



The contribution of fungi to the global economy

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Abstract

Fungi provide ecological and environmental services to humans, as well as health and nutritional benefits, and are vital to numerous industries. Fermented food and beverage products from fungi are circulating in the market, generating billions of USD. However, the highest potential monetary value of fungi is their role in blue carbon trading because of their ability to sequester large amounts of carbon in the soil. There are no conclusive estimates available on the global monetary value of fungi, primarily because there are limited data for extrapolation. This study outlines the contribution of fungi to the global economy and provides a first attempt at quantifying the global monetary value of fungi. Our estimate of USD 54.57 trillion provides a starting point that can be analysed and improved, highlighting the significance of fungi and providing an appreciation of their value. This paper identifies the different economically valuable products and services provided by fungi. By giving a monetary value to all important fungal products, services, and industrial applications underscores their significance in biodiversity and conservation. Furthermore, if the value of fungi is well established, they will be considered in future policies for effective ecosystem management.

Keywords Fungi-based food · Medicinal mushrooms · Market value · Environmental biotechnology

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Introduction

It is irrefutable that fungi play a pivotal role in any ecosystem. Detrital pathways are necessary for carbon and nutrient cycling (Liu et al. 2020a). Fungi have very essential functions in addressing major global challenges. Wild mushrooms, especially if they can be cultivated, constitute a significant non-timber forest resource that provides various benefits, especially food and income for local communities in many parts of the world (Mortimer et al. 2012). They can be instrumental in improving resource efficiency as renewable substitutes for fossil resources. Moreover, they can be valuable sources of food, nutraceuticals, cosmeceuticals, amino acids, proteins, carbohydrates, vitamins, fats, and minerals (Ślusarczyk et al. 2021; Badalyan et al. 2022). They produce manifold bioactive compounds with medicinal, pharmaceutical, and industrial applications (Hyde et al. 2019; Niego et al. 2021; Galappaththi et al. 2022).

These numerous benefits of fungi are often overlooked, and the general population is often unaware of their value. Applied research has unfolded the role and potential of fungi in environmental services, such as bioremediation, mitigation of pollution, and as a resource for the development of drugs to combat various human diseases (Hyde et al. 2019). To fully utilize the potential of fungi, we need to understand their services rendered in ecosystems on a global scale. With the move towards a biobased circular economy (Meyer et al. 2020), we now consider it appropriate to make the world aware of the immense value of fungi for sustainable global development. Economic valuation is essential to create transparency with respect to the services rendered by fungi in ecosystems compared to other economic assets. This will provide clarity in political discussions, often dominated by monetary worth since ecosystem conversion appears to be more profitable than

conservation. Economic criteria represent as well key elements during decision-making processes regarding conservation policies (Martin-Lopez et al. 2008; Takala et al. 2021).

The current review paper narrates the contribution of fungi in bio-economies. A greater understanding of the roles and value of fungi can be used to build global support for mycological appreciation. It will, in particular, raise policymakers' awareness of the importance of fungi, leading to future research and conservation efforts.

Methods used to give monetary value to fungal services

Data sources

The available data were collected and extrapolated from published studies in scientific journals, databases, online market research, and reliable news and articles. Scientific journals were the major sources of reports for this paper. The published academic papers considered are from reliable journals, not listed in Beal's list of potential predatory journals and publishers (<https://beallist.net/>). Key databases, which are listed below, provided reliable data for chemical/drug information (ChEBI 2022; Drugbank Online 2022a; National Center for Biotechnology Information 2022a; Special Chem 2022), industry reports and international trade reports (DEFRA 2006; OEC 2022a; Tridge 2022a), agricultural production (Food Data Central 2019; UNData 2022) and information on the populations (World Population Review 2022). Online market research reports are the main source for the market value of fungal products used in our study (Table 1). They provided reliable sources of data since they are based on literature analysis, annual reports, technical papers, news releases, white papers, conference papers, government publications, trade data and other literature for market studies. News on TV and social media, as well as articles in newspapers and magazines featuring economy news and market reviews can also provide the needed knowledge for fungal-marketed products, since many marketed values are not published in scientific journals (Table 1). However, we had experienced that some of the provider companies requested substantial fees when we asked them for details. This is why we were not able to add data on some of the included product lines.

Identification of economically important products and services of fungi

The first and most relevant method for this article is to identify and list the major individual products and services of fungi that contribute to the global economy. The marketable products and services are categorized into (i) wild and cultivated mushrooms traded for food, (ii) industrial uses of fungi (e.g. medicines and pharmaceuticals, food and beverages,

Table 1 Data sources of market value of fungal products

Data sources	Name	Website
Databases	ChEBI	https://www.ebi.ac.uk/chebi/
	Drugbank Online	https://go.drugbank.com/
	FAOSTAT	https://www.fao.org/faostat/
	FoodData Central	https://fdc.nal.usda.gov/
	International Trade Center	https://intracen.org/
	National Center for Biotechnology Information	https://www.ncbi.nlm.nih.gov/
	OEC	https://oec.world/
	Special Chem	https://www.specialchem.com/
	UNData	https://data.un.org/
Online Market Research	World Population Review	https://worldpopulationreview.com/
	Allied Market Research	https://www.alliedmarketresearch.com/
	Business Research Insights	https://www.businessresearchinsights.com/
	Data Bridge Market Research	https://www.databridgemarketresearch.com/
	Dataintel	https://dataintel.com/
	Fior Market	https://www.fiormarkets.com/
	Fortune Business Insight	https://www.fortunebusinessinsights.com/
	Future Market Insights	https://www.futuremarketinsights.com/
	Global Market Insights	https://www.gminsights.com/
	Grand View Research	https://www.grandviewresearch.com/
	Imarc	https://www.imarcgroup.com/
	InsightAce Analytic	https://www.insightaceanalytic.com/
	Market Data Forecast	https://www.marketdataforecast.com/
	Markets and Markets	https://www.marketsandmarkets.com/
	Maximize Market Research	https://www.maximizemarketresearch.com/
	Mordor Intelligence	https://www.mordorintelligence.com/
	Persistence Market Research	https://www.persificmarketresearch.com/
	Polaris Market Research	https://www.polarismarketresearch.com/
	PS Market Research	https://www.psmarketresearch.com/
	Reportlinker	https://www.reportlinker.com/
	Research and Markets	https://www.researchandmarkets.com/
	Statista	https://www.statista.com/
	Straits Research	https://straitsresearch.com/
	The Brainy Insights	https://www.thebrainyinsights.com/
	The Business Research Company	https://www.thebusinessresearchcompany.com/
	Tridge	https://www.tridge.com/company
	Verified Market Research	https://www.verifiedmarketresearch.com/
News	Globe Newswire	https://www.globenewswire.com/
	Market Watch	https://www.marketwatch.com/
	Refinitiv	https://www.refinitiv.com/en
	Scynexis	https://www.scynexis.com/news/
	The Spirit Business	https://www.thespiritsbusiness.com/

and commodities), (iii) emerging biomaterial industries (e.g. myco-based materials, biofuels), (iv) marketable ecosystem services (carbon stock, fungal foraging). Only the top products, considered as those with a minimum global market value of at least a million dollars, were included. The valuation of the included products was taken from 2017 to 2022 or the latest available data point, respectively.

Literature reviews

Whenever possible, the monetary value of each product or service was identified based on reliable data sources, which were listed above. However, when there were not enough direct data available in the literature, monetary values were determined by using the value transfer method (Johnston and Wainger 2015).

Value transfer method

The value transfer or benefit transfer method refers to applying quantitative estimates of ecosystem service values from existing studies to another context. The values given in the literature are monetary estimates of benefits or costs. Data have been extrapolated from a study site and applied with adjustments to other policy sites. Value transfer is a continuum of approaches depending on the information available (Johnston and Wainger 2015). This method is applicable in giving monetary value to fungal traded services such as carbon stocking and recreational foraging.

Summation of values

Market values are categorized as definite value, product value and traded value, respectively. Definite value is the monetary value of a fungus itself (e.g., *Agaricus bisporus* and “*Cordyceps*”—i.e., *Ophiocordyceps*; edible fungi: wild and cultivated fungi). Product value is the market value of the products derived from fungi or with the involvement of fungi in the production process (e.g., medicines and pharmaceuticals, fermented food and beverages, commodities and mycobased-material). Traded value is the market value from the services of fungi (e.g., carbon stock, recreational foraging). All these marketed values are combined to give an estimate of the monetary value of the fungal contribution to the global economy. All monetary values are given in US dollars (USD). For numerous industries that rely on fungi for the production processes, we have assumed the total industry value as the value of fungi, as it is impossible to disentangle the values of individual ingredients, and these products would not exist without the fungi involved.

Scope and limitation of the study

This study focusses on consumptive and marketed products and services rendered by fungi with direct effect on human well-being. Only those with a large impact on the global economy (minimum of USD 1 million) are included in the summation of values. Other ecosystem services and important roles in ecosystem functioning by fungi listed in Niego et al. (2023) with an indirect effect on humans will not be considered for valuation in this study, but future research is recommended to give them monetary value.

Value of carbon stocks being traded from forests

According to the Kyoto protocol, the Clean Development Mechanism (CDM) promotes afforestation and reforestation as carbon sequestration activities. It was expected to be the most effective and easily measurable method for impounding carbon as biomass above and below the ground. During the

negotiation of the Kyoto Protocol under the United Nations Framework Convention on Climate Change, 38 countries were required to reduce greenhouse gas (GHG) emissions by at least 5.2% below the 1990 levels. This goal was achieved by reducing greenhouse gas emissions or increasing greenhouse gas sinks (Tulpule et al. 1998; Grubb et al. 1999). A carbon price is an instrument used to capture the cost of greenhouse gas emissions, such as the damage caused to the environment. Governments and business sectors increasingly agree that carbon pricing plays a vital role in the transition to a decarbonized economy. In addition to charging emitters for carbon dioxide (CO₂) emissions, carbon pricing also provides incentives to individuals who emit less (Barron et al. 2019). Global carbon trading was valued at €760 billion (USD 817 billion) in 2021 with EU emission allowances above €80/t (USD 86/t) (Refinitiv 2022).

Carbon stock in forests can be found as 31% biomass and 69% in the soil (IPCC 2005). In the study by Clemmensen et al. (2013), it was stated that 50–70% of sequestered carbon in the soil was derived from roots and root-associated microorganisms such as mycorrhizal fungi. Approximately 85% of the terrestrial plants form mycorrhizal associations with fungi. The ectomycorrhizal and ericoid mycorrhizal plants associates are the majority of trees (92%) and shrubs (85%), while arbuscular mycorrhizal plant associates are mostly herbaceous (50%) (Soudzilovskaia et al. 2020).

Different types of mycorrhizal association present in forest ecosystems can affect the global distribution of carbon stock. Soudzilovskaia et al. (2019) estimated the storage of carbon in arbuscular (AM), ectomycorrhizal (EcM) and ericoid (ER) mycorrhizal vegetation in above-ground biomass as 241 ± 15 , 100 ± 17 , and 7 ± 1.8 billion metric tons, respectively. We assumed that the EcM and ER vegetations are in the forest, since these groups of fungi are mostly associated with trees. Based on the recent study of Edy et al. (2022) AM fungi are also present in 75% of tropical forests. The monetary values of carbon sequestered by different mycorrhizal vegetation were estimated by multiplying the values by the carbon emission allowance of USD 86/t of carbon (Refinitiv 2022) (Table 2). The total monetary value of the carbon stock from above-ground biomass by mycorrhizal vegetation worldwide is USD 24,768 billion, equivalent to 31% of the carbon stock in the forest (IPCC 2005). From this value, the total value of carbon stock in the forest is estimated to be USD 79,897 billion, of which USD 55,129 billion is contributed by soil carbon of 69% (IPCC 2005). Since 50–70% of the sequestered carbon in the soil is associated with root-associated microorganisms, we can roughly assume that the value of the carbon stock in the soil related to mycorrhizae is at least USD 27,565 billion. Thus, the total market value of the carbon stock associated with mycorrhizae is **USD 52,333 billion**.

Industrial uses of fungi

Fungi and the welfare obtained from them have been instrumental in the development of essential industrial processes worldwide. Among others, the secondary metabolites produced by these organisms represent a valuable resource in the development of medicines and pharmaceuticals. Fungal-based processes and fungal enzymes also play a key role in the production of food and beverages, as well as different commodities. The market value of these products steadily increases as the years go by. This chapter will discuss the different products and their market values, based on the available data.

Medicines and pharmaceuticals

Fungi have been explored for their medicinal value over thousands of years (Zhang et al. 2015). Aside from nutritional benefits, their ability to produce secondary metabolites makes them an important source for innovative chemistry, which led to the development of several important pharmaceuticals that have been beneficial for the advance of human civilization over time. While natural products and secondary metabolites in general have resulted in many drugs for the treatment of various diseases (Newman and Cragg 2020), fungal metabolites have been only developed for part of these indications, as amply summarized by Bills and Gloer (2016). For instance, contrary to what is stated in many reviews that have been published on the subject, there are no ethical anticancer drugs from fungi on the market. Taxol, for instance, is exclusively produced using plants as sources and the recent classification of the fungal “endophyte” that was reported to be able to produce the metabolite as a member of the Basidiomycota (Cheng et al. 2022) raises serious concerns as to whether fungi can produce this metabolite at all. In any case, fungal metabolites have given rise to the development of several drugs that gained a rather high commercial value in other indications, above all as anti-infectives, but even cardiovascular and immunomodulatory agents. However, even the discovery of some blockbuster drugs like cyclosporin has been attributed to their ability to exert antibiosis, and their true potential was discovered later when they were tested in more sophisticated bioassays. Growth inhibitory or toxic properties of fungal secondary

metabolites have regularly been linked with ensuring their survival in competitive natural environments (Keller 2019). Of the fungal natural product—derived drugs found on the market, the majority were originally isolated from species of the Ascomycota, while a few are derived from Basidiomycota (Bills and Gloer 2016; Sandargo et al. 2019). Compared to the vast number of described compounds, only a handful have been followed up upon to be further developed into marketable drugs (Mapook et al. 2022) (Table 3). Nevertheless, the secondary metabolite-inspired drugs that are on the market have been proven indispensable for modern medicine and managing diseases in general, displaying important sources of economic revenue.

Antibacterials

Penicillins are the first β -lactam antibiotics explored for their medicinal value and are still one of the most widely used antibiotic agents to fight bacterial infectious diseases. They were first described from *Penicillium rubens* (Houbraken et al. 2011) but also reported from other species such as *P. chrysogenum* and *P. griseofulvum* (Laich et al. 2002). Penicillins are still in use to treat a wide range of bacterial infections (Lobanovska and Pilla 2017). Aside from the formulated naturally occurring derivatives penicillin G and V, other semi-synthetic derivatives among the vast diversity of analogues are Amoxicillin, Ampicillin, Piperacillin, Dicloxacillin, Nafcillin and Oxacillin (Wright 1999). The global Penicillin market size is estimated to be worth **USD 1.96 billion in 2022** and is forecasted to increase to USD 2.4 billion by 2028 with a compound annual growth rate of 3.8% (Market Watch 2022a).

Cephalosporins are another class of β -lactam antibiotics originally isolated from strains of the genus *Acremonium*. Following its first report by Newton and Abraham (1955), a semi-synthetic derivative of cephalosporin C named cephalothin reached the market in 1964 (Asbel and Levison 2000). Since then, in total five generations of cephalosporin-derived antibiotics were developed, further improving upon its selectivity against drug resistant bacteria (Lin and Kück 2022). Among the indications are skin infections, with and without multi drug resistant bacteria and meningitis, to name a few (Lin and Kück 2022). The global cephalosporin market size

Table 2 Monetary value of the aboveground biomass of carbon stock associated with different types of mycorrhizal vegetation (Soudzilovskaia et al. 2019)

Type of mycorrhizal vegetation	Amount of carbon stored in above-ground biomass (billion metric tons)	Calculated value of carbon stock in billion USD
Arbuscular	$241 \pm 15 \times 0.75 = 181$	15,566
Ectomycorrhizal	100 ± 17	8,600
Ericoid	7 ± 1.8	602
Total		24,768

Table 3 Medicines and pharmaceutical products of fungi

Category	Products	Fungi involved	Market value (USD billion)	Year	source
Antibacterials	Penicillins	<i>P. rubens</i> , <i>P. chrysogenum</i> and <i>P. griseofulvum</i>	1.960	2022	Market Watch (2022b)
	Cephalosporins	<i>Acremonium</i> spp.	18.700	2022	Imarc (2022a)
	Fusidic acid	<i>Ramularia coccinea</i>	0.170	2021	Market Watch (2022a)
	Pleuromutilin (Lefamulin)	<i>Clitopilus</i> spp. Basidiomycota	0.267	2025	Joseph (2019)
Antimycotics	Echinocandins	Leotiomycetes and Eurotiomycetes	0.510	2021	Data Bridge Market Research (2022)
	Enfumafungin (Brexafemme®)	<i>Hormonema</i> sp.	0.004	2022	GlobeNewswire (2022); Scynexis (2022)
	Griseofulvin	<i>Penicillium</i> spp.	N/A		
Cardiovascular drugs	Statins	<i>Aspergillus terreus</i> , <i>Monascus ruber</i> , <i>Penicillium citrinum</i>	14.300	2021	Imarc (2022b)
Immunosuppressive and immunomodulatory agents	Cyclosporin	<i>Tolypocladium inflatum</i>	1.990	2021	Verified Market Research (2022a)
	Fingolimod	<i>Melanocarpus albomyces</i>	3.340	2018	Miller (2019)
	Mycophenolic acid (mycophenolate mofetil)	<i>Penicillium stoloniferum</i> and related <i>Penicillium</i> species	1.581		
	Mizoribine	<i>P. brefeldianum</i>	No value available		
Nematicidal	Emodepside	<i>Rosellinia</i> spp.	No value available		
Traditional Chinese Medicines	<i>Cordyceps</i>	<i>Ophiocordyceps sinensis</i> , <i>Cordyceps militaris</i> , <i>Cordyceps guangdongensis</i> , and <i>Isaria cicadae</i>	1.500	2004	Dong et al. (2015)
	<i>Ganoderma</i>	<i>Ganoderma</i> spp. Mostly <i>G. lingzhi</i>	3.100	2019	Allied Market Research (2022a)
		Total	ca. 47.422		

was valued at **USD 18.7 billion in 2022**, and it is expected to reach USD 22.3 billion by 2028, exhibiting a CAGR of 2.83% during 2023–2028 (Imarc 2022a).

First generation cephalosporins are commonly used to manage skin and soft tissue infections caused by susceptible strains of *Staphylococcus aureus* and group A *Streptococcus*. Those include cefazolin, a parenteral formulation, and cephalexin, an oral equivalent, among others (Lin and Kück 2022).

Second generation cephalosporins have a better performance against Gram-negative bacterial infections than the first-generation derivatives and are used to treat urinary and tract infections, and skin and soft tissue infections. A variety of orally administered second-generation agents (cefactor, cefprozil, loracarbef, cefpodoxime) are commonly used in the outpatient management of sinopulmonary infections and otitis media (Lin and Kück 2022).

Third generation cephalosporins are typically used for serious pediatric infections, including meningitis and sepsis (Lin and Kück 2022).

Fourth generation cephalosporins include, e.g. cefepime, which is active against *Pseudomonas aeruginosa* and retains good activity against methicillin-susceptible staphylococcal infections (Lin and Kück 2022).

An example for **Fifth generation cephalosporins** is ceftaroline, the active metabolite of the prodrug ceftaroline fosamil. This is a broad-spectrum cephalosporin with bactericidal activity against resistant Gram-positive bacteria, including Methicillin-resistant *Staphylococcus aureus* (MRSA), and common Gram-negative pathogens (Lin and Kück 2022). The development of cephalosporins is a prime example of how a basic structure derived from natural sources can be gradually improved via semisynthesis and medicinal chemistry approaches, finally leading to broad

spectrum antibiotics. However, this development has taken several decades of hard work.

In this context, it is also worthwhile to mention the **carbapenems**, which are also β -lactam antibiotics but were discovered from *Streptomyces* species, which are Gram-positive Actinobacteria. Olivanic acids were the first isolated carbapenems from *S. clavuligerus* in a screening campaign for β -lactamase inhibitors (Brown et al. 1976), but the compound family only went into clinical relevance with the isolation of thienamycin from *S. cattleya*, which exhibited superior physicochemical properties (Kahan et al. 1979; Papp-Wallace et al. 2011). Carbapenems combine two activities as being able to bind to the same target as other β -lactams, in addition to their inherent property to act as a β -lactamase inhibitor. The first carbapenem to enter the market was the semi-synthetic analogue imipenem (Miyadaira et al. 1983) in 1985, which was followed by other synthetic analogues like meropenem (Sunagawa et al. 1990), biapenem (Ubukata et al. 1990), ertapenem (Sundelof et al. 1997), doripenem (Tsuji et al. 1998), and panipenem (Neu et al. 1986). These compounds are used to treat a broad band of bacterial infections, including complicated nosocomial bacteriosis, or infections caused by multi-drug resistant staphylococci and *Pseudomonas* (Papp-Wallace et al. 2011). Due to their inability to pass the gastrointestinal tract, they are commonly administered intravenously. However, the new drug tebipenem is currently in clinical trials as the first orally available carbapenem (Jain et al. 2018). The global carbapenem market was valued at **USD 3.9 billion in 2021** and is expected to exhibit a growth rate (CAGR) of 4.5% during 2022–2030 (Polaris Market Research 2022).

Fusidic acid is a bacteriostatic triterpene derived from the fungus *Ramularia coccinea* (Godtfredsen et al. 1962; as *Fusidium coccineum*) and used as a topical medication for the treatment of skin infections with Gram-positive bacteria (Fernandes 2016). It acts as a bacterial protein synthesis inhibitor by binding to the elongation factor G (EF-G) bound to ribosomes. This effectively prevents the translocation of the newly assembled polypeptide chain during protein synthesis. Recycling of ribosomal subunits is thus inhibited after completion of transcription (Gao et al. 2009). The global fusidic acid market value was estimated at **USD 171.89 million in 2021** with projection to reach up to USD 271.84 million by 2028, exhibiting a CAGR of 6.77% during the forecast period (Market Watch 2022b).

Pleuromutilin and its derivatives are antibacterials produced by Basidiomycota that inhibit protein synthesis in bacteria by inhibiting peptide bond formation through binding to the 50S subunit of ribosomes (Paukner and Riedl 2017). For details we refer to the recent review by (Mapook et al. 2022). The pleuromutilin derived compounds tiamulin and valnemulin covered 2.5% of total sales of antimicrobials used for food producing animals (European Medicines

Agency 2013). Lefamulin, a new pleuromutilin antibiotic with the brand name XENLETA™, which is used for the treatment of community-acquired pneumonia (CAP), is expected to peak sales of **USD 267 million** by the end of 2025 (Joseph 2019). As this drug is fairly new to the Pharma market and has a molecular target that is not addressed by the conventional antibiotics, a substantial increase in the sales is to be expected in the coming years (Fig. 1).

Antimycotics

Echinocandins are a group of cyclic non-ribosomal lipopeptides reported from Ascomycota of the classes Leotiomyces and Eurotiomyces (Hüttel 2021). Currently, there are three semi-synthetically modified drugs, derived from echinocandin B (producer: *Aspergillus delacroixii*; Benz et al. 1974), pneumocandin A₀ (*Glarea lozoyensis*; Schwartz et al. 1989) and FR901379 (*Coleophoma empetri*; Iwamoto et al. 1994) on the market. All three drugs, **anidulafungin**, **caspofungin** and **micafungin** are used to treat and prevent invasive fungal infections including candidemia, abscesses, esophageal candidiasis, and certain other invasive *Candida* infections (Hüttel 2021). Furthermore, these pharmaceuticals are used as prophylaxis for *Candida* infections during stem cell transplantation. Antifungal effect relies on the inhibition of the synthesis of β -(1,3)-D-glucan, an integral component of the fungal cell wall (Sawistowska-Schröder et al. 1984). The global market size for echinocandins was valued at **USD 515.20 million in 2021** and is expected to reach USD 796.69 million by 2029, with a CAGR of 5.6% (Data Bridge Market Research 2022).

Enfumafulvin is a triterpene glycoside and hemiacetal derived from the endophytic fungus *Hormonema* sp. (Peláez et al. 2000). It is a potent antimycotic which, similarly to the echinocandins, inhibits the biosynthesis of β -(1,3)-D-glucan (Jallow and Govender 2021). Its semi synthetic derivative Ibrexafungerp was the first-in-class triterpenoid antifungal drug with broad spectrum antifungal activity (Ghannoum et al. 2020) that has been approved for the treatment of vulvovaginal candidiasis (VVC) and only recently entered the market (Espinell-Ingroff and Dannaoui 2021). It is sold under the brand name Brexafemme® approved by the FDA in June 2021 with net revenues of **USD 0.7, 1.3, and 1.16 million in the first three quarters of 2022** respectively (GlobeNewswire 2022; Scynexis 2022).

Griseofulvin is a secondary metabolite produced by *Penicillium* spp. and was first discovered from *P. griseofulvum* (Oxford et al. 1939). It has been developed as an orally available, fungistatic drug used to treat superficial fungal skin infections such as tinea capitis and pedis (Gupta et al. 2017). The onychomycosis treatment market value exceeded USD 4.2 billion in 2020 and expected to reach USD 6.2 billion in 2027 (Global Market Insights 2022a). Although there is no market value reported in the literature for griseofulvin,

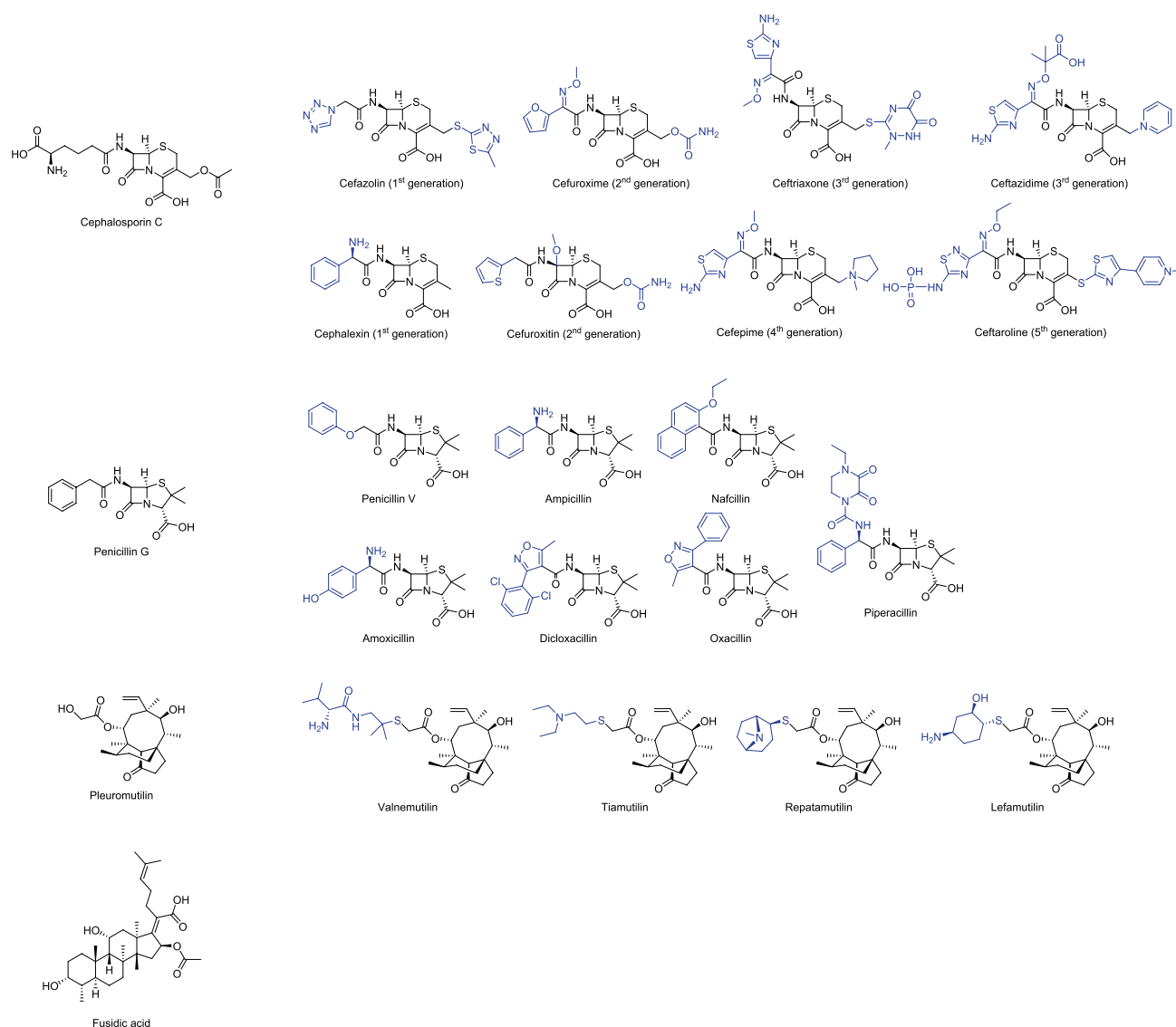


Fig. 1 Chemical structures of antibacterial drugs

it is worth mentioning this important product because it is one of the most valuable treatments for onychomycosis on the market (Fig. 2).

Cardiovascular drugs

Statins are prescribed for their cholesterol-lowering capacity to prevent mortality linked towards cardiovascular diseases, such as coronary artery disease and stroke (Endo 2008). Among the marketed statins are **pravastatin**, the semi-synthetic product of **compactin** (or mevastatin) isolated from *Penicillium citrinum* (Endo et al. 1976), **lovastatin** and its semi-synthetic derivative **simvastatin** (Pedersen and Tobert 2004). In addition, some of the synthetic statins inspired by nature introduced to the market are fluvastatin,

atorvastatin, rosuvastatin and pitavastatin (Endo 2010). Lovastatin was concurrently isolated from *Aspergillus terreus* and *Monascus ruber* (reported as Monacolin K, Endo 1979) and was one of the first statins to be extensively used for its cholesterol-lowering ability (Steinberg 2006) and even discussed as auxiliary drugs in treatment regiments against cancer (Jiang et al. 2021). The global statins market size was valued at **USD 14.3 billion in 2021**, and was expected to reach USD 17.5 billion by 2027, with a CAGR of 3.4% during 2022–2027 (Imarc 2022b) (Fig. 3).

Immunosuppressive and immunomodulatory agents

Cyclosporin A represents the first calcineurin inhibitor, which was reported from the hypocrealean soil fungus

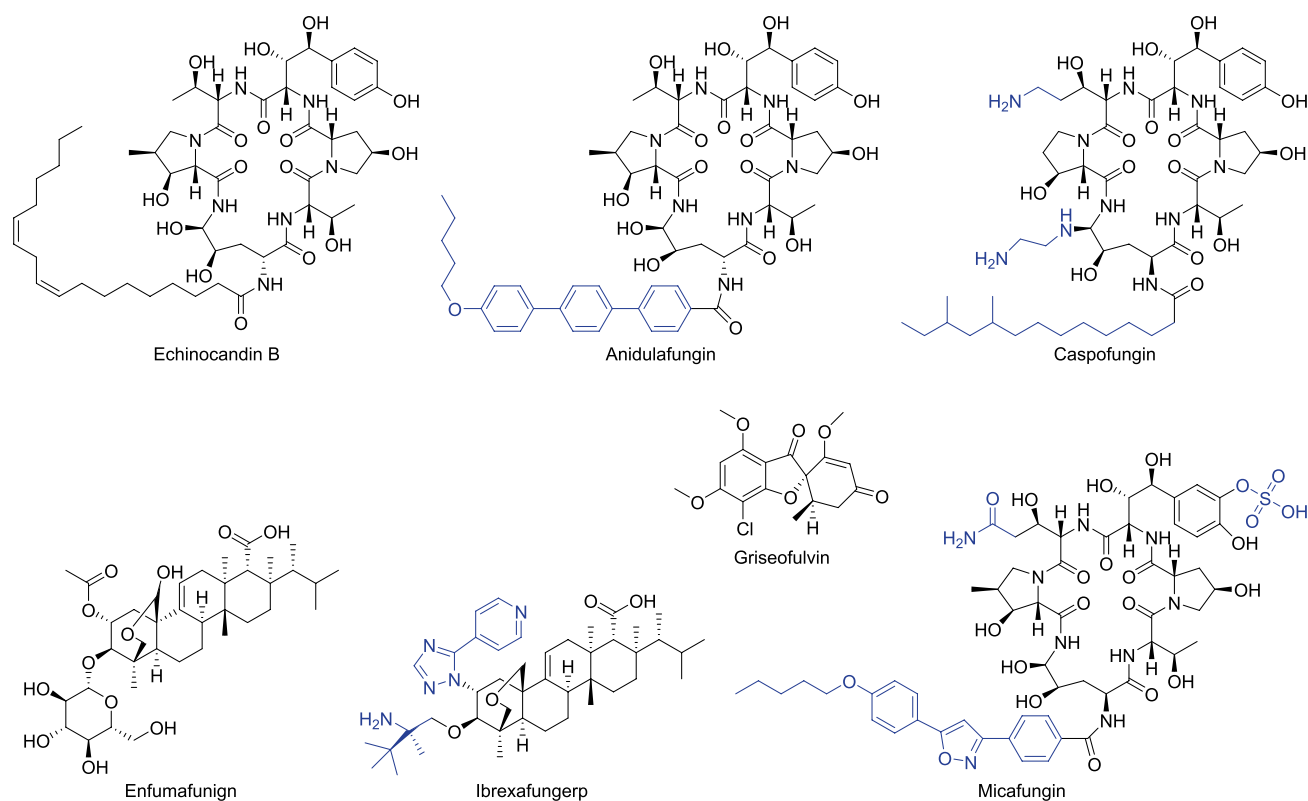


Fig. 2 Chemical structures of antimycotic drugs

Tolypocladium inflatum (originally identified as “*Trichoderma polysporum*” by Rügger et al. 1976) and entered the market in 1983 (Survase et al. 2011). This substance was shown to exhibit a better bioactivity profile in terms of its immunosuppressive activities as compared to other synthetic drugs on the market, which turned out to be a game changer in the field of transplantation medicine (Demain and Sanchez 2009; Survase et al. 2011). The market sales of cyclosporin A totaled to USD 1.5 billion in 2009. Recently, cyclosporine was valued at **USD 1.99 billion in 2021**, and it is projected to reach the value of USD 6.08 billion in 2030 (Verified Market Research 2022a).

Fingolimod is an immunomodulating drug developed from myriocin. It was first reported from *Melanocarpus albomyces* (previous name: *Myriococcum albomyces*; cf. Kluepfel et al. 1972). The semi-synthetic derivative was shown to modulate the sphingosine 1-phosphate receptor, which is exploited to treat patients with a relapsing–remitting form of multiple sclerosis (MS, Volpi et al. 2019). It is sold since 2010 (Thomas et al. 2017) under the brand name Gilenya (Drugbank Online 2022b). Gilenya has a market share of USD 79,411 per 1000 Medicare beneficiaries in 2014 (San-Juan-Rodriguez et al. 2019) with annual sales worth **USD 3.34 billion in 2018** (Miller 2019).

Mycophenolic acid is derived from *Penicillium brevicompactum* and originally reported by Gosio (1893) as the first

fungal antibiotic. However, it was only much later that systemic studies and semi-synthetic derivatization improved its toxic side effects to enable its usage as an immunosuppressant for organ transplantations as of starting from 1995 (Lipsky 1996). The compound itself, however, is toxic and commonly prescribed as its formulated prodrug, mycophenolate mofetil. Upon release of its active component (mycophenolic acid), it inhibits the inosine monophosphate dehydrogenase, which is required for the de novo synthesis of guanosine (Lenihan and Tan 2020). The global market value of mycophenolate mofetil was **USD 1581.34 million in 2022** (Market Watch 2023a). Mycophenolate sodium was later introduced to the market as an enteric-coated slow-release formulation of mycophenolic acid to decrease the gastrointestinal side effects of mycophenolate mofetil (Lenihan and Tan 2020). This drug has been in discussion for its application in other medical conditions associated with an apparently hyperactive immune systems as well, such as psoriasis (Bentley 2000).

Mizoribine is an immuno-suppressive sold in Japan, Korea, and China and commonly used for treatment of renal diseases and prevention of renal transplants rejection (Kawasaki 2009). The compound was first isolated from *Penicillium brefeldianum* (Mizuno et al. 1974) and came on the market in 1984, however, limitations concerning its efficacy allegedly limits its use worldwide (Kawasaki 2009). Mizoribine is

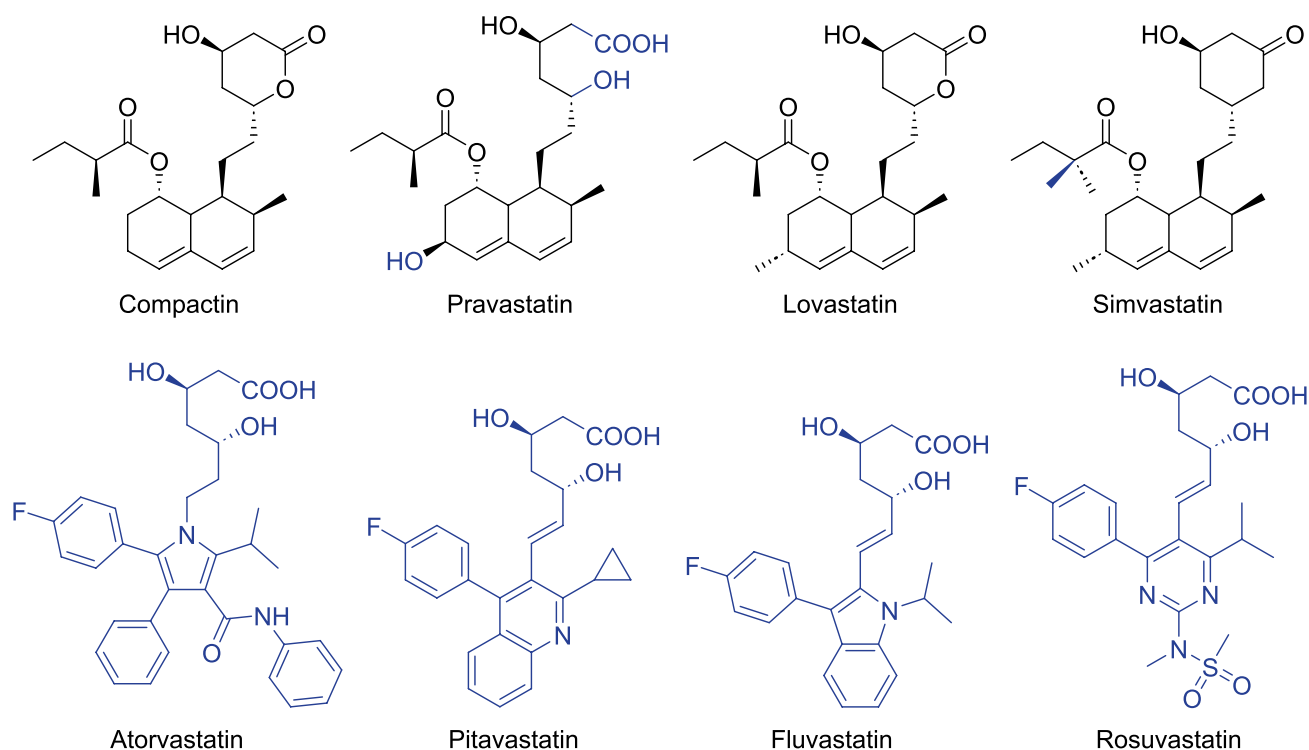


Fig. 3 Chemical structures of cardiovascular drugs

estimated to be worth several million USD in 2021, however, the exact value was not available to us (Fig. 4).

Nematicides

Emodepside has been the first drug on the market that is derived from a secondary metabolite produced by a fungal endophyte (Sasaki et al. 1992; Scherckenbeck et al. 2002; Helaly et al. 2018). Molecular Data in patents already pointed towards this fungus, which was isolated from a tea plant in Japan, being a member of the genus *Rosellinia* (Harder et al. 2011). However, it was only shown recently that ascospore-derived isolates of the latter xylariaceous genus can indeed be linked with the production of the nematicidal PF1022 derivatives (Wittstein et al. 2020). The semi-synthetic derivative is marketed under Emodepside and used as an anti-helminthic drug in veterinary medicine (Willson et al. 2003). Currently, attempts are ongoing to develop the compound as a remedy for human pathogenic nematode infections. In this sense, emodepside appears as a promising candidate with a novel mode of action against human river blindness (onchocerciasis), a disease caused by the filarial worm *Onchocerca volvulus*, and which treatment relies on the natural product ivermectin (Krücken et al. 2021). Recently, it has been validated that emodepside exhibits good in vitro efficacy against microfilarial, third larval, fourth larval, and adult stages of various filarial genera and species (Hübner et al. 2021). There are no data available on the current market value of emodepside. The compound is

only administered with another synthetic anthelmintic agent, praziquantel, in veterinary medicine (Fig. 5).

Traditional Chinese medicines (TCM)

Traditional Chinese medicine (TCM) has existed for almost 5000 years and was historically used by the Chinese to combat diseases. Until now, interest and acceptance of TCM continue to grow worldwide (Lin et al. 2018). Fungi have always been part of TCM, and the most explored species belong to the genera *Ophiocordyceps*, *Cordyceps*, and *Ganoderma* (Paterson 2006, 2008).

Ophiocordyceps/Cordyceps preparations are commonly used in traditional Chinese medicines in China, Japan, Korea, and other eastern Asian countries (Zhu et al. 1998). They were used in China for at least 2000 year (Zhu et al. 1998). *Ophiocordyceps sinensis*, *Cordyceps militaris*, *Cordyceps guangdongensis*, and *Isaria cicadae* are the most explored and commercialized “*Cordyceps*” fungi in China (Zhu et al. 1998; Zhang et al. 2014). There is a huge demand in Chinese markets for *O. sinensis*, with an annual yield of 100–150 tons (of which approximately 100 tons are produced in China). The market price is USD 8 to USD 25 each or USD 25,000 to 60,000 per kilogram (Zha et al. 2018). The national annual value of natural Chinese *Cordyceps* is estimated to be over 10 billion RMB (USD 1.5 billion) in 2004 (Dong et al. 2015).

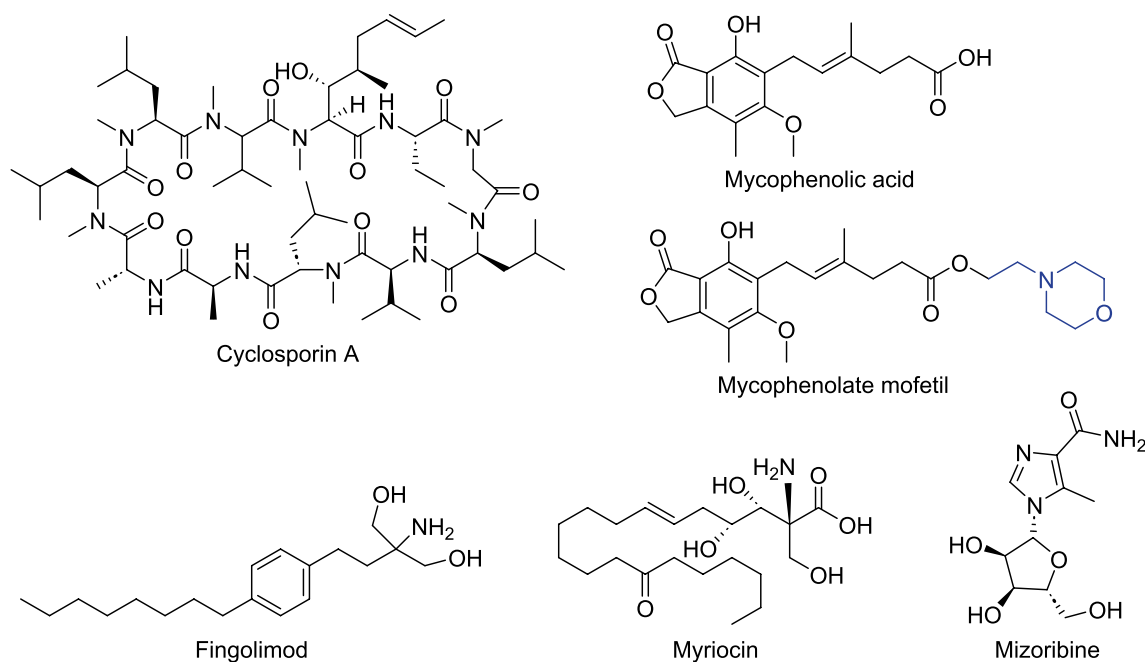


Fig. 4 Chemical structures of immunosuppressive and immunomodulatory agents

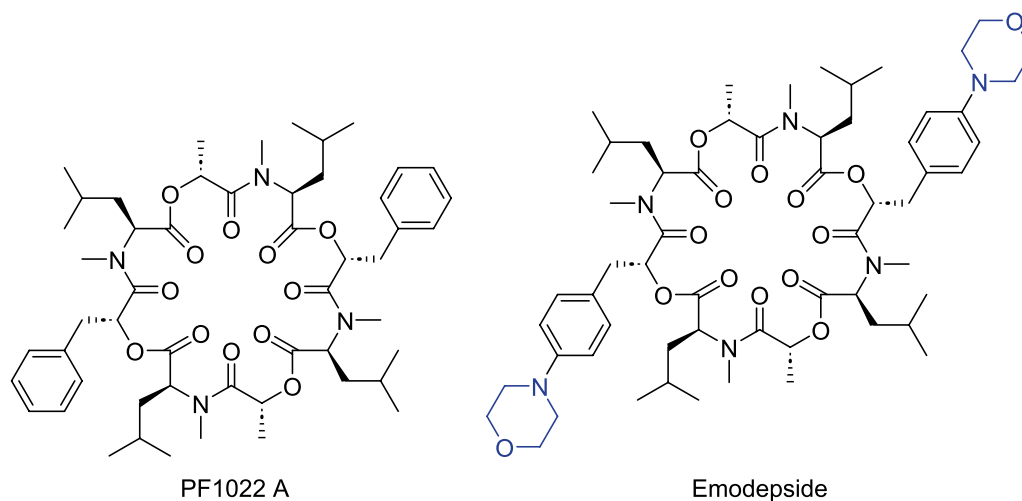


Fig. 5 Chemical structures of nematicidal agents

Ganoderma-based products are marketed in many Asian, European and North American countries, although South Asian countries such as China, Japan, Korea, Malaysia and Singapore are the main producers of the food products (Chang and Miles 2004b). The annual global market turnover of *Ganoderma*-based products was approximately USD 2.16 billion in 2002 (Lai et al. 2004). In 2019, the global market value of *Ganoderma*-based products was **USD 3.1 billion**, and projected to reach USD 5.1 billion in 2027 (Allied Market Research 2022a).

Food and beverages

Functional food and nutraceuticals

Fungi have long been explored due to their medicinal value (De Silva et al. 2013; Hyde et al. 2019; Badalyan and Raprior 2021) and many fungal products are produced as nutraceuticals, including cosmeceuticals (Bandara et al. 2015; Badalyan et al. 2022). Nutraceuticals are a group of products

from edible sources, proven to be safe for consumption and can be considered a supplement to effective pharmacological treatment (Niego et al. 2021). Fungal products are being consumed as functional foods, dietary supplements, and sources of bioactive compounds with a range of medicinal applications (Hyde et al. 2019; Badalyan et al. 2021). Some of the most explored genera are *Agaricus*, *Hericium*, *Lentinula*, and *Ophiocordyceps* (Valverde et al. 2015; Hyde et al. 2019; Niego et al. 2021). The reported bioactivities include antibacterial, antidiabetic, antifungal, antihypercholesterolemia, antioxidant, antiparasitic, antitumor, antiviral, cardiovascular, hepatoprotective, immunomodulatory and radical scavenging effects (Hyde et al. 2019; Zeb and Lee 2021; Niego et al. 2021). The bioactive principles causative for those effects are polysaccharides, proteins (El Enshasy and Hatti-Kaul 2013), glycoproteins (Cohen et al. 2014), phenolic compounds (Gupta et al. 2018; Hamwenye et al. 2022), ergosterol (Diallo et al. 2020) and other terpenoids, or unsaturated fatty acids (Galappaththi et al. 2022). The health-promoting properties of many fungi are the driving force for increasing their market value and incorporation into the nutraceutical industry (Niego et al. 2021). The following are economically important fungi explored in the nutraceutical and functional food industries (Table 4).

The bioactivities of *Agaricus bisporus* have been quite established. It is one of the most explored mushrooms for nutraceuticals (Gopalakrishnan et al. 2005). *Agaricus bisporus* was valued globally at **USD 16.69 billion** in 2022 (Market Data Forecast 2022a).

Hericium species (and in particular *H. erinaceus*) are highly valued for their medicinal properties. China is the main exporter of *Hericium* with a market value of USD 270 million, followed by Italy (USD 90.97 million) and Poland (USD 65.83 million) in 2021 (Tridge 2022a). The global export value of *Hericium* was USD 963.4 million and the import value was **USD 978.83 million** in 2021 (Tridge 2022b).

The nutraceutical properties of *Lentinula edodes* have been well documented (Liu et al. 2020b; Wang et al. 2020; Raghoonundon et al. 2021). The global market value of *Lentinula* (Shiitake) is **USD 4.31 billion** in 2022 and is expected to reach USD 4.7 billion in 2030 at a CAGR of 8.3% (The Brainy Insights 2022).

Red yeast rice was created by fermenting *Monascus purpureus* on white rice. In traditional Chinese medicine, the powdered yeast-rice mixture has been utilized as a staple food in Asia (Nguyen et al. 2017). For heart disease and high cholesterol, people consume red yeast rice orally as a supplement. (Dufossé 2019). The cholesterol-lowering properties and other beneficial effects that have been proven for the product is, however, not due to the pigments (Li et al. 1998). The substance monacolin K (see above under “statins”) is one of them (Nguyen et al. 2017). The red yeast rice had a market value of **USD 380.6 million** in 2022 (Persistence Market Research 2022).

Ophiocordyceps sinensis is one of the most well-known and most expensive fungal species worldwide, with a market price that reached up to USD 60,000/kg in 2015 (Lei et al. 2015). Various nutraceutical products have been derived from *Ophiocordyceps sinensis*. In China, more than 1000 nutraceutical products are prepared from this species (Rakhee et al. 2021). The global market value of *O. sinensis* was around **USD 5–11 billion** in 2018 (He 2018).

The market value of these economically important mushrooms, however, was mainly due to the fact that they are also food sources and not solely functional food or nutraceuticals, particularly *A. bisporus* and *L. edodes* which are also some of the most cultivated mushrooms for food, thus will not be included in the summation for functional food to avoid double inclusion. By definition, functional food refers to food or food ingredients providing health benefits beyond basic nutrition (Colorado State University Extension 2023). The global functional mushroom market was then valued at **USD 12.34 billion**.

Fermented food

Fungi are beneficial to humans both industrially and commercially, especially in food and beverage production (Koul and Farooq 2020). Fermented foods and alcoholic beverages have long been an essential part of the human diet around the world. These foods are often well preserved with high nutrient content such as proteins, vitamins, minerals, and other nutrients (Tamang et al. 2020). The availability of nutrients in fermented foods and beverages is mainly due to the fermentation process performed by living microorganisms such as bacteria and fungi (Rezacc et al. 2018). These

Table 4 The most explored fungi in the nutraceutical and functional food industries

Fungal species	Market value (USD billion)	Year	Sources
<i>Agaricus bisporus</i>	16.69 (food source)	2022	Market Data Forecast (2022a)
<i>Hericium</i> spp.	0.96	2022	Tridge (2022b)
<i>Lentinula edodes</i>	4.31 (food source)	2022	The Brainy Insights (2022)
<i>Monascus purpureus</i>	0.38	2022	Persistence Market Research (2022)
<i>Ophiocordyceps sinensis</i>	11.00	2018	He (2018)

microorganisms may also improve gastrointestinal health and provide other health benefits as probiotics (Rezac et al. 2018) that contribute to the popularity of fermented products (Fortune Business Insight 2022a). *Saccharomyces cerevisiae*, *Candida* spp., *Debaryomyces* spp. and *Wickerhamomyces anomalus* are the most common yeasts associated with traditional fermentations of fermented foods and beverages (Bhalla and Savitri 2017). *Saccharomyces cerevisiae* is the yeast species most frequently involved in alcoholic fermentation and is also used in most other fermented products (Walker and Stewart 2016). Fermentation of foods and beverages changes the flavor and taste of the product, as well as its nutritional value and digestibility (Fortune Business Insight 2022a). Table 5 lists some economically important fermented foods and beverages along with their global market value.

Baked goods are an essential part of human food. *Saccharomyces cerevisiae* is a very important fungus in the food production industry and is known as Baker's Yeast. It converts

sugars and starches into alcohol and carbon dioxide during the fermentation process. *Saccharomyces cerevisiae* has been bred into various strains which produce significantly more CO₂, and thus can achieve faster fermentation than wild type strains (Lahue et al. 2020). The global value of the market for bakery products reached **USD 497.50 billion in 2022** (Imarc 2023). The top exporters are Germany (USD 4.3 billion), Canada (USD 3.14 billion), Italy (USD 2.73 billion), France (USD 2.28 billion) and the USA (USD 2.04 billion) (OEC 2022b).

Cheese is a widely consumed dairy product with numerous varieties such as cheddar, feta, gouda, parmesan and camembert, produced in different parts of the world. Filamentous fungi and yeasts are used in the production of different kinds of cheese (Metin 2018; Chourasia et al. 2021). Filamentous fungi that thrive in cheese include *Aspergillus*, *Cladosporium*, *Geotrichum*, *Mucor*, *Penicillium*, and *Trichoderma* (Hymery et al. 2014). There are two categories of mold-ripened cheeses: internally ripened and surface-ripened. The most well-known examples of internally ripened

Table 5 Market value of fermented food and beverages

Category	Products	Fungi involved	Market value (USD billion)	Year	Sources
Food products	Baked Goods	<i>S. cerevisiae</i>	497.50	2022	Imarc (2023)
	Cheese	<i>Aspergillus</i> , <i>Cladosporium</i> , <i>Fusarium</i> , <i>Geotrichum</i> , <i>Mucor</i> , <i>Penicillium</i> , <i>Scopulariopsis</i> , <i>Sporendonema</i> , <i>Trichoderma</i> , <i>Trichothecium</i>	231.65	2022	The Business Research Company (2023)
Alcoholic beverages	Beer	<i>S. cerevisiae</i> , <i>S. eubayanus</i>	605.20	2020	Allied Market Research (2022b)
	Wine	<i>S. cerevisiae</i>	339.53	2020	Fortune Business Insight (2022b)
	Vodka	<i>S. cerevisiae</i>	39.00	2020	Conway (2022)
	Gin	<i>S. cerevisiae</i>	14.03	2020	Allied Market Research (2022c)
	Tequila	<i>S. cerevisiae</i>	12.89	2021	The Spirit Business (2022)
	Rum	<i>S. cerevisiae</i>	15.00	2021	Market Data Forecast (2022a)
	Whiskey	<i>S. cerevisiae</i>	59.63	2019	Allied Market Research (2022d)
	Brandy	<i>S. cerevisiae</i>	23.17	2020	Globe Newswire (2022a, b)
Non-alcoholic beverages	Chocolate	<i>Galactomyces geotrichum</i> , <i>Hanseniaspora opuntiae</i> , <i>Pichia kudriavzevii</i> , <i>S. cerevisiae</i> , <i>Wickerhamomyces anomalus</i>	130.56	2019	Grand View Research (2022b)
	Coffee	<i>S. cerevisiae</i>	102.02	2020	OEC (2022d)
	Vinegar	<i>Candida lactis-condensi</i> , <i>C. stellata</i> , <i>Hanseniaspora osmophila</i> , <i>H. valbyensis</i> , <i>S. cerevisiae</i> , <i>Saccharomyces ludwigii</i> , as well as <i>Zygosaccharomyces bailii</i> , <i>Z. bisporus</i> , <i>Z. lentus</i> , <i>Z. mellis</i> , <i>Z. pseudorouxii</i> , <i>Z. rouxii</i>	2.27	2021	Imarc (2022a, b, c)
	Kombucha	<i>Brettanomyces/Dekkera</i> , <i>Candida</i> , <i>Torulaspora</i> , <i>Pichia</i> , <i>Schizosaccharomyces</i> , <i>Saccharomyces</i> , <i>Zygosaccharomyces</i>	2.59	2021	Polaris Market Research (2021)
	Total value		2,075.04		

Notably, fungi are not essential for all product lines listed and the non-alcoholic beverages are partly produced without them

cheeses are the blue cheeses caused by *Penicillium roqueforti* creating blue veins, as the name suggests. The ripening of the famous Camembert-type soft cheeses relies on *Penicillium camemberti* (Lessard et al. 2014; Ropars et al. 2020). Another example is Norwegian Gamalost with its ripening caused by *Mucor* with a yellow–brown color. Surface-ripened cheeses can be hard, semi-hard, and soft. The most common examples of hard surface-ripened cheeses are French Cantal, Salers, and Rodez, which involve species of *Scopulariopsis* or *Sporendonema casei*. The Saint Nectaire semi-hard cheese uses *Mucor* spp. and *Bisifusarium domesticum* as ripening molds (Zhang and Zhao 2010; Zhang et al. 2012; Metin 2018).

The global value of the cheese market was **USD 231.65 billion in 2022** (The Business Research Company 2023). The top exporters were Germany (USD 4.79 billion), Netherlands (USD 4.11 billion), Italy (USD 3.57 billion), France (USD 3.49 billion), and Denmark (USD 1.71 billion) (OEC 2022c). Blue cheese production had a total net trade of USD 624 million in 2020 wherein the top exporters are Italy (USD 185 million), Denmark (USD 122 million), France (USD 121 million), Germany (USD 94.8 million), and the United Kingdom (USD 17.1 million) (OEC 2022a).

Alcoholic beverage and spirits

Yeasts, especially *Saccharomyces cerevisiae*, play a vital role in the production of fermented beverages. They are involved in the production of all alcoholic beverages and the selection of suitable yeast strains is essential not only to maximize alcohol yield, but also to maintain beverage sensory quality (Walker and Stewart 2016). *Saccharomyces cerevisiae* is the most common yeast used for many years in the production of beverages associated with the fermentation process (de Almeida Silva Vilela et al. 2020). Fermented beverages are made by yeast by converting sugar together with other essential nutrients such as amino acids, minerals, and vitamins into alcohol and carbon dioxide (primary fermentation metabolites) and other chief secondary metabolites (Walker and Stewart 2016; Vilela 2019). Secondary metabolites produced by yeast act as important flavor congeners of beverages that influence the final taste and aroma of alcoholic beverages such as beer and wine, as well as other distilled beverages such as brandy, rum, and whiskey (Walker and Stewart 2016). Yeasts are also involved in the production of white spirits such as gin and vodka (Pauley and Maskell 2017).

Beer is the most popular low-alcohol beverage consumed in huge amounts globally each year. It is important in the economy of many countries around the world (Maicas 2020). In Europe, traditional distinctions of beers are influenced by the different brewing practices, the water properties used in brewing, the type of malt and the yeast strains used

(Britannica 2022a). The European countries are some of the major producers and consumers of beers. The primary yeast involved in beer making is *S. cerevisiae*; however, other species such as *S. eubayanus* were also recently utilized in the brewing process (Gibson et al. 2017). Brewing is a complex fermentation process used in the beverage industries with huge annual revenues (Maicas 2020). Global beer production was valued at **USD 605.20 billion** in 2020 (Allied Market Research 2022b).

Wine is an alcoholic drink made from fermented grapes. The varieties of grapes are the main factor in wine production. *S. cerevisiae* is also the main microorganism used in wine making. The global wine market size was **USD 339.53 billion in 2020** which is projected to grow to USD 456.76 billion in 2028 (Fortune Business Insight 2022b).

White spirits

Vodka is the most popular beverage in eastern Europe, traditionally made from potatoes and grain, especially rye (Menezes et al. 2016; Britannica 2022b). The alcohol content of vodka is unaged and high concentration (40%) alcohol by volume (ABV), thus, can cause poisoning if over-consumed (Kanny et al. 2015; Pauley and Maskell 2017). The vodka industry was worth **USD 39 billion in 2020** (Conway 2022).

Gin is an alcoholic beverage from junipers that has evolved greatly over the past 300 years from its origin with an alcohol content of 35–55% ABV (Abel 2001; Alcohol Rehab Guide 2022). It was previously invented as a remedy for military troops suffering from ‘East Indian fevers’ (Abel 2001). The global gin market was valued at **USD 14.03 billion in 2020**, and is expected to reach USD 20.17 billion by 2028 (Allied Market Research 2022c).

Tequila is a distilled beverage made from the blue agave plant (*Agave tequilana*) originating from the western Mexican state of Jalisco (Graham 2022). It has an alcohol concentration of 38–55% ABV (Alcohol Rehab Guide 2022). The size of the tequila market has reached **USD 12.89 billion in 2021** (The Spirit Business 2022).

Dark spirits

A dark spirit is a type of alcohol that has been aged in oak barrels, resulting in a dark color. With the exception of brandy, which is distilled from wine, dark spirits are beverages distilled from grains.

Rum is a distilled drink made from fermented sugarcane or molasses that originated in the Americas. It has an alcohol concentration of 40% ABV, but can go “overproof” with an alcohol concentration of 57.5–75% ABV (Alcohol Rehab Guide 2022). The highest valued rum comes from countries such as Barbados, Cuba, Guyana, Jamaica, and the

Philippines (Brick 2022). The global value of the rum market was **USD 15 billion** in 2021, and is expected to reach USD 21.5 billion by 2027 (Market Data Forecast 2022b).

Whiskey is a spirit made from fermented grains such as barley, corn, rye, and wheat aged in wooden casks. It has a typical alcohol concentration of 40–50% ABV (Alcohol Rehab Guide 2022). The global whiskey market was valued at **USD 59.63 billion** in 2019, and is projected to reach USD 86.39 billion by 2027 (Allied Market Research 2022d).

Brandy is produced by distilling wine with an alcohol concentration of 35–60% ABV (Alcohol Rehab Guide 2022). Brandy varieties are well known throughout the world, such as Cognac and Armagnac from southwestern France (BBC 2022). The global brandy market was valued at **USD 23.17 billion** in 2020 and is expected to reach USD 25.32 billion by the end of 2027 (Globe Newswire 2022a).

Our economy is significantly impacted by alcohol. Beer and wine were the most popular alcoholic beverages on the market. The total market value for alcoholic beverages made from fungi was **USD 1,108.45 billion**, demonstrating how popular drinking is worldwide.

Non-alcoholic fermented beverages

Chocolate is primarily produced from cocoa beans (*Theobroma cacao*). Cocoa trees are native to the tropical regions of Central and South America. Most of the flavors that we recognize in chocolate only start to develop during the fermentation of beans (Carvalho 2016). Yeasts are also involved in nonalcoholic fermentation of chocolate production to improve chocolate flavor properties and add a new collection of aromas to chocolate (Maicas 2020). Yeasts are also responsible to produce several secondary metabolites that are flavor-active that add different fruity aromas to chocolate. These fruity volatile compounds include aldehydes, esters, fatty acids, higher alcohols, organic acids, phenols and sulphur-containing compounds (Carvalho 2016). The main yeasts involved in cocoa fermentation are *Hanseniaspora opuntiae*, *Pichia kudriavzevii*, and *S. cerevisiae*, which produce higher alcohols and acetyl-CoA to make acetate esters that give floral and fruity aromas (Gutiérrez-Ríos et al. 2022). Other yeasts found in cocoa formation that produce aromas are *Galactomyces geotrichus* and *Wickerhamomyces anomalus* (Koné et al. 2016). *Saccharomyces*, *Pichia*, *Hanseniaspora*, *Kluyveromyces*, *Hansenula*, *Wickerhamomyces* and *Torulaspora* are the predominant wild genera of yeast in cocoa fermentation in Colombia (Sandoval-Lozano et al. 2022).

There are approximately 4 million exporters of cocoa beans worldwide (International Trade Center 2022). The top exporters of chocolate and other food preparations containing cocoa in 2021 with their exported value were

Germany (USD 32.82 billion), Belgium (USD 5.37 billion), Italy (USD 2.47 billion), Poland (USD 2.34 billion) and The Netherlands (USD 2.12 billion) (International Trade Center 2022). The global chocolate market value reached **USD 130.56 billion** in 2019 (Grand View Research 2022a).

Coffee is one of the most consumed nonalcoholic beverages in the world. Due to its popularity and high demand for coffee quality from consumers, constant improvement and increase in variety are deemed necessary (Martinez et al. 2019; Ruta and Farcasanu 2021). Yeast processing can help to improve the quality and complexity of coffee (Walbank 2022). Coffee is an essential commodity exported to around 70 tropical and subtropical countries (FAO 2015). The global coffee market was valued at **USD 102.02 billion** in 2020 (Research and Markets 2022a). The top coffee exporters according to net traded value were Brazil (USD 5.08 billion), Switzerland (USD 2.71 billion), Germany (USD 2.59 billion), Colombia (USD 2.54 billion), and Vietnam (USD 2.24 billion) (OEC 2022d). However, like with other goods, it is unclear how much of the world coffee output is dependent on yeast fermentation, so the value provided here is an overestimation, but without more detailed market information, no further breakdowns of this amount can be calculated.

Vinegar is a liquid product formed from alcoholic fermentation and subsequent acetous fermentation of carbohydrate sources. It has been reported as medication in many cultures and documented for its beneficial health effects when consumed regularly (Ho et al. 2017). Vinegar is the product of a two-step fermentation: In the first step, yeast converts sugars from fruits and grains to ethanol anaerobically, while in the second step, ethanol is oxidized to acetic acid aerobically by bacteria of the genera *Acetobacter* and *Gluconobacter*. However, alcohol formation is necessary to produce the required percentage of acetic acid (4–5%) for the liquid not to spoil (Tonkinson 2022). Several yeast species are involved in the fermentation of vinegar such as in traditional balsamic vinegar including *Candida lactis-condensi*, *C. stellata*, *Hanseniaspora osmophila*, *H. valbyensis*, *S. cerevisiae*, *Saccharomycodes ludwigii* as well as *Zygosaccharomyces bailii*, *Z. bisporus*, *Z. lentus*, *Z. mellis*, *Z. pseudorouxii* and *Z. rouxii* (Solieri and Giudici 2008). Vinegar has been an important household commodity and is used around the world. The global vinegar market reached a value of **USD 2.27 billion** in 2021 (Imarc 2022c).

Kombucha is a beverage produced from the fermentation of tea (*Camellia sinensis*) by acetic bacteria and osmophilic yeasts (De Filippis et al. 2018). It is a good source of probiotics with numerous health benefits. Kombucha is an ancient drink dating back to as early as 220 B.C (Jayabalan et al. 2014). The yeasts involved are *Brettanomyces/Dekkera*, *Candida*, *Torulaspora*, *Pichia*, *Schizosaccharomyces*, *Saccharomyces* and *Zygosaccharomyces* (May et al. 2019). The

global market value for kombucha was **USD 2.59 billion** in **2021** (Polaris Market Research 2021).

Fungal food additives: organic acids

Organic acids are one of the fastest growing sectors of the fermentation market globally, in which biotechnological production is an imperative economic alternative to chemical synthesis (Sharma et al. 2021). Organic acids are extensively used as ingredients in modern food processing (Copetti 2019). They are used mostly as buffers, preservatives, flavor enhancers, and adjuvants (Copetti 2019). Some organic acids from fungi have already made it to the market, such as citric, gluconic, and lactic acids made from fermentation of glucose or sucrose by *Aspergillus niger* (Copetti 2019). Other organic acids produced mostly by filamentous fungi but used to a lesser extent are fumaric, itaconic, malic, oxalic, succinic, and tartaric acids (Magnuson and Lasure 2004; Liaud et al. 2014; Dörsam et al. 2017).

Citric acid is an α -hydroxylated tricarboxylic acid found in citrus fruits. It has numerous applications in the food, pharmaceutical, and industrial fields. It is used to prevent the crystallization of sucrose in candies, as an acidulant in carbonated drinks, buffering agent, pH stabilizer in fruit and vegetable juices, and antioxidant as preservatives (Grewal and Kalra 1995; Magnuson and Lasure 2004; Carochio et al. 2018). Commercial citric acid production was initially done using *A. niger* in surface fermentation in 1916 by James Currie (Grewal and Kalra 1995; Show et al. 2015). Over the years, a variety of other microorganisms were studied, but *A. niger* is still superior among them in terms of production yield (Show et al. 2015). Citric acid production using this filamentous fungus is a multi-billion dollar industry (Cairns et al. 2018). Citric acid market was valued at **USD 2.81 807 billion** in 2021 and reached to **USD 2.89 billion** in 2022 due to increased demand (Future Market Insights 2022a).

Fumaric acid is an unsaturated dicarboxylic acid with various industrial applications in the food industry as a food acidulant in beverages and baking powders, feedstock for the synthesis of polymeric resins, and renewable energy resources (Yang et al. 2011). Fumaric acid is produced from glucose fermentation by the filamentous fungus *Rhizopus arrhizus* via a reductive tricarboxylic acid (TCA) pathway (Pan et al. 2016; Martin-Dominguez et al. 2022) and had an estimated market value of **USD 654.4 million** in 2020 (Reportlinker 2022).

Gluconic acid was first isolated from a strain of *A. niger* in 1922 (Goldberg and Rokem 2009). The production of gluconic acid can be done on an industrial scale using the enzymes glucose oxidase and catalase, derived from *A. niger*, which can efficiently convert glucose to gluconic acid (Copetti 2019). Other filamentous fungi, such as *Gonotobotrys*, *Gliocladium*, *Penicillium* and *Scopulariopsis* were found to produce gluconic acid (Goldberg and Rokem 2009;

Dowdells et al. 2010). Gluconic acid and its derivatives have various applications in pharmaceuticals, cosmetics, and food products as additive or buffer salts (National Center for Biotechnology Information 2022b; Yadav et al. 2022). The market size of gluconic acid was more than **USD 50 million** in 2017 (Global Market Insights 2022b).

Itaconic acid is a dicarboxylic acid with an α,β -unsaturated functionality that can be used as a monomer for the production of resins, plastics, paints, and synthetic fibers (Steiger et al. 2013). *Aspergillus* species such as *A. itaconicus* and *A. terreus* have the ability to synthesize itaconic acid (Steiger et al. 2013) as well as *Ustilago maydis* (Wierckx et al. 2020). The value of the itaconic acid market was **USD 98.4 million** in 2021 (Market Data Forecast 2022c).

Lactic acid is also one of the most common organic acids produced from renewable substrates using bacteria and fungi such as *Rhizopus* species (Zhang et al. 2007). Lactic acid became also interesting due to its high added value (Castillo Martinez et al. 2013). It has various applications in the food and food-related industries (Ameen and Caruso 2017). Other potential applications are the production of biobased itaconic acid substitutes for petrochemical derivatives, such as biodegradable and biocompatible polylactate polymers (Zhang et al. 2007; Teleky and Vodnar 2019). Lactic acid market value was estimated to be **USD 1.1 billion** in 2020 (Markets and Markets 2022a).

Fungi-based protein also called mycoprotein, is a sustainable protein source produced from single-cell protein (SCP) production technologies that could address the demands of protein worldwide (Nigam and Singh 2014). The global demand on vegetarian opportunities is currently rising, so the market share of mycoprotein is bound to increase. Moreover, mycoprotein consumption has been associated with numerous bioactivities such as antioxidant, antidiabetic, reduced cholesterol level, and fungal proteins are a potential source of amino acids that could induce muscle protein synthesis (Derbyshire and Delange 2021; Stoffel et al. 2021). Formerly, mycoproteins were produced for animal consumption, but the market for human feed is constantly growing (Nigam and Singh 2014; Derbyshire 2022). The commercially marketed Quorn™ mycoprotein is derived from *Fusarium venenatum* (Nigam and Singh 2014), which remains the most important source. *Pleurotus albidus* can also be used to produce mycoproteins flour that was used to replace wheat flour to produce cookies (Stoffel et al. 2021). The company “Nature Fynd” promotes Fy produced by a strain of *Fusarium flavolapis*, collected in the Yellowstone National Park, as an alternative producer. Due to the numerous food applications of mycoprotein, it was valued at **USD 156.6 million** in 2020 (Allied Market Research 2022e) and is estimated to attain a market worth of USD 397.5 million in 2029 (Globe Newswire 2022b) (Table 3).

Food enhancers/staple food

Soy sauce is the oldest food flavoring ingredient that is eminent, particularly in Asian countries (Hong et al. 2015). It is an all-purpose seasoning used in around 100 countries around the world (Ito and Matsuyama 2021). Fungi responsible for brewing soy sauce are known as koji molds and belong to the genus *Aspergillus* (e.g. *A. flavus* var. *oryzae*, *A. sojae*, and *A. tamarii*) (Terada et al. 1981). Soy sauce is produced by fermenting soybean, wheat, and salt by the action of koji mold, halophilic lactic acid bacteria, and salt-tolerant yeasts such as *Candida etchellsii*, *C. versatilis*, and *Zygosaccharomyces rouxii* (Ito and Matsuyama 2021). The market value of soy sauce was around **USD 39.5 billion** in 2019 (Verified Market Research 2022b).

Miso is another condiment, a fermented soybean paste made of *Aspergillus* species that are involved in making soy sauce, specifically *A. flavus* var. *oryzae* and *A. sojae* (Yokotsuka and Sasaki 1998; Allwood et al. 2021). Other fungi involved in accelerating miso ripening process are *Zygosaccharomyces* spp. together with the lactic acid bacterium, *Pediococcus halophilus* (Wilson 1995; Batt and Tortorello 2014; Allwood et al. 2021). There are several kinds of miso products depending on the type of koji used in fermentation (e.g. rice, barley, soy bean) (Wilson 1995; Allwood et al. 2021). The market size for miso was valued at **USD 67.8 million** in 2022 (Future Market Insights 2022b).

Indonesian tempeh is a mold-facilitated fermented product produced from fermented soy beans mostly consumed as staple food in Indonesia (Dinesh Babu et al. 2009), but is widely accepted globally (Ahnan-Winarno et al. 2021). The fungi involved in soybean fermentation for tempeh production are *Rhizopus* species such as *R. microporus* (formerly *R. oligosporus*), and *R. arrhizus* (formerly *R. oryzae*) (Maheshwari et al. 2021; Sjamsuridzal et al. 2021). The mycelia of the *Rhizopus* species hold the soy beans together, thus forming a compact structure like a cake (Gandjar 1999; Handoyo and Morita 2006). The global tempeh market was valued at **USD 4.53 billion** in 2021 (The Business Research Company 2022).

Food colorants/pigments

Food colorants are pigments added to food to enhance quality and add color to the food to make it more presentable and attractive to consumers (Hyde et al. 2019). Natural colors are generally regarded safer than synthetic ones and some may even have medicinal benefits. Furthermore, food colorants are also added to preserve food products (Christiana 2016). Nevertheless, the compounds should undergo extensive toxicity tests before they can be added to food, as some fungal toxins are also pigments. With the growing demand for natural food colorants globally, filamentous fungi have

become important and readily available sources of food coloring (Dufossé et al. 2014; Hyde et al. 2019). Several genera of filamentous fungi such as *Fusarium*, *Monascus*, *Penicillium*, and *Talaromyces* have been explored for colorant production (Caro et al. 2017; Lagashetti et al. 2019). Marine fungi are also potential sources of pigments with various color hues and atypical chemical structures (Dufossé et al. 2014). Filamentous fungi can produce an extraordinary range of pigments, including some chemical classes such as carotenoids, melanins, flavins, phenazines, quinones, azaphilones, and violacein or indigo (Dufossé et al. 2014; Poorniammal et al. 2021). For instance, the strain *Penicillium oxalicum* var. *armeniaca* CCM 8242 isolated from soil was able to produce the first commercial red color Arpink red™ pigment (Natural red™) (Caro et al. 2017). The high demand for natural food colorants was reflected in its global market value of **USD 1.6 billion** in 2020 (Mordor Intelligence 2022) (Table 4).

Astaxanthin is a red–orange carotenoid belonging to the xanthophyll family (Aneesh et al. 2022). The natural sources of astaxanthin include bacteria, fungi, algae, crustaceans, and certain fishes. Important fungal astaxanthin producers are the yeasts *Phaffia rhodozyma* (Pandey et al. 2015) and *Xanthophyllomyces dendrorhous* (Rodríguez-Sáiz et al. 2010). The market price of astaxanthin ranges from USD 2500 to USD 7000/kg with the global market value of **USD 1.94 billion in 2022** (Grand View Research 2023a). However, we did not find a way to discriminate between fungal and non-fungal sources during our literature search.

Carotenoids are terpenoid pigments commonly produced by vascular plants, algae, bacteria, and fungi (Avalos and Carmen Limón 2015). Various fungi produced various carotenoids. Among these carotenoid-producing fungi are *Blakeslea trispora* (zygomycete), *Neurospora crassa* (sordariomycete) and *Xanthophyllomyces dendrorhous* (basidiomycetous yeast) (Avalos and Carmen Limón 2015; Sandmann 2022). The provitamin β-carotene has also been described in *Aspergillus giganteus*, *Penicillium* sp., *Rhodospiridium* sp., *Sclerotium rolfsii*, *Sclerotinia sclerotiorum*, and *Sporidiobolus pararoseus*. Aside from the food market, there are potential applications for carotenoids in the textile industries (Venil et al. 2020). The global market size for carotenoids was **USD 1.4 billion** in 2019 (Fortune Business Insight 2022c), but once again, the share of fungal products remains obscure.

Monascus pigments are natural food colorants widely used in the food industries worldwide, but especially in China and Japan (Feng et al. 2012). They are produced by fungi belonging to the genus *Monascus*. The six main pigments produced by strains of the genus *Monascus* are orange (monascorubrine, rubropunctatin), red (monascorubramine, rubropunctantamine), and yellow (monascine, ankaflavin) (Agboyibor et al. 2018). Furthermore,

Monascus pigments have a variety of biological activities, such as antimutagenic, anticancer properties, antimicrobial activities, and potential anti-obesity activities. *Monascus* pigments already had a market value of **USD 1 million** in Japan at the end of the 1990s (Dufossé 2019), but we did not find hard data on the current market (Fig. 6).

Another application of natural dyes from fungi is the textile industry (Chadni et al. 2017). Some wood rotting fungi are utilized in the production of textile dyes (Hernández et al. 2019). Other filamentous fungi can also produce various pigments with application in dyeing cotton, silk, and wool (Sudha et al. 2016; Kalra et al. 2020). *Neurospora* spp. are ascomycetous yeasts that can also be a great source of pigments (Lagashetti et al. 2019; Kalra et al. 2020).

Commodities

Agarwood

Agarwood is a dark resinous heartwood that forms in mainly *Aquilaria* and *Gyrinops* trees naturally infected with endophytic fungi such as *Cladosporium*, *Fusarium*, *Melanospora* spp., and “*Mycelia sterilia*” (Hyde et al. 2019), however, fungi reported have not been identified accurately according to the current standards. Agarwood is used as a fragrance in cosmetics and some important religious rituals (Chowdhury et al. 2016). The global market value of the **agarwood chip** market is worth **USD 8.30 billion** in 2018 (Straits Research 2021). **Agarwood oil** also has applications in the chemical, cosmetics, and personal care product industries with a global market value of **USD 278.03 million** in 2021 (Maximize Market Research 2021) (Tables 6, 7).

Cosmetics

Fungi synthesize natural active biomolecules that can be applied to develop cosmetic products due to their important

biological functions and applications such as antiaging, antioxidants, skin revitalization, skin whitening, and hair products (Hyde et al. 2010; Wu et al. 2016; Badalyan et al. 2022). Numerous bioactive metabolites such as polysaccharides and glycoproteins, as well as other metabolites such as phenolic compounds, terpenoids, and several lipid components, have been explored due to their functions in skin health (Usman et al. 2021).

Lentinula edodes and *Ganoderma* species are two of the most popular fungal sources used in skin care products. Lentinan extracted from *L. edodes* has the potential to protect the skin against environmental pollutants (Zi et al. 2020). *Agaricus subrufescens* residues were also used as cosmetic ingredients (Hyde et al. 2010; Wisitrassameewong et al. 2012). Other macrofungal species utilized in skin care preparations include *Taiwanofungus camphoratus*, *Grifola frondosa*, *Inonotus obliquus*, *Ophiocordyceps sinensis*, and *Schizophyllum commune* (Wu et al. 2016). The following compounds are economically important isolated from fungi.

β-Glucans are polysaccharides that constitute around 30–80% of the fungal cell wall (Free 2013). Among these β-glucans, lentinan had a market value of **USD 10 million** in 2022 (Market Watch 2023b). However, yeast is the main source of β-glucans in the market with a global value of **USD 174.2 million** in 2021 (Grand View Research 2023b). The global β-glucan market was over **USD 329.4 million** in 2019 (Global Market Insights 2022c) and increased to **USD 403.8 million** in 2020 (Markets and Markets 2022b).

Ergothioneine is a natural sulphur derivative of histidine, which was originally isolated from the ascomycete *Claviceps purpurea* (Tanret 1909). It has antioxidant activity and is nowadays more commonly produced from edible mushrooms (Fu and Shen 2022). Some sources of ergothioneine are *A. bisporus*, *Boletus edulis* *Flammulina “velutipes”* (probably *F. filiformis* according to the current taxonomy established by Wang et al. 2018), *Pleurotus eryngii*, *P. ostreatus* and *Lentinula edodes* (Lee et al. 2009; Kalač 2016). The global market value of L-ergothioneine

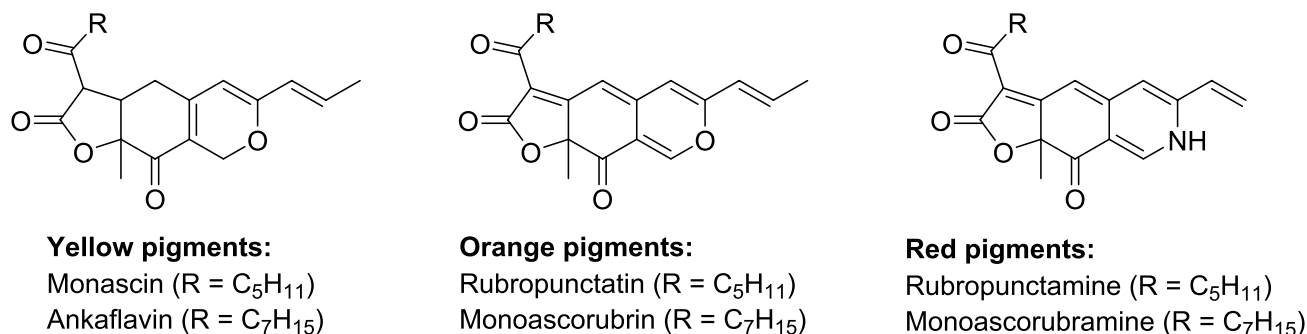


Fig. 6 Chemical structures of *Monascus* pigments

Table 6 Other food products produced with the involvement of fungi

Category	Products	Fungi involved	Market value (USD billion)	Year	Sources
Organic acids	Citric acid	<i>A. niger</i>	2.81	2021	Future Market Insights (2022a)
	Fumaric acid	<i>Rhizopus</i> spp.	0.65	2020	Reportlinker (2022)
	Gluconic acid	<i>A. niger</i> , <i>Penicillium</i> , <i>Scopulariopsis</i> , <i>Gonotobotrys</i> , and <i>Gliocladium</i>	0.05	2017	Global Market Insights (2022a, b, c)
	Itaconic acid	<i>A. itaconicus</i> , <i>A. terreus</i>	0.98	2022	Market Data Forecast (2022b)
	Lactic acid	<i>Rhizopus</i>	1.10	2020	Markets and Markets (2022a, b)
Fungi-based protein		<i>Fusarium</i> , <i>Hericium erinaceus</i> , <i>Pleurotus</i>	0.16	2029	Globe Newswire (2022b)
Food enhancers	Soy sauce	<i>Aspergillus oryzae</i> , <i>A. sojae</i> , <i>A. tamarii</i> , <i>Candida versatilis</i> , <i>C. etchellsii</i> , <i>Zygosaccharomyces rouxii</i>	39.50	2019	Verified Market Research (2022a, b)
	Miso	<i>A. oryzae</i> , <i>A. sojae</i> , <i>Zygosaccharomyces</i> spp.	0.68	2022	Future Market Insights (2022c)
	Indonesian tempeh	<i>Rhizopus arrhizus</i> , <i>R. microporus</i>	4.53	2021	The Business Research Company (2022)
Food colorants	Astaxanthin	<i>Phaffia rhodozyma</i>	1.94	2022	Grand View Research (2023a)
	Carotenoids	<i>Blakeslea trispora</i> , <i>Neurospora crassa</i> , and <i>Xanthophyllomyces dendrorhous</i>	1.40	2019	Fortune Business Insight (2022c)
	Monascus pigments	<i>Monascus</i> spp.			
Total value			53.80		

was around **USD 15.02 million** in 2021 (Market Data Forecast 2022d).

Kojic acid, a pyrone derivative, is a byproduct in the fermentation process of producing sake, an alcoholic drink made from rice and almost exclusively produced in Japan (Goldberg and Rokem 2009). It is a metabolite of *Aspergillus* species, including *A. oryzae* and *A. flavus*. Kojic acid inhibits tyrosinase in the synthesis of melanin and is documented for its numerous bioactivities (Saeedi et al. 2019). It is known for its radioprotective and skin lightening effect and therefore has been used as ingredients in the production of skin creams, lotions, soaps and dental care products (Saeedi et al. 2019; Phasha et al. 2022). Kojic acid has a global market value of **USD 36 million** in 2022 (Market Watch 2022c).

Mycopesticides

Fungi have been used as biological control agents of crop pests in agricultural and urban areas for several decades. (Wraight and Carruthers 1998). Almost 50% of the registered microbial biopesticides are based on fungi (Mascarin et al. 2018). Mycopesticides have been on the market since 1981, and the first of these products was registered in the United States as Mycar. It was composed of *Hirsutella thompsonii*, which causes epizootics in some species of spider mites (Rechcigl and Rechcigl 2000). Mycoinsecticides

are interesting organic alternatives to chemical insecticides because they tend to be less harmful to human health and the environment. They are also target-specific with less detrimental effects to human and pets (Moore et al. 2011).

The most explored entomopathogenic fungal genera are *Akanthomyces*, *Beauveria*, and *Metarhizium*, which can infect a wide variety of insect hosts such as dipterans, lepidopterans, and coccidae. Numerous studies have explored the efficacy of these genera as biocontrol agents. *Beauveria bassiana* is one of the most explored entomopathogenic species worldwide (Fancelli et al. 2013). It has high genetic variability, virulence and adaptability to local conditions (Fancelli et al. 2013). *Metarhizium*, on the other hand, has been widely studied because of its general safety, narrow host range, environmentally friendliness and ease of mass production (Aw and Hue 2017). The global biopesticides market is estimated to be valued at \$ 5.5 billion in 2022 (Research and Markets 2022b). Mycopesticides account for around 10% of the global market value of biopesticides (Zaki et al. 2020), thus the global market value of mycopesticides can be estimated to be approximately **USD 550 million** in 2022.

Strobilurins are economically important bioactive compounds first reported by Anke et al. (1977) from cultures of the basidiomycete *Strobilurus tenacellus*. These compounds have later also been extracted from numerous Basidiomycota such as *Oudemansiella canari* and *Mucidula mucida* (Rosa et al. 2003, 2005; Iqbal et al. 2018). Strobilurins became

Table 7 Commodities produced with the involvement of fungi

Category	Products	Fungi involved in the production	Market value (USD billion)	Year	Sources
Agarwood	Agarwood chips	<i>Aquilaria</i> , <i>Aetoxylon</i> , <i>Gyrinops</i> , and <i>Gonystylus</i>	8.30	2018	Straits Research (2021)
	Agarwood oil		0.28	2021	Maximize Market Research (2021)
Cosmetics	β -(1–3)-D-glucan	<i>Agaricus subrufescens</i> , <i>Lentinula edodes</i> , <i>Ganoderma lucidum</i> , <i>Antrodia cinnamomea</i> , <i>Cordyceps sinensis</i> , <i>Grifola frondosa</i> , <i>Inonotus obliquus</i> and <i>Schizophyllum commune</i>	0.40	2020	Markets and Markets (2022b)
	L-ergothioneine	<i>A. bisporus</i> , <i>Boletus edulis</i> <i>Flammulina velutipes</i> , <i>Pleurotus eryngii</i> , <i>P. ostreatus</i> and <i>L. edodes</i>	0.015	2021	Market Data Forecast (2022d)
	Kojic acid	<i>Aspergillus flavus</i> var. <i>oryzae</i>	0.036	2022	Market Watch (2022c)
Mycopesticides		<i>Akanthomyces</i> , <i>Beauveria</i> , and <i>Metarhizium</i>	0.55	2022	Zaki et al. (2020)
Fungicides	Strobilurins	<i>Mucidula</i> , <i>Oudemansiella</i> and <i>Strobilurus</i>	4.65	2022	Market Watch (2022d)
Mycorrhiza-based biofertilizers		<i>Pisolithus tinctorius</i> , <i>Rhizophagus</i> Sebaciales and <i>Trichoderma</i>	0.27	2021	Market Data Forecast (2022e)
Fungal enzymes	Laccase	<i>Aspergillus</i>	0.003	2021	Business Research Insights (2022)
	Invertase	<i>Aspergillus</i> , <i>Penicillium</i> , <i>Rhizopus</i> and <i>Saccharomyces</i>	0.058	2022	Future Market Insights (2022c)
	Amylase	<i>Aspergillus awamori</i> , <i>A. niger</i> , <i>A. oryzae</i> , <i>Penicillium</i> and <i>Rhizopus</i>	0.28	2018	Fior Market (2022)
	Protease	<i>Aspergillus</i> , <i>Humicola</i> , <i>Mucor</i> , <i>Penicillium</i> , <i>Rhizopus</i> , <i>Thermoascus</i> , and <i>Thermomyces</i>	1.30	2021	Dataintelo (2022a)
	Cellulases	<i>Trichoderma reesei</i>	1.62	2022	Future Market Insights (2022d)
	Pectinase	<i>Aspergillus niger</i> , <i>A. awamori</i> , <i>Mucor piriiformis</i> , <i>Penicillium restrictum</i> , <i>Trichoderma viride</i> , and <i>Yarrowia lipolytica</i>	1.40	2020	PS Market Research (2022)
	Lipase	<i>Aspergillus</i> , <i>Penicillium</i> , <i>Fusarium</i>	0.69	2022	Future Market Insights (2022e)
	Galactosidase	<i>Aspergillus</i> , <i>Cluyveromyces lactis</i> , <i>Guehomyces pullulans</i>	1.50	2021	Grand View Research (2022b)
	Lactase	<i>Aspergillus</i> , <i>Cluyveromyces</i> , <i>Trichoderma</i> , <i>Penicillium</i> , <i>Rhizopus</i> , <i>Fusarium</i>	0.18	2019	Dataintelo (2022b)
	Total value		21.53		

an inspiration in developing the β -methoxyacrylate class of agricultural fungicides (Nofiani et al. 2018) such as azoxystrobin (Quadris), trifloxystrobin (Flint), pyraclostrobin (Cabrio), or Pristine (pyraclostrobin and boscalid, a premix of a Group 11 and a Group 7 fungicide). The global market value for strobilurin fungicides was estimated to be **USD 4.65 billion** in 2022 (Market Watch 2022d).

Mycorrhiza-based biofertilizers

Mycorrhizal fungi such as arbuscular mycorrhiza and ectomycorrhiza are considered natural biofertilizers since they provide important nutrients to the plant in exchange for photosynthetic products (Berruti et al. 2016; Domínguez-Núñez et al. 2020). A mycorrhiza-based biofertilizer is a substrate containing fungi colonizing the rhizosphere or the interior of the plant when applied to seeds, plant surfaces, or soil (Hyde et al. 2019; Karima and Samia 2020). It helps in plant

growth by enhancing the supply of primary nutrients to the host plant and promoting growth hormones (Berruti et al. 2016).

The most widespread EcM product inoculum is *Pisolithus tinctorius* with a wide host range that can be applied as a vegetative mycelium peat vermiculite carrier used in nursery and forestry plantations (Gentili and Jumpponen 2006; Sebastiana et al. 2018). Other fungi used are *Rhizophagus* (formerly *Glomus*), Sebaciales and *Trichoderma* species (Kaewchai et al. 2009; Molla et al. 2012). The market value of mycorrhiza-based biofertilizers was **USD 271.8 million** in 2021 (Market Data Forecast 2022e).

Fungal enzymes

Fungi grow ubiquitously on complex organic matter, prone to recycle nutrients and decompose complex substrates. In order to successfully accomplish this endeavor, they are

equipped with a great portfolio of enzymes. Compared to chemical reactions, enzymes, used as biocatalysts, are highly specific, have few side products, and show mild reaction conditions with a low environmental and toxicological impact. Besides highly specific ones, also enzymes with a broad substrate spectrum are present. In general enzymes are classified in six classes by the International Enzyme Commission: EC1 oxidoreductases, EC2 transferases, EC3 hydrolases, EC4 lyases, EC5 isomerases, and EC6 ligases. In 2019 fungal enzymes had an overall marked share of 50% on all enzymes available (Kango et al. 2019). Despite of the large share, solely few species, namely *Aspergillus*, *Trichoderma*, *Rhizopus*, and *Penicillium*, contribute significantly to the market (El-Gendi et al. 2021).

In the food processing industry, fungi are the primary source for enzymes. They are applied to influence for example food quality, shelf life, texture, color, aroma but may also simplify production steps and yields (Zhang et al. 2018). Due to their unique properties, they are also used in the pharmaceutical, chemical, textile, detergent, cosmetic, and flavor or fragrance industry (He et al. 2017; Haile and Ayele 2022; El-Gendi et al. 2021). Whereas in 1983 about 30 enzyme classes, half of fungal origin, were commercialized, in 2020, the industrial enzymes market was valued at **USD 5.7 billion** (PS Market Research 2022). Though no detailed information on product origins is available, several global acting companies for enzyme production use fungi as production organisms. Among them are Novozymes (Denmark), DSM (Netherlands), Chr. Hansen (Denmark), DuPont (USA), BASF (Germany), Advanced Enzymes (India), and AB Enzymes (Germany). Here, production processes are diverse. Besides cultivation of the native producer strain, also heterologous hosts are widely spread. Second helps to overcome to long cultivation times, process in homogenities and simplifies the overall process. However, in case of technical enzymes, partially purified enzyme mixtures decrease production costs significantly. In bioremediation, wastewater treatment and bioethanol production, the use of whole-cell bioconversion of non engineered strains in mixed cultures is preferred to enzyme preparations (El-Gendi et al. 2021). Continuous fermentation simplifies processes and keeps them at low costs. Modern bioinformatics pushes the identification of novel enzymes with unique properties. Furthermore, genome mining approaches are on the verge, which increases product portfolios drastically.

Oxidoreductases are catalyzing redox reactions, therefore are typical housekeeping enzymes i.e., involved in the glycolysis and amino acid metabolism. Despite the great potential and the formation of several products of industrial interest, oxidoreductases are nowadays solely used in niche applications (Gygli and van Berkel 2015). However, fungi have a large share of this market, especially in bioremediation applications and wastewater treatment (Verma et al.

2020). This is due to the fact that mainly white rot Basidiomycota grow on lignocellulolytic biomass hitherto secretes robust enzymes of high redox-potential for the substrate degradation (Martínez et al. 2018). Especially Laccases, monooxygenases, and dioxygenases are of commercial use (El-Gendi et al. 2021).

Laccases have a great potential to oxidize phenolic and non-phenolic substrates cofactor independently. They are commercially used in destaining processes, paper industry, medical applications, and for biosensors. Usually, fungi are applied in microbial consortia to degrade pollution i.e. *Aspergillus* consortia that are used in wastewater treatment to degrade heavy metals chromium and cadmium (Talukdar et al. 2020). The global market value for laccase was **USD 3 million** in 2021 (Business Research Insights 2022).

Reactions involving the transfer of functional groups are catalyzed by **transferases**. Especially enzymes, catalyzing the transformation of higher sugars, are of commercial use. Invertases are breaking down sucrose into fructose and glucose (Nadaroglu and Polat 2022). Fungi that produce invertases are *Aspergillus*, *Penicillium*, *Rhizopus* and yeasts such as *Saccharomyces* (Kulshrestha et al. 2013; Matei et al. 2017). **Invertase** is prevalent in the food industry, especially in making confectioneries and baking as well as extending the shelf life of the food products (Infita 2022). Inverted sugar prevents crystallization in food products and increases sweetness of soft fillings like soft caramel (Verma et al. 2020). Moreover, fructosyltransferase activities are used to produce fructooligosaccharides (FOS) which are known for their health promoting effects. FOS are applied as an alternative sweetener with a viscous texture in food industry (Lateef et al. 2012). The overall invertase market was valued at **USD 57.6 million** in 2022 (Future Market Insights 2022c).

Hydrolases can cleave substrates via the addition of water. They display the most extensively studied enzyme class with the largest potential for commercialization (Gurung et al. 2013). Especially fungal amylases, proteases, cellulases and lipases are widely commercialized, but also other enzymes of industrial interest are known.

Among them, α -amylases are randomly hydrolyzing α -1,4-glycosidic bonds converting complex carbohydrate to simple sugars (Akinfemiwa et al. 2022). This unique property allows cleavage of non-reduced sugar residues unlike other amylolytic enzymes (Gupta et al. 2003). **α -Amylases** have the largest share of enzyme preparations used in industry (Monteiro de Souza and De Oliveira e Magalhães 2010). The global market size was valued at **USD 278.2 million** in 2018 and expected to increase up to USD 353 million by 2026 (Fior Market 2022). Among others, they are applied in the food, detergent, pulp and paper, and textile industry to hydrolyze starch (Gupta et al. 2003). The main applications of α -amylases are in the production of bakery products and food processing i.e. for glucose production (Copetti 2019).

Herein, fungal enzymes are preferred to other sources due to their GRAS-status (Gupta et al. 2003). In bakeries, they are applied since 1995 and lead to a higher dough volume, better color, softer doughs, higher toasting quality, and a softer crumb (Pritchard 1992). They are commercially produced by *Aspergillus* (e.g. *A. awamori*, *A. niger* and *A. oryzae*), *Penicillium* and *Rhizopus* (Pandey et al. 2000; Copetti 2019).

Proteases hydrolyze peptide bonds of proteins into smaller polypeptides or single amino acids (Flores-Gallegos et al. 2019). Various fungi such as *Aspergillus*, *Humicola*, *Mucor*, *Penicillium*, *Rhizopus*, *Thermoascus*, *Thermomyces*, etc. can produce proteases (Monteiro de Souza et al. 2015). These enzymes are easier to purify than their bacterial counterparts (Vishwanatha et al. 2010). Proteases have various industrial applications in the food industry, as pharmaceuticals and in biomedical therapies (Monteiro de Souza et al. 2015; Agbowuro et al. 2018; Naeem et al. 2022). Fungal proteases are cost effective and have faster production compared to other microbial sources (Monteiro de Souza et al. 2015). The global market value of fungal proteases was valued at **USD 1.3 billion** in 2021 (Dataintel 2022a).

Increasing demand on biofuels opens the potential of cellulose as cost effective substrate. Degradation is catalyzed by **cellulases**. Apart from biofuels, cellulases are also applied in combination with pectinases to clarify juices and in biopolishing of textiles (Gurung et al. 2013). Because of its high product titers, exceeding 100 g/L in submerged processes, *Trichoderma reesei* is widely used in industry (Gupta et al. 2016). The global market value of cellulases was **USD 1.62 billion** in 2022 (Future Market Insights 2022d).

Pectinases are catalyzing the hydrolysis of pectin and pectic substances. Pectinases have wide application in food industry especially in fruit juice extraction to increase pressing efficiency and to clarify the former turbid drink (Jayani et al. 2005). Enzyme treatment in combination with cellulases decreases filtration times by 50% (Blanco 1999). During textile production an enzymatic cocktail containing among others pectinases is applied to remove non-cellulolytic impurities from clothes, called biosourcing (Hoondal et al. 2002). Some of the most efficient fungal species in producing pectinases are *Aspergillus awamori*, *A. niger*, *Mucor piriformis*, *Penicillium restrictum*, *Trichoderma viride*, and *Yarrowia lipolytica* (Haile and Ayele 2022). About 25% of global share of food enzyme in 2005 sales pectinases with the market value of **USD 1.4 billion** in 2020 based on the global industrial market value of industrial enzymes (Jayani et al. 2005; PS Market Research 2022).

Lipases hydrolyze triacylglycerols to glycerol and fatty acids which is of commercial interest as biological laundry detergents, cosmetics additive, fine chemical production, paper pitching, leather defatting, wastewater treatment, and biodiesel production (El-Gendi et al. 2021). Fungal lipases stand out due to its alkaline and temperature stability (Singh and Mukhopadhyay 2012). In food production i.e. offered

by Rohm and Haas Co. USA, lipases are used to improve cheese aroma (Singh and Mukhopadhyay 2012). Important sources for fungal lipases are for example *Aspergillus*, *Penicillium*, and *Fusarium* (El-Gendi et al. 2021). The global lipase market value in 2022 was **USD 694 million** (Future Market Insights 2022e).

Galactosidases, specifically β -galactosidases isolated from bacteria, filamentous fungi and yeasts, are responsible to hydrolyze lactose (Saqib et al. 2017). Yeasts, such as *Kluyveromyces lactis* and *Guehomyces pullulans*, but also filamentous fungi like *Aspergillus niger* are commercially important sources of β -galactosidases for food processing, waste disposal, and prebiotic production (Hu et al. 2010; Saqib et al. 2017). This enzyme is also used in whey disposal, a byproduct of cheese industry (Karasova et al. 2002). Enzymatically treated waste streams are rich in ethanol and a sweet syrup that is used further in food production including bakery (Zhou and Chen 2001). **Lactase** is a β -galactosidase, with a special importance for the production of lactose-free milk and dairy products (Copetti 2019). This enzyme is industrially obtained from fungal sources such as *Aspergillus*, *Kluyveromyces*, *Trichoderma*, *Penicillium*, *Rhizopus*, and *Fusarium* (Mahoney 1985; Zhou and Chen 2001; Seyis and Aksoz 2004; Jesus and Guimarães 2021). The lactases produced by filamentous fungi are more heat-stable compared with the ones originating yeasts (Copetti 2019). Whereas the global market of galactosidases was valued at **USD 1.5 billion** in 2021, lactase take about 12% of the overall market share with around **USD 185.2 million in 2019** (Grand View Research 2022b; Dataintel 2022b).

Lyases mediate elimination reactions. Among them is the pectin lyase of industrial interest, catalyzing the non-hydrolytic cleavage of pectin. As previously described for pectinases, the lyases are present in preparations for fruit and juice processing (Suhaimi et al. 2021). These enzymes are also applied in a cocktail with various hydrolases in wine making as well as paper production processes. As for pectinases fungal sources play an important role in production due to their unique enzyme properties, namely temperature and pH stability. Prominent sources are *Aspergillus*, *Candida*, *Penicillium*, *Trichoderma*, and some yeasts.

Isomerases catalyze rearrangement processes. The most notable is the isomerization of glucose to generate high fructose corn syrup (HFCS), which has various applications in the food sector owing to its sweetness. HFCS has a high solubility, low crystallization tendency, and a high freezing point depression, which makes its use in drinks and frozen desserts advantageous. Besides food, HFCS is used in the detergent, and pharmaceutical industries (Singh et al. 2017). Commercially available pectin lyases have been solely reported from *Aspergillus*.

Ligases catalyze the formation of new bonds. Despite the high importance in intercellular mechanisms (besides

niche applications in diagnostics, and molecular biology), hardly any commercialization is reported. Solely yeasts were reported as promising producer strains.

Value of wild and cultivated mushrooms being traded for food

Edible mushrooms

Wild and commercial fungi can be resources of low-calorie functional food and nutraceuticals (Hyde et al. 2019; Lu et al. 2020). The popularity among consumers is due to the pleasant and unique flavors and health benefits of these mushrooms (Barros et al. 2008; Ache et al. 2021). Fungi are rich in crude fibers, proteins, vitamins, and minerals; they contain low fat, calories and high quality carbohydrates (Bandara et al. 2017; Thakur 2020). Fresh fungi have a moisture content of about 90% while dry matter consists of carbohydrates (50–65%), proteins (19–35%), essential fatty acids (2–6%) with some vitamins and minerals (Rathore et al. 2017; Jacinto-Azevedo et al. 2021). Consumption of edible fungi promotes good health caused by synergistic effects of the bioactive compounds present such as β -glucans, ascorbic acid, lectins, unsaturated fatty acids, phenolic compounds, tocopherols, and carotenoids (Varghese et al. 2019). Cultivated (54%), medicinal (38%), and wild fungi (8%) are the three major components of the global mushroom industry (Royse et al. 2017).

The world production of mushrooms was 42,590 thousand tons from the 20 largest producing countries, mainly contributed by China (93.93%) in 2020 (Table 8) (FAOSTAT 2022a). The mushroom and truffle production and yield in Asia was around 7 million tons and 3.2 million hg/ha yield, respectively, in 2018. China is the largest contributor with 6.7 million tons production (FAOSTAT 2022a). The total value for each country was determined by multiplying the production by the 2020 mushroom price (USD/ton) (FAOSTAT 2022b). The total value of mushroom was USD 45.42 billion in 2020. The value of mushrooms being traded for food which only include cultivable and wild edible fungi constitute to 62% of the mushroom production or **USD 28.16 billion** in 2020.

Cultivable fungi

Cultivated edible mushroom production is attributed to 54% of global production, amounting to USD 34 billion in 2013 (Royse et al. 2017). Around 60 species of fungi are commercially cultivated (Chang and Miles 2004a). The most cultivated mushroom genera in global production are *Agaricus bisporus*, followed by “*Lentinus*” (*Lentinula edodes*, *Pleurotus* spp., and *Flammulina* “*velutipes*” (or *F. filiformis*) (cf. Valverde

et al. 2015 with the names corrected to the currently valid taxonomy). These genera accounted for 85% of global mushroom production in the world (Royse et al. 2017; Kant Raut 2019). The market value of edible cultivated fungi in 2020 accounted to 54% of global production was **USD 24.53 billion**.

Wild edible fungi

Approximately 2000 species of wild fungi are edible and can be consumed safely (Li et al. 2021). About 470 species have medicinal values, and another 180 species have been attributed value in other activities, such as religious purposes. In Tanzania, for instance, macrofungal collectors were able to collect up to 1500 kg of fruiting bodies of wild fungi that can earn around USD 500 to 600 per season (Tibuhwa 2013; Chelala et al. 2014). The retailers were also able to sell 750 to 800 kg with seasonal earnings of USD 750 to 1000 (Chelala et al. 2014). Wild edible fungi are collected each year in several million tons, accounting for 8% of global macrofungal production (Royse et al. 2017), therefore it was accounted to around **USD 3.63 billion in 2020**.

Emerging myco-based material industry

Facing the transition towards a sustainable economy based on reduction of non-renewable materials and minimization of waste, fungal biotechnology offers a fascinating opportunity with high innovation potential (Meyer et al. 2020). In the last two decades, fungal biomaterials attracted growing attention in academic and commercial fields. Transferring organic agricultural or industrial waste into new bio-based products, they constitute a new form of a cost-effective and low energy bio-fabrication (Jones et al. 2020). Fungal mycelium has the capacity to degrade lignocellulosic materials and form composite networks (Sun et al. 2019) with insulating, non-flammable or hydrophobic properties and an improved mechanical strength (Jones et al. 2020). The mycelium binder constituent interfaces a dispersed phase of agricultural residue (substrate filler) and functions as a load transfer medium between the typically fibrous agricultural residue within the composite in a manner similar to the matrix phase of a polymer composite (Jones et al. 2020). Produced as an eco-friendly alternative to petroleum-based products, mycelium-based materials are considered to play a pivotal role in construction, automotive, transportation, electronic, and fashion sectors as well as design or applied arts. They comprise a great opportunity for substitution of traditional materials, such as timber, steel, concrete, foams or leather might (Karana et al. 2018; Attias et al. 2020; Silverman et al. 2020; Stelzer et al. 2021). Across the diverse disciplines, potential applications for mycelium-based products are reaching from packaging materials, bricks, acoustic

Table 8 Mushroom production of top 20 producing countries with market value in 2020 (FAOSTAT 2022a)

Rank	Country	Tons (thousand)	% of Top 20	Total value (million USD)
1	China	40,005	93.9	39,510
2	Japan	472	1.1	1,041
3	United States of America	370	0.9	1,107
4	Netherlands	260	0.6	441
5	India	201	0.5	443
6	Poland	183	0.4	229
7	Spain	166	0.4	321
8	Canada	133	0.3	463
9	United Kingdom	106	0.2	315
10	Iran	100	0.2	220
11	Russia	86	0.2	191
12	France	80	0.2	110
13	Germany	79	0.2	247
14	Ireland	69	0.2	138
15	Italy	69	0.2	170
16	Turkey	55	0.1	55
17	Australia	51	0.1	244
18	Hungary	39	0.1	34
19	Indonesia	34	0.1	74
20	Belarus	32	0.1	70
	Total	42,590		45,423

panels, insulation panels, wall panels, fireproof material to leather and clothes.

Consistent with an increasing number of patent documents and scientific publications since 2007, the field of mycelium-based materials is currently under rapid development (Cerimi et al. 2019; Sydor et al. 2021). Sydor et al. (2021) identified 153 patent applications and 55 patents granted until April 2021, demonstrating the immense attraction for commercialization. US-based companies, such as Ecovative (Ecovative Design LLC 2023) and MycoWorks (MycoWorks 2023), pioneer companies focusing on dehydrated mycelium materials for packaging, insulation, fire protection or the production of a fungal leather alternative, respectively, have become key players on the market during the last fifteen years. Another up-coming label based in the US and Netherlands is Bolt Threads. In 2018, nine years after their foundation, they have developed the sustainable leather-like material Mylo™ attracting the attention of serious partners like Adidas, Kering, Lululemon or Stella McCartney. Furthermore, the success of European startups indicates the surging demand on the market for economical and eco-friendly sustainable technologies (Jones et al. 2020; Bitting et al. 2022). Striking examples are MycoTex (NEFFA 2023), the winner in 2018 of the Global Change Award created by the H&M foundation, or Grown.Bio (GrownBio

2022), featured as the most innovative SME (small and medium-sized enterprise) of the Netherlands in 2021.

Industries like packaging, plastic, and fashion have shown great interest in eco-friendly products (Research and Markets 2022c). This shift goes hand in hand with an increasing economic impact of mycelium-based products. According to market analyses, the global market for mycelium materials, including food and beverage products, is valued at USD 2.48 billion in 2020 (Research and Markets 2022c). A year later, the global mycelium market has increased to **USD 2.95 billion** with North America having the highest share of the mycelium market in 2021, followed by Europe and the Asia Pacific (InsightAce Analytic 2021). Driven by an ongoing trend to a bio-based circular economy around the world, governmental regulations, such as the styrofoam and polystyrene bans in various nations, increasing R&D investments and further application opportunities (e.g. mycorrhizal fungal concentrate for organic farming and tree nurseries, health-conscious products), the demand for eco-friendly mycelium-based products is continuously increasing. In 2030, the mycelium market is expected to reach USD 5.49 billion, with a CAGR of 7.3% during a forecasted period of 2022–2030 (InsightAce Analytic 2021). One of the key factors in hampering the market growth is the conversion from a small-scale of commercial products into an industrial-size scale. Limiting factors can be depicted by

the lack of infrastructure facilities and challenging scale-up processes. Applicable solutions are needed for deficiencies in scalability (e.g. long cycles of production, risk of contamination, complex multi-step manufacturing processes), reproducibility (e.g. missing levels of standardization), and automation (InsightAce Analytic 2021; Bitting et al. 2022). The monopoly of mycelium-related patents in the industry together with a disconnect between industry and academia is further strengthening this dilemma and prevent the distribution of knowledge and progress (Bitting et al. 2022).

Recreational fungal foraging

Recreational mushroom picking is another service provided by forest ecosystems in which people can also sell the fungi they collected at the local market (Martínez de Aragón et al. 2011; Cutler II et al. 2021). Mushroom pickers benefited both from the recreational experience and the product collected (Martínez de Aragón et al. 2011; Debnath et al. 2019). Public demand for recreational mushroom picking has increased in the past decades in the forest ecosystems, affecting forest land owners (Frutos et al. 2009). Many people pick mushrooms for recreational purposes and not for economic reasons; thus, environmental valuation methods allow the benefits of this recreation activity to be assessed. The most common method used to measure the monetary value of recreational mushroom picking is the travel cost method. This method is used to approximate the difference between the willingness to pay for the good of the consumer (demand function) and the actual spending (price) (Bockstael 2007).

Mushroom picking is an upward leisure activity in European forests (Schulp et al. 2014; Marini Govigli et al. 2019). Along with the economic growth of European countries, fungal picking has transformed its profile to that of a primarily recreational activity (Kotowski 2016). Most studies of mushroom picking activities are done in Spain (Table 4). It shows that Europeans enjoy mushroom foraging activities as leisure activities. For instance, in Spain many studies were conducted in forested areas using the travel cost method to estimate the amount paid for mushroom hunting, which ranged from 10 to 60 €/trip (10.5–63 USD/trip) (Frutos et al. 2009). The estimated recreational surplus in Catalonia, Spain was €39 (40.9 USD) per journey (Martínez de Aragón et al. 2011). The average recreational surplus in Spain is USD 33.0 per trip, with 23% of the adult population experiencing mushroom picking at least once a year (Martínez de Aragón et al. 2011). Spain has around 38.6 million adults (World Population Review 2022), which, multiplied to 0.23 is equal to 8.9 million adults, which are experiencing mushroom picking once a year. Each of these 8.9 million adults has a recreational surplus of USD 33.0 per trip, thus

the total recreational surplus is **USD 293 million** per year in Spain.

Other potential biotechnological applications of fungi

With filamentous fungi and yeasts being veritable cellular factories, they are major contributors to biotechnology, providing virtuous outlets for the protection of the environment and health by breaking down various industrial waste.

Biofuel

The spent mushroom substrate (SMS) is composed of fungal mycelia, extracellular enzymes, and unused lignocellulosic substrates. Production of industrially important hydrolytic enzymes by fungi has various economic applications, which can be an inexpensive alternative energy source (Grujić et al. 2015). SMS is suitable in a fermentative process with easy and low-energy sugar conversion through various hydrolysis methods, such as that leading to the production of economically important bioethanol (Antunes et al. 2020). SMS use could be a strategy to improve yield and reduce the cost of the production process (Corrêa et al. 2016). It could also be incorporated as a substrate for biogas generation (Pérez-Chávez et al. 2019).

Biofuels produced from renewable lignocellulosic biomass are projected to meet increasing energy demands without increasing greenhouse gas emissions as do fossil fuels (Saini and Sharma 2021), with butanol as the most promising for its high energy density (Cascone 2008). The spent mushroom substrate was also used as a potential substrate for butanol production using biodiesel removal in situ (Antunes et al. 2020). The old macrofungal-growing substrates harbor bacteria that can convert cellulose to biobutanol. Biobutanol is an alternative fuel that can directly replace gasoline in engines (Zhen et al. 2020). However, traditional methods in producing biofuels require a lot of energy and water. They are costly and require complicated pretreatments (Saini and Sharma 2021).

The global biofuels market was valued at nearly **USD 110 billion** in 2021 and is projected to continue to increase until 2030 with a forecast value of USD 201.2 billion (Statista 2022a).

Bioremediation

Environmental pollutions, especially synthetic organic compounds such as xenobiotics, have become a major problem worldwide. These compounds are recalcitrant and many microorganisms cannot degrade them (Embrandiri et al. 2016). Fungi can act as remediation tools due to their ability to enzymatically convert different type of pollutants into

less complex components, even including a wide range of xenobiotics (Kulshreshtha et al. 2014; Zhen et al. 2022). White-rot fungi are able to produce extracellular ligninolytic enzymes consisting of three groups: lignin peroxidase (LiP), manganese-dependent peroxidases (MnP) and laccases, which play important roles in the transformation and mineralization of organic contaminants (Wang et al. 2009; Bulkan et al. 2020).

In agriculture, contaminated soil with heavy metals has negative effects on crop quality and yield (Kumar et al. 2018). There are three general effective strategies involving fungi to address contaminated soil: biodegradation, bioconversion, and biosorption. Toxicity reduction by fungi depends on their ability to produce different enzymes to degrade pollutants. Fungi can degrade pollutants and transform them into simpler mineral constituents (Chugh et al. 2022). They can also convert waste and other pollutants into more useful forms. Fungi can also absorb heavy metals from substrates without production of secondary pollution produced, which could be a very effective method to reclaim polluted land (Prenafeta-Boldú et al. 2019). Fungi have the potential to accumulate heavy metals in their network of hyphae and convert them into their mineral constituents. Fungi can also degrade recalcitrant hydrocarbon contaminants. They can turn hydrocarbon pollutants present in the environment into an energy source, increasing the selection of the hydrocarbon-metabolizing fungal population (Prenafeta-Boldú et al. 2019). Some fungal species are effective degraders of high molecular weight polycyclic aromatic hydrocarbons (Al Farraj et al. 2020). Some genera of fungi used for degradation of polycyclic aromatic hydrocarbons and polycyclic aromatic hydrocarbons are *Agaricus* (Li et al. 2010), *Armillaria* (Hadibarata and Kristanti 2013), *Ganoderma* (Agrawal et al. 2018), *Marasmiellus* (Vieira et al. 2018), *Phanerochaete* (Wang et al. 2009), *Pleurotus* (Li et al. 2010; Hadibarata and Teh 2014), and *Trametes* (as *Coriolus*) (Jang et al. 2009). However, these projects are all at experimental stages. Among the different potential fungi, only *Phanerochaete chrysosporium* has been explored in large-scale biodegradation programs. Although global bioremediation has a large market value of **USD 12.38 billion** in 2021 (Grand View Research 2023c), contribution of fungi is yet to be determined.

Monetary valuation of fungi

Fungi have been utilized in different industries (Hyde et al. 2019). Fungal products and services have a great impact in the global economy. High-value products biosynthesized

by fungi can generate millions of dollars, which can help the country's economy. The valuation of fungi at the global level is exceptionally difficult, and, in this account, we do not claim to accurately estimate this. However, we have used our knowledge and the available literature to derive a starting figure that can be used and built upon openly. Without such a figure, the value of fungi will not be recognized and there will be no monetary value for these amazing organisms, extrapolate decisions from stakeholders to further protect and conserve the mycobiota. This is our first attempt to give monetary value to the contributions of fungi in global economy that focus on marketed products and services. Our evaluation is carried out to derive an internationally accepted figure. The most significant fungal products and services with great economic value are listed in Table 9. Fungi can be primary source in making products such as medicines and pharmaceuticals, TCM, functional food and nutraceuticals, pigments, and others or they can be involved in the production process especially in fermentation. For instance, production of fermented food and beverages such as baked goods, cheese, alcoholic beverages (e.g. beer, wine, whiskey) and non-alcoholic beverages (e.g. chocolate and coffee) with high market value will not be possible without the activity of yeast and filamentous fungi in fermentation in combination with bacteria. Therefore, involvement of fungi in this important process is also considered as contribution of fungi to global economy.

Our attempt to give monetary value to the contributions of fungi includes the definite value of fungi itself (e.g. wild and cultivated mushrooms), product value from the products made from fungi or through the involvement in the production process, and traded value from fungal services such as carbon stock and recreational foraging. Table 10 is the summation of the market values of fungal products and services that are economically of great importance. The contribution of fungi to the global market through fungal products and services is estimated to be **USD 54.59 trillion**.

The traded value of fungal services accounted for 95.90% of the total estimated value of fungi, or USD 52.33 trillion (Table 11). However, because this is just a monetary estimate of services rendered by fungi and has not been in the actual market, it can only be considered potential market value and not actual market value that affect the global Gross Domestic Product (GDP). The actual market value is made up of definite and product values that are already considered market revenue, totaling **USD 2.24 trillion**. The **GDP is USD 88.44 trillion** (Statista 2022b), thus fungal products constitute for **2.53% of the GDP**.

Table 9 List of economically important products and services from fungi, their contribution in production and type of market value

	Products and services from fungi	Contributions of fungi	Type market value
i)	Value of carbon stocks being traded from forests	Involved in the process	Traded value
ii)	Industrial uses of fungi		
	<i>Medicines and pharmaceuticals</i>		
1	Antibacterials		
	Penicillins	Primary source material	Product value
	Cephalosporin	Primary source material	Product value
	Fusidic acid	Primary source material	Product value
	Pleuromutilin -no value	Primary source material	Product value
2	Antimycotics		
	Echinocandins	Primary source material	Product value
	Enfumafungin	Primary source material	Product value
	Griseofulvin -no value	Primary source material	Product value
	Micafungin	Primary source material	Product value
3	Cardiovascular drugs		
	Statins	Primary source material	Product value
4	Immunosuppressive and immunomodulatory agents		
	Cyclosporin	Primary source material	Product value
	Fingolimod	Primary source material	Product value
	Mycophenolic acid (mycophenolate mofetil)	Primary source material	Product value
	Mizoribine	Primary source material	Product value
5	Nematicidals		
	Emodepside	Primary source material	Product value
6	Traditional Chinese Medicines		
	<i>Ophiocordyceps/Cordyceps</i>	Primary source material	Definite value
	<i>Ganoderma</i>	Primary source material	Definite value
	<i>Food and beverages</i>		
7	Functional food and nutraceuticals		
	Functional mushrooms	Primary source material	Definite value
8	Fermented food		
	Baked goods	Involved in production process	Product value
	Cheese	Involved in production process	Product value
9	Alcoholic beverages and spirits		
	Beer	Involved in production process	Product value
	Wine	Involved in production process	Product value
	Vodka	Involved in production process	Product value
	Gin	Involved in production process	Product value
	Tequila	Involved in production process	Product value
	Rum	Involved in production process	Product value
	Whiskey	Involved in production process	Product value
	Brandy	Involved in production process	Product value
10	Non-alcoholic fermented beverages		
	Chocolate	Involved in production process	Product value
	Coffee	Involved in production process	Product value
	Vinegar	Involved in production process	Product value
	Kombucha		
11	Fungal food additives: Organic acids		
	Citric acid	Involved in production process	Product value
	Fumaric acid	Involved in production process	Product value
	Gluconic acid	Involved in production process	Product value
	Itaconic acid	Involved in production process	Product value

Table 9 (continued)

	Products and services from fungi	Contributions of fungi	Type market value
	Lactic acid	Involved in production process	Product value
12	Fungi based proteins	Primary source material	Product value
13	Food enhancers		
	Soy sauce	Involved in production process	Product value
	Miso	Involved in production process	Product value
	Indonesian tempeh	Involved in production process	Product value
14	Food colorants/pigments		
	Astaxanthin	Primary source material	Product value
	Carotenoids	Primary source material	Product value
	<i>Monascus</i> pigments- no values yet	Primary source material	Product value
Commodities			
15	Agarwood		
	Agarwood chips	Involved in production process	Product value
	Agarwood oil	Involved in production process	Product value
16	Cosmetics		
	β -glucan	Primary source material	Product value
	Ergothioneine	Primary source material	Product value
	Kojic acid	Primary source material	Product value
17	Mycopesticides	Primary source material	Product value
	Strobilurin fungicide	Primary source material	Product value
18	Mycorrhiza-based biofertilizer	Primary source material	Product value
19	Fungal Enzymes		
	Laccase	Primary source material	Product value
	Invertase	Primary source material	Product value
	Amylase	Primary source material	Product value
	Protease	Primary source material	Product value
	Cellulases	Primary source material	Product value
	Pectinase	Primary source material	Product value
	Lipase	Primary source material	Product value
	Galactosidase	Primary source material	Product value
	Lactase	Primary source material	Product value
iii)	Value of wild and cultivated mushrooms being traded for food	Primary source material	Definite value
iv)	Emerging myco-based material industry	Primary source material	Product value
v)	Recreational fungal foraging	Involved in the process	Traded value

Future perspectives/implication to policy makers

Fungi are being exploited in the forest and other ecosystems for their food production, medicinal and pharmaceutical applications; hence, they represent a major economic source worldwide (Zotti et al. 2013). Fungal products are sustainable, which could also create a biobased circular economy, which aims to eliminate waste and transform the production and use of goods (Valavanidis 2018). The circular economy is estimated to offer up to USD 4.5 trillion in global economic benefits by 2030 (World Economic Forum 2022).

Some services offered by fungi are eminent, especially those with direct effect to humans such as food source, medicines, commodities, and cultural services. These services also have available market values and thus are quantifiable. However, ecosystem services provided by fungi and their role in ecosystem functions, are not recognized, especially those which belong to supporting and regulating services. These services are not generally considered within policy appraisal at present. They represent an area where a greater and more methodical focus would be very valuable. To recognize and improve their strategic importance, several conservation strategies are necessary (Zotti et al. 2013). Institutional environment moves towards regulating mycological resources, with estimating

Table 10 Market value of fungal products and services by category

Category	Group	Market value (USD billion)
(i) Value of carbon stocks being traded from forests		52,333.00
(ii) Industrial uses of fungi	Medicines and pharmaceuticals	47.42
	Food and beverages	2141.18
	Commodities	21.53
(iii) Value of wild and cultivated mushrooms being traded for food		28.16
(iv) Emerging myco-based material industry		2.95
(v) Recreational fungal foraging (Spain)		0.29
	Total	54,574.53

Table 11 Monetary value by type of market value

Type market value	Monetary value (USD billion)	Percentage
Definite value	45.10	0.08
Product value	2,196.14	4.02
Traded value	52,333.29	95.90
	54,574.53	

the value of this ecosystem service becoming a key tool for policy-makers and rural entrepreneurs (Marini Govigli et al. 2019).

A formal ecosystem assessment could provide the necessary information on the larger suite of ecosystem services contributed by fungi in the ecosystems and for beneficiaries to value these services. Smaller and more specific studies should also be performed for each service to capture the true values of fungi. The under-representation of fungal ecosystem services and functions in ecosystem assessments potentially limits the information available for decision-making about regional and global activities that impact forest ecosystems. The concept of ecosystem services was developed as part of the Millennium Ecosystem Assessment project in the early 2000s to analyze and quantify the true and total value of an ecosystem. Valuation of fungi is essential, as it will contribute toward better decision making in policy appraisals considering the full costs and benefits to the natural environment and human wellbeing, while providing policy development with new insights (DEFRA 2006). Monetary valuation, or monetarization, is used in translating measures of social and biophysical impacts into monetary units so that they can be compared against each other and against the costs and benefits already expressed in monetary units (Marquina et al. 2022). This is very helpful in assessing the global value of fungi. Humans tend to give value to expensive things because they enjoy the pleasure of price. Studies show that people tend to value expensive

items over their cheaper or free counterparts (Schmidt et al. 2017). The global value of fungi in ecosystems is missing or is not recognized since we get them for free. No studies have been conducted yet to give the overall value of fungi. Under-representation of the services rendered by fungi can lead to an underestimation of the global significance of the contribution of fungi in forest ecosystems. Moreover, many potential applications of fungi in biotechnology and industry have not been fully explored. Fungi have the potential to generate money, especially in their role as a bioremediator, mycoinsecticide, mycofertilizer, and biofuel. Quantifying ecosystem services provided by fungi and giving them a monetary price can help appraise their value to be taken into account in policy making and development. Formal and comprehensive ecosystem assessment would require considerable investment but could substantially improve coordination between management bodies, such as legislators and beneficiaries that could help in the conservation of fungal resources both on the regional and global scale.

Conclusion

In this study, using data from a number of industries, we estimated the global market value of fungi at **USD 54.57 trillion**. We acknowledge this is the first attempt to evaluate fungi in monetary terms, and that future assessments building on our work will perhaps be able to improve on the accuracy of this value. We have had to assume the value of fungi for some key industries, especially the food and beverages industries, as the total value of the products produced in those industries was based on the assumption that the final products would not be able to be produced, without the contribution of fungi.

This study emphasizes that fungi have an enormous market value, having an undeniable impact on the global economy. Monetary valuation of global products and services by fungi as well as their roles in ecosystem functioning is crucial to drive policy regarding the conservation and

industrialization of this natural resource. With the rapid advancement of new technologies and related industries, the market presence of fungi will only increase, and thus fungi are prone to unsuitable exploitation if not properly monitored and managed in the future. The huge financial value of fungi adds weight to the argument that landscapes need to be conserved in order to conserve the natural resources found within. We have only discovered a small percentage of the fungi found in nature; thus, it is highly probable that there are untold billions of dollars' worth of fungal resources yet to be discovered, or lost if their habitats are destroyed.

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Data availability No data were generated for this study.

Declarations

Competing interests The authors declare no competing interests.

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