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Review article

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The biodiversity, genomics, ecology and evolution of mushroom-forming fungi

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Abstract

The class Agaricomycetes represents the mushroom-forming fungi; it is a diverse group within the Basidiomycota with an evolutionary history spanning over 350 million years. Interest in Agaricomycetes has grown considerably over the past decades because of their important roles in nature, their developmental biology, and their use in green technologies and medicine. In this Review, we discuss how genomics approaches have contributed to important breakthroughs in understanding their ecology, evolution, development and conservation. We also explore the central challenges constraining further research. We postulate that the surge in omics exploration of Agaricomycetes over the past decade will be followed by a postgenomic era combining experimental, reverse genetics, ecological and functional genomics tools, helping to resolve the recalcitrant questions surrounding the complex biology of these fungi.

Sections

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Key points

- The class Agaricomycetes is a taxonomically and functionally diverse group of fungi with >350 million years of evolutionary history.
- They are among the most important recyclers of dead plant biomass and are mutualistic partners of woody plants.
- A robust phylogenetic framework allows reconstruction of ancestral morphologies and lifestyles with high confidence.
- Agaricomycete genomics has advanced tremendously in the past decade. Further progress will require a shift to postgenomic and functional approaches.

Introduction

The class Agaricomycetes is a diverse class of fungi within the Basidiomycota, encompassing mushrooms, bracket fungi, puffballs and other fruiting body-forming species. Agaricomycetes are found on all continents, including Antarctica, in habitats ranging from tropical rainforests to arctic and alpine ecosystems. They have important ecological roles as decayers, mycorrhizal symbionts and parasites of plants and fungi. Some have formed symbioses with insects; for example, with leaf-cutter ants. Only a few Agaricomycetes are animal pathogens. The Agaricomycetes' evolutionary history spans over 350 million years with about 40,000 described species, comparable in evolutionary age to tetrapods or seed plants (spermatophytes) (Fig. 1). The class displays a remarkable diversification in morphology, ecology and metabolic capabilities[1].

With rare exceptions (such as yeast forms cultivated by leaf-cutter ants), all Agaricomycetes produce fruiting bodies (Fig. 1), the macroscopic sexual reproductive structures of fungi[2]. Fruiting bodies, also known as sporocarps or basidiomes, aid sexual reproduction by embedding basidia and spore production within a protected environment and increasing the spore-to-biomass ratio via a large spore-producing surface of gills, pores or other structures. The diversity of fruiting bodies is sorted into morphotypes, a simplistic categorization useful for comparative analyses and discussions, but it often oversimplifies diversity. The most familiar types are agarics, which typically have a cap, stalk and gills, such as the iconic fly agaric *Amanita muscaria*, the cultivated button mushroom *Agaricus bisporus* or the psychedelic *Psilocybe cubensis*. Roughly 70% of Agaricomycetes are agarics; other types include boletes, polypores, crust and coral fungi, puffballs and cyphelloid fungi (Fig. 1). Not all fruiting bodies are produced by Agaricomycetes, indicating multiple independent origins of complex multicellular forms[3].

Agaricomycetes manifest diverse adaptations to life on, under and above ground, including the challenge of spore dispersal. Most mushrooms forcibly discharge spores into the air from the surfaces of their gills, pores, teeth and other structures[4]. Others, the so-called gasteroid forms, produce spores internally and release them through a variety of ingenious mechanisms including splash cups and puffballs, harnessing the force of raindrops to eject spores[5] (Fig. 1). Some Agaricomycetes exploit animals: flower-like stinkhorns attract insect agents of dispersal with visual and olfactory cues, whereas basidiomycetous false truffles produce volatile compounds to attract the animals that eat them and disperse spores.

Advances in omics technologies have revolutionized research with Agaricomycetes, including genomics (for understanding genetic diversity and resolving evolutionary relationships), transcriptomics (insight to mechanisms of growth, development and infection) and metabolomics (elucidating the diversity of small molecules the Agaricomycetes deploy in their interactions with other organisms). Popular interest in Agaricomycetes has also surged in the past decade, driven by potential applications in industry. Agaricomycetes have been implicated as useful tools in developing green technologies, including in biofuel production, biopulping, biomaterials and mycoremediation[6], to varying degrees of commercial success[7]. Mycelia of some species are used to make meat substitutes, leather substitutes and packing materials. Psychedelic mushrooms are one group among a diverse array of medicinal mushrooms in the class, and they show promise for treating depression and substance use disorders. Research progress of the past decade, combined with renewed interest in Agaricomycetes, necessitates a synthesis and outlook on current knowledge regarding the class.

In this Review, we introduce the diversity of mushroom-forming fungi and provide an overview of current trends and major challenges in the research with this unique group. We cover the diversity, ecology, evolutionary history and genomics of Agaricomycetes, focusing on key recent discoveries and remaining knowledge gaps. We describe the main lifestyles of agaricomycetes and their genomic underpinnings, evolutionary transitions between lifestyles and morphologies, genomic correlates of traits of interest as well as breakthroughs in understanding the history of diversification in the class. Finally, we explore remaining open questions and challenges for future of the field.

Ecological diversity of Agaricomycetes

Agaricomycetes provide a wide range of ecological services associated with their feeding strategies, from breaking down organic matter and forming mutually beneficial relationships with plants to living as commensal endophytes, lichens, parasites or even carnivores (Fig. 2). Their feeding strategies are often classified according to how they obtain nutrients (Fig. 2) and described as lifestyles, a loosely defined but practical term best viewed as an ecological niche. Databases such as fungaltraits[8] help to coarsely categorize species into groups, but within each category, there exists a large diversity and, possibly, a continuum of strategies[9]. A major trend in eco-genomic research on Agaricomycetes is the continuous refinement of the definition of lifestyles and the use of gene content to recognize subgroups. In this section, we explore some key Agaricomycetes lifestyles and their importance to ecosystems, and we explain how comparative genomics sheds light on their evolution.

Saprotrophic wood rotters and litter decomposers

Terrestrial ecosystems hold an enormous amount of organic carbon in plant tissues and soil, with forests alone estimated to harbour 861 ± 66 Pg of carbon[10]. Agaricomycetes are the primary decomposers of lignin and thus greatly influence the fate of that carbon.

Saprotrophic Agaricomycetes are broadly categorized into wood decayers and litter decomposers. Wood-decayer Agaricomycetes are further classified into white rot and brown rot based on the chemical and anatomical characteristics of the decayed wood. White-rot fungi depolymerize all wood components and are the only microorganism able to fully mineralize lignin[11]. White-rot fungi are estimated to have evolved in the Carboniferous (359–299 million years ago (Ma)), and one hypothesis suggests they contributed to the slowdown of organic

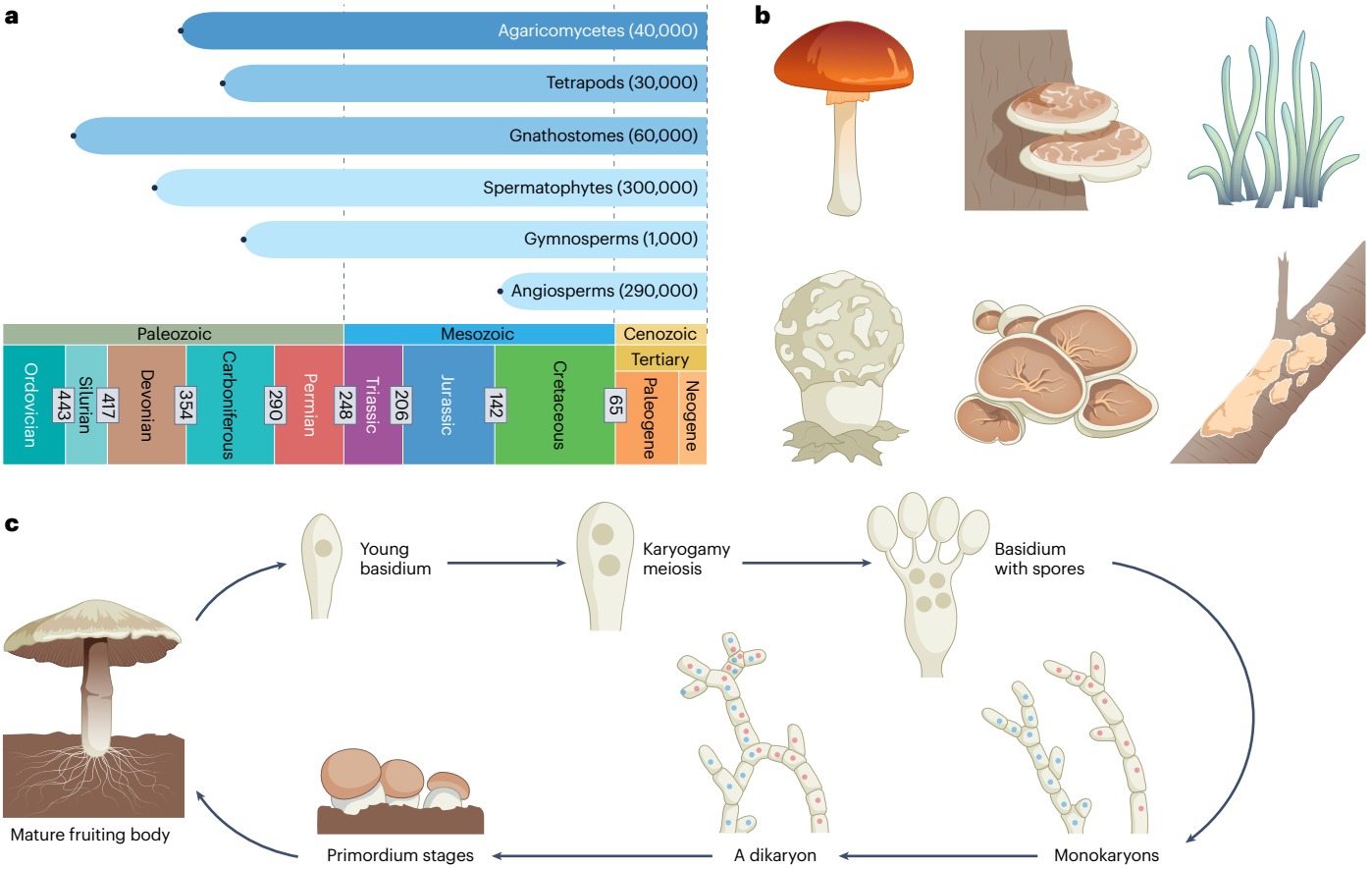


Fig. 1 | The evolutionary age and morphologies of Agaricomycetes. **a**, The evolutionary age (in millions of years) of Agaricomycetes based on molecular clock data, in comparison to well-known animal and plant lineages. The numbers in brackets indicate the estimated number of species in each group. **b**, Representative fruiting body morphologies of Agaricomycetes. Top (from left to right): the agaricoid morphology, bracket fungi and coralloid fungi. Bottom: gasteroid, cyphelloid and resupinate (crust-like) fungi. **c**, The typical life cycle of a mushroom-forming fungus. The data in part **a** are from refs. 95,204,205.

carbon burial at the end of the Carboniferous period[12,13]. Today, several wood-decay Agaricomycetes, especially in the timber decaying brown-rot fungi (such as *Serpula lacrymans*), cause economic damage.

White-rot fungi possess hydrolytic and oxidative carbohydrate-active enzymes (CAZymes) acting on various wood components[11] (Fig. 2). By contrast, all sequenced brown-rot fungi so far[12,14–16] lack most of the enzymes involved in crystalline cellulose and lignin decomposition and so leave behind partly oxidized lignin residues[17]. Brown-rot fungi instead decompose cellulose through a Fenton reaction, via small secreted quinones, which reduce iron and can also contribute to hydrogen peroxide production[18–20], forming hydroxyl radicals to oxidize carbohydrates. Many mechanistic aspects of brown rot remain unclear, however[21,22]. The nitrogen economy of wood decay has also received considerable attention. Wood is a strongly nitrogen-limited environment, in which wood-decay fungi thrive via unknown adaptations to access nitrogen. Some Agaricomycetes, such as oyster mushrooms (*Pleurotus* spp), obtain nitrogen by trapping nematodes[23], but for most species, the major sources of nitrogen are unknown.

Although white rot and brown rot have traditionally been considered as the two dominant wood-decay strategies, there are several wood-decaying Agaricomycetes that do not fit into either category. The CAZyme diversity inferred from genomic data indicates that decay strategies vary across a gradient, rather than a dichotomy[24,25]. For example, although ligninolytic enzymes are abundant in typical white-rot species, other saprotrophic fungi possess only a few. Some atypical decayers are thought to have either reverted to an ancestral decay strategy or evolved unique wood-decay mechanisms[15,24,26]. Finally, some unsequenced Agaricomycetes, in particular corticioid fungi[27], have both poorly understood ecology and decay and could offer important insights into the evolution of wood decay.

Litter decomposers represent an ecologically diverse group of fungi found across a wide range of terrestrial environments, including arid habitats, grasslands, forest ecosystems and even tundra regions[28]. Litter decomposers have varying niches within the litter; for example, growing in specific soil layers[29,30]. These fungi possess a remarkably rich repertoire of CAZymes, both in terms of diversity and copy number[25,31], and their CAZyme gene diversity might even surpass that of white-rot fungi.

There is a wide range of Agaricomycetes litter decomposers with interesting natural histories, including tropical spider or horse-hair fungi (Marasmiaceae), which capture falling leaves using a litter-trapping network (of rhizomorphs) dispersed by nest-building birds[32]. A peculiar group of litter decomposer fungi include ant and termite symbionts. These mutually beneficial relationships

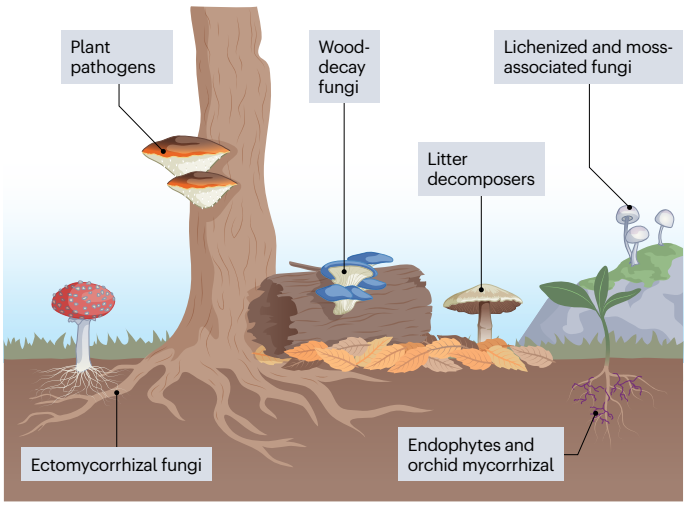


Fig. 2 | The ecological diversity of Agaricomycetes. A representative ecosystem visualizing the various lifestyles of mushroom-forming fungi.

are often viewed as agricultural[33] and the domestication of fungi by the animal partner[34], though these descriptions might reflect an anthropocentrically biased view of coevolution towards a stable mutualism[35,36]. The interactions involve genomic changes in both fungal and insect genomes[37], including the evolution of specialized metabolites[38]. Termite–fungus associations might have originated in African rainforests[36]. The fungal partner might have had morphological and dispersal adaptations predisposing it towards the evolution of mutualism[39].

ECM fungi

Ectomycorrhizal (ECM) fungi colonize the roots of trees and shrubs, driving forest productivity[40] (Fig. 2). Although the first fossils of ECM fungi are approximately 48.7 million years old, the origins of the ECM symbiosis probably occurred much earlier[41], and ECM fungi represent a polyphyletic lifestyle thought to have evolved independently >80× from saprotrophic ancestors[42,43]. Extant species comprise >250 genera and are found across tropical[44,45], temperate and boreal forests[46,47], often dominating in the latter two. The fungi support plant health by increasing nutrient uptake in return for host-supplied carbon[48], although the exchange is not always reciprocal[49,50]. Beyond their hosts, ECM fungi depend on interactions with soil bacteria and other fungi to mine organic nutrients[51,52]. ECM fungi can further benefit plant partners by buffering abiotic and biotic stresses, making them of interest to the horticultural industry[53]. Some ECM fungi mediate metal tolerance in their hosts via metal exclusion, immobilization and detoxification[54–57].

Evolution of the ECM lifestyle is associated with convergent genome changes including the loss or co-option of decay-associated genes[58–61] and the expansion of transposable elements and small secreted proteins (SSPs), although the universality of latter two phenomena has been challenged. Several effector-like secreted proteins are necessary for symbiotic establishment[62–64]. Most sequenced ECM Agaricomycetes lack the GH6 and GH7 CAZyme families, class-II lignin peroxidases and CBM1-binding domains[43,59], potentially explaining the lack of evidence for ECM fungi reverting to free-living saprotrophy[59].

Advances in the sequencing of ECM fungal genome have driven substantial insights into macroevolution[59,65–67] and microevolution[55,68,69], physiology, molecular mechanisms[70,71] and ecology[72]. Ongoing challenges include the ability to link genotypes to phenotypes and decode the functional mechanisms underpinning essential processes such as population dynamics, partner specificity, nutrient trading and non-nutritional partner benefits. Efforts to develop ECM taxa into new models[73–79] systems, such as *Pisolithus* and *Suillus*[80], might help to address these outstanding questions.

The discovery of (ecto)mycorrhizal networks connecting across trees in a forest[81] has led to strong claims of trees communicating and sharing resources with each other, and the possibility of a hidden world of cooperating individuals in a forest community has captured the popular imagination. However, the main claims of the mother tree narrative[82] are not well supported by scientific literature. Claims of common mycorrhizal networks, in which resources are often being moved from one tree to another through fungal individuals and of mature trees preferentially allocating benefits to their own offspring through common mycorrhizal networks, remain largely untested[82]. The benefits provided by a fungus to a plant depend on the species involved in any particular symbiosis, as well as the surrounding environmental context[50,83]. Integrating popular and scientific narratives and building a cohesive model of how ECM symbioses shape forests remains a challenge.

Pathogens and parasites

Plant pathogenic and parasitic Agaricomycetes are relatively rare but form an important guild within the class. These fungi have evolved repeatedly from saprotrophic ancestors, and some species have a substantial ecological and economic impact. For example, *Armillaria* spp. (honey mushrooms) can devastate temperate forests[84], and they form some of the largest clonal organisms on Earth[85]. *Moniliopthora* spp. (sexual form: *Crinipellis*) cause diseases to cacao and jeopardize chocolate production[86], *Heterobasidion annosum* infects conifers, *Laetisaria fuciformis* (pink patch fungus) damages turfgrasses and *Rhizoctonia solani* infects crops, including rice and potato.

Many agaricomycete pathogens infect tree stems or roots (Fig. 2), aided by their extensive CAZyme repertoire[80,87]. Most are white-rot fungi in their saprotrophic phase (for example, *Armillaria*, *Rigidoporus*, *Phellinus* and *Ganoderma*), although some are brown rotters (such as *Phaeolus schweinitzii*). Many species can infect healthy trees, acting as weak parasites or feeding off of dead parts[88]. Such species can be particularly adept at becoming necrotrophic pathogens, eventually killing their host and thus having prime access to dead wood, avoiding microbial competition[87].

The importance of effectors, secreted proteins and horizontally acquired genes in agaricomycete pathogenicity has been highlighted in the past few years[89–93], although key gaps remain in researchers' understanding of host recognition, penetration, immune system manipulation and microbiome interactions. Many of these insights are derived from the non-pathogenic endophyte *Serendipita indica*, one of the best-studied plant-associated agaricomycete fungi[94], and the insights could be relevant to fungal pathogens more generally.

Biodiversity and conservation

The class Agaricomycetes encompasses ~40,720 formally described species distributed unevenly between its orders (Fig. 3a). Agaricomycete species diversity seems to be higher at temperate as compared with tropical regions, defying the ecological pattern known as the latitudinal

diversity gradient[95,96]. New species are being described at a steady rate, with no apparent deceleration, indicating that plenty of undescribed species await discovery or formal taxonomic description. A striking uptick in the description of new taxa is visible in Asia over the past decade (Fig. 3b). To approximate the dimensions of dark fungi – potentially undescribed species known only from DNA sequencing – species hypotheses based on molecular data from UNITE[97] (a database for the molecular identification of eukaryotes) in each order can be compared with the number of formally described species in each order. The greatest disparities in species count were identified in the Thelephorales, Sebacinales and Trechisporales (Fig. 3a) and the lowest disparities in Polyporales, Agaricales and Gloeophyllales. Orders with a large number of potentially undescribed taxa house organisms frequently found in soil; molecular species definitions are predominantly drawn from soil metagenomics studies. In line with the considerable number of potentially undescribed species in Agaricomycetes, metabarcoding databases reveal there may be considerable numbers of dark ECM taxa; these are unevenly distributed across the globe[98].

Further support for the existence of large numbers undescribed species can be found in case studies. The charismatic red-and-white-spotted mushroom *Amanita muscaria* is an example of a fungus perceived as a single species but made up of multiple morphologically similar, cryptic species. It appears to grow on multiple continents, but the name is being used to describe a complex of distinct evolutionary lineages, most of which are restricted within smaller biogeographic ranges[99]. Descriptions of mushroom biodiversity also contend with a complex history of naming. When many fungi in the New World, Southern Hemisphere and Asia were named, European names were given to them, for example, *Amanita phalloides*, to a similar-looking but different *Amanita* species found in Michigan[100]. European names are still used and often, the names are used for species complexes, aggravating the problem of counting species and describing their ranges. Although the data suggest there are many dark taxa in the Agaricomycetes, the number of undescribed species is orders of magnitudes lower than the numbers extrapolated from estimated ratios of 10–50×, described to undescribed taxa given for the whole fungal kingdom[101].

Earth is at the early stages of a sixth mass extinction event[102], but mushrooms are rarely considered as threatened. Nonetheless, mushroom-forming fungi are threatened by competition from invasive species, habitat loss, global warming, extinction and other global change drivers[103]. Fungal fruiting seasons have shifted in time compared with decades ago, and document substantial phenological change. For example, fruiting patterns in fungi from southern England show shifts to both earlier and later dates compared with their history, depending on the species[104], but the mean annual day of fruiting body formation is now later for most species[105]. In addition, invasive species, such as the octopus stinkhorn (*Clathrus archeri*[106]) or the golden oyster (*Pleurotus citrinopileatus*), are probably displacing native species[107]. The golden oyster is a cultivated, edible mushroom and invasive in North America. Trees colonized by golden oyster have been found to have on average half of the native species of any organism compared with trees without the species. The effects of most other invasive agaricomycetes, especially ECM species, are less clear[108], but many species have been moved deliberately by people (for example, to enable plantation forestry), contributing to the establishment of invasive populations[109]. The overharvesting of popular edible and medicinal species may also contribute to population declines, although most studies do not find clear evidence of harm[110].

A total of 1,300 fungi have been assessed for extinction threats so far, and 1,105 of them are Agaricomycetes species[103]. Nearly 40% of these are classified as threatened based on current Red List criteria[103]. However, only 2% of all Agaricomycetes have been included in the assessments completed so far, leaving 98% of the class unassessed. Current data are both geographically and taxonomically biased (Box 1). The most common threats to fungi are commercial and residential development, agriculture and logging, according to an assessment of species currently found on the International Union for Conservation of Nature (ICUN) Red List[103]. Although there is not yet a global

a

Order	Number of described species	Number with DNA-based evidence
Agaricales	25,546	7,205
Thelephorales	498	7,820
Russulales	3,547	3,412
Cantharellales	933	4,331
Polyporales	4,064	283
Boletales	2,473	757
Sebacinales	124	3,045
Hymenochaetales	1,446	865
Auriculariales	378	1,055
Trechisporales	175	1,256
Geastrales	149	890
Gomphales	530	419
Atheliales	111	669
Corticiales	212	216
Amylocorticiales	71	252
Hysterangiales	151	159
Phallales	197	104
Tremellodendropsidales	10	130
Gloeophyllales	58	5
Other	57	143

b

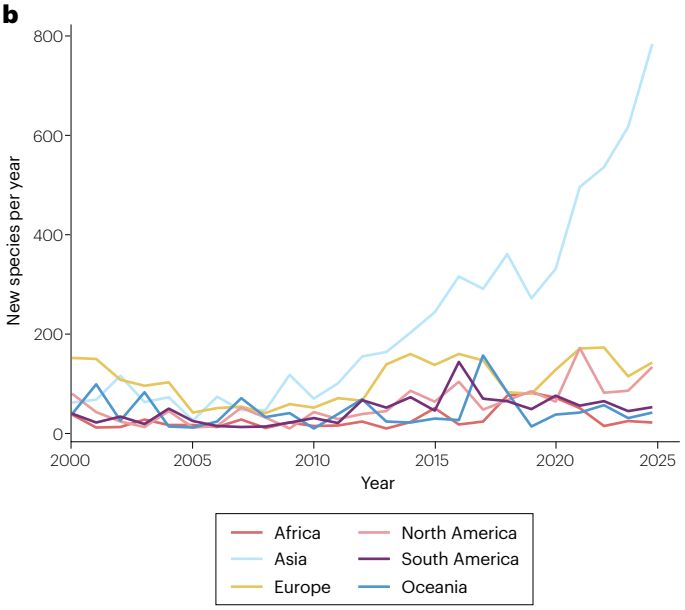
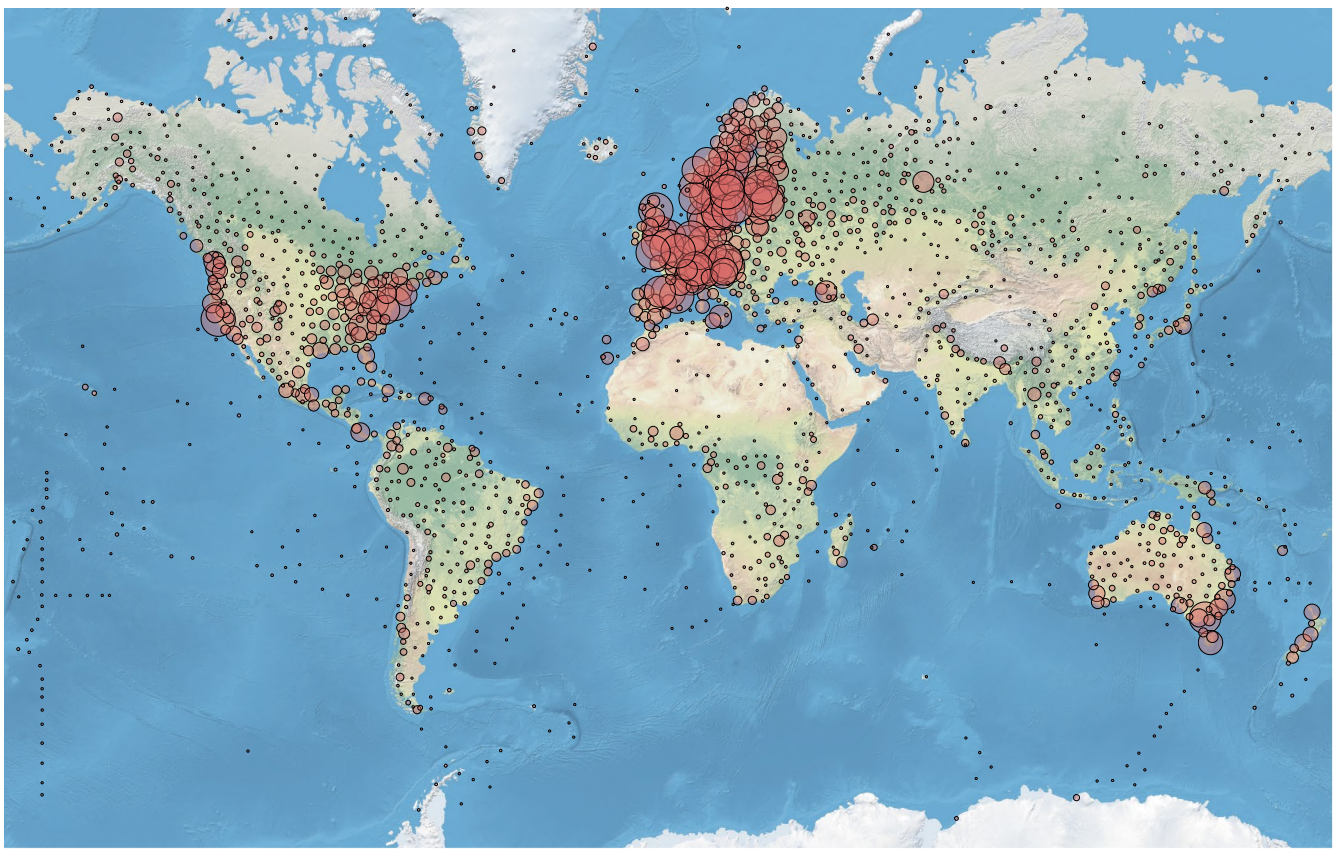


Fig. 3 | Species diversity in Agaricomycetes. a, The estimated numbers of species in the largest nine Agaricomycetes orders, based on formal descriptions[206] or inferred from DNA-based evidence[207]. **b**, The rate of new species descriptions over the past 25 years by geographic region. The data in part **b** are from ref. 208.

Box 1 | Geographic bias

Research efforts are often unevenly distributed across species and geographic regions, commonly biased towards macroscopic, familiar organisms (such as vertebrates) and towards Europe and North America[209,210]. Although many scientists researching fungi now target for global analyses[211], the Global Biodiversity Information Facility (GBIF[212]) indicates that these same geographic biases are present in studies of mushroom-forming fungi. The majority of 17,898,496 records of 34,329 Agaricomycetes species[212] are from Europe and North America (73.6% and 15.8% of records, respectively), whereas all other parts of the world accounted for only 10.5% of the entries (see the figure; the circles indicate georeferenced entries in the GBIF). The distribution of Agaricomycetes observations probably reflects a sampling bias rather than an actual distribution of fungal biodiversity, with over-representation in areas with more mycologists, citizen science initiatives and better infrastructure and funding. In contrast to the low availability of registered records from Asia in GBIF, the number of new agaricomycete species described in MycoBank has increased considerably over the past decade (Fig. 3), suggesting increased interest in agaricomycete taxonomy in Asia not currently represented in western-biased databases such as the GBIF. Agaricomycete biologists should aim to build a more inclusive environment to encourage globally diverse contributions, for example, by holding conferences in currently underrepresented and under resourced regions, including the Global South.



framework for fungal conservation, the 2022 Kunming-Montreal Global Biodiversity Framework identifies 23 targets for global action to conserve biodiversity[111], most of which are relevant to fungi.

Vulnerability in fungi generally receives less attention than threats to animals or plants for at least two reasons. First, there are perhaps more undescribed fungal species than animals and plants[101], and the disproportionate number of undescribed species emphasizes discovery over loss. Second, scientists have assumed most fungi are globally distributed[112], and if a species has a global range, its local extinction would be less concerning than if it has a narrow range. Ideas of global distribution are tied to understanding of fungal dispersal; large numbers of very small spores were assumed to be capable of global dispersal. In situ studies of spore dispersal in nature are rare[113,114], but some patterns can be inferred. For example, *Amanita muscaria* suggests that spore dispersal can be quite limited, as most spores for this species fall within metres of their fruiting body[115].

Phylogenetics and evolution

Agaricomycetes is nested within the Agaricomycotina subphylum of the Basidiomycota. Its close relatives are the Dacrymycetes, which

includes jelly fungi, and the Tremellomycetes, which also includes jelly fungi as well as the human pathogen *Cryptococcus neoformans*. Phylogenetic and phylogenomic analyses have established a robust phylogenetic framework, leaving only a few ambiguous nodes (Box 2). In this section, we explore the evolutionary origins and diversification of Agaricomycetes and the evolution of their morphology and lifestyle, as well as traits crucial to their success.

Reconstructing the last common agaricomycete ancestor

The origin of the Agaricomycetes is estimated to occur in the Devonian–Carboniferous (350–270 Ma[12,43,95]) period, according to molecular clock studies (Fig. 4), at approximately the same time as tetrapods[116] and seed plants emerged on Earth. The diversification of order-level clades is dated to the Jurassic, coinciding with a humid, warming climate and with the radiation of angiosperms[117].

The ages of agaricomycete divergences are probably conservative estimates with considerable uncertainty. Fossil-informed molecular dating of fungi is notoriously difficult because of a scarce fossil record. Very few well-preserved fossils with taxonomically informative characters are known, comprising mostly the fruiting bodies of wood-decaying polypores and other fungi able to survive drying out (such as marasmioid fungi, puffballs). Specimens are often preserved in amber[118]. The oldest evidence for the Agaricales is *Palaeoagaricites antiquus* and four unnamed fossils from the Cretaceous (around 100 Ma[118,119]). Fossil evidence for polypores extends somewhat earlier in the Cretaceous[120]. Although the fossil record can provide minimum age estimates for some groups, it is too limited to provide maximum age constraints, for example, based on the disappearance of clades from the record. Accordingly, molecular clock studies in this class rely on somewhat ad hoc maximum calibrations, rendering upper estimates of agaricomycete ages more uncertain than minima.

The last common ancestor (LCA) of the Agaricomycetes was probably a saprotroph with crust-like fruiting bodies with simple, smooth, spore-producing surfaces, according to molecular phylogenies[24] (see figure 1 of ref. 95). This ancestor might have had either a dry crust-like or gelatinous form resembling jelly fungi[121] (Fig. 4a), though most studies treat these two forms as the same, introducing uncertainty. Over the past ~300 million years, Agaricomycetes has diversified into a wide array of morphotypes and lifestyles, each being evolutionarily dynamic and with frequent examples of transition and homoplasy.

The saprotrophic Agaricomycetes LCA was initially inferred to be a white rotter[122], though the ancestral lifestyle is now considered unresolved[16,123], owing to the occurrence of brown rot in the Dacrymycetes and the uncertain or white or soft-rot-like decay mode of many Cantharellales[16,24] (Fig. 5). Nevertheless, the inferred absence of class-II peroxidases suggest that this ancestor was not degrading lignin and that lignin degradation evolved in the LCA of Auriculariales and residual Agaricomycetes[12,16].

Convergence in morphology and lifestyle

In mushroom-forming fungi, both lifestyle and fruiting body morphology show remarkable evolutionary plasticity. Convergence in both traits transcends phylogenetic scales and cannot be tied to specific geological ages, suggesting the main drivers of these transitions are not global changes in biotic parameters.

One of the greatest challenges in agaricomycete biology is explaining the diversity of fruiting body morphologies. Fruiting bodies evolve to maximize spore numbers[124], spores' efficient dispersal and, ultimately, their fitness, and selection to maximize reproduction is likely to be a key driver of morphological evolution[125]. Several fruiting body traits are adaptations to water regulation and thermoregulation, as well as defence against grazing animals or other physical damages. Spore dispersal is facilitated by ballistospory, a forcible spore discharge mechanism that is the defining synapomorphy of Basidiomycota. On basidia, each spore is balanced at the tip of a structure named the sterigma and is launched by the energy generated via the merger of two liquid droplets (one called Buller's drop, reviewed in ref. 125). The initial acceleration of the spores is the fastest documented so far in nature[126]. The genetics of spore formation is an emerging target of research[127] but is far from being fully understood. Nevertheless, because fruiting body morphologies evolved to optimize spore success, each extant morphology should reflect morphometric fine-tuning to optimally launch the spores of any given species, a process already well documented among ascomycetes[128].

At first glance, mushroom morphologies can appear endless. Closer inspection, however, reveals there are a finite number of solutions produced by evolution (Fig. 4). The ancestral crust-like morphology characterizes the backbone of the agaricomycete phylogeny and morphological diversity evolved independently in order-level clades, often with a trend towards higher complexity[129]. The evolution of morphological complexity is characterized by frequent convergence, with the same morphologies evolving repeatedly in independent clades (reviewed in ref. 130). For example, resupinate, coralloid and pileate-stipitate fruiting bodies are each present in several orders (Fig. 4), even though the ancestors of each of these orders were crust-like. Two studies inferred 462 and 151–204 transitions among five fruiting body morphologies[123] and three hymenophore (spore-producing tissue) types[131], respectively (Fig. 4). Enclosed development, a trait provides protection to vulnerable developing

Box 2 | Phylogeny of Agaricomycetes and resolving challenging relationships

Resolving the phylogenetic relationships of the Agaricomycetes has been instrumental to addressing key evolutionary questions. Early single-gene and multigene phylogenetic studies[213] have subsequently been replaced by genome-scale analyses[12,16,95], leading to a well-resolved phylogenetic framework of the class, with a total of 22 recognized orders, including the Xenasmatellales established in the year 2023 (ref. 214). Researchers recognize two subclasses, the Agaricomycetidae and Phallomycetidae, and an unnamed clade comprising the Polyporales, Russulales, Jaapiales, Gleophyllales, Corticiales and Thelephorales[16,59] (see figure 1 of ref. 95) (Fig. 4). In some studies, the order Russulales branches outside of the latter grouping. The Cantharellales has been resolved as the earliest branching order[12,16,43]. Coral fungi related to *Tremellodendropsis* have been grouped in their own order[215], although genome-scale data have yet to confirm this placement. The taxonomy of the class is in more flux[216] than phylogenetic relationships are, especially in certain groups, such as in white-spored Agaricales where ten new families and a new suborder were recognized in the year 2024 (ref. 217). Among the corticioid fungi, dozens of new genera and families have been described in the past few years, and more await taxonomic definition. Dedicated databases, such as Index Fungorum[218] and MycoBank, facilitate the implementation and tracking of the changing taxonomy of the class.

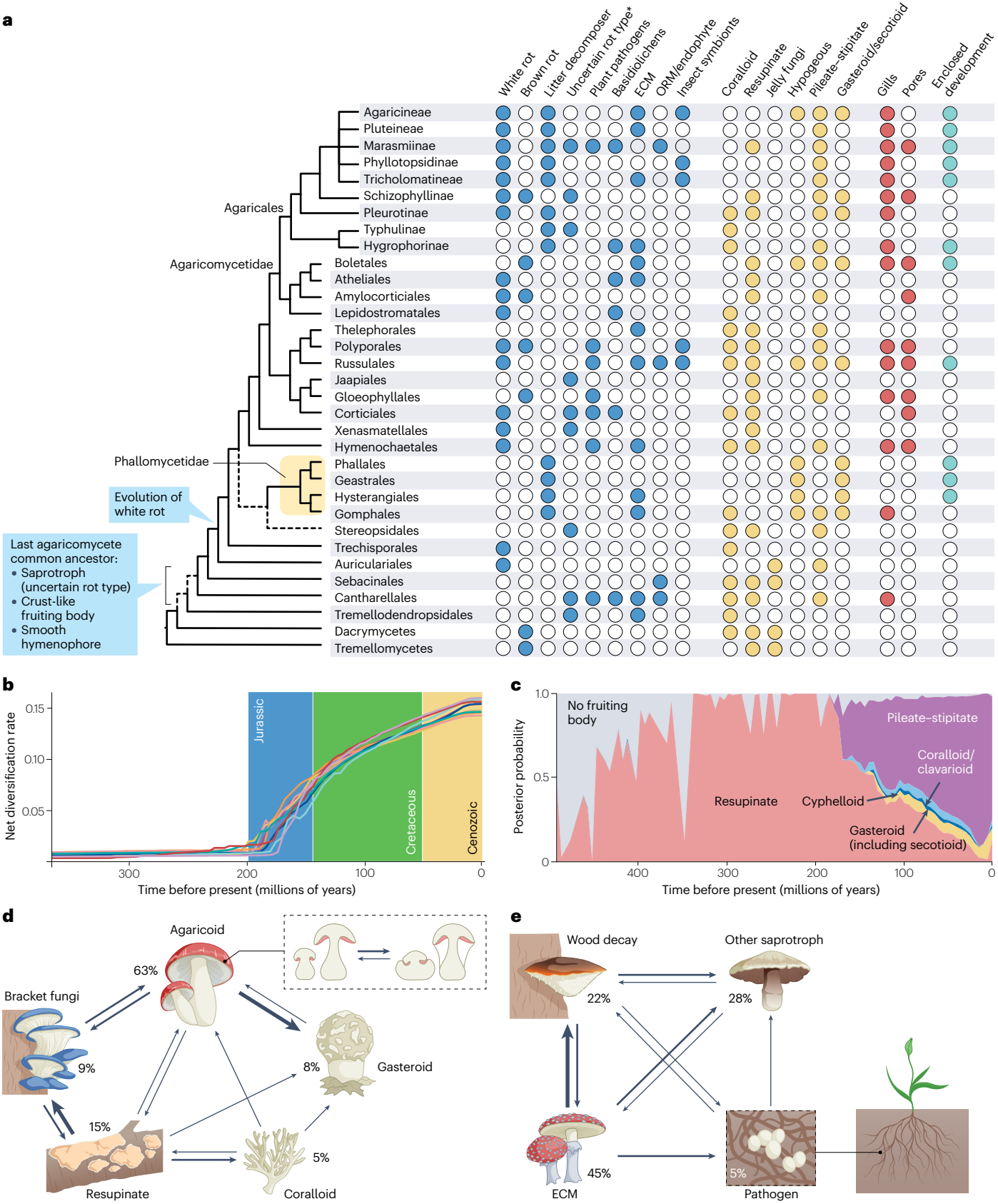

a
White rot
Brown rot
Litter decomposer
Uncertain rot type*
Plant pathogens
Basidiolichens
ECM
ORM/endophyte
Insect symbionts
Coralloid
Resupinate
Jelly fungi
Hypogeous
Pileate–stipitate
Gasteroid/secotioid
Gills
Pores
Enclosed development
Agaricineae
Pluteineae
Marasmiinae
Phyllotopsidinae
Tricholomatineae
Schizophyllinae
Pleurotinae
Typhulinae
Hygrophorinae
Agaricales
Agaricomycetidae
Boletales
Atheliales
Amylocorticiales
Lepidostromatales
Thelephorales
Polyporales
Russulales
Jaapiales
Gloeophyllales
Corticiales
Xenasmatellales
Hymenochaetales
Phallomycetidae
Phallales
Geastrales
Hysterangiales
Gomphales
Stereopsidales
Trechisporales
Auriculariales
Sebacinales
Cantharellales
Tremellodendropsidales
Dacrymycetes
Tremellomycetes
Evolution of white rot
Last agaricomycete common ancestor:
• Saprotroph (uncertain rot type)
• Crust-like fruiting body
• Smooth hymenophore
b
Net diversification rate
0.15
0.10
0.05
Jurassic
Cretaceous
Cenozoic
300
200
100
0
Time before present (millions of years)
c
Posterior probability
1.0
0.5
0
No fruiting body
Pileate–stipitate
Coralloid/ clavarioid
Resupinate
Cyphelloid
Gasteroid (including secotioid)
400
300
200
100
0
Time before present (millions of years)
d
Agaricoid
63%
Bracket fungi
9%
8%
Gasteroid
15%
5%
Resupinate
Coralloid
e
Wood decay
22%
Other saprotroph
28%
45%
ECM
5%
Pathogen

Fig. 4 | The evolution of Agaricomycetes. a, An order-resolved phylogenetic tree of Agaricomycetes. The dot matrix illustrates presence (filled) or absence (empty) of key traits and their evolutionary convergence. The dotted lines represent uncertain branches in the phylogeny. Uncertain rot type includes only literature-reported cases. **b**, The net diversification rate (defined as speciation minus extinction) for Agaricomycetes through time. Species diversification accelerated in the Jurassic. The lines of different colour refer to ten distinct phylogenetic trees analysed in ref. 95. **c**, Propensity of fruiting body morphologies in ancestors of the class through time, inferred from phylogenetic reconstructions of ancestral forms. Resupinate morphologies were dominant until the emergence of the agaric (pileate-stipitate) forms after the Jurassic. **d**, A summary of evolutionary transitions between fruiting body morphologies. Enclosed development is shown above the agaricoid morphology. **e**, A summary of evolutionary transitions between the main agaricomycete lifestyles. The arrow thickness in parts **d** and **e** reflects the frequency of the transitions. The percentages in parts **d** and **e** reflect genome-sequenced species proportions and are not representative of species diversity. The data in parts **b** and **c** are from ref. 95. Part **e** is based on data from ref. 59. ECM, ectomycorrhizal; ORM; orchid mycorrhizal. Parts **b** and **c** are adapted from ref. 95, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part **d** adapted from with permission from ref. 131, Elsevier.

structures by producing specialized tissues (veils), in a way that is functionally analogous to viviparity in metazoans, has independently evolved at least 49 times[131].

Explaining how and why similar morphotypes have evolved dozens of times is a challenge. One hypothesis posits that some morphologies are stable attractors in morphospace[95,129] (for example, pileate-stipitate), whereas other morphologies might be developmentally inevitable stepping stones towards these attractors[130,132]. For example, coralloid morphologies are concentrated in some branches of the phylogenetic tree, the same branches where transitions from resupinate to pileate-stipitate occurred, suggesting the coralloid morphology might be a transitional state. Puffball-like (gasteroid) fruiting bodies might have evolved through secotioid or sequestrate intermediates, which resemble an agaric with a closed cap. Some evolutionary adaptations are geared towards specific ecologies. For example, the continuum from gasteroid fruiting bodies to false truffles might have resulted from adaptation to dry environments[130,133], whereas rapidly growing coprinoid fungi could have adapted to habitats that quickly dry out[134,135]. Morphological simplification has also had a key role in the evolution of fruiting bodies; around 100 reversals from more complex to resupinate[95,123] and cyphelloid[136] forms have been inferred. Fruiting body coloration is quite labile and correlated with exposure to sunlight[137].

Perhaps, in addition to adaptation to surrounding environments, internal factors (such as predisposing mutations), morphometric constraints and mathematical laws also drive morphological evolution. For example, the Turing model (a simple mathematical law)[138] has been hypothesized to be a driver of hymenophoral patterning via interference between local and long-range signalling. It follows that homoplasy could then stem from the simplicity of the underlying laws, although this idea remains to be tested experimentally.

Most ancestors along the backbone of the agaricomycete phylogeny were probably white-rot fungi (Fig. 4), suggesting white rot has served as the basis for the evolution of lifestyles. White rot has evolved into diverse, often highly specialized nutritional strategies, including brown rot, ectomycorrhizae, insect symbiotic saprobes and plant pathogens and litter decomposers, among others. The best understood transitions are from white rot to brown rot and to ECM mutualisms, which are conservatively estimated to have evolved at least 7 and 36 times, respectively[12,16,31,123]. ECM fungi also evolved from brown-rot ancestors, such as in the Boletales. Transitions from litter decomposers to white rot might have also occurred in the Pleurotaceae[139]. Several groups, such as *Armillaria* or the Schizophyllaceae, have a modified white-rot strategy, in that they degrade lignin differently or to a different extent[15,26,89].

Symbioses with termites and ants evolved independently across four species groups: Atheliaceae (*Fibularhizoctonia* spp) and Lyophyllaceae (*Termitomyces* spp) are symbiotic with termites and Pterulaceae (*Pterula* spp.) and Agaricaceae (*Leucoagaricus* spp.) with leaf-cutter ants.

The evolution of lifestyles shows more directionality than the evolution of fruiting body morphologies. Brown-rot and ECM symbioses seem to be evolutionarily stable states with no reversals to white rot[123], probably because irreversible losses of lignocellulose-degrading enzyme genes preclude the re-evolution of lignin degradation. The evolution of ECM from saprotrophy more generally has been hypothesized to be irreversible[140–142], but a reversal to brown rot in the Boletales cannot be excluded[43,140].

Diversification history, drivers of speciation

The diversification of the Agaricomycetes LCA into >40,000 extant species can be inferred using evolutionary models and time-calibrated trees. Diversification, or species birth minus species extinction, accelerated during the Jurassic period (Fig. 4), marking a turning point in the evolution of the class[1,95,123,143]. This diversification rate increase coincided with the breakup of Pangaea, a warming climate and the radiation of gymnosperms and angiosperms[95]. However, the class-wide pattern is the product of lineage-specific effects, which can include rapid radiation (bursts of speciation) and extinction events. In total, 85 such events have been inferred, with more than half of these occurring in species with a cap. One example of a rapid radiation is in dung-inhabiting *Coprinellus* species[134], which perhaps occurred in response to grassland expansion or the evolution of specialized hair-like cells (cystida) that protect against grazing insects[144].

Even though inferring extinction is challenging, there is evidence for a mass extinction in the late Jurassic[95]. Interestingly, there is no evidence for the Cretaceous–Palaeogene (K–Pg, 66 Ma) mass extinction event that affected most animals and plants[145]. This result is also supported by micro-fossil records[146], suggesting the Agaricomycetes might have, interestingly, evaded this cataclysm.

Some agaricomycete radiations might be linked to key innovations, traits that spur rapid radiations by opening new adaptive zones[147]. For example, lineages with a cap, with complex spore bearing tissue or with enclosed development show a higher diversification rate compared with other lineages[131]. The ECM lifestyle and gasteroid fruiting body morphology have also been hypothesized to be key innovations[148]. Although class-wide and some taxon-specific studies do not provide support for either hypothesis[123,149,150], some taxon-specific studies report faster diversification in ECM clades and in gasteroids, suggesting these traits might have facilitated rapid species birth in certain lineages[148,151,152].

The evolutionary history of clades can be a result of complex interactions at multiple scales. Complexity is exemplified by the evolution of the Amanitaceae family. A global diversification rate shift in the

a

Lifestyle	Sequenced genomes
White rot	185
ECM	168
Litter decomposer	81
Brown rot	38
Endophyte	28
Unknown rot	26
Pathogen	19
Orchid mycorrhizal	11
Insect symbiont	8
Lichenized	0

b

Order	Sequenced genomes
Agaricales	205
Polyporales	94
Boletales	92
Russulales	43
Cantharellales	24
Hymenochaet.	18
Amylocorticiales	8
Sebacinales	7
Gloeophyllales	5
Atheliales	4
Auriculariales	4
Corticiales	4
Geastrales	3
Gomphales	3
Trechisporales	3
Xenasmatellales	3
Thelephorales	2
Hysterangiales	1
Jaapiales	1
Phallales	1
Tremellodendr.	0
Lepidostromatales	0

c

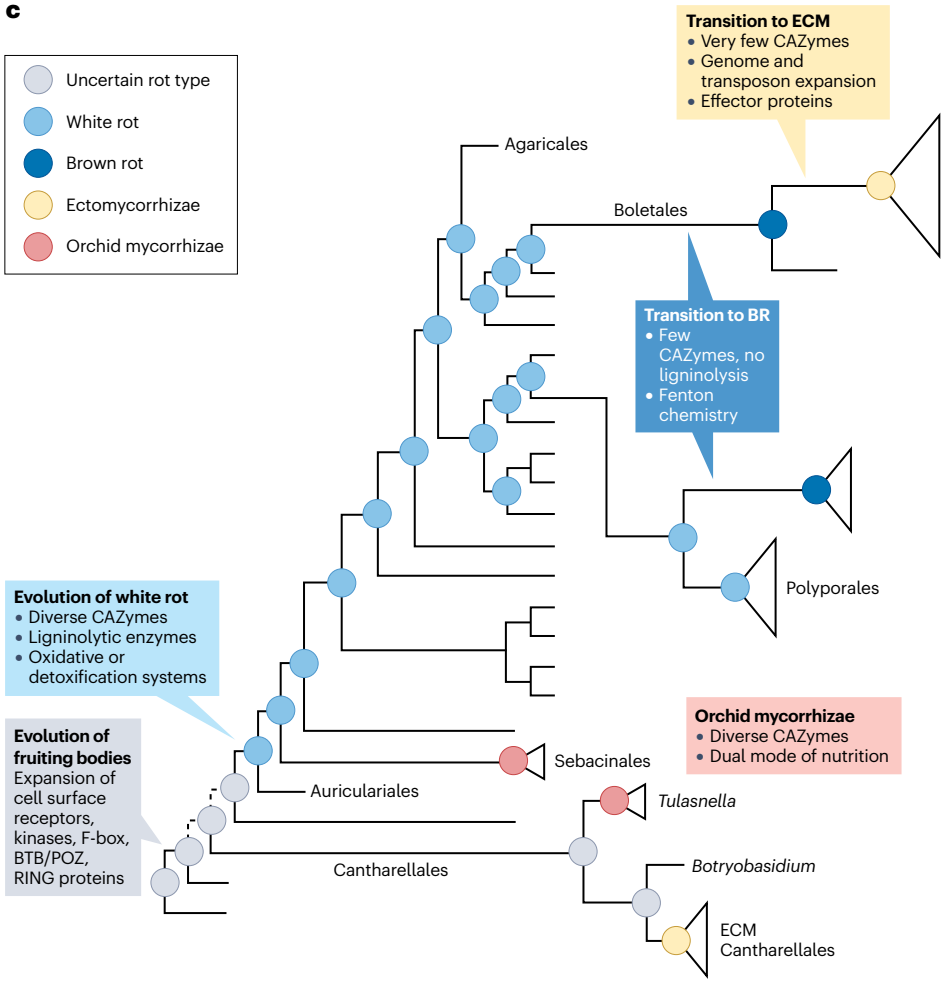


Fig. 5 | Key traits and associated genomic trends in the Agaricomycetes. **a**, The distribution of sequenced agaricomycete genomes of by lifestyle (as of March 2025). **b**, The distribution of sequenced genomes of Agaricomycetes by taxonomy (as of March 2025). **c**, Simplified phylogeny of the Agaricomycetes depicting the emergence of complex fruiting bodies, white rot and illustrative examples of transitions to brown rot (BR), ectomycorrhizal (ECM) and orchid mycorrhizal lifestyles. Note that this figure highlights a limited sample out of the many origins of brown rot and ectomycorrhizae. CAZymes, carbohydrate-active enzymes.

Amanita genus coincided with the evolution of an ECM lifestyle[95,145]. However, rate shifts in five subgenera could have been driven by multiple factors, including radiation to temperate niches[153,154] and speciation in refugia and during glacial oscillations[155,156].

The evolution of Agaricomycetes has been dynamic and episodic; the class has not experienced a steady and constant increase of species diversity. Future challenges include testing the robustness of published results by accounting for confounding factors of diversification analyses (such as taxon sampling) and better understanding of the drivers and types of radiation (adaptive versus non-adaptive).

Agaricomycete genome evolution

Genomics has transformed scientists' understanding of agaricomycete evolution and lifestyle transitions, and has supported research into various life history traits of Agaricomycetes. Over the past two decades, extensive genomic research has contributed to a thorough understanding of genome evolution and dense genomic sampling within the class (Fig. 5a,b). Early efforts to produce a taxonomically diversified sampling have now been complemented by lineage-specific genome projects at a fine resolution (as in Polyporales[157], Hymenochaetales[158], Boletales[65] and Russulales[159]). For example, *Mycena* spp. (bonnet mushrooms) genomes evidence a massive and unspecific genome expansion in which hundreds of novel gene families emerged, with some genes potentially acquired from ascomycetes by horizontal gene transfer[160] (HGT; the horizontal transmission of genomic DNA between species). Yet, genome sequencing remains biased towards certain lineages, and more work is needed to fill in taxonomic gaps (Fig. 5a,b). Sequencing species collected from ongoing field excursions and museum collections should efficiently complement culture-based approaches for the species that are difficult to culture in the laboratory[161,162].

Agaricomycetes display diverse macroevolutionary trends in genome evolution. For example, the evolution of multiple mating types can be observed in the Basidiomycota, which has reached its most sophisticated manifestations in mushroom-forming fungi (reviewed

in refs. 163,164). Agaricomycetes possess multiallelic mating loci which promote outcrossing, with estimates that *Schizophyllum commune* and *Trichaptum abietinum* have ~30,000 and 17,550 compatibility groups (similar to reproductive sexes), respectively, resulting in >98% outcrossing efficiency[165,166]. Convergent transitions in lifestyle and gene duplications and losses are another well-established evolutionary trend in the class. Lignocellulose-degrading CAZymes expanded in white-rot fungi but were lost in brown-rot and ECM fungi, probably by DNA decay via point mutations[65] (Fig. 5; reviewed in ref. 11). ECM fungi have more repetitive DNA in their genomes (transposons) than saprotrophs[43,59,167]. Whether this repetitive DNA is adaptive (for example, enabling the fast evolution of symbiotic genes), a result of relaxed selection and drift or is causally uncoupled from lifestyle (for example, by increased transposon activity in monokaryons[168]) remains to be established. SSPs, such as symbiosis-related effectors, are also suggested to be more diverse in ECM fungi[167], though genome-size normalized measures SSP content[58] challenge this assumption. Nevertheless, experimental evidence supports the role of specific SSPs in mycorrhizae[169], ligninolysis[170] and pathogenesis[89].

An important innovation in Agaricomycetes was the emergence of complex fruiting bodies — complex multicellular structures in which cell–cell adhesion, communication and gene expression regulation have key roles[171] (Fig. 5c). In contrast to lifestyle evolution, obvious expansions of functionally linked gene families have remained elusive so far. An expansion of classical G-protein-coupled receptors, fungal-specific kinase families and selective protein ubiquitylation systems (for example, F-box proteins) has been noted in Agaricomycetes[3,172], but in contrast to complex multicellular animals and plants, no expansion in transcription factor families was inferred. Uncovering the mechanisms of fruiting body development has been a longstanding target for Agaricomycetes researchers. Some transcriptomic signatures in fruiting bodies are conserved across species, such as the regulation of genes encoding proteins involved in cell wall remodelling, defence against insects and bacteria, certain cell-surface protein and SSP families or the meiotic apparatus in gills (reviewed in ref. 173). Despite some advances, information on the fundamental principles of pattern formation and tissue differentiation in fruiting bodies remains scarce compared with that of developmental processes in model plant or animal species.

Several exciting mechanisms of genomic novelty in Agaricomycetes have been uncovered in the last few years. An unusually low mutation rate in Agaricomycetes has been postulated, compared with other multicellular organisms. This low mutation rate was first identified in long-lived *Armillaria*[174] and ascribed to their unique biology. However, low mutation rates have also been identified in *Marasmius oreades* (the fairy ring mushroom[175]), a species with a very different life history. The mechanisms[176] underlying these unusual mutation rates remain elusive, although some data point to the existence of populations of cells that behave similar to germline[177]. HGT has been identified as an alternative source of genetic novelty in the class, with intriguing cases of HGT affecting pathogenicity[89], genome expansion in *Mycena*[160] and natural product repertoires[178]. For example, the psilocybin gene cluster has been subject to multiple HGTs in hallucinogenic *Psilocybe* spp. (magic mushrooms)[179]. The evolution of the bioluminescence gene cluster in *Mycena* spp. presents a perplexing scenario, with one potential explanation being HGT across lineages of Agaricomycetes[180]. However, among fungi more broadly, the Agaricomycetes might be the least prone to HGT[181].

Secondary or specialized metabolites (also termed natural products) are often defined as organismal compounds unrelated to primary growth, development or reproduction. A dizzying array of specialized metabolites are produced by Agaricomycetes, and they seem to be important in ecological interactions[78,182] and toxicity[183]. Specialized metabolites are often exploited by humans, for example, the drug psilocybin is derived from *Psilocybe* species and is emerging as a useful treatment for depression[184], whereas the toxin α-amanitin, found in the lethal clade of the genus *Amanita* and in a few other genera, has long been used to understand the mRNA synthesis[185]. α-Amanitin is often cited as the leading cause of fatal mushroom poisonings, by *A. phalloides* and its relatives. Yet from an ecological perspective, why some Agaricomycetes are poisonous to humans is unknown. Strobilurins, originally isolated from fruiting bodies of *Strobilurus tenacellus*[186], are the most widely used fungicides in cereal and turf management. Beyond a few well-known examples (reviewed in ref. 187), the vast diversity and the functions of specialized metabolites within mushroom-forming fungi remain to be discovered. Moreover, agaricomycetes appear to follow different paradigms for specialized metabolites synthesis compared with ascomycetes, and the typical genetic architecture of biosynthetic genes in Agaricomycetes more generally is another unknown. In ascomycete fungi, specialized metabolites are typically encoded by genes clustered within a biosynthetic gene cluster[188]. Clustering facilitates coordinated gene expression. Although some mushroom specialized metabolites are arranged as biosynthetic gene clusters, many are not, complicating their discovery. Nevertheless, the biosynthesis of some metabolites, such as psilocybins[179], amatoxins[185] or those underlying bioluminescence[189], are well investigated.

A saprotrophism to symbiosis continuum

Agaricomycetes exhibit a fluid ecological spectrum, ranging from saprotrophic to symbiotic relationships, and from mutualistic to parasitic interactions. This spectrum correlates with evolutionary modifications, including the reduction of saprotrophic traits and development of symbiotic capabilities. Some species, such as the highly prized matsutake or pine mushroom (*Tricholoma matsutake*), possess both saprotrophic and symbiotic abilities, with shifts between these modes depending on environmental factors. Similarly, ecological versatility has been demonstrated in a laboratory model system of root-invading *Mycena* spp. and birch (*Betula*) seedlings[190]. This versatility might provide an evolutionary advantage in many habitats.

The shift from saprotrophy to symbiosis has been a key theme in fungal evolution[123] and has been extensively investigated in Agaricomycetes. ECM fungi have evolved independently multiple times from soil decomposer or wood-decayer ancestors[43] via mechanisms that include the loss of genes encoding plant cell wall degrading enzymes. The shift from saprotrophic to biotrophic lifestyles often occurs incrementally along a spectrum, as shown in Russulales[159] and Boletales[191]. Some ECM lineages retained diverse arrays of degradative enzymes reflecting their varying degradative capabilities and phylogenetic origins. Some ECM fungi (for example, in Boletales and Cortinariaceae) have a limited saprotrophic capacity when disconnected from their host or during periods of host plant inactivity, such as winter[192]. These fungi can use their degradative enzyme repertoire to mobilise nitrogen from organic matter, rather than obtaining carbon[193].

Orchid mycorrhizal (ORM) fungi follow unique evolutionary paths compared to ECM fungi (Fig. 5). Genera such as *Ceratobasidium*, *Tulasnella* and *Sebacina* (Cantharellales and Sebacinales), all of which are ORM fungi, retain a very large repertoire of degradative enzymes to break down organic matter[59]. These genera have a dual mode of

Table 1 | Main and emerging mushroom model organisms and their genomic features

Species name	Lifestyle	Main topics	Reverse genetics	Number of Pubmed records, 2015–2025
Agaricus bisporus	Litter decomposer	Breeding, degradative enzymes	Transformation	791
Agrocybe aegerita	WR	Fruiting body development, degradative enzymes	Transformation	142
Coprinopsis cinerea	Litter decomposer	Fruiting body development	KO (CRISPR)	175
Dichomitus squalens	WR	Emerging model of wood decay, degradative enzymes	KO (CRISPR)	31
Various edible mushrooms	Mixed	Strain breeding, wood decay and fruiting body development	RNA interference/CRISPR	N/A
Ganoderma lucidum/lingzhi	WR	Medicinal properties, degradative enzymes and biocomposites	KO (CRISPR)	1,584
Laccaria bicolor	ECM	Physiology of ECM, plant–fungal interaction	RNA interference	85
Phanerochaete chrysosporium	WR	Bioremediation, plastic degradation and degradative enzymes	Transformation	495
Pleurotus ostreatus	WR	Fruiting body development, degradative enzymes	KO (CRISPR)	1,998
Rhizoctonia solani	Pathogen	Plant pathogenicity	–	1,859
Schizophyllum commune	Uncertain rot type	Fruiting body development and wood decay	KO (CRISPR)	373
Serendipita indica	Endophyte	Plant–fungal interaction	–	139
Suillus spp.	ECM	Physiology of ECM, heavy metal tolerance	–	207
Trametes versicolor	WR	Wood decay, degradative enzymes and bioremediation	–	643

ECM, ectomycorrhizal; KO, knockout; N/A, not applicable; WR, white rot.

nutrition, as they can flourish in many habitats and are efficient decomposers. ORM fungi help orchids to obtain nutrients, including soluble carbohydrates, during their early growth stages. The preservation of decomposition abilities in ORM species indicates transitional stages in the evolution from saprotrophic to mutualistic lifestyles.

Several species that are primarily considered soil and litter decomposers can form mycorrhizal, endophytic or parasitic interactions. For example, bonnet mushroom species (*Mycena* spp.) have been documented in the roots of multiple plant host species in the temperate and Arctic regions[194]. These species possess an extensive repertoire of CAZymes that act on all components of plant and microbial cell walls. No reduction in the CAZyme repertoire has been observed in species capable of colonizing plant roots[160], suggesting that the expression of these degrading enzymes is suppressed during plant ingress.

ECM fungi can also interact with non-mycorrhizal plants[195–198]. Some ECM fungi, such as *Russula* spp., are found in the roots of non-ECM herbaceous plants, creating stable endophytic structures and promoting lateral root growth. These findings underscore the potential overlap between endophytic and ECM fungi, prompting suggestions to broaden the definition of mycorrhizal fungi. Associations, such as those established by *Ceratobasidium* spp. (Cantharellales) often shift along a spectrum from mutualism to parasitism.

Postgenomics of Agaricomycetes

Agaricomycetes research has been one of the first to embrace new genomic techniques, as exemplified by the early publication of the first genome sequences. However, it is becoming increasingly clear that (comparative) genomics has limited explanatory power for many traits of interest. Dynamics have started to change in the past 5 years. Scientists have started developing new model systems and deploying postgenomic/functional genomics tools for Agaricomycetes.

Agaricomycetes model species have not received as much attention as model species in the Ascomycota. The imbalance materializes in a shortage of established protocols for experimental mycology of mushrooms, a dominance of descriptive and omics studies and an underrepresentation of experimental research and lack of knowledge on gene function. Thus, agaricomycete research often uses genomics for analysing gene copy numbers and their correlation with traits of interest. However, many traits require consideration of finer genomic changes, which traditional genomics cannot consider. An exciting development in this regard is the transition from draft genomes to haplotype-resolved telomere-to-telomere assemblies, which will allow scientists to extend agaricomycete biology to phenomena such as *cis*-regulatory changes, allele-specific expression[199,200], alternative polyadenylation[201] or the currently controversial RNA editing[202]. In parallel, efforts to improve existing model systems and to develop new ones have established several new functional genomics or reverse genetics tools (Table 1). Emerging model systems require independent lines of technique development, and these will require coordination and consolidation across laboratories in the future. The field also requires model fungi outside the most frequently researched groups (such as Agaricales), which will facilitate discovery of both common and unique features among different lineages of mushroom-forming fungi.

Studies of Agaricomycetes biology might currently be most strongly limited by a lack of knowledge on gene function. The majority of genes in agaricomycete genomes have no functional descriptions, or those that they do have are vague. This poor functional annotation is because automated annotation approaches, which use homology-based extrapolation from well-studied model systems (such as yeasts) rarely apply well to the most characteristic traits of agaricomycetes, such as fruiting body development, wood decay or ectomycorrhizae. Understanding how Agaricomycetes use their genes under

conditions relevant to ecology, organismal development or applied medical and industrial contexts will require better functional annotations and an agaricomycete-specific vocabulary of gene function based on large-scale studies of model systems.

Summary and future directions

The past two decades have seen breakthroughs in the understanding of several aspects of agaricomycete biology. Scientists now have a good understanding of phylogenetic relationships and a stable order-level taxonomy, although the shortage of fossils means molecular clock studies remain notoriously difficult. The genomic coverage of Agaricomycetes is taxonomically balanced, which has contributed to the discovery of several genomic trends and genetic correlates of lifestyle transitions. The dynamic evolution of morphologies, with extensive convergence and some broad patterns of the tempo and mode of the emergence of extant species diversity, have also been documented in detail, yielding a good understanding of the evolution of morphologies and lifestyles. In many cases, the genetics and specific genes related to the development of fruiting bodies are identified, and a comprehensive understanding of developmental genes is under development[173].

Many of these discoveries have been driven by phylogenetics and genomics research, though these tools for uncovering patterns and generating hypotheses have limited explanatory power in many cases. A major future challenge is transitioning agaricomycete biology from primarily descriptive omics to functional and experimental approaches and introducing hypothesis validation in laboratory-friendly model systems. Some studies can bypass this need, for example, by combining microbiology, multiomics and genomics in the non-model genus *Clitopilus*[203] (Fig. 5) or studying mutation accumulation in naturally occurring fairy rings[175], whereas for most studies, experimental validation is currently a bottleneck. Much work is needed to fully shift agaricomycete biology into the postgenomic era.

Much of the natural history of mushroom-forming fungi remains challenging to understand. Scientists have little information on agaricomycete generation times, population sizes, natural phenologies, life cycles, genome stability[168], longevity and other aspects of basic ecology — knowledge that has long been established for animals and plants. Ecological interactions of agaricomycetes with insects, viruses, bacteria or other fungi matter to both individual species as well as local community and broader ecosystem dynamics; however, data on these interactions are currently limited. More research is needed on many fundamental aspects of autecology. Ecological and functional studies are capable of increasingly more holistic analyses and hold promise for understanding how Agaricomycetes really function in nature. Genome-informed ecology, built on multiomics datasets (including metagenomics and transcriptomics) can help to build knowledge of the natural history of species. Amid the developments of high-throughput techniques, it is probably more important than ever to emphasize how knowledge of the organisms themselves, their life history, morphology and taxonomy, is instrumental to the crafting of ideas and testable hypotheses.

We expect the near future to see a continued surge in interest in Agaricomycetes, and research will uncover the under- and above-ground secrets of these fascinating organisms. Studies will build on classic and established methodologies — to which genomics could now belong — as well as on novel developments to allow an increasingly better understanding of mushroom biology.

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A.P. is vice president of Mushroom Observer, a US non-profit dedicated to cataloguing fungal mushroom biodiversity. All other authors declare no competing interests.

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