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Pushing the Frontiers of Biodiversity Research: Unveiling the Global Diversity, Distribution, and Conservation of Fungi

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Abstract

Fungi comprise approximately 20% of all eukaryotic species and are connected to virtually all life forms on Earth. Yet, their diversity remains contentious, their distribution elusive, and their conservation neglected. We aim to flip this situation by synthesizing current knowledge. We present a revised estimate of 2–3 million fungal species with a "best estimate" at 2.5 million. To name the unknown >90% of these by the end of this century, we propose recognition of species known only from DNA data and call for large-scale sampling campaigns. We present an updated global map of fungal richness, highlighting tropical and temperate ecoregions of high diversity. We call for further Red List assessments and enhanced management guidelines to aid fungal conservation. Given that fungi play an inseparable role in our lives and in all ecosystems, and considering the fascinating questions remaining to be answered, we argue that fungi constitute the next frontier of biodiversity research.

Contents

1. INTRODUCTION

Fungi: a monophyletic group of heterotrophic eukaryotes with chitinous cell wall

Mycorrhiza: a mutualistic association between a fungus and a plant root (fungus–root)

Fungi underpin nearly all life on Earth, being vitally important to land plants, ecosystem functioning and, ultimately, us. Mutualistic fungi improve the uptake of essential nutrients to plants (e.g., mycorrhiza) and stimulate their immunity and stress resistance (e.g., endophytes) (1). They can also recycle rigid natural polymers, such as lignin, cellulose, and chitin, and thus are significant biomass decomposers (2). At the same time, many pathogenic fungi attack plants and cause significant crop loss worldwide (3, 4). Parasitism on animals is comparatively rare, but includes, e.g., an amphibian chytrid fungus that is devastating populations of tropical frogs around the world (5).

The human interactions with fungi are manifold. Fungi have become an increasingly valuable source of bioactive compounds, such as antibiotics, immunosuppressants, statins, or organic acids

for industry and medicine (6) and provide eco-friendly materials for daily life (7). The digestive enzymes secreted by fungi are used in food and livestock feed, textile and paper manufacturing, and biofuel production, and some fungi can also be used in remediation of polluted sites (6, 8). The ability of some fungi to combat pests and stimulate plant growth means they are also useful as biopesticides and biofertilizers for sustainable agriculture (9, 10). The small size of fungal genomes makes them a powerful target for genetic research on eukaryotic biology and an efficient microbial cell factory for biotechnology and bioengineering (11–13). The excellent nutritional properties of many macrofungi were recognized thousands of years ago, and the current global market of mushroom farms is worth billions per year. Moreover, yeasts and filamentous fungi are widely used in the food industry (6, 9). Alongside their many benefits, fungi can also be quite harmful to humans, through specialist parasitism either permanently or intermittently in some stages of their life cycle, or opportunistically when their host's immune system gets compromised. Fungal infections are estimated to kill approximately 1.6 million people every year (14, 15).

Fungal evolution started approximately 1.3 billion years ago, when the true Fungi diverged from the common ancestor of the animal kingdom and other related eukaryotes (16). In contrast to animals, fungal cells are covered by a rigid chitinous cell wall, and their mode of nutrition is therefore also different—the rigid cell wall precluding the engulfment of food particles. Their nutrition is instead based on the absorption of dissolved small molecules, which are digested outside the cell. Absorptive nutrition can only be efficient if the surface-to-volume ratio is large and the environment is wet. This type of nutrition determines the shape of fungal bodies—either multicellular, consisting of thin filaments called hyphae which form a network (mycelium), or simple spherical, single-celled (yeasts)—and forces them to live either inside their food or in direct contact with it, in moist habitats. Consequently, fungi mainly live an ecologically cryptic life: The vast majority of their mycelium is usually hidden in organic substrata such as soil, water, or dead wood or leaf litter for saprotrophs, or other organisms for biotrophs. Yeasts and aquatic fungi usually form biofilms on wet nutritious surfaces.

Most fungi disperse their spores by air, animals, or water droplets (17). This requires the formation of spore-bearing structures, such as the familiar mushrooms, truffles, cup and bracket fungi, moulds, or rusts, among others. Many of these structures are ephemeral and, in some cases, show seasonality. In contrast, lichen-forming fungi have a perennial appearance, with permanent spore-bearing structures, as they feed on carbohydrates photosynthesized by their symbiotic partners (bacteria and/or algae) and are able to withstand extreme desiccation (18). Fungi come in a vast array of sizes; they hold the record for being the largest organism on Earth [e.g., *Armillaria ostoyae*, spanning more than 10 km^2 in Oregon, USA (19, 20)], but they can also have diminutive bodies hard to examine with conventional morphometric techniques.

The arrival of DNA technologies around 30 years ago opened an exciting new era in mycology, including a new understanding of how fungi diversified (**Figure 1**), and now with genomics we are seeing a second wave of revolution (see also the sidebar titled How DNA Technology Is Rewriting Everything We Thought We Knew About Fungi). It has become clear that we only know a fraction of the global Funga (21, 22) and that the highest diversity of traits underlying the evolution and speciation of fungi is hidden not in their morphology but in their physiology, biochemistry, and genetics (23–25). Here, we review and summarize our current knowledge on fungal diversity, distribution, and conservation research and propose future directions for research and conservation.

Endophyte: a fungus living within a plant causing no disease symptoms

Saprotroph: an organism feeding on dead organic matter

Biotroph: an organism feeding on living organisms, e.g., as a parasite causing a disease (pathotroph) or a mutualist (symbiotroph)

Mycology: the study of fungi

Funga: the entire fungal life of a given region, habitat, or geological stratum, similar to flora for plants and fauna for animals

2. DIVERSITY

Fungi rank third among the major kingdoms in terms of known taxa, with approximately 155,000 species scientifically documented to date (26, 27). Animals number 1.45 million (28) and plants

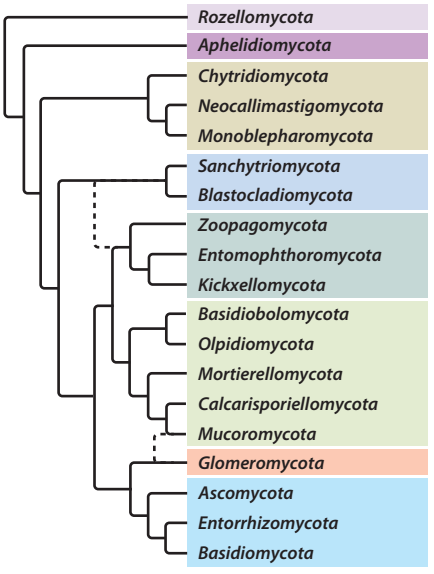

Figure 1

Synopsis of the current classification of phyla in the kingdom Fungi, compiled from References 152 (phylogenomics), 148 (multimarker), 84 (phylogenomics), 150 (phylogenomics), and 151 (multimarker). For comparison, see also the synoptical tree by Spatafora et al. (153). Some conflicts in the placement of individual phyla across these studies are indicated (*dashed line*): Glomeromycota has been either placed as sister to Asco-, Basidio-, and Entorrhizomycota in multimarker studies or nested with Mucoromycota in phylogenomic approaches; Blastocladiomycota appears as an early emerging lineage in some phylogenomic approaches (150, 152) or as a supported sister to Sanchytriomycota next to Zoopagomycota, Entomophthoromycota, and Kickxellomycota or included in the clade formed by these latter three phyla in other phylogenomic and in multimarker studies (61, 84, 151). The phylum Caulochytriomycota, proposed for the genus Caulochytrium (see 151), is here considered a synonym of Chytridiomycota, following Ahrendt et al. (152). Background colors set apart major clades.

345,000–390,000(–435,000) (26, 29–31). Estimated global species richness varies considerably among these three kingdoms and between authors (lowest and highest estimates given in parentheses): (3–)8–9(–30) million for animals (32–34), 450,000–500,000 for plants (30, 35–37), and (0.5–)1.5–6.3(–19.35) million for fungi (38–43). The most current figures given here suggest that a large proportion of plant species (80–85%) is likely already known, whereas the full diversity of animals, particularly invertebrates (less than 20% known), and fungi (less than 5–10% known) remains largely undescribed.

HOW DNA TECHNOLOGY IS REWRITING EVERYTHING WE THOUGHT WE KNEW ABOUT FUNGI

DNA sequences provide a wealth of data, dramatically improving our understanding of fungal biology, diversity, distribution, and evolution. Nowadays we have tools to efficiently read DNA barcodes or even genomes of hundreds of species from environmental samples (i.e., metabarcoding and metagenomics, respectively), at relatively low costs and to place any fungus in the evolutionary tree of life. DNA data are, consequently, transforming fungal taxonomy and the classification of fungi at all levels (**Figure 1**). In the past four years alone, five new phyla have been established (84, 148), and in most recent studies, the number of accepted phyla ranged from 12 to 20 (149–151). DNA has also brought the unveiling of many new fungal orders, families, genera, and species (57, 151).

2.1. Estimating the Global Richness of Fungi

Global richness predictions are based on extrapolation of existing data, and the level of uncertainty associated with them—mainly due to insufficient sampling—makes reliable estimates challenging. Historically, global fungal richness has been estimated since the early works of Elias Fries, the father of mycology (see **Supplemental Figure 1**). Estimates of fungal species richness published since Hawksworth's (44) seminal work range from half a million (45) to more than 12 million (46) and even 19.35 when extrapolating the figures given by Tedersoo et al. (41), but many of these predictions are made ad hoc, without quantitative assessments, or make misguided assumptions, as discussed below. In addition, (semi)quantitative assessments often only focus on particular groups of fungi, missing insights that may come from looking across the full range of diversity. The large range of variation in these numbers invites a critical look at the underlying data and the extrapolation methods used.

Supplemental Material >

2.1.1. Global estimation derived from scaling laws. Mora et al. (33) provided global richness predictions for all major groups of organisms, using scaling laws in taxonomic hierarchies, that is, predicting species numbers from patterns in numbers of higher taxa. Their estimates were also used in a recent overview of global biodiversity by Díaz & Malhi (47). For fungi, Mora et al. (33) estimated 611,000 species; however, their input of 43,271 species known was less than half the actual number accepted at the time, approximately 100,000 (48–50). Using the correct figure, one would arrive at approximately 1.4 million (**Table 1**). This figure would not include, however, higher taxa not known at the time, such as Archaeorhizomycetes (51). In addition, Mora et al. (33) assumed saturation effects for the accumulation of higher taxa, as demonstrated in animals. However, in fungi there have been additions even at high ranks over the past decade, so even the corrected number given above could underestimate the actual global richness of fungi.

2.1.2. Global estimation derived from fungus:plant ratios. The fungus:plant (F:P) ratio has been used in various prediction scenarios, based on selected localities, larger geographic areas including countries, or specific plant taxa. The exact definition of the F:P ratio is not clear: It can relate only to fungi directly associated with plants or to all fungi known from a given area for which the number of plants is known. As a result, proposed global F:P ratios oscillate between 6:1 and 10:1, and ratios for individual sites or hosts reach up to 89:1 (**Supplemental File 1**). With a growing number of known plant species, global estimates for fungi thus range between 1.5 and 3.8 million (38, 42, 44). However, F:P ratios are not constant across environmental gradients, vary across latitudes (39), and may show a saturation effect with increasing area. While site-based ratios often exceed 10:1, country-based ratios were calculated at between 2.5:1 and 5.1:1 for Japan, the United States, Canada, Germany, and France (52, 53). The United Kingdom appears to be an exception, with a ratio of 9:1 when taking into consideration only native plants. The inclusion of alien plants, which also bear fungi included in the national species list, would decrease the ratio to only 2.6:1 (54). We therefore propose a more conservative ratio of 5:1 (53) for temperate areas and a lower ratio of 3.5:1 for tropical areas [applying the correction proposed by Tedersoo et al. (39)]. With one-third of the estimated 390,000 known plant species occurring outside and two-thirds inside the tropics, this would result in a prediction of 1.56 million fungi (**Table 1**). While considerably lower than the 3.8 million proposed by Hawksworth & Lücking (42), this revised figure does not fully take into account hidden diversity within presumably known taxa, and it ignores fungal groups that are usually not detected in such inventories; it is therefore likely to be an underestimate.

2.1.3. Global estimation derived from actual versus previously known number of species. Hawksworth & Lücking (42) analyzed hidden diversity in presumed known fungal species, entities

Table 1 Extended list of global fungal diversity predictions, proposed corrections, and proposed totals including fungal groups (largely) not considered in prediction methods[a]

Reference	Approach	Original	Adjusted	Total adjusted
Martin (156)	F:P ratio (pathogens)	0.25 million	1.20 million	3.10–3.17 million
Pascoe (73)	F:P ratio (pathogens)	2.70 million	0.94 million	2.45–3.01 million
Hawksworth (44)	F:P ratio (general)	1.50 million	1.63 million	2.30 million
Hawksworth (44)	F:P ratio (general), F:I ratio	3.00 million	2.13 million	2.30 million
Hywel-Jones (162)	F:I ratio	1.50 million	0.55 million	2.77 million
Shivas & Hyde (74)	F:P ratio (tropical pathogens)	0.27 million	0.40 million	2.57 million
Cannon (157)	Species-area relationships	9.90 million	2.23 million	2.33 million
Aptroot (158)	Ascomycota (tropical)	0.04–0.07 million	0.20–0.70 million	0.58–1.86 million
Fröhlich & Hyde (159)	F:P ratio (general)	8.68 million	1.49 million	2.36 million
May (45)	F:P ratio (general)	0.50 million	1.56 million	2.43 million
Arnold et al. (160)	F:P ratio (endophytes)	>1.50 million	0.50 million	2.57 million
Hawksworth (38)	F:P ratio (general)	2.27 million	2.01–2.45 million	2.68–3.12 million
O'Brien et al. (58)	Metabarcoding (soil; 97%)	5.1 million	1.34 million	2.84 million
Schmit & Mueller (161)	F:P ratio and others	0.71 million	1.12 million	2.58 million
Mora et al. (33)	Scaling laws (taxonomy)	0.62 million	1.42 million	1.52 million
Taylor et al. (59)	F:P ratio (general), metabarcoding (soil; 97%)	5.91 million	1.56 million	3.11 million
Tedersoo et al. (39)	F:P ratio (general), metabarcoding (soil; 97%)	2.04–3.00 million	0.54–0.79 million	2.16–2.41 million
Hawksworth & Lücking (42)	F:P ratio (general)	3.8 million	1.56 million	2.21 million
Hawksworth & Lücking (42)	Hidden diversity (known taxa)	1.70 million	1.47 million	1.57 million
Wu et al. (46)	Metabarcoding versus culturable fungi	11.7–13.2 million	3.06 million	3.23 million
Baldrian et al. (43)	Metabarcoding (general; 97%)	6.28 million	1.66 million	1.73 million
Tedersoo et al. (40)	Metabarcoding	>1.53 million	>1.53 million	>3.03 million
Tedersoo et al. (41)	Metabarcoding (98%); hidden diversity	19.35 million	2.28 million	3.83 million
Senanayake et al. (77)	Ascomycota (teleomorphic)	(1.37–)1.86(–2.56) million	1.50 million	2.69 million

[a]The following are details on the original estimates and corrections: original, original prediction; adjusted, adjusted prediction (see comments on each entry above); total, total prediction including fungal groups not considered in the prediction approach (see comments on each entry above). Cells are colored according to number ranges: gray, <1 million; light green, 1–2 million; bright green, 2–3 million; yellow, 3–5 million; orange, 5–10 million; red, >10 million. Abbreviations: F:I, fungus:insect; F:P, fungus:plant.

treated as single species that in reality represent several to many species. They came up with a weighted mean of 11.3:1 for the number of actual versus presumed species across a large taxonomic sample. This factor would increase the currently known 150,000 species to 1.7 million, if it holds across all fungal lineages. However, the base reference should be corrected to 130,000, the number of known species at the onset of most studies on species complexes, resulting in a prediction of 1.47 million instead (**Table 1**).

A critical issue related to this approach is the precise definition of species (55), requiring integrative taxonomy to combine different lines of evidence (sequence data, phenotype, distribution) through quantitative approaches (56). Unfortunately, it is not possible to apply this approach to species only known from DNA data, although guidelines can be derived from the comparison of phylogenetically defined lineages of other fungi that have been assessed through integrative taxonomy.

Metabarcoding: production of DNA barcodes of species present in an environmental sample

Endemic: geographically constrained to one particular region, such as a country, continent, or biome

2.1.4. Global estimation derived from metabarcoding studies. Environmental metabarcoding has emerged as the most powerful approach for documenting fungal diversity globally (40, 41, 43, 57). Several studies using metabarcoding data to extrapolate on global fungal species richness have been published, with predictions ranging from (1.5–)3.5–5.1(–6.3) million (38, 40, 41, 43, 58, 59). Tedersoo et al. (41) used long-read PacBio sequences to estimate species richness for the ten largest genera of fungi in soil, including *Cortinarius* (14,375 species) in the Basidiomycota, *Cladophialophora* (15,968) in the Ascomycota, and *Glomus* (7,610) in the Glomeromycota, resulting in the factor of 80–115:1 compared to currently accepted species in these genera (27). Extrapolation would result in a global estimation of more than 19 million fungi (**Table 1**).

A pitfall of these methods is that they rely on operational taxonomic unit (OTU) clustering, which requires a fixed threshold and is sensitive to sequencing errors and stochastic point variation (60, 61). The aforementioned metabarcoding studies used a 97% or 98% threshold for OTU clustering, which, in theory, should underestimate taxonomic diversity, as species-level thresholds are often closer to and even above 99% (56). However, even such conservative thresholds considerably overestimate taxonomic diversity due to nontaxonomic sequence variation. Rather, accurate estimates of taxonomic diversity are achieved through multiple alignment-based methods or phylogenetic read placement (62–64).

Applying a corrective factor of 3.8:1 (**Supplemental File 2**) to the global estimates of 5.1, 6.0 and 6.3 million fungal species based on metabarcoding data and 97% OTU clustering, we arrive at adjusted predictions of 1.34, 1.58, and 1.66 million species, respectively (**Table 1**). Applying a correction factor of 8.6:1 to the genus-based figures provided by Tedersoo et al. (41) would result in a ratio of 8–6:1, reducing the estimate of 19 million to 2.28 million.

Supplemental Material >

Although here we apply corrections to metabarcoding extrapolations, these studies mostly focus on data from soil fungi (except 43), omitting aboveground fungi, such as plant and animal pathogens, endophytic fungi, or lichens. Another issue with metabarcoding data is their representativity in terms of taxonomic and functional composition (see Section 2.3). Considering these issues, estimates of global fungal diversity derived from metabarcoding samples are to be interpreted with care. For reliable estimations, data should represent all habitats and consider different types of substrata (soil, water, plants, etc.); additionally, certain lineages of fungi should not be left uncovered because of methodological biases affecting particularly those fungi that diverge at the base of the fungal tree (40, 65).

2.1.5. Comparison of the results from different methods. While original predictions of global fungal diversity oscillate between 70,000 and more than 19 million species, the adjusted figures presented here using scaling laws in taxonomic hierarchy, species-area relationships, F:P ratios, metabarcoding, and hidden diversity are remarkably in line, many oscillating around 1.5 million (**Table 1**). As mentioned, however, these numbers are not inclusive in terms of all known functional or phylogenetic groups and still require upward corrections. Using F:P ratios may ignore fungi not associated with plants, whereas metabarcoding may miss aboveground plant pathogens, endophytes, lichens, arthropod-related fungi, and those in aquatic and marine environments. Adding these corrections to the adjusted estimates resulted in surprisingly homogeneous

global predictions, ranging from 1.5 to 3.2 million (**Table 1**), with a mean of 2.53 million and a standard deviation of 20% (±0.49). We thus propose a revised range of (2–)2.5(–3) million fungi globally. This revised estimate is above the 1.5 million first predicted by Hawksworth (44) but below more recent extrapolations of up to 6.3 (or even 19.35) million from metabarcoding studies (40, 41, 42, 43, 58, 59). The 2–3 million proposed here would still place Fungi as the second largest kingdom of eukaryotes, after animals. Given that only approximately 155,000 fungal species are known, an estimated 92.5–95% of all fungi remains to be found and scientifically described.

2.2. Documenting and Describing the Unknown Diversity

Despite how high the true number of fungi is, the daunting task thus remains to discover and catalogue perhaps millions of unrecognized fungi. Specimen- or culture-based taxonomy can achieve only a fraction of this. Even if we speed up the process by an order of magnitude from currently approximately 2,000 (see **Supplemental Figure 2**) to 20,000 new species per year, we would still need 100 years to catalogue, e.g., 2 million additional fungi. Classification of fungi known from environmental metabarcoding data could deal more efficiently with such a staggering number, with formal names entirely based on sequence data (57), which could render viable 50,000 new species catalogued per year. In addition, a concerted effort should be made to produce sequence data from the world's fungal collections: (*a*) Data from type specimens would anchor the use of names described to date, simultaneously revealing which species are new to science, and remove one of the biggest bottlenecks currently hindering the description of new species; (*b*) non-type collections contain a wealth of already collected but not yet named species just waiting to be described. Together, data from these two sources would enable the creation of a global phylogenetic framework for merging voucher-based and environmental sequence data.

2.3. Taxonomic and Functional Groups: Current Versus Predicted Patterns

Besides species numbers, unknown aspects of the world's total fungal diversity also include its taxonomic and functional composition. Predicting these is challenging; the most parsimonious assumption would be that the composition derived from known species would not notably change. However, given that the predicted numbers are at least an order of magnitude higher, shifts in the proportion of major taxonomic and functional groups should be expected, reflecting the notion that some groups are much better studied than others. The best example is lichen-forming fungi; they currently constitute 13% of known fungi, but with a predicted 2–3 million fungi worldwide, they are only likely to account for 1–2% of the total diversity.

Comparing metabarcoding studies (39, 40, 43) with the current classification in Species Fungorum (27), marked differences arise in the composition of fungal phyla (**Figure 2**). The findings from Baldrian et al. (43) reflect the proportions of described Ascomycota and Basidiomycota well, whereas in Tedersoo et al. (39, 40) the percentages of these phyla are in part much lower. Concerning fungal traits (**Figure 3**), Tedersoo et al. (39) show the proportions of saprotrophs and symbiotrophs from DNA metabarcoding data are relatively close to those derived from known species (27) and genera (66), whereas the proportion of pathotrophs is substantially smaller, because pathotrophs are naturally underrepresented in soil samples.

In the global soil dataset analyzed by Tedersoo et al. (39), Dothideomycetes, Lecanoromycetes (both Ascomycota), and Pucciniomycetes (Basidiomycota) are particularly underrepresented, supporting the notion that studies focused on soil fungi neglect aboveground fungal guilds, in particular pathogens and lichens. A reliable estimate of the composition of taxonomic and functional groups extrapolated from a global metabarcoding dataset would therefore require a sampling strategy that is representative of the major global ecosystems, habitats, and substrata, further expanding

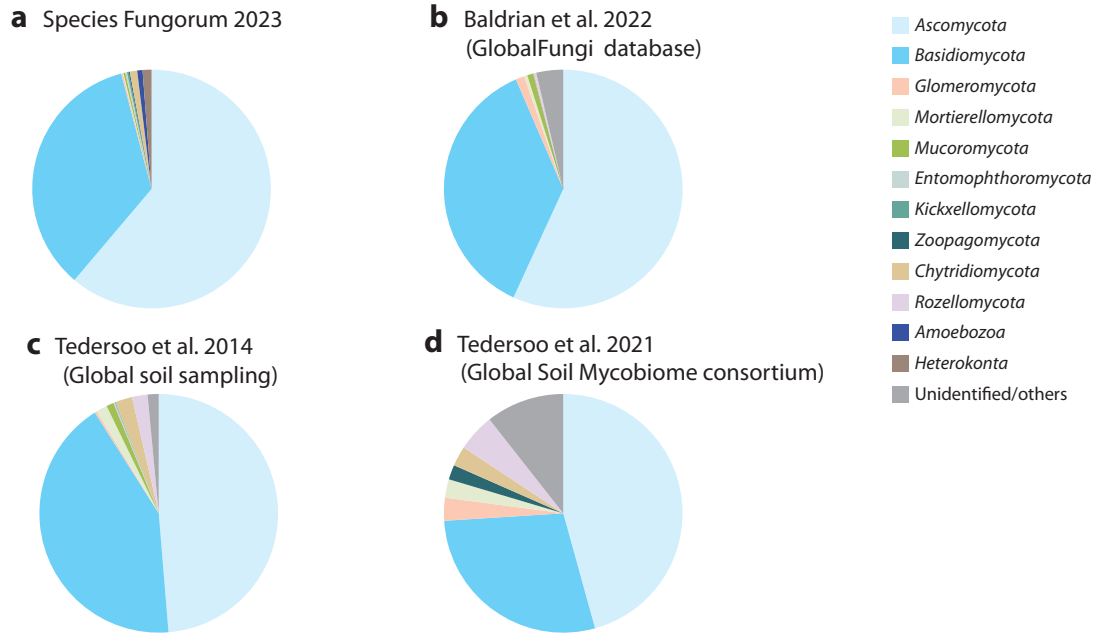

Figure 2

Composition of the proportion of fungal phyla in terms of taxon richness detected in three major global metabarcoding studies (including both described and undescribed species) versus Species Fungorum (including only species described to date) (27). (*a*) Species Fungorum (27): fungi, all phyla, and terrestrial and aquatic habitats (155,603 species); (*b*) Baldrian et al. (43): fungi from terrestrial habitats above- and belowground [1,080,072 operational taxonomic units (OTUs) (97%)]; (*c*) Tedersoo et al. (39): soil fungi [80,486 OTUs (98%)]; (*d*) Tedersoo et al. (40): soil fungi [722,682 OTUs (98%)].

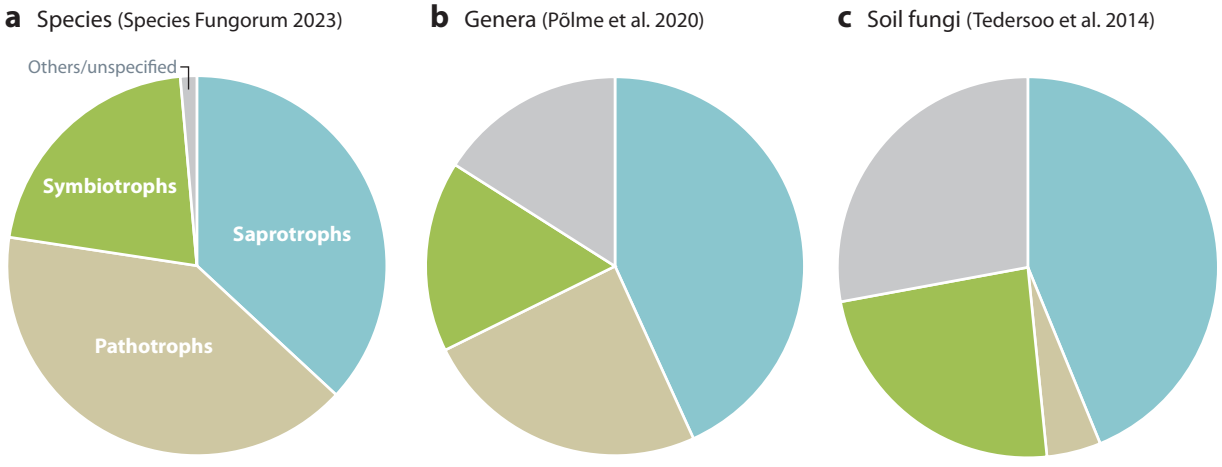

Figure 3

Composition of the proportion of fungal traits [main life forms, simplified based on the FungalTraits database (66)] in terms of taxon richness detected in (*a*) Species Fungorum (27; species level), (*b*) FungalTraits database (66; genus level), and (*c*) global metabarcoding of soil fungi [39; operational taxonomic units (OTUs), soil fungi]. Species Fungorum (27) lists all accepted species of fungi, currently 155,603 species, whereas FungalTraits (66) provides lifestyle classifications for more than 10,000 genera of fungi; Tedersoo et al. (39) focus on soil fungi, covering 80,486 OTUs from clustering at 97% identity.

on studies such as Tedersoo et al. (39–41) and Baldrian et al. (43), to represent the wealth of ecologically hidden fungi.

3. DISTRIBUTION

Until the past decade, our knowledge on fungal distribution was mainly based on traditional, often broad, species concepts, which we now know include many closely related species that were challenging to delimit based on morphology only. Moreover, the knowledge was mainly based on collectable species, i.e., mushrooms, truffles, lichens, rusts, and visible sac fungi, excluding a large proportion of "hidden" fungal diversity such as early-diverging fungal lineages and Glomeromycota. Besides their classification, the adoption and widespread use of DNA techniques also transformed our views on fungal distributions (see the sidebar titled How DNA Technology Is Rewriting Everything We Thought We Knew About Fungi).

3.1. How Is Fungal Diversity Distributed Globally?

Two key studies have investigated global fungal diversity based on metabarcoding techniques, and these showed a dual pattern: Whereas most groups indeed have their highest diversity in the tropics, mirroring general patterns for plants and animals, others—ectomycorrhizal fungi and several fungal classes—are most diverse in temperate ecosystems (39, 67). At least for ectomycorrhizal fungi, this may be explained by the presence of suitable hosts and more structured soils in temperate compared to tropical areas (39). However, as mentioned, both studies were based on soil samples, and no comparable global study on the biogeography of the whole kingdom Fungi has been published that also includes extensive sampling of the aboveground fungal diversity.

To synthesize current knowledge on this topic, we combined the data from different studies (40, 68–72) to produce the most up-to-date map on the global diversity of soil fungi (**Figure 4**). Our estimate shows that some of the most species-rich areas in the world are in tropical lowland and montane forests and woodlands, but high-diversity temperate areas are also evident.

3.1.1. Fungal diversity and biomes. Among the main biomes of the world, forests, such as the Amazon and the Atlantic Forest in South America, host the greatest diversity of soil fungi, but grasslands and tundra also host a significant number of species, whereas far fewer fungi are found in dry and cold areas, such as deserts and polar regions (**Figure 4**). For aboveground fungi, in particular plant pathogens and endophytes, but also insect-associated fungi, this holds true as well (73, 74). Aquatic habitats around the world may contain up to 100,000 species (75–77) belonging to at least eight phyla. Some habitats with fewer fungal species may still host diverse lineages of early colonizing fungi, e.g., lichens in rocky, otherwise hostile areas of tundra and deserts, and in the Interior Antarctic (78).

The two most species-rich phyla of fungi, Ascomycota and Basidiomycota, as well as the smaller phyla Chytridiomycota, Mucoromycota, and Glomeromycota (**Figure 1**), are found on all continents and in all biomes (39, 76, 79–82). In terrestrial habitats, early diverging fungi—those that evolved before the rise of Dikarya [Asco-, Basidio-, and Entorrhizomycota (**Figure 1**)]—seem to be relatively more common in nonwooded ecosystems (39). An example of an early diverging fungal clade predominantly found in terrestrial habitats is the phylum Calcarisporiellomycota, its members being saprotrophic in soil. Some of the early diverging lineages are either aquatic or their hotspot of diversity is in aquatic habitats, such as Olpidiomycota, which are saprotrophs or parasites of algae, aquatic fungi, and rotifers, and Aphelidiomycota and Sanchytriomycota, which are parasites of mostly algae (83, 84). Some others are very restricted in their ecology: For instance, members of the phylum Neocallimastigomycota live in anaerobic conditions within the guts and dung of herbivores (85).

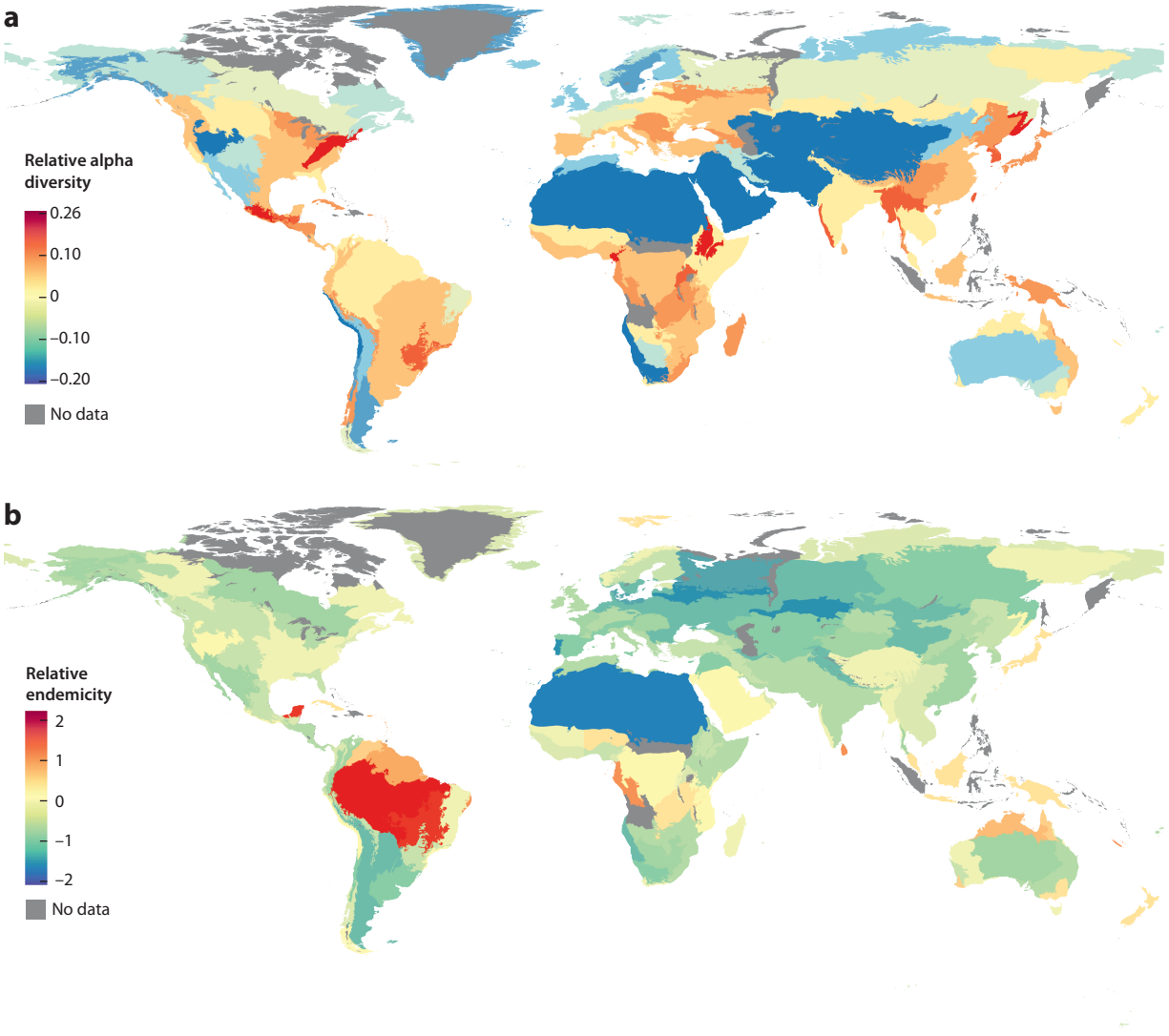

Figure 4

(*a*) Average global taxonomic richness (alpha diversity) of soil fungi (see **Supplemental File 3** for details). (*b*) Average endemicity of soil fungi according to Tedersoo et al. (41).

All three main functional groups—saprotrophs, pathotrophs, and symbiotrophs—are present in all terrestrial habitats. Saprotrophs and pathotrophs have the broadest distribution ranges, the latter partially due to anthropogenic spread through human movement or via crops (86), and animal parasites are particularly widely distributed (39, 41, 67). Mycorrhizal fungi seem to have the narrowest climate niche (39, 41, 67). When looking at the species level, only a few species are known to have a cosmopolitan distribution, the majority of them being saprotrophs and pathogens in the Ascomycota (87). In freshwater and marine aquatic habitats, saprotrophs and pathotrophs are the most commonly recorded lifestyles (75, 79). Mutualistic symbiotrophs are less well-known from these habitats, but endophytes, mainly representing Ascomycota, seem to be the most diverse

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group inhabiting marine plants (i.e., algae, seagrass and mangrove trees), invertebrates (i.e., corals and crustaceans), and fishes (88).

3.1.2. Biotic similarities across regions and biomes. The northern regions (Europe, West and East Asia, and North America) host the most similar fungal communities, with many circumboreal species (41, 89). Other areas with a clear linkage are (*a*) New Zealand, Australia, and southern South America, driven especially by the species associated with Nothofagaceae (90); (*b*) Southeast Asia and New Guinea; and (*c*) regions of sub-Saharan Africa (39). Among Northern Hemisphere biomes, tundra and boreal and temperate forests are linked together, but they also have an affinity with tropical montane forests (see **Supplemental Figure 3**). Other tropical biomes form a separate group. This can be seen, for example, in South America, where ectomycorrhizal fungi associated with Fagaceae in the Andean region belong to Holarctic lineages, whereas species in the Colombian Amazonian Region associated with the Fabaceae or Dipterocarpaceae originate from tropical lineages of Gondwanan origin (91) and *Nothofagus*-associated taxa belong to southern temperate lineages (92). The current distribution patterns are partially explained by the comigration with hosts over Pleistocene land bridges such as Beringia, Wallacea, and the Isthmus of Panama (93, 94). Compared to plants and animals, the distribution patterns of fungi are somewhat conflicting, since the Holarctic lineages in plants and animals are nested within larger tropical groups (39). Additional bioregionalization analyses would be required to further clarify the high-level organization of fungal taxonomic clusters worldwide (95).

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3.2. Distribution Range Size and Endemism

Before the arrival of molecular methods, many fungi were considered to be widespread, and the same species were found on different continents. Now we know that many of these "species" are in fact groups of species: For example, the golden chanterelle (*Cantharellus cibarius*), once thought to be a single subcosmopolitan species, has been shown to include at least 14 different species with regionally limited distributions (42, 96, 97). An even more extreme example comes from the lichen genus *Cora*; it was once thought to include one species but now nearly 200 species are recognized (60, 98). The replacement of traditional taxon concepts with species delimitation based on integrative taxonomy, including sequence data, has also dramatically changed our knowledge of the proportion of widespread versus narrowly distributed species: In a study encompassing eight lichen genera in Colombia, based on traditional taxonomy, 45% of the species were considered widespread (on at least two continents) and less than 25% endemic to the country. When examining the same genera after phylogenetic revisions, only approximately 10% remained genuinely widespread, whereas 75% were considered nationally endemic (91).

3.2.1. Global patterns of distribution range size. In general, the spatial patterns of range size for soil fungi resemble those of vascular plants and animals in that they also have many narrowly distributed species in tropical habitats (99, 100). The largest difference, however, is that in plants and animals, islands or island-like continental habitats usually contain the greatest proportion of narrowly distributed species, whereas in fungi the island habitats do not necessarily have greater endemicity compared with continental habitats (41). For example, for soil fungi, the forests of Amazonia and the Cerrado savanna of Brazil stand out as some of the regions with the highest average of regionally endemic fungi (**Figure 4**). This does not mean that islands, e.g., Hawaii and Madagascar, would not have endemic species of soil fungi, but, according to the current knowledge, the proportion of species endemic to those island groups is not as high as in the top-ranking regions, at least when measured in absolute rather than area-corrected terms [crucial for considering patterns of endemism (e.g., 101)]. However, including the above-ground diversity may change

the picture since some groups of lichens in Hawaii, New Zealand and Galapagos show high island endemism (e.g., 102–104).

Furthermore, in plants, large islands can host even endemic families, but in fungi island endemism seems to be more at the species level, e.g., Hawaii (102) and Madagascar (105). This may be the result of a greater long-distance dispersal capacity of fungal spores relative to propagules of plants and animals (17). For instance, the currently dominant families of fungi forming ectomycorrhizal associations with the plants in Madagascar seem to have arrived on the island after its separation from mainland Africa, and recent studies would also indicate multiple dispersal events within genera or families to the island (105, 106). The difference between plants and fungi in the proportion of endemic genera and families, however, could be smaller than currently observed since growing understanding on fungal diversity is also affecting the classification, and many previous families and genera have been divided into smaller units; in addition, higher plants and animals allow for much more refined genus- and family-level classifications due to their richness of phenotypic characters, and so these ranks are not directly comparable among kingdoms (107). A recent revision of a cosmopolitan ectomycorrhizal genus *Cortinarius* (Agaricales), for example, concluded that instead of one genus, the group contains ten genera, of which one is currently only known from New Zealand and Australia and one is only associated with the species of Nothofagaceae in the Southern Hemisphere (108).

3.3. Global and Regional Drivers of Fungal Richness

Drivers of fungal species richness vary from local to global scales and between different functional groups of fungi, which show different patterns of diversity, distribution range size, and vulnerability to climate change (41, 109). At the global scale, efforts to disentangle fungal richness and their drivers have mostly focused on soil-inhabiting fungi, identifying climate and soil pH as key factors, with fungal richness peaking in slightly acidic soils (39, 41, 110). Climate has a strong direct effect on plant and fungal richness, but also an indirect effect by altering soil conditions (e.g., soil pH and C:N ratio). Soil pH influences nutrient availability, metal solubility (essential for enzymatic activities), and nitrogen speciation, potentially affecting fungal competition with bacteria. Vegetation variables and organic carbon content have also been found to be significant drivers of fungal community composition (67, 111). Deserts and Antarctic habitats, where plant coverage and richness are lower, support the lowest fungal richness (39, 41). Aboveground fungal diversity has been poorly studied, but its drivers might differ from those growing in soil. There are also limitations to inferring responses to drivers from variations in their DNA detection in soil, as dormant propagules and spore banks might differ from their active communities (112).

At regional scales, in temperate and boreal habitats in Europe, soil pH is the main predictor of fungal species richness, together with atmospheric nitrogen deposition, which drives richness and community composition of different groups of mycorrhizal fungi in roots of forest trees (113–115), grasslands (116), and ericoid plants in bogs and heathlands (117). The richness of epiphytic lichens is also affected by these factors (118), while host and seasonality affect endophyte richness (119, 120). In Amazonia, habitat type is the strongest factor explaining fungal diversity, whereas soil properties show conflicting signals or appear less important (121). In the Brazilian Atlantic Forest, latitudinal diversity gradients differ according to families, suggesting differential climate adaptations as drivers of diversity (122).

4. CONSERVATION AND THREATS

Judging what to prioritize for conservation actions depends on knowledge from biology, social sciences, and economy, and ultimately, decisions are significantly affected by our values. For too

long, the conservation of fungi—with the exception of certain lichens—has been largely overlooked. This is in part due to their cryptic nature and the challenges in studying and detecting them with traditional methods that have often led to the earlier held incorrect perception that fungi are intractable for conservation initiatives (123, 124).

Red-listing: the process of categorizing species into a set of threat categories, which reflect the estimated extinction risk

Red List: a list of species that have had their risk of extinction assessed according to formal criteria, such as those set by the IUCN

4.1. Conservation Assessments of Fungi

Reports of lichen and macrofungal decline (e.g., 125–127) and the early success of the red-listing of animals and plants inspired the development of the first national Red Lists of threatened macrofungi and lichens, starting in the late 1980s. Red List assessments, based on International Union for Conservation of Nature (IUCN) criteria (128) and leading to entries on the IUCN Red List of Threatened Species™ or national equivalents, are the global standard for identifying species under threat, informing conservation needs and leading to the initiation of conservation actions. Although not legally binding per se, Red Lists influence political decisions and the effectiveness of conservation measures, by being recognized as official documents of the best available knowledge of species' status and trends. National Red Lists of fungi are increasingly being used to identify and prioritize areas and habitats to set aside for conservation, as reference points for including fungi in conservation management guidelines, and to initiate species action plans, e.g., waxcap grassland in the United Kingdom (129), numerous conservation management efforts in Fennoscandia and Denmark, and forest protection in Chile. Red List data on fungi are also starting to be incorporated into conservation actions in Australia, New Zealand, and the United States. A few countries have protected species, such as the United Kingdom and Croatia, and a few have linked their national fungal Red Lists to protection and legislation, e.g., Chile and Poland. Fungal Red Lists are also increasingly considered in guidelines and legislation governing land use, together with animals and plants, e.g., in Fennoscandian national biodiversity plans and by the Forest Stewardship Council. The number of countries with official or unofficial national Red Lists, or corresponding lists of conservation values for macrofungi, stands at approximately 58 in 2022, and for lichens is 17 (**Figure 5**). The extent of species assessed, and amount and type of documentation, varies, but even with these limitations, collectively more than 20,000 species have been assessed at national levels.

Building on these national red-listing efforts, the Global Fungal Red List Initiative was established in 2013 (130) to facilitate global assessment efforts by the fungal specialist groups of the IUCN and volunteer mycologists across the world. Fungi on the global Red List draw attention to and highlight threats to fungi that should be considered in any country regardless of whether national fungal Red Lists are present or not. The IUCN Red List (130) includes 625 fungi, of which 352 (56%) were assessed as globally threatened or near threatened (131) (**Figure 5**). Only 0.4% of the fungi described to date and 0.02% of those estimated to occur on Earth have therefore been assessed. Fungi and invertebrates are the two most species-rich and poorly known groups containing multicellular eukaryotes (**Figure 6**).

The classification of extinction risk for species on Red Lists, regardless of taxonomic group, is based on the size of, and trends in, their population size (past and potential future changes), and range (see 128). For many fungi, these estimates are often indirect and based on estimates of the quantity and quality of their habitat, host plants and substrata (127, 132). However, the knowledge of fungal distributions and their ecologies, primarily based on spore-bearing structures and thalli, has substantially increased over the past decades, thanks to increasing interest from scientists and field mycologists, the arrival of DNA techniques, surveys, for example, those required for forest certification, and targeted citizen science initiatives focused on locating threatened species.

Because red-listing includes a population analysis, efforts at generating assessments have raised challenging questions, otherwise infrequently addressed in fungi, about the biology and

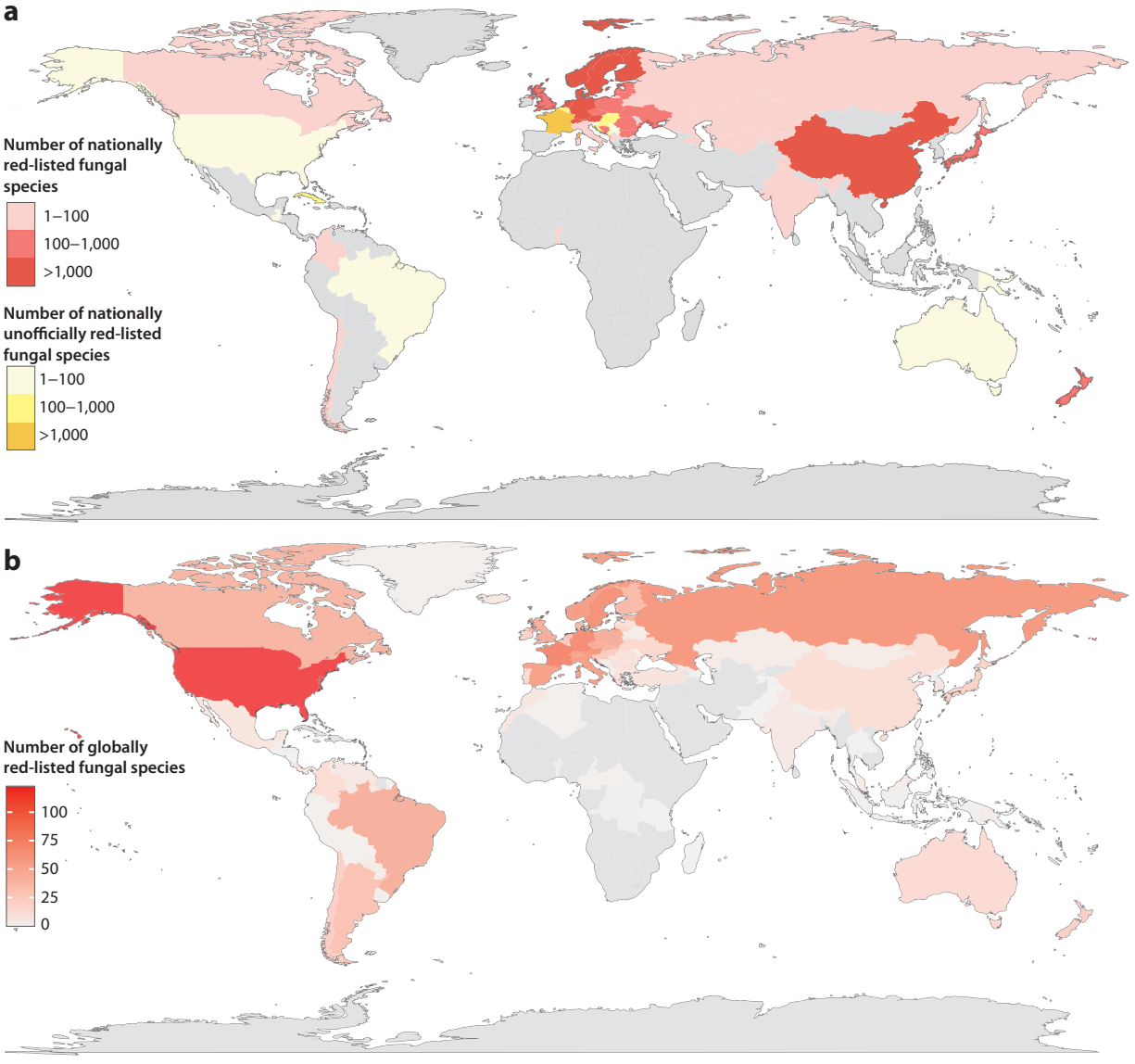

Figure 5

(*a*) Countries with officially approved national Red Lists of lichens or macrofungi (those acknowledging appropriate government agency endorsement) are shaded red, with increasing intensity indicating greater numbers of taxa red-listed as Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), or Data Deficient (DD). Corresponding shading in yellow highlights countries with unofficial national Red Lists or not using IUCN criteria. Countries shaded in gray have no national Red Lists of lichens or macrofungi. Data compiled from Dahlberg et al. (133), Willis (154) and Leonardi et al. (155) together with updated information and comments from the IUCN SSC Lichen Specialist Group and IUCN SSC Mushroom, Bracket and Puffball Specialist Group in January 2023. (*b*) The distribution of the 352 globally red-listed fungi, with shading in red highlighting the numbers of taxa listed as CR, EN, VU, NT, and DD in different countries as of December 2022 (130) (**Supplemental File 4**).

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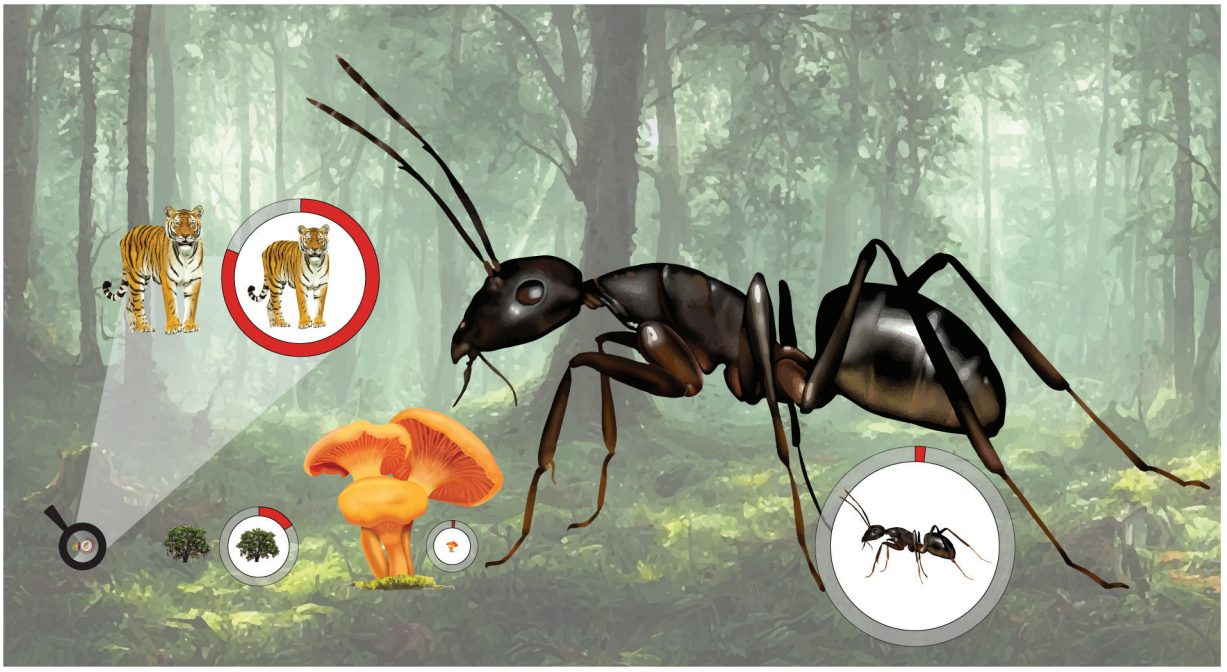

Figure 6

Diversity of species in the three kingdoms: fungi, plants, and animals (vertebrates and invertebrates shown separately). The size of an organism within a circle is drawn in proportion to the number of described species; the size of the bigger version of the organism reflects the total estimated number of species. The outer red portion of the circle represents the percentage of species assessed under the Global Red List of Threatened Species (in relation to the species described). Numbers and references used for compiling the figure are provided in **Supplemental File 5**. Artwork by Inessa Voet, with background image generated by DeepAI (**https://deepai.org/**).

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life-history features such as (*a*) turnover and longevity of individuals; (*b*) required conditions for establishment of mycelia; (*c*) the presence and significance of a spore bank, since most species appear to have short-lived spores and a limited spore bank; (*d*) the significance of mycelial fragmentation and clonality; and (*e*) symbiont/host specificity. It is also critical to consider factors influencing whether individuals form sexual spore-bearing structures or not, the geographical distribution of species, their commonness, and, importantly, if the data are of sufficient quality to estimate potential sizes of fungal populations. These data are needed to better manage macrofungal and lichen habitats at different spatial and temporal scales to strengthen populations of individual threatened species (124).

4.2. Threats to Fungi

Information provided by the global IUCN Red List indicates that the underlying threats to fungal species are essentially the same as those to animals and plants, as threats that impact fungal hosts and their substrata will have a substantial impact on fungi as well. They include, in decreasing order of frequency, (*a*) land use change (comprising natural system modifications, forestry, agriculture, residential and commercial development); (*b*) climate change; (*c*) invasive species; (*d*) pollution (such as the deposition of nitrogen); and (*e*) direct exploitation (collection of economically valuable sporing bodies, e.g., *Butyriboletus loyo*, *Fomitopsis officinalis* and *Ophiocordyceps sinensis*) (114, 123, 130, 131, 133–135).

Threats identified through national Red Lists show similarities to global patterns, although few regions have been thoroughly surveyed. In Europe, assessments in Sweden and the Netherlands (136, 137) show that habitat loss and fragmentation are mainly due to (*a*) decline of areas of older natural forest and the intensification of timber production; (*b*) decline in the availability of coarse dead wood and old trees; (*c*) impoverishment and decline of old seminatural and unfertilized grasslands (due to fertilization, reforestation, and lack of grazing); and (*d*) high anthropogenic nitrogen deposition, particularly affecting ectomycorrhizal fungi in naturally nutrient-poor soils (133). Although threatened animals, fungi and plants often occur in the same habitat, several habitats differ in importance; for example, threatened fungi are more frequent in seminatural grassland (i.e., ancient pastures and meadows traditionally managed by grazing or mowing, without the use of pesticides or fertilizers in modern time) and sandy natural pine forests.

Although fungal species may be lost from an area as a result of environmental degradation, it is difficult to effectively document fungal extinction through survey data, as absence of evidence is not evidence of absence. So perhaps not surprisingly, only 34 species are officially listed as Critically Endangered (Possibly Extinct) on the Red List. However, the most important purpose of the Red List is to document and bring attention to threatened species so that declines can be counteracted, or at least mitigated.

4.3. Advancing Fungal Research and Conservation

Although efforts to fill the large gaps in our knowledge of fungal diversity and distribution need to continue, the key objective in fungal conservation today should be to raise scientific, public, and political interest and awareness of fungi and their vital roles that benefit people, nature, and the climate. Ultimately, public awareness and appreciation of biodiversity set the foundation for conservation to take place. The increasing public interest in fungi, thanks to committed mycologists and their organizations together with recent popular science books, series, short videos, TED Talks, documentaries, podcasts, and other media, may help conservation as much as improved science (e.g., 138). Three of the most important actions needed for preventing the decline and enhancing the protection of threatened fungi are (*a*) to formally protect areas of conservation interest; (*b*) to identify, design, and implement appropriate management actions inside and outside protected areas, including ecological restoration measures, to ameliorate habitat conditions for threatened fungi; and (*c*) to integrate fungal conservation with efforts to preserve plant and animal life and to coordinate conservation of these three kingdoms across the network of protected areas and among countries.

In light of climate change and increased pressure on natural areas, there is also a great need to generate evidence-based, user-friendly guidelines for how land could be managed to support different aspects of fungal biodiversity, particularly in areas of resource use such as forestry. Being immobile and often long-lived, fungal species benefit from many of the general conservation efforts employed for other species, such as site protection and sustaining processes and management of habitats of conservation interest. But additional management practices are often needed to conserve fungal diversity and function. For example, preservation of veteran trees to serve as species reservoirs, maintaining a continuity of trees and forest structures and maintaining the succession and amount of deadwood are essential to preserve many threatened lichens, and mycorrhizal and wood-inhabiting fungi. Seminatural grassland fungi are best preserved by maintaining the current management of the land and its nutrient-poor condition (132). The recognition of fungal conservation practices both supports and strengthens overall conservation, and importantly also preserves sites and habitats of importance for threatened fungi, irrespective of animals and plants, to be identified, prioritized, and protected. May et al. (124) set out a research agenda for conservation mycology, including identifying management needs beyond basic site conservation.

Ex situ conservation: for fungi, refers to the cultivation or live storage of individuals that can be regrown in suitable substrates

Furthermore, advancing fungal conservation will require increased mycological expertise, human and financial resources, and utilization of new tools and analyses, for example using available satellite surveillance data and other information to document and analyze status and changes in land cover and habitat degradation (131). Metabarcoding offers a new additional tool to detect and monitor fungal distributions and species populations, but rare species are typically not detected, limiting the utility of the technique. Thus, combining the manual search for spore-bearing structures with environmental DNA data is recommended for the best outcome (139, 140). As more global Red List assessments are carried out, we may soon reach suitable sizes of training datasets to use machine learning approaches to help identify the putative threat status of unassessed fungal species, especially those of Least Concern. This will enable efforts to focus on those most likely to be threatened and therefore in need of expert-based evaluations for conservation actions to be developed. To be efficient, documentations, assessments, and actions for fungal conservation should be focused on species and habitats likely to be declining and threatened.

Whereas in situ conservation should always be a priority, the increasing number of severely threatened habitats may require the complementarity of ex situ methods. Unlike in plants and animals, ex situ conservation in fungi is still rare, with only a few examples such as translocations in lichens (141, 142). A road map for potential translocations of native wood-inhabiting fungi to their original habitats has been recently proposed as a means to strengthen threatened local populations and prevent further decline (143). Considering that saprotrophic culturable fungi represent 40% of fungal diversity, that brings in potential for ex situ conservation. According to the World Data Centre for Microorganisms, more than 900,000 cultured strains of fungi, corresponding to approximately 54,000 species, are being held in 824 culture collections worldwide. If we account for redundancy, misidentifications, and synonyms, the actual number drops down to approximately 20–25,000 species (A. Buddy, D. Smith, personal communication). Unfortunately, from the 352 species assessed as globally threatened or near threatened, only 25 are preserved in culture collections, demonstrating that there is little connection between these collections and conservation initiatives. In addition, many symbiotic fungi, especially mutualists, cannot be grown apart from their symbionts and thus are not suitable for living collections and further cryopreservation. To secure ex situ conservation success, it is therefore important to improve the diversity of culture collections and develop alternative methods of preservation and propagation for non-culturable fungi, as well as to establish long-term studies to monitor the success of population augmentation and relocation.

Although species and habitat conservation are heavily based on the information from Red Lists, there are other conservation approaches to consider. One is to maximize phylogenetic diversity by ensuring representation of many fungal clades (e.g., 144). Another is to heed hotspots, i.e., areas with a high number of species of conservation interest including endemic species with restricted distributions (see 41). A third approach is to pay attention to fungal ecosystem services identified as ecologically and economically important, and this focuses on frequently and abundantly occurring species that perform most fungal processes in a habitat (145, 146). These approaches rely largely on species identification through molecular analyses, which enable identification of fungi from not only spore-bearing structures but also from mycelia present in environmental samples.

5. CONCLUSIONS

Fungi are immensely important to the world's ecosystems and humankind. Yet, probably because they are mostly small, live hidden lives to our human eyes, and have complicated and unfamiliar names and unknown functions, they have often been left in the shadow of plants and animals.

There is an urgent need to bring the knowledge on Funga to the same level as Flora and Fauna. Our knowledge on fungi was long limited because of their cryptic nature and difficulty to assess

them with traditional methods, but the arrival of DNA techniques has transformed our ability to study them (see the sidebar titled How DNA Technology Is Rewriting Everything We Thought We Knew About Fungi). Molecular and other novel techniques have allowed and continue to enable us to understand the basic biological questions related to fungi, achieve natural classifications, and gather data on fungi at a speed never seen before. However, while the technologies to generate data on a large scale have advanced rapidly, the analytical methods to assess those data lag strongly behind. Furthermore, improvements to avoid methodological biases during the data generation are needed.

Our conclusions on global patterns of fungi are currently based on far less data than that of plants and vertebrates, in relation to the expected diversity for those three groups. Also, global efforts have concentrated mainly on soil fungi and less data are available for aboveground diversity and aquatic fungi. For gaining better data for the basis of diversity estimates and knowledge on distribution patterns of fungi, a well-balanced and dense global sampling of all fungi from all habitats will be needed. Recent global initiatives such as the Global Lichen Holobiont, FunAqua, and FunLeaf projects will offer ample fungal biodiversity data from substrata other than soil. Currently, the Sequence Read Archive contains approximately 150,000 environmental samples corresponding to fungal DNA, and this number is growing exponentially (147). A concerted global effort could easily generate ten times this number of samples within a period of five years, allowing a global terrestrial grid cover of 20 × 20 km to cover most of the global fungal diversity. The key challenges for achieving these are not scientific, but logistical: securing the resources, permits, collaborations, and coordination required.

The underlying overall threats to fungal diversity are essentially the same as those to animals and plants, including habitat destruction and fragmentation, climate change, pollution, and invasive species, and fungi benefit from the same general conservation measures and priorities as animals and plants, i.e., protection of sites and appropriate habitat management. However, additional actions can be required to conserve fungi. Fungi have largely been neglected in conservation, but the situation is improving, and fungi are starting to increasingly be considered. Key tasks in conservation will be to significantly increase the number of assessed species, enhance and increase the interest and understanding of the importance of including fungi in conservation, and provide user-friendly knowledge and guidelines to facilitate efficient conservation of threatened fungi. Conservation knowledge needs to be spoken with "one voice," to make it easy for decision makers and stakeholders to understand and act upon.

SUMMARY POINTS

1. Our assessment of the scientific literature and consideration of biases and gaps lead us to propose a new estimate for global fungal richness ranging between 2 and 3 million species, with a "best guess" at 2.5 million (representing both the mean and median across calculations).
2. Between 92.5% and 95% of all fungal species remain unknown, and with the current speed it will take 750–1,000 years to formally describe those remaining.
3. Our maps integrating datasets of soil-inhabiting fungi support the earlier findings that the most species-rich areas in the world are in tropical lowland and montane forests, as well as in some temperate areas.
4. Drivers of fungal species richness vary from local to global scales and differ between functional groups.

5. The average distribution ranges of fungi are wider than those of plants and many groups of animals, and there is no detectable relationship with insularity in certain groups of fungi, such as soil fungi, whereas in others, such as lichen fungi, island endemism matches that of plants and even some animals.
6. Although threatened animals, fungi, and plants often occur in the same habitats, certain habitats such as European grasslands and calcareous conifer forests are more important for fungal conservation than for other groups of organisms, and fungi with specialized ecologies; e.g., host and substrate specificity, need special consideration.
7. Extensive fungal conservation initiatives are being carried out in only a few countries, and only 625 species (0.4% of the total described, and 0.02% of those estimated) have so far been assessed for their extinction risk in the global (IUCN) Red List.
8. The most effective way to protect fungal species is in situ, by formally protecting areas and improving land use management. Ex situ conservation, through storage in cryobanks or cultures, provides an additional way to safeguard fungal species amenable to cultivation and storage and to help with their re-establishment in nature.

FUTURE ISSUES

1. The topmost priority for advancing fungal knowledge is undertaking a taxonomically and functionally comprehensive global sampling effort of fungi from all habitats and regions.
2. The mycological community needs to discuss and agree on appropriate sampling protocols, building on the integration of environmental DNA (e.g., from soils, leaves, animals) into fungal classifications, along with expert surveys likely needed to detect rare species.
3. To accelerate scientific description of the >90% undocumented species, taxonomic nomenclature rules may be revised to allow descriptions from molecular data only, pending the addition of morphological examinations. Alternatively, a separate classification system could be established for this purpose. However, scientific guidelines must be developed and broadly agreed upon that guarantee a high quality of classifications derived from DNA sequence data only.
4. A concerted effort should be made to produce sequence data from the world's fungal collections. Data from type specimens would be needed to anchor the use of names described to date, and data from other already collected specimens to reveal the yet unnamed species. Together, voucher-based and environmental sequence data will enable the creation of a complete fungal tree of life.
5. Whenever possible, the identification, delimitation, and mapping of fungal species from environmental DNA should be based on phylogenetic methods and multiple sequence alignments, rather than operational taxonomic unit clustering, due to recognized problems in species delimitation with the latter approach. This will require further development of methods and tools.
6. Thousands more fungal species, particularly from Africa, Latin America, and Asia, should be red-listed in order to support identification of habitats and critical areas for fungal

conservation. This should be done as much as possible in concert with fauna and flora to identify more efficient procedures for species not yet assessed by experts.

7. Advancing fungal conservation requires the compilation of evidence-based management guidelines for species and areas, the integration of fungi into existing conservation programs, and further investigation on the potential of cryobanks to support ex situ storage of fungal strains for conservation, research, and reintroductions.
8. Advancing fungal knowledge through research, training, and partnerships must ensure fair and equitable sharing of benefits across the globe, with high potential to bring tangible benefits to people and nature.

DISCLOSURE STATEMENT

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