Received: 3 May 2024 | Revised: 26 July 2024 | Accepted: 28 August 2024

DOI: 10.1111/1750-3841.17390

Journal of Food Science WILEY

REVIEW ARTICLE

Concise Reviews and Hypotheses in Food Science

Fungi as biotechnological allies: Exploring contributions of edible and medicinal mushrooms

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Funding information
CIDET—Secretaría de Ciencia y Técnica de la Univ. Nacional de Misiones (Argentina), Grant/Award Number: 16/Q1557-TI; Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, Grant/Award Number: PICT2020-0652

Abstract

Edible and medicinal mushrooms possess excellent nutritional properties due to their incredible versatility in growing on different substrates and producing extracellular enzymes with a wide range of specificity. These features make them excellent candidates for various biotechnological applications. In this context, biotechnological applications using edible and medicinal mushrooms can focus on the bioprocessing of agro-industrial wastes, an economical and environmentally friendly strategy. This review, based on recent original research and scientific reviews, highlights the versatility and potential of mushrooms in terms of sustainability and efficiency. We emphasized the biotechnological applications of edible and medicinal mushrooms and their enzymes including food production with high nutraceutical value by enhancing the quality and flavor of food industry products. Other biotechnological applications addressed in this review were cosmeceutical and biomedical development using mushroom extracts with bioactive compounds; wood pulp pretreatment processes in the pulp and paper industry; bioethanol production; and bioremediation for decontaminating soils and polluted effluents. These applications explain how edible and medicinal mushrooms have gained significance in biotechnology over the years, opening new avenues for innovation. The current tendency to study edible and medicinal mushrooms has gained the attention of researchers because these are still less known organisms becoming an attractive and natural source of novel bioactive compounds that could be integrated into a circular model production.

KEYWORDS
bioactive compounds, bioprocessing, biotechnology, edible mushrooms, enzymes

1 | INTRODUCTION

Mushrooms are fungi whose fruiting body or reproductive structure, named sporoma, is large enough to be recognized by the naked eye and collected manually (Chang & Wasser, 2017; Itria et al., 2021).

Edible mushrooms are highly valued for their attractive aroma, texture, and flavor, making them popular in global culinary traditions (Chang & Wasser, 2017; Ghorai et al., 2009). Medicinal mushrooms are macrofungi used in extract or powder form to prevent, alleviate, or treat specific health conditions and maintain a balanced diet for

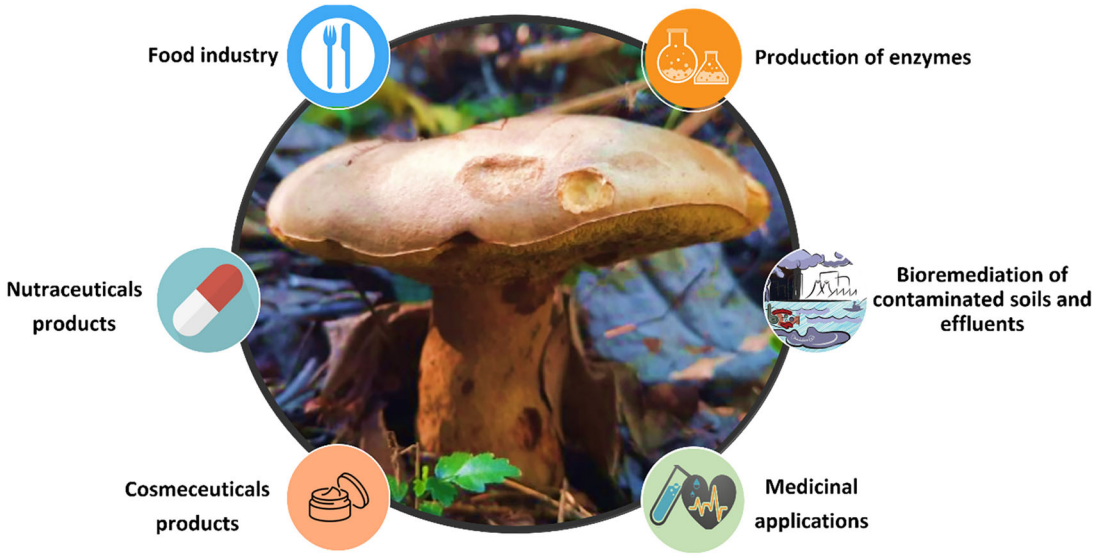

FIGURE 1 Use of edible and medicinal mushrooms in biotechnology.

optimal health (Gargano et al., 2017). Edible and medicinal mushrooms find extensive applications in various biotechnological fields.

Fungal biotechnology, a specialized area within biotechnology, harnesses mushrooms and metabolites to produce biodegradable products. This approach offers significant advantages by reducing energy consumption and minimizing waste generation during production processes (Roth et al., 2023; Yadav et al., 2019). Extensive compilations of literature exist on the biotechnological applications of filamentous fungi and mushrooms (Challa et al., 2019; Jouzani et al., 2020; Meyer et al., 2020; Nevalainen, 2020). However, there remains a need for enhanced literature compilations focused on edible and medicinal mushrooms in different biotechnological applications and their associated advantages (Badalyan & Zambonelli, 2023; Chang & Wasser, 2017; Petre, 2016; Rashidova et al., 2021; Sekan et al., 2019). Therefore, this review aims to consolidate recent research and contribute to understanding the biotechnological potential of edible and medicinal mushrooms (Figure 1). This review explores the versatility of different species across diverse biotechnological applications, with a primary emphasis on their contributions to the food industry. The biotechnology of edible and medicinal mushrooms represents a safe way to obtain nutritious foods, constituting a source of bioactive compounds with beneficial health properties that can be consumed safely. The use of edible and medicinal mushrooms or their enzymes for food biotechnology is crucial as it avoids the potential toxic effects that could arise from the use of fungi or chemicals that are not suitable for consumption. The initial section will discuss the lifestyle habits of edible and medicinal mushrooms, and the bioprocessing methods involving these organisms, aiming to improve the comprehension of their diverse biotechnological applications. Additionally, the review will briefly discuss other biotechnological uses, such as the utilization of bioactive compounds from edible and medicinal mushrooms in cosmeceutical products and in the medicinal field, the application of enzymes in biofuel production, their roles in the pulp and paper industry, and bioremediation. Furthermore, for better clarity, in this review, the term "edible mushrooms" will specifically refer to species primarily valued for culinary purposes, and "medicinal mushrooms" will denote species used for medicinal extracts or powders, even if they are not widely consumed as food.

2 | MUSHROOM LIFE HABITS AND ENZYMATIC FUNCTIONS

Mushrooms represent one of the most diversified groups of biological species, adapted to thrive in extreme environmental conditions worldwide (Coleine et al., 2022; Petre, 2016). Their diverse ecological and functional attributes are evident in the wide variety of forms and their physiological and biochemical properties (Sánchez et al., 2018). Edible and medicinal mushrooms can be categorized as mycorrhizal, saprophytic, or parasitic. Some mushrooms can even be initially parasitic and then adopt a saprophytic lifestyle such as *Armillaria mellea, Laetiporus sulphureus*, and *L. cincinnatus* (Díaz-Godínez & Téllez-Téllez, 2021). Mycorrhizal mushrooms form beneficial symbiotic associations with tree roots through their hyphae. Ectomycorrhizal genera have their sporocarps grow on the root surface; examples include *Russula, Lactarius*, and *Boletus*

(Reddy, 2015; Sharma, 2017). Saprophytic mushrooms grow on dead and decaying wood. Examples include *Lentinus edodes, Ganoderma lucidum, Agaricus bisporus*, and *Pleurotus sp*. Parasitic species grow on trees and can cause their death; examples include *A. mellea, Polyporus squamosus*, and *Hericium erinaceus* (Jones & Buttolph, 2012; Meena et al., 2020; Reddy, 2015).

Understanding the nutritional habits of edible and medicinal mushrooms enables better recognition of the required substrate types for their growth. It helps to define potential biotechnological applications because identifying optimal conditions contributes to optimizing and maximizing their cultivation and effectiveness yield for multiple purposes (Table 1).

Mushrooms' life habits and substrate greatly influence the production of enzymes and metabolites. For instance, the biological efficiency and the composition of the bioactive compounds vary during the cultivation of edible and medicinal mushrooms depending on the substrate, as will be developed in section 4.1.3.

Because saprophytic and parasitic mushrooms can act as wood decomposers through an enzyme battery (Janusz et al., 2017), it is not surprising that they have significant biotechnological applications related to the degradation of lignocellulosic biomass. Therefore, it is important to highlight that one approach to utilizing lignocellulosic biomass for biotechnological applications involves the bioprocessing of underutilized biomass from agricultural activity, named agro-industrial wastes because these residues contain proteins, starch, and lignocellulosic components (Yafetto, 2022). Lignocellulosic biomass comprises three primary fractions: cellulose, hemicellulose, and lignin. In addition to these components, lignocellulose presents pectins, extractives, and ash (Yousuf et al., 2020). Based on the ability to degrade lignocellulosic biomass by active enzymes, mushrooms are traditionally classified as white-rot fungi (WRF), brown-rot fungi (BRF), and soft-rot fungi (SRF) (Table 1) (Couturier et al., 2018; Kües, 2015).

During the bioprocessing of lignocellulosic biomass, WRF can degrade lignin and cellulose biopolymers, producing powerful extracellular enzymes (Bilal & Iqbal, 2020; Manavalan et al., 2014). In contrast, BRF can effectively depolymerize cellulose polymers into simple sugars but they can partially degrade lignin (Arantes & Goodell, 2014; Sánchez, 2009); hence, lignin is attacked and chemically modified into a brown oxidized and enzymes can access cellulose for oxidative depolymerization (Kijpornyongpan et al., 2022; Kües, 2015; Levasseur et al., 2014). On the other hand, SRF prefer polysaccharides; they can also remove methylated side chains (R–O–CH_3) and break aromatic rings but cannot completely degrade the lignin structure (Horwath, 2015). This restricted activity produces a softwood texture in environments with abundant moisture (Kameshwar & Qin, 2018; Sigoillot et al., 2012).

The WRF group is involved in the degradation of lignocellulosic biomass through various enzyme systems, some of which are also present in BRF. These enzyme systems are composed of enzyme consortia that are classified based on the type of substance they degrade and the mode of catalytic action. Some of these systems include the lignin-degrading enzyme system, cellulose-degrading enzyme system, hemicellulose-degrading enzyme system, and pectin-degrading enzyme system (Table 2) (Díaz-Godínez et al., 2016; Manavalan et al., 2014; Naghdi et al., 2018).

Lignocellulosic enzymes hold potential for various industrial biotechnological applications, including the food industry. Thus, a comprehensive understanding of the enzymes responsible for lignocellulosic biomass degradation is essential.

Laccase (Lac; EC 1.10.3.2) and peroxidases represent the ligninolytic enzyme system. Lac is copper-containing phenol oxidase that oxidizes phenolic compounds by catalyzing the one-electron subtraction of phenolic hydroxyl groups from phenolic lignin model compounds, such as vanillyl glycol, 4,6-di(t-butyl) guaiacol, and syringaldehyde, to form phenoxy radicals, which generally polymerize by radical coupling; the enzyme Lac facilitates a chemical reaction wherein the substrate undergoes oxidation through a single-electron mechanism (Cajthaml, 2015; Khatami et al., 2022). The main fungal peroxidases involved in the biodegradation of lignocellulose from organic and inorganic substrates are lignin peroxidases (LiPs; EC 1.11.1.14) containing a heme group, manganese peroxidases (MnPs; EC 1.11.1.13) and versatile peroxidases (VPs; EC 1.11.1.16) (Kües, 2015). LiP enzymes can oxidize various aromatic compounds, whereas MnP enzymes degrade phenolic compounds and almost exclusively oxidize Mn^{+2} to Mn^{+3}. Both are enzymes of the heme peroxidase system and require H_2O_2 as an electron acceptor to oxidize lignin and related compounds (Ruíz-Dueñas & Martínez, 2009). Moreover, VP enzymes are broad substrate enzymes capable of oxidizing phenolic and nonphenolic compounds and are highly valued in biotechnological processes, such as bioremediation (Deshmukh et al., 2016; Karigar & Rao, 2011).

For the conversion of cellulosic biomass to fermentable sugars, the synergistic action of cellulase enzymes is required (Bilal & Asgher, 2016). Among these, endoglucanases (EGs; EC 3.2.1.4) catalyze the random cleavage of internal bonds in the cellulose chain releasing cellobiose units and oligosaccharides of various lengths. Cellobiohydrolases (CBHs; EC 3.2.1.91) are monomeric proteins with low or absent glycosylation, and these enzymes cleave

TABLE 1 Biotechnological importance of some edible and medicinal mushroom species classified according to their ability to degrade wood and nutritional mode.

Group	Nutritional mode	Examples	Biotechnological importance	References
Lignicolous mushrooms				
White-rot fungi	Saprophytic	*Armillaria gallica*	Bioactive compounds	Sun et al., 2023
		Lentinula edodes	Bioremediation Production of enzymes Functional food Bioactive compounds and nutraceutical properties	Chen et al., 2022 Kumla et al., 2020 Chmelová et al., 2022 Dimopoulou et al., 2022 Gargano et al., 2017 Kumar et al., 2021 Nam et al., 2021
		Lentinus tigrinus	Production of enzymes	Chmelová et al., 2022
		Pleurotus eryngii	Production of enzymes Nutraceutical properties Bioactive compounds Functional food	Kumla et al., 2020 Chmelová et al., 2022 Gargano et al., 2017 Kumar et al., 2021 Otieno et al., 2021
		Pleurotus ostreatus	Bioremediation Production of enzymes Decolorizer Bioactive compounds and nutraceutical properties Functional food	Chen et al., 2022 Kumla et al., 2020 Chmelová et al., 2022 Eichlerová & Baldrian, 2020 Gargano et al., 2017 Kumar et al., 2021 Mkhize et al., 2022 Pilafidis et al., 2023 Otieno et al., 2021
		Pleurotus pulmonarius	Production of enzymes Nutraceutical properties Bioactive compounds	Chmelová et al., 2022 Gargano et al., 2017 Kumar et al., 2021
		Pleurotus sajor-cajú	Functional food Enzyme production and decolorizer	Otieno et al., 2021 Eichlerová & Baldrian 2020
		Trametes versicolor	Bioremediation Production of enzymes Decolorizer Bioactive compounds	Chen et al., 2022 Kumla et al., 2020 Chmelová et al., 2022 Eichlerová & Baldrian, 2020 Gargano et al., 2017 Pilafidis et al., 2023
		Volvariella volvacea	Nutraceutical properties Bioactive compounds	Gargano et al., 2017 Kumar et al., 2021
		Flammulina velutipes	Nutraceutical properties Bioactive compounds	Gargano et al., 2017 Kumar et al., 2021
	Parasitic/saprophytic[a]	*Armillaria mellea*	Bioactive compounds Functional food	Kumar et al., 2021 Erbiai et al., 2021 Ren et al., 2022
		Fomes fomentarius	Production of enzymes Decolorizer	Kumla et al., 2020 Chmelová et al., 2022 Ilić et al., 2022 Eichlerová & Baldrian, 2020
		Ganoderma lucidum	Bioremediation Production of enzymes Decolorizer Functional food Bioactive compounds	Chen et al., 2022 Kumla et al., 2020 Chmelová et al., 2022 Eichlerová & Baldrian, 2020 Dimopoulou et al., 2022 Gargano et al., 2017 Kumar et al., 2021

(Continues)

TABLE 1 (Continued)

Group	Nutritional mode	Examples	Biotechnological importance	References
		Hericium erinaceus	Functional food Bioactive compounds	Dimopoulou et al., 2022 Gargano et al., 2017 Kumar et al., 2021 Pilafidis et al., 2023
Brown-rot fungi	Parasitic	*Fistulina hepatica*	Nutraceutical properties Bioactive compounds	Gargano et al., 2017 Lee et al., 2020
		Fomitopsis pinicula	Biodegradation	Purnomo et al., 2020
		Laetiporus sulphureus	Nutraceutical properties	Gargano et al., 2017
Soft-rot fungi	Parasitic	*Armillaria ostoyae*[b]	Bioremediation Bioactive compounds	Champramary et al., 2023 Gargano et al., 2017 Wang et al., 2024
Nonlignicolous mushrooms				
	Saprophytic	*Agaricus arvensis*	Bioactive compounds	Gąsecka et al., 2017
		Agaricus bisporus	Functional food Bioactive compounds	Dimopoulou et al., 2022 Gargano et al., 2017 Gąsecka et al., 2017 Kumar et al., 2021
		Agaricus campestris	Functional food	Gupta et al., 2019
		Morchella elata	Functional food	Dimopoulou et al., 2022
		Morchella esculenta	Bioactive compounds	Kumar et al., 2021 Pilafidis et al., 2023
	Mycorrhizal	*Amanita caesarea*	Functional food	Dimopoulou et al., 2022
		Boletus edulis	Bioactive compounds Food	Kumar et al., 2021 Díaz-Godínez & Téllez-Téllez, 2021
		Lactarius deliciosus	Food	Dimopoulou et al., 2022
		Russula sp.	Nutraceutical properties Bioactive compounds	Gargano et al., 2017 Kumar et al., 2021
		Suillus brevipes	Food Tree growth-promoting	Pérez-Moreno et al., 2021
		Suillus granulatus	Nutraceutical properties	Gargano et al., 2017

[a]Parasitic/saprophytic: refers to mushrooms that can be initially parasitic and then adopt a saprophytic lifestyle.

[b]A recent study suggests that wood decay by *A. ostoyae* resembles more closely that of soft-rot fungi, as they exhibit a reduction in genes encoding ligninolytic enzymes (Sahú et al., 2021).

the cellulose chains at their terminal ends to release cellobiose. β-glucosidases (BGLs; EC 3.2.1.21) are monomeric, dimeric, or trimeric proteins capable of acting on cellobiose and releasing glucose molecules (Manavalan et al., 2014). The delignified cellulosic biomass-degrading system also involves copper-dependent lytic polysaccharide monooxygenase enzymes (LPMOs; AA9/EC 1.14.99.54) that depolymerize cellulose through an oxidative mechanism involving hydroxylation of cellulose at the C_1 or C_4 and cleaving the glycosidic bond (Beeson et al., 2015).

Xylanases are part of the hemicellulose-degrading xylanolytic enzyme system, which include endoxylanases (EXs, EC 3.2.1.8), β-xylosidases (BXLs, EC 3.2.1.37), α-glucuronidases (EC 3.2.1.131), α-L-arabinofuranosidase (EC 3.2.1.55), and acetyl-xylan esterase (EC 3.1.1.72) (Juturu & Wu, 2012; Manavalan et al., 2014). EXs and BXLs are the key enzymes responsible for the total hydrolysis of xylan (Burlacu et al., 2016; Díaz et al., 2019).

Due to pectin's heterogeneous and complex structure, its complete degradation includes the action of different enzymes. Among these enzymes, polygalacturonases (endo-polygalacturonase EC 3.2.1.15 and exo-polygalacturonase EC 3.2.1.67) degrade homogalacturonan and hydrolyze glycosidic bridges; depolymerase enzymes, pectate lyase (EC 4.2.2.2.2) and pectin lyase (EC 4.2.2.10) cleave α−1,4 bonds by a trans-elimination mechanism. The degradation of acetyl, methyl, and feruloyl residues is carried out by pectin-methylesterase (EC 3.1.1.11), pectin-acetylesterase (EC 3.1.1.1.6), and feruloyl esterase (EC 3.1.1.73), respectively (Manavalan et al., 2014).

TABLE 2 Different enzyme systems of edible and medicinal WRF for degrading lignocellulosic biomass according to the type of substance they degrade and their mode of catalytic action.

Enzymatic system	Enzyme types	Enzymes	Examples of edible and medicinal WRF	References
Lignin degrader	Hemeperoxidases	LiP[a]	*Agrocybe cylindracea* *Fistulina hepatica* *Grifola frondosa* *Lepista irina* *Pholiota nameko* *Trametes versicolor*	Manavalan et al., 2014
		MnP[a]	*Agaricus bernardii* *Agaricus bisporus* *Agaricus campestris* *Agrocybe cylindracea* *Fistulina hepatica* *Grifola frondosa* *Lentinus edodes* *Lentinus tigrinus* *Lentinus irina* *Pholiota nameko* *Pleurotus dryinus* *Pleurotus ostreatus* *Pleurotus pulmonarius* *Trametes versicolor*	Manavalan et al., 2014
		VPs[a]	*Pleurotus ostreatus* *Trametes versicolor*	Fernández-Fueyo et al., 2014 Carabajal et al., 2013
	Phenoloxidase	Lac[a]	*Agaricus bernardii* *Agaricus bisporus* *Agaricus campestris* *Lentinula edodes* *Lentinus tigrinus* *Pleurotus dryinus* *Pleurotus ostreatus* *Pleurotus pulmonarius* *Trametes versicolor*	Manavalan et al., 2014
	Monooxygenase	CYP450[a]	*Pleurotus ostreatus*	Golan-Rozen et al., 2011
Cellulose degrader	Cellulases	LPMOs-AA9[a]	*Pleurotus ostreatus* *Trametes versicolor* *Schizophyllum commune*	Bentil et al., 2018
		CDH[a]	*Agaricus bisporus*	Manavalan et al., 2014
		EGs[b]	*Agaricus arvensis* *Auricularia polytricha* *Lentinula edodes* *Lentinus tigrinus* *Pleurotus dryinus* *Pleurotus ostreatus* *Pleurotus pulmonarius*	Manavalan et al., 2014
		CBHs[b]	*Agaricus arvensis* *Auricularia polytricha* *Lentinula edodes* *Lentinus tigrinus* *Pleurotus ostreatus* *Pleurotus pulmonarius*	Manavalan et al., 2014

(Continues)

TABLE 2 (Continued)

Enzymatic system	Enzyme types	Enzymes	Examples of edible and medicinal WRF	References
		BGLs[b]	*Agaricus arvensis* *Auricularia polytricha* *Lentinula edodes* *Lentinus tigrinus* *Pleurotus ostreatus*	Manavalan et al., 2014
Hemicellulose degrader	Xylanases	Endoxylanase[b]	*Auricularia polytricha* *Lentinula edodes* *Lentinus. tigrinus* *Pleurotus dryinus* *Pleurotus ostreatus* *Trametes versicolor*	Manavalan et al., 2014
		β-Xylosidase[b]		
		α-Glucuronidase[b]		
		α-L-Arabinofuranosidase[b]		
		Acetylxylan esterase[b]		
Pectin degrader	Pectinases	Endo-polygalacturonase[b]	*Pycnoporus sp.* *Pleurotus djamor var. roseus* *Lentinula boryana* *Lentinus sp.* *Schizophyllum commune*	Díaz-Godínez et al., 2016 Manavalan et al., 2014
		Exo-polygalacturonase[b]		
		Pectate lyase[c]		
		Pectin lyase[c]		
		Pectin methyl esterase[c]		
		Pectin acetyl esterase[c]		
		Feruloyl esterase[c]		

Abbreviations: LiP, lignin peroxidases; MnP, manganese peroxidase; VPs, versatile peroxidases; Lac, laccases; CYP450, cytochrome P450; LPMOs-AA9, lytic polysaccharide monooxygenases; CDH, cellobiose dehydrogenase; EGs, endoglucanases; CBHs, cellobiohydrolases; BGLs, glycosidases or β-glucosidases.
Enzyme groups according to their mode of action: [a]Oxidoreductases; [b]Hydrolases; [c]Lyases.

In addition, mushrooms possess enzymatic mechanisms to degrade recalcitrant organic compounds, the xenome, responsible for the detection, transport, and metabolism of xenobiotics (Aranda, 2015; Edwards et al., 2005; Morel et al., 2013). Mushrooms have to handle toxic compounds resulting from the degradation of organic matter and the secondary metabolism of antagonistic organisms and human activities, particularly mushrooms that interact with wood. These mushrooms can degrade recalcitrant lignin and cope with the complex compounds synthesized by plant species (Morel et al., 2013). The detoxification pathways of the xenome are constituted by multigenic families of intracellular cytochrome P450 monooxygenases (EC 1.14.14.1). These enzymes are intracellular hemothiolate-containing oxidoreductases that act on a wide range of substrates in a stereoselective and regioselective manner under O_2 consumption. These enzymes are activated by reduced heme iron and usually add a molecular oxygen atom to a substrate by a hydroxylation reaction (Kües, 2015). However, other reactions such as epoxidation, alcohol and aldehyde oxidation, oxidative dehalogenation, and oxidative cleavage of C–C bridges, among others, can also occur (Sakaki, 2012).

There are also enzymes not related to the hydrolysis of lignocellulosic biomass, but still of biotechnological importance, for example, amylolytic and proteolytic enzymes. Amylases are key enzymes in the beer and bakery industries. These enzymes have also been applied in the textile, paper, chemical, pharmaceutical, and biofuel industries (Paludo et al., 2023). Amylases are hydrolytic enzymes belonging to glycoside hydrolase family 13 (GH-13) that can hydrolyze glycosidic bonds in starch molecules. Depending on the hydrolysis site, at the reducing end or within the starch molecule, they are

classified as exo-amylases and endo-amylases, respectively. Among mushrooms amylases, the α-amylase subtype (EC 3.2.1.1), known as α−1,4-glucan-4-glucanohydrolase, is a metalloenzyme that uses calcium as a cofactor. It is an endo-amylase that cleaves α–d-(1,4) glycosidic bonds. The α-amylase has a three-dimensional structure that helps it bind to the substrate, conferring high specificity (Farooq et al., 2021). In addition to amylases, proteases are another important group of enzymes with diverse biotechnological applications. Proteases can be classified into extracellular and intracellular proteases; the extracellular ones are responsible for hydrolyzing large proteins into peptides or amino acids then absorbed by the cells, whereas the intracellular proteases regulate metabolism. The extracellular proteases are particularly valuable for industrial applications such as pharmaceutical, leather, detergent, and food industries to make wine and beer or improve wheat gluten properties (Naeem et al., 2022; Solanki et al., 2021). Furthermore, some proteases from mushrooms, such as the fibrinolytic enzymes, are of interest in medical research for their role in the degradation of fibrin in blood clots (Altaf et al., 2021; Krishnamurthy et al., 2018).

As has been described/discussed, mushrooms can produce a wide variety of enzymes with different functions, which makes them an object of interest for multiple biotechnological applications, which will be addressed in the following sections.

3 | MUSHROOM BIOPROCESSING STRATEGIES

In biotechnology, obtaining desired products from mushrooms requires using bioprocessing strategies. Bioprocessing involves using living organisms or their components to convert solid or liquid materials into valuable products (Ashok et al., 2017). Bioprocessing strategies often utilize lignocellulosic biomass as a substrate, resulting in the production of monomeric sugars that can be fermented to obtain secondary products (Tsegaye et al., 2019; Usmani et al., 2021). The most common substrate for bioprocessing is food or agro-industrial waste.

According to the physical state of the substrate used, there are two bioprocessing types: submerged-state and solid-state bioprocessing. In submerged-state bioprocessing, the concentration of water and solid substrate is maintained at least at an equal level; thus, mushrooms thrive in liquid growth media enriched with vital nutrients (Arango & Nieto, 2012; Dey et al., 2016). This kind of bioprocessing is the most used for industrial applications due to the advantages over solid-state bioprocessing: It is simple, and several variables can be controlled, such as pH, culture medium, carbon source, nitrogen source, temperature, and agitation; and the final product is easy to recover. The organisms grow on the surface under static conditions; filamentous fungi can form small mycelial spheres named "pellets" when they grow under agitation. However, this bioprocessing sometimes becomes a problem because the viscosity of the broth due to the mycelium development limits the transfer between oxygen and fungal biomass (Arango & Nieto, 2012; Liu & Kokare, 2017).

In contrast to submerged-state bioprocessing, solid-state bioprocessing involves the growth of mushrooms on a solid substrate with a low percentage of moisture, sufficient to support fungal growth and metabolism. This bioprocessing is suitable for enzyme production using natural substrates, such as agricultural residues, because these substrates mimic the natural conditions where mushrooms grow. In addition, solid-state bioprocessing has four significant advantages over submerged-state bioprocessing: high volumetric productivity, high product concentration, low effluent generation, and simple fermentation equipment. However, it has been reported that the solid-state bioprocessing technique can use up to 20%–30% substrate, in contrast to the maximum 5% used in submerged-state bioprocessing; this leads to a major required space for production (Liu & Kokare, 2017). Table 3 summarizes the advantages and disadvantages of submerged-state and solid-state bioprocessing, providing a detailed comparison of characteristics such as growth medium, control of variables, productivity, effluent generation, substrate requirements, and preferred applications of each method.

Cultivation of edible and medicinal mushrooms in solid-state bioprocessing can convert various lignocellulosic wastes into high-value-added products such as bioactive compounds (e.g., enzymes, polysaccharides) and animal feeds (Economou et al., 2017; Koutrotsios et al., 2016; Mandeel et al., 2005; Philippoussis, 2009; Philippoussis et al., 2001). This type of culture can also present disadvantages such as low O_2 and CO_2 transfer rate, heat removal, and bacterial contamination; it is also a slow process and very few organisms are suitable due to its low humidity; monitoring and scaling up can be challenging. However, industries such as the pharmaceutical industry prefer this type of bioprocessing over submerged-state bioprocessing (Arango & Nieto, 2012).

4 | BIOTECHNOLOGICAL APPLICATIONS IN THE FOOD INDUSTRY OF EDIBLE AND MEDICINAL MUSHROOMS

Edible mushrooms are widely used for their culinary uses, providing flavor, texture, and nutritional value to numerous dishes. On the other hand, medicinal mushrooms

TABLE 3 Comparison of submerged-state and solid-state bioprocessing properties.

Properties	Submerged-state bioprocessing	References	Solid-state bioprocessing	References
Preferred application	Enzyme production at industrial scale Production of bioactive compounds of pharmacological and food interest	Hemansi et al., 2019 Arango & Nieto, 2012	Enzyme production by utilizing agro-industrial wastes Production of bioactive compounds and animal feeds Production of food and beverages	Behera & Ray, 2016 Koutrotsios et al., 2016 Economou et al., 2017
Growth medium	Liquid enriched with essential nutrients	Dey et al., 2016	Solid substrates with low moisture content. Agro-industrial wastes or agricultural residues	Hemansi et al., 2019 Liu & Kokare et al., 2017
Variables	pH, temperature, agitation, C and N sources are easily controllable	Arango & Nieto, 2012 Liu & Kokare, 2017	pH: the use of urea instead of ammonium salts is suggested Temperature: It is a critical factor that requires specific strategies for its management such as forced ventilation. Moisture: Low Aeration: Air flow is the main means for heat removal Agitation: a critical parameter that must be carefully controlled as it has positive and negative effects that must be balanced	Chilakamarry et al., 2021
Productivity	Lower volumetric productivity and product concentration	Hemansi et al., 2019	High volumetric productivity and concentration	Liu & Kokare, 2017
Advantages	Easy to handle and monitor Easy dilution of nutrients and O_2 Efficient heat and mass transfer management	Hemansi et al., 2019	Efficient fermentation Stable product Easy recovery Economic Low effluent generation	Behera & Ray, 2016 Hemansi et al., 2019 Liu & Kokare, 2017
Disadvantages	Viscosity limits the transfer of O_2 to the fungal biomass. Higher generation of liquid effluents High costs	Arango & Nieto, 2012 Liu & Kokare, 2017 Hemansi et al., 2019	Low O_2–CO_2 transfer Low heat removal Bacterial contamination Slow process Difficult monitoring and scaling	Arango & Nieto, 2012 Hemansi et al., 2019

are extensively used for their beneficial health properties. In this section, we will examine in detail how and why these edible and medicinal mushrooms are of great interest and relevance for various biotechnological applications, exploring how they can be utilized as foods with high nutritional value and their potential uses in the food industry.

4.1 | Production of mushrooms as high nutritional value foods

The most cultivated edible mushrooms globally encompass a wide variety of genera. The most cultivated genera constitute approximately 85% of the global supply, where it is highlighted that Shiitake (*L. edodes*) represents 22%, followed by Oyster mushrooms (*Pleurotus sp.*) with 19%, Wood ear mushrooms (*Auricularia sp.*) with 17%, Champignons and Portobellos (*A. bisporus* and *Agaricus brunnescens*) with 15%, and Enoki (*Flammulina sp.*) with 11% (Figure 2). The cultivation of edible mushrooms represents the main component of the global mushroom industry, with an estimated value of approximately US$34 billion (Anusiya et al., 2021; Grimm & Wösten, 2018; Royse et al., 2017). Among *Pleurotus* species, some are particularly popular in the industry, such as *P. citrinopileatus, P. djamor, P. eryngii, P. florida, P. ostreatus*, and *P. pulmonarius* (Bellettini et al., 2019; Krakowska et al., 2020).

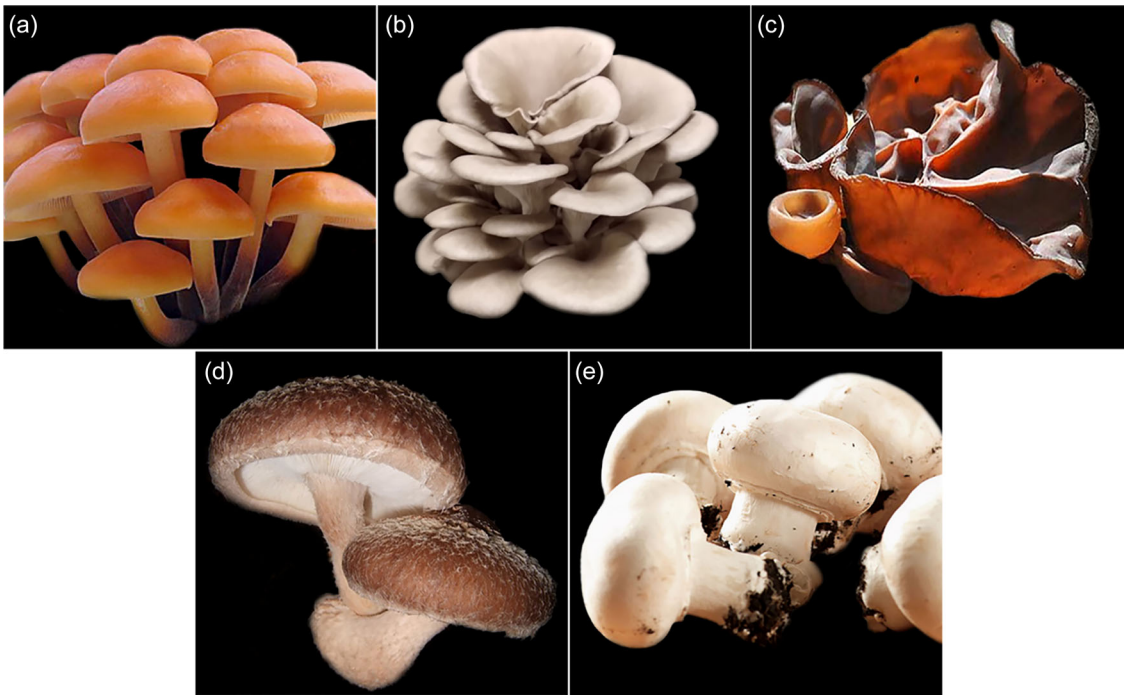

FIGURE 2 Edible mushrooms. (a) Enoki, (b) Oyster mushroom, (c) Juda's ear, (d) Shiitake, and (e) Champignon.

4.1.1 | Nutritional benefits of edible and medicinal mushrooms

Edible and medicinal mushrooms are attractive as food due to their high nutritional value because they are sources of dietary fiber; minerals such as iron, phosphorus, potassium, and selenium; fatty acids; and vitamins, in particular, vitamin D (Barros et al., 2008; Chang & Wasser, 2017; Ren et al., 2012) (Table 4). In addition, mushrooms have a higher protein content than most vegetables (Valverde et al., 2014), containing the nine essential amino acids required by humans, making them suitable for vegetarian diets (Kumar, 2015).

According to Chang and Wasser (2017), it is important to highlight several nutritional benefits of edible mushrooms: they contribute to low caloric intake, making them advantageous for weight loss; they possess a nonsignificant purine level that is beneficial for individuals with metabolic diseases; they exhibit a deficient level of glucose and high mannitol content, helpful for people with diabetes; and they present low sodium concentration deems them suitable for individuals with high blood pressure. Furthermore, edible and medicinal mushrooms have a significant water content ranging from 80% to 90%, with low caloric values, ranging between 50 and 70 kcal per 100 grams of fresh mushroom (Golianek & Mazurkiewicz-Zapałowicz, 2016; Łysakowska et al., 2023).

4.1.2 | Cultivation methods of edible and medicinal mushrooms

In biotechnology based on cultivating edible mushrooms for food, assessing the difficulty level of their cultivation is crucial. Mycorrhizal mushrooms are challenging to reproduce due to their specific requirement for establishing direct relationships with other organisms (Dias & de Brito, 2017; Díaz-Godínez & Téllez-Téllez, 2021). In contrast, saprophytic mushrooms are the most cultivable, because they can grow and produce sporoma in multiple substrates. The cultivation techniques are based on duplicating the natural process of lignocellulosic decomposition with similar organic matter and mineral composition (Albertó, 2017). When large-scale production is necessary, mushrooms are cultivated by solid-state bioprocessing or submerged-state bioprocessing (see section 3) when their bioactive compounds are required for food ingredients and agents for flavors (Lu et al., 2020).

Edible and medicinal mushrooms can be cultivated on wood-log or non-wood-log. The non-wood-log can be realized under non-aseptic conditions with composted substrates (*A. bisporus, Volvariella volvacea*) or sterilized conditions with pasteurized substrates (*L. edodes*, *Auricularia sp., Pleurotus sp., Schyzophylum commune*, among others) (Thuy & Suzuki, 2019). It is important to highlight that the disinfection of substrates for the culture of mush-

TABLE 4 Proximal composition of some of the mushrooms commonly consumed in Asia and Europe.

Mushrooms species	% Protein	% Fats	% Carbs	Crude fiber	Content of minerals %				References
					Ca	K	Na	P	
Lentinus sajor-caju	62.27%	2.3%	6.81%	7.02%	-	0.020	-	0.024	Han et al., 2016 Ao & Deb, 2019 Zahid et al., 2020
Lentinula edodes	43.81%	4.2%	38.44%	3.6%	0.002	0.304	0.009	0.112	Li et al., 2018 Ao & Deb, 2019 Ho et al., 2019
Schizophillum commune	24.42%	1.34%	5.31%	6.02%	0.00037	1.12	0.000073	0.79	Shin et al., 2007 Ao & Deb, 2019 Singh et al., 2021 Paul et al., 2022
Termitomyces heimii	60.53%	3.58%	22.74%	8.11%	21.08	-	0.15	0.32	Due et al., 2016 Ao & Deb, 2019 Rajoriya et al., 2023
Auricularia auricula-judae	56.92%	1.7%	18.67%	11.1%	1.6	1.2	0.8	-	Kadnikova et al., 2015 Ao & Deb, 2019 Bandara et al., 2019
Auricularia polytricha	42%	4.37%	16.03%	10.45%	0.016	0.043	0.009	0.014	Usha & Suguna, 2014 Ao & Deb, 2019 Bandara et al., 2019
Lentinus tigrinus	31.85%	4%	16.09%	7.09%	0.049	0.049	0.020	-	Dulay et al., 2014 Ao & Deb, 2019
Agaricus bisporus	21.3%	2.53%	38.3%	17.7%	0.107	2.92	0.028	1.23	Tsai et al., 2006 Ao & Deb, 2019 Krishnamoorthi et al., 2022
Amanita sp.	16.3%	4.7%	22.5%	7.4%	0.15	4.82	0.85	0.73	Greeshma et al., 2018 Ao & Deb, 2019

rooms is crucial to assess optimal growth and biological efficiency. For instance, González et al. (2022) have studied the critical role of substrate disinfection methods for *P. ostreatus* cultivation. The study concluded that thermal pasteurization, specifically scalding at 80°C for less than 30 min, is the optimal method for achieving higher yields.

The techniques to produce edible and medicinal mushrooms to obtain sporoma include bags with holes, open bags, jars, mycelium blocks, and bags with casing (Alberti et al., 2021). The bags with hole technique consist of mixing the spawn of mushrooms with the chosen substrate moistening and pasteurizing in sterile plastic bags with holes for aeration and incubation in a dark room. After colonizing the content bag for mycelium these were moved to the cropping room at an appropriate temperature for growth maintaining the moisture (Tesfay et al., 2020). For the open bag technique, the chosen substrate with adequate moisture is placed in polypropylene bags and sterilized, then inoculated with the corresponding spawn. After incubation at room temperature, bags are open and exposed to scattered light maintaining the moisture and aeration for the induction of sporoma formation (Hassan et al., 2010). The jar technique consists of inoculating the mushroom under aseptic and controlled conditions in a glass jar with the substrate selected. During the incubation, the temperature requires adjustment for the sporoma formation (Tie et al., 2017). On the other hand, the mycelium block technique consists of solid substrates in block form to cultivate the mushroom and is usually utilized for shiitake cultivation. However, this method requires special techniques for visualizing the mushroom growing because the blocks can be colonized by fungi such as *Penicillium* (Ogawa & Yashima, 2019). The technique of bags with casing can be used for the production of *A. bisporus*. It consists of utilizing a composted substrate for the mycelium colonizing followed by the addition of a special casing for the induction of growth of the sporoma. The casing is important because it constitutes physical support for the sporoma and maintains adequate moisture with sufficient aeration (Pardo-Giménez et al., 2017).

It should be noted that the chosen substrates for cultivating edible and medicinal mushrooms influence their biological efficiency and the production of enzymes and bioactive compounds. For example, when sunflower seed husks are used to cultivate saprophytic mushrooms such as *Grifola gargal* and *G. sordulenta*, their sporomas show high protein content and increased laccase activity (Díaz & Díaz-Godínez, 2022; Postemsky &Curvetto, 2015). Similarly, saprophytic medicinal mushrooms such as *Fomes fomentarius* and *S. commune* have demonstrated higher production of Lac and xylanases when grown on lignocellulosic biomass such as sunflower meal and brewer's spent grain, respectively, compared with substrates such as coffee residues and soybean meal (Ilić et al., 2022). Furthermore, Wanzenböck et al. (2017) reported that *P. ostreatus* and *P. eryngii* exhibit better quality when grown on wheat bran instead of other substrates. Additionally, the incorporation of wheat bran (18%–20%) into commonly used substrates such as sugarcane bagasse for cultivating *P. ostreatus* has led to extracts with higher levels of vitamin E, phenols, fatty acids, terpenoids, and greater reducing power. Variations in the amount of wheat bran (14%–20%) used as a supplement have also been found to improve the antimicrobial activity of *P. ostreatus* extracts against *Escherichia coli* (Mkhize et al., 2022).

Sustainable cultivation methods are essential for long-term mushroom availability for direct consumption and utilizing their bioactive compounds or enzymes for biotechnological applications. There are several factors involved in the culture methods for the production of mushrooms (type and proportion of substrates, temperature, humidity, type and percentage of supplements, pH, CO_2 concentration, etc.). However, these exceed the scope of the present review.

4.1.3 | Future foods

Edible mushrooms are increasingly recognized for their potential in biotechnological applications, particularly within the food industry. Although research on developing edible mushrooms as protein-based meat analogs is at the beginning compared with other plant-based protein alternatives, there are promising signs of progress.

Recently, the advantages of incorporating edible mushrooms as ingredients in meat products have started to be studied. Various studies have evaluated the effect of partially substituting meat with different mushroom species in these products. Guinard et al. (2016) have studied and evaluated the effect of replacing part of the beef with *A. bisporus* in taco mixtures and roast beef and its use as a mitigating agent to reduce sodium content. The results showed that for the roast beef, overall acceptance decreased when half of the meat was substituted with *A. bisporus*. However, for the taco mixture, there were no significant differences in overall acceptance between the recipes with full sodium and those with 25% less sodium. Most consumers preferred the recipes with *A. bisporus* substitution, demonstrating that this mushroom can be fully used to replace meat and reduce sodium without significantly affecting acceptance.

Similarly, Wong et al. (2017) incorporated *A. bisporus* into the filling of meat tacos, replacing up to 50% of the meat. They observed that this addition minimized the physical differences compared with a control with 100% meat, and the sensory tests showed that most consumers

preferred the filling mixed with *A. bisporus* and reduced sodium. Also, Wong et al. (2019) demonstrated that when *A. bisporus* is added as a meat extender for hamburgers, this mixture also presents physical characteristics similar to pure meat, thus providing a healthier product.

On the other hand, Wang et al. (2019) evaluated the effects of adding *P. eryngii* as a replacement for fat in pork sausages. The results showed that by replacing pork fat with this mushroom, less fatty and caloric products are obtained, with higher protein, moisture and dietary fiber content being well-accepted.

Some edible mushroom-based meat analog products, such as pickled fish fillets made from *H. erinaceus* and mushroom meat snacks derived from *L. edodes*, are already available in the market (Wang & Zhao, 2023). In 2020, Xuerong Bio, a prominent player in China's edible mushroom industry, took proactive steps to explore the possibilities of deep-processing edible mushrooms. By collaborating with other food companies, they developed edible mushroom protein as a viable raw material for meat analogs, making a significant advancement in the production of edible mushroom-based meat analogs. This initiative underscores the growing recognition of the importance of edible mushrooms in biotechnology within the food industry. It suggests their potential to reshape the landscape of alternative protein sources in the future (Wang & Zhao, 2023).

4.2 | Nutraceutical's products based on bioactive compounds from mushrooms

Investigations on mushroom biotechnology increasingly evidence that these are not just culinary delights but potent sources of bioactive compounds. Bioactive compounds are those compounds that confer bioactivity, meaning they have the potential to be used in the treatment of various diseases (Venturella et al., 2021). Bioactive compounds included phenolic compounds, polysaccharides, proteins, and terpenes. Phenolic compounds mainly exhibit antioxidant activity; polysaccharides exhibit antitumor, immunomodulatory, antioxidant, anti-inflammatory, antimicrobial, and antidiabetic activity; proteins possess cytotoxic, and anticancer properties with immunomodulatory, antitumor, and antiproliferative effects, and terpenes have anti-inflammatory, antioxidant, and antitumor properties (Venturella et al., 2021).

Phenolic compounds of edible and medicinal mushrooms are mainly represented by phenolic acids, cinnamic acid, flavonoids, ascorbic acid, ergosterol, and tocopherols (Cardoso et al., 2017; Barros et al., 2008; Sharma & Gautan, 2016). Some polysaccharides are lentinan of *L. edodes*, schizophyllane of *S. commune*, pleurane of *Pleurotus sp.*, and ganoderan of *G. lucidum* (Liu et al., 2015; Ma et al., 2018; Ruthes et al., 2016). Proteins are lectins, mushrooms immunomodulatory proteins (FIPs), ribosome-inactivating proteins; and other specific proteins (PEP) from *P. eryngii* (Xu et al., 2011; Yuan et al., 2017). Terpenes include monoterpenoids, sesquiterpenoids, diterpenoids, and triterpenoids. Flammulinol and flammulinolides are sesquiterpenoids present in *Flammulina velutipes*, whereas methyl ganoderate A acetonide and n-butyl ganoderate H are lanostane triterpenoids present in *G. lucidum* (Rathore et al., 2017).

Edible and medicinal mushrooms are considered nutraceuticals because of their beneficial properties for human health (Pirillo & Catapano, 2014). Bioactive compounds can be extracted from mycelial biomass or sporoma. The content of bioactive compounds varies with mushroom species, the part of the mushroom, and the type of substrate (Cardoso et al., 2017). Besides the direct consumption of the mushroom, the bioactive compounds can be incorporated into nutraceutical products as capsules or tablets (Arango & Nieto, 2012; Singh et al., 2009; Wasser, 2014). It should be noted that nutraceutical products derived from mushrooms are based on the combinations of several compounds that together contribute to total bioactivity (Srivastava et al., 2019). Commercially, there are several mushroom-based nutraceutical products. Organic ReiShi-Gen contains 50% *L. edodes* and 50% *G. lucidum* and is marketed as a daily supplement to strengthen the immune system. Pure Red-Reishi and Organic Reishi in capsules based on *G. lucidum* increase the body's resistance to stress and support the immune system, respectively. Capsules based on *Agaricus blazei* contribute to overall physical health (Rathore et al., 2017). *G. lucidum* extract powders from the commercial brands Urban Platter and Terrasoul Superfoods strengthen the immune system. *Cordyceps militaris* extract powder from the brand Organic Mushroom Nutritions increases energy levels, and physical endurance and supports cardiovascular and respiratory health (Srivastava et al., 2019), among others (Table 5).

Regarding the techniques for bioactive compound extraction, studies conducted in the last decade have highlighted methods such as ultrasound-assisted extraction (MAE), pulsed electric field extraction (PEF), and others. You et al. (2013) reported that utilization of pulsed countercurrent ultrasound-assisted extraction (CCPUE) resulted in the highest extraction of polysaccharides from *Boletus edulis*, with lower energy consumption. They used a liquid-to-solid ratio of 16:1, an extraction time of 40 minutes, and a temperature of 60°C. On the other hand, Xue and Farid (2015) demonstrated that PEF provided high yields in the extraction of polysaccharides (98%), polyphenols (51%), and proteins (49%) from *A. bisporus*. This method

TABLE 5 Products derived from nutraceutical mushrooms marketed in powder and capsule form. Extracts from different mushrooms can be combined in the same product. Products manufactured by alohamedicinals.

Product	Composition	Description
Immune Asist Critical Care^{TM}	Heteropolysaccharides, including approximately 300 mg of 1,3-β glucan and 1,6-β glucan per capsule from *Cordyceps sinensis, Agaricus blazei* (Almond mushroom), *L. edodes, G. frondosa, G. lucidum*, and *Coriolus versicolor*	A safe, natural, capsule dietary supplement that combines six potent mushroom species to provide immune support
Immune Asist^{TM} *Micron*	Purified powder of *C. sinensis, A. Blazei, L. edodes, G. frondosa, G. lucidum*, and *C. versicolor*	Provides immune support, supports cardiac and respiratory function, helps maintain healthy energy and brain function
Pure Agaricus Blazei^{TM}	β-Glucans from *A. blazei*. More than 300 mg of polysaccharides (60%) in each capsule	Provides blood sugar regulation, improves digestion and immunity
Pure Shiitake^{TM}	It contains more than 15% of lentinan, from Shiitake (*L. edodes*), and more than 300 mg of polysaccharides (60%) in each capsule	Provides immune support, supports heart function, skin and muscle health.
Pure Maitake^{TM}	More than 300 mg of polysaccharides (60%) of *G. frondosa* in each capsule	Supports weight control, blood sugar balance, and healthy digestion

applied electric pulses with a field intensity of 38.4 kV/cm for 272 μs and a treatment temperature of 85°C, thereby minimizing losses of bioactive compounds due to high temperatures. Additionally, Özyürek et al. (2014) evaluated the effectiveness of MAE, highlighting its advantage over other methods. They found that methanolic extracts of *B. edulis* obtained by MAE with 80% methanol, at 80°C for 5 minutes, showed the highest yield of phenolic compounds with antioxidant properties. These methods represent only some of the options available for bioactive compound extraction from edible and medicinal mushrooms. Other methods include conventional techniques and new approaches such as enzyme-assisted, supercritical and subcritical fluid extraction, and subcritical water extraction (Kumar et al., 2021).

4.3 | Production of enzymes for improving quality and enhancing flavor in the food industry

Edible and medicinal mushrooms, and their abundant enzyme content, offer practical solutions for biotechnological processes. Using enzymes from mushrooms in the food industry is an opportunity to enhance product quality and sensory attributes while addressing various processing challenges. Enzymes can be produced through solid-state or liquid-state bioprocessing of agro-industrial wastes, and enzyme immobilization techniques allow for enzyme reuse and improved catalytic stability in different environmental conditions (Lettera et al., 2015; Sheldon, 2007).

Fungal enzymes such as amylase, cellulase, xylanase, pectinase, lipase, protease, and others are used in various food industries including baking, brewing, dairy processing, fruit juice production, meat and fish processing, food coloring, and fermented food production (Alam et al., 2021). However, filamentous fungi are the most common sources of these enzymes, and fewer studies use enzymes from edible and medicinal mushrooms. Among them, the most cited enzyme is laccase.

Numerous enzymes from edible and medicinal mushrooms can be used as additives in food and beverage processing (Table 6). Lac can be applied to processes that improve or modify the color of food or beverage (Mayolo-Deloisa et al., 2020; Osma et al., 2010; Sun et al., 2021). Proteins and polyphenols in clear fruit juices can create turbidity or sediment. Hence, Cantarelli (1986) used mutant Lac from *Trametes versicolor* to treat black grape juice, obtaining 50% removal of total polyphenols and more stabilization than physicochemical treatment. Lac has been used for odor control, flavor enhancement, or reduction of undesirable products in several food products. Takemori et al. (1992) used crude *T. versicolor* Lac to improve the flavor and taste of cocoa nib and its products. The treatment with this Lac eliminated the bitterness and other unpleasant flavors, and the resulting chocolate tasted better than the control. Other studies using Lac from *T. versicolor* reported the removal of phenolic compounds from wines; more than 90% of ferulic acid was removed from a model solution, and 34% of phenolic compounds from wines (Minussi et al., 2002). Recently, Lettera et al. (2015) concluded that juice treatment with Lac is highly effective for clarifying and reducing phenols, improving the quality of the juices. These authors optimized a covalent immobilization of the recombinant Lac POXA1b from *P. ostreatus* on epoxy-activated poly (methacrylate) beads using a Response Surface Methodologies approach. The

TABLE 6 Edible and medicinal mushroom enzymes with applications in the food industry.

Enzyme application	Benefits	Example study
Laccase	Removal of phenolics compounds and improvement of stabilization of black grape juice	Cantarelli, 1986
Laccase	Improve flavor and taste of cocoa nib	Takemori et al., 1992
Laccase	Removal of phenolics compounds from wine	Minussi et al., 2002
Laccase	Phenol removal in musts for wine stabilization	Minussi et al., 2006
Laccase	Reduction of phenolic compounds in pomegranate juice	Neifar et al., 2009
Laccase	Color enhancement in beverages improved clarity and stability	Osma et al., 2010
Laccase	Improvement in elasticity and viscosity of gluten-free amadumbe dough	Manhivi et al., 2018
Laccase	Clarification and removal of reducing phenols	Lettera et al., 2015
Amylases Cellulases Pectinases	Food additive for seasoning	Tatsumi et al., 2016
Lipoxygenase	Potential as a biocatalyst for aroma transformation	Krahe et al., 2021
Ferulic acid decarboxylase	Production of 4-vinylguaiacol by decarboxylation of ferulic acid	Günther et al., 2021

juice treatment using Lac achieved up to 45% phenol reduction. In addition, the treatment did not affect flavanones, which are beneficial for health. After being treated, the flavor of the juice improved because vinyl guaiacol was reduced, which is an unpleasing taste.

Tatsumi et al. (2016) have reported that dried shiitake mushrooms are suitable for enzymatic preparations, remain stable, and can be reactivated to function as an enzymatic food additive or seasoning. The authors observed that cellulases, pectinases, and amylases were still present in the powder of dried shiitake mushrooms, even at temperatures from 35°C to 50°C. This study confirms the practicality and effectiveness of dried shiitake mushrooms as enzymatic food additives in the food industry.

5 | EXTENDED BIOTECHNOLOGICAL APPLICATIONS

In addition to their recognized use as food and in the production of nutraceuticals with bioactive compounds, edible and medicinal mushrooms can be utilized in other biotechnological applications such as cosmeceuticals, medicine, and other emerging industries, where they significantly contribute and the scope of novel solutions will be addressed in this section.

5.1 | Utilization of extracts with bioactive compounds for cosmeceutical production

Mushroom extracts have antioxidant and anti-inflammatory properties, and therefore, these extracts are often used to solve cosmetic problems, such as wrinkles, uneven skin tone, and texture (Wu et al., 2016a). Compounds of cosmetic products can induce changes in the skin, improving its appearance and health. In this context, the term cosmeceuticals refers to the combination of cosmetics and pharmaceuticals. Cosmeceuticals are applied topically as creams, lotions, and ointments, and they also have biologically active compounds with benefits similar to those of medical drugs (Mukherjee et al., 2024; Sharma, 2011).

Cosmeceuticals formulated from mushroom extracts are relatively complex mixtures of metabolites in liquid, semisolid, or dry powder form (Wu et al., 2016a). Among the components of mushroom extracts, ceramides, lentinan, omega 3, 6, and 9, fatty acids, carotenoids, resveratrol, and others are used more in the cosmetic industry (Camassola, 2013; Hyde et al., 2010). Also, β-glucans are of interest for producing creams, ointments, and powders because they can increase collagen production, reduce age lines, and treat eczema (Aboushanab et al., 2019).

Some mushrooms are valuable for making cosmeceutical products due to their bioactive compounds. For example, *L. edodes* has been reported to produce antioxidant enzymes that protect the skin and reverse oxidative damage (Cheung et al., 2003). Extracts from *F. velutipes* can lighten the skin by inhibiting melanin synthesis (Nagasaka et al., 2015). *Auricularia fuscosuccinea* offers hydration due to its ability to retain moisture (Liao et al., 2014), while *Tricholoma matsutake* extract reduces elastase activity, which is helpful against wrinkles (Kim et al., 2014; Wu et al., 2016a). Furthermore, bioactive compounds present in ethanolic extracts of edible mushrooms such as *A. bisporus, P. ostreatus*, and *L. edodes* maintain antioxidant and anti-inflammatory properties in cosmetic products, as

do extracts from *S. commune*, combating skin aging and hyperpigmentation (Razak et al., 2018; Taofiq et al., 2016).

5.2 | Utilization of bioactive compounds in medicinal research

Medicinal mushroom biotechnology is rapidly developing in cancer therapy because the anticancer activity of purified and extracted glucan polysaccharides and polysaccharide peptides has been demonstrated in animal models (Muhammad & Suleiman, 2015). *L. edodes*, native to East Asia, is cultivated, consumed, and considered medicinal in many Asian countries. Studies indicate prolonged survival and improved quality of life in patients with irremediable gastric cancer or recurrent diseases when patients are treated with lentinan, a component of *L. edodes*, in combination with other chemotherapies. *P. ostreatus* is considered medicinal due to statins such as lovastatin, which help reduce cholesterol (Chowdhury et al., 2015; Talkad et al., 2015).

Some mushrooms have also been shown to possess antimicrobial activities (Reis et al., 2017), mainly due to secondary metabolites, such as terpenes, steroids, anthraquinones, benzoic acid derivatives, and quinolones, and primary metabolites, such as oxalic acid, peptides, and proteins (Valverde et al., 2014). Chowdhury et al. (2015) evaluated and compared the antibacterial properties of edible mushrooms *Hypsizygus tessulatus*, *L. edodes*, and *P. ostreatus*. The authors found that methanolic extracts of the mushrooms used in their study exhibited antimicrobial activity against the microorganisms tested. *L. edodes* showed the best in vitro antibacterial activity against *Basillus subtilis*, followed by *P. ostreatus* and *H. tessulatus*. Also, *P. ostreatus* showed broad-spectrum antibacterial and antifungal activities. Other similar studies evaluating the antimicrobial activity of edible mushroom extracts were also carried out (Table 7). Moreover, recent studies have reported new substances, sesquiterpenes 1–4 and 6–12, from a strain of the edible mushroom *Gloeostereum incarnatum* BCC41461 having antimicrobial properties in association with two already known compounds, chondrosterin B and (E)-dichthiochromenol. These substances showed antimalarial, antituberculosis, and anti-*Basillus cereus* activity (Bunbamrung et al., 2017).

5.3 | Utilization of enzymes to enhance processes in the pulp and paper industry

The stringent environmental regulations in the pulp and paper industry have necessitated the adoption of new technologies to mitigate contaminants in bleach plant effluents. A pivotal step involves separating and degrading lignin from wood pulp, with pretreatment utilizing ligninolytic enzymes emerging as a cleaner and milder alternative to chemical bleaching (Dwivedi et al., 2010). The combined action of xylanases and Lac has facilitated the bleaching of mixed wood pulp, showcasing promising results (Liu & Kokare, 2017; Money, 2016). Mushroom pretreatment of wood chips offers a solution to issues such as pitch deposition and effluent toxicity, with studies highlighting the efficacy of strains like *T. versicolor* LaVec94-6 in reducing lipophilic compounds (van Beek et al., 2007). Moreover, thermostable and pH-stable xylanases from species such as *P. eryngii* can enhance the processes within the pulp and paper industry (Altaf et al., 2016).

5.4 | Utilization of enzymes to facilitate eco-friendly bioethanol production

Second-generation biofuels, exemplified by lignocellulosic ethanol, hold promise for reducing greenhouse gas emissions from conventional petrol fuels (Jouzani et al., 2020). Bioethanol, an eco-friendly alternative, boasts 37.4% oxygen content, unlike gasoline (Zabed et al., 2017). Yafetto (2022) argues that various agro-industrial wastes are used in bioethanol production. Although submerged-state bioprocessing of agro-industrial wastes is traditionally used for biofuel production, studies suggest that solid-state bioprocessing is a more viable alternative. This approach allows the utilization of agro-industrial wastes as both a solid support and carbon source, while also requiring less water and minimizing potential environmental contamination.

Nevertheless, the viability of lignocellulosic bioethanol hinges on achieving competitive yields vis-à-vis fossil fuels, presenting a significant challenge (Coniglio, 2017; Dashtban et al., 2009). Bioethanol production entails four primary stages: pretreatment, hydrolysis, fermentation, and distillation (Aditiya et al., 2016) (Figure 3). Pretreatment involves lignin removal, which is crucial for the enzymatic degradation of biomass (Agbor et al., 2011; Binod et al., 2011). Traditional pretreatment methods include physical or chemical techniques or combined using acids, alkalis, oxidative delignification, and organic acids to enhance lignocellulose breakdown. Although highly effective, they require careful management of operational conditions, which can result in adverse effects and the need for special elimination processes (Edeh, 2020). In contrast, biological pretreatment using enzymes from edible and medicinal mushrooms offers several advantages: It is an eco-friendlier strategy, does not require recycling of chemical substances after pretreatment, involves reduced

TABLE 7 Antibacterial activity of extracts from edible and medicinal mushroom species.

Mushroom specie	Bacterial inhibiting	Reference
Armillaria mellea	*Moraxella catarrhalis*	Liktor-Busa et al., 2016
Fistulina hepatica	*Bacillus subtilis* *Staphylococcus aureus* *Morganella morganni* *Pasteurella multocida* *Staphylococcus epidermidis* *Staphylococcus hominis*	Liktor-Busa et al., 2016 Alves et al., 2012
Lactarius volemus	*Moraxella catarrhalis*	Liktor-Busa et al., 2016
Lactarius deliciosus	*Streptococcus agalactiae* *Streptococcus pyogenes*	Alves et al., 2012
Megacollybia platyphylla	*Moraxella catarrhalis*	Liktor-Busa et al., 2016
Agaricus bisporus	*Bacillus cereus* *Staphylococcus aureus* *Salmonella enteritidis* *Escherichia coli* *Pasteurella multocida* *Streptococcus agalactiae*	Bach et al., 2019 Alves et al., 2012
Agaricus brasiliensis	*Bacillus cereus* *Staphylococcus aureus* *Salmonella enteritidis* *Escherichia coli*	Bach et al., 2019
Flammulina velutipes	*Bacillus cereus* *Staphylococcus aureus* *Escherichia coli*	Bach et al., 2019
Lentinula edodes	*Bacillus cereus* *Staphylococcus aureus* *Salmonella enteritidis* *Escherichia coli*	Bach et al., 2019
Lepista nuda	*Proteus mirabilis* *Staphylococcus epidermidis* *Listeria monocytogenes*	Alves et al., 2012
Russula delica	*Escherichia coli* *Morganella morganni* *Pasteurella multocida* *Staphylococcus saprophyticus* *Enterococcus faecalis* *Listeria monocytogenes*	Alves et al., 2012

costs for subsequent processes, minimizes the formation of inhibitory substances, is straightforward to operate, and has low energy consumption (Rezania et al., 2020). Hydrolysis also includes the treatment of products from pretreatment with concentrated, diluted acids or enzymes to separated lignin and cellulose (Panahi et al., 2019). In this sense, WRF secrete enzymes such as LiP, MnP, and Lac, facilitating biomass delignification and enhancing sugar conversion efficiency (Jouzani et al., 2020). These enzymes, utilized in hydrolysis enable cellulose breakdown into fermentable sugars, are less costly to maintain, mild conditions of temperature and pH do not affect the glucose formed, and inhibitory byproducts are not formed (Coniglio, 2017; Panahi et al., 2019). Some studies explore edible and medicinal mushroom enzymes for bioethanol production. Fang et al. (2015) isolated Glac15 Lac from *G. lucidum* 77,002, enhancing ethanol yield by 10% via pretreatment of substrate, whereas Yu et al. (2008) combined ultrasound pretreatment with enzymatic hydrolysis using Lac, LiP, and MnP from *P. ostreatus* BP-035, boosting substrate conversion and delignification (Yadav et al., 2019).

These findings highlight mushroom enzymes' versatility and promise in advancing the development of sustainable technologies. Further exploration and optimization of mushroom enzyme applications hold significant implications for the future of bioethanol production and renewable energy initiatives.

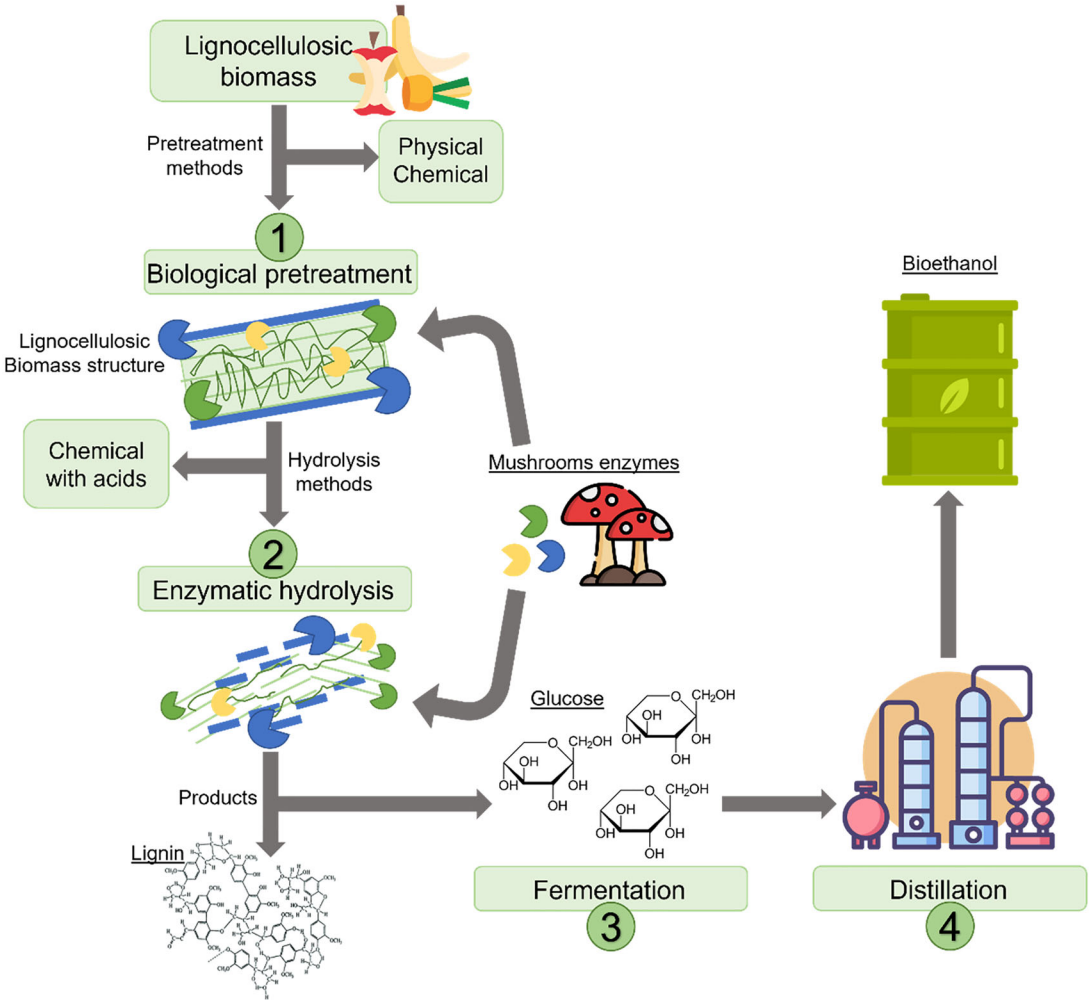

FIGURE 3 Diagram of bioethanol production using mushroom enzymes in pretreatment and hydrolysis steps.

5.5 | Utilization of enzymes for the bioremediation of contaminated soils and effluents

Bioremediation is an alternative to conventional methods for treating effluents and contaminated soils and harnesses mushrooms' enzymatic systems to convert pollutants into less toxic byproducts (Kulshreshtha et al., 2014). WRF has demonstrated prowess in removing diverse organic pollutants such as polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), pesticides, and endocrine disruptors (EDCs) (Asgher et al., 2008; Cajthaml, 2015). WRF produces extracellular oxidoreductase enzymes such as LiP, MnP, VP, and Lac, along with the intracellular system involving CYP450, enabling broad-spectrum xenobiotic degradation (Hata et al., 2010; Naghdi et al., 2018; Nguyen et al., 2013).

Edible mushrooms, particularly *Pleurotus* species, exhibit promise in bioremediation, degrading various contaminants, including insecticides such as endosulfan and biodegradable plastics (Mendoza et al., 2008; Petre, 2016; Rodrigues da Luz et al., 2013). For instance, *Pleurotus sajor-cajú*, reclassified as *P. pulmonarius* LBM 105, efficiently eliminated over 90% of PCBs in liquid media, with a concomitant reduction in toxicity attributed to a threefold increase in Lac enzyme activity (Chelaliche et al., 2021; Sadañoski et al., 2019). Similarly, the potential of *P. florida* has been assayed for the biodegradation of gas oil (Roshandel et al., 2021). *P. florida* inoculated in liquid media with 10% gas oil produced more biosurfactant and the enzymes Lac and tyrosinase. Therefore, the surface and interfacial tension were reduced and the solubilization of hydrocarbons and detoxification were increased.

Furthermore, studies have explored the bioremediation potential of species like *P. eryngii* for manganese and phenanthrene removal, with enhanced Lac production aiding in the degradation of pollutants (Wu et al., 2016b). Solid-state fermentation techniques have also bolstered Lac production in WRF, facilitating the remediation of PAHs such as phenanthrene and pyrene (Rosales et al.,

2013). Additionally, alkaline proteases from organisms like *Termitomyces clypeatus* have shown efficacy in multifunctional bioremediation processes such as tanning, making them suitable for applications in skin depilation, feather disintegration, and bactericidal activities (Majumder et al., 2014).

Maisto et al. (2024) advanced the study of plastic biodegradation with *P. ostreatus* and *A. bisporus* by evaluating genes involved in the expression of Lac, MnP, and LiP isoenzymes. This study revealed that exposure of these mushrooms to low-density polyethylene oxidized led to the overexpression of Lac6, Lac7, Lac9, Lac10, and MnP12 genes in *P. ostreatus*, and Lac2 and Lac12 genes in *A. bisporus*. This emergent work represents an opportunity for further research into genetic engineering and gene manipulation for synthesizing mushroom enzymes with significant potential for bioremediation processes especially for plastics degradation.

6 | CONCLUSION

An exhaustive search and interpretation of the studies of edible and medicinal mushrooms have outstanding nutritional and medicinal value. They are versatile, able to grow on different substrates and have a great capacity to produce extracellular enzymes with a wide range of specificities. All these characteristics make them excellent organisms for different biotechnological industries.

Although most studies of bioactive compounds have focused on plants, there is a tendency to research these compounds from edible and medicinal mushrooms because they are less known organisms becoming an attractive source of probably novel bioactives with nutraceutical and medicinal properties. Moreover, the ability of edible and medicinal mushrooms to produce extracellular enzymes represents an excellent opportunity for the bioprocessing of agro-industrial wastes because these can be transformed into value-added products. From the bioprocessing of plant matrices, enzymes can be recovered that can be used in different industrial activities, such as the food industry, the pulp and paper industry, and the second-generation fuel industry. Also, mushrooms or their enzymes can be used directly for the bioremediation of contaminated soils and effluents, allowing decontamination by degrading pollutants, textile dyes, and other xenobiotic compounds. All these biotechnological activities with edible and medicinal mushrooms could be integrated into a circular economy model that allows sustainable development, recycling agro-industrial waste for the production of mushrooms on a large scale. However, there is still work to be done to learn about the biotechnological potential of other edible and medicinal mushroom species, in addition to those already examined and cited in this article.

To take more advantage in the food industry, it will be interesting for further research to focus on the enzymes of edible mushrooms for improving food rheological properties and bioprocesses because most works are related to commercial enzymes or enzymatic extracts from filamentous fungi. A deeper exploration of enzymes from edible mushrooms will offer a promising alternative for consumption due to their natural and edible origin and sustainable production.

AUTHOR CONTRIBUTIONS

Ramona C. Barua: Conceptualization; investigation; writing—original draft; visualization; writing—review and editing; resources. **Romina O. Coniglio**: Writing—review and editing; visualization; supervision; conceptualization; resources. **Melisa A. Molina**: Visualization; investigation; writing—original draft; writing—review and editing. **Gabriela V. Díaz**: Visualization; writing—review and editing; conceptualization; supervision. **Maria I. Fonseca**: Conceptualization; visualization; writing—review and editing; supervision; resources.

ACKNOWLEDGMENTS

This work was funded by CIDET—Secretaría de Ciencia y Técnica de la Univ. Nacional de Misiones (Argentina) (16/Q1557-TI). Ramona C. Barua has a CONICET PhD fellowship, Romina O. Coniglio, Gabriela V. Díaz, and Maria I. Fonseca are career members of CONICET (Argentina).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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How to cite this article: Barua, R. C., Coniglio, R. O., Molina, M. A., Díaz, G. V., & Fonseca, M. I. (2024). Fungi as Biotechnological Allies: Exploring Contributions of Edible and Medicinal Mushrooms. *Journal of Food Science*, 1–28. https://doi.org/10.1111/1750-3841.17390