



# Current trends, limitations and future research in the fungi?

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## Abstract

The field of mycology has grown from an underappreciated subset of botany, to a valuable, modern scientific discipline. As this field of study has grown, there have been significant contributions to science, technology, and industry, highlighting the value of fungi in the modern era. This paper looks at the current research, along with the existing limitations, and suggests future areas where scientists can focus their efforts, in the field mycology. We show how fungi have become important emerging diseases in medical mycology. We discuss current trends and the potential of fungi in drug and novel compound discovery. We explore the current trends in phylogenomics, its potential, and outcomes and address the question of how phylogenomics can be applied in fungal ecology. In addition, the trends in functional genomics studies of fungi are discussed with their importance in unravelling the intricate mechanisms underlying fungal behaviour, interactions, and adaptations, paving the way for a comprehensive understanding of fungal biology. We look at the current research in building materials, how they can be used as carbon sinks, and how fungi can be used in biocircular economies. The numbers of fungi have always been of great interest and have often been written about and estimates have varied greatly. Thus, we discuss current trends and future research needs in order to obtain more reliable estimates. We address the aspects of machine learning (AI) and how it can be used in mycological research. Plant pathogens are affecting food production systems on a global scale, and as such, we look at the current trends and future research needed in this area, particularly in disease detection. We look at the latest data from High Throughput Sequencing studies and question if we are still gaining new knowledge at the same rate as before. A review of current trends in nanotechnology is provided and its future potential is addressed. The importance of Arbuscular Mycorrhizal Fungi is addressed and future trends are acknowledged. Fungal databases are becoming more and more important, and we therefore provide a review of the current major databases. Edible and medicinal fungi have a huge potential as food and medicines, especially in Asia and their prospects are discussed. Lifestyle changes in fungi (e.g., from endophytes, to pathogens, and/or saprobes) are also extremely important and a current research trend and are therefore addressed in this special issue of Fungal Diversity.

**Keywords** AMF · Biocircular economy · Biocontrol · Data repositories · Drug discovery · Ecology · Emerging diseases · Functional genomics · Fungal classification · HTS · Machine learning · Mycoremediation · Nanotechnology · Novel compounds · Phylogenomics · Plant pathology · Species numbers

## Introduction

Studies on fungi were previously frowned upon. Alison Pouliot (2023) wrote in The Guardian “*Fungi have endured a long history of neglect and disdain. In 1887 the British mycologist William Hay commented that he who studied*

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*fungi “must boldly face a good deal of scorn ... and is actually regarded as a sort of idiot among the lower orders”. A few years earlier the nature writer Margaret Plues observed how the stranger “blinded by conventionalities” sneered at those seeking fungi. Unlike birders who look upwards for their charismatic avian delights, fungus hunters glance downwards, for what the “father of modern taxonomy”, Swedish biologist Carl Linnaeus, referred to as “thievish and voracious beggars”.*” This has certainly changed with studies on fungi now being looked at much more positively, especially with their importance in human, animal and plant disease (Hyde et al. 2018; Mapook et al. 2022; Niego et al. 2023a, b), potential in novel compound discovery (Hyde et al. 2019; Mapook et al. 2022), value in industrial applications (Hyde et al. 2019) and potential in the biocircular economy (Kirchherr et al. 2017; Meyer et al. 2016, 2020).

### The effect of metrics on mycology

An often-overlooked topic is the effect of Metrics on the study of Mycology. We can only speak from our experience, but it would be interesting to see how this affected other mycologists. In the 1990s the Web of Science started to influence university assessments (1996 onwards) and promotions. At the time the highest impact mycology journals, *Mycologia* and *Mycological Research*, had impact factors of 1–2, while some ecological journals had impact factors of 3–4. Therefore, the peer pressure led some of us to turn towards ecological research, so we published several papers at the end of the Century with an ecological slant (e.g., Hyde and Lee 1998; Taylor et al. 1999; Luo et al. 2004; Tao et al. 2008). At the turn of the century, molecular research was becoming important and journals specialising in this topic also had higher impact factors of 3–4. So again, the trend was to do molecular research and publish in these high impact journals (e.g., Liew et al. 2000, 2002; Guo et al. 2001).

During the early 2000s the ecological and molecular trends continued, whereas after 2010 some mycological journals overtook the ecological journals, so ecological studies in mycology became less important. As time progressed, the impact factors of some mainstream mycological journals (*Fungal Diversity*, *Persoonia*, *Studies in Mycology*) increased and these became the desired journals to publish in. The focus of these journals was mainly diversity, taxonomy, and phylogeny and thus these topics became popular. Thus, our research also focused on this area and we published many important papers during this period (e.g., Shearer et al. 2010; Hyde et al. 2013, 2014a, b). More recently it has become important to publish in Quartile 1 journals and *Fungal Biology Reviews*, *Fungal Diversity*, *IMAfungus*, the *Journal of Fungi*, *Mycosphere* and *Studies in Mycology* have become desirable journals. The future

is hard to predict, phylogenomics and functional genomics have become hot topics, however in mycology this is not matched by the high-impact journals where such papers are published, but this may change. At least for the time being biodiversity, taxonomy and phylogenetics will remain important topics as papers can be published in high-impact journals.

The effect of Web of Science metrics on books has been extremely detrimental. During the mid stages of the careers of some of us published more than 20 books. At the time books were needed for promotions. As for now, there is very little kudos from publishing books, as they have no impact factor and scientific books make little profit. This is why very few comprehensive monographs are presently published.

In conclusion, there is no doubt that the Web of Science has had a profound influence on the research and publications in mycology. Whether one considers this a good or bad thing will depend very much on the researcher’s interests.

### The golden era of mycology

We the senior authors of this paper began their careers in the 1980s, the number of mycologists was declining and places such as CBS, IMI, Kew, and British Universities were shedding these specialists at an alarming rate. In this period, it was hugely difficult to obtain funding and as stated above, the impact factor of mycological journals was low. Thus, it was almost impossible for a young Ph.D. to obtain a university position. Fast forward to the present day, the emerging economies of Asia and South America are recruiting large numbers of mycologists. Even The Royal Botanical Gardens, Kew, has realised the importance of mycology and created several new positions for mycologists. It has become much easier to obtain funding and the impact factors of some mycology journals are some of the highest in specialised science. Thus, it is the golden era of mycology and this should last for some time to come because of the applied potential of the fungi (Hyde et al. 2019).

Below we provide notes on 15 important research trends and discuss their current research, limitations, and future expectations. We use these trends to indicate the expected research in mycology in the future.

### Current trends, limitations, and future research in emerging diseases and their control

As an applied area of research that is directly linked to human health, medical mycology is probably one of the most rapidly evolving subdisciplines. Fundamental changes are taking place in all aspects: in the fungi and their evolution,

in the hosts and their immunity, in the environmental conditions of human lifestyles, and at a global scale in climate and sustainability.

From a fungal perspective, hosts have become available with dramatically altered susceptibility to infection due to immunological alterations, constitutional diseases, or as a side effect of medical intervention. The second half of the twentieth century is marked by the emergence of patient populations that were immunocompromised in view of the treatment of life-threatening or chronic inflammatory and systemic diseases, while also organ transplants became standard therapy. In the USA, an estimated 2.7% of the population may have evidence of immunosuppression (Harpaz et al. 2016), and this number is growing due to increasing life expectancy and eldering demography in large parts of the world. Immunosuppression generally aims for a temporary or local decrease of innate cellular immune responses. Inevitably, this highly successful intervention has a downside in the emergence of a wide diversity of environmental fungi as opportunistic pathogens (de Hoog et al. 2020), many of which were previously unknown to medical mycology. The ability of these fungi to adapt to the compromised conditions within the debilitated host and potentially tolerate human endothermic conditions are the key factors in the pathogenic processes of environmental fungi (Köhler et al. 2014). At the scale of the individual patient, management and control of fungal disease is dependent on the level of diagnostics, understanding of pathogenic processes, knowledge of fungus-host interaction, and available therapy. This enables precision medicine focused on defined patient groups (Märtson et al. 2021), with antifungal stewardship leading to the design of personalised, tailored therapy preventing inappropriate use of prophylaxis (Singh et al. 2018).

### More epidemics are expected

Microbial epidemics have always battered humanity and are expected to increase in frequency. The early pandemics, like plague and cholera, mostly originated from polluted water, as urban hygiene was at a low level until the nineteenth century, but the majority of the recent pandemics are zoonotic, and the intervals between the epidemics are decreasing. We recently witnessed the HIV, MERS, SARS, and COVID-19 pandemics that originated from primates, camels, and possibly from bats and intermediate hosts. Among novel threats are avian and swine flu which already are associated with human infection, having reached stage 2 (in a scale of 5; Piret and Boivin 2021) in adaptation to humans. Large-scale animal breeding, global trade of exotic animals, increased population density, and intercontinental travel enhance the spread, spill-over, and adaptation of microbial pathogens. In fungi, these often concern multiple infections from a single source, e.g., with *Sporothrix schenckii* from plant material

(Dooley et al. 1997; Govender et al. 2015) or *Verruconis gallopava* from contaminated straw in a chicken coop (Blalock et al. 1973). Others are promoted by viral infections damaging the human cellular immune system. The HIV pandemic led to pronounced infections of true pathogens (Carpouren et al. 2022) in *Cryptococcus*, *Sporothrix*, *Talaromyces*, and *Histoplasma*. The COVID-19 pandemic enhanced the infection of opportunists in *Rhizopus* (Singh et al. 2021; Nehara et al. 2021) and *Aspergillus* (Calderón-Parra et al. 2022). Serious problems are looming in the monoculture of animal farming, where large numbers of animals are packed within limited space. The agent of goat Q-fever, *Coxiella burnetii* and that of bird flu, H7N9 Influenza-A are already becoming endemic in Europe, and both can be transmitted to humans with serious consequences. Unexpected fungi may follow in their slipstream. As a result, bioindustry plants today are close to implementing similar biosafety measures as microbiological laboratories.

Changes in lifestyle follow a global trend. In the past, endemic infectious diseases and regional epidemics were associated with agricultural labour on the field. Traumatic eye and subcutaneous infections from plant material and dermatophytoses acquired from farm animals were prevalent. Today, the farmer is placed at a distance from infectious agents by modern technology. In addition, rural populations diminish worldwide as a result of urbanization. Diseases like chromoblastomycosis by black fungi or cattle-borne *Trichophyton verrucosum* infection are disappearing. They are replaced by infections particularly involving from pet animals (Zhan et al. 2015). For example, 44.5% of U.S. households own dogs, and 29% cats ([www.forbes.com](http://www.forbes.com)). The spectrum of animals held is becoming wider, with novel agents from exotic animals appearing, such as the emergence of *Trichophyton erinacei* from the African pygmy hedgehog (Hsieh et al. 2010).

An interdisciplinary One-health approach is mandatory to prevent unforeseen and expected consequences of intensive agriculture. Evaluation of emerging infectious diseases can be done in a broader sense e.g. by reducing monoculture, regardless of the specific etiologic pathogen, and comparative genomics will allow further investigation of genetic and biological characteristics, especially in terms of adaptation to new habitats. Population translocation is accelerated by human-made climate change (Kimutai et al. 2022), as large areas are likely to become uninhabitable (<https://www.un.org/africarenewal/>). Human populations will spread disease at an unprecedented pace, conversely, in the wealthy part of the world, global travel is likely to increase. Also, fungal biodiversity patterns and mycobiomes are changing under the pressure of changing environmental conditions (Větrovský et al. 2019; Case et al. 2022), making it harder to predict epidemic expansions. Future pandemics will be very hard to control.

## Problematic therapy and future solutions

Fungi are expected to be the infectious health problem of the future, because infections are chronic and recalcitrant, often with poor host response despite in vitro susceptibility (Vinh et al. 2023; Berman et al. 2020). The emerging resistance to commonly used antifungals in some of the major opportunists is a global concern in medical mycology. In addition, the discordance between overall treatment outcome and low levels of clinical resistance may be attributable to antifungal drug tolerance (Berman et al. 2020). Acquired antifungal resistance (Fisher et al. 2022) is a probable result of similar compounds being used in agriculture (Barber et al. 2020). In regions with intense farming, *Aspergillus fumigatus* comprises up to 20% of azole-resistant strains in natural populations (Chowdhary et al. 2013). The dermatophyte *Trichophyton indotineae* is often resistant to terbinafine, which is the main antifungal used by the public (Singh et al. 2018). In several orders of the fungal kingdom, such as Hypocreales, Microascales, and Mucorales, resistance is not acquired, but intrinsically present, even in the absence of previous exposure to antifungals (Caramalho et al. 2017). Also, some yeasts, among which is the emerging hospital agent *Candida auris* have reduced susceptibility, causing problems comparable to those of MRSA. Despite advances in antifungal therapy, there are few drug classes. New generations of antifungals are being developed with novel targets, such as echinocandins and orotomides, which are promising but generally are effective in only a limited number of species, or luliconazole which can only be applied topically. Currently, several promising antifungal agents undergoing clinical investigation, each with unique mechanisms of action. These include novamycin, an antifungal peptide that disrupts the plasma membrane, leading to cell lysis. Another agent, olorofim, belongs to the orotomide class of drugs and inhibits pyrimidine biosynthesis by reversibly inhibiting mitochondrial dihydroorotate dehydrogenase. Additionally, fosmanogepix, a GPI inhibitor, hinders the activity of Gwt1, preventing GPI anchoring. These agents exemplify novel drug targets and showcase their potential in the field of antifungal drug development. There are multiple bottlenecks to the successful development of antifungal drugs due to the unique characteristics of fungal cells. These challenges include the need to establish high-throughput screening methods, optimize target specificity and bioavailability, and minimize host toxicity to ensure efficacy. In silico approaches have the potential to expedite the early stages of drug development; however, their effectiveness relies on the availability of high-resolution protein structures and a strong mechanistic understanding of signaling pathways and the impact of therapeutic intervention on fungal physiology (Velazhahan et al. 2023).

Novel types of therapy have been applied to some of the classical, severe, and previously untreatable diseases that ultimately led to the death of the patient. In the past these were ascribed to supposedly uncommon, highly virulent fungi (Rajendran et al. 2003); particularly the mutilating diseases by black fungi (Bonifaz et al. 2013) and *Mucor irregularis* (Kang et al. 2014) have been mysterious. Today, these fungi are understood as being opportunists in patients with inherited immune disorders (Lanternier et al. 2015). Mutations in the essential dectin-signalling CARD9 protein increase susceptibility to particular fungal infections (Song et al. 2020). These primary immunodeficiencies include several hundreds of single-gene inborn errors of immunity and occur in close to 1% of the human population (Quinn et al. 2022). Similar to the increase in allergic diseases in the developed world, this problem is likely to grow in the future. Classical antifungal therapy is only temporarily successful in these patients due to emerging resistance. Immunotherapy or stem cell transplantation seems to provide a successful cure (Grumach et al. 2015) and may open new ways of therapy in chronic infections. For pathogens that are controlled by adaptive cellular immunity, the development of preventative tools such as vaccines might be an option (Oliveira et al. 2021).

## The need for reliable diagnostics

Medical mycology comprises 778 species in 250 genera ([www.atlasclinicalfungi.org](http://www.atlasclinicalfungi.org), dd 01–04–2023), and this number is increasing nearly every month. General knowledge of the great majority of these species is scant, while a very limited number of prevalent clinical taxa have been thoroughly investigated. The recent emergence of novel agents, such as *Candida auris* and *Sporothrix brasiliensis*, demonstrates severe gaps in understanding sources and routes of infection, potential pathology, immune response, and therapy. Numerous taxa are described on the basis of just a few isolates, neglecting intraspecific variability. Without an understanding of clonality, recombination, uniparental sex, and horizontal gene transfer, it is difficult to develop reliable diagnostics for hospital routines (Song et al. 2023). Diversity studies and taxonomy are fundamental but need a stronger integration with the sciences that follow (de Hoog et al. 2023). The focus on molecular phylogeny overshadows the comprehension of the practical significance of the described entities for applied sciences and patient care. Phylogeny provides insight into adaptive trends between species, and nomenclature opens the doors toward existing literature. However, phylogeny-based rearrangement of classical genera leads to fragmentation, such that the coherence between pathogens is lost again. For example, the 52 medically relevant candida-like species are now dispersed over 19 genera and this process is continuing. This underlines



the responsibility of the taxonomist to provide a workable system.

One limitation in controlling emerging diseases is the lack of rapid diagnostic tools and surveillance systems. Timely detection and identification of pathogens are essential for implementing effective control measures. Diagnostic methods are reliable only when based on sound taxonomy. The future of diagnostics may include multi-microbial tools that can provide a comprehensive view of microbial diversity and detect bacteria, fungi, and viruses simultaneously in clinical samples. Currently, protein- and DNA-based methods are available such as PCR, gene and genome sequencing, metagenomics, and MALDI-ToF, but these are not suitable for point-of-care diagnosis (POD), particularly in resource-limited settings or during outbreaks. Based on advanced knowledge, simplified techniques can be developed that are applicable in a wide range of settings and require less human implementation (Prattes et al. 2016) and are therefore particularly useful in developing regions (Osaigbovo and Bongomin 2021). An artificial intelligence approach has been evaluated for the autodetection of fungal hyphae from a microscopic image and seems promising (Koo et al. 2021). Additionally, microfluidic approaches such as lab-on-chip (Richter et al. 2022) can be utilized to promote fast detection of host/microbial biomarkers.

Overall, developing and improving diagnostic techniques and surveillance capabilities should be a priority. Future research should focus on enhancing our understanding of the ecological factors contributing to disease emergence. Exploring the complex interactions between pathogens, hosts, and the environment can help identify high-risk areas and predict disease outbreaks. Furthermore, strengthening international collaborations, data sharing, and communication networks is essential for a coordinated global response to emerging fungal infections.

## Current trends, limitations, and future research in novel compound and drug discovery

### Role of fungi in classical natural product-based drug discovery

Natural products have historically been one of the most important sources for human therapeutics, and they remain indispensable for the discovery and development of new drugs (Atanasov et al. 2021; Newman and Cragg 2020). As summarized by Bills and Gloer (2016), several of the most important pharmaceuticals and agrochemicals are derived from fungi. Aside from the blockbuster cardiovascular drugs like statins and the immunomodulating compounds like cyclosporine and fingolimod (Mapook et al. 2022; Niego

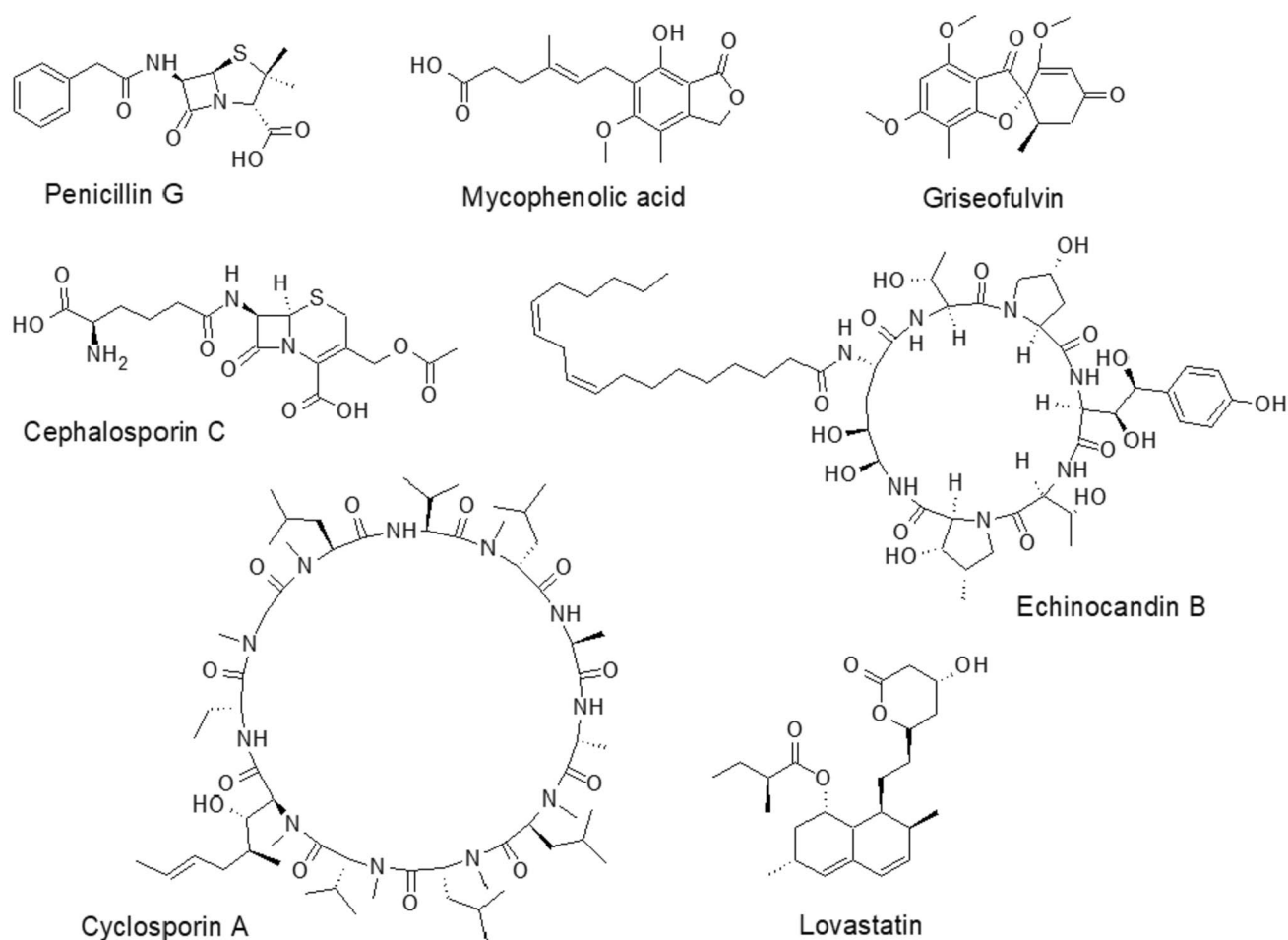
et al. 2023b), the beta-lactams are certainly the best-known class of fungi-derived drugs (Fig. 1).

Since the discovery of penicillin, scientists have turned to fungi to find cures for mankind's diseases. Out of this arose the blooming age of antibiotics in the late 1940s which lasted until the 1960s (Karwehl and Stadler 2016; da Cunha et al. 2019), followed by a period of neglectful thinking that such drugs would always be available and last for eternity. This has given rise to resistance against these drugs and has slowly become a mass problem (Mitra et al. 2022). Roughly 60 years later, the focus has now turned on having to find new drugs predominantly against superbugs, strains of, e.g. bacteria, which are resistant to multiple classes of antibiotics, if not all, as in the case of some recalcitrant strains of *Mycobacterium tuberculosis* (Gygli et al. 2017). By far the most dangerous bacterial pathogens, however, are the organisms that are classified in the ESKAPE panel: *Enterococcus faecium*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Acinetobacter baumannii*, *Pseudomonas aeruginosa* und *Enterobacter* spp. often become multi-resistant and are responsible for an increasing number of deaths (Miethke et al. 2021).

The main research focus in the medical field over the last four decades has shifted to different topics, such as finding chemotherapeutics for cancerous diseases (a field, in which natural products also are playing a major role), but in particular for diabetes and other metabolic disorders, cardiovascular drugs and other indications in which higher revenues can be expected. One of the reasons for this shift was the fact that the development costs for drugs have exploded, and regardless of the indication, the development of novel drugs from scratch may now cost up to a billion USD (Wouters et al. 2020). Especially because of the extremely high attrition rates, it became less fashionable to develop totally novel molecules from natural sources to drugs, and the antibiotics and other anti-infective sectors in which the natural products are particularly strong have been heavily affected by this trend. (Atanasov et al. 2021).

With this focal shift, many biomedical research branches are now devoted to drug development for these and other types of diseases of affluence. Therefore, the major contributor to new FDA-approved drugs over the past 30 years has been “biologicals” (macromolecular medicinal products of fermentative origin) (Rader 2008; Newman and Cragg 2020; Butler et al. 2023). Its most prominent representative is of course recombinant human insulin (Falcetta et al. 2022). Generally, their use is currently focused primarily on oncology, rheumatology, gastroenterology, and cardiology (Walsh and Walsh 2022).

Thus, the main problem remains: finding new drugs against superbugs and bringing them to the market as quickly as possible, and counteracting their resistance. Therefore, classical drug discovery research, which is



**Fig. 1** Some of the most prominent fungal natural products-derived drugs currently on the market

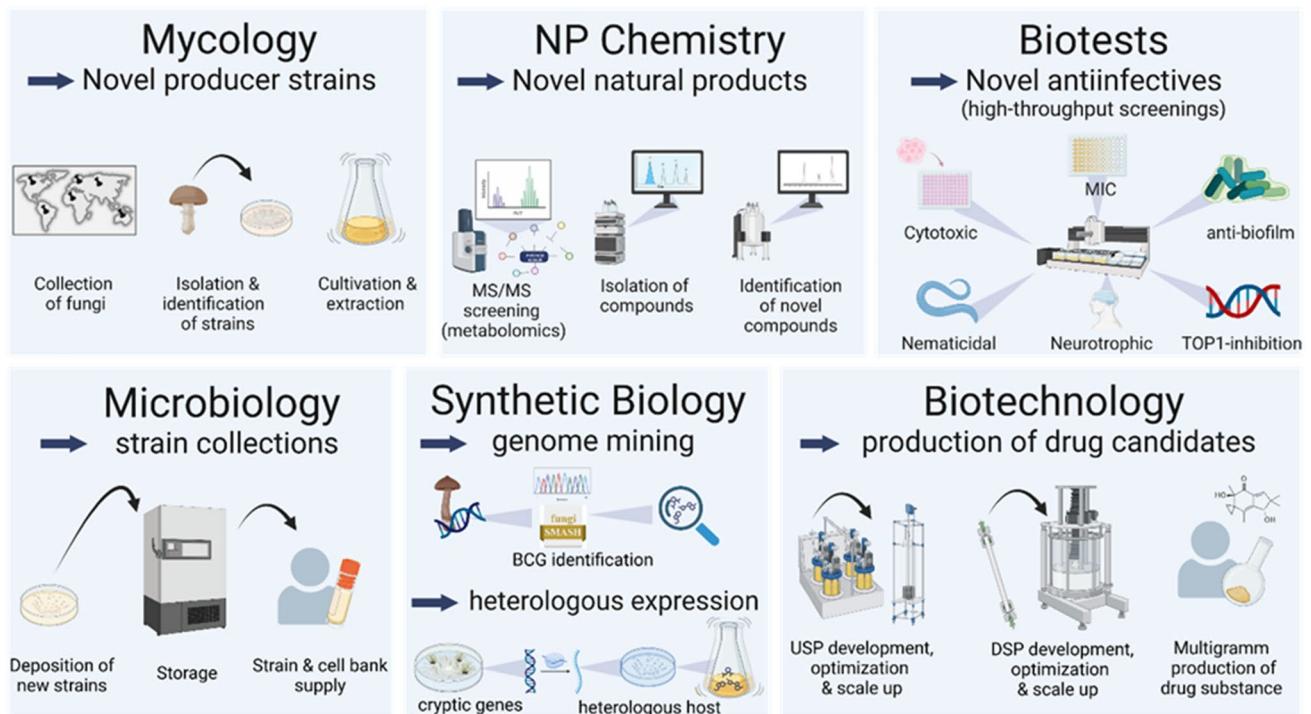
based on natural product chemistry, has been given new attention in the last few years. Natural products have their fair share in the approval of new drugs by the FDA, while in contrast, the approval of new synthetic drugs has almost disappeared (Newman and Cragg 2020; Butler et al. 2023), the proportion of fungal natural products among the newly approved drugs is relatively small.

Yet, at the same time, the last approved new compound class of antibiotics, pleuromutilins, that came onto the market are derived from fungi (Paukner and Riedl 2017; Mapook et al. 2022). With the diverse range of natural products fungi have to offer, they remain one of the most promising sources for new lead structures. In addition, science has dedicated itself to the development of new dosage forms, particularly nanotechnology, which is a cutting-edge research topic at present. One of the most promising fungal metabolites with biomedical use in this regard is chitosan, a fungal chitin-derivative under investigation as a drug delivery system, as hemostatic, and as medical material for wound healing (Nawawi et al. 2020). This

would make natural products more bioavailable and thus a lot more interesting for use as drugs.

One big problem of the pharmaceutical industry is that all large companies have given up or outsourced their capacities for natural product research and development. Not only for the mycological field, but the search for novel compounds from nature also requires the availability of interdisciplinary resources and expertise, ranging from classical microbiology via know-how in biotechnology to analytical and preparative natural product chemistry (Fig. 2). Once a given company has abandoned these R&D activities, which had historically been built up over several decades, it may take decades to get back the know-how.

On the other hand, there is hope. A large number of bioactivity screening systems are nowadays available for newly discovered natural products, which often only require small amounts compared to the past. This does not mean that already known natural products cannot be tested in these new assays as well, and stand out as hits. One such example would be rubiginosin C (Quang et al. 2004), which has been



**Fig. 2** Overview of current state of fungal drug research (created with [www.BioRender.com](http://www.BioRender.com))

known from *Hypoxylon rubiginosum* for almost 20 years, yet only recently stood out to be a highly promising biofilm inhibitor of pathogenic *Candida* spp. (Zeng et al. 2023).

Just as bioactivity assays need less and less amount of material, classic natural products drug discovery has changed in this regard. New technologies in the field of structure elucidation, mainly nuclear magnetic resonance spectroscopy (NMR) and mass spectrometry (MS) allow for structure elucidation of smaller and smaller amounts. One look into the respective literature shows that natural product isolation and characterization of less than 1 mg has become the norm, with a trend to even lower amounts (<0.5 mg), such as five unprecedented diketopiperazines from the endophytic fungus *Batnamyces globulariicola*, cultured from the medicinal plant *Globularia alypum*, native to Algeria (Noumeur et al. 2020). This opens up drug discovery in completely new territories, which have previously been disclosed. Not only geographical territories, where in recent times fungal natural products research has had and is focusing predominantly on tropical, understudied regions (Sandargo et al. 2019), but also specialized ecological niches, can thus now be investigated for potential drug producers.

A challenge here can be the adherence to all legal procedures, such as the Nagoya protocol (Heinrich and Hesketh 2019). However, the greater limitation in all these cases lies with the cultivation conditions, which in turn can lead

to challenges in the reproduction of interesting drug candidates and makes an upscaling of these more difficult, as well as potentially elaborate isolation procedures. After all, a complex upstream process (USP) followed by a lavish downstream process (DSP) leads to a high cost of goods, which makes a drug candidate unappealing (Suresh and Basu 2008).

A frequent solution to this problem is the fermentation of an easier-to-produce precursor molecule which is then chemically modified in further steps, called “semisynthesis”. A majority of fungal drugs on the market have at least one step of semisynthesis, not only to increase production, but largely to improve bioavailability (like micafungin, an antifungal agent semi-synthesized from fermentative echinocandin; Hashimoto 2009), or to improve its (selective) bioactivity (like ceftaroline fosamil (teflaro® / Zinforo®) the last generation semisynthetic cephem to enter the market with improved selectivity for multi-resistant Gram-positive bacteria, Newman and Cragg 2020). In some cases, semisynthesis is also used to lower the actual bioactivity, such as in the case of irofulven, a lesser toxic derivative of illudin S (Chaverra-Muñoz and Hüttel 2022). These chemical modifications, a part of a vast field of medicinal chemistry, are becoming increasingly important and it is impossible to imagine a future without them. The best example of the success of a semisynthetic approach based on fungal metabolites is probably the cephalosporins, where five generations

of compound families were synthesized over several decades, resulting in substantial improvements in efficacy against human pathogens (Lin and Kück 2022).

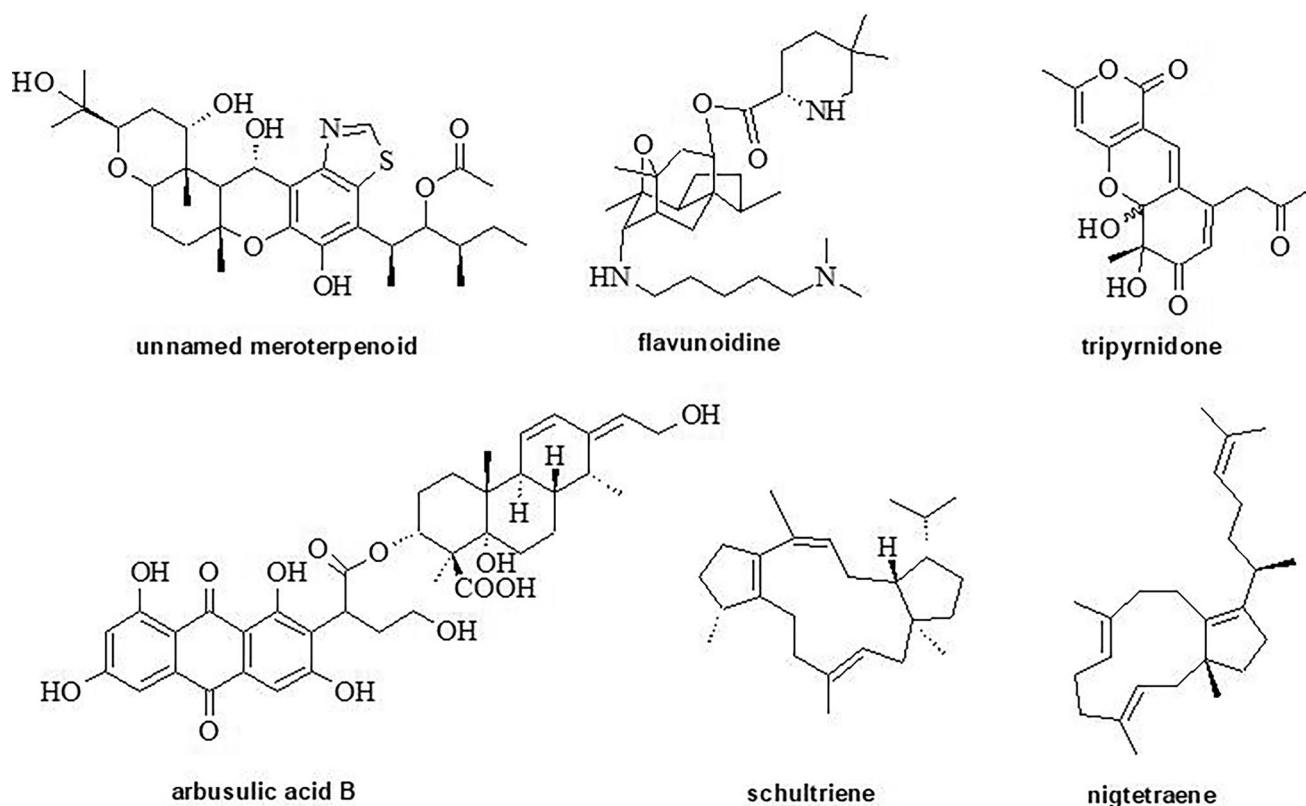
However, the now-established way of producing non-synthesizable natural substances more cost-effectively is synthetic biology, which introduces the BGCs into a new, easier-to-cultivate host via heterologous production or can even allow for total biosynthesis of novel natural products. As shown for strobilurins (Nofiani et al. 2018) and pleurotulinins (Alberti et al. 2017a, b) it has even been possible to transfer the BGC from Basidiomycota into workhorses like *Aspergillus (flavus var.) oryzae* that belong to the Ascomycota. It has even been possible to synthesize natural products using enzymes, as recently demonstrated for psilocybin by Fricke et al. (2017). The mechanisms of many biosynthetic pathways, including those that encode for rather rare and complicated metabolite classes, have been elucidated over the past years (Feng et al. 2020; Tian et al. 2020; Schotte et al. 2020).

### Current trends and future potential

When the first genomes of filamentous fungi became available, the large number of biosynthetic gene clusters in these fungi surprised the researchers, as the number of clusters by

far exceeded the diversity of SMs known from these fungi during previous natural product isolation studies. Since then, genome mining has been established as an alternative way for the discovery of new secondary metabolites. Its common workflow is the identification of biosynthetic gene clusters (BGCs), the heterologous expression or activation of interesting BGCs, followed by metabolite characterization. Examples (Fig. 3) yielded in novel carbon skeletons include the discovery of new meroterpenoids from a gene cluster encoding polyketide synthase, prenyltransferase, terpenoid cyclase, and other tailoring enzymes (Zhang et al. 2018); the discovery of flavunoidine, whose gene cluster contains two terpene gene clusters and a nonribosomal peptide synthetase (Yee et al. 2020) and the sesterterpenes schultriene and nigtetraene discovered by heterologous expression of fungal bifunctional terpene synthases (Jiang et al. 2022). Arbuselic acid was isolated besides other compounds after epigenetic activation of the endophytic fungus *Calcarisporium arbuscula* (Mao et al. 2015), whereas the production of tripyridone in *Aspergillus nidulans* was induced by co-cultivation with filamentous *Streptomyces* bacteria producing antifungal glycopeptide antibiotics (Gerke et al. 2022).

Precondition for the genome mining is the availability of full genome information to be mined. Although fewer fungal genomes have been sequenced compared to the bacterial



**Fig. 3** Novel compounds isolated from genome mining approaches



kingdom, more than 1000 fungal genomes have already been interpreted for secondary metabolite production (Robey et al. 2021). However, most of those studies focused on well-studied genera such as *Aspergillus*, *Fusarium*, and *Penicillium*.

Thus, it is important to expand sequencing efforts to less studied, nevertheless very prolific groups of fungi. Based on high-quality genome sequences for 13 representative species of Hypoxylaceae, Kuhnert et al. (2021) surveyed the diversity of biosynthetic pathways and found 783 biosynthetic pathways across the 14 studied species, the majority of which were arranged in biosynthetic gene clusters. Of the 375 gene cluster families (GCF) found, only ten GCFs were conserved across all of these fungi, indicating that a high degree of speciation is accompanied by changes in secondary metabolism. Besides giving insights in the genetic background that drives the production and diversification of secondary metabolites, this and similar studies will help to systematically access the secondary metabolites of prolific fungal secondary metabolite producers.

A drawback of the genome mining approaches is that often compounds with no obvious bioactivity are isolated. Thus, target-directed genome mining efforts try to increase the odds of finding bioactive compounds. Because antimicrobial producers must be self-resistant to their own metabolites, fungi often encode resistance genes to avoid self-toxicity in the BGCs of corresponding bioactive compounds. FunARTS, the Fungal bioActive compound Resistant Target Seeker, is a recent exploration engine to specifically mine for these resistance genes (Yilmaz et al. 2023).

So far, genome mining has largely focused on unknown metabolites from predicted BGCs with known core enzymes, like PKS, NRPS, and terpene synthases. However, the most spectacular findings are expected in the search for unknown secondary metabolites with so far unidentified types of core enzymes, the so-called “unknown-unknowns”. Yee et al. (2023) identified a new arginine-containing cyclodepsipeptide synthase, which is responsible for a highly modified cyclo-arginine-tyrosine dipeptide. However, since the scaffold of this compound was already known from derivatives, it remains to be seen if this method can meet the high expectations.

Metabolomics is a recently developed, complementary research field. The identification of known compounds, a process known as dereplication, is readily possible with HPLC–MS/MS data from crude extracts if reference data are available. Thus, the integration of genomics and metabolomics has the potential to revolutionize fungal natural product research (Hautbergue et al. 2018). Beyond metabolomics, the integration of transcriptomics and proteomics data may provide an additional layer of information for pathway analysis (“multi-omics”). However, it is very important to reduce the complexity of the vast amount of data in a

sensible way (Rinschen et al. 2019). Of particular interest is the systematic connection of pathway data to biological activities. However, it is, of course, not possible to assess the biological effects of single components in mixtures like extracts unless the respective compounds can be isolated to purity. The same holds true for their unambiguous identification, for which techniques like 2D-NMR spectroscopy, crystallization, or derivatization remain indispensable.

Furthermore, synthetic biology, designing and constructing biological modules, biological systems, and biological machines or re-design of existing biological systems for useful purposes, will greatly help to access the chemical diversity uncovered by genome mining (Skellam et al. 2019; Keller 2019). The combination of genome mining with a synthetic biology-based method of heterologous biosynthesis is a promising approach to rationally access NPs with novel structures and biological activities. As an example, this method was used to explore the biological activity-related chemical space of fungal decalin-containing diterpenoid pyrones (Tsukada et al. 2020). Even though these compounds do not have very prominent and selective biological activities, the latter study shows the feasibility of the approach to expand the chemical space. Meroterpenoids (Matsuda and Abe 2016), NRPS-PKS hybrids (Boettger and Hertweck 2013), and other compounds of mixed biosynthetic origin are increasingly being studied, also because their BGC can be made out in the genomes rather easily.

Finally, yet importantly, the application of artificial intelligence (AI) to natural product drug discovery has grown tremendously in recent years, due to ever-increasing computing power, extensive storage, and accessible software (Saldivar-Gonzalez et al. 2022). Thus, we expect the rational application of AI to assist in discovering bioactive natural products and capturing the molecular “patterns” of these privileged structures for combinatorial design or target selectivity. Main help will most likely be the prediction of chemical structures from microbial genomes and automation of the natural product dereplication process, the identification of NP substructures, computer-assisted structure elucidation, and virtual screening approaches. Additionally, the prediction of biological functions of the NPs will be afforded by the recent advances in machine learning having leveraged to accelerate the accurate atomic-resolution structure prediction of proteins (Lin et al. 2023a, b).

## Conclusion

Above we have summarized the classical development of natural product-based drug discovery with fungi as well as various modern options that recently became available via the –OMICS technologies. Curiously, the options to quickly improve the production and activities of natural compounds nowadays appear higher than ever before, while the lack of

relevant expertise in the pharmaceutical industry steadily contributes to the innovation gap regarding novel drugs that can be brought to the market. A further increase of public funding and incentives for the industry to re-establish capacities and know-how for natural product-based drugs would be highly desirable, especially with respect to indications like anti-infectives, where the greatest need is going to arise in the future.

## Current trends, limitations, and future research in fungal classification and phylogenomics

The term "phylogenomics" was introduced by Jonathan Eisen in 1998 for improving functional predictions for uncharacterized genes and to study the evolution of gene families in the genome-scale phylogenetic analysis (Eisen 1998). Compared with multi-locus phylogenetic analysis, genomes contain more species evolution information, and a larger dataset can decrease sampling errors. Reconstruction of phylogeny based on genome-scale data can more realistically reflect the evolutionary relationship between taxa (Virendra and Somnath 2009). In the last 20 years, advances in next-generation sequencing technologies and bioinformatics have made the genomic era now a reality. Phylogenomics has since become a widely used approach in evolutionary biology and genomics (Guttmacher and Collins 2003; McGuire et al. 2020; Eisen and Fraser 2003; Virendra and Somnath 2009). There has been a rapid increase of fungal genome data in public databases, such as NCBI database (<https://www.ncbi.nlm.nih.gov/datasets/genome/?taxon=4751>) and 1000 Fungal Genomes Project (<https://mycocosm.jgi.doe.gov/mycocosm/home/1000-fungal-genomes>). Researchers are therefore increasingly using genomic data to infer the evolutionary relationships among fungi, and have obtained remarkable progress in fungal taxonomy. A number of long-standing taxonomic questions have been resolved, and at the same time, the accuracy of fungal classification and the understanding of fungal evolution have been improved greatly (Zhang et al. 2017). Pizarro et al. (2018) utilized a genome-scale dataset of 2556 single-copy protein-coding genes to reconstruct a phylogeny of the most diverse group of lichen-forming fungi. This study strongly supported the monophyly of major clades and resolved previously unresolved relationships in the family Parmeliaceae. Based on morphological characters and two-locus phylogenetic analysis, the important plant-pathogenic genus *Pythium* sensu lato was split into five genera: *Pythium*, *Elongisporangium*, *Globisporangium*, *Ovatisporangium*, and *Pilasporangium* (Uzuhashi et al. 2010). This revision however, was not generally accepted by the scientific community due to the

lack of phylogenetic support until a phylogenomic study of *Pythium* was conducted by Nguyen et al. (2022).

In higher-level taxonomic studies, phylogenomic analysis helps in resolving several problematic lineages, including the grouping of microsporidia + *Rozella* with Cryptomycota (James et al. 2013), the formal phylogenetic classification of splitting zygomycete taxa into Mucoromycota and Zoopagomycota (Spatafora et al. 2016), and the systematic placement of the xerotolerant mold *Wallemia* as the earliest diverging group in Agaricomycotina (Padamsee et al. 2012). In addition, Li et al. (2021b) discovered that ~85% of fungal taxonomy ranks used in the dataset were broadly consistent with both genome sequence divergence and divergence times at higher taxonomic levels, suggesting the effectiveness of using the divergence time approach to rank taxonomic lineages.

## Limitations

While phylogenomics has brought powerful analytic methods to fungal taxonomy, there are some limitations that should be considered. Current phylogenomic studies suffer from limited taxon sampling, which can lead to incomplete or inaccurate phylogenetic reconstructions. The phylogenomic study by Chen et al. (2023a) included all available genomes of Sordariomycetes from the public database. The final dataset only comprised 156 genera, 50 families, 17 orders, and five subclasses, which is much lower than the number of existing taxa (1619 genera, 184 families, 46 orders, and seven subclasses) summarised in the latest outline (Wijayawardene et al. 2022a, b). Most genomes in the public database are from pathogenic or biotechnologically useful fungi, with whole genome sequencing was conducted by non-fungal specialists for non-taxonomic purposes. This led to poor sampling in many groups, which may be underrepresented in genomic databases. Furthermore, because most genomes are not from ex-type or representative strains, there are no morphological characterizations for these genomes. This impedes the combination of phylogenomic analysis and morphological studies. In fungal species delineation, there have been several attempts to differentiate species using genome data; however, this kind of application has been hampered by the lack of clear and universal criteria (Sepúlveda et al. 2017; Gostinčar 2020; Matute and Sepúlveda 2019). The cost of whole genome sequencing has been decreasing due to advancements in sequencing technologies. However, it remains relatively more expensive as compared to Sanger sequencing, which is used in multigene phylogenetic analysis. Furthermore, whole genome sequencing instruments are not available in underdeveloped countries. The subsequent requirements of extensive computational resources, sophisticated bioinformatic skills and poor collaborations between bioinformaticians and taxonomists

also limit the promotion of phylogenomics in fungal taxonomy to some extent.

## Future

The main limitation of phylogenomics in fungal taxonomy is an unbalanced genomic sampling. As more fungal genomes are sequenced, including those from understudied and diverse fungal lineages, phylogenomic studies can benefit from increased genomic sampling. This will enable a more comprehensive understanding of fungal diversity and evolution, filling in gaps in the fungal tree of life and improving the resolution of phylogenetic relationships. The vast majority of fungal taxonomic groups do however, not have the ability and conditions to perform phylogenomics analysis. Therefore, the use of morphology and multi-locus analysis will be the main methodologies used in fungal taxonomy. Phylogenomic approaches will be supplements to solve some taxonomic problems. The fungal taxonomy community should support and advocate for the implementation of phylogenomics into taxonomy. It is hoped that phylogenomics will provide a more comprehensive and accurate understanding of fungal diversity and evolution in the future.

## Current trends, limitations, and future research in genomics and ecology of fungal plant pathogens

### A brief history of the origin and evolution of fungi

Some studies have shown that the ability of fungi to colonise plants is ancient, suggesting a correlation between streptophyte algae (embryophytes and their closest green algal relatives) and the lineages of fungi Ascomycota, Basidiomycota, and Chytridiomycota around 1 billion years ago (Jones et al. 2015). The application of genome analysis and comparative studies has supported this hypothesis. For instance, the presence of pectinases and cellulases through millions of years of evolutionary history suggests that most of the ancestors of fungi evolved using plant-based nutrition (Berbee et al. 2017). Moreover, as algae evolved into land plants, and as the polysaccharides in their cell walls differentiated, fungal enzymes accompanied this evolution process (Lange et al. 2019). In this regard, fungi developed strategies to invade complex substrates, making them the principal degraders of biomass, and efficient saprotrophs and pathogens able to infect a wide range of hosts (Bucher et al. 2004; Berbee et al. 2017; Howlett et al. 2015). In natural ecosystems, the interaction between plants and their pathogens drives a co-evolutionary dynamic (Howlett et al. 2015). However, in managed ecosystems, as crops evolve through artificial selection (e.g., selection of desired traits), pathogens need

to rapidly evolve and adapt to new environmental conditions and niches leading to the increase of virulent phenotypes (Möller and Stukenbrock 2017). Consequently, the awareness of mycologists and plant pathologists to study fungal pathogens and to evaluate their evolutionary relationships based on genome data has been considerable in recent studies (Ball et al. 2020; Garcia et al. 2021; Priest et al. 2020).

### What does genomics offer?

Genome analysis is pivotal to understanding the mechanisms underlying the infection processes (Schikora-Tamarit and Gabaldón 2022) and adoption patterns involved in fungal lifestyles and ecological niches (Gonçalves et al. 2022; Janusz et al. 2017). Additionally, genome data provides information on gene families and their functional potential for virulence and host infection (Ball et al. 2020). This is of paramount importance for the plant pathology sector to understand the biology of diseases, to improve diagnostic methods, and ultimately to manage and/or prevent disease outbreaks (Aylward et al. 2017; Weisberg et al. 2021). Therefore, current efforts on fungal genome sequencing have been made to cover the above-mentioned purposes by unveiling:

- (1) carbohydrate-active enzymes responsible for the degradation of plant cell walls, showing the ability of fungi to penetrate and colonise plant tissues.
- (2) biosynthetic gene clusters for the discovery of bioactive compounds with pharmaceutical, biomedicine, and agricultural applications.
- (3) transmembrane transporters of ions, sugars, and molecules that contribute to fungal virulence.
- (4) pathogenicity/virulence genes and candidate effectors that manipulate the host immune defense.
- (5) candidate genes involved in evolutionary processes that shape fungal pathogens' adaptation to different environments (e.g., increasing temperatures, drought, high levels of salinity).
- (6) the role of secreted effectors on fungal virulence and lifestyle switching.
- (7) genes related to morphological, physiological, and reproduction among different isolates.
- (8) genetic basis for multi-omics analyses to offer a complete overview on plant-pathogen interactions.
- (9) genomic variants linked to virulence through the analysis of single nucleotide polymorphisms (SNPs) (Constantin et al. 2021; Garcia et al. 2021; Gonçalves et al. 2022; Grandaubert et al. 2019; Xu 2020).

### Current limitations on genome analysis

The important roles of fungi and their ubiquity and plurivorous nature, coupled with the advances in next-generation

sequencing (NGS) have driven researchers to sequence numerous fungal genomes (Möller and Stukenbrock 2017; Priest et al. 2020). This has led to a greater availability of fungal genomes in public databases (e.g., NCBI, JGI Genome Portal) which significantly expanded our knowledge of the infection processes, fungal ecology, and genome evolution (Aylward et al. 2017; Xu 2020). However, there is a limited understanding of the impact of genome architectures on the upsurge of pathogenicity changes and the adaptation to changing environments mainly due to:

- (1) increasing numbers of fungal genomes published as genome announcements lacking functional gene annotations.
- (2) interpretation of genomes based mostly on low-quality assemblies, weak annotations, and homology-based predictions.
- (3) shortage of sufficient funding to obtain whole genome sequencing and to access publicly available databases and web surfaces for data analysis.
- (4) wrongly identified fungal species and misidentification of the submitted genomes in databases which introduce errors and deceive further analysis.
- (5) requirement of experts in data sciences and plant pathology for a correct and careful interpretation of data.
- (3) Comparing the genomes of different fungi can assist in the identification of common features and differences between species. This can shed light on the evolutionary relationships and the genetic basis of unique properties of certain fungi.
- (4) In environmental mycology, metagenomics allows for the analysis of all the genetic material present in a sample. In this regard, bioinformaticians can handle the vast amounts of data generated from such studies and help in the identification of different fungal species.
- (5) Bioinformatics tools can aid in predicting the functions of genes and proteins in fungi, even for species where experimental validation may be challenging or time-consuming.
- (6) Understanding the genetic factors involved in fungal pathogenicity can lead to the discovery of potential drug targets. Bioinformatic analysis can assist in identifying crucial genes and pathways related to fungal virulence.
- (7) Bioinformaticians can facilitate the sharing of large datasets and help establish collaborative efforts between different research groups and institutions in the field of mycology.
- (8) Bioinformaticians can create software tools and databases tailored specifically for mycological research, making it easier for mycologists to analyse and interpret their data.

These limitations are challenging for researchers impairing the achievement of high-quality and large-scale comparative analysis (Gabaldón 2020; Stavrou et al. 2018).

### The close relationship between bioinformaticians and basic mycology

Mycology is integrative and requires experts with diverse skills in fungal biology, bioinformatics, and molecular biology (Hibbett et al. 2013). Despite the efforts to understand the biology and ecology of fungi, mycologists and plant pathologists need to establish a close collaboration with bioinformaticians. Combining their expertise can be beneficial to deepen our knowledge of fungi and their role in biological processes and lead to several advantages (Aylward et al. 2017; Gautam et al. 2022; Roth et al. 2023; Wijayawardene et al. 2022a, b):

- (1) Bioinformaticians can assist mycologists in analysing the genomes of several fungal species, thus providing valuable insights into their evolution, physiology, and potential applications.
- (2) By analysing the gene expression (transcriptomics) and protein profiles (proteomics) of fungi, bioinformaticians can help mycologists understand how genes are regulated and the biological functions of proteins.

Overall, the collaboration between bioinformaticians and basic mycologists can accelerate research, increase the accuracy of analyses, and provide a better understanding of fungi (Roth et al. 2023). As technologies and computational methods continue to advance, this partnership will play an increasingly critical role in advancing mycological research and its applications in various fields, including medicine, agriculture, and industry (Weisberg et al. 2021; Wijayawardene et al. 2022a, b).

### Future perspectives in untangling genome architectures

Despite the above-mentioned challenges, further efforts should be made to continue pursuing knowledge on the mechanisms of virulence, processes of genome evolution, environmental adaptations, and speciation events (Aylward et al. 2017; Ball et al. 2020). This information can be achieved through the analysis of genome compartments that are enriched in effectors and transposable elements, responsible for genomic plasticity and the evolution of new virulence phenotypes (Möller and Stukenbrock 2017). Therefore, comparative whole genome analysis between pathogenic and non-pathogenic isolates will contribute to.



- (1) identifying those compartments and determining their roles in the rapid evolution of fungi.
- (2) monitoring the population dynamics of pathogens.
- (3) revealing fungal ecological adaptations.
- (4) understanding evolutionary dynamics (Ball et al. 2020; Grandaubert et al. 2019).

Moreover, bearing in mind that fungi can adopt different lifestyles (e.g., endophytes, pathogens, saprotrophs), genome analysis should be considered in future studies for a deep understanding of the molecular traits and mechanisms that determine lifestyle switches (Constantin et al. 2021; Hilário and Gonçalves 2023). As a single reference genome cannot reflect the genetic diversity of a species, it is also vital to increase the number of sequenced genomes of closely related and divergent isolates within a given species to assess evolutionary relationships (Gabaldón 2020; Xia et al. 2022). High-quality genomes are required to obtain more accurate and correct information from a fungal genome and its functional annotation. In this regard, it has been suggested that plant pathology programs must provide their students with more opportunities to deepen their skills in data sciences (Xu 2020). This will surely help them to gain experience and expertise in working with genomic datasets, thus improving the quality of the published data (Weisberg et al. 2021).

The integration of all these approaches provided by genomics will certainly enable new perspectives in untangling fungal-pathogen interactions, shed light on the biology, ecology, and evolution of pathogens, and ultimately in identifying diagnostic markers for agricultural settings (Hilário and Gonçalves 2023; Weisberg et al. 2021; Xia et al. 2022).

### Current trends, limitations and future research in functional genomics

Functional genomics is an interdisciplinary field that integrates molecular biology and cell biology, utilizing the massive amount of data generated by genomic and transcriptomic projects. This has the aim of deciphering how genes and their regulatory elements work together to carry out biological processes and determine the functions of specific genes in various biological systems (Smit et al. 2017). These functional genomic approaches to fungi enable researchers to shed light on the molecular mechanisms underlying fungal biology, focusing on their growth, development, metabolism, and response to environmental stimuli (Chethana et al. 2020; Peng et al. 2022; Huang et al. 2023). The significance of fungal functional genomics lies in its ability to elucidate gene function, paving the way for advancements in various fields, including medicine, agriculture, and biotechnology (Huberman 2021). Furthermore, identifying these genes and proteins that are essential for critical processes like fungal

survival and pathogenicity provides the knowledge required to develop targeted therapies and antifungal drugs that disrupt vital processes in pathogenic fungi impacting plants, animals, and humans, improving the treatment of fungal infections and reducing the emergence of drug resistance (Sanz et al. 2017; Segal et al. 2018; Chethana et al. 2020; Bruno et al. 2021; Peng et al. 2022; Huang et al. 2023). Moreover, functional genomics provides insights into evolutionary relationships, gene family expansions or contractions, and the acquisition of novel traits that are important to understand the processes that shaped fungal diversity and adaptation to different ecological niches (Kim et al. 2014; Liu et al. 2017; Ball et al. 2020; Garcia et al. 2021; Priest et al. 2020).

As fungi play essential roles in agriculture, both as beneficial symbionts and devastating plant pathogens (Hyde et al. 2019), functional genomics research also provides insights into fungal-plant interactions, including symbiosis, disease resistance, and nutrient uptake (Seo et al. 2015). Understanding these interactions can lead to the development of strategies for crop protection, enhancing plant health, and improving agricultural productivity (Bhardwaj et al. 2014; Yang et al. 2023). Hyde et al. (2019) discussed the immense biotechnological potential of fungi to produce a wide range of enzymes, bioactive compounds, and secondary metabolites for industrial processes or pharmaceutical compounds. This knowledge can be harnessed to optimize fungal strains for biotechnological applications and develop new bio-products. Overall, fungal functional genomics is essential for expanding our knowledge of fungal biology, enhancing food security, boosting human health, and spurring innovation across various industries (Wijayawardene et al. 2023a, b). By uncovering the functions of fungal genes and their interactions, this field contributes to the development of new strategies, therapies, and biotechnological applications with broad societal impacts.

### Current trends in fungal functional genomic studies

The advent of genomics research has revolutionized our understanding of fungi by generating an unprecedented volume of data, serving as the foundation for functional research in this diverse group of organisms. The sequencing of fungal genomes has produced enormous datasets that provide valuable insights into the genetic makeup of various fungal species (Noble and Andrianopoulos 2013; Ma et al. 2014; Yan et al. 2018; Grandaubert et al. 2019; Constantin et al. 2021; Garcia et al. 2021; Gonçalves et al. 2022; Greener et al. 2022). Integrating this massive data with other "omics" approaches, such as transcriptomics and proteomics, offers a holistic perspective of fungal functional genomics, paving the way for groundbreaking discoveries and innovative applications in industries such as agriculture,

medicine, and biotechnology (Muller et al. 2013; Abram 2015; Grandaubert et al. 2019; Chethana et al. 2020; Xu 2020; Constantin et al. 2021; Garcia et al. 2021; Gonçalves et al. 2022; Peng et al. 2022; Huang et al. 2023). In recent years, several prominent trends have emerged in fungal functional genomics. These trends encompass a range of techniques and approaches that are reshaping our understanding of fungal biology and offering new avenues for applications in various fields.

A prominent trend in functional genomic research is the integration of multi-omics datasets, such as genomics, transcriptomics, proteomics, and metabolomics, into functional research, providing a deeper understanding of the functional elements within fungal genomes and their relationships to fungal biology (Chethana et al. 2020; Presley et al. 2020; Constantin et al. 2021; Garcia et al. 2021; Gonçalves et al. 2022; Li et al. 2022a, b, c; Peng et al. 2022; Huang et al. 2023). Such research has the potential to uncover novel insights into the biology, evolution, and biotechnological potential of fungi by correlating genomic information with gene expression profiles, protein interactions, and metabolic pathways. For instance, Presley et al. (2020) integrated functional research with transcriptomics (comparative RNA-Seq) and proteomics to identify various interaction methods and the individual proteins mediating these relationships among two model brown rot fungi of softwood timber. Additionally, the integration of metabolomics and functional genomics in the study by Li et al. (2022a, b, c) elucidated the metabolic adaptations of *Trichoderma reesei* under cellulase-inducing circumstances, revealing key regulatory mechanisms for efficient cellulase synthesis. Furthermore, comparative genomics research combined with functional genomic research in fungi facilitates the identification of conserved genes, orthologs, regulatory elements, and lineage-specific adaptations, and provides insights into the evolutionary innovations and specialised functions that contribute to the diversity of fungal lifestyles, including pathogenicity, symbiosis, and environmental adaptation (Muller et al. 2013; Abram 2015; Yan et al. 2018; Grandaubert et al. 2019; Xu 2020; Constantin et al. 2021; Garcia et al. 2021; Gonçalves et al. 2022). For example, comparative analysis of the transcriptome and genome data of *Aspergillus* species identified genes responsible for carbon utilization, secondary metabolism, and stress response, laying the foundation for exploiting them for biotechnological and medical applications (Terabayashi et al. 2010; de Vries et al. 2017). Furthermore, functional studies, in conjunction with comparative analysis, revealed the evolution of the fungal chitin synthase (CHS) gene family, as well as its relationship to fungal morphogenesis and adaptability to ecological niches (Liu et al. 2017). Large-scale comparative analysis of 135 genomes of mycorrhizal species revealed their complex symbiotic traits through gene duplications and diversifications and provided evidence for

convergent evolution, and identified key genetic components involved in the nutrient exchange between mycorrhizal fungi and their plant hosts (Miyachi et al. 2020). Similar research can aid in understanding the origin and development of plant-fungal relationships and their impact on ecosystem function.

Another emerging trend in the study of pathogenic fungi is using functional genomic techniques in conjunction with transcriptomics, proteomics, and gene editing to uncover the genetic mechanisms underlying their pathogenicity and host interactions. These studies lay the groundwork for identifying virulence factors, comprehending host–pathogen interactions, and developing tailored antifungal therapies (Chethana et al. 2020; Chakraborty et al. 2021; Duan et al. 2021; Kowalski et al. 2021; Peng et al. 2022; Przybyla and Gilbert 2022; Yu et al. 2022; Huang et al. 2023). A recent study used a combination of functional genomics and solid-state NMR spectroscopy to identify key genes involved in the cell wall assembly and remodeling of the fungal cell wall architecture of *Neurospora crassa*, and provided new insights into the spatial arrangement and interactions of cell wall components, improving our understanding of the structural response of fungal pathogens to stresses and revealing potential targets for antifungal therapies (Chakraborty et al. 2021). Advances in genome editing tools, such as CRISPR-Cas9, have opened up new paths for functional genomics research in fungi, enabling precise modifications to fungal genomes and accelerating the advances in fungal biology and pathogenicity (Kowalski et al. 2021; Duan et al. 2021; Wang et al. 2023a, b, c). Kowalski et al. (2021) used CRISPR-Cas9 to discover the critical role of its gene *CZF1* in *Candida glabrata* virulence and biofilm formation, highlighting its potential as a therapeutic target, while Duan et al. (2021) used a similar approach to identify the function of *FgHOG1*, in regulating stress responses and virulence in *Fusarium graminearum*. Characterizing these genes is crucial, as they can be utilized in developing green super crops that exhibit superior productivity and resilience to abiotic/biotic stresses using functional genomics and multi-omics technologies, holding great potential for addressing global food security challenges and reducing the environmental impact of agriculture (Varshney et al. 2019; Yu et al. 2022).

### Limitations on functional genomic studies

Several constraints limit the progress of functional genomics research and our understanding of fungal biology and interactions. In general, fungal genomes are complex, with varied genome sizes, repeated sequences, and high levels of genetic plasticity (Noble and Andrianopoulos 2013; Möller and Stukenbrock 2017). One major challenge for conducting functional genomic research is that the functions of a significant portion of fungal genes remain unknown or

hypothetical, making it challenging to interpret complex regulatory networks and pathways (Bouhired et al. 2007; Schäpe et al. 2019). While advanced genetic manipulation tools are available in many fungal species, these genetic tools and techniques are lacking in certain fungal species, hindering the efficient, targeted manipulation and functional analysis of specific genes (Huang and Cook 2022; Wang et al. 2023a, b, c). Furthermore, functional genomic research has focused primarily on well-studied model fungi (Magee et al. 2003; Lee and Dighton 2013), leaving many fungal species of ecological or industrial value with a scarcity of data. Gene and functional redundancy is often associated with fungal genomes (Noble and Andrianopoulos 2013; Herzog et al. 2020), affecting and restricting the success of functional genomics studies, as knocking out a single gene might not result in a noticeable phenotype due to the presence of redundant or compensatory mechanisms that contribute to similar or overlapping functions (El-Brolosy and Stainier 2017). Additionally, functional genomic studies often rely on phenotypic assays, which can be complex and time-consuming for characters that are difficult to quantify or visualize. These assays may not fully capture interactions in natural fungal habitats (Franco-Duarte et al. 2019), limiting their applicability to fungi. Environmental factors, developmental phases, and interactions with other organisms impact fungal gene functions (Rangel et al. 2015; Momin and Webb 2021; Lin et al. 2023a, b). A further limitation of functional genomics research is that it often focuses on specific circumstances or time points, which may not capture the entire range of fungal gene functions. Addressing and overcoming these limitations requires continuous advancements in genetic manipulation techniques, improvements in genome annotations, and the development of standardized methodologies, leading to a more thorough and complete understanding of fungal biology and interactions.

### Future perspectives for functional genomic research in fungi

The future of functional genomic research in fungi holds great promise. Advancements in high-throughput sequencing technologies, including single-cell genomics and long-read sequencing integrated with multi-omics approaches, facilitate the comprehensive characterization of fungal genomes and transcriptomes, thereby providing a more holistic understanding of fungal biology (Lorrain et al. 2019; Li et al. 2021a, b; Tedersoo et al. 2021a, b; Massart et al. 2022). The future of functional research should be expanded to a broader array of fungal taxa, including non-model fungi and those with agricultural, biotechnological, economical, and ecological relevance to overcome one of the previously mentioned limitations (Swift et al. 2019). In addition, future research should delve into the genetic basis of symbiotic

relationships, pathogenicity, and host-microbe interactions (Bosch et al. 2019; Fiorilli et al. 2020). Understanding the molecular mechanisms underlying these interactions will affect agriculture, human health, and ecosystem dynamics.

The widespread application of cutting-edge gene editing tools such as CRISPR-Cas9, pathway engineering, and synthetic gene circuits will be increasingly applied to functional fungal research (García-Granados et al. 2019; Xia et al. 2019; Otero-Muras and Carbonell 2021). This research will facilitate the design and engineering of fungi to produce valuable compounds, bioremediation, and other biotechnological applications (Arun et al. 2023; Ghosh et al. 2023). Further research is needed to improve these tools to achieve more efficient delivery methods, increased precision, and the ability to target specific genomic loci, thereby facilitating the identification of key genes and regulatory elements for synthetic biology applications with greater precision and scalability (Porto et al. 2020). Furthermore, rapidly advancing technologies such as single-cell genomics, transcriptomics, and automated, high-throughput phenotyping tools will be applied to fungal functional genomics research for studying cellular processes and gene expression at the single-cell level and enable understanding of the contributions of specific cell populations to fungal physiology and development (Maviane-Macia et al. 2019; Wösten 2019; Jansen et al. 2021; Seto et al. 2023). The automated, high-throughput phenotyping tools are specifically used to simultaneously investigate multiple phenotypic traits across a large fungal population, thereby accelerating research progress (Maviane-Macia et al. 2019; Jansen et al. 2021). Automated imaging, robotic systems, and machine learning algorithms assess the functions of genetic modifications and aid in identifying novel gene functions, characterizing gene networks, and discovering phenotypes associated with specific genetic variants (Shariff et al. 2010; Wainaina and Taherzadeh 2022). Moreover, future functional genomic research should increasingly be integrated into environmental metagenomics studies to investigate the gene expression patterns, metabolic adaptations, and functional traits of fungi in diverse environmental conditions, thereby contributing to our understanding of fungal ecology, ecosystem dynamics, and the impact of environmental changes on fungal communities (Gómez-Silva et al. 2019; Zhao et al. 2023).

In addition to those mentioned above, functional research integrated with multiple omics data sets (genomics, transcriptomics, proteomics, metabolomics, and epigenomics) to provide a system-level understanding of fungal biology and its responses to environment will continue to be a major trend in the future as well (Gómez-Silva et al. 2019; Swift et al. 2019; Li et al. 2021a, b; Wijayawardene et al. 2023a, b; Zhao et al. 2023). Therefore, data integration methods and computational analysis tools require advancements to successfully uncover intricate regulatory networks, metabolic

pathways, and molecular interactions within fungal cells and communities (Wijayawardene et al. 2023a, b). Functional annotation tools and methods require further improvements to ensure the accuracy and reliability of gene function predictions in fungal genomes. This can be achieved by establishing improved, reliable annotation pipelines by integrating experimental data, comparative genomics, and functional assays. The future of fungal functional genomics relies on collaborative research efforts and data sharing among research communities. Therefore, establishing a centralized database, repositories, and platforms for sharing functional genomics data will be of utmost importance (Byrd et al. 2020; Schatz et al. 2022) as they can accelerate discoveries and enable the broader scientific community to access and utilize the wealth of information generated through functional genomics studies.

## Current trends, limitations, and future research in fungi and the biocircular economy

### Current trends

Fungi are versatile organisms. They can produce a wide range of products, from food and feed to chemicals and fuels (Lübeck and Lübeck 2022; Copetti 2019; Hyde et al. 2019; Meyer et al. 2021; Vandeloos et al. 2021; Strong et al. 2022). They can also break down organic and inorganic materials and compounds, making them a potential waste management and pollution control tool (Vaksmas et al. 2023; Dashtban et al. 2010; Harms et al. 2011; Deshmukh et al. 2016). As a result, fungi are increasingly seen as critical players in the biocircular economy, an economic system that aims to minimise waste and maximise the reuse of resources (Kirchherr et al. 2017). With their ability to grow on various organic feedstocks and be functionalised into a range of diverse material types, fungi have the potential to revolutionise the way we think about and approach sustainability.

Fungi decompose, meaning they break down organic matter into smaller molecules that other organisms can reuse (Osono 2007; Holden et al. 2013; Niego et al. 2023a, b), a vital process for the ecosystem's functioning. This ability makes them a potential tool for waste management and pollution control. Fungi can be crucial in utilising farm waste and producing fertiliser or food. Agricultural waste, such as crop straw and livestock manure, can be treated through composting or aerobic fermentation to produce organic fertiliser. This process can help reduce dependence on chemical fertilisers and improve the application rate of organic fertiliser in soil (Mengqi et al. 2021).

Additionally, agro-industrial wastes can be used as raw materials for producing biofuels, enzymes, vitamins,

antioxidants, animal feed, antibiotics, and other chemicals through solid-state fermentation using fungi and other microorganisms (Sadh et al. 2018). Varma et al. (2015) showed that the decomposition rate of agricultural waste increased when inoculated with a white-rot fungus, while *Aspergillus niger* was efficient in producing cellulases and agro-waste materials (Jasani et al. 2016). Inoculating *Trametes versicolor* and *Fomes fomentarius* on the compost of an organic fraction of municipal solid waste led to a higher degrading ratio and increase of enzymatic activities (Voběrková et al. 2017).

Fungi can produce high-value food and feed products like mushrooms, Quorn, and tempeh (Amara and El-Baky 2023). These products are often considered more sustainable than traditional animal-based products, requiring less land and water to produce (Boland et al. 2013). Some species or isolates can synthesise chemicals like enzymes and antibiotics (e.g., Jakubczyk and Dussart 2020; Sanchez and Demain 2017; Khan et al. 2014; Conrado et al. 2022; De Silva et al. 2012, 2013). These products can be used in different industries, including the food, pharmaceutical, and energy sectors. Others can produce several materials, such as biopolymers, biocomposites, and mycelium-based foams, that can be used in various applications, including packaging, construction, and medical devices (e.g., Sydor et al. 2022; Yang et al. 2021; Manan et al. 2021; Alemu et al. 2022; Vandeloos et al. 2021; Bitting et al. 2022; Biala and Ostermann 2022).

Fungal biotechnology also produces biomaterials that can replace petroleum-based ones in various industries, including food, packaging, textile, leather, and automotive (Cerimi et al. 2019; Raman et al. 2022; Meyer et al. 2020). For example, the production of lipase by strains of *Aspergillus niger*, used in several industries, including food, pharmaceutical, and cosmetics, has been studied and optimised (Colla et al. 2016; Alabdallal et al. 2020). A new and more efficient bioprocess has been developed to produce bioethanol from agricultural waste (starch of avocado seeds) by using a natural strain of *Saccharomyces cerevisiae* (Caballero-Sanchez et al. 2023). A new mycelium-based biodegradable and recyclable foam that could be used in many applications, such as packaging and insulation, has been developed (Gandia et al. 2021; Karana et al. 2018; Yang et al. 2009). This could lead to the construction of healthier buildings made of components that are grown instead of manufactured and can be triggered to biodegrade at the end of their life.

Fungi, especially mycelium, are increasingly recognized for their potential in carbon sequestration and as a source of bio-based materials, keeping climate-warming carbon dioxide out of the atmosphere. Indeed, using biodegradable building materials can contribute significantly to carbon sequestration. Bio-based materials integrate various mitigation techniques, including low embodied energy and carbon, affordability, recyclability, utilisation of locally sourced



materials, and the ability to repurpose waste and byproducts (Alemu et al. 2022). Biological materials offer indirect benefits in reducing organic waste. This is because the raw materials used to produce microbial-based materials are often locally available organic wastes. This promotes recycling and waste reduction, contributes to local economies, and reduces the carbon footprint associated with transporting materials. According to Kumarappan et al. (2018), using biological materials in construction could reduce carbon emissions by nearly 800 million tons annually.

Fungi have also been found to break down contaminants such as polyaromatic hydrocarbons, heavy metals, herbicides, pesticides, cyanotoxins, pharmaceuticals, antibiotics, phthalates, dyes, and detergents (Akhtara and Mannana 2020). In this process, fungi produce enzymes that can break down specific types of waste. For example, fungi can produce enzymes that can break down plastics (e.g., Andler and Goddard 2018; Okal et al. 2023; Ekanayaka et al. 2022; Temporiti et al. 2022; Ren et al. 2021), wood, and other materials (e.g., Orth et al. 1993; Hammel et al. 1997; Azelee et al. 2020; Goodell et al. 2020; Beltrán-Flores et al. 2022; Geethanjali et al. 2020). These enzymes can then treat waste materials in various settings, such as industrial wastewater treatment plants and landfills, and grow them directly on the substrate. In this way, fungi can also be used to produce biogas from different organic materials, including food waste, agricultural waste, and sewage sludge. They can break down these materials and produce methane, the main component of biogas (Dollhofer et al. 2015; Kazda et al. 2014; Kovács et al. 2022). In addition to their natural ability to break down waste materials, scientists are also developing new biotechnological solutions to harness the power of fungi for waste disposal and ecosystem restoration (Kulshreshtha et al. 2014; Akhtar and Mannan 2020; Akpasi et al. 2023).

## Limitations

Even though fungi have great potential and diverse applications, several downsides must be addressed. One of the critical areas of research in fungi and the biocircular economy is the development of new fungal strains and bioprocesses to produce high-value products (Tiwari and Dufossé 2023). The development of even more sustainable and cost-effective ways to make these products, will significantly impact the biocircular economy. Developing new fungal strains and bioprocesses for producing high-value products is however, complex and challenging. For example, there is a need for further research and development to optimise the use of fungi as sources for novel compounds and as cell factories for the large-scale manufacture of bio-based products (Lübeck and Lübeck 2022; Meyer et al. 2016; Vandellook et al. 2021).

Additionally, controlling fungal pathogenicity is a significant challenge that needs to be addressed to improve the efficiency and safety of using fungi in biotechnology (Meyer et al. 2016). Also, their slow growth rate, the intrinsic characteristics of a species and the ecological conditions it is exposed to (Gostinčar et al. 2022), and sensitivity to environmental conditions (Bakar et al. 2020) are constraints to their utilisation on the industrial scale. Research should address these limitations by developing or selecting faster-growing and more efficient fungal strains, optimising bioprocesses for producing high-value products from fungi and developing new methods for their use.

There is also the potential for fungi to produce harmful metabolites such as toxins (Bennett and Klich 2003). This includes mycotoxins such as aflatoxins, ochratoxins, and trichothecenes that can cause a variety of health problems, including food poisoning, liver damage, and cancer (World Health Organization 2023; Bennett and Klich 2003; Omotayo et al. 2019; El-Sayed et al. 2022), alkaloids such as psilocybin, psilocin, and ergot alkaloids that can have a variety of effects on humans, including hallucinogenic, stimulant, and sedative effects (Plazas and Faraone 2023); Polyketides including penicillin, griseofulvin, and lovastatin that can act antibiotic, antifungal, and anti-inflammatory effects on humans (Prescott et al. 2023; Conrado et al. 2022). However, several steps can be taken to mitigate this risk of exposure to harmful metabolites produced by fungi, such as growing fungi in controlled environments, testing fungi for the presence of harmful metabolites, and processing fungi in ways that can inactivate toxic metabolites.

Furthermore, while mycelium-based materials have excellent properties and ecological advantages, challenges remain to overcome. One of the primary challenges is their variable structural strength depending on the substrate, strain, incubation time, and fabrication process (Alemu et al. 2022), which means they cannot support much weight and restricts their use in specific applications, making it challenging to produce consistent, high-quality materials. While the raw materials for growing mycelium are inexpensive, the initial costs associated with mass production and distribution, typical of industrial fabrication, are high. Furthermore, mycelium, like any living organism, can be unpredictable, which could lead to inconsistencies in the final product.

Another challenge is scaling up the production of mycelium biomaterials to a level that can significantly contribute to global carbon sequestration. Also, the longevity of mycelium materials in different environments is not fully understood, and if these materials degrade quickly, they may release stored carbon back into the atmosphere. It becomes evident that the lack of established standards or regulations for using these materials in many applications, could slow their adoption. Besides, as with any new technology, public perception and acceptance will play a role in the widespread

adoption of mycelium materials. These challenges underscore the need for further research and development in this field.

### Future research

Fungi play a significant role in the biocircular economy by providing sustainable alternatives to traditional products and materials. Despite many challenges, fungal biotechnology has a growing trend towards producing fungal-based biomaterials that can contribute to a more sustainable and circular economy (Meyer et al. 2016; Kržišnik et al. 2023; Delvendahl et al. 2023; Wikandari et al. 2022). However, some challenges and limitations must be addressed, such as the slow growth rate of some fungi, their sensitivity to environmental conditions, and the potential for some fungi to produce harmful metabolites.

Future research in fungi and the biocircular economy will likely focus on overcoming these limitations and developing new and innovative ways to use fungi to create a more sustainable future. Developing new methods to drive more sustainable ways to deal with waste materials using fungi is a crucial area of research in the biocircular economy. This may include developing more robust fungal strains, optimising bioprocesses for producing high-value products and developing new methods for degrading and recycling waste materials using fungi. Developing new fungi-based materials with improved properties, studying the potential of fungi to produce harmful metabolites, and developing strategies to mitigate this risk are also important. By addressing the challenges and unlocking the full potential of fungi, we can create new opportunities to develop bio-based products.

Several key factors underscore the necessity for research on mycelium-based composites. Firstly, A deeper understanding of the properties of mycelium materials and how

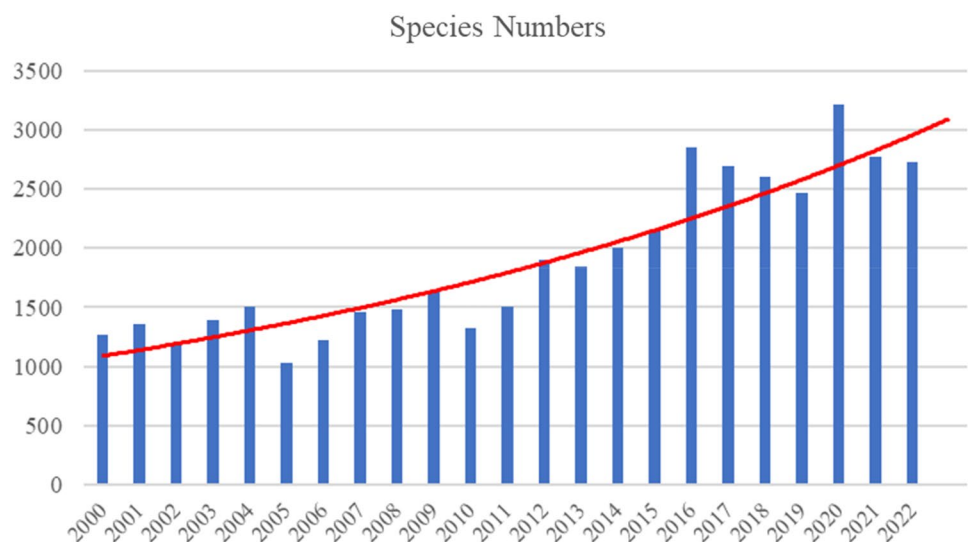
to manipulate them is required. Secondly, research can aid in devising more efficient and cost-effective production techniques. Thirdly, the absence of established standards or regulations for using mycelium materials in many applications necessitates research to help formulate these standards and regulations, thereby facilitating the adoption of these materials. Furthermore, mycelium-based materials hold potential in various applications, from construction to carbon sequestration. Research can assist in exploring these applications and optimising the materials for each use. Lastly, more research is imperative to comprehend the environmental impact of mycelium materials, such as their longevity and potential for carbon sequestration. This research needs to underscore the potential of mycelium-based composites and emphasize the importance of continued investigation in this field.

Finally, selecting highly promising strains is also an active area of investigation. Researchers are working on large-scale phenotyping of fungal strains to evaluate their potential for degrading non-natural, industrial compounds (Navarro et al. 2021). Additionally, using innovative approaches, such as genetic engineering for enzymes, fuels, and chemicals from lignocellulose biomass is important (Madhavan et al. 2022). These efforts aim to unlock the full potential of fungi as sources for novel compounds and as cell factories for the large-scale manufacture of bio-based products.

### Current trends, limitations, and future research in the quest for species numbers

The number of fungal species is a hotly debated topic among mycologists (Hawksworth et al. 1991; Hawksworth and Lücking 2017; Hyde et al. 2020a, b). The estimated number is currently higher than the known species (Phukhamsakda

**Fig. 4** Number of new species introduced from 2000 to 2023. (Numbers extracted from Index Fungorum.org (<https://www.indexfungorum.org/names/Names.asp>))



et al. 2022). A large number of novel taxa have been introduced in recent years (Fig. 4). In this section, we discuss current trends in introducing and estimating species numbers. How do these methods and approaches result in novel species. Do the current papers dealing with the topic, overestimate the species number? We address future direction needs in the quest for the species number?

## Current trends

### Novel fungi, are they an untapped potential?

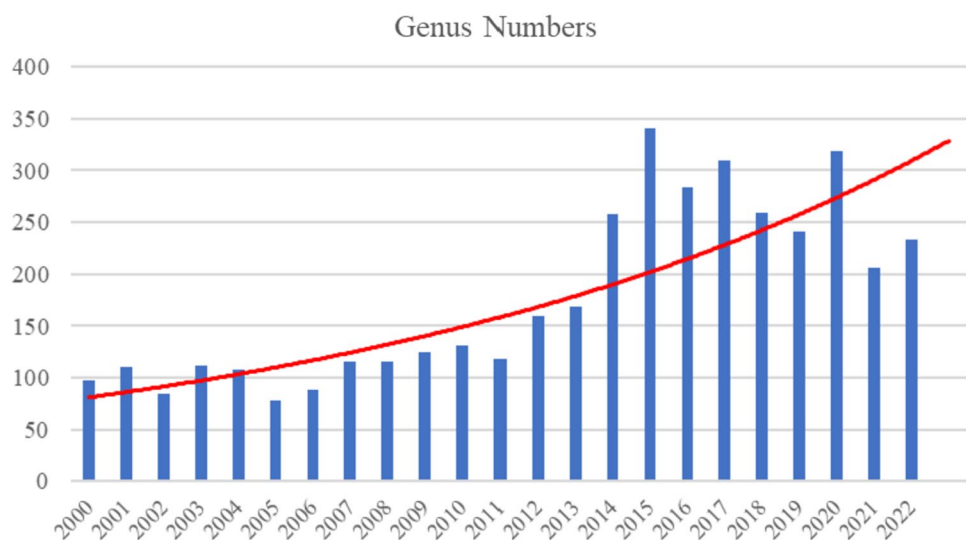
Introducing novel species is common practice, but what is the point? Besides the need to understand fungal diversity worldwide, taxa also have a huge potential in biotechnology (Sandargo et al. 2019; Hyde et al. 2020a, b; Niego et al. 2023a, b) and therefore it is essential to search for and describe novel taxa. Figure 5 illustrates the number of novel species introduced in the last 22 years. Although there have been yearly fluctuations, since the turn of the century, the number of new species that have been described has increased from 1264 (in 2000) to 2734 (in 2022), peaking at 3216 in 2020. The figures for 2021 and 2022 were slightly lower (2772, 2734), probably due to the restrictions due to Covid-19. Similarly, the number of new genera described has increased from 98 in 2000, tripling to 319 in 2020, with a peak of 340 in 2015. Again, figures for 2021 and 2022 were lower (206, 233).

The increase in the number of novel fungi described yearly might be as a result of expanding collection sites or increased studies in certain countries (e.g., China, Thailand) and advancement of DNA techniques which have become standard practice (Cheek et al. 2020). Based on the ratio of plants to fungi, Hawksworth (1991) estimated there could be around 1.5 million fungal species, of which only about 10%

had been described. However, based on high-throughput sequencing (HTS), it is estimated that the number of fungal species could be as high as 11.7 to 13.2 million (Blackwell 2011; Baldrian et al. 2021). However, HTS results in a large number of unidentified taxa and technically compromised sequences (Nilsson et al. 2014), thus estimations based on HTS might be an overestimation.

In 2022, a study series was published to estimate the global numbers of fungi. In this series, Wijayawardene et al. (2022a, b) reported that around 30,000 anamorphic (or asexual) species belonging to 3800 genera have been described, while Senanayake et al. (2022) estimated 1.37 to 2.56 million teleomorphic (sexual) species of which 83,000 have been described. The number of basidiomycetes species is estimated to be between 1.4 and 4.2 million (He et al. 2022), whereas single-celled yeast species are estimated to be 20,000 (Boekhout et al. 2021). New yeast species have been introduced at a very rapid rate, particularly due to an extensive research contribution from Asia, in which China has yielded many taxonomic novelties (Boekhout et al. 2021). Several studies have focused on estimating the number of species based on ecological niches. Mora et al. (2011) predicted that there could be over 50,000 (0.005 million) marine species. On the other hand, Sarma (2019) showed that the number of marine species increased from 530 in 2009 to 1112 species by 2015. Jones et al. (2019) listed 1257 marine species, which included 943 ascomycetes. Thus, the number of species of from marine environments is increasing gradually. However, we are far behind in ocean exploration as compared to that in terrestrial habitats. Research on freshwater fungi has also greatly increased and numerous new species have been described, particularly from China and Thailand (Calabon et al. 2023; Yang et al. 2023). Dong et al. (2020) introduced nine new genera of freshwater Dothideomycetes and 33 new species, whereas Luo et al. (2019)

**Fig. 5** Number of new genera introduced from 2000 to 2023. (Numbers extracted from Index Fungorum.org (<https://www.indexfungorum.org/names/Names.asp>))



introduced two new families, three new genera, and 47 new species belonging to Sordariomycetes.

Hyde et al. (2020a, b) considered that the newly introduced species curve had not reached asymptote, based on studies in Asia. Mycology was well-established in Australia, Europe, New Zealand, South Africa and the USA, whereas in the past two decades it has been increasing in Asia and South America (Hyde et al. 2020a, b). The earliest studies on fungal taxonomy were by European mycologists (Wijesinghe et al. 2023). However, based on the State of the World's Plants and Fungi (Royal Botanic Gardens (Kew; Antonelli et al. 2020), the proportion of fungi introduced since 2019 from Europe is lower (23%) as compared to the Asia (41%).

The current introduction of novel species and genera introduced from 2020 to 2022 is likely to continue to increase due to several factors. (1) There are no longer travel restrictions and forays will become commonplace. (2) Annually published collections such as in the Fungal diversity notes (Boonmee et al. 2021; Jayawardena et al. 2022), Fungal planet description sheets (Crous et al. 2022; Tan et al. 2022) and Mycosphere notes (Thambugala et al. 2018; Manawasinghe et al. 2022) which encourage collections of novel taxa and have higher citation scores as compared to the average of other papers in mycology. Some open-access journals are also encouraging papers comprising novel species with designated special issues as this is beneficial for improving journal citation indexes.

### What is a fungal species?

In order to estimate fungal numbers, it is crucial to understand what a species is. The definition of a genus and species has received much attention (Liu et al. 2016; Chethana et al. 2021; Lücking et al. 2021). Publications have focused on providing recommendations to introduce new species. Aime et al. (2021) provide a basis to accurately introduce a new species or a name. Chethana et al. (2021) provided overall recommendations for introducing new species. Recommendations for establishing species for specific groups of fungi include namely lower fungi (Voigt et al. 2021), ascomycetes (Maharachchimbura et al. 2021), plant pathogens (Jayawardena et al. 2021; Manawasinghe et al. 2021), and yeasts (Boekhout et al. 2022). In all cases, a polyphasic approach has been recommended, which includes the combination of morphology, phylogeny, ecology, chemistry, and any other useful evidence. It is not clear that these recommendations have been followed in recent publications. Introducing new taxa based on only one strain, only sequence variations, missing required gene regions, invalid species names, and poor taxon sampling (Kularathnage et al. 2023; Tang et al. 2023; Yasanthika et al. 2023; Zhu et al. 2023) are some examples.

With the increased availability of molecular data, the phylogenetic species concept has resulted in a number species becoming cryptic such as in pestalotioid genera (Maharachchimbura et al. 2014a, b), *Diaporthe* (Udayanga et al. 2014) and *Colletotrichum* (Jayawardena et al. 2022). When introducing new species, it is essential to establish a complete sampling of representative taxon in the phylogenetic analysis. For example, the *Diaporthe eres* species complex is highly diverse and *D. eres* is polyphyletic (Udayanga et al. 2014). Therefore, it is necessary to add additional strains as well as the type species when introducing a new species in this complex. *Diaporthe rosicola* (Manawasinghe et al. 2018) and *D. mahothocarpus* (as *mahothocarpus* in Gao et al. 2015) were introduced without adding adequate strains. A combined multigene (ITS, *tub2*, calmodulin (*cal*), and *tef1*) analysis, *D. rosicola* and *D. mahothocarpus* clustered together with *D. eres* with an increased number of strains *D. eres* (Manawasinghe et al. 2019) suggesting that both *D. rosicola* and *D. mahothocarpus* are genotypes of *D. eres*.

Fungi are one of the most diverse groups of organisms, and therefore it is necessary to take into account population biology when introducing novel taxa. Inter-species diversity is based on the host or geographical regions. Bhunjun et al. (2022) predicted that specious genera could contain more species than expected. The limiting factor in defining a species in a specious genus however, depends on the ability to determine the amount of variation that can be accepted in a single species. For example, *Colletotrichum* has 14 species complexes and 248 accepted species, of which *C. gloeosporioides* is one of the most diverse and widely distributed species (Jayawardena et al. 2022). *Colletotrichum gloeosporioides* has 12% and 88% genetic differentiation between and within host populations, respectively, based on the genetic diversity of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) region (Liu et al. 2023). Therefore, to define a new species which is closely related to *C. gloeosporioides*, we assume that it should exceed this genetic variation. Therefore, within-species diversity that must be concisely dealt with for most of the asexual and specious genera. In the present era of the phylogenetic species concept, morphology tends to have become less important. Most novel introductions of species provide excellent descriptions. However, environmental factors may affect characters such as spore length and width. Thus, describing a novel species using a single strain may be questionable. Therefore, when introducing a new species, it is recommended to use more than one strain (Manawasinghe et al. 2021). The use of the single strain has the risk of introducing a new genotype with sequencing errors. There are numerous examples of this. *Pseudopithomyces kunmingensis* was introduced by Karun and Hyde [as '*kunmingensis*'], in Hyde et al. (2017) using a single strain. Abeywickrama et al. (2023) found no significant nucleotide differences in



GAPDH and *tef1- $\alpha$*  sequence data between *P. chartarum* and *P. kunmingensis*. Thus, they synonymised *Pseudophthomyces kunmingensis* under *P. chartarum*, based on morphological similarities and phylogenetic analysis. Zhang et al. (2021a, b) synonymised recently published *Botryosphaeria* species; *B. auasmontanum*, *B. minutispermata*, *B. quercus*, *B. sinensis*, *B. wangensis* and *B. qinlingensis* under *B. dothidea* based on sequence similarities where all these species share 99% or over similarities with the type sequence of *B. dothidea*. Zhang et al. (2023a, b) reduced *C. pandanicola* (Tibpromma et al. 2018) to *C. siamense* as there are only few variations in four gene regions (ITS four bp, *gapdh* six bp, *chs-1* four bp, *act* two bp, and *tub2* one bp).

There is no universal method to characterise a new species and species concepts and approaches in mycology will always be subjective. However, it is necessary to standardise sequence-based novel species introduction. Otherwise rather than describing distinct novel taxa we may separate a single taxon into several species.

## Limitations

There are many under-studied geographic regions (e.g., Africa, South America) and more research effort is needed in these areas (Antonelli et al. 2020). Contributions to the fungi in North America and Europe have, however, decreased in recent years as compared to those in Asia (Hyde et al. 2020a, b). One possible reason for this could be the lack resources allocated for basic mycological research (Rambold et al. 2013). African rainforests have a huge plant biodiversity, which is subjected to climate change, forest expansion, deforestation and human interactions (Mahli et al. 2013) and therefore the study of their fungi is important before they become extinct.

The multifarious regulatory measures adopted by individual nations greatly restrict access and exploration of biological hotspots for those interested in sampling and studying their fungal biodiversity. Ironically, most such biodiversity hotspots are based in tropical and subtropical regions (Kumar et al. 2017; Deharveng and Bedos 2019) and fall within the category of developing countries. As the name suggests, these countries have limited financial and physical resources. Therefore, the economic policies of these developing nations cannot afford biodiversity explorations. This situation gets more complex when these countries are signatory to the Convention on Biological Diversity (CBD), Access and Benefit-sharing (ABS) rules and other bureaucratic barriers preventing joint research or international collaborations. One example is the status of mycology in Sri Lanka. Even though mycology in Asia has a rapid growth, Sri Lanka, with its most prominent biodiversity, lacks sufficient studies due to limited resources and stringent biodiversity policies (Wijayawardene et al. 2023a, b).

Despite being poorly studied ecological niches, studies of fungi in terrestrial habitats have been greater as compared to aquatic and marine habitats (Jones et al. 2019). The fungi associated with freshwater streams, mangroves, karst regions, and rocks are some habitats that have recently been explored (Osorio et al. 2017; Norphanphoun et al. 2019; Calabon et al. 2023; Yang et al. 2023). Mangrove fungi represent the second-largest ecological group of marine fungi (Deshmukh et al. 2018). Several novel taxa were introduced in early studies on marine fungi (Hyde and Jones 1988; Hyde et al. 1992). The majority of these taxa lacked sequence data, and need to be recollected, sequenced and published as new collections. Studies on rock fungi are less common, despite their diversity, probably because these species being slow-growing, poor competitors, widespread in nature, and occurring commonly (Coleine et al. 2021). Entomopathogenic fungi are well-researched due to their potential as biocontrol agents, yet compared to phytopathogenic fungi, the introduction of novel species associated with ants and arthropods is comparatively low. A recent study by Zhang et al. (2023a, b) introduced five novel nematode-trapping fungi associated with soil and freshwater sediment samples. Thus, it reflects expanding studies on fungi associated with arthropods, nematodes and other animals that have a high potential to result in novel taxa.

Fungal lifestyles are diverse and have been discussed in detail. Yet, several lifestyles have been either poorly studied or overlooked. Endophytes are one of the most studied fungal lifestyles (Purahong and Hyde 2011) yet remain far behind in numbers of new taxa because not many species were sequenced. Concurrently, the HTS approach presupposes very high fungal numbers within the same community (Dissanayake et al. 2018; Jayawardena et al. 2018; Abeywickrama et al. 2023). It has been estimated that number of endophytes be approximately one million (Sun and Guo 2012) however, current isolation techniques and the inability to culture them on artificial media have become limiting factors to finding new species.

## Future research needs

Fungi have an amazing potential in resolving future global needs such as renewable energy, human nutrition, health, and sustainable agricultural. Fundamental research in mycology is a separate discipline to zoology and botany (Christensen 1989; Rambold et al. 2013) and should be treated as such (Rambold et al. 2013). Though fungi play a crucial role in ecosystem stability, the involvement of mycologists in ecological and diversity studies is less when compared to botanists and zoologists (Schmit and Mueller 2007; Rambold et al. 2013). This is the case even when dealing with topical studies such as climate change (Tibpromma et al. 2021). Fungi need to be appreciated as a key component in

ecosystem stability, and their contribution should never be underestimated. Simultaneously mycologists need to diversify and integrate their research into subdisciplines, such as biotechnology, biochemistry, ecology, genetics, natural products and nutritional science, and pathology.

Over the last two decades, DNA sequencing, high-throughput technology and molecular methods have advanced significantly (Nilsson et al. 2019a, b; Mapook et al. 2022). It is important to verify species in genera such as *Colletotrichum*, *Diaporthe*, *Fusarium* and *Pestalotiopsis* as they are important phytopathogens and may also produce a number of metabolites (Manawasinghe et al. 2019; Matio Kemkuignou et al. 2022).

The use of polyphasic approaches and other techniques to justify the introduction of novel species has been stipulated (Chethana et al. 2021). However, in a situation where the answer to ‘What is a fungal species?’ changes constantly, introducing a new species will continue to be a challenge. At present, most studies rely on the phylogenetic species concept combined with morphology. Poor taxon sampling and biased referencing must be avoided. However, taxonomy is subjective and open to critical evaluations.

The quest for fungal numbers should be expanded to understudied regions and habitats including Africa, Australia, South America, and some Asian countries. Furthermore, a concerted effort must be in place for future collections to adequately cover all the underexplored niches like forest ecosystems, deep sea, marine, and extreme conditions, including caves, hot springs, and rock-associated fungi. The necessity to explore fungal species from extreme environments is important because that is where the potential lies for the development of new secondary metabolites due to the adaptive nature of fungi to extreme environmental conditions (Gostinčar et al. 2022; Yu et al. 2023).

Fungal species number estimations require further research (Hyde et al. 2020a, b). Even though the actual number of species might be lower or higher than the present estimates, it is obvious that there are a numerous understudied and unexplored regions with hidden mycota. Without a doubt, these novel species will contribute to the development of agriculture, industrial biotechnology, medicine, and disease management.

## Current trends, limitations, and future research in machine learning in mycology

As a subfield of artificial intelligence, machine learning is normally categorised into two primary types: unsupervised and supervised learning (Mahesh 2020). Unsupervised learning algorithms recognize hidden patterns, structures, or relationships within the given observations where the input data does not have corresponding output labels or

target values. K-means clustering and principal component analysis are the most typical unsupervised learning methods to find elusive patterns in high-dimensionality datasets (Ding and He 2004). In some sense, phylogenetic trees can be treated as outcomes of unsupervised algorithms that the algorithm does not have prior knowledge of the tree topology or relationships between the sequences. Instead, it seeks to find the most likely tree that best explains the observed sequence data without relying on predefined classifications. While supervised learning algorithms rely on well-constructed training datasets with input data and the corresponding outputs, develop a predicting model by learning the hidden associated patterns, and use the model to predict the outputs of new input instances. In the era of data explosion, a large number of biological data are being generated by advanced analytic instruments, and machine learning algorithms have been a widely used analytical method to extract information and reveal hidden patterns from overwhelming amounts of data or complex data (Ma et al. 2014; Greener et al. 2022). Some image-recognition-based fungal classification and disease diagnosis models have been developed for fungi to identify fungal species or detect specific morphological features. Zahan et al. (2021) developed a deep learning-based approach to classify the edible, inedible, and poisonous mushroom types. Also, they developed a model to detect mushroom diseases (Zahan et al. 2022). Mikhail et al. (Genaev et al. 2020) developed a model to recognize wheat rust diseases and can differentiate between leaf rust and stem rust. In genomics, some machine learning algorithms were used in well-known programs, such as AUGUSTUS, to de novo annotate gene models in new sequenced fungal and other eukaryotic genomes, and effectorP to predict fungal effector protein candidates from entire secreted protein datasets (Sperschneider and Dodds 2022). Machine learning algorithms are being used to predict the ecological roles and functional traits of fungi based on genomic traits (Fijarczyk et al. 2022; Chen et al. 2023b), which can help in the early identification of devastating fungal species with potential high pathogenicity to humans or plants. There have been some applications of machine learning algorithms in mining secondary metabolites (Aghdam and Brown 2021; Skinnider et al. 2016, 2020).

## Limitations

In mycology, the limited availability of comprehensive and reliable datasets, particularly for rare or understudied fungi, can be challenging. Machine learning models by image recognition to identify fungal species have been developed only for economic macrofungi, whereas researchers cannot obtain enough morphological images for training the predictive model for most wild macrofungi. In the study of microfungi, it is not easy to obtain the image data because we

cannot directly observe the useful diagnostic characteristics without the assistance of optical microscopes. Highly similar characteristics in the morphology of some plant pathogens make image recognition useless in identifying microfungi. Machine learning algorithms, especially deep learning, often act as "black boxes" with limited interpretability (Azodi et al. 2020). However, mycologists need to understand the specific biological mechanisms and identification processes.

## Future

For image recognition in macrofungi, a shared database of image data checked by taxonomists should be developed for obtaining more diverse and reliable morphological images of some rare fungi species. Integration of multi-omics data, such as genomic, transcriptomic, proteomic, and metabolomic data, can provide a more comprehensive understanding of fungal biology. Machine learning models can uncover the hidden association between the genomic traits and the capacity of producing beneficial secondary metabolites, which avoids duplicated screening and expands screening populations in genome mining, helping to quickly target the fungal strains that are candidates for producing candidate drugs (Fungal genomes scoured for drugs 2018). Collaborations between mycologists and data scientists and the availability of high-reliable data and advanced computational techniques will drive further progress in this field.

## Current trends, limitations, and future research in detecting plant pathogens

Plant pathology is the field of study of plant diseases and disease-causing agents, across a diverse range of natural and man-made environments. They cause substantial yield losses in several economically important crops, resulting in economic and social adversity (Venbrux et al. 2023). Plant pathogens can be microfungi, macrofungi, and fungus-like organisms (Hyde et al. 2014a, b; Jayawardena et al. 2019). Human practices such as monoculture farming and global trade affect the spread of plant pathogens and the emergence/reemergence of diseases (Gomdola et al. 2022). Accurate estimates of disease incidence, severity, and the negative effects of the disease on quality are very important. Hence, the early detection and identification of pathogens are important to reduce the associated agricultural and social losses. These pathogens have been identified and are based mainly on morphology and molecular analyses (Senanayake et al. 2020; Dissanayake et al. 2020). Several techniques are available to detect plant pathogens including culture-based, PCR-based, sequencing-based, and immunology-based techniques. The evolutionary processes of these pathogenic fungi were often fuelled by genetic variation in pathogen

populations (Manawasinghe et al. 2021). Based on multi-loci analyses, a better understanding of pathogenic fungi has been obtained. Many cryptic species, in genera such as *Colletotrichum*, and *Diaporthe* were identified (Talhinhas and Baroncelli 2021; Norphanphoun et al. 2022).

Non-invasive optical and spectral detection methods such as imaging efficiently detect plant diseases (Venbrux et al. 2023). It has been shown that stressed or diseased plants produce a different spectral signature compared to that of healthy plants (Zubler and Yoon 2020). According to Singh et al. (2021), spectral analysis can be applied at different scales, ranging from taking high-resolution images from a single leaf to an entire field. In large cultivation areas, imaging can help to detect a 'hot spot' that is experiencing biotic stress. *Fusarium virguliforme*, the causative agent of sudden death syndrome in soybean can be detected via satellite imaging (Raza et al. 2020). This technique provides real-time detection and detects biotic stress without any sample collection.

Cultivation-based methods are used to isolate and grow the pathogen on a selective or semi-selective medium (Senanayake et al. 2020). Isolates obtained via this method need to be confirmed by morphological, molecular, and biochemical assays (Ferone et al. 2020). Different types of PCR-based diagnostic methods have been used to identify fungal phytopathogens (Table 1). For a better resolution of the pathogens, analytical profile index, microplates, matrix-assisted laser desorption/ionisation, and fatty acid profiling (Chen et al. 2020; Ferone et al. 2020). Fatty acid profile analysis allows taxonomic identification of the pathogen up to the species level and is cost-effective as well as a rapid method in species identification (Lacey et al. 2021). In taxonomic identification, DNA barcoding also plays an important role (Hyde et al. 2014a, b; Chethana et al. 2021). In recent years various molecular techniques such as Amplified Fragment Length Polymorphism (AFLP), Inter Simple Sequence Repeats (ISSR), Random Amplified Polymorphic DNAs (RAPD), Simple Sequence Repeats (SSR), Sequence-Related Amplified Polymorphism (SRAP), and Inter Primer Binding Site (iPBS) amplification techniques have been successfully used in plant pathogen identification (Cannon et al. 2012; Longya et al. 2020). Genealogical Concordance Phylogenetic Species Recognition is used to differentiate species that lack distinguished morphological characteristics when enough independent samples per lineage are provided (Jayawardena et al. 2021a, b). Bhunjun et al. (2020; 2021) highlighted the importance of using different molecular approaches such as Automatic Barcode Gap Discovery (ABGD), General mixed Yule-coalescent, and Objective clustering in plant pathogen identification. *Fusarium* head blight caused by *Fusarium graminearum* can be identified by a CRISPR-Cas12a-based dual recognition technique

**Table 1** Different types of PCR used in phytopathogen identification

Type of PCR	Phytopathogen	Host	References
End-point	<i>Cercospora tezpurensis</i>	<i>Capsicum assamicum</i>	Meghvansi et al. (2013)
	<i>Exobasidium maculosum</i>	<i>Vaccinium</i> sp.	Brewer et al. (2014)
	<i>Golovinomyces cichoracearum</i> sensu lato	<i>Cannabis sativa</i>	Pépin et al. (2018)
	<i>Cercospora flagellaris</i>	<i>Cannabis sativa</i>	Doyle et al. (2019)
	<i>Neopestalotiopsis clavisporea</i>	<i>Macadamia</i> sp.	Prasannath et al. (2020)
	<i>Colletotrichum siamense</i>	<i>Macadamia</i> sp.	Prasannath et al. (2020)
Nested PCR	<i>Puccinia striiformis</i> f. sp. <i>tritici</i>	<i>Triticum</i> sp.	Wang et al. (2009)
	<i>Phytophthora cactorum</i>	<i>Fragaria</i> × <i>ananassa</i>	Bhat and Browne (2010)
	<i>Colletotrichum gloeosporioides</i>	<i>Dioscorea</i> spp.	Raj et al. (2013)
Multiplex PCR	<i>Coniella granati</i>	<i>Punica granatum</i>	Yang et al. (2017)
	<i>Fusarium verticillioides</i> and <i>F. subglutinans</i>	<i>Zea mays</i>	Faria et al. (2012)
	<i>Neofabraea alba</i> , <i>N. perennans</i> and <i>N. keinholtzii</i>	<i>Malus domestica</i>	Michalecka et al. (2016)
Quantitative PCR	<i>Fusarium oxysporum</i> f sp. <i>cubense</i> lineage VI strains	<i>Musa</i> spp.	Ndayihanzamaso et al. (2020)
	<i>Didymella bryoniae</i>	Cucurbits	Ling et al. (2010)
	<i>Ramularia collo-cygni</i>	-	Havis et al. (2014)
	<i>Rhizoctonia solani</i>	<i>Nicotiana tabacum</i>	Zhao et al. (2014)
	<i>Magnaporthe oryzae</i>	<i>Oryza sativa</i>	Sun et al. (2015)
	<i>Verticillium longisporum</i>	<i>Brassica napus</i>	Depotter et al. (2017)
	<i>Pyrenophora tritici-repentis</i> and <i>Parastagonospora nodorum</i>	<i>Triticum</i> spp.	Abdulla et al. (2018)
	<i>Fusarium culmorum</i>	Cereals	Bilska et al. (2018)
	<i>Fusarium guttiforme</i>	<i>Ananas cosmosus</i>	Carnielli-Queiroz et al. (2019)
	End-point PCR and quantitative PCR	<i>Phacidiopycnis washingtonensis</i> and <i>Sphaeropsis pyriputrescens</i>	<i>Malus domestica</i>
<i>Guignardia citricarpa</i>		<i>Citrus</i> spp.	Faganello et al. (2017)

developed to detect this pathogen as low as 1 fg/μL of total DNA (). For the detection of *Botrytis cinerea* and *Didymella bryoniae*, two DNA targets were used in the development of a reusable microfluidic bioassay. Thermal denaturation of DNA was then performed to regenerate the oligonucleotide sequence and a quick assessment of multiple target detection using the laser-induced fluorescence detection technique was done in less than 10 min (Qu et al. 2017). Loop-mediated isothermal amplification (LAMP) assays have been used recently in plant pathogen detection. A quick, sensitive, and focused LAMP-based test has been used to detect *Sclerotinia sclerotiorum* (Grabicoski et al. 2020). Wang et al. (2020) mentioned that highly specific LAMP primers for *Fusarium proliferatum* are appropriate for the TEF-1 region. The use of LAMP assay for quick detection of *F. proliferatum* causing ear and kernel rot in maize was also described by Wang et al. (2020). Karimi et al. (2019) described the detection of *Colletotrichum*

*nymphaeae* infection in asymptomatic strawberry plants based on LAMP assays.

To speed up the identification of plant pathogens and allow their identification in the field, a number of serological methods have been developed, mainly based on the enzyme-linked immunosorbent assays (ELISA), which can be considered an immunological method (Luchi et al. 2020). Different immunoassay methods have been used to visualise the binding of a specific antibody to its related antigen (Miller and Martin 1988). As ELISA needs a laboratory facility, a simple paper-based dip-stick assay, namely lateral flow devices (LFD) to detect the presence or absence of a target analyte in a liquid sample was developed. This method is widespread as it allows rapid in-field detection of plant pathogens in a few minutes (Boonham et al. 2014; Tomlinson et al. 2010). Quantum dots offer a unique optical property known as fluorescence resonance energy transfer between two reactive molecules (Sanzari et al. 2019). This property is



exploited by QT-FRET immunoassays for visual identification of pathogen infections such as *Aspergillus amstelodami* (Safarpour et al. 2012).

Digital agriculture is an innovative approach to farming that uses modern technologies to enhance agricultural practices. High-resolution remote sensing and data analytics are being utilised to monitor and predict disease outbreaks. This digital agriculture technology allows for timely and targeted interventions, reducing the need for blanket applications of pesticides. Biosensors comprise devices that consist of a biorecognition element combined with a physicochemical transducer that generates a measurable signal upon the binding of the target analyte with the biorecognition element (Bridle and Desmulliez 2021). Biosensors are promising tools for point-of-care applications, as they are generally low-cost, easy to use, and can provide fast results (Bridle and Desmulliez 2021).

Studies of the population genetics of fungi and fungi-like pathogens are essential to identify and clarify the disease epidemiology as well as to devise management strategies (Atallah and Subbarao 2012). Genome sequencing of fungal pathogens has provided information on extensive variation in genome structure and composition between species, especially between individuals of the same species (Eschenbrenner et al. 2020). Hundreds of fungal pathogen genomes are now available and analysing these genomes provide information about the genes that are responsible for causing the diseases (Plissonneau et al. 2017). A study done by Zhang et al. (2023a, b) revealed that the comparative genome of *Colletotrichum* species from different lineages revealed that expanded gene families encoding CAZymes are thought to be one of the likely explanations for the widespread and polyphagous nature of species in the *C. acutatum*, *C. boninense* and *C. gloeosporioides* species complexes. Liu et al. (2022) used 94 *Colletotrichum* species based on 1893 single-copy orthologous genes to provide the most comprehensive genome tree. Datasets from population genomics built on NGS can be used to identify variations including single nucleotide polymorphisms (SNPs), insertions and deletions (INDELS), and structural variations (Potgieter et al. 2020). Next-Generation Sequencing (NGS) is another popular current trend in the identification of phytopathogenic fungi. *Calonectria pseudonaviculata* was detected by using NGS (Malapi-Wight et al. 2016). *Puccinia striiformis* f. sp. *tritici* is the causative agent of the wheat yellow stripe. In order to identify the population of this emerging pathogen field pathogenomics was done using RNA-Seq-based NGS of pathogen-infested wheat leaves (Hubbard et al. 2015). It was shown that there is a dramatic shift in the pathogenic population in the UK, probably due to an introduction of a different set of emerging and exotic pathogen lineages. Molecular diagnostics for the cucurbit downy mildew pathogen *Pseudoperonospora cubensis*, was conducted via RNA

and DNA-based NGS approaches. Based on the comparative genomic analyses based on RNA-Seq of closely related species of *Pseudoperonospora humuli*, seven specific regions were identified in *P. cubensis* (Withers et al. 2016).

A hybrid and hierarchical de novo association strategy was used to sequence the genome of *Monilinia fructicola* (Mfrc123), the brown rot pathogen, through a combination of Illumina short-read NGS and Pacific Biosciences (PacBio) long-read third-generation sequencing platforms (Angelini et al. 2019). The genome of the coffee rust fungus *Hemileia vastarix* was sequenced using PacBio RS II and Illumina HiSeq platforms (Porto et al. 2019).

## Limitations

The major limitation in plant pathology is the emergence and resurgence of pathogens. New plant pathogens or more aggressive strains evolve due to climate changes, global trade, and human activities (Olsen et al. 2011). Identifying these novel pathogens and managing their threats is a significant challenge for plant pathologists (Zeilinger et al. 2016). Karnal bunt is a fungal disease of wheat, durum, and rye triticale caused by *Tilletia indica*. This disease first emerged in Karnal, India during 1931 and was initially restricted to South Asia and Iraq (Singh et al. 1989). It became of global importance following its discovery in Mexico in 1972, and USA in 1996 (Bonde et al. 1997). The disease decreases seed viability and flour quality and wheat consisting of 3% or greater bunted kernels is considered unfit for human consumption (Bansal et al. 1984; Brennan et al. 1992). The causative agent of chestnut blight is *Cryphonectria parasitica* and it was restricted to East Asia. Japanese chestnut (*Castanea crenata*) which is resistant to this disease was introduced from Japan to North America during the late nineteenth century. The causative agent has been moved with imported chestnut plants and infected to American chestnut and has killed most mature American chestnut (*C. dentate*) trees within their natural range (Anagnostakis 2001). Anderson et al. (2004) listed many emerging and resurgent cases of plant pathogens worldwide.

Morphological observations and interpretations in pathogen identification can be rather difficult and are often based on the interpretative skills and experience of the analyst (Rajapaksha et al. 2019). Not all pathogens can be cultivated in an artificial environment (Jayawardena et al. 2018), leading to reliance on sequence data obtained directly from the infected material, which has proven to be difficult. With the use of DNA sequence data, mycologists came up with different genes that can be used to give a better resolution in species identification. However, there is no standard as to which gene(s) should be analyzed or how much sequence divergence is needed, or what statistical support is required at both the individual locus

and the combined concatenated sequence levels to determine whether different strains belong to different species (Lücking et al. 2020). This has resulted in dubious species identification.

Another limitation is that some taxonomic studies rely on relatively few samples (one strain) when introducing phytopathogens. However, further analyses of closely related DNA sequences based on ‘phylogenetic or genotypic cluster species’ with a larger sample size, may reveal an abundance of recombination (Liu et al. 2016; Zhang et al. 2023a, b). The best examples of this are *Colletotrichum siamense* and *Diaporthe eres*. Separate species designations are mainly due to the inadequate sampling size (Liu et al. 2016). In the use of the GCPSR concept, the resulting trees are only as informative as the specific loci chosen for sequencing and the alignment used as input data (Taylor et al. 1999). If the sequences that are used are wrong, the result will also be wrong leading to misidentification of species. The major limitation in NGS is the time consumption during assembly and analysis of large amounts of sequence data (Espindola et al. 2015) as well as low yield and/or integrity, stability and impurities (Cortés-Maldonado et al. 2020). Also, expertise in bioinformatics and mycology are necessary for NGS analysis and are mandatory to avoid any misinterpretations.

Plant diseases can be caused by multiple fungal genera that affect diverse hosts with different tissue specificities involving a range of symptoms (Bhunjun et al. 2021). In order to confirm whether a species is actually the disease-causing agent, a pathogenicity assay is needed. There are limitations from selecting inoculation methods (wounded, non-wounded, spore suspension, mycelium plug) to analysing the disease symptoms (disease charts) (Bhunjun et al. 2021). Determining whether a fungus is a true pathogen needs more studies. Some species have been introduced or reported as associated with a disease when Kochs’ postulates cannot be implemented. In the case of *Colletotrichum*, a pathogenic genus, pathogenicity assay data are available for only one-third of its species. Disease epidemiology of fungal genera or species is not well-studied or identified. Hence, this makes it difficult to identify how the diseases are spread and when to apply the control measures.

Due to the changes in climate and weather patterns, global trade, and human activities, many new fungal pathogens are emerging, or more aggressive strains are re-emerging (Gomdola et al. 2022). Identifying and managing these novel threats is a significant challenge for plant pathologists. While imaging techniques can detect biotic stress in the plant before visual symptoms appear, the technique lacks capability to identify specific pathogens. More novel approaches for determining, characterising, and monitoring fungal pathogens are required as traditional methods are time-consuming and have other limitations.

## Future

Incorporating a new disease paradigm such as pathobiome can provide more information about the disease epidemiology. The pathobiome concept, has been invoked in cases where the disease is believed to result from interactions between a set of organisms (including eukaryotic, microbial and viral communities) within the plant and its biotic environment, leading to the deterioration of host health status is needed (Collinge et al. 2022). Although the concept of pathobiome is relatively new in plant pathology, several studies have reported on diseases caused by multi-species “disease complexes” (Mazzola and Freilich 2017). Examples of diseases caused by multi-species complexes include tomato pith necrosis, soft rot in broccoli, and young grapevine decline. These diseases are caused by multiple bacterial or fungal species that interact synergistically to impact disease development. It is suggested that the pathobiome concept be applied to postharvest diseases, providing a more comprehensive perspective on disease development involving intricate assemblages of microorganisms (Droby et al. 2022).

The developments in omics approaches in plant disease ecology have been particularly important as fungi can be spread around the world via globalisation changing the composition and ecology of habitats. Invasive pathogens with a broad range of hosts can cause chaotic results in ecosystems. Shifting temperatures and the frequency and duration of weather conditions over time result in phenomena such as the rapid evolution of microbial pathogens or environmental stress which can weaken plant hosts. Omics are primarily aimed to enhance the understanding of plant-pathogen interactions at the molecular level (Crandall et al. 2020). A multi-omics approach allows for a detailed account of plant-microbial interactions and can eventually allow us to build predictive models for how microbes and plants will respond to stress under environmental changes (Santini et al. 2015; Gilbert et al. 2010; Rizzo et al. 2002). These technologies will identify new targets for disease control and improve the development of resistant plant varieties (Filgueiras et al. 2019). Pangenomics can be used to identify virulence processes in a rapidly evolving fungal plant pathogen (Chen et al. 2023a).

Climate-resilient plant pathology is studying the impact of climate change on plant diseases and developing adaptive strategies to combat disease outbreaks under changing climatic conditions (Velásquez et al. 2018). Disease forecasting tools are not used abundantly at present. This can help the farmers to identify when a disease is going to occur as well as the best time to use fungicides (El Jarroudi et al. 2017; Maddalena et al. 2023).

## Current trends, limitations, and future research in HTS

The study of fungal diversity is a rapidly growing field, with researchers worldwide working to understand their distribution in diverse ecosystems. The development of high-throughput sequencing (HTS) technology and the application of meta-approaches, such as microbiome sequencing, has revolutionised how researchers analyse and interpret fungal diversity (Gutleben et al. 2018). High-throughput sequencing is based on the sequencing of the internal transcribed spacer (ITS) region (as the primary barcode), followed by the small (SSU) and large subunit ribosomal ribonucleic acid (LSU) and their combinations (Taberlet et al. 2012; Nilsson et al. 2019a, b; Tedersoo et al. 2020a, b; Semenov 2021). The sequencing generates multiple sequences from the same samples, which have output as operational taxonomic units (OTUs) (Nilsson et al. 2019a, b; Tedersoo et al. 2020a, b). Runnel et al. (2022) demonstrated the effectiveness of long-read HTS, specifically PacBio HTS, for the taxonomic identification of fungal specimens. Their study showed the advantages of long-read HTS over the traditional Illumina sequencing (Sanger method), including higher success rates and the ability to detect gene polymorphism, taxonomic delimitation, and ecological and population-level studies.

High-throughput sequencing can provide comprehensive insights into taxonomic and functional diversity of fungal communities. High-throughput sequencing techniques have enabled the identification and characterisation of diverse fungal species in various environments such as soil, plants, and the human body. It can recover DNA sequences in extreme environments (Tedersoo et al. 2020a, b; Rämä et al. 2017; Ogaki et al. 2021a, b) where cultivation is difficult or impracticable (Semenov 2021). These methods have also shed light on fungal microbiome diversity, composition, and functional potential (D'Hondt et al. 2021; Fan et al. 2023). In the most recent studies, HTS has significantly impacted estimating the number of fungi (Wu et al. 2019; Baldrian et al. 2022a, b). Pölme et al. (2020) introduced the user-friendly database FungalTraits, a stand-alone spreadsheet dataset covering 17 lifestyle-related traits of fungal and *Stramenopila* genera, and the endemicity of soil taxa (Tedersoo et al. 2022). The GlobalFungi (<https://globalfungi.com/>, Větrovský et al. 2020) and the Global Soil Mycobiome consortium dataset (Tedersoo et al. 2021a, b) have attempted to gather information on soil fungal diversity and construct a curated HTS sequence database, respectively. Other studies have focused on fungi to answer specific questions. For example, Baldrian et al. (2022a, b) estimated the number of fungi; Sun et al. (2019) used different HTS platforms for measuring Fungi and Oomycetes.

Several examples have highlighted the potential of HTS in fungal studies. In clinical settings, it has been used for the early identification of infection in culture-negative and food-borne pathogens. In ecology, it has been used to study fungi in several environments, such as aerial (Mbareche et al. 2019), aquatic (Hassett et al. 2017; Lepère et al. 2019; Souza et al. 2021; Garmendia et al. 2021) and soil (e.g., Young et al. 2016; Tedersoo et al. 2020a, b, 2021a, b, 2022; Yasanthika et al. 2022; Wydro et al. 2022). It has also been used in plant pathogen detection and surveillance (Bérubé et al. 2018; Piombo et al. 2021).

## Limitations

While high-throughput sequencing has revolutionised microbiome research, it is not without its limitations. HTS methods have challenges and possible sources of error, which require careful consideration when using and interpreting HTS data and outcomes. One major challenge is the high rate of erroneous base calls produced by HTS technologies, such as Illumina sequencing machines, which have errors at approximately  $0.1-1 \times 10^{-2}$  per base sequenced (Lou et al. 2013). This error rate can present a profound barrier in contexts where rare genetic variants are sought. Methods are also unable to differentiate living and dead cells or organisms, amplifying inactive DNA (Tuininga et al. 2009). This can lead to inaccurate estimations of microbiome structures and, consequently, functional capacities (Dlott et al. 2015; Carini et al. 2020; Nagler et al. 2021). This effect would be most noticeable if artefact DNA is abundant and if the taxa represented in the relic DNA pool do not accurately reflect the taxa present as living cells (Carini et al. 2020).

Additionally, during the analysis stage, the absence of reference databases and the amplification of selected barcodes, results in challenges in assigning OTUs at lower taxonomic ranks, resulting in erroneous or unclassified taxa (Hong-sanan et al. 2018; Wu et al. 2019). Comparisons between datasets such as the Global Fungi dataset (Větrovský et al. 2020) and GSMc (Tedersoo et al. 2021a, b) have shown significant levels of contradictions in the richness of certain fungal groups due to different sampling strategies and analytical biases such as the use of different primers for metabarcoding and lack of properly annotated reference sequences (Tedersoo et al. 2021a, b).

High-throughput sequencing requires storage facilities, computational power, and specialised personnel (Rincon-Florez et al. 2013; Sota et al. 2014; Nilsson et al. 2019a, b; Wu et al. 2019), which are limited to a few research institutions or specialised companies. However, the successful implementation of high-throughput sequencing extends beyond these resources. It requires a close collaboration between bioinformaticians and mycologists. This interdisciplinary collaboration is crucial for meaningful results.

Bioinformaticians bring their expertise in managing and interpreting large datasets and help design experiments and analyse data in ways that answer the specific questions which mycologists are interested in, while mycologists provide the necessary biological context and understanding of the studied organisms and guide bioinformaticians in understanding the biological significance of their findings.

HTS analysis lacks standardised methods for sample collection, DNA extraction, library preparation, and data analysis. The variability introduced by these differences can hinder the comparability of findings across studies. Standardisation of protocols and methodologies is necessary to ensure reproducibility and facilitate meta-analyses (Li et al. 2022a, b, c). Accurately identifying and classifying fungal species using HTS data is another limitation in mycobiome research. Fungal taxonomy is complex and constantly evolving, and reference databases for fungal sequences are often incomplete or inadequate. Additional techniques or curated databases may be required to accurately assign taxonomy to fungal sequences (D'Hondt et al. 2021). To overcome these limitations and shape future research, several promising directions have emerged. Integrating multi-omics data, such as metagenomics, metatranscriptomics, and metabolomics, can provide a holistic understanding of microbial community dynamics (Muller et al. 2013; Abram 2015). Establishing standardised protocols for sample collection, storage, and data analysis is crucial to ensure the reliability and comparability of results (Bella et al. 2013; Wang et al. 2023a, b, c). Moreover, exploring microbiome-based therapeutics and the role of microbiomes in environmental sustainability, including soil health and sustainable agriculture, holds promise for addressing global challenges (Tedersoo et al. 2017).

## Future research

Notwithstanding these limitations, HTS remains a powerful tool for microbiome research, providing comprehensive insights into the taxonomic and functional diversity of microbial communities. Advancements in DNA and RNA sequencing technologies have enabled the integrative study of fungal communities, including their taxonomic profiles and functional and ecological attributes. This allows for a better interpretation of communities and the ability to address questions related to ecosystem functioning, including intra- and interkingdom interactions. However, standardisation, taxonomy challenges, and multi-omics data integration remain critical focus areas in mycobiome research. Ongoing advancements in HTS technology, such as long-read sequencing and data analysis, help to address some of these limitations and improve the accuracy and reliability of HTS-generated data. As HTS data accumulate, it becomes

increasingly important to use those data to explore new research questions, hypotheses, and theories.

Fungal metabarcoding is an interdisciplinary and reproducible research strategy that requires expertise in mycology, ecology, Earth sciences, bioinformatics, statistics, and laboratory and analytical procedures. Indeed, while HTS does present technical challenges, it also opens up a world of opportunities for interdisciplinary collaboration. This collaboration is beneficial and essential to fully harness the potential of HTS in mycology and other biological fields. The synergy between bioinformatics and mycology can lead to what were previously impossible breakthroughs within a single discipline. It allows for a more comprehensive understanding of the data, leading to more accurate and meaningful results. By working together, bioinformaticians and mycologists can unlock new insights and push the boundaries of what is possible in mycology. Mycology must ask significant scientific questions and target large-scale patterns and processes. Producing reproducible results by following applicable standards and protocols, providing ample detail on data processing and analysis, and making all relevant data freely and openly available is crucial. Failure to do so will maintain the view that fungi matter only to mycologists, a belief that has haunted mycology for far too long.

## Fungal nanotechnology: fungi-based nanoparticles, current applications, challenges and prospects for future research

Nanotechnology is a rapidly advancing field that involves manipulating and controlling substances at the nanoscale, which is about  $10^{-9}$  m in size (Bayda et al. 2020). It encompasses a wide range of scientific disciplines, i.e., biology and engineering, to understand and harness the unique properties of materials at the atomic and molecular levels (Paramasivam et al. 2021). This field holds tremendous potential for various industries, including electronics, medicine, energy, and manufacturing, by enabling the development of novel materials and devices with enhanced properties and functionalities (Green et al. 2015; Peer et al. 2007; Meyers et al. 2006). In nanotechnology, nanoparticles have become an integral part of our daily lives, often working behind the scenes to enhance product functionality and user experience. A prevalent example is in the field of cosmetics, where nanoparticles, particularly of titanium dioxide and zinc oxide, are employed in sunscreens to offer broad-spectrum UV protection without leaving a white residue on the skin (Smijs and Pavel 2011). In medicine, nanoparticles have shown promise in targeted drug delivery, allowing for increased drug efficiency and reduced side effects (Yusuf et al. 2023). The electronics industry harnesses the unique electronic, optical, and mechanical properties of nanoparticles to develop



improved displays, batteries, and memory storage devices (Malik et al. 2023). Nanoparticles also enhance the protective nature of some textiles, filling them with water-repellent, stain-resistant, or even antimicrobial properties (Saleem and Zaidi 2020). In the environmental sector, nanoparticles aid in water purification processes by binding to and removing contaminants (Kumar 2023). Thus, from personal care products to high-tech gadgets and environmental solutions, nanoparticles play an essential role in driving advancements and refining everyday experiences.

The demand for clean, non-toxic, and environmentally friendly approaches, commonly referred to as "green chemistry", in nanoparticle synthesis and assembly is increasing. This has prompted researchers to explore biological systems for inspiration (Mukherjee et al. 2001). Recently, the utilization of microorganisms and plants for synthesising metal nanoparticles (MtNPs) has gained recognition as an efficient and sustainable method, enabling further exploration of microorganisms as "nanofactories". Microorganisms, cultivated on a large scale, play a crucial role as nanofactories due to their ability to accumulate and detoxify heavy metals. This capability is attributed to the presence of diverse reductase enzymes that facilitate the reduction of metal salts into MtNPs.

Fungi, as a diverse group of organisms, have gained significant attention in recent years for their potential application in various fields, including nanotechnology. Moreover, fungi present a convenient option for cultivation as nanofactories, allowing for the production of nanoparticles with precise control over their size and morphology (Gade et al. 2008; Ahluwalia et al. 2014; Azmath et al. 2016; Khan et al. 2017; Guilger-Casagrande de Lima 2019). The utilization of fungi in nanoparticle synthesis represents a promising and sustainable approach within the rapidly evolving field of nanotechnology, with applications in areas such as medicine, agriculture, and environmental remediation (Guilger-Casagrande de Lima 2019; Moond et al. 2022; Sharma et al. 2023). Myconanotechnology, as it is commonly known, is thus defined as the interface between nanotechnology and mycology (Hanafy 2018; Sousa et al. 2020; Adebayo et al. 2021). In this section of the article, our aim is to discuss the fungi-based nanoparticles, current applications, limitations, and potential future prospects in this captivating field of research.

### **Biosynthesis of nanoparticles by fungi**

Fungi have become a valuable addition to the microorganisms used in nanoparticle production. They are effective candidates for synthesizing metal nanoparticles, both intracellularly and extracellularly. In intracellular synthesis, fungi serve as nanofactories for the production of metal nanoparticles within their cellular structures. This process entails

the uptake and accumulation of metal ions by fungal cells, subsequently reducing these ions to generate nanoparticles. Conversely, extracellular synthesis involves the utilization of fungal biological systems to generate metal nanoparticles outside the confines of the cells. This mechanism is facilitated through the secretion of enzymes or biomolecules by fungi, which act as reducing agents to convert metal ions into nanoparticles within the surrounding environment. Fungal-synthesized nanoparticles have excellent dispersion and stability. Fungi offer advantages such as the presence of specific enzymes, ease of handling in the lab, scalability, and cost-effectiveness (Castro-Longoria et al. 2012; Siddiqi and Husen 2016; Guilger-Casagrande and Lima 2019; Bourzama et al. 2021). Fungi can produce various metal nanoparticles, including silver, gold, platinum, palladium, copper, iron, selenium and tellurium nanoparticles.

### **Silver nanoparticles**

The utilization of fungi for the biological synthesis of silver nanoparticles (AgNPs) has garnered significant attention in scientific research over the past two decades. Notably, more than 120 fungal species from diverse taxa, including Ascomycota, have demonstrated the ability to produce nanosilver (Loshchinina et al. 2023). Basidiomycota, in particular, have attracted considerable interest as bio-objects for nanoparticle fabrication, as highlighted by Loshchinina et al. (2023). Their unique properties and potential applications make the mycosynthesis of AgNPs a compelling area of investigation in the field of nanotechnology. These nanoparticles have been found to possess remarkable antibacterial, antifungal, anticancer, antioxidant, and larvicidal activities, among other beneficial properties (Khan et al. 2018; Ratan et al. 2020). Notably, the same nanoparticles have been shown to exhibit a diverse range of biological activities, underscoring their versatility and potential for various applications (Rafique et al. 2017a, b; Razak et al. 2021). The broad spectrum of therapeutic and functional attributes displayed by mycosynthesized AgNPs reinforces their significance in fields such as medicine, biotechnology, and environmental science.

### **Gold nanoparticles**

Gold nanoparticles (AuNPs) have found widespread application in diverse processes, ranging from chemical and biological sensing to bio-imaging, nonlinear optics, catalysis, targeted drug delivery, and gene delivery (Elahi and Baghersad 2018). Additionally, they exhibit antimicrobial and antioxidant properties, making them valuable in cancer and infectious disease therapy (Ahmed et al. 2016). The biological synthesis of AuNPs by fungi has also been extensively investigated, with various species demonstrating the ability

to form these nanoparticles. Notably, these AuNPs show promise as dual-modal (chemo-photothermal) therapeutic agents for anticancer applications. It was observed that synthesized gold nanospheres (10–50 nm) effectively inhibited the growth of clinically significant Gram-positive and Gram-negative bacteria, as well as pathogenic fungi (Loshchinina et al. 2023). These findings highlight the potential of mycosynthesized AuNPs as versatile and effective therapeutic candidates.

### Platinum nanoparticles

Platinum nanoparticles (PtNPs) have catalytic, magnetic, and optical properties, as well as antimicrobial, antioxidant, and anticancer properties (Jeyaraj et al. 2019; Fahmy et al. 2020). While the mycosynthesis of PtNPs has been less well-studied compared to silver and gold nanoparticles, some Ascomycota species have been found to have the ability to form PtNPs. In a study by Borse et al. (2015), PtNPs synthesized by *Saccharomyces boulardii* showed anticancer activity.

### Palladium nanoparticles

The synthesized PdNPs exhibit unique physicochemical properties, such as excellent catalytic activity and enhanced stability. These properties make them suitable for various applications, such as the development of novel photothermal, photoacoustic, antimicrobial, and antitumor agents, gene/drug carriers, prodrug activators, and biosensors (Phan et al. 2019). The mycosynthesis of palladium nanoparticles (PdNPs) in fungal cultures has received limited attention, with only a few publications reporting its occurrence in *Agaricus bisporus*, *Inonotus obliquus*, and *Saccharomyces cerevisiae* (Mohana et al. 2020, Gil et al. 2018, Sriramulu et al. 2018, Saitoh et al. 2020).

### Copper nanoparticles

Biosynthesized copper nanoparticles (CuNPs) possess a range of beneficial properties, including antibacterial, antifungal, antiviral, and anticancer activities. These nanoparticles have potential applications in targeted drug delivery, cosmetics, catalysis, microelectronics, gas sensors, high-temperature superconductors, solar cells, bactericide agents, wound dressings, biopesticides, bioremediation, biodegradation, and energy storage (Rafique et al. 2017a, b; Al-Hakkani 2020; Chaerun et al. 2022). However, the mycosynthesis of CuNPs remains an area of limited research, with species such as *Agaricus*, *Aspergillus*, *Fusarium*, *Hypocrea*, *Shizophyllum*, *Stereum*, and *Trichoderma* reported to be capable of producing CuNPs (Loshchinina et al. 2023).

### Iron nanoparticles

Iron nanoparticles (FeNPs) and iron-based nanomaterials play a crucial role in addressing environmental pollution through their ability to degrade organic dyes, remove heavy metals, and treat wastewater. In addition, these nanomaterials hold promise in biomedicine as antimicrobial agents (Saif et al. 2016; Pasinszki and Krebsz 2020). The production of FeNPs has been primarily investigated in Ascomycota micromycetes, with species such as *Alternaria*, *Aspergillus*, *Fusarium*, *Penicillium*, *Pleurotus*, *Rhizopus*, and *Trichoderma* being reported as capable of synthesizing FeNPs (Loshchinina et al. 2023).

### Selenium nanoparticles

Selenium nanoparticles (SeNPs) have garnered significant attention due to their reduced toxicity compared to inorganic and organic selenium compounds, as well as their biocompatibility, bioavailability, and biomedical properties. Nanoselenium demonstrates remarkable antimicrobial, anticancer, antidiabetic, antiparasitic, and antioxidant activities (Bisht et al. 2022). SeNPs find applications in targeted drug delivery, bioremediation, nanobiosensors, food supplements, and various other fields (Shoeibi et al. 2017). Selenium nanoparticles (SeNPs) synthesized through mycosynthesis using culture liquid of *Aspergillus flavus* and *Candida albicans* have demonstrated potent antifungal activity. These nanoparticles exhibit the ability to inhibit fungal growth at lower concentrations compared to conventional antifungal drugs (Bafghi et al. 2021). The biological synthesis of SeNPs has been observed in a substantial number of fungal species, with *Aspergillus*, *Penicillium*, and *Trichoderma* being among the most extensively studied genera in this regard (Loshchinina et al. 2023).

### Tellurium nanoparticles

These nanoparticles possess a wide range of properties, including photoconductivity, thermoconductivity, piezoelectricity, non-linear optical behavior, antioxidant activity, antimicrobial activity, anticancer effects, immunomodulation, and cytotoxicity. Moreover, TeNPs show potential for applications in drug delivery, bioremediation, and biorecovery, making them an area of significant interest (Zambonino et al. 2021). However, the formation of TeNPs in fungi remains relatively understudied. Thus far, tellurium nanospheres have been successfully obtained from species such as *Aspergillus welwitschiae*, *Aureobasidium pullulans*, *Mortierella humilis*, *Penicillium chrysogenum*, *Phanerochaete chrysosporium*, *Phoma glomerata*, and *Trichoderma harzianum* (Loshchinina et al. 2023).

## Current trends in fungal nanobiotechnology

Current trends in myconanotechnology applications highlight the significant potential of this field across various sectors. The unique properties and capabilities of fungi make them valuable tools in medicine, agriculture, environmental remediation, and materials science. Recent developments in fungal nanoparticle synthesis and manipulation have paved the way for novel applications and outcomes. Over the years, significant advancements have been made in the synthesis and manipulation of fungal-derived nanoparticles, leading to innovative applications and results. The combination of fungal biology and nanotechnology holds great promise for addressing societal challenges and revolutionizing industries.

### Medicine and biomedical applications

Fungal nanotechnology has shown great promise in the field of medicine. Fungal-derived nanoparticles have been utilized in drug delivery systems, diagnostics, and therapeutics. For example, the antifungal properties of silver nanoparticles synthesised by fungi have been explored for the treatment of fungal infections (Gajbhiye et al. 2009; Liang et al. 2022). These nanoparticles exhibit enhanced efficacy and reduced toxicity compared to traditional antifungal drugs (Bafghi et al. 2021). Furthermore, fungal nanocarriers have been developed to deliver drugs to specific target sites, improving drug bioavailability and reducing side effects (Bafghi et al. 2021). Fungal nanoparticles have also been used in biosensing and imaging applications (Ahmed et al. 2016, Elahi and Baghersad 2018, Kalimuthu et al. 2020). Their unique optical and magnetic properties make them suitable for developing biosensors, imaging agents, and contrast agents for various imaging modalities, including magnetic resonance imaging (MRI) and fluorescence imaging. Fungal nanotechnology holds great potential in early disease detection, personalized medicine, and targeted therapy (Rai et al. 2019; Mota et al. 2023).

### Agriculture and crop improvement

Fungal nanotechnology has found applications in agriculture and crop improvement. Fungal nanoparticles can be used as biofertilizers, biopesticides, and growth promoters (Mishra and Kumar 2009; Prasad et al. 2014; Ponmurugan et al. 2016). For example, nanoparticles synthesized from fungal extracts have been shown to enhance plant growth, improve nutrient uptake, and increase crop yield (Tripathi et al. 2017; Khalifa and Hasaneen 2018). These nanoparticles can also act as carriers for delivering nutrients, pesticides, and genetic materials to plants, enabling more efficient and targeted delivery (Kumar et al. 2017; Tripathi et al. 2017;

Cao et al. 2018). Additionally, fungal nanotechnology has the potential to address challenges in plant disease management (Wang et al. 2021). Fungal nanoparticles can inhibit the growth of plant pathogens and suppress the development of diseases (Abbacia et al. 2014; Adebayo et al. 2021). They can also be used in the development of nanosensors for the early detection of plant diseases, allowing for timely interventions and reduced crop losses.

### Environmental remediation

Fungal nanotechnology offers promising solutions for environmental remediation and pollution control. Fungi have the ability to synthesize nanoparticles with unique properties that can be employed in the removal of pollutants from soil, water, and air. Fungal nanoparticles can act as efficient adsorbents, catalysts, or photocatalysts for the degradation of organic pollutants, heavy metal ions, and even radioactive contaminants (Viswanath et al. 2008, 2014; Bahrulolum et al. 2021). These nanoparticles can be used in water treatment, wastewater purification, and soil remediation processes, contributing to sustainable environmental management.

### Industrial science

The industrial application of fungal nanobiotechnology holds significant potential for various sectors. Fungal nanoparticles can be utilized in the development of advanced materials, such as nanocomposites, coatings, and membranes, with improved properties and performance (Muñoz et al. 2006; Tsivileva et al. 2021). These materials find applications in the automotive, aerospace, electronics, and packaging industries. Fungal nanobiotechnology also offers opportunities for the production of high-value chemicals, enzymes, and biofuels through the use of fungal bioreactors (Williamson et al. 1998, Polizeli et al. 2005, Azin et al. 2007, Shraddha et al. 2011, Uday et al. 2016, Elegbede and Lateef 2018). The ability of fungi to synthesize nanoparticles with unique properties, combined with their scalability and sustainability, makes them attractive candidates for industrial processes.

## Current challenges in fungal nanobiotechnology

Since fungi-based nanotechnology is developing, it faces several limitations and challenges that need to be overcome for successful implementation. One of the major hurdles is the limited exploration of fungal diversity suitable for nanotechnology applications. The availability of fungal species with the ability to produce nanoparticles and possess desired properties is restricted, hampering the discovery of potential fungal candidates (Adebayo et al. 2021).

Another challenge lies in the incomplete understanding of fungal nanoparticle synthesis mechanisms (Guilger-Casagrande de Lima 2019). The complex interplay between fungal cells and the surrounding environment during nanoparticle synthesis is a subject of ongoing research. Gaining a deeper understanding of these mechanisms is crucial to optimize and control the synthesis process.

Scalability and reproducibility pose significant challenges when transitioning from laboratory-scale to industrial-scale production of fungal nanoparticles (Ganeshan et al. 2021). Maintaining consistent and reproducible synthesis conditions, ensuring the quality and desired properties of the nanoparticles, and developing scalable and reliable production methods become increasingly complex at larger scales. Therefore, it is necessary to focus on the development of robust and efficient production processes to enable the practical implementation of fungi-based nanotechnology.

Precise control over nanoparticle properties is another limitation that needs to be addressed. Factors such as size, shape, composition, and surface characteristics significantly influence the functionality of nanoparticles (Loshchinina et al. 2023). However, achieving precise control over these properties is challenging in fungi-based nanotechnology, limiting the customization and optimization of fungal nanoparticles for specific applications. Further research and innovation are required to enhance control over these properties and enable tailored nanoparticle design.

Biocompatibility and toxicity concerns are critical considerations, particularly in applications involving medicine and environmental remediation (Deng et al. 2018; Dasari et al. 2014). A thorough assessment of the impact of fungal nanoparticles on living organisms and ecosystems is necessary to ensure their safe use. Understanding the long-term effects and potential risks associated with exposure to fungal nanoparticles is an ongoing challenge that requires comprehensive research and evaluation.

The regulatory landscape for fungi-based nanotechnology is evolving, with a lack of clear guidelines and regulations specific to fungal nanoparticles. Addressing potential safety concerns, establishing standardized protocols, and developing appropriate regulations are essential to ensure responsible and ethical implementation (Arnaldi and Muratorio 2013; Loshchinina et al. 2023). Collaboration between researchers, industry stakeholders, and regulatory bodies is crucial to develop a robust regulatory framework that ensures the safe and effective use of fungal nanoparticles.

The cost-effectiveness and commercial viability are significant factors for the widespread adoption of fungi-based nanotechnology. Large-scale production processes need to be developed to reduce production costs and make fungal nanoparticles economically competitive with other nanomaterials (Singh et al. 2016). Additionally, optimizing the

scalability and stability of fungal nanoparticle synthesis methods is necessary to meet the demands of industrial applications.

## Way forward in fungal nanobiotechnology

Fungal nanotechnology is an emerging field with significant potential for advancement. Overcoming the limitations and challenges in fungi-based nanotechnology requires interdisciplinary research, collaboration, and innovation. Expanding the exploration of fungal diversity, gaining a deeper understanding of synthesis mechanisms, developing scalable and reproducible production methods, enhancing control over nanoparticle properties, addressing biocompatibility and toxicity concerns, establishing regulatory frameworks, and optimizing cost-effectiveness and commercial viability are crucial steps towards harnessing the full potential of fungi-based nanotechnology in various sectors.

Researchers are actively exploring different fungal species and refining synthesis methods to improve the efficiency, scalability, and reproducibility of producing fungal nanoparticles. Additionally, there is a growing focus on unravelling the intricate mechanisms involved in fungal nanoparticle synthesis, enabling better control over their size, shape, and surface properties. Moving forward, fungal nanotechnology offers promising applications in personalized medicine, with the development of targeted therapies and diagnostic tools customized to individual patients. It also has the potential to revolutionize sustainable agriculture practices by reducing reliance on chemical inputs and enhancing crop productivity. Furthermore, the application of fungal nanoparticles in environmental remediation presents an opportunity to address pressing challenges in pollution control and waste management.

To fully harness the potential of fungal nanotechnology, efforts should be dedicated to the comprehensive exploration and study of a wider range of fungal species. This can be achieved through biodiversity surveys, screening programs, and collaborations between researchers and fungal collections. Further research is needed to enhance our understanding of the mechanisms underlying fungal nanoparticle synthesis, utilizing interdisciplinary collaborations and advanced techniques such as genomics, transcriptomics, and proteomics.

The scalability and reproducibility of production methods are crucial considerations, necessitating optimization of growth conditions, synthesis parameters, and downstream processing steps. Collaboration between academia and industry is key to bridging the gap between laboratory-scale research and industrial-scale production. Investment in advanced characterization techniques, such as electron microscopy and spectroscopic methods, can provide valuable insights into the morphology, composition, and surface



properties of fungal nanoparticles. To achieve better control over nanoparticle properties, research efforts should focus on studying the influence of fungal species, growth conditions, and synthesis parameters. Strategies such as genetic engineering, surface modification, and controlled synthesis techniques can enable precise control over desired properties. Rigorous safety assessment protocols and risk management strategies are essential to evaluate the toxicity and biocompatibility of fungal nanoparticles and ensure their responsible and safe implementation. Collaboration between researchers, industry stakeholders, and regulatory bodies is vital for developing a robust regulatory framework for fungi-based nanotechnology. Clear guidelines and regulations should be established through active engagement with the scientific community. Additionally, research should aim to enhance cost-effectiveness and commercial viability by optimizing production processes and exploring alternative substrates.

Moreover, fungal nanotechnology offers the capability to create innovative materials with distinctive structures and functionalities. Fungal mycelium, the vegetative component of fungi, has been harnessed as a sustainable and biodegradable material for the production of bioplastics, construction materials, and even 3D-printed objects (Holt et al. 2012; Haneef et al. 2017; Gantenbein et al. 2023). This field holds significant promise in the advancement of tailored materials with specific properties to cater to diverse applications.

## Current trends, limitations and future research in AMF

Arbuscular Mycorrhizal Fungi (AMF) form symbiotic associations with plant roots that provides benefits to both parties. Most currently described AMF taxa belong to the phylum Glomeromycota (or subphylum Glomeromycotina) (Wijayawardene et al. 2020). Within this phylum, there are five orders, 16 families and 49 genera. Here is a summary of current trends, limitations, and future research in AMF.

### Current trends

Through their symbiotic relationship with plants, AM fungi receive up to 20% of the total photosynthetic C fixed by the plant (Smith et al. 1997) with an estimated global average of 6.2% (Hawkins et al., 2018). Plants can transfer photosynthate C via arbuscular fungal structures in the root cortex to external hyphae in soil within hours (Terrer et al. 2016). As exchange, plants receive from their mycorrhizal fungal symbionts mineral nutrients and a higher capacity for water uptake. Arbuscular mycorrhizal symbiosis also enhances host plant protection against biotic stress. Recent developments in the field of mineral nutrients (particularly

phosphorus and nitrogen) uptake by AM plants via their mycorrhizal symbionts was covered by several review papers (Kuyper and Jansa 2023; Xie et al. 2022), therefore we do not aim to comprehensive overview of this topic in this chapter.

Besides the ongoing research on AM physiology, significant attention is given to the ecological aspects of AM symbiosis. By interacting with approx. 75% of vascular plants, AM fungi play important role in all terrestrial ecosystems having large effects on vegetation and ecosystem processes (Brundrett and Tedersoo 2018). Therefore, response of AMF to global change and their role in mitigating its adverse effects have gained much interest. The climatic niche optima and width differ among the species of AM fungi. While Acaulosporaceae has a realized niche optima in low temperature conditions, Gigasporaceae has a realised niche optima in high temperature and high precipitation conditions (Davison et al. 2021). The width of the AM fungal temperature niche appears to be limiting, likely narrower than in other fungal guilds (Davison et al. 2021; Vetrovsky et al. 2019). These findings indicate that changes of MAT and MAP can particularly affect the composition of AM fungal communities. Climate change factors such as warming and precipitation changes can indeed affect AMF abundance and community composition directly (Cotton et al. 2015). While the increase of CO<sub>2</sub> and temperature does not seem to affect AMF profoundly, drought and nitrogen deposition often decrease AM biomass in soils and all of the above factors can bring about changes in AMF community composition (Baldrian et al. 2022a, b). A study by Jia et al. (2021) has shown that mycorrhizal fungi can maintain plant community stability by mitigating the negative effects of nitrogen deposition in Central Asia. Another study by Mei et al. (2019) also showed that AMF can alleviate phosphorus limitation by reducing plant N:P ratios under warming and nitrogen addition in meadow soils.

There is increasing research focusing on how AMF perform their ecological function at a community level and how AMF communities respond to climate changes (Xu et al. 2022). Based on a grassland extreme drought experiment in Inner Mongolia, research by Fu et al. (2022) found that the robustness of the AM fungal community response increased with drought intensity. The use of effective AMF communities may stand better chances to mitigate some drawbacks under field conditions. In the forest ecosystems of the temperate zone, the increase of nitrogen deposition with warming leads to the transition from forests dominated by ectomycorrhiza-forming trees to those forming arbuscular mycorrhiza, best described from the continental USA (Baldrian et al. 2023). Since the rates of microbial processes in AM forest soils including N cycling and C storage differs from ECM forests (Averill and Hawkes 2016), this transition has a far-reaching importance for global biogeochemistry.

The interaction between AMF and other microorganisms also gains increasingly interest in recent years, especially the increasing research about microbiome of AM fungal hyphosphere (Zhang et al. 2022). AM fungal hyphae recruit distinct microbes into their hyphosphere, the narrow region of soil influenced by hyphal exudates (Zhang et al. 2022). Recent research have also found that natural and agricultural ecosystems, various bacteria can live in the AM fungal hyphosphere and the hyphosphere microbiome is unique compared with other microbial communities when compared with the bulk soil (Zhang et al. 2022). In addition, various functions of the hyphosphere microbiome were also reported and focused on. The hyphosphere microbiome has been believed to be able to mobilize soil P and interact with soil bacteria (Svenningsen et al. 2018).

In addition, there is an increased interest in the use of AMF in sustainable agriculture due to its potential to improve plant growth, nutrient uptake, and soil health. AMF can improve soil structure and quality, increase nutrient availability and uptake, enhance plant resistance to diseases and pests, and reduce water usage (Otun and Achilonu 2023). This makes them a valuable tool in sustainable agriculture and ecological restorations, especially in low-input systems. Vahter et al. (2020) indicated that co-introduction of native AM fungi and plants is an efficient means of initializing species-rich vegetation recovery in barren post-mining landscapes. The practical application of AMF in sustainable agriculture—especially as biofertilizers—has been also frequently addressed (Madawala 2021). For instance, Al-Karaki and Williams (2021) showed that AMF inoculation can affect the growth, nutrition, and physiological responses of soybean to water deficit. Many research articles have already reported the beneficial roles of AMF protecting their hosts against fungal pathogens (Krzyzaniak et al. 2021). Overall, the current trend in the use of AMF in sustainable agriculture is to enhance plant growth and yield while reducing the environmental impact of agriculture.

## Limitations

Limited understanding of the mechanisms behind the symbiotic association between AMF and plant roots, which hinders the optimization of AMF use in agriculture or other application. Though in recent years, the whole genome of several AM fungal species and isolates have been sequenced (i.e. *Diversispora epigaea* (Sun et al. 2019), *Rhizophagus clarus* (Kobayashi et al. 2018)), which are helpful to explore the diverse functions of AM fungi. But the mechanism underlying these effects needs more exploration (Shi et al. 2023). However, the limited understanding of the cellular and molecular basis of forming AM symbiosis can also hinder the applications of AMF.

Another limitation of AM research seems to be the difficulty in transforming the success stories of AMF under glasshouse conditions to real farmer fields (Helander et al. 2018). Challenges in mass production and application of AMF in agriculture due to the need for living inoculum and the difficulty in maintaining fungal viability during storage and transportation. The outcomes of mycorrhizal symbiosis on plant health and nutrient cycles are affected by many diverse biotic and abiotic environmental factors. The effects of environmental factors, such as soil type, pH, and climate, on the effectiveness of AMF remain poorly understood (Powell and Rillig 2018).

For the exploration of the relative importance of AMF in ecosystem processes, the main limitation is represented by the absence of a reliable molecular marker that is common to AMF and other fungi. The recent progress at least has led to the design of molecular barcoding markers that are able to capture well the composition of the AMF communities through sequencing of long stretches of rDNA (Kolarikova et al. 2021) Also the complexity of AMF genomes (Miyachi et al. 2020) represents a grand challenge for the use of genomics, metagenomics and metatranscriptomics as a tool to explore AMF biology and ecology.

## Future research

New technologies such as next-generation sequencing (NGS) provide insight into how AMF interact with indigenous counterparts and to screen beneficial microbial candidates with specific functional traits. In the grassland soil, mycorrhizal fungi alter root exudation to cultivate a beneficial microbiome for plant growth (Xu et al. 2023).

Investigating the genetic and molecular mechanisms involved in the symbiotic association between AMF and plant roots to better understand the factors that determine AMF effectiveness. It has been reported that these compounds, known as strigolactones, induce hyphal branching in an arbuscular mycorrhizal (AM) fungus, and subsequent work by Besserer et al. (2006) showed that a synthetic strigolactone stimulated spore germination in two other species of AM fungi. The roles of strigolactones or other root exudes in the formation of AMF in plant roots need further research (Kuyper 2023).

Beside the root exudes, the identification of genes and gene products that are responsible for controlling the growth and development of AMF under stressful conditions also need more focus (Begum et al. 2019).

One of the key areas of research is focused on the molecular signals that are exchanged between the plant and the AMF. Studies have shown that the exchange of signals involves a range of molecular components, including receptor-like kinases, transcription factors, and small signaling molecules. For example, a study by Gomez-Roldan et al.

(2008) identified a receptor-like kinase in the plant that is essential for the recognition of AMF and the initiation of symbiosis.

Another area of research is focused on identifying the genes involved in the symbiotic association. This has been facilitated by advances in high-throughput sequencing technologies, which have allowed researchers to identify candidate genes involved in the symbiotic association. For example, a study by Tisserant et al. (2013) identified several genes in the AMF that are involved in nutrient exchange with the plant.

Furthermore, researchers are also exploring the role of epigenetic mechanisms in the symbiotic association. Epigenetic modifications, such as DNA methylation and histone modifications, can play a crucial role in regulating gene expression and the development of the symbiotic association between the plant and the AMF. For example, a study by Zouari et al. (2014) showed that DNA methylation is involved in the regulation of genes related to nutrient transport in the symbiotic association.

Exploring the potential of AMF to mitigate the effects of climate change on plant growth and nutrient uptake in different soil types and environmental conditions is also essential, especially in those ecosystems that are so far understudied, namely tropical AM forests (Baldrian et al. 2023). Soil microplastic (MP) pollution has emerged as a main factor of global change. A recent study by Moreno-Jiménez et al. (2022) has shown that the use of AMF to sustainably manage agricultural ecosystems contaminated with MP, buffering and counteracting the effects of MP.

AMF can enhance plant nutrient uptake under different soil conditions, including nutrient-poor soils and soils with imbalanced nutrient ratios. This is because AMF can access nutrients that are not available to the plant through their extensive mycelium network, which can reach into deeper soil layers (Lehmann et al., 2015). AMF can also facilitate the uptake of essential nutrients such as nitrogen, phosphorus, and micronutrients, which can be limiting in some soils. The identification of genes and gene products that are responsible for controlling the growth and development of AMF under stressful conditions also need more focus from the researchers (Begum et al. 2019).

Besides members of the phylum Glomeromycota, there is a growing body of research suggesting that also other fungal groups may act as arbuscular mycorrhizal symbionts. Specifically, fine endophytes, *Glomus tenue*, traditionally considered to be AM fungus are related to Mucoromycotina, not Glomeromycota (Orchard et al. 2017). Recent study provides that these Mucoromycotina ‘fine root endophytes’ are nutritional mutualists with flowering plants (Hoysted et al. 2023). Understanding the similarities and differences in character of the symbioses between plants and fungi from

Glomeromycotina and Mucoromycotina may shed more light on co-evolution of land plants and fungi (Field et al. 2019).

Further better understanding of AM fungal ecology should be stimulated by a recently compiled GlobalAM-Fungi database, which collates a comprehensive collection of published data on the composition of AM fungal communities (Větrovský et al. 2023). This open source and open access database contains almost 50 million observations of AM fungal amplicon DNA sequences across almost 8,500 samples with geographical locations and additional metadata.

One of the important challenges for better understanding of AM ecology represents independent development of AM fungal taxonomy and AM fungal ecology. While studies aiming to describe AM fungal community composition have so far largely relied on sequencing the SSU rRNA region ((Opik et al. 2014) but see e.g., Kohout et al. 2014; van Geel; (Schlaeppli et al. 2016), AM fungal morphospecies are molecularly described using different marker. Moreover, only a subset of AM fungal species is available in pure culture collections, due to the obligatory symbiotic lifestyle (e.g., INVAM (Sturmer et al. 2021)). Therefore, morphologically described AM fungal species corresponds to a subset of the AM fungal molecular diversity (Öpik et al. 2014). Although this schism dates back more than a decade, there are only limited attempts to at least into some extant interconnect these two field by sequencing longer DNA molecules, spanning all commonly utilized barcoding regions of AM fungi (de Souza et al. 2018; Kolarikova et al. 2021; Kruger et al. 2012). However, AM fungal phylogroups that are identified only on the basis of their DNA are categorised differently by studies using different AM fungal barcoding regions, which limits the direct comparability of such data.

## Current trends, limitations and future research in data repositories

In the realm of biological sciences, the study of fungi has gained remarkable momentum, uncovering their intricate roles in ecosystems, medicine, agriculture, and industry. As our understanding of fungal diversity and significance expands, so does the need for robust data management and dissemination platforms. Data repository is basically termed as data archive or library. Data repositories dedicated to fungi have emerged as crucial hubs for storing, sharing, and analyzing a wealth of fungal-related information. In recent years, the world of data repositories for fungi has undergone notable transformations, aligning with broader advancements in technology and research practices, such as genomic data, taxonomy, and phylogeny, open access and collaboration, and visualization and data integration tools.

## Current trends

An increased number of online data repositories has become a significant and convenient resource for all genomic information for fungal variety research and development. An online open data repository has made fungal research more accessible, faster, and more systematic. High-quality and functional genomic data and DNA sequencing technologies have led to an explosion of genomic data for various fungal species. Data repositories are increasingly focused on curating and hosting high-quality fungal genome sequences, along with associated metadata. Detailed metadata and annotations for fungal sequences were becoming increasingly important. Repositories were working to improve the quality and completeness of metadata to enhance the usability and interpretability of the stored data. The advancement of molecular phylogenetics in fungi involved creating and maintaining comprehensive phylogenetic databases that helped in understanding the evolutionary relationships among different fungal species. New species identification requires phylogenetic analysis and comparison among a large number of closer species, which is possible only with the availability of a large number of DNA sequence datasets and is solved with the availability of this facility (Nilsson et al. 2006).

Several efforts have been made to provide information on fungi collection and compilation, but systematic and online databases were only developed a few years ago. These tools enabled the scientific community and academic sector to study the diversity and evolution of fungi. Ullah et al. (2022) have compiled a collection of 76 fungal databases based on scientifically published literature. Research centers, universities, private companies, etc. are more interested in developing these kinds of websites, and the number is growing. With the opening of a broad spectrum of fungal applications, today's generation of researchers is intensively engaged in research, including the discovery of new species and secondary metabolites and their applications in medicine and biomaterials. Mycobank, GenBank, Index Fungorum, Fungal Names, Species Fungorum, FacesofFungi, e-fungi, Global Biodiversity Information Facility (GBIF), etc. are some examples of data repositories covering fungal nomenclature and details (Table 2).

## Limitations

Despite many benefits, using online data repositories is crucial and challenging to study fungal biogeography as the current depositories have some limitations. Many data repositories might have inconsistent or incomplete data entries, which can hinder the reliability and usefulness of the information available. Ensuring high data quality and completeness requires continuous efforts and strict data curation

processes. The molecular evolutionary study is never-ending and primary research is based on the availability of DNA sequences. Also, advancements in science and technology will scrutinize problems in the latest online database system. Taxonomic identification's accuracy relies more on the quality of data available in online repositories (Smith et al. 2016). With the addition of new species or fungal sequences, there is a proportionately increased probability of errors like duplication, incorrect naming, and incomplete species details. These issues have not been solved completely and must be cured on time. The scientific community has an important topic of discussion on whether to have single or multiple databases.

The research on fungal diversity has not covered the entire geography, creating complications in using repository data (Phillips et al. 2009; Troia and McManamay 2016; Hao et al. 2021). A uniform and systematic study of their geographic origin and evolutionary evidence can minimize artificial patterns about their common characteristics. Data repositories not only cannot provide all features but also require laboratory facilities to manage all the locally produced experimental data (Garwood 2006). The description of all fungal species should be scientifically understood and be uniform in every part of the world. For this, the global standard has to be established and operated accordingly. The Nagoya Protocol, agreed by 117 countries, ensures benefits that arise from the use of genetic resources of respective countries (Ryan et al. 2019); however, there are a considerable number of informally collected fungal specimens in countries with poor infrastructure and experts, which have to be analyzed and merged into the online data repositories. Additionally, ensuring the accuracy, consistency, and standardization of fungal data remains a challenge. Differences in data formats, metadata, and annotation practices can hinder data integration and analysis. We propose that the fungal taxonomic challenges are continually evolving, and there can be discrepancies and uncertainties in the classification and naming of fungal species. This can complicate data retrieval and interpretation.

## Future

The potential future research directions and trends in the field of data repositories for fungi might emphasize greater community involvement, enabling researchers, citizen scientists, and enthusiasts to contribute data, share observations, and collectively build a more comprehensive understanding of fungi. Fungal research on macroecological and biogeographic patterns is possible only with an accurate, reliable, and complete database, which can be made with the currently used databases. According to Wang et al. (2023a, b, c), "One fungus, one name" is the easiest, correct, and most effective standard for fungal



**Table 2** List of important fungal data depositories

Database	Webpage	References
Barcode of Life Database (BOLD)	<a href="http://www.barcodinglife.org/">http://www.barcodinglife.org/</a>	Ratnasingham and Hebert (2007)
Basidiochecklist	<a href="http://www.basidiochecklist.science.kew.org">www.basidiochecklist.science.kew.org</a>	Basidiochecklist (2023)
Botryosphaerales	<a href="http://botryosphaerales.org">botryosphaerales.org</a>	Wu et al. (2021a, b)
BPI Fungarium	<a href="https://www.ars.usda.gov">https://www.ars.usda.gov</a>	U.S. National Fungus Collections (2023)
CABI Culture collection	<a href="https://www.cabi.org">https://www.cabi.org</a>	CABI Culture Collection (2023)
CBS Fungus Collection	<a href="https://wi.knaw.nl">https://wi.knaw.nl</a>	CBS-KNAW collections (2023)
Coelomycetes	<a href="http://coelomycetes.org">coelomycetes.org</a>	Huanraluek et al. (2021)
Checklist of the Lichens of Australia and its Island Territories	<a href="https://www.anbg.gov.au/abrs/lichenlist/introduction.html">https://www.anbg.gov.au/abrs/lichenlist/introduction.html</a>	
Consortium of Lichen Herbaria	<a href="https://lichenportal.org/portal/">https://lichenportal.org/portal/</a>	
Cyberliber	<a href="http://www.cybertruffle.org.uk">http://www.cybertruffle.org.uk</a>	Cyberliber (2023)
Cybertruffle	<a href="http://www.cybertruffle.org.uk/eng/index.htm">http://www.cybertruffle.org.uk/eng/index.htm</a>	Minter (2015)
Central <i>Aspergillus</i> Data Repository (CADRE)	<a href="http://www.cadre-genomes.org.uk">http://www.cadre-genomes.org.uk</a>	Mabey et al. (2004), and Mabey Gilsenan et al. (2012)
DEEMY	<a href="http://www.deemy.de">www.deemy.de</a>	Agerer and Rambold (2021)
Discomycetes	<a href="http://discomycetes.org">discomycetes.org</a>	Discomycetes (2023)
Dothideomycetes	<a href="http://dothideomycetes.org">dothideomycetes.org</a>	Pem et al. (2019)
e-fungi	<a href="http://www.cs.man.ac.uk">http://www.cs.man.ac.uk</a>	Hedeler et al. (2007) and Cornell et al. (2015)
Ensembl Genomes	<a href="http://www.ensemblgenomes.org/">http://www.ensemblgenomes.org/</a>	Kersey et al. (2010)
EPPO-Q-bank	<a href="https://qbank.eppo.int/fungi">https://qbank.eppo.int/fungi</a>	Trontin et al. (2022)
Faces of Fungi	<a href="https://www.facesoffungi.org/">https://www.facesoffungi.org/</a>	Jayasiri et al. (2005)
Fungal Genetics Stock Center (FGSC)	<a href="https://www.fgsc.net/">https://www.fgsc.net/</a>	McCluskey et al. (2010)
Fungal Genome Database (FGDB)	<a href="https://bio.tools/fgdb">https://bio.tools/fgdb</a>	Güldener et al. (2006)
Fungal Growth Database	<a href="https://www.fung-growth.org">https://www.fung-growth.org</a>	Fungal Growth Database (2023)
Fungal ITS Database Commons	<a href="https://ngdc.cncb.ac.cn/databasecommons/database/id/4155">https://ngdc.cncb.ac.cn/databasecommons/database/id/4155</a>	Fungal ITS Database Commons (2023)
Fungal MLST	<a href="https://mlst.mycologylab.org/">https://mlst.mycologylab.org/</a>	Fungal MLST (2023)
Fungal Names	<a href="https://nmdc.cn/fungalnames/">https://nmdc.cn/fungalnames/</a>	Wang et al. (2023a, b, c)
FungiDB	<a href="https://fungidb.org">https://fungidb.org</a>	Stajich et al. (2012)
Fungi of Brazil	<a href="http://www.cybertruffle.org.uk">http://www.cybertruffle.org.uk</a>	Minter (2011)
Fusarium-ID database	<a href="https://www.fusarium.org/">https://www.fusarium.org/</a>	Torres-Cruz et al. (2022)
Global Biodiversity Information Facility (GBIF)	<a href="http://www.gbif.org">www.gbif.org</a>	Telenius (2011)
GlobalAMFungi	<a href="https://globalamfungi.com/">https://globalamfungi.com/</a>	Větrovský et al. (2023)
GenBank	<a href="https://www.ncbi.nlm.nih.gov/genbank/">https://www.ncbi.nlm.nih.gov/genbank/</a>	Benson et al. (2015)
GlobalFungi	<a href="https://globalfungi.com/">https://globalfungi.com/</a>	Vetrovsky et al. (2020)
Index Fungorum	<a href="https://www.indexfungorum.org/">https://www.indexfungorum.org/</a>	Indexfungorum (2023)
ISHAM Barcoding Database	<a href="http://www.its.mycologylab.org">www.its.mycologylab.org</a>	Irinyi et al. (2015)
JGI MycoCosm	<a href="https://mycocosm.jgi.doe.gov/mycocosm/home">https://mycocosm.jgi.doe.gov/mycocosm/home</a>	Ahrendt et al. (2022)
Mycobank	<a href="https://www.mycobank.org/">https://www.mycobank.org/</a>	Crous et al. (2004), Robert et al. (2005, 2013)
Mycology Collections Portal	<a href="https://www.mycportal.org">https://www.mycportal.org</a>	Miller and Bates (2017)
PHYMYCO-DB	<a href="https://phymycodb.genouest.org/">https://phymycodb.genouest.org/</a>	Mahé et al. (2012)
Saccharomyces Genome Database	<a href="https://www.yeastgenome.org">https://www.yeastgenome.org</a>	Cherry et al. (1998)
Smithsonian Libraries	<a href="https://www.sil.si.edu">https://www.sil.si.edu</a>	Smithsonian Libraries (2023)
Species Fungorum	<a href="https://www.speciesfungorum.org">https://www.speciesfungorum.org</a>	Speciesfungorum (2023)
Trichoblast	<a href="https://trichokey.com">https://trichokey.com</a>	Kopchinskiy et al. (2005)
UNITE database	<a href="http://www.unite.ut.ee">www.unite.ut.ee</a>	Nilsson et al. (2019a, b)

nomenclature. Combined morphological and phylogenetic analysis of fungal species avoids duplication and misinterpretation of the species worldwide, thereby demanding a global standard. Some researchers have practised and published on data cleansing in data repositories (Hao et al. 2021). All the authorised data depositories can be cleaned for higher accuracy and reliability of the information in modern research. The biogeographic regionalization function requires details about species, including geographic coordinates and collection dates. The problem of species duplication and incorrect naming in databases is a significant concern that must be addressed.

In addition, the DNA barcoding technique, a general sequencing approach, is highly used to identify fungal species, and has to be applied uniformly to all the specimens (Herbert and Gregory 2005). With the availability of an increased number of sequences, evolutionary relationships at a higher level of resolution can be performed (Gabaldon 2020). For this, large-scale scientific research has to be conducted effectively at every level and form of life, like marine, freshwater, terrestrial, desert, snow-covered regions (Polar Regions and snow-capped mountains), living body associations, and so on. Furthermore, most fungal genetic resource collections are generally kept in industrialized countries, whereas least developed or developing countries are rich in resources and diversity without appropriate infrastructure on a global scale (Ryan et al. 2019). Fungal research and infrastructure in the least developed countries are lacking, and future steps can be taken to strengthen them around the globe. The worldwide biodiversity reports and depositories reflect this discrepancy. Collaboration among developed and underdeveloped countries and international culture collections in fungal specimen registration, taxonomic study, compilation in data repositories, and publication is the prime remedy for overall progress and development in fungal biodiversity research. The global scientific community has a huge scope to study a vast fungus diversity to upgrade present lead online data repositories.

Future repositories will emphasize greater community involvement, enabling researchers, citizen scientists, and enthusiasts to contribute data, share observations, and collectively build a more comprehensive understanding of fungi. The development of interactive data visualization and exploration will be used as user-friendly interfaces, and interactive visualization tools could be developed within repositories, making it easier for researchers to explore and analyze complex fungal datasets. Future repositories may focus on predictive modeling using machine learning and AI techniques. Researchers might use these models to predict fungal behavior, interactions, and responses to environmental changes. Through enhanced functional annotations, researchers could focus on exploring biological pathways and both ecological and environmental.

## Current trends, limitations and future research in biocontrol

Biocontrol, also known as biological control, is a strategy for managing pests in an eco-friendly way and making a sustainable environment without any adverse impact on humans, plants, and animals. The use of beneficial microorganisms, such as fungi, bacteria, and viruses, as biocontrol agents against plant pathogens has become more prevalent. This approach harnesses the natural antagonistic interactions between beneficial microorganisms and plant pathogens to suppress disease development.

### Current trends

The research on biocontrol of plant diseases, including postharvest diseases of fruits and vegetables, has undergone significant development over the past four decades. Biocontrol research was initiated in response to concerns regarding the potential carcinogenicity of numerous synthetic fungicides that were being utilised, and the anticipated withdrawal or prohibition of various classes of chemical fungicides. In fact, this has remained a driving force behind postharvest biocontrol research, as many governmental regulatory agencies have imposed increasingly stringent limits on the number of residues allowed on fruits and vegetables (Droby et al. 2016). Numerous studies have identified and screened various types of microorganisms from soil and other substrates and environments, which exhibit varying degrees of control efficacy against different plant diseases (Abdelhai et al. 2019; Ahima et al. 2019). Some of these microorganisms have been successfully applied in agricultural production, resulting in significant social and economic benefits (Hyde et al. 2019).

Due to the necessity of enhancing biocontrol activity through multiple strategies, the scope of biocontrol has been expanded to encompass natural products derived from plants or animals as well as compounds produced by other organisms that can be utilised for pathogen control (Li et al. 2022b). Integrated pest management (IPM) is gaining traction as a sustainable approach to managing plant diseases and pests. It involves combining various control methods, such as biological control, cultural practices, and judicious use of pesticides, to minimise the impact on the environment and human health while effectively controlling plant pathogens. Nanotechnology in plant pathology such as nanoparticles and nanoformulations is being explored for their potential in delivering biocontrol agents or plant defense elicitors more effectively. Nanotechnology offers precise and targeted delivery, increasing the efficiency of disease control and minimizing

environmental impacts. High-resolution remote sensing and data analytics are being utilized to monitor and predict disease outbreaks. This digital agriculture technology allows for timely and targeted interventions, reducing the need for blanket applications of pesticides. Besides the strategy for plant disease control, numerous studies have been conducted on the mechanisms of action. Tjamos et al. (2004) demonstrated that *Paenibacillus alvei* K165 released chitinolytic compounds in an LB growth medium supplemented with glycol chitin, which suggests the potential of K165 to inhibit the growth of *Botrytis cinerea* causing grapevine bunch rot through extracellular chitinases.

With the advance in technology, the use of next generation sequencing technology in combination with universal primer sets, has provided insights into the global microbial community present on plant microbiome. For example, Abdelfattah et al. (2021) conducted a global analysis of the microbiome of 'Royal Gala' apples and investigated the composition and diversity of microbial communities present in various fruit tissues at harvest. The fungal and bacterial communities associated with apple fruit exhibit variations in composition and structure, which are significantly influenced by geographical location. This can be utilized to develop novel approaches for managing fruit quality and safety, as well as reducing losses caused by the establishment and proliferation of postharvest pathogens. Li et al. (2022b) provided current and future trends in the biocontrol of postharvest disease and discussed the use of marker-assisted selection (MAS) to identify markers for resistance to disease including the use of double-stranded RNA (dsRNA) to protect plants from phytopathogen.

## Limitations

Biocontrol methods do not result in the accumulation of toxic residues within the environment. However, many biocontrol agents have a limited scope in eradicating diseases and pests as compared to chemicals as well as they are specific to certain diseases, pathogens, or environmental conditions. Therefore, the efficacy of microorganisms is restricted to certain types of diseases and pests with unique features, while other factors such as application techniques, duration of use, air quality, temperature, humidity levels, sunlight exposure, and storage conditions for each type of biological agent can also impact their effectiveness. The lack of broad-spectrum biocontrol agents poses a challenge in the search for effective biocontrol agents capable of controlling a wide range of plant pathogens. Ethical and regulatory considerations are also a limitation for studies and applications. The release of genetically modified organisms (GMOs) and other biocontrol agents may raise ethical concerns and regulatory

challenges. Striking a balance between environmental safety and effective control is an ongoing issue.

Fungi develop resistance against fungicides and the over-reliance on chemical fungicides has led to the development of resistance in many plant pathogens which is one of the major limitations in plant pathology. As a result, some pathogens have become more difficult to control using conventional chemical methods. *Plasmopara viticola* is an oomycete that causes Downy mildew. This is one of the major threats for grapevine production, due to the yield losses that are associated with severe disease epidemics (Gessler et al. 2011). *Plasmopara viticola* is an obligate parasite of grapevine (*Vitis vinifera*). Most *V. vinifera* cultivars are highly susceptible to the pathogen (Toffolatti et al. 2018a, 2020). This high susceptibility makes chemical control of the pathogen to ensure an adequate yield. *Plasmopara viticola* is a polycyclic pathogen, able to undergo numerous infection cycles during a single grapevine growing season. It overwinters as oospores in dead leaves on the vineyard floor and oospores produce a single macrosporangium with favourable weather conditions in spring. The zoospores infect the receptive grapevine tissues through stomata by rain or dew (Massi et al. 2021). Therefore, frequent fungicide applications are needed in vineyards located in areas with frequent rainfall and moderate temperatures during the grapevine growing season (Toffolatti et al. 2018b).

## Future

Research into natural or synthetic compounds such as elicitors that can activate plant defenses against pathogens without causing harm to beneficial organisms could revolutionise disease control. Future research should prioritize the development of more environmentally friendly biological control methods. This includes exploring more efficient natural control agents and integrating diverse control strategies to decrease dependence on chemical pesticides, as well as mitigate environmental contamination and ecosystem degradation. Microbiome-based approaches are another future trend that will understand the plant microbiome and its influence on disease development. This can open new avenues for disease management. Manipulating the plant microbiome or introducing beneficial microbes could offer innovative biocontrol strategies (Afridi et al. 2022).

The development of biotechnology and gene editing technology is expected to provide new tools and methods for biological control. Gene editing techniques can be employed to enhance the attributes of natural predators or beneficial insects, fungi, and bacteria thereby enhancing their efficacy in pest and disease management. In addition, gene editing can also be used to develop crop varieties that are resistant to pests and diseases. For instance, CRISPR-Cas9 and Gene Editing hold promise for developing disease-resistant

plant varieties. Further research in this area could lead to the development of more resilient crops (Rivero et al. 2022).

It is also important to seek more efficient methods to forecast and monitor the occurrence and distribution of pests and diseases. This will help agriculturalists and ecosystem managers in implementing strategies to mitigate economic losses and ecological harm during disease outbreaks. Further integrating precision agriculture techniques and artificial intelligence can enhance disease monitoring, prediction, and management at a finer scale (Talaviya et al. 2020). Research into the identification of virulent genes and their functions are needed to implement better control strategies (John et al. 2021). Future research should pay more attention to the service functions of biological control in ecosystems, with a particular focus on elucidating the fungal role in biodiversity maintenance and ecosystem stability (Liu et al. 2022). This will help us to better utilize ecosystem services for biological control while protecting and restoring ecosystem functions.

## Current trends, limitations and future research in edible fungi and functional foods

### Current trends in the introduction of new mushrooms to the table

Edible fungi are consumed as both food, and in traditional Chinese medicine as well as used as productive sources of various food products and chemicals (Alam et al. 2021). Ascomycetes, have played an important role in the production of food and medicinal compounds. According to Kirk et al. (2008) many ascomycetes producing substantial fruit bodies are edible. Many genera, such as *Cordyceps*, *Morchella*, *Tuber* and truffle-like fungi are used in medicine due to their bioactive substances (Wasser 2011; 2014). *Ophiocordyceps sinensis* has been used in Chinese medicine due to its biological activity (Lin and Li 2011). However, natural *Ophiocordyceps sinensis* yields have declined by over 90% over the past 25 years, leading to a rapid increase in price and reduced affordability (Feng et al. 2008). As a consequence of this scarcity, natural alternatives such as *C. liangshanensis*, *C. militaris*, and *C. cicadicola* have been promoted in markets (Yang et al. 2009). *Morchella*, is a popular, valuable and palatable mushroom which has been determined to be rich with bioactive components (Ali et al. 2011; Fu et al. 2013; Zhang et al. 2021a, b). Truffles and truffle-like fungi are also well-known revered taxa which are in high demand for both culinary as well potential use to offset climate change (Thomas and Büntgen 2019).

Mushrooms in basidiomycetes are also consumed, and their use is a significant part of folk medicine. The mushroom industry, including cultivation of mushrooms and key

derivatives, has had a direct and observable benefit to human health, and as a result has grown rapidly (Lu et al. 2020). Parallel to this trend of industry growth and discovery, consumers of various nations have been increasingly exposed to using wild ingredients in novel gastronomic experiences, while considering sensory, cultural, social, and historical factors (Adapon 2008; Youssef and Spence 2021). Table 3 is a summary of how novel mushrooms are currently being used.

### Current trends in edible fungi as meat replacements

There is a growing trend for consuming edible fungi for use as part of a sustainable and healthier diet for human muscle growth (Das et al. 2021). The majority of fungi used as food are macrofungi, or mushrooms, with fleshy fruiting bodies, distinct flavors and aromas, and strong nutritional qualities (Lesa et al. 2022). Importantly, mushrooms are largely made up of protein, and includes all nine of the essential amino acids that humans require but cannot synthesize (González et al. 2020; Yuwa-Amornpitak et al. 2020; Davila and Du 2023). Additionally, mushroom compounds contain antibacterial and antioxidant properties can extend the shelf life of meat products (Pérez Montes et al. 2021).

As a result of their high protein content and bioactive properties, consumers are more frequently using edible fungi as meat substitutes. Products of the mushroom group that are especially suitable for vegetarian diets and a good option for those who do not consume meat include *Agaricus*, *Auricularia*, *Boletus*, *Flammulina*, *Grifola*, *Hericium*, *Lentinus*, *Phallus*, *Pleurotus*, *Tremella*, *Tuber* and *Volvariella* (Prasad et al. 2015; Li et al. 2021a, b). Furthermore, in the development of more sustainable meat products, mushrooms have been used as an addition or supplement to a diet including meats (Table 4). In the contemporary world, consumers perceive meat substitutes as ethical, nutritious, and eco-friendly alternatives. There is, however, a need for further changes in consumer ideas, perceptions, as well as understanding and more clean-label healthy meat substitute innovations (Aschemann-Witzel et al. 2020). Furthermore, many studies are developing healthy meat replacements, and it remains necessary to demonstrate whether edible fungi can be used as a viable replacement for meat consumption.

### Current trends in edible fungi as dietary supplement products and/or functional foods

Edible fungi are regarded as high-quality food products with nutritional and functional properties (Al-Obaidi et al. 2021). While fungi have been consumed by humans for centuries, their status as a key food with potential benefit to many aspects of human health has increased in recent years (Assemie and Abaya 2022). With the discovery of novel



**Table 3** Summary of the current trend of introducing mushrooms for consumption

Genus	Species	References
<i>Agaricus</i>	<i>Agaricus augustus</i> <i>Agaricus bisporus</i> <i>Agaricus campestris</i> <i>Agaricus pampeanus</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)
<i>Albatrellus</i>	<i>Albatrellus aff. ovinus</i>	Santiago et al. (2016)
<i>Amanita</i>	<i>Amanita basii</i> Ram. Guill <i>Amanita calyptroderma</i> <i>Amanita grupo caesarea</i> <i>Amanita tecomate</i> <i>Amanita flavoconia</i> <i>Amanita aff. jacksonii</i> <i>Amanita aff. laurae</i> <i>Amanita sect. caesarea</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)
<i>Boletus</i>	<i>Boletus edulis</i> <i>Boletus edulis var. clavipes</i> <i>Boletus aff. aereus</i> <i>Boletus barrowsii</i> <i>Boletus appendiculatus</i> <i>Boletus atkinsonii</i> <i>Boletus edulis s.l.</i> <i>Boletus pinophilus</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)
<i>Calvatia</i>	<i>Calvatia aff. cyathiformis</i>	Santiago et al. (2016)
<i>Cantharellus</i>	<i>Cantharellus cibarius</i> <i>Cantharellus subalbidus</i>	Molina-Castillo et al. (2023)
<i>Gomphus</i>	<i>Gomphus floccosus</i>	Molina-Castillo et al. (2023)
<i>Helvella</i>	<i>Helvella lacunosa</i> <i>Helvella crispa</i>	Molina-Castillo et al. (2023)
<i>Hohenbuehelia</i>	<i>Hohenbuehelia petaloides</i>	Santiago et al. (2016)
<i>Hydnum</i>	<i>Hydnum repandum</i>	Santiago et al. (2016)
<i>Lactarius</i>	<i>Lactarius indigo</i> <i>Lactarius aff. mitissimus</i> <i>Lactarius luculentus</i> <i>Lactarius volemus</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)
<i>Laccaria</i>	<i>Laccaria</i>	Molina-Castillo et al. (2023)
<i>Lyophyllum</i>	<i>Lyophyllum decastes</i> <i>Lyophyllum shimeji</i>	Molina-Castillo et al. (2023)
<i>Morchella</i>	<i>Morchella esculenta</i> <i>Morchella conica</i>	Molina-Castillo et al. (2023)
<i>Marasmius</i>	<i>Marasmius oreades</i>	Santiago et al. (2016)
<i>Neolentinus</i>	<i>Neolentinus lepideus</i>	Santiago et al. (2016)
<i>Pleurotus</i>	<i>Pleurotus opuntiae</i> <i>Pleurotus ostreatus</i> <i>Pleurotus aff. dryinus</i> <i>Pleurotus aff. eryngii</i>	Molina-Castillo et al. (2023)
<i>Pseudofistulina</i>	<i>Pseudofistulina radicata</i>	Santiago et al. (2016)
<i>Ramaria</i>	<i>Ramaria abietina</i> <i>Ramaria araiospora</i> <i>Ramaria aurea</i> <i>Ramaria botrytis</i> <i>Ramaria cystidiophora</i> <i>Ramaria fenica</i> <i>Ramaria flava</i> <i>Ramaria formosa</i> <i>Ramaria aff. sanguinea</i>	Molina-Castillo et al. (2023), Santiago et al. (2016)

**Table 3** (continued)

Genus	Species	References
<i>Russula</i>	<i>Russula cf. chloroides</i> <i>Russula brevipes</i> <i>Russula mexicana</i> <i>Russula rosacea</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)
<i>Schizophyllum</i>	<i>Schizophyllum commune</i>	Santiago et al. (2016)
<i>Suillus</i>	<i>Suillus luteus</i>	Molina-Castillo et al. 2023
<i>Ustilago</i>	<i>Ustilago maydis</i>	Molina-Castillo et al. (2023) and Santiago et al. (2016)

**Table 4** Use of edible fungi as a meat replacement

Edible fungi species	Product	References
<i>Agaricus bisporus</i>	Ground meat and beef taco	Wong et al. (2017)
<i>Agaricus bisporus</i>	Meat product	Rangel-Vargas et al. (2021)
<i>Agaricus bisporus</i>	Beef patties	Wong et al. (2019)
<i>Agaricus bisporus</i>	Meat analogue	Kim et al. (2011)
<i>Auricularia cornea</i>	Pork fat in sausages	Fu et al. (2021)
<i>Boletus edulis</i>	Beefburgers	Grangeia et al. (2010)
<i>Flammulina filiformis</i>	Meat analogs	Zou et al. (2023)
<i>Flammulina velutipes</i>	Goat meat nuggets	Banerjee et al. (2020)
<i>Lentinula edodes</i>	Sausages	Wang et al. (2019a)
<i>Lentinula edodes</i>	pork lean meat	Wang et al. (2019a)
<i>Pleurotus</i> spp.	Patties, sausages, paste, and suchlike	Torres-Martínez et al. (2022)
<i>Pleurotus eryngii</i>	Pork sausages	Wang et al. (2019b)
<i>Lentinus sajor-caju</i>	Chicken patties	Wan Rosli et al. (2011)
<i>Lentinus sajor-caju</i>	Beef patties	Wan Rosli and Solihah (2012)
<i>Lentinus sajor-caju</i>	Chicken meat	Husain and Huda-Faujan (2020)
<i>Tremella fuciformis</i>	Pork patties	Cha et al. (2014)
<i>Pleurotus ostreatus</i>	Meat product	Rangel-Vargas et al. (2021)
<i>Volvariella volvacea</i>	Cantonese sausages	Wang et al. (2018)

benefits of edible fungi, the global market for functional mushroom food is expected to continue to increase from the 2022 market value of USD 15.3 billion (Globe Newswire 2022). Fungal products have traditionally been used as functional foods, nutritional supplements, and sources of bioactive chemicals for a variety of medical purposes (Hyde et al. 2019). Recent research has shown that as next-generation ingredients in healthy food (Das et al. 2021), they can enhance health and immunity with their proteins, polysaccharides, terpenes and lipids. Critically, these components have been shown to have anticancer, antidiabetic, antihypercholesterolemia, anti-inflammatory, antiviral and immunomodulatory effects (Hamza et al. 2023).

In addition to medicinal qualities and use in muscle-building diets, edible fungi are suitable for the formation of low-caloric functional meals due to their low-fat content, high-quality proteins, dietary fiber and presence of bioactive compounds (Das et al. 2021). The edible fungi that are being most actively explored for use as functional foods include *Agaricus bisporus*, *Hericium* spp., *Lentinus edodes*, *Monascus purpureus*, *Ophiocordyceps sinensis*, and *Pleurotus* spp.

(Gopalakrishnan et al. 2005; He 2018; Niego et al. 2021; Thongbai et al. 2015). The popularity of these edible mushrooms has resulted in increased attention, leading to breakthroughs in mushroom research and further promotion of various discoveries regarding their health-promoting benefits. (Kumar et al. 2021a, b).

Such research has led to unexpected discoveries including the benefits of edible fungi as a nutritional supplement (Bell et al. 2022). This research has not been ignored by the public, leading to an increase in their use as dietary supplements and functional foods. Furthermore, studies have suggested that the bioactive compounds found in mushrooms and other edible fungi can be extracted and used as supplements or adjuvant therapies for various health conditions (Valverde et al. 2015). The most optimal fungal supplements have been shown to provide critical daily advantages, such as improved brain function, a stronger immune system, greater energy, and better sleep (Healthline 2023; Lovering 2021).

Numerous edible fungi dietary supplements are on the market and are currently economically valuable (Bell et al. 2022). The inclusion of mushroom powder in food items

increased consumer approval by improving taste and juiciness. In the aftermath of the SARS-CoV-2 (COVID-19) epidemic, people are focused on increasing their antioxidant activity through nutrition. Various bioactive substances from fungi, such as ergosterol, gallic acid, and cordycepin, have been shown to be important in preventing or lowering the severity of COVID-19 (Hamza et al. 2023). Therefore, using dried mushroom powder to develop added value coproducts is crucial (Hamza et al. 2023). Mushroom products are available in powder capsule, pill, and in liquid form. Due to their ease of use and extensive availability, capsules and tablets dominate the global market (Market Research Report 2023). The market value of functional fungi is promising and worth exploring.

### Current trends in edible fungi are cosmeceuticals

The combination of cosmetics and pharmaceuticals is known as cosmeceuticals. Cosmeceuticals are topically applied products such as creams, lotions, and ointments that contain biologically active ingredients with benefits similar

to prescription medications (Sharma 2011). According to Hyde et al. (2010), cosmetic products have substances that modify the skin's biological function by providing nutrients and improving its appearance, radiance, texture, as well as having anti-aging activity. Natural ingredients are sought for the cosmetic industry due to their competitive efficacy and lower toxicity effects (Taofiq et al. 2016a, b). Many mushroom extracts have been reported with various bioactivities; see Table 5, 6 based on literature reviews (Taofiq et al. 2016a). The most common bioactivities were antityrosinase, anticollagenase, antihyaluronidase, and antielastase. However, more research may be needed to uncover further activity. Abd Razak et al. 2020 reported that the extract of four edible mushrooms, namely *Pleurotus ostreatus*, *Ganoderma lucidum*, *Auricularia polytricha* and *Schizophyllum commune*, were examined for antioxidant, antihyaluronidase and antityrosinase activity. Based on Hyde et al. (2010), some cosmetic products have extracts of *Ophiocordyceps sinensis* (Berk.) G.H. Sung, J.M. Sung, and *Tremella fuciformis* Berk. to increase the moisturizing effect. In the Center of Excellence for Fungal Research of Mae Fah Lung University,

**Table 5** Reported mushroom extracts with cosmeceutical potential

Mushroom species	Bioactivity	Types of Chemical Compounds	References
<i>Agaricus bisporus</i> (J.E.Lange) Imbach	Anti-tyrosinase, anti-aging	2-Amino-3H-phenoxazin-3-one	Miyake et al. (2010) and Taofiq et al. (2016b)
<i>Agaricus subrufescens</i> Peck (= <i>Agaricus brasiliensis</i> ) Fr	Anti-tyrosinase	Extract	Huang et al. 2014
<i>Coriolus versicolor</i> (L.:Fr.) Qué	Anti-tyrosinase	Extract	Park et al. (2015)
<i>Ganoderma lucidum</i> (Curtis) P. Karst	Anti-tyrosinase, Hyaluronidase activity	Extract, hot-water extract	Chien et al. (2008), Taofiq et al. (2019), Abd Razak et al. 2020
<i>Grifola frondosa</i> (Dicks.) Gray	Anti-collagenase, Anti-tyrosinase	Exopolysaccharide, Mycelia extract	Bae et al. 2005, Kim (2007)
<i>Inonotus mikadoi</i> (Lloyd) Gilb. & Ryvardeen	Anti-tyrosinase	Extract	Park et al. (2015)
<i>Lentinula edodes</i> (Berk.) Pegler	Anti-tyrosinase, Anti-aging	Extract	Yan et al. (2014), Taofiq et al. (2016b)
<i>Lentinus lepideus</i> (Fr.) Redhead & Ginns	Anti-tyrosinase	Extract	Yoon et al. (2011)
<i>Pleurotus citrinopileatus</i> Singer	Anti-hyaluronidase, Anti-tyrosinase	Extract	Yoon et al. (2011)
<i>Pleurotus ferulae</i> (Lanzi) X.L. Mao	Anti-tyrosinase	Extract	Uchida et al. 2014
<i>Pleurotus nebrodensis</i> (Inzenga) Qué	Anti-tyrosinase	Extract	Meng et al. (2011)
<i>Pleurotus ostreatus</i> (Jacq. ex Fr.) P.Kumm	Anti-tyrosinase, Anti-aging	Extract	Alam et al. (2012), Hapsari et al. (2012), Taofiq et al. (2016b), Taofiq et al. (2019),
<i>Pleurotus tuber-regium</i> (Rumph. ex Fr.) Singer	Anti-hyaluronidase	Extract	Dandapat and Sinha, (2015)
<i>Tricholoma matsutake</i> (S. Ito & S. Imai) Singer	Anti-elastase, Anti-collagenase	Extract	Kim et al. (2014)
<i>Volvariella volvacea</i> (Bulliard ex Fries) Singer	Anti-collagenase	Phenolic compounds, polysaccharide	Ruksiriwanich et al. 2014

**Table 6** Cosmetic products containing some edible mushrooms and their function (Wu et al. 2016)

Mushroom species	Product Name	Function
<i>Agaricus subrufescens</i> (also known as <i>A. brasiliensis</i> )	Vitamega Facial Moisturizing Mask, Brazil	Renew and revitalize skin
<i>Cordyceps sinensis</i> (Berk.) Sacc	Kose Sekkisei Cream, Japan	Moisturizer and suppress melanin production
<i>Inonotus obliquus</i> (Fr.) Pilát	Root Science RS Reborn Organic Face Mask, U.S	Anti-inflammatory to help soothe irritated skin
<i>Lentinula edodes</i>	Aveeno Positively Ageless Daily Exfoliating Cleanser, U.S	Lift away dirt, oil and makeup and fight signs of aging
	One Love Organics Vitamin D Moisture Mist, U.K	Part lightweight moisturizer and part toner
	Osmia Organics Luz Facial Brightening Serum, U.S	Skin looking bright and luminous
<i>Ganoderma lucidum</i>	CV Skinlabs Body Repair Lotion, U.S	Wound-healing and anti-inflammatory
	Dr. Andrew Weil for Origins Mega-Mushroom Skin Relief Face Mask, U.S	Anti-inflammatory properties
	Four Sigma Foods Instant Reishi Herbal Mushroom Tea, U.K	Immunity boost
	Kat Burki Form Control Marine Collagen Gel, U.K	Boost collagen, improve elasticity and provide hydration
	Menard Embellir Refresh Massage, France	Skin anti-aging
	Moon Juice Spirit Dust, U.S	Immune system
	Tela Beauty Organics Encore Styling Cream, U.K	Provide hair with sun protection and prevent color fading
	Yves Saint Laurent Temps Majeur Elixir De Nuit, France	Anti-aging
	<i>Schizophyllum commune</i>	Alqvimia Eternal Youth Cream Facial Máxima Regeneración, Spain
Sulwhasoo Hydroaid, Korea		Hydrating cream promoting clear, radiant skin
<i>Tremella fuciformis</i>	La Prairie Advanced Marine Biology Night Solution,	Moisturizer which nourishes, revitalizes and hydrates skin
<i>Ganoderma lucidum</i> and <i>Pleurotus ostreatus</i>	Hankook Sansim Firming Cream (Tan Ryuk SANG)	Make skin tight and vitalized
and <i>Lentinula edodes</i>	La Bella Figura Gentle Enzyme Cleanser, Italia	Antioxidants and vitamin D
<i>Ganoderma lucidum</i> , <i>Lentinula edodes</i> , and <i>Mucor miehei</i>	Pureology NanoWorks Shineluxe, France	Anti-aging

Chiang Rai, Thailand, The King's Cordy Serum product is produced, which contains *Cordyceps militaris* (L.) Fr. extract and this extract has been shown to facilitate anti-wrinkle effects and add moisture and antioxidants to the skin (Hyde et al. 2019).

The bamboo mushroom or *Phallus indusiatus* Vent. is an edible mushroom but can be eaten at the egg stage only (Habtemariam 2019). The bamboo mushroom has been studied and investigated regarding the cultivation of bamboo pulp, and the potential consumption of further products of the fungi (Thaisuchat et al. 2022). Bamboo mushroom extract has benefits for skin care; it has been developed into natural cosmetics in various forms (Razif and Fung 2021). Of note, extracts from the mucus cover of bamboo mushrooms were found to be rich in hyaluronic acid, the same substance which has been isolated from snail slime

(Chumkhiao 2021). This extract has been shown to help the skin's nourishing properties, reduce irritation, and add moisture. Furthermore, gluconic acid of the bamboo mushroom extract helps exfoliate skin cells and strengthen collagen under the skin as well as moisturize the skin which helps reduce premature aging (Shivhare et al. 2013; Chumkhiao 2021). The skin care products of the extract of straw mushrooms (*Volvariella* sp.) are effective in reducing the pigmentation of melanin in the skin, making the skin appear radiant, reducing wrinkles, and adding moisture to the skin. Straw mushrooms contain polysaccharides that have the ability to add moisture to the skin and antioxidant properties (Sangthong et al. 2022). Wu et al. (2016) reported cosmetic products containing mushrooms and their function, various edible mushroom species, and substances that are now used in cosmetics or that are patented to be used in these products.



## Limitations

Instead of using techniques that are damaging to the environment such as burning, mushrooms can be grown with relative ease using a variety of low value agricultural and forest by-products (Okuda 2022). As a result, mushroom production is proposed to be a lucrative industry, particularly in underdeveloped nations. Furthermore, mushroom cultivation is an example of cyclical agriculture that supports the sustainability of forests and the environment by preventing soil degradation (Kohsaka et al. 2021). Both the "bright" features of mushroom farming that promote sustainability and the "dark" ones that work against such impacts must be addressed. Unfortunately, despite its contribution to sustainability, there is a lack of worldwide awareness and stagnation in global uptake in mushroom cultivation (Elisashvili 2012). The explosive growth and expansion of the mushroom industry in China is a remarkable illustration of rural development fueled by bio-innovation and the dissemination of technology (Zhang et al. 2014). In addition to being a good example of a traditional recycling economy, sustainable agriculture, and forestry, it is also a great example of rural economic development and poverty relief (Zhang et al. 2014). Furthermore, it will be critical to exchange fundamental know-how and experience with facilities that deal with mushrooms (Okuda 2022).

The introduction of sustainability certification schemes is another effective strategy to highlight the environmental benefits of the mushroom industry (Okuda 2022). On the downside, the massive amount of mushroom spores produced by indoor cultivation endangers the health of growers, pollutes facilities, and erodes the natural genetic variety. Despite having both a "bright" and a "dark" side, the mushroom industry appears to be moving in the direction of greater environmental sustainability as a result of trends and new findings (Okuda 2022). Profits are only a small portion of the benefit to a nation's total mushroom production. Despite this, the working climate in this sector may not be sustainable due to the extreme competitiveness of prices. The working environment must also be taken care of if mushroom cultivation is to be sustainable. Although this type of issue could be overly generic, it should not be dismissed and should be acknowledged as a widespread difficulty in many sectors, not just mushroom farming. An efficient way to raise the perceived value of mushrooms internationally and ensure the profitability of mushroom production as a marketing strategy is to address sustainability issues associated with mushroom production as soon as possible (Okuda 2022). Additional enhancements in the production of currently cultivated species are also required, such as year-round cultivation of "seasonal" species and greater quality control. We can test a non-green (white agricultural) revolution in underdeveloped nations and the rest

of the world using mushrooms, a special group of fungi. On a local, national, and international scale, mushrooms have the ability to significantly improve the socioeconomic and environmental conditions that affect human welfare (Chang and Wasser 2017a, b).

The health-promoting qualities of mushrooms are mainly attributable to their high content of fiber, particularly chitin and glucans (Stachowiak and Reguła, 2012; Jayachandran et al. 2017). The glucans, whether homo- or heteroglucans, play an important role in the structure of the fungal cell wall (Manzi and Pizzoferrato 2000; Ferreira et al. 2015; Vetter 2023). These are made up of sugar (mainly glucose) chains, and the linear or even branching structure is created by normal glycosidic linkages (Vetter 2023). The integrity of this triple helix structure and the unique configuration of  $\beta$ -glucans appear to be crucial for the biological actions of the molecule (Vetter 2023). Antitumor (anticarcinogenic) and immune-stimulating activities are two of glucans' key biological effects (Kothari et al. 2018; Wu et al. 2021a, b; Vetter 2023). Some glucan types may also have additional categories of benefits (such as anti-diabetic, antioxidant, etc.) linked with them (Vetter 2023). Moreover, the chitin molecule is made up of monomers of 1,4-N-acetyl-D-glucosamine chemically (Vetter 2023). All fungi in the Eukaryota kingdom typically have cell walls that contain chitin, which is an extremely resilient and water-insoluble component (Vetter and Siller 1991; Vetter 2007; 2023; Zhang et al. 2016). Because the needed chitinase activity in the digestive systems of animals and humans is quite low, the actual chitin content of a mushroom fruit body seems to be a significant determinant in its digestibility (Vetter 2023). However, there is another side to the significance of the chitin content in nutritional physiology: it contributes significantly to the dietary fiber fraction and, as a result, helps to meet the fiber needs of typical digestive processes (Vetter 2023).

Nevertheless, new initiatives are needed to elucidate the bioactive compounds yet to be identified in various mushrooms and their medicinal potential (Raghavendra et al. 2017). To promote preclinical and clinical research and ensure its safety, innovative toxicological studies are required (Elkhateeb 2020; Frost 2016; Jeitler et al. 2020). More research on mushrooms would be useful to find active components that contribute to functional food properties, health promotion, and disease prevention (Bell et al. 2022; Rousta et al. 2023). Although the study of medicinal mushrooms has recently rapidly advanced, more work remains. Regarding their pharmacological effects, many species are still unstudied or underappreciated. Identifying the compounds in the extracts, the metabolites responsible for their effects, their chemical characterization, and their mode of action are also of utmost importance (Venturella et al. 2021). The majority of studies that have been reported on the immunomodulatory actions were carried either in vivo or

in vitro, which may not accurately reflect the function in the human body (Yin et al. 2021; Kozarski et al. 2023). Therefore, more research is still needed to understand the mechanism and use of in the body (Yin et al. 2021). Moreover, to maintain quality, it is essential to regulate, monitor and standardize the production of mushroom supplements along the supply chain, from cultivation to extraction and preparation of the commercial formulation (Venturella et al. 2021).

### Future research

The current demand to maintain human well-being, and to focus on healthy lifestyles, is a key driver of fungi and fungus products research (Al-Obaidi et al. 2021; Hyde et al. 2019; Mapook et al. 2022). The medical, health, and beauty businesses have grown significantly due to the demand for herbal products, especially new drugs, dietary supplements, beverages, and cosmetics (Ekor 2014). Along with the increase in the aging society this has resulted in a preference for natural products. These help to build immunity and promote health. Global wellness institute predicts that in 2020, the market value of health and wellness products was worth US\$ 4.4 trillion and is expected to increase to US\$ 6 trillion by 2025 (Global wellness institute 2020). Therefore, research and development (R&D) of human welfare products from natural products such as plants, animals, microorganisms, and particularly fungi will be important.

Fungi are important producers of natural products (Alberti et al. 2017a, b; Sanchez and Demain 2017). However, only about 150,000 species of fungi and fungus-like taxa have been reported, although far more than 1.5 million species are estimated to exist (Gautam et al. 2022). Therefore, studies on the biodiversity of edible and other fungi and their uses are important as it should result in new mushrooms and mushroom products. Research to find new sources of fungi that produce novel medicinal compounds, studies on the genetic levels of biosynthetic gene expression to increase the efficiency of biological metabolites and research to verify health claims of consuming fungi, clinical trials, new innovations, and market research are areas for future study.

### Mycoremediation of polluted soils—trends, limitations and future research

Fungal-based bioremediation, also known as mycoremediation, is defined as the degradation, removal, or isolation of environmental pollutants using fungi (Stamets 2005; Akhtar and Mannan 2020). Fungi have a broad range of enzymes capable of degrading complex inorganic and organic pollutants, making them ideal candidates for the remediation of contaminated soils. They have been successfully used

for the removal of hydrocarbons, heavy metals, pesticides, industrial waste products, and even radioactive materials from soils (Singh et al. 2020). Mycoremediation holds great promise for further development, offering a broad range of cost-effective mechanisms for alleviating contaminated soil systems.

Current trends in this field include the use of genomics-based toolkits coupled with traditional culture methods for the screening of fungal species from different environments, with the aim of discovering fungi that have the capacity to be used in the bioremediation of contaminated soils (Park and Choi 2020; Akpasi et al. 2023). Fungi found growing in polluted soils or on complex substrates can be tested in the laboratory for their ability to break down, bio-transform, or hyperaccumulate various pollutants. An extension of this work is the use of nanoparticles derived from fungi which can be used for the targeted delivery of enzymes and the adsorption of contaminants in the soil, thus increasing the overall efficiency of the process (Alazaiza et al. 2021; Kumar et al. 2021a, b; Sharma et al. 2023). Another trend in mycoremediation is the investigation of fungi with the ability to hyperaccumulate heavy metals, and how to not only increase the scale and efficiency of hyperaccumulation but also the successful removal of pollutants after the fungi have assimilated the heavy metals (Hu et al. 2021; Borovička et al. 2022). In addition to the hyperaccumulation of heavy metals, the ability of certain fungal groups, such as white rot fungi, to remove xenobiotics from soils is of particular interest to restoration scientists as xenobiotics are finding their way into soils systems at alarming rates as a result of anthropogenic activities (Khatoun et al. 2021).

### Limitations

Despite the positive applications of mycoremediation and the potential for these practices to effectively remove pollutants from soil systems, there are certain limitations that need to be addressed. Compared to bacterial-based bioremediation methods, fungi can be slow in degrading pollutants. Furthermore, the rate of fungal growth and the associated degradation of substrates is influenced by soil factors such as soil pH, temperature, moisture, and nutrient availability (Soares and Rousk 2019). These constraints will impact how effectively fungi can be used for bioremediation purposes. In addition, the large-scale use of fungi has not been widely tested and the lack of knowledge surrounding how to use fungi at scale for soil restoration efforts remains a key limitation in developing this technology (Chen et al. 2020). Lastly, in order to effectively use fungi for bioremediation purposes, there are numerous site-specific considerations that need to be addressed. Not only the type of pollutant, but also the environmental and biophysical conditions at each site will influence the success of the mycoremediation program.

## Future

Mycoremediation of soil systems holds great promise for future applications, but it is currently limited in the scale of application due to knowledge gaps and constraints in our ability to effectively harness the full potential of the fungi involved. As such, there are numerous areas of research required to improve the mycoremediation process. At the field level, large-scale trials are needed to test how effectively fungi can be used for bioremediation in real-world scenarios. However, such trials should be performed in conjunction with laboratory-based research. An improved understanding of fungi and their life cycles will enable scientists to select and breed fungi for targeted use in specific environments or for certain types of pollutants. Network analyses of soil microorganisms can provide insight into how different microbes interact in the soil, allowing scientists to understand the synergistic behavior between fungi and other soil organisms, such as bacteria, and archaea (Matchado et al. 2021). This will enable the development of broader bioremediation strategies, potentially employing a range of organisms and thus enhancing the overall efficiency of the bioremediation process.

The genetic modification of fungi to enhance their capacity for pollutant degradation will be a key area of research in the future, including the upregulation of existing enzymes or the integration of enzymes from other organisms (Stein et al. 2018; Kumar et al. 2020). This work should be coupled with omics-based research. A deeper understanding of genomics, proteomics, transcriptomics, and metabolomics will allow scientists to better understand the bioremediation processes and, thus, potentially manipulate the genes and metabolic pathways involved.

Therefore, a multidisciplinary approach, combining taxonomists, molecular biologists and field practitioners, is required if we are to benefit from the use of fungi in large-scale bioremediation programs. The vast array of pollutants found in soils and the impact these have on soil biodiversity, agricultural productivity, and ecosystem health requires direct action on our behalf if soils are to be successfully restored. Fungi offer great potential to help in the restoration process, and future research programs should contribute to making mycoremediation a realistic strategy for use at the landscape level.

## Conclusion and appraisal of papers of Special Issue

In this paper we have reviewed 16 topics that we consider as important current trends in fungal biology research. A further topic, not covered in this paper are changes in the lifestyles of fungi as it is the subject of this special issue. Fungi

can occupy numerous life modes and their abilities to produce enzymes with multivarious functions outside the fungal mycelial allow them to cross the different lifestyle barriers. Many fungi are thought to have evolved from endophytic ancestors and this is the theme of the paper by Bhunjun and coauthors. Endophytes live symptomless within plant hosts. When the plant is stressed, they may become opportunistic pathogens or at leaf senescence they become active saprobes using their armoury of enzymes to degrade the dying plant cells. Chen and coauthors use genomics to show how opportunistic pathogens of Botryosphaeriaceae evolved from saprobic or endophytic ancestors. Necrotic pathogens may also kill the host and then digest the dead cells using enzymes also commonly found in endophytes and saprobes (Bucher et al. 2004, Shao et al. 2021). With their ability to degrade chitin and keratin, fungi can infect other fungi cells walls, living and dead insects, human and animal skin and hair. In this special Quan and coauthors examine the evolution of human pathogens in Chaetothyriales, Tang and coauthors the evolution of hair pathogens, Yu and coauthors discuss the fungal pathogens of cultivated mushrooms and Coleine and co-authors discussed the effect of harsh environments such as high and low temperatures, and industrial pollution on the lifestyle changes of black fungi based on comparative genomic analyses.

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**Data Availability** There are no datasets in this paper.

## Declarations

**Conflict of interest** The authors have no conflicts of interest, competing interests or relevant financial or non-financial interests to disclose.

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