How Many Species of Fungi are there in the World?

Jim Cornish

"How many species of fungi are there in the world?" is a fundamental question in mycology. Yet, after more than three centuries of collecting and classifying fungi, we still don't know with any degree of certainty the diversity (species richness) of the Fifth Kingdom on our planet. This immense gap in our knowledge of fungi exists largely because of unexplored niches, underexplored habitats, ambiguities in both traditional and molecular sequencing identification methodologies, species complexes, and a worldwide shortage of field mycologists, taxonomists, to name a few. Consequently, mycologists have resorted to estimating fungi, often by extrapolating data collected from local and regional plant and fungi associations to a global scale (Blackwell et al., 2019; Lücking et al., 2020). Although these estimates are often based on some questionable assumptions and are usually conservative in number, they remain an important part of discussions related to climate change, ecosystem protection, biodiversity loss, development goals, and the spread of fungal pathogens. Estimates are also used when investigating fungi as potential sources of food, medicines, and other products on which human life depends (Wu et al., 2019). This article covers a few of the thirty or so notable estimates of global fungal diversity published since the early nineteenth century and briefly covers where most of the missing fungi are likely hiding.

The Estimates

One of the earliest estimates of fungal diversity was made by Elias Fries, the renowned taxonomist who helped develop the traditional classification system for fungi. In 1825, Fries compared known species across multiple kingdoms and reportedly estimated fungi at more than 140,000 species. He conceded that the actual number could be higher and predicted that fungi would rival the insects in diversity and become the largest group within "orbis vegetabilia" (Hawksworth and Lücking, 2017). Another nineteenth century estimate came from the botanist Anton de Bary, an ardent promoter of symbiosis. In 1872, de Bary estimated fungi at 150,000 species (Hawksworth, 1991). While critics considered the estimate modest, de Bary's promotion of fungal associations with plants and animals as mutualists, commensalists, parasites, and pathogens with ranges the same as their hosts, undoubtedly inspired the future use of ratios as a model to estimate fungal species.

In 1943, mycologists Guy Bisby and Geoffrey Ainsworth used "f:p" (fungi:plant) ratios derived from Iowan forests to estimate fungal diversity at 100,000 species, more than double the described species at that time (Bisby and Ainsworth, 1943). Mycologist George Martin considered the estimate the most "thoughtful in recent times," but he believed that it was low and that fungi were at least the same order of magnitude as flowering plants (Martin, 1951). Martin also proposed his own estimate of 250,000 species (Blackwell, 2011) based on a 1:1 f:p ratio that obviously did not reflect the plant-fungi associations easily observed in the field. Although both estimates were considered conservative, they were among the first to be based on fungi-plant associations, a methodology that would continue to form the basis of dozens of new estimates hypothesized in the decades that followed.

The first "respectable" estimate of fungal diversity came in a "landmark paper" published by mycologist David Hawksworth in 1991 (Blackwell, 2011). Hawksworth used an updated f:p ratio and revised Martin's estimate upward, mainly as "an effort to ensure fungi were duly considered in the scientific and political debates on biodiversity" that began in earnest in the early 1990s. Extrapolating globally a 6:1 f:p ratio derived from native plants on the well-studied British Isles and on average f:p ratios from other European and American locations, Hawksworth estimated fungi at 1.5 million species (Hawksworth, 1991). Although a significant increase over previous estimates, many mycologists, including Hawksworth, thought the figure was also conservative. Mathematician and biologist Robert May, on the other hand, thought the estimate was too high and argued that while Hawksworth's ratio might be accurate for well-known plant and fungi associations in the temperate forests of North America and Europe, it did not represent the species richness of tropical forests and should have been applied globally (May, 1991). This criticism of Hawksworth's approach clearly recognized that determining global fungal diversity required data from more than one ecotype.

To his credit, Hawksworth was a critic of his own work. In his 1991 and subsequent papers, Hawksworth admitted not including what he considered unreliable data from the tropics and often overlooked microhabitats. He had also not included unreliable data from lichenized fungi, soil fungi, fungi associated with insects, and the ever-elusive species complexes (Hawksworth, 1991; Bass and Richards, 2011). Despite these omissions and criticisms from his contemporaries, Hawksworth's 1.5 million figure was considered a "benchmark" and was widely accepted as a "working hypothesis" and frequently cited by researchers and writers of popular science articles for the duration of the 1990s (Hawksworth, 2012). By the end of the decade, at least ten new estimates ranging from 500,000 to 9.9 million species, largely based on revised f:p ratios, were proposed (Wu et al., 2019). In response, in 2000 Hawksworth reconsidered his original 1.5 million figure. Regardless of the new and promising data sets available, Hawksworth deemed it was "prudent" to stick with his 1991 estimate until a consensus on a new working figure based on fresh and independent data sets emerged and the evidence to change it was overwhelming (Hawksworth, 2001).

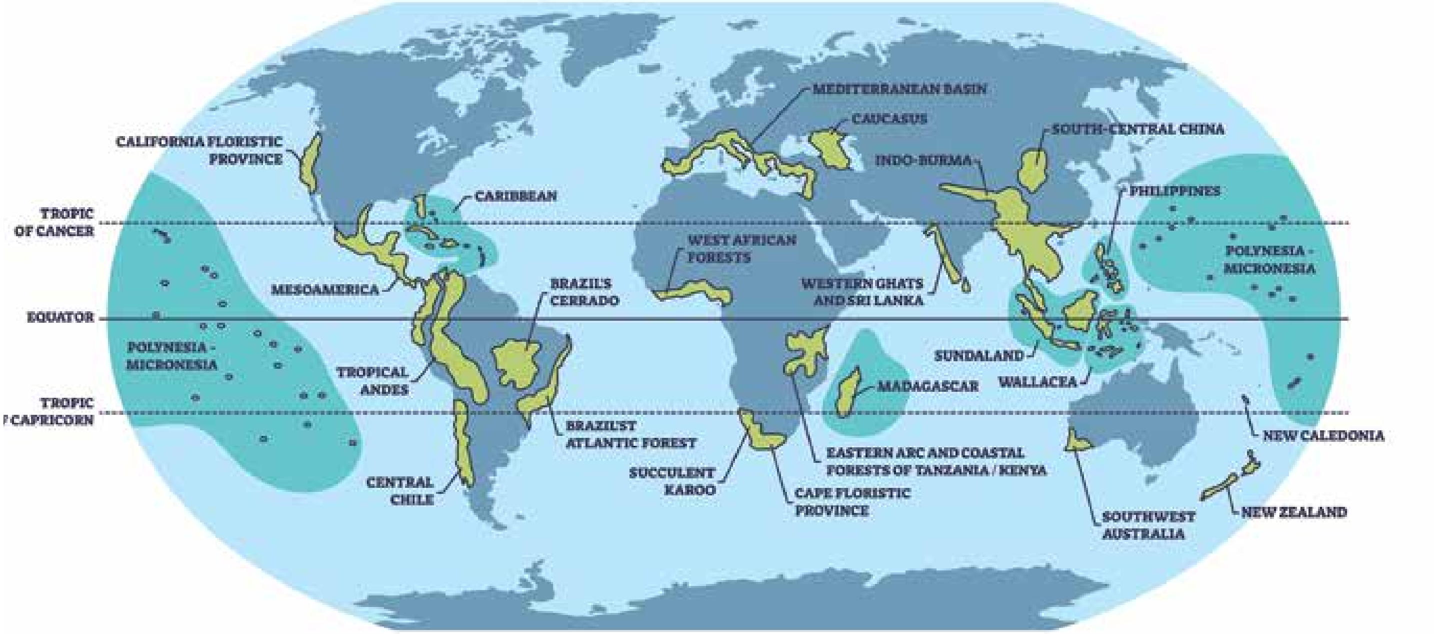
Most efforts in describing and cataloguing fungal species have focused on macro fungi (Bass and Richards, 2011). In 2005, biologist Heath O'Brien and colleagues conducted a large-scale sequencing study to inventory nonculturable soil fungi, a diverse group often overlooked because they lack conspicuous fruiting bodies and invariably do not produce in vitro the voucher specimens required for visual identification. O'Brien found 463 OTUs (i.e., operational taxonomic unit or digital types, equivalent to unnamed species) of fungi in 863 sequences derived from a few grams of soil sampled in a temperate North Carolina forest. The OTU count was then coupled with local plant numbers to create a 19:1 f:p ratio. Extrapolated globally based on a total plant population of 270,000 species, O'Brien proposed a new global estimate of 3.5 to 5.1 million fungal species. Upon reflection, he suggested the actual number could be an order or two of magnitude higher (O'Brien et al., 2005).

The use of sequencing in O'Brien's study had major implications for determining global fungal diversity. Although O'Brien's level of species richness was deemed comparable with studies in Switzerland, it had taken the Swiss twenty years of sampling and identification using traditional means to accomplish what O'Brien had achieved in one season (O'Brien et al., 2005). This clearly demonstrated that sequencing could be used reliably to identify fungi faster and cheaper than microscopy and in vitro cultures. Some mycologists even argued that if sampling coverage was sufficient, in due time sequencing could reduce the need to resort to unreliable extrapolations and assumptions about fungal species richness (Bass and Richards, 2011). Sequencing would also enable mycologists to revisit explored sites to find species previously overlooked by traditional methods. But sequencing on an environmental scale also created problems. The "digital types" revealed by sequencing are being dumped into gene banks, adding tens of thousands of new fungi to await the time-consuming and unregulated process of assigning binomial names to sequenced, new-to-science species (Hawksworth, 2012; Lücking and Hawksworth, 2018).

Elias Fries (1794 –1878). Public domain image source: digitaltmuseum.se.

In 2007, American mycologists John Schmit and Gregory Mueller presented another notable fungal species richness estimate of 712,000 species. Although well short of Hawksworth's "working number," the estimate was notable because its calculation was based on f:p ratios derived from ecologically defined groups of fungi in well-studied temperate and tropical climatic zones across six continents. The estimate also included data based on levels of endemism in fungal groups with allowances made for overlapping species, on widely accepted fungus:insect ratios and on estimates of soil fungi diversity. Schmit and Mueller promoted their estimate as a "lower boundary" (Schmit and Mueller, 2007) but despite their efforts, the estimate did not displace Hawksworth's popular number. It may have, however, demonstrated the

BIODIVERSITY HOTSPOTS



importance of including data from regions of the world that were previously ignored.

In 2011, biologist Camilo Mora and colleagues used a "predictive algorithm" to estimate global fungi as part of a study to assess species diversity across all kingdoms. They argued that taxonomic classification from genus to phylum follows a consistent and predictable pattern in the total number of species in a taxonomic group. Based on a fungal species count of 43,271 taken from the *Catalogue of Life*, Mora estimated fungi at 611,000 species (Mora et al., 2011). If the study had used 100,000 as the number of fungi widely accepted at the time, as Hawksworth pointed out, a recalculation would have generated a fungal estimate around 1.4 million species, close to Hawksworth original figure. Because Maro's estimate was well below the "working hypothesis," very little significance was given to the study (Hawksworth, 2012). But other critics, including Hawksworth and Blackwell, saw it as a "call-to-arms for a concerted and continued effort to improve our knowledge of fungal diversity by all means available" (Bass and Richards, 2011; Hawksworth, 2012).

In 2017, Hawksworth and Robert Lücking revisited Hawksworth's 1991 estimate. Over the intervening twenty-six years, a lot had changed in our understanding of fungal species richness. Morphological, ecological, and phylogenetic fungal species concepts had been combined and increasingly supported by mycologists as a new species concept. This caused a resurgence in species descriptions that delimited many new species while consolidating others. Each year since 1991 had also shown an increase in newly discovered species with no signs of the numbers plateauing. New evidence obtained from species discovery rates had increased f:p ratios to better reflect nature and the inclusion of molecular sequence data from environmental samples had been considered in new extrapolations. When these new data were combined with new mathematical modelling techniques for estimating species richness, Hawksworth revised his 1991 estimate to between 2.2 and 3.8 million species. He yet again acknowledged that it too was subject to change as new analytical methodologies were applied (Hawksworth and Lücking, 2017).

In 2019, mycologist Bing Wu headed a study that revisited fungal species estimates, some of which have been mentioned here. Wu noted that some of these estimates were based mostly on fungi that associate with plants and excluded the nonhost-specific fungi in soils and the fungi associated with insects. Wu's team suggested that the actual number of fungi can only be determined once we have a thorough understanding of the ecology and life strategies of all fungi, goals probably as difficult to achieve as counting all the fungi. Wu also made his own estimate. Building on Hawksworth and Lücking's 2017 figure, Wu suggested about 12 million fungal species globally (Wu et al., 2019), probably the largest estimate to be taken seriously and the one more frequently appearing in recent studies.

Polar Night in the Arctic - Spitsbergen, Svalbard.

The Missing Fungi

If there are at least 3.8 million species of fungi on Earth, as Hawksworth proposed in 2017, but only 148,000 of them are named (Cheek et al., 2020), then 3.752 million species or 98% of all fungi are missing! If true, it begs an intriguing question. Where are all the undescribed fungi hiding?

In their 1997 paper, Hawksworth and Amy Rossman felt that answering the missing species question was "essential for mycologists and plant pathologists if they are to anticipate and respond to problems resulting from emerging diseases caused by previously unknown or understudied species and to prioritize and direct resources toward understanding the systematics of the most important and unknown groups of fungal plant pathogens. Additionally, the answer to this question will test the hypothesis itself and, thereby, address the skepticism of some nonmycologists about the number of undescribed species of fungi" (Hawksworth and Rossman, 1997).

So, where do we look for missing species? The short answer is everywhere! Fungi live in every biome from the tropics to the poles and occupy nearly every habitat from deep ocean sediments to high mountain peaks and beyond. Many of these habitats are understudied or completely unexplored and studying all of them for new fungi will be a daunting task. Some of the most promising and unusual sources of missing species are briefly covered below.

Biodiversity Hotspots

Biodiversity hotspots are defined as biogeographic regions with at least 1,500 endemic vascular plants and 30% or less of their original natural vegetation remaining (Mittermeier et al., 2011). Thirty-six *biodiversity hotspots* representing 17.3% of the Earth's land surface have been identified around the globe. Collectively, they maintain about 77% of all endemic plant species, 43% of vertebrates including 60% of threatened mammals and birds, and 80% of all threatened amphibians (Marchese, 2015). Because hotspots offer a rich variety of substrates on and in which fungi can grow, they are likely to yield a plethora of missing fungal species.

Microhabitats

There are many potential sites for fungal growth in any locality, including one's own backyard. Some of these locales are likely to have niches or microhabitats with small natural features where abiotic factors such as light, temperature, moisture and pH create growth conditions for unique and diverse lifeforms not found in the larger environment. During the 1980s, novel fungi were found in microhabitats associated with nearly 2,000 hosts including rumens of herbivorous mammals, algae, lichens, mosses, marine plants, rocks, insect scales, and plant litter. Often understudied, many microhabitats are likely to be hotspots of novel fungi too (Hawksworth and Rossman, 1997).

Lichenicolous Fungi

Lichenicolous fungi form a specialized and relatively inconspicuous group composed largely of ascomycetes living exclusively as host specific parasites on lichens or as

Yellow crotal lichen (*Xanthoria parietina*) and beard moss lichen (*Usnea*) growing on rock in southern Shetland, UK.

Slate grey saddle (*Helvella lacunosa*), Moenchbruch Nature Reserve, Hesse, Germany.

Lady Slipper orchid (*Cypripedium calceolus*), an endangered European species.

Endangered Philippine Tarsier (*Tarsius syrichta*).

Endangered froghopper species (*Cercopis sanguinea*).

saprotrophs on dead lichen thalli. Usually unrelated to their fungal hosts, lichenicolous fungi commonly appear as galls and have been documented since the mid-1800s but largely ignored until the mid-1970s. Only 457 described species were known worldwide during the 70s, but by 2018 that number had increased to more than 2,300. It is predicted that at least 4,000 species of lichenicolous fungi will be found in the future (Diederich, 2018). While certainly not a source of significant numbers of novel species, they are one of the more unusual places to look for novel fungi.

Novel Plant and Animal Species

An astonishing 86% of all plants and animals on land, and 91% of those in the seas, have yet to be named. On average, thousands of new species of plants, animals, and insects are discovered each year. Like most other species on the planet, these new ones cannot survive without some type of relationship with fungi, some of which will undoubtedly prove to be novel (Mora et al., 2011).

Cryptic Species

Taxonomists have long suspected that many novel fungi lie hidden within known species. Called species complexes or cryptic species, these fungi are a group of “morphologically indistinguishable species” that share a single taxonomic name but are in fact phylogenetically distinct. Complexes are commonly seen among pathogens and among many macrofungi that have European binomial names but are in fact different from their European cousins (Hawksworth, 2012). The European elfin saddle *Helvella lacunosa*, described in western North America is now known as a complex of eleven separate species (Nguyen at al., 2013). Prior to the mid-1970s, species complexes were discovered based on failed cross breeding attempts, but since then restudies via molecular sequencing have unmasked hidden species in many basidiomycetes and ascomycetes which make up the bulk of all fungi (Crespo and Pérez-Ortega, 2009). Hawksworth predicted that the number of novel species hidden within complexes is likely around 1.4 million and once discovered, they alone will increase lichen totals eleven-fold and the known number of fungi five-fold (Hawksworth, 2012).

Insects

Fungi that are associated with insects are so poorly known, fungal:insect ratios have rarely been included in fungal estimates. Today, it is believed some 20,000 to 50,000 species of fungi associate with insects. Gut yeasts that help mycophagic insects digest chitin are believed to be a species-rich source of new fungi. Additionally, many fungi are known as insect parasites. Given that 80% of the estimated 5 million insect species remain undiscovered, it is likely these invertebrates will be another insect-related source of new fungi that could easily outnumber the entire insect population as Fries suggested nearly two centuries ago (Blackwell and Vega, 2018; Shang et al., 2015). But there may be a problem identifying these fungi as there are few specialists in mycology or entomology to do this work.

Soil

Fungi account for about half of all living organisms found in soil. The mushrooms we commonly see growing from soil are but a fraction of the actual mycota present. Many soil fungi are asexual ascomycetes that can only be identified by molecular analysis. In a recent study, environmental DNA sequencing of samples taken just meters apart in an Alaskan forest produced 200 different taxonomic units with only a 14% overlap in species. Soil studies around the world extended Hawksworth's 2017 estimate by nearly two million new species (O'Brien et al., 2005). Because many soils throughout all ecological zones remain unexplored and changes in plant type often help to define these zones, environmental analyses will likely reveal a far higher microbial species level diversity than their morphological diversity suggests (Bass and Richards, 2011).

Aquatic Fungi

Fungi are present in most fresh and marine water bodies where they play crucial roles in nutrient and carbon cycling. Aquatic fungal are typically microscopic and their diversity varies depending on the water layer. Some 3,000 species of aquatic fungi are known, about one-sixth of which live in marine waters. Given that 96.5% of our planet's water is oceanic, the species richness of marine fungi is likely to be huge, making this group another major source of missing species. Other aquatic fungi are fragments of terrestrial fungi that find their way into streams, lakes, and oceans. These fragments can stay suspended in water or settle into bottom sediments where they can be easily collected and identified via environmental sequencing (Wurzbacher et al., 2010). No doubt, terrestrial novel species not found on land will be discovered in various types of aquatic environments in the future.

Existing Reference Collections

For several hundred years, fungi have been collected and deposited in reference collections (fungaria) and used to support research, especially in taxonomy. Most reference collections, whether they are dried sporocarps or living cultures, include fungi that are named only to the genus or orphaned, i.e., not named at all. Many of these fungaria specimens have yet to be studied using modern standards. Hawksworth has suggested that as many as 20,000 fungaria specimens are misidentified, a situation he attributes to the dwindling numbers of mycologists and increasing demands created by ever expanding collections and sequencing. With sequenced species being added faster than they are named, the number of orphaned fungi cited are likely conservative (Meyer et al., 2016; Andrew et al., 2018).

Extreme Habitats

While fungi are better known in forested and grassland regions of the world, other unlikely locations are emerging as unexplored sources of undiscovered extremophilic fungi. These locations include hot and cold desert soils and rocks (Blackwell, 2011), deep biosphere environments along crustal fault lines (Sohlberg et al., 2015), deep oceanic crusts and sediments (Ivarsson et al., 2016), hydrothermal vents, and permafrost (Taylor and Sinsabaugh, 2015). Depending on the location, the fungi found in these habitats likely include many previously unknown species of yeasts, thermophiles, lichens, and maybe fungal forms we have not yet found or envisioned (Taylor and Sinsabaugh, 2015).

Many soils are full of fungal mycelia, like *Agaricus bisporus* seen here.

Conclusions

By the end of 2020, the total number of described fungi stood at around 148,000 species (Cheek et al., 2020), less than 10% of what is estimated to exist based on Hawksworth's conservative 2017 estimate. This means that fungi now rank third among eukaryotes in terms of known species richness (Wu, 2019). At the current average rate of ~2,000 new species named annually, it will take at least 2,100 years, (the 41st century) to describe Hawksworth's high estimate of 3.8 million fungi. It is estimated that within a hundred years, half of the known species that exist on earth today will be extinct. If we want to identify the hidden species that might provide cures to today's health issues and environmental problems, we must quicken the pace of finding new species. Just as mycologists have learned that estimating fungal diversity requires a global approach, finding all the missing novel mycota will require a global effort by bio-scientists and citizen scientists alike.

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