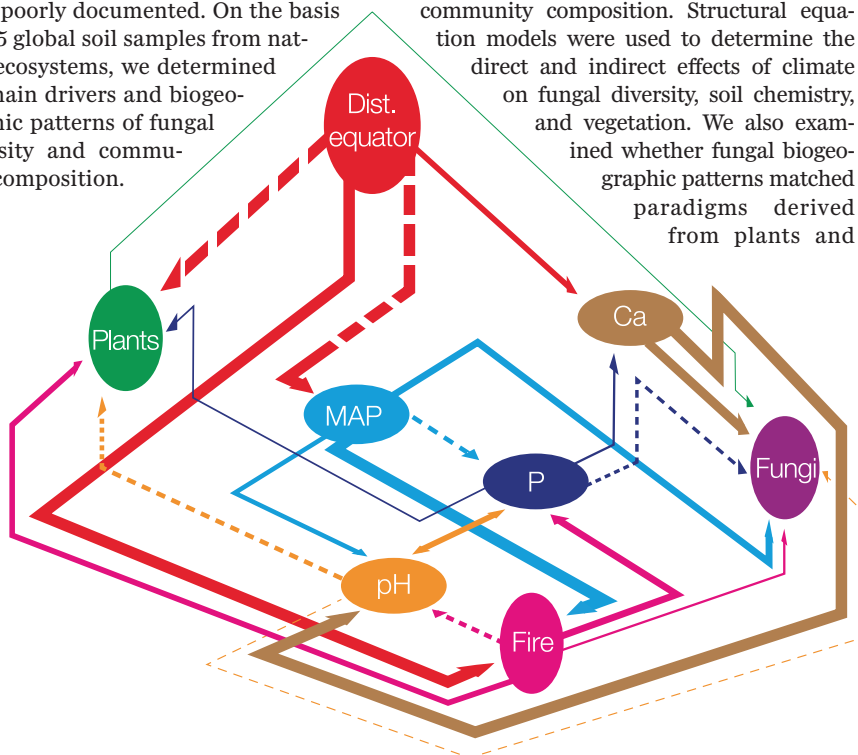**FUNGAL BIOGEOGRAPHY**

Global diversity and geography of soil fungi

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INTRODUCTION: The kingdom Fungi is one of the most diverse groups of organisms on Earth, and they are integral ecosystem agents that govern soil carbon cycling, plant nutrition, and pathology. Fungi are widely distributed in all terrestrial ecosystems, but the distribution of species, phyla, and functional groups has been poorly documented. On the basis of 365 global soil samples from natural ecosystems, we determined the main drivers and biogeographic patterns of fungal diversity and community composition.

RATIONALE: We identified soil-inhabiting fungi using 454 Life Sciences (Branford, CN) pyrosequencing and through comparison against taxonomically and functionally annotated sequence databases. Multiple regression models were used to disentangle the roles of climatic, spatial, edaphic, and floristic parameters on fungal diversity and community composition. Structural equation models were used to determine the direct and indirect effects of climate on fungal diversity, soil chemistry, and vegetation. We also examined whether fungal biogeographic patterns matched paradigms derived from plants and

animals—namely, that species' latitudinal ranges increase toward the poles (Rapoport's rule) and diversity increases toward the equator. Last, we sought group-specific global biogeographic links among major biogeographic regions and biomes using a network approach and area-based clustering.

RESULTS: Metabarcoding analysis of global soils revealed fungal richness estimates approaching the number of species recorded to date. Distance from equator and mean annual precipitation had the strongest effects on richness of fungi, including most fungal taxonomic and functional groups. Diversity of most fungal groups peaked in tropical ecosystems, but ectomycorrhizal fungi and several fungal classes were most diverse in temperate or boreal ecosystems, and many fungal groups exhibited distinct preferences for specific edaphic conditions (such as pH, calcium, or phosphorus). Consistent with Rapoport's rule, the geographic range of fungal taxa increased toward the poles. Fungal endemicity was particularly strong in tropical regions, but multiple fungal taxa had cosmopolitan distribution.

CONCLUSIONS: Climatic factors, followed by edaphic and spatial patterning, are the best predictors of soil fungal richness and community composition at the global scale. Richness of all fungi and functional groups is causally unrelated to plant diversity, with the exception of ectomycorrhizal root symbionts, suggesting that plant-soil feedbacks do not influence the diversity of soil fungi at the global scale. The plant-to-fungi richness ratio declined exponentially toward the poles, indicating that current predictions—assuming globally constant ratios—overestimate fungal richness by 1.5- to 2.5-fold. Fungi follow similar biogeographic patterns as plants and animals, with the exception of several major taxonomic and functional groups that run counter to overall patterns. Strong biogeographic links among distant continents reflect relatively efficient long-distance dispersal compared with macro-organisms. ∎

Direct and indirect effects of climatic and edaphic variables on plant and fungal richness. Line thickness corresponds to the relative strength of the relationships between the variables that affect species richness. Dashed lines indicate negative relationships. MAP, mean annual precipitation; Fire, time since last fire; Dist. equator, distance from the equator; Ca, soil calcium concentration; P, soil phosphorus concentration; pH, soil pH.

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Global diversity and geography of soil fungi

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Fungi play major roles in ecosystem processes, but the determinants of fungal diversity and biogeographic patterns remain poorly understood. Using DNA metabarcoding data from hundreds of globally distributed soil samples, we demonstrate that fungal richness is decoupled from plant diversity. The plant-to-fungus richness ratio declines exponentially toward the poles. Climatic factors, followed by edaphic and spatial variables, constitute the best predictors of fungal richness and community composition at the global scale. Fungi show similar latitudinal diversity gradients to other organisms, with several notable exceptions. These findings advance our understanding of global fungal diversity patterns and permit integration of fungi into a general macroecological framework.

Fungi are eukaryotic microorganisms that play fundamental ecological roles as decomposers, mutualists, or pathogens of plants and animals; they drive carbon cycling in forest soils, mediate mineral nutrition of plants, and alleviate carbon limitations of other soil organisms. Fungi comprise some 100,000 described species (accounting for synonyms), but the actual extent of global fungal diversity is estimated at 0.8 million to 5.1 million species (1).

Globally, the biomass and relative proportions of microbial groups, including fungi, co-vary with the concentration of growth-limiting nutrients in soils and plant tissues. Such patterns suggest that the distribution of microbes reflects latitudinal variation in ecosystem nutrient dynamics (2–4). Richness of nearly all terrestrial and marine macroorganisms is negatively related to increasing latitude (5)—a pattern attributed to the combined effects of climate, niche conservatism, and rates of evolutionary radiation and extinction (6). Although morphological species of unicellular microbes are usually cosmopolitan (7), there is growing evidence that the distribution of microorganisms is shaped by macroecological and community assembly processes (8). Only a few of these biogeographic processes have been demonstrated for fungi at the local scale (9). Despite their enormous diversity and importance in ecosystem function, little is known about general patterns of fungal diversity or functional roles over large

geographic scales. We used a global data set to disentangle the roles of climatic, edaphic, floristic, and spatial variables governing global-scale patterns of soil fungal diversity. We also address macroecological phenomena and show that fungi largely exhibit strong biogeographic patterns that appear to be driven by dispersal limitation and climate.

Materials and methods

We collected 40 soil cores from natural communities in each of 365 sites across the world using a uniform sampling protocol (Fig. 1A and data file S1). Most plots (2500 m^2) were circular, but in steep mountain regions and densely forested areas, some plots were oblong. We randomly selected 20 trees located at least 8 m apart. In two opposite directions, 1 to 1.5 m from each tree trunk, loose debris was removed from the forest floor. Polyvinyl chloride (PVC) tubes (5 cm in diameter) were hammered into the soil down to 5 cm depth. These soil cores almost always included fine roots and comprised both the organic layer and top mineral soil. Although deep soil may contain some distinctive organisms adapted to anoxic conditions or low nutrient levels, our sampling was limited to topsoil for the following reasons. First, in the vast majority of soil types, >50% of microbial biomass and biological activity occur in the topmost organic soil layer. Second, deeper sampling was impossible in shallow, rocky

soils or those with high clay concentrations and hardpans. Third, differences among soil horizons may be masked by other variables across large geographic scales (10). The 40 soil cores taken in each site were pooled, coarse roots and stones were removed, and a subset of the soil was air-dried at <35°C. Dried soil was stored in zip-lock plastic bags with silica gel in order to minimize humidity during transit. In the laboratory, we ground dried soil into fine powder using bead beating.

We extracted DNA from 2.0 g of soil using the PowerMax Soil DNA Isolation kit (MoBio, Carlsbad, CA) following manufacturer's instructions. We performed polymerase chain reaction (PCR) using a mixture of six forward primers (in equimolar concentration) analogous to ITS3 and a degenerate reverse primer analogous to ITS4 (hereafter referred to as ITS4ngs). We shortened and modified forward and reverse primers to

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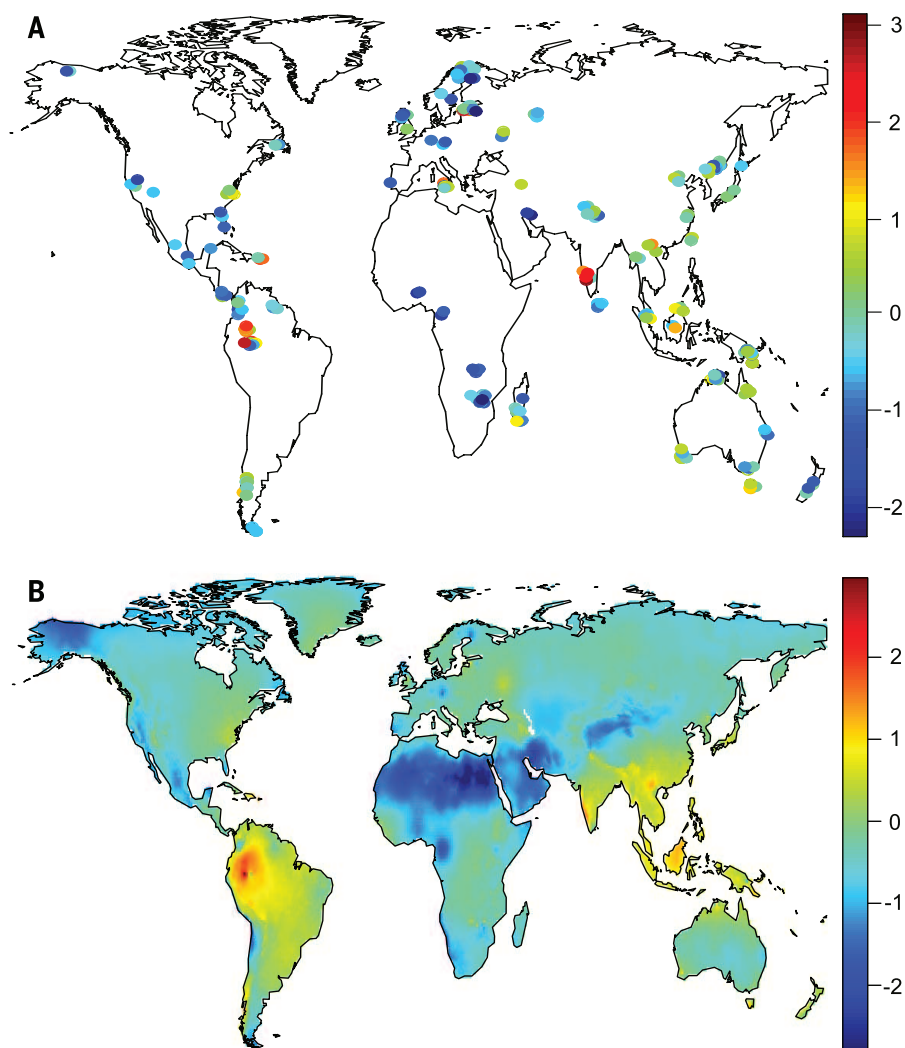*Corresponding author. E-mail: leho.tedersoo@ut.ee †These authors contributed equally to this work.

Fig. 1. Maps of global sampling and interpolated taxonomic richness of all fungi. (**A**) Map of global sampling. Circles indicate study sites. (**B**) Interpolated taxonomic richness of all fungi using IDW algorithm and accounting for the relationship with mean annual precipitation (based on the best multiple regression model). Different colors depict residual OTU richness of all fungi accounting for sequencing depth. Warm colors indicate OTU-rich sites, whereas cold colors indicate sites with fewer OTUs.

completely match >99.5% of all fungi [except ~60% of Tulasnellaceae that exhibit highly divergent 5.8S ribosomal DNA (rDNA) and Microsporidia that exhibit rearrangements in rDNA] (table S1). The ITS4ngs primer was tagged with one of 110 identifiers (multiplex identifiers, 10 to 12 bases) that were modified from those recommended by Roche (Basel, Switzerland) to differ by >3 bases, start only with adenosine, and consist of between 30 and 70% adenosine and thymidine in order to optimize the adaptor ligation step. The PCR cocktail consisted of 0.6 µl DNA extract, 0.5 µl each of the primers (20 pmol), 5 µl 5xHOT FIREPol Blend Master Mix (Solis Biodyne, Tartu, Estonia), and 13.4 µl doubledistilled water. We carried out PCR in four replicates using the following thermocycling conditions: an initial 15 min at 95°C, followed by 30 cycles at 95°C for 30 s, 55°C for 30 s, 72°C for 1 min, and a final cycle of 10 min at 72°C. PCR products were pooled, and their relative quantity was estimated by running 5 µl amplicon DNA on 1% agarose gel for 15 min. DNA samples yielding no visible band were reamplified by using 35 cycles in an effort to obtain sufficient PCR product, whereas samples with a very strong band were reamplified with only 25 cycles. It is important to use as few cycles as possible to minimize chimera formation and to be able to interpret sequence abundance in a semiquantitative manner (*11*). We used negative (for DNA extraction and PCR) and positive controls throughout the experiment. Amplicons were purified with Exonuclease I and FastAP thermosensitive alkaline phosphatase enzymes (Thermo Scientific, Pittsburgh, PA). Purified amplicons were subjected to quantity normalization with a SequalPrep Normalization Plate Kit (Invitrogen, Carlsbad, CA) following manufacturer's instructions. We divided normalized amplicons into five pools that were subjected to 454 adaptor ligation, emulsion PCR, and 454 pyrosequencing by using the GS-FLX+ tech-nology and Titanium chemistry as implemented by Beckman Coulter Genomics (Danvers, MA).

Bioinformatics

Pyrosequencing on five half-plates resulted in 2,512,068 reads with a median length of 409 bases. The sequences were reassigned to samples in mothur 1.32.2 (www.mothur.org) based on the barcodes and then trimmed (parameters: minlength = 300; maxambigs = 1; maxhomop = 12; qwindowaverage = 35; qwindowsize = 50; and bdiffs = 1) to exclude short and low-quality sequences, resulting in 2,231,188 high-quality sequences. We used ITSx 1.0.7 (http://microbiology.se/software/itsx) to remove the flanking 5.8S and 28S rRNA genes for optimal resolution of ITS2 clustering and removal of compromised and nontarget sequences. As a filter to remove most of the partial sequences, we retained only sequences >99 base pairs (bp) in length. Chimera control was exercised through UCHIME 4.2 (www.drive5.com/uchime). After these filtering steps, 1,397,679 sequences were retained and further clustered at 90.0% and 95.0 to 99.0% sequence similarity thresholds (*12*) as implemented in CD-Hit 4.6.1 (www.cd-hit.org). Clustering revealed 37,387, 59,556, 66,785, 77,448, 94,255, and 157,956 taxa based on 90.0, 95.0, 96.0, 97.0, 98.0, and 99.0% sequence similarity thresholds, respectively. The longest sequence of each Operational Taxonomic Unit (OTU), based on clustering at 98.0% sequence similarity, was selected as the representative for BLASTn searches (word size = 7; penalties: gap = −1; gap extension = −2; and match = 1) against the International Nucleotide Sequence Databases Collaboration (INSDC; www.insdc.org) and UNITE (unite.ut.ee) databases. In addition, we ran BLASTn searches against established reference sequences of all fungi in 99.0% similarity clusters that include third-party taxonomic and metadata updates (*12*) as implemented in the PlutoF workbench (*13*). For each query, we considered the 10 best-matching references to annotate our global sequences as accurately as possible. If no reliable taxon name was available, we ran manual BLASTn searches against INSDC with 500 best-matching sequences as output. We typically relied on 90, 85, 80, and 75% sequence identity as a criterion for assigning OTUs with names of a genus, family, order, or class, respectively. Sequence identity levels were raised in subsets of Sordariomycetes, Leotiomycetes, and Eurotiomycetes, because these taxa contain multiple genera and families that have unusually conserved internal transcribed spacer (ITS) sequences. As a rule, we considered e-values of BLASTn search results e^{-50} reliable to assign sequences to the fungal kingdom, whereas those $>e^{-20}$ were considered "unknown." E-values between e^{-20} and e^{-50} were manually checked against the 10 best matches for accurate assignment. We followed INSDC for higher-level taxonomy of eukaryotes (*14*) and the Index Fungorum (www.indexfungorum.org) for species through class-level taxonomy of fungi. Our group of taxonomic experts assigned each fungal genus, family, or order to functional categories (data file S2). If different functional categories

were present within a specific genus, we chose the dominant group (>75% of species assigned to a specific category) or considered its ecology unknown (<75% of species assignable to a single category). All Glomeromycota were considered to be arbuscular mycorrhizal (AM). Taxa were considered to be ectomycorrhizal (EcM) if they best matched any sequences of known EcM lineages (*15*) and exhibited sequence length/BLASTn scores above lineage-specific thresholds. For several taxonomic groups, we constructed phylogenetic trees to assess the performance of clustering, sequence quality of singletons, accuracy of OTU separation, and taxonomic assignments (fig. S1). In the course of this project, we provided 10,232 third-party taxonomic reannotations to INSDC sequences to improve subsequent identification of fungal sequences and made these available through the UNITE database.

Statistical analyses

Estimates of the mean annual temperature (MAT), mean annual precipitation (MAP), soil moisture, and soil carbon at 30 arc second resolution were obtained from the WorldClim database (www.worldclim.org). Estimates of potential evapotranspiration (PET) and net primary productivity (NPP) at 30 arc minute resolution were obtained from the Atlas of the Biosphere (www.sage.wisc.edu/atlas/maps.php). Variation coefficients for MAT and MAP were computed based on the average monthly values to represent seasonality of temperature and precipitation. We also calculated the difference of MAP to PET in order to evaluate the effect of rainfall surplus or deficit. On the basis of vegetation type and geographical distribution, sites were categorized into biogeographic regions and biomes following the classification of the World Wildlife Foundation (http://worldwildlife.org) with a few exceptions: (i) temperate deciduous forests in the Northern and Southern hemispheres were treated separately; (ii) tropical montane forests (>1500 m elevation) were separated from the tropical lowland moist forests; and (iii) grasslands and shrublands of all geographic origins were pooled. At each site, we also determined the age of vegetation, time since the last fire, and EcM plant species along with their relative contribution to stand basal area. EcM plants are usually conspicuous trees or prominent shrubs that are relatively easy to identify, and their mycorrhizal status is verifiable in the field by using root excavation and microscopy. Complete lists of tree species were available for <10% of the sites, so we did not directly include plant community composition parameters in our analyses.

Concentrations of N, C, $^{13}C/^{12}C$, and $^{15}N/^{14}N$ were determined from 1 to 20 mg of soil by using GC-combustion coupled to isotope-ratio mass spectrometry (*16*). Concentrations of soil calcium, potassium, magnesium, and phosphorus were determined as in (*16*). Soil pH was measured in 1 N KCl solution.

For analyses of fungal richness, we calculated residuals of OTU richness in relation to the square root of the number of obtained sequences to

account for differences in sequencing depth. This method outperformed the commonly used rarefaction to the lowest number of sequences method, which removes most of the data (*17*). We also calculated the richness of major class-level taxonomic and functional groups (comprising >100 OTUs). We excluded outlying samples dominated by a few OTUs of molds, which are indicative of poor sample preservation (relative abundance of sequences belonging to Trichocomaceae >5%, Mortierellaceae >20%, or Mucoraceae >20% that exceeded three times the mean + SD). Although these samples were fairly homogeneously distributed across the world, they had conspicuously lower fungal richness. We also excluded samples that yielded less than 1200 sequences per sample.

To determine the relationship between plant and fungal richness, we relied on co-kriging values from the global vascular plant species richness data set (*18*), which covered 96.7% of our sites. These scale-free values of plant richness were then regressed with residuals from the best-fit models for fungal richness and fungal functional groups. We further calculated the ratio of relative plant richness to fungal richness and fitted this ratio with latitude using polynomial functions to test the assumed uniformity of plant-to-fungal richness ratios at the global scale (*1, 19, 20*). To account for potential latitudinal biases in plant-to-fungal diversity estimates, we took into account the nonuniform distribution of land surfaces by calculating an inverse distance weighting (IDW) spatial interpolation of standardized ratios of plant-to-residual fungal diversity using the "gstat" package in R (*21*). We then used IDW to interpolate total fungal diversity beyond sampling sites by accounting for MAP as based on the best-fitting multiple regression model.

Distance from the equator, altitude, age of vegetation, time since last fire, climatic variables, and concentrations of nutrients were log-transformed before analyses in order to improve the distribution of residuals and reduce nonlinearity. To account for potential autocorrelation effects, we calculated spatial eigenvectors using SAM version 4 (*22*). To determine the best predictors of global fungal diversity, we included edaphic, climatic, floristic, and spatial variables in multiple regression models. Because of the large number of predictors, we preselected 16 candidate predictors that were revealed through exploratory multiple linear and polynomial regression analyses based on coefficients of determination and forward selection criteria. The most parsimonious models were determined according to the corrected Akaike information criterion (AICc), which penalizes over-fitting. Last, components of the best models were forward-selected to determine their relative importance as implemented in the "packfor" package in R.

To test the direct effects of climatic variables on richness of fungi and their functional groups, and indirect climatic effects (via soil nutrients and vegetation), we used Structural Equation Modeling (SEM) in Amos version 22 (SPSS Software, Chicago, IL). Model fits were explored based on both χ^2 test and root-mean-square error of

approximation (RMSEA). First, we included all potentially important variables (inferred from both the multiple regression models and correlations for individual response variables) to construct separate SEM models. We tested all direct and indirect relations between exogenous and endogenous variables, including their error terms. Then, we used backward elimination to remove nonsignificant links to maximize whole-model fit. Last, we combined the obtained SEM models in a unified path model, following the same elimination procedure.

In addition to full models, we specifically tested the relationships between OTU richness and distance from the equator and soil pH because these or closely related variables were usually among the most important predictors. For these analyses, we calculated residuals of richness that accounted for other significant variables of the best models. To address nonlinear relationships, we fitted up to fifth-order polynomial functions and selected best-fit models on the basis of AICc values.

The relative effects of climatic, edaphic, spatial, and floristic variables on the total fungal community composition and on particular functional groups were determined by using Hellinger dissimilarity (calculated if >90% sites were represented by >1 shared OTUs), exclusion of all OTUs that occurred once, and a multistage model selection procedure as implemented in the DISTLM function of Permanova+ (www.primer-e.com/permanova.htm). Considering computational requirements, 15 candidate variables were preselected based on unifactorial (marginal test based on largest F_{pseudo} values) and multifactorial (forward selection) models. Spatial eigenvectors were not included in these analyses because they typically were of minor importance in variation partitioning analyses and to avoid making the models computationally prohibitive. Optimal models were selected based on the AICc. To obtain coefficients of determination (cumulative $R^2_{adjusted}$) and statistics (F_{pseudo} and P values) for each variable, components of the best models were forward selected. In parallel, we prepared Global Nonmetric Multidimensional Scaling (GNMDS) graphs using the same options. Significant variables were fitted into the GNMDS ordination space by using the "envfit" function in the "vegan" package of R. We also grouped all climatic, edaphic, spatial, and floristic variables into a variation partitioning analysis by integrating procedures in the "vegan" and "packfor" packages of R. Besides group effects, variation partitioning estimates the proportion of shared variation among these groups of predictors.

For global biogeographic analyses, we excluded OTUs from the order Hypocreales and family Trichocomaceae (both Ascomycota) because the ITS region provides insufficient taxonomic resolution, and known biological species are grouped together within the same OTU (*23*). We tested the differences among fungal taxonomic and functional groups for the occurrence frequency (number of sites detected) and latitudinal range of OTUs using a nonparametric Kruskal-Wallis

test and Bonferroni-adjusted multiple comparisons among mean ranks. To test the validity of Rapoport's rule in soil fungi, we calculated the average latitudinal range of OTUs for each site (24). The average latitudinal range was regressed with the latitude of study sites by means of polynomial model selection based on the AICc criterion. This analysis was run with and without OTUs only detected at a single site (range = 0). Because the results were qualitatively similar, we report results including all OTUs. To construct biogeographic relationships among major regions and biomes, we generated cross-region and cross-biome networks based on the number of shared OTUs. We excluded occurrences represented by a single sequence per site. Ward clustering of biogeographic regions and biomes were constructed

by using the Morisita-Horn index of similarity, which is insensitive to differences in samples size, by use of the "pvclust" package of R. In this procedure, P values are inferred for nonterminal branches based on multiscale bootstrap resampling with 1000 replicates.

Taxonomic and functional diversity

Pyrosequencing analysis of global soil samples revealed 1,019,514 quality-filtered sequences that were separated into 94,255 species-level OTUs (supplementary materials). Altogether, 963,458 (94.5%) sequences and 80,486 (85.4%) OTUs were classified as Fungi. Most other taxa belonged to animals (Metazoa, 3.3%), plants (Viridiplantae, 3.1%), alveolates (Alveolata, 2.8%), and amoebae (mostly Rhizaria, 1.3%). Kingdom-level assign-

ment of 3.8% OTUs remained elusive. The fungal subset included 35,923 (44.6%) OTUs that were represented by a single sequence; these were removed from further analyses in order to avoid overestimating richness based on these potentially erroneous sequences (25). The remaining 44,563 nonsingleton fungal OTUs in our data set numerically correspond to approximately half of the described fungal species on Earth (1). For comparison, there are currently 52,481 OTUs based on 98.0% similarity clustering of all fungal ITS sequences in publicly available databases (12). Global soil sampling revealed representatives of all major phyla and classes of Fungi. Of fungal taxa, Basidiomycota (55.7%), Ascomycota (31.3%), Mortierellomycotina (6.3%), and Mucoromycotina (4.4%) encompassed the
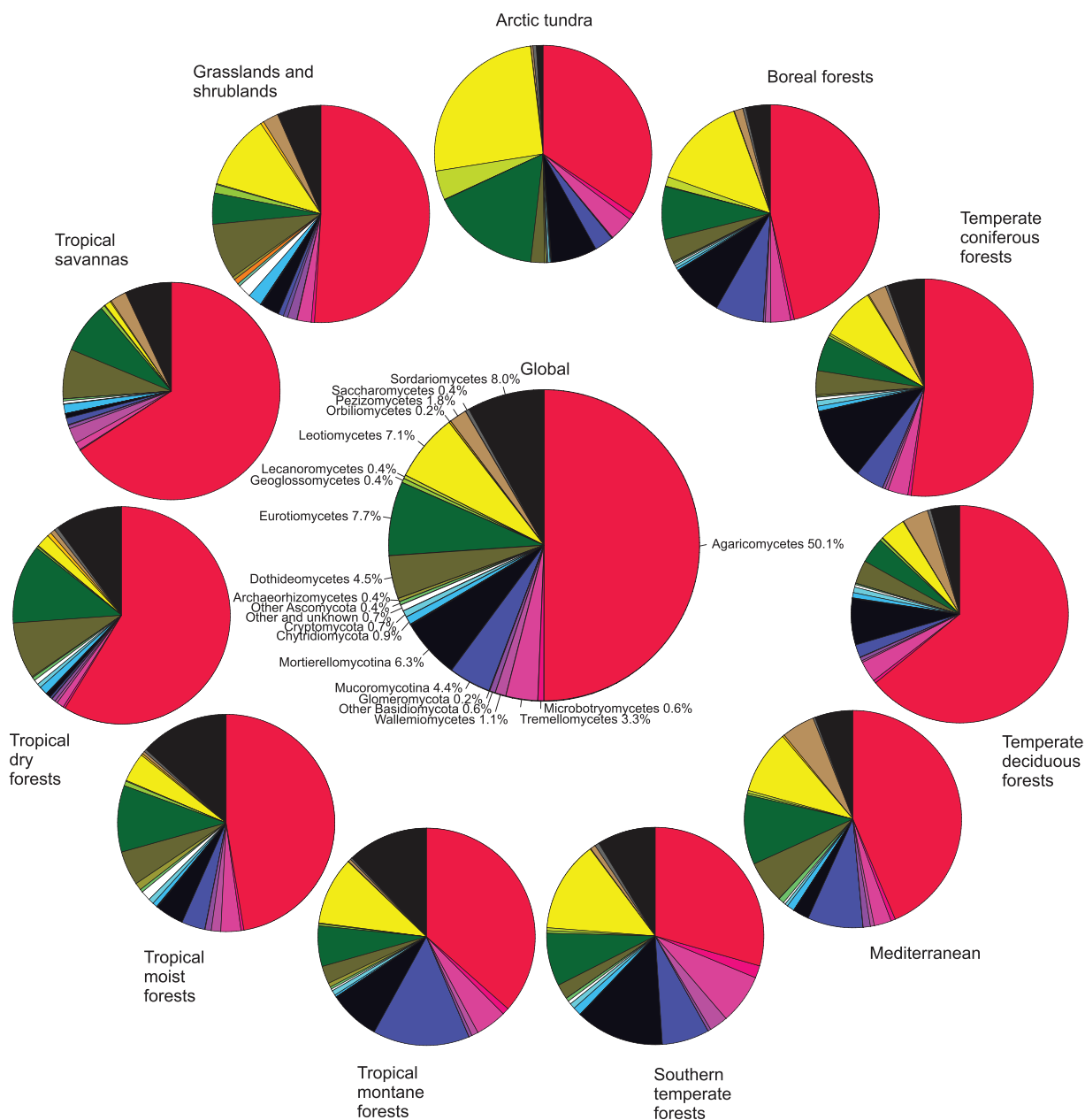

Fig. 2. Relative proportion of fungal sequences assigned to major taxonomic groups in different biomes.

largest proportion of sequences (Fig. 2), whereas the most OTU-rich phyla were the Ascomycota (48.7%), Basidiomycota (41.8%), Chytridiomycota (2.3%), and Cryptomycota (syn. Rozellida; 2.1%) (fig. S2 and data file S1). Except for the recently described phylum Cryptomycota (*26*), the relative proportions of major phyla correspond to the proportional distribution of taxa described and sequenced to date (www.indexfungorum.org) (*12*). Below the phylum level, ~6% of all fungal OTUs could not be assigned to any known class of fungi. Further clustering of unidentified fungal sequences at 70% sequence similarity revealed 14 distinct taxonomic groups comprising >7 OTUs, suggesting that there are several deeply divergent class-level fungal lineages that have not yet been described or previously sequenced.

Our classification revealed that 10,801 (24.2%) fungal OTUs exhibited >98% sequence similarity, and 33.8% exhibited >97% similarity, to pre-existing ITS sequences in public databases. This is consistent with (*19*), reporting 48% of OTUs amplified from Alaskan soils with >97% similarity to any database sequences. In our study, only 4353 fungal OTUs (9.8%) were matched to sequences from herbarium specimens or fully described culture collections at >98.0% sequence similarity. Although many type collections are yet to be sequenced, the paucity of matches to database entries indicates that a majority of soil-inhabiting fungal taxa remain undescribed (*19, 20*). These results highlight the current lack of data from understudied tropical and subtropical ecosystems. The phenomenon of high cryptic diversity and low success in naming OTUs at the genus or species level have been found in other groups of soil microbes and invertebrates, emphasizing our poor overall knowledge of global soil biodiversity (*27, 28*).

The main fungal phylogenetic and functional groups were present in all ecosystems, but their relative proportions varied severalfold across biomes (Fig. 2 and figs. S2 to S4). The ratio of Ascomycota to Basidiomycota OTUs was highest in grasslands and shrublands (1.86) and tropical dry forests (1.64) but lowest in the temperate deciduous forests (0.88). Chytridiomycota, Cryptomycota, and Glomeromycota were relatively more diverse in the grasslands and shrublands, accounting for 4.6, 3.6, and 1.4% of OTU richness, respectively. The relative OTU richness of Mortierellomycotina and Mucoromycotina (including most fast-growing molds but also some plant symbionts) peaked in the tundra biome (4.8 and 2.7%, respectively), but their abundance was lowest in tropical dry forests (1.0 and 0.6%, respectively). Archaeorhizomycetes, a recently described class of Ascomycetes from a boreal forest (*29*), was most diverse in tropical moist and montane forests, particularly in northern South America and New Guinea.

Among all fungal taxa, OTUs assigned to saprotrophs, EcM mutualists, and plant pathogens comprised 19,540 (43.8%), 10,334 (23.2%), and 1770 (4.0%), respectively (fig. S4). Other trophic categories contained <1% of remaining OTUs. EcM fungi contributed 34.1% of all taxa

in the northern temperate deciduous forests but accounted for a relatively low proportion (11.9%) in grasslands and shrublands, reflecting the paucity of host plants in these ecosystems. Similarly, the proportion of EcM fungal taxa was lowest in northern South America (8.0%), where AM trees often dominate. Plant pathogens were relatively more abundant and diverse in lowland tropical moist (6.2%) and dry (6.3%) forests.

Predictors of global richness

Structural equation models revealed that climate has both a strong direct effect on plant and fungal richness and functional groups, but it also indirectly affects these metrics by altering edaphic conditions (fig. S5). Both SEM and regression models suggest that the best predictors of diversity differed among phylogenetic and functional groups of fungi. Positive effects of mean annual precipitation (MAP) and soil calcium (Ca) concentration were the strongest predictors of total fungal diversity, explaining 7.2 and 8.9 of residual richness, respectively (table S2). Richness of EcM fungi responded positively to the relative proportion and species richness of EcM plants (explaining 18.3 and 8.5% of variance, respectively), as well as soil pH (13.0%). EcM host species richness (5.9%) and soil pH (20.4%) remained the strongest predictors in the best model for sites with EcM vegetation, accounting for >60% of basal area, a critical point above which the proportion of EcM plants had no further effect on EcM fungal richness. MAP had a strong positive effect (14.8%) on richness of saprotrophs. Diversity of plant pathogens declined with increasing distance from the equator (17.8%) and soil carbon/nitrogen (C/N) ratio (11.6%). Animal parasites responded positively to MAP (20.3%), whereas monthly variation of precipitation (MAP CV) had a negative impact on richness of mycoparasites (fungus-parasitic fungi; 8.2%). Richness of the AM Glomeromycota was negatively related to the age of vegetation (7.3%) but positively related to PET (3.5%) and soil pH (4.3%). Of the major taxonomic groups, the richness of Ascomycota in general (18.5%) and that of Archaeorhizomycetes (21.7%) were negatively related to distance from the equator in best-fit models. Climatic variables were the best predictors for richness of Mortierellomycotina (MAT, negative effect, 26.1%) and the ascomycete classes Dothideomycetes (MAT, positive effect, 20.9%), Lecanoromycetes (MAT, negative effect, 26.7%), Leotiomycetes (MAT, negative effect, 30.1%), Orbiliomycetes (MAT, positive effect, 12.8%), and Sordariomycetes (MAP, positive effect, 33.4%). The richness of Chytridiomycota and the ascomycete class Pezizomycetes was best explained by a positive response to soil pH (8.6 and 40.5%, respectively). Concentration of soil nutrients or their ratio to other nutrients were the strongest predictors for OTU richness of Cryptomycota (N concentration, positive effect, 10.1%), Geoglossomycetes [N/phosphorus (P) ratio, positive effect, 3.7%], Mucoromycotina (C/N ratio, positive effect, 19.0%), and Wallemiomycetes (P concentration, negative effect, 14.9%). The richness of Basidiomycota and

its class Agaricomycetes were best explained by a positive response to soil Ca concentration (13.5 and 12.8%, respectively).

Although geographical distance per se had negligible effects on richness (Moran's I = 0.267), spatial predictors were included in the best richness models of nearly all functional and phylogenetic groups (except Glomeromycota), indicating regional- or continental-scale differences in OTU richness (Fig. 1B). Compared with other tropical regions, richness of fungi was conspicuously lower in Africa, independent of biome type. These results might reflect the relatively lower MAP in much of Africa as compared with other tropical continents. Alternatively, lower fungal richness could be related to the disproportionately strong shifts in biomes during the Pleistocene, which impoverished the African flora (*18*).

Among edaphic variables, soil pH and Ca concentration were typically the most important predictors of fungal OTU richness. These variables positively correlated with fungal richness at the global scale ($F_{1,335}$ = 290.7; $R_{Pearson}$ = 0.682; $P < 0.001$). The strong positive influence of soil Ca concentration on richness of fungi, in particular Basidiomycota, is congruent with a similar positive relationship found for Ca and EcM fungal richness associated with Northern Hemisphere *Alnus* spp. (*30*). Exchangeable Ca is important for many physiological processes in plants and microorganisms and influences the turnover rate of soil organic matter (*31*). In soil geochemical processes, pH and Ca concentration affect each other and thus may have both direct and indirect effects on soil biota. Fungal functional groups were differentially affected by pH. Richness of EcM fungi was greatest in slightly acidic to neutral soils (fig. S6), whereas saprotrophs, especially white rot decomposers, were more diverse in moderately to strongly acidic soils. Richness of Pezizomycetes peaked distinctly in neutral soils.

Macroecological patterns

In general agreement with biogeographic patterns of plants, animals, and foliar endophytic fungi (*5, 32*), the overall richness of soil fungi increased toward the equator (Fig. 3A). However, major functional and taxonomic groups showed dramatic departures from the general latitudinal richness patterns (Fig. 3 and fig. S7). Namely, diversity of saprotrophic fungi, parasites, and pathogens increased at low latitudes, whereas richness of EcM fungi peaked at mid-latitudes, especially in temperate forests and Mediterranean biomes of the Northern Hemisphere (40° to 60°N) (fig. S8). In contrast, saprotrophic fungi had a broad richness peak spanning from ~45°S to 25°N. Richness of Ascomycota—in particular, that of Archaeorhizomycetes, Dothideomycetes, Eurotiomycetes, Orbiliomycetes, and Sordariomycetes—peaked in tropical ecosystems (fig. S7). Conversely, the ascomycete classes Lecanoromycetes and Leotiomycetes, as well as Microbotryomycetes (basidiomycete yeasts), Mortierellomycotina, and Mucoromycotina increased in diversity toward
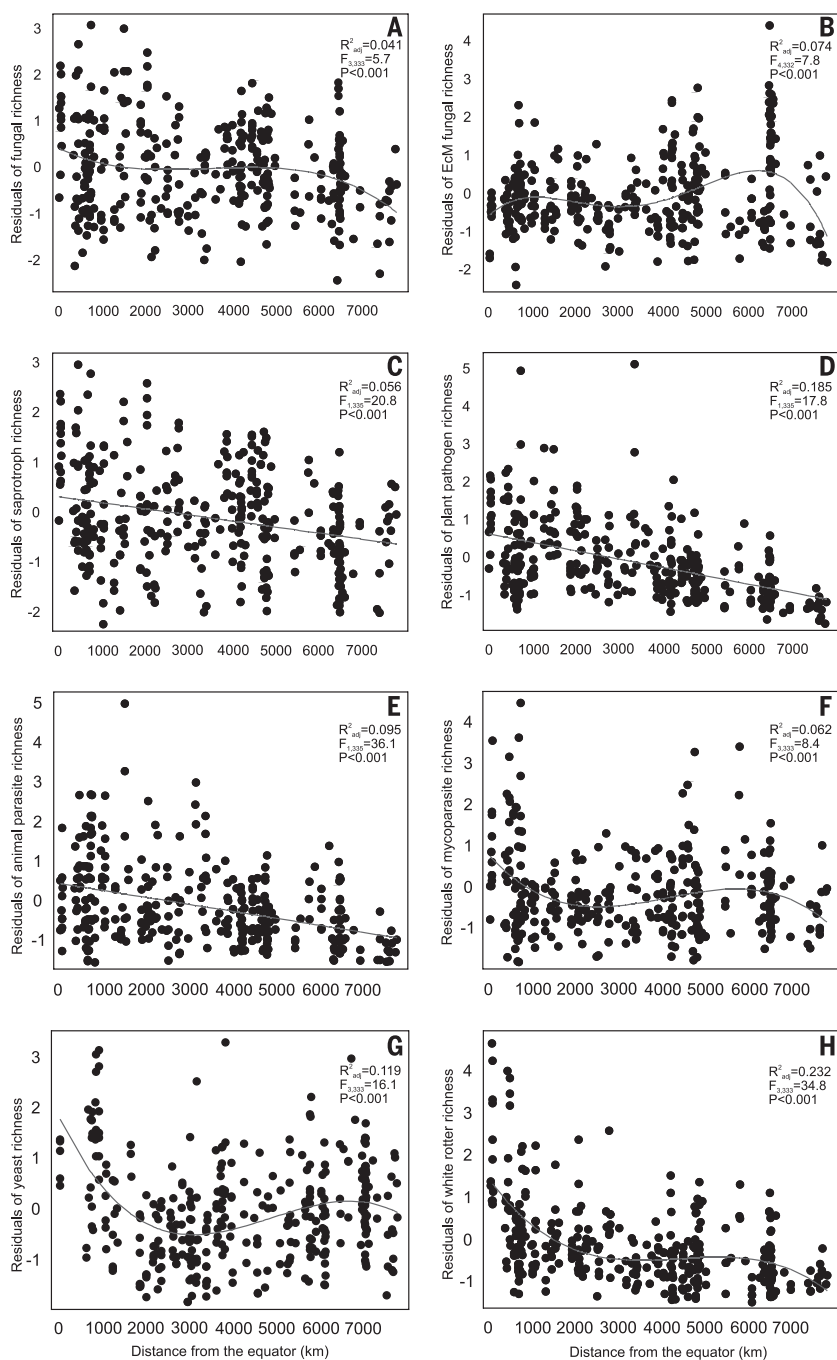
Fig. 3. Relationships between residual richness of fungal taxonomic or functional groups and distance from the equator. (**A**) All fungi. (**B**) EcM fungi. (**C**) Saprotrophic fungi. (**D**) Plant pathogens. (**E**) Animal parasites. (**F**) Mycoparasites. (**G**) White rot decomposers. (**H**) Yeasts. Lines indicate best-fitting linear or polynomial functions.

the poles, with no noticeable decline in boreal forests and tundra biomes. Agaricomycetes, Pezizomycetes, and Tremellomycetes exhibited distinct richness peaks at mid-latitudes. Richness of Agaricomycetes was greater in the Northern Hemisphere, whereas that of Microbotryomycetes, Tremellomycetes, and Wallemiomycetes peaked in the Southern Hemisphere temperate ecosystems (fig. S8).

All of these phylogenetic groups originated >150 million years ago on the supercontinent Pangaea (*33*) and have had sufficient time for long-distance dispersal. However, our data suggest that particular regional biotic or abiotic conditions (such as soil pH and favorable climatic conditions) have likely stimulated evolutionary radiations in certain geographic areas and not in others. Adaptation to cold climate in younger fungal phyla has been suggested to explain differential latitudinal preferences among fungal groups (*34*). However, our global analysis provided no support for this hypothesis (fig. S9).

Instead, it revealed that ancient lineages are relatively more common in nonwooded ecosystems.

Relation of plant and fungal richness

Plant and fungal richness were positively correlated (fig. S10), but plant richness explained no residual richness of fungi according to the best regression model ($R^2_{adj} < 0.01$; $P > 0.05$). These results and SEM path diagrams suggest that correlations between plant and fungal richness are best explained by their similar response to climatic and edaphic variables (covariance) rather than by direct effects of plants on fungi. However, when separating functional categories, trophic groups of fungi exhibited differential response to plant diversity and relative proportion of potential hosts.

Plant pathogens usually attack a phylogenetically limited set of host plants (*35*), suggesting that plant pathogens have at least partly co-evolved with their hosts and may have radiated more intensively in the tropics, where high plant diversification and richness permit greater diversification. Strong phylogenetic signals in soil feedbacks, adaptive radiation, and negative density dependence (the Janzen-Connell hypothesis) have probably contributed to the pronounced richness of both plants and their pathogens at low latitudes (*36*, *37*). However, our analyses revealed no significant effects of plant richness per se on residual richness of pathogens in soil. Similarly to pathogens, richness of AM fungi was unrelated to the proportion of AM host trees or interpolated host richness, which may result from nonspecific associations with tree and understory species. Hence, both AM and soil pathogen richness were unaffected by plant richness. In contrast, host richness explained 6% of variation in EcM fungal richness, indicating either niche differentiation of fungi in forests of mixed hosts or sampling effects (forests with higher host diversity are more likely to include plant species that harbor high fungal diversity). With a few notable exceptions, most studies have found low levels of host preference or host specificity among EcM fungi (*38*). We found that relative EcM host density had a strong influence on EcM fungal richness, suggesting that greater availability of colonizable roots in soil provides more carbon for EcM fungi and thereby yields greater species density and local-scale richness regardless of latitude. The peak of EcM fungal taxonomic and phylogenetic richness in northern temperate biomes coincides with the geographical distribution and dominance of Pinaceae, which is the oldest extant EcM plant family (*15*, *39*).

The ratio of plant-to-fungal richness decreased exponentially with increasing latitude because plant diversity dropped precipitously toward the poles relative to fungal diversity (Fig. 4). This finding calls into question present global fungal richness estimates. These estimates assume similar spatial turnover of plant and fungal species and a constant plant-to-fungus ratio and have been formulated mostly based on data from temperate and boreal ecosystems (*1*, *19*, *20*). Yet, local-scale beta diversity of both plants and fungi
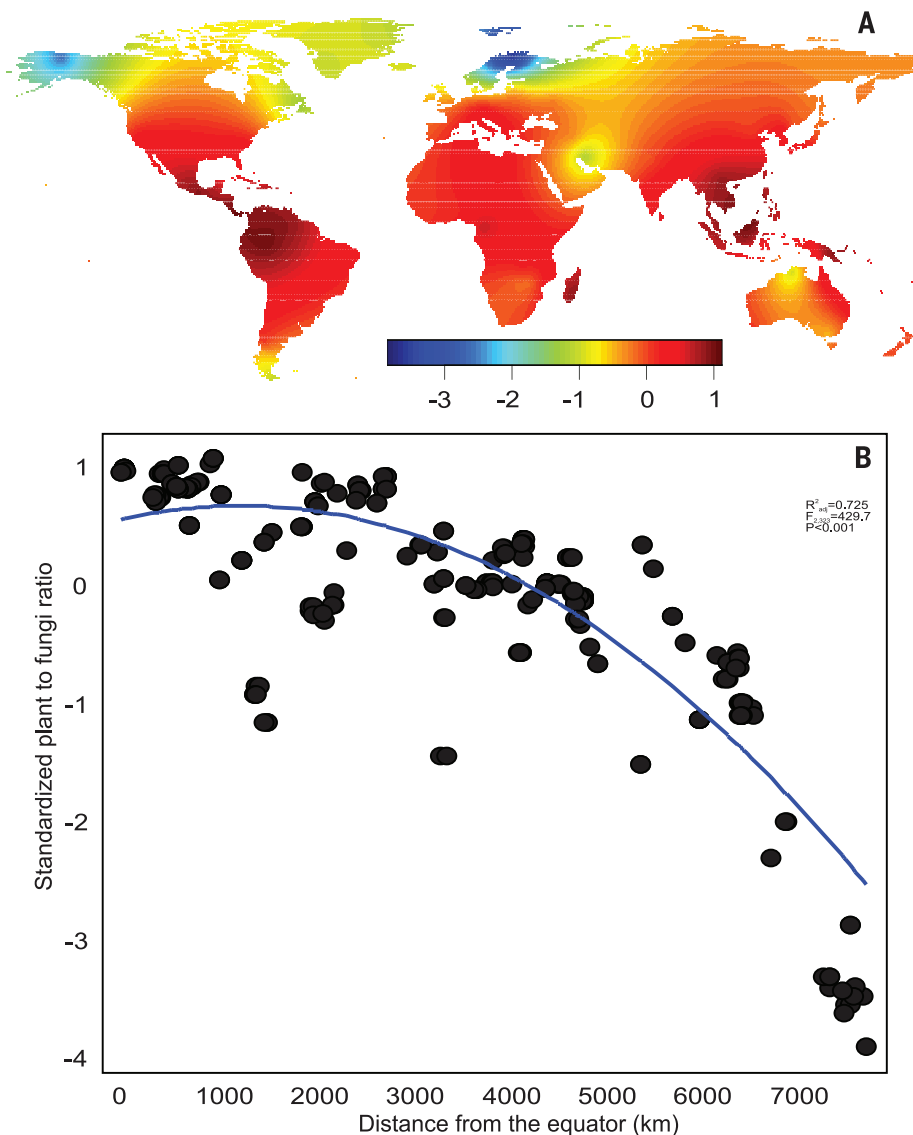
Fig. 4. Relationship between standardized plant richness to fungal richness ratio and distance from the equator. (**A**) Interpolated values. (**B**) Polynomial regression. Residuals of fungal richness are taken from the best linear regression model accounting for other significant predictors. Warm colors indicate high plant-to-fungal richness ratio, whereas cold colors indicate low plant-to-fungal richness.

differ among temperate and tropical sites (*40, 41*), and there are profound differences in plant species turnover depending on propagule size (*42*). Natural distribution of very few vascular plant species encompass several continents, but there are multiple fungal species with circumpolar or cosmopolitan distribution (*43, 44*). Although we cannot directly compare plant and fungal beta diversity, spatial turnover of plant species is inarguably greater (*42*). Based on the function of fungi-to-plant richness ratio to latitude and latitudinal distribution of land, we calculated that fungal richness is overestimated by 1.5- and 2.5-fold on the basis of constant temperate (45° latitude) and boreal (65° latitude) richness ratios, respectively.

Because richness estimates are calculated based on the frequency of the rarest species, the reliability of singleton data call into question biologically meaningful extrapolations (*11*). In

metabarcoding studies such as ours, sequencing errors tend to give rise to singleton sequences, and the number of rare artificial taxa grows rapidly with increasing sequencing depth (*25*). Therefore, despite the size of our data set, it cannot readily be used to produce reliable taxonomic richness extrapolations.

Community ecology

Variation partitioning analysis revealed that climatic, edaphic, and floristic variables (and their shared effects) are the strongest predictors for community composition of all fungi and most of their functional groups (fig. S11). However, the saprotroph community composition was most strongly explained by purely spatial variables. More specifically, PET and soil pH explained 2.4 and 1.5%, respectively, of the variation in total fungal community composition

(table S3 and fig. S12). PET contributed 3.8, 2.8, and 11.7% to community structure of saprotrophs, plant pathogens, and yeasts, respectively. Distance from the equator (1.3%) and soil pH (0.7%) were the strongest predictors of EcM fungal community composition, whereas mean annual temperature (4.0%) was the strongest predictor for animal parasites, and distance from the equator (3.5%) was the best predictor for mycoparasites (table S3 and fig. S12).

These results indicate that both environmental and spatial predictors generally have a minor influence on species-level composition of fungi at the global scale. Nonetheless, the significant global-scale pH effect in several groups of fungi is consistent with the substantial influence of pH on the phylogenetic structure of soil fungal and bacterial communities in both local and continental scales (*27, 45*). The relatively stronger climatic and edaphic drivers of richness at the class and phylum level suggest that phylogenetic niche conservatism in fungal lineages is similar to cross-biome distribution patterns in vascular plants (*46*) and protists (*47*).

Global biogeography

Consistent with Rapoport's rule formulated for macro-organisms (*24*) and later applied to marine bacteria (*48*), the mean latitudinal range of fungi strongly increased toward the poles (fig. S13). These results also suggest that a greater proportion of fungi are endemic within tropical rather than extratropical ecosystems.

Major taxonomic and functional groups of fungi differed markedly in their distribution range (figs. S14 and S15). Animal parasites were more widely distributed as compared with all other groups, suggesting that there are many generalist OTUs with global distribution. Saprotrophs and plant pathogens had broader distribution ranges than EcM and AM root symbionts. Taxa belonging to Mortierellomycotina, Mucoromycotina, Tremellomycetes, and Wallemiomycetes—groups that include a large proportion of saprotrophs and parasites that produce exceptionally large quantities of aerially dispersed mitospores—were generally most widely distributed. Besides the AM Glomeromycota, OTUs belonging to the ascomycete classes Archaeorhizomycetes, Geoglossomycetes, and Orbiliomycetes were detected from the fewest sites.

The northernmost biogeographic regions (Europe, West Asia, East Asia, and North America) had the most similar fungal communities as revealed by shared fungal OTUs (Fig. 5). According to the Morisita-Horn similarity index, the northern and southern temperate regions clustered together with marginally nonsignificant support (*P* = 0.064) (Fig. 6A). In spite of the large geographical distance separating them, paleo- and neotropical biogeographic regions clustered together (*P* = 0.059). However, biogeographic clustering of regions deviated markedly in certain functional groups of fungi (Fig. 6). For instance, EcM fungi in the southern temperate and tropical regions had greater similarity as compared with northern temperate ecosystems
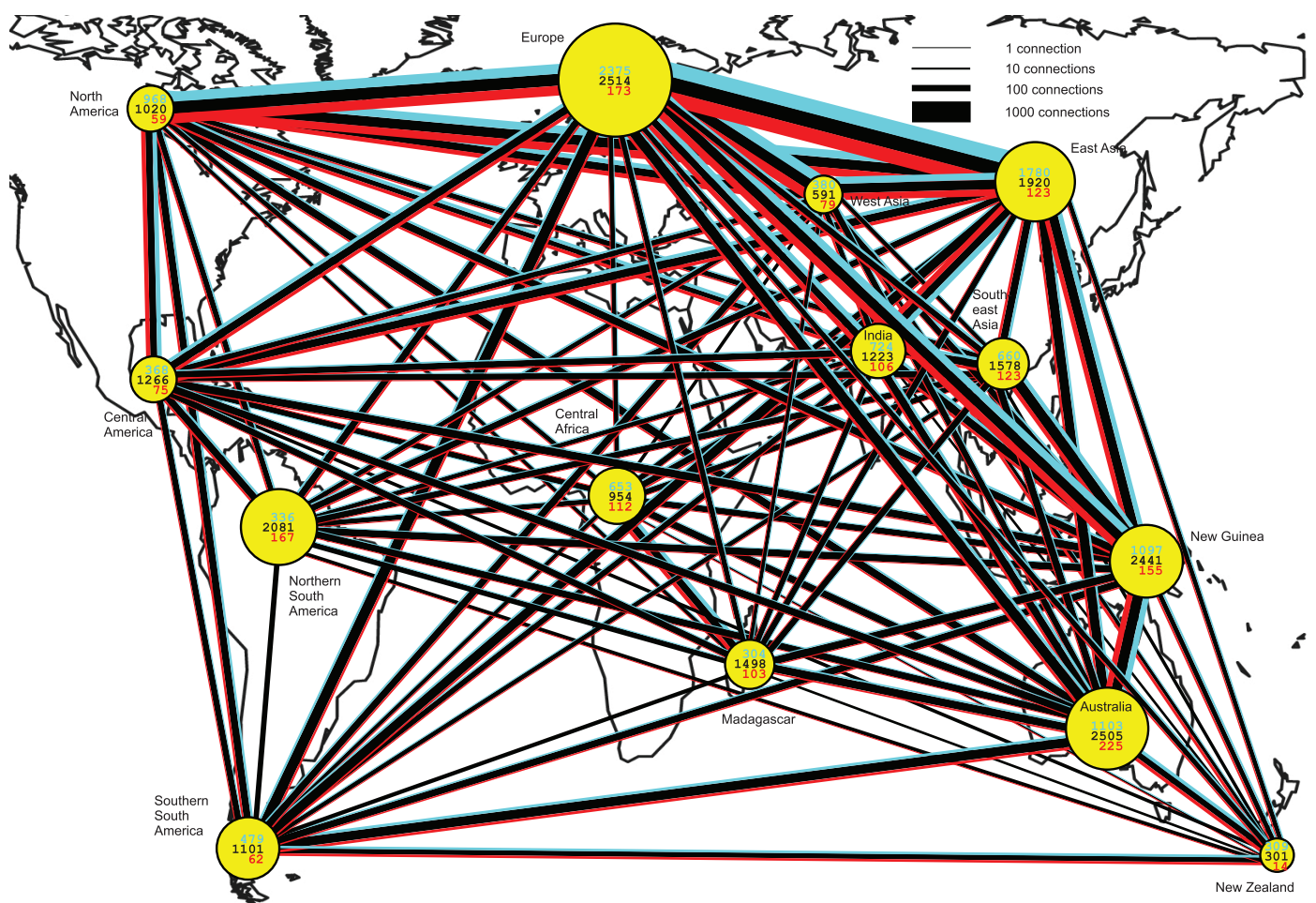
Fig. 5. Connectedness of biogeographic regions by shared OTUs of EcM fungi, saprotrophs, and plant pathogens. Blue, EcM fungi; Black, saprotrophs; and red, plant pathogens. The width of lines and diameter of circles are proportional to the square root of the number of connections and sample size (number of sites), respectively. Numbers in circles indicate the number of OTUs found in each region. OTUs with a single sequence per site and OTUs belonging to Hypocreales and Trichocomaceae (in which the ITS region is too conservative for species-level discrimination) were excluded.

(P = 0.001). Among biomes, boreal forests, temperate coniferous forests, and temperate deciduous forests shared the largest numbers of fungal OTUs (fig. S16). Fungal OTUs in temperate deciduous forests were highly similar to Mediterranean and tropical montane forests, whereas fungal OTUs in tropical montane forests were linked to tropical moist forests, which in turn exhibited substantial connections with tropical dry forests and savannas. As a result, cluster analysis supported separation of tropical and nontropical biomes (Fig. 6B). Consistent with biogeographic region-level analysis, lowland tropical biomes, arctic tundra and boreal forests biomes, and temperate biomes formed three well-supported clusters. Tropical montane forests and grasslands and shrublands were clustered with temperate biomes according to distribution of all fungi and most functional groups. However, in EcM fungi, taxa from southern temperate forests, tropical montane forests, and grass/shrublands clustered with tropical lowland and Mediterranean biomes. A relatively large proportion of EcM fungal taxa were shared across various biomes in Australia and New Guinea, which explains these

deviating patterns. In contrast, plant pathogens from tropical montane forests clustered with tropical lowland biomes rather than with temperate biomes.

Our biogeographic analyses complement the community-level results, suggesting that both climate and biogeographic history shape macroecological patterns of fungi. Comigration with hosts over Pleistocene land bridges (such as Beringia, Wallacea, and Panamanian) and long-distance dispersal by spores appear to have played important roles in shaping current fungal distribution patterns (30, 43). The relative influence of climate and biotrophic associations with host plants of varying extant distributions probably contribute to differences in the range and biogeographic relationships among fungal functional groups (49). In addition, taxon-specific constraints for dispersal, such as shape and size of propagules and sensitivity to ultraviolet light, may differentially affect long-distance dispersal among taxa (7). For instance, Glomeromycota OTUs, which form relatively large non–wind-dispersed asexual spores, had the lowest average geographical range. In general, region-based dis-

tribution patterns of fungi are somewhat conflicting with clustering of plants and animals, where Holarctic lineages are deeply nested within larger tropical groups (50). Consistent with macroorganisms, fungi from the Southern Hemisphere temperate landmasses cluster together. Differences observed in macroecological patterns among fungi, plants, and animals may originate from the relative strength of dispersal limitation and phylogeographic history, but exaggeration from methodological differences among studies cannot be discounted. The use of homogenous sampling and analytical methods, as done in this study, are necessary to confidently compare macroecological patterns among distinct life forms and to reliably test degrees of consistency among all kingdoms of life.

Conclusions and perspectives

Climatic variables explained the greatest proportion of richness and community composition in fungal groups by exhibiting both direct and indirect effects through altered soil and floristic variables. The strong driving climatic forces identified here open up concerns regarding the
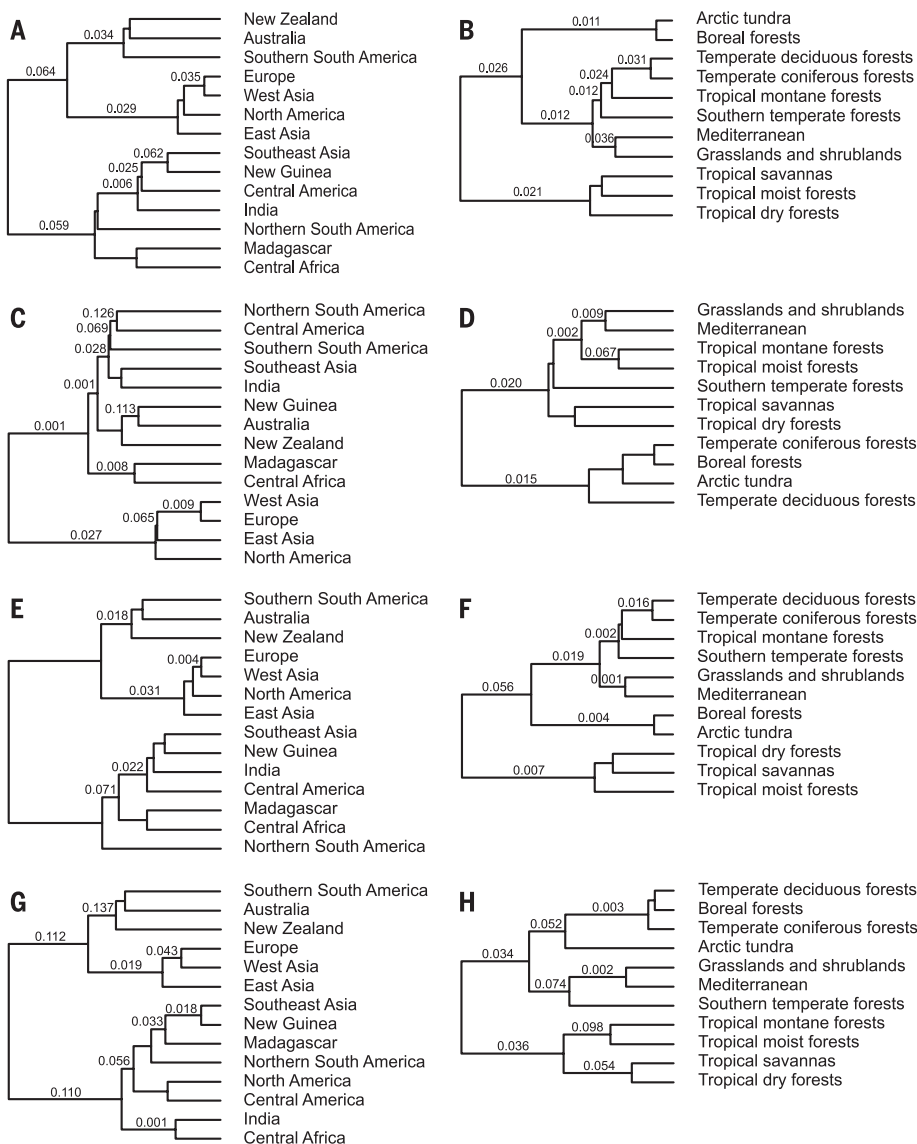
Fig. 6. Ward clustering of biogeographic regions and biomes based on the Morisita-Horn pairwise similarity index. Left, biogeographic regions; right, biomes. (**A** and **B**) All fungi. (**C** and **D**) EcM fungi. (**E** and **F**) Saprotrophs. (**G** and **H**) Plant pathogens. Numbers above branches indicate *P* values.

impact of climate change on the spread of disease (*51*) and the functional consequences of altered soil microorganism communities (*52*). The observed abrupt functional differences between fungal communities in forested and treeless ecosystems, despite spatial juxtaposition, suggests that plant life form and mycorrhizal associations determine soil biochemical processes more than plant species per se. Loss of tree cover and shrub encroachment resulting from drying and warming may thus have a marked impact on ecosystem functioning both above- and belowground.

In addition to natural mechanisms, such as long-distance dispersal and migration over past land bridges, global trade has enhanced the spread of some non-native soil organisms into other ecosystems, where they sometimes become hazardous to native biota, economy, and human health (*53*). Our results highlight how little insight we still

have into natural microbial distribution patterns, and this undermines our ability to appraise the actual role of humans in shaping these biogeographic processes. Even larger-scale sampling campaigns are needed to provide data for establishing natural distributions and building species distribution models (*52*), which will enable us to predict the spread and habitat suitability of non-native microorganisms.

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SUPPLEMENTARY MATERIALS

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Figs. S1 to S17
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