.* 2012). This pattern is broadly consistent with our observations, as most ectomycorrhizal fungi belong to the Dikarya. In contrast, the richness of fungal endophyte communities (primarily Ascomycota) peaks in the tropics, where host plant diversity is likewise high (Arnold & Lutzoni 2007). Within southern Europe, epiphytic lichen diversity (also mostly Ascomycota) peaks in latitudes with higher water availability (Aragon *et al.* 2012). In a global synthesis, Kivlin *et al.* (2011) reported that latitude, temperature, and precipitation each significantly influenced the community composition of arbuscular mycorrhizal fungi (Glomeromycota). Moreover, community compositions of ericoid fungi and forest soil fungi vary by latitude in western China (Sun *et al.* 2012).

A number of caveats should be considered within the context of this study. First, the observed relationships between environmental preferences and other traits are correlative, so causal mechanisms must be interpreted with caution. Selection experiments are a more definitive test of underlying mechanisms and would be a worthwhile next step. Second, although our complement of study sites is fairly large, it does not comprehensively represent all environments and geographical regions within North and South America. Likewise, it is based solely in the Western Hemisphere. Third, we focused on soil fungi; environmental controls over the biogeography of aquatic, endophytic, or epiphytic fungi could be quite different. Fourth, our survey did not capture all fungal phyla, and did not include Zoopagomycotina, Kickxellomycotina, or the microsporidia. Our interpretations are necessarily limited to those taxa represented in the survey. Finally, we sequenced the 18S region because it allowed us to identify taxa from the phylum to the family level. Had we targeted the ITS region, its high degree of sequence variation would have allowed us to resolve fungal taxa closer to the species level, but with the trade-off of lower confidence at the phylum level (Schoch *et al.* 2012).

In conclusion, we found that the evolutionary history of fungal taxa was related to their biogeographic distribution at large scales. Specifically, responses to past changes in the Earth’s climate might have determined the latitudinal distribution of fungal phyla today. We propose that extreme ice ages that occurred early in the history of fungi elicited the evolution of greater drought or cold tolerance. The responsible trait might be the loss of the zoospore stage in favour of the maintenance of protective cell walls throughout the life cycle. The potential underlying mechanism, addressed by the Tropical Conservatism Hypothesis, has previously been implicated for plants and animals; our results indicate that it could be even more broadly applicable across the tree of life.

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AUTHORSHIP STATEMENT

KT led the analyses and wrote the manuscript; MM & JS investigated the fungal traits and evolutionary history; BH provided input on the Tropical Conservatism Hypothesis and its analyses; NF supplied the samples, extracted the DNA, and provided advice on the phylogenetic analyses; and KM amplified and prepped the fungal DNA and contributed to the sequence analyses. All authors provided feedback during manuscript preparation.

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