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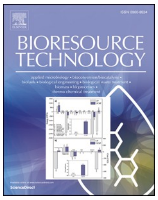

Review

Fungal fermentation: The blueprint for transforming industrial side streams and residues

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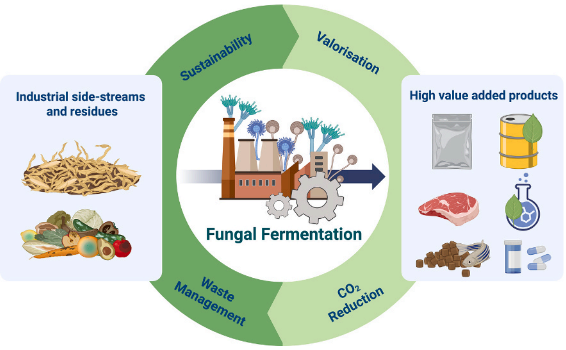
HIGHLIGHTS

- Fungal fermentation valorizes diverse industrial residues into high value products.
- Mycoproteins, enzymes and biochemicals produced from waste derived substrate.
- Sequential SSF-SmF strategy enhances fungal yield and process efficiency.
- Circular bioeconomy advanced through integrated fungal valorization pathways.

GRAPHICAL ABSTRACT



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ABSTRACT

The escalating generation of industrial side streams and organic residues presents both a challenge and an opportunity for sustainable biotechnological solutions. Filamentous fungi, with their metabolic versatility and ability to secrete a wide spectrum of enzymes, have emerged as promising agents for transforming diverse waste substrates into high-value products within the biorefinery concept. This review explores the multifaceted applications of fungal fermentation (submerged, solid-state, and sequential) for valorizing agri-food, lignocellulosic, and marine residues into mycoproteins, enzymes, biochemicals, biomaterials, and agricultural applications. Emphasis is placed on the scalability, functional diversity, nutritional potential, and environmental relevance of fungal-derived products, particularly in addressing global protein demand, chemicals, materials and sustainable biomanufacturing. Furthermore, challenges, substrate heterogeneity, safety concerns, and emerging tools, such as AI and multi-omics, are discussed in the context of process optimization and regulatory acceptance. This paper highlights fungal fermentation as a pivotal biotechnology tool in advancing circular bioeconomy goals by contributing to sustainable food production, resource recovery, and the development of novel compounds of interest.

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1. Introduction

Burgeoning environmental concerns and increasing public awareness of the consequences of current consumption and production models have propelled the circular economy and bioeconomy to the forefront of scientific, industrial, and policymaking discourse, particularly within EU legislations (European Commission, 2018). As a result, the circular bioeconomy has emerged as a pivotal strategy for fostering sustainability and ensuring economic activities remain within earth's biophysical limits (Muscat et al., 2021). Built on the principles of waste minimization and valorization, circular economy is a cornerstone in the sustainable development frameworks. By embedding reduction, reuse and recycling across the entire value chain, it aims to enhance resource efficiency while mitigating environmental impact (Kumar et al., 2025).

Biorefineries play a pivotal role in translating these principles into practice, providing a sustainable platform for converting biomass into a diverse range of valued-added products, including food, feed, energy, biomaterials, and chemicals (Ianda et al., 2024; Van Der Hauwaert et al., 2024). They utilize biomass from various sources, such as forestry, agriculture, aquaculture, and organic waste generated by industrial and urban sectors (Ianda et al., 2023). Given that global municipal solid waste generation is projected to reach 3.4 billion tonnes annually by 2050 (Kaza et al., 2018), with food waste alone accounting for nearly 1.05 billion tonnes per year (United Nations Framework Convention on Climate Change (UNFCCC), 2024), biorefineries offer a crucial solution for waste management and resource recovery. The biorefinery distribution report indicate the existence of 803 biorefineries in the European Union (EU), with the majority dedicated to production of bio-based chemicals (507), while 363 focus on liquid biofuels and 141 specialize in bio-based composites and fibers (European Commission. Joint Research Centre., 2018). The potential for biorefineries is expected to expand significantly in the coming decades, with the demand for bioproducts projected to reach 113 Mt/year by 2050, corresponding to an estimated annual growth rate of 15 % (Arias et al., 2023).

Fungal fermentation, a robust and versatile biotechnological approach has been utilized for centuries (Cairns et al., 2018). Its effectiveness in biomass valorization makes it a key enabler of the biorefinery concept, offering sustainable solutions for resource utilization. Filamentous fungi can produce a wide range of enzymes including, cellulase, xylanase, lignin peroxidase, laccases, among others (El-Gendi et al., 2021; Liu and Qu, 2019). Leveraging this enzymatic capability and their metabolic versatility, fungal technology can degrade a wide range of complex substrates such as lignocellulosic residues, proteinaceous byproducts, and lipid-rich waste, converting them into high-value compounds (Dukare et al., 2024). Additionally, their capacity to accumulate intracellular storage molecules and synthesize bioactive metabolites makes them highly suitable for applications in food, feed, biopolymers, and bioenergy (Fan et al., 2025; Li et al., 2024a).

Beyond biotransformation efficiency, fungal fermentation offers key advantages in sustainability and scalability. Operating under mild conditions, it requires lower energy inputs than conventional chemical processes while reducing waste accumulation and carbon emissions. Moreover, several filamentous fungi are edible and hold generally recognized as safe (GRAS) status, facilitating their use in food applications. Comparing fungal fermentation with bacterial or algal valorization, it offers clear economic advantages primarily by reducing upstream and downstream costs. Filamentous fungi can directly act on complex substrates such as lignocellulose and agro-industrial residues, minimizing pretreatment requirements and lowering capital and operational expenses (Banerjee et al., 2023; Dhiman et al., 2024). Their superior enzyme secretion capacity enables efficient substrate utilization and faster lignin breakdown, while the easy separation of fungal biomass from the fermentation medium simplifies downstream processing and allows further valorization of proteins and lipids, enhancing circularity (Varriale and Ulber, 2023). Simultaneous saccharification and fermentation further decreases costs by combining enzymatic hydrolysis and fermentation in a single vessel, as demonstrated for lactic acid production from industrial waste paper sludge using *Rhizopus oryzae* (Dhandapani et al., 2021).

At industrial scale, fungal fermentation underpins diverse processes, from mycoprotein production (e.g., Quorn™) to enzyme-assisted biomass degradation (e.g. Carbios, Abengoa) and enzyme production (e.g. Novozymes), demonstrating its broad commercial relevance. As advancements in process optimization continue, fungal-based valorization is poised to play a central role in the evolution of biorefineries and low-carbon principles.

In light of the growing importance of circularity and a thriving bioeconomy, this review explores the valorization of industrial side streams and wastes through fungal fermentation, examining biomass types, fermentation strategies, applications, challenges, and future prospects. Fig. 1 exhibits a general overview of the feedstocks, fermentation and products that are discussed in the coming sections.

2. Fungal fermentation

Fermentation, as first described by Pasteur, is a microbial process that enables energy production in the absence of oxygen (Pasteur, 1879). Complex molecules are degraded and converted into simpler ones such as alcohols or acids mediated by myriads of enzymes (Chai et al., 2022a). This biological transformation has become a pillar of modern industrial biotechnology, supporting applications in food, medicine, energy, and environmental sustainability.

Fungal fermentation, in particular, offers distinct advantages due to the metabolic versatility of filamentous fungi. Their ability to secrete diverse enzymes and secondary metabolites enables the breakdown of complex biomass, including cellulose, hemicellulose, and lignin, the latter being particularly resistant due to its highly branched, aromatic structure (Hsin et al., 2025; Ren et al., 2024; Zhang et al., 2024a; Liang et al., 2025). Efficient biomass conversion hinges on maximizing the utilization of each component, yet lignin degradation remains a major bottleneck (Chai et al., 2022b). Unlike many microorganisms, fungi possess specific ligninolytic enzymes that facilitate lignin breakdown, improving cellulose accessibility and enhancing subsequent saccharification (De Oliveira et al., 2023; Sun et al., 2014). Due to this characteristic, fungal fermentation is not only a core bioconversion process, but it can also serve as a powerful pretreatment step in other biomass valorization processes. For instance, biological pretreatment of sugarcane bagasse with *Trametes villosa* 82I6 has been found to selectively degrade lignin, making cellulose more accessible for enzymatic hydrolysis. This process significantly enhances sugar recovery from bagasse, ultimately improving ethanol production (Hartmann et al., 2022).

Beyond their enzymatic capabilities, fungi exhibit remarkable resilience to environmental stressors such as pH, aeration and water activity, further reinforcing their industrial applicability.

Filamentous fungi are predominantly saprophytic eukaryotes, which means they obtain carbon from nonliving organic matter. Their structure is made up of thin, thread like units called hyphae, which together form a larger network known as mycelium. Among the industrially prominent filamentous fungi, we can mention *Peniccillium*, *Fusarium*, *Aspergillus*, *Rhizopus* and *Neurospora*.

Fungal fermentation processes can be categorized as submerged, solid-state or sequential method. Fig. 2, exhibits fungal fermentation modes and position of polysaccharides and proteins in the hyphae cell walls.

2.1. Submerged fermentation

Submerged fermentation (SmF), or liquid fermentation, involves cultivating microorganisms in a liquid medium enriched with essential nutrients such as carbon, nitrogen, and micronutrients (Amobonye et al., 2023). This method is widely used in industrial-scale operations, due to its precise control, efficient automation, and robust monitoring of

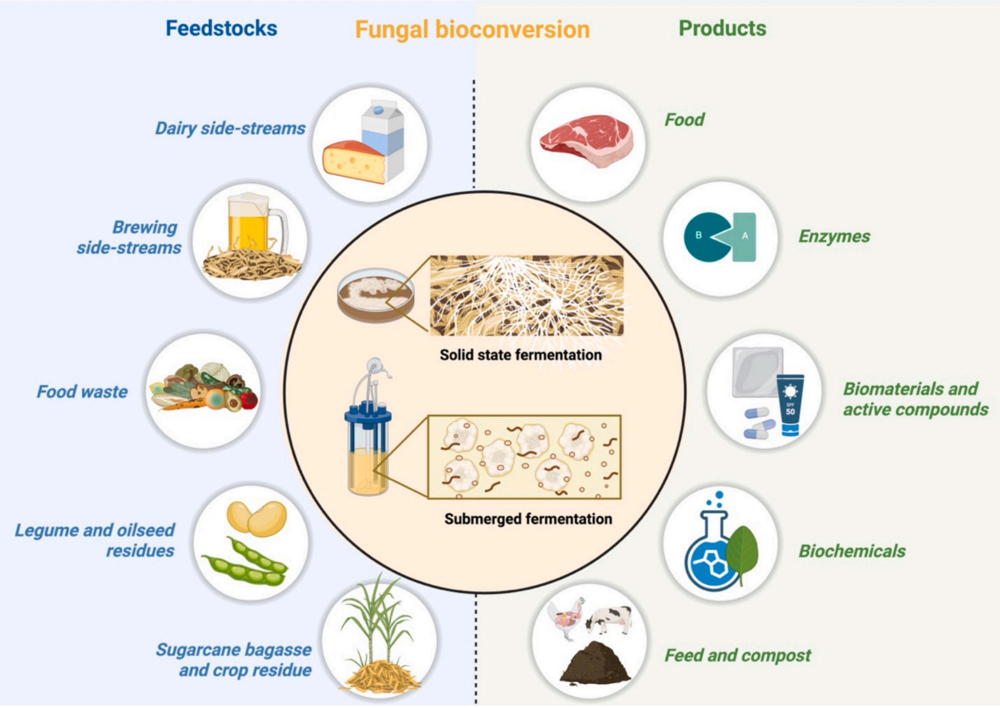

Fig. 1. General overview of the feedstocks, fermentation bioconversion and products discussed in this review.

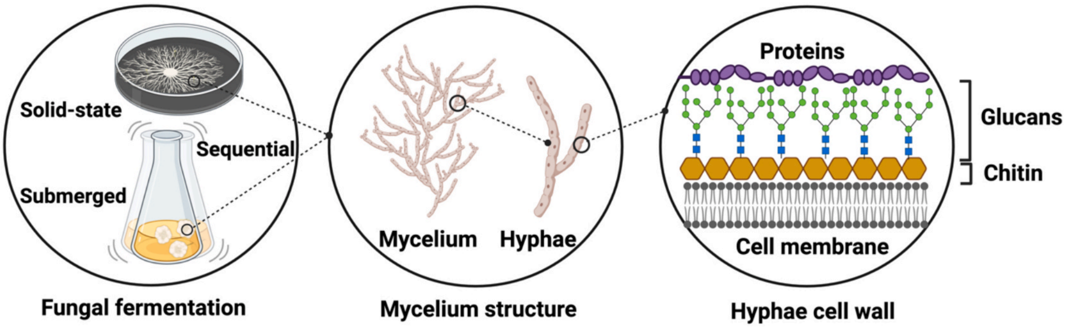

Fig. 2. Fungal fermentation modes, structure of mycelia and hyphae cell wall.

parameters like pH, temperature, aeration, and dissolved oxygen (Thakur et al., 2023). Typically performed in stirred-tank or airlift bioreactors, SmF is preferred for large-scale enzyme production as it enhances microbial growth and simplifies process control while minimizing heat and mass transfer limitations. Beyond enzymes, SmF plays a key role in the industrial production of citric acid, antibiotics, vitamin supplements, flavoring agents, biopesticides, animal feed and bioplastic for packaging production (Haque et al., 2024; Książek, 2023; Mascarin et al., 2024; Show et al., 2015).

2.2. *Solid state fermentation*

The other major mode of fungal fermentation is solid state fermentation (SSF), with a moisture content between 34–75 % (Ahmad et al., 2022). In SSF, microbes are grown with minimal free-flowing liquid on moist, insoluble substrates which serves as both the source of nutrients and physical support (Couto and Sanromán, 2006; Wang et al., 2023a).

While SmF remains more prevalent in bioprocessing, SSF is increasingly getting valued for its advantages, including high productivity, reduced energy and water demands, lower contamination risks, and minimal wastewater generation and lower operational costs (Majumder et al., 2024; Wang et al., 2023a). Notably, SSF is becoming favored for fungal cultivation, when maximizing biomass production or secondary metabolite synthesis (Amobonye et al., 2023) for instance in mycoprotein production (Wang et al., 2023b). However, despite its potential, SSF has yet to be fully realized on an industrial scale due to challenges in process monitoring and control, substrate heterogeneity as well as heat and mass transfer (Bamidele et al., 2025; Jin et al., 2024).

2.3. *Sequential fermentation*

Coupling solid and submerged fermentations in a sequential SSF-SmF strategy leverages the strengths of both techniques, creating a synergistic effect that improves fungal fermentation efficiency. SSF facilitates strong microorganism-substrate interactions, which leads to higher enzyme concentrations (Gmoser et al., 2019). By providing a favorable microenvironment with improved oxygen availability, SSF promotes mycelial germination and enzyme synthesis (Cunha et al., 2012), making it an effective pre-culture step. The subsequent transition to SmF optimizes mass and heat transfer, ensuring effective substrate utilization and nutrient diffusion, which maximizes fungal metabolism and enzymatic activity. This combined approach has demonstrated superior performance in cellulase and glucoamylase production (Martău et al., 2021), and improved bioconversion of lignocellulosic residues (Intasit et al., 2021). Combining SSF and SmF not only enhances fungal adaptability and productivity but also optimizes resource utilization, making it a highly effective strategy for industrial biotechnology applications. However, despite its promising potential, the industrial deployment of this dual-mode strategy remains limited. Existing bioprocessing infrastructure is generally optimized for either SSF or SmF, and lacks the flexibility to accommodate the sequential integration of both modes at scale. Further technological innovation and process engineering are thus required to overcome operational and scale-up challenges before the SSF–SmF approach can be widely adopted in industrial biotechnology. To achieve high fungal biomass yields, critical factors such as temperature, pH, oxygen availability, and agitation must be carefully controlled throughout the process. However, significant techno-economic barriers remain. The intrinsic heterogeneity of SSF complicates reactor design, scale-up, and automated control compared to the more uniform conditions of SmF (López-Gómez and Venus, 2021). Challenges in ensuring efficient heat and mass transfer, maintaining appropriate moisture content, supplying adequate aeration, and achieving precise pH regulation further limit industrial adoption. Moreover, the absence of scalable, rationally designed bioreactors supported by mathematical modeling and automated control systems prevents robust aseptic operation under heterogeneous conditions (Arora et al., 2018). Transitioning from the initial SSF phase to the liquid SmF stage also poses difficulties, requiring careful coordination of nutrient transfer, microbial dynamics, and metabolite stability (De Oliveira et al., 2024). In addition, the physical and chemical complexity of solid substrates often impedes efficient product recovery and integration into the subsequent submerged phase. Beyond these technical barriers, realistic scale-up is further challenged by increased contamination risks during phase transfer (Abraham et al., 2013), difficulties in cleaning heterogeneous residues, and regulatory hurdles associated with food- and feed-grade approval of waste-derived substrates.

3. Industrial biomass as potential feedstocks

A wide range of organic side streams are generated across industries, each varying in composition, structure and biodegradability. The following subsections explore representative industrial side streams and residues that have shown potential as suitable feedstocks for fungal valorization. Table 1 summarizes the key characteristics of the main feedstocks, including C/N ratio, lignin content, potential inhibitory compounds, fungal strain compatibility, and commonly reported pretreatment methods. The data are compiled from multiple case studies to provide a comprehensive comparative overview.

3.1. Food and beverage industry byproducts

The food and beverage industry is one of the world's largest producers of organic waste, contributing significantly to environmental pollution, economic inefficiencies, and increasing burdens on waste management systems (Hadj Saadoun et al., 2021). However, many of these byproducts are rich in proteins, fibers, and carbohydrates, making them highly suitable for bioconversion (Borkertas et al., 2025; Yu et al., 2025). Fungal fermentation, in particular, offers a promising approach to valorizing these residues.

The waste and side streams in food and beverage industries can generally be categorized into two main groups; 1: Processing byproducts and residues generated during or at the end of production, such as whey, cheese, and milk residues. 2: Defective or discarded products including faulty batches, expired, spoiled, or contaminated items.

Among these, dairy byproducts hold immense potential for biotechnological valorization. Dairy waste streams contain high organic loads, with chemical oxygen demand (COD) values reaching 1.13 kg for lactose, 1 kg for protein, and 3 kg for fat per kg of waste (Ahmad et al., 2019). In 2023, global cheese production reached 22.15 million metric tons, with the EU contributing approximately 47 % (10.4 million metric tons) (USDA Foreign Agricultural Service, 2024). Since 9–10 L of whey are generated per kg of cheese produced, this results in vast amounts of

Table 1
Potential feedstock properties for using as substrate in fungal fermentation.

Feedstock	C/N ratio	Lignin content (%)	Inhibitory compounds/by products	Fungal strain compatibility	Pretreatment	Reference
Whey	~18–70	NA	Lactose derived inhibitors, salt	*A. oryzae, A. Niger, P. chrysogenum, P. purpurogenum,*	Acid precipitation and thermal denaturation if needed	(Bansfield et al., 2024; De Carvalho et al., 2020; Usmani et al., 2022)
Brewer's spent grain	19.2	10–25	Phenolics, HMF	*A. niger, R. oryzae T. aurantiacus, T. reesei,* *T. Neurospora, N. intermedia*	Physical, chemical (acid, alkaline, organosolv), hydrothermal, enzymatic	(Gmoser et al., 2020; Llimós et al., 2022; Parchami et al., 2023; Saldarriaga-Hernandez et al., 2025)
Wheat straw	55–110	11–26	Phenolics, HMF, furfural, acetic acid	*T. versicolor, P. ostreatus*	Physical, dilute acid, alkali, enzymatic	(Gao et al., 2016; Li et al.. 2025a,; Shamshitov et al., 2025; Sun et al., 2025)
Rice straw	43–110	5–24	Silica, HMF, furfural, phenolics	*T. versicolor,* *C. subvermispora, P. ostreatus,* *A. niger, P. janthinellum,* *T. reesei, S. cerevisiae*	Physical, thermal, and acid	(Binod et al., 2010; Gao et al., 2026; Nozoe et al., 2025; Panda and Maiti, 2024)
Corn stover	40–60	17–22	Furan aldehydes organic acids, aldehydes, phenolics	*P. ostreatus, T. longibrachiatum*	Grinding, soaking in water, chemical	(Jazmín Edith et al., 2019; Nichols et al., 2008; Wuaku et al., 2025)
Rice bran	16.54–19.7	11.5–24.8	Lipids, phenolics, phytic acid	*T. harzianum, A. oryzae, A. niger, N. sitophila,*	Milling, defatting, extrusion	(Abduh et al., 2025; Hernaman et al., 2024; Huervana et al., 2024; Nozoe et al., 2025)
Soybean okara	5.83	1.14–11.5	Phytic acid, lectins	*P. citrinopileatus, A. oryzae, A. niger A. ficuum*	NA	(Devanthi et al., 2024; Joo et al., 2023; Mok et al., 2019; Thi Bich et al., 2024)
Sugarcane bagasse	66	10–26	Acetic acid, phenolics, 5-HMF, furfural	*Wickerhamomyce, Aspergillus, Trichoderma, Rhizopus, Mucor, Penicillium, Fusarium*	Acid and alkali, hot water cleaning to remove sugar, steam explosion, detoxification by liquid–liquid extraction	(Bonfiglio et al., 2024; Dhandapani et al., 2021; Mili et al., 2025)

HMF: Hydroxymethyl furfural
NA: not applicable.

cheese whey, a byproduct with a high biochemical oxygen demand (BOD) and COD. Some whey is processed into more valuable products, such as whey protein concentrates, whey powder, whey permeate. However, a significant portion of the liquid whey produced during cheese manufacturing is still discarded or used as livestock feed (Tunick et al., 2025). Rich in proteins and lactose, whey serves as an excellent substrate for fungal fermentation, enabling the production of functional and bioactive compounds (Malos et al., 2025; Pires et al., 2021; Usmani et al., 2022).

Brewer's spent grain (BSG) is among the abundant cereal-based byproducts and waste. BSG, the primary by-product of beer production, is the solid residue after the malting, mashing, and lautering stages (Sibhatu et al., 2021). It accounts for approximately 85 % of total brewing waste, with an average of 20 kg of BSG generated per 100 L of beer (Qazanfarzadeh et al., 2024). Global BSG production is estimated at 36.4 million tons annually, with the EU contributing to approximately 3.4 million tons (Li et al., 2021; Pilafidis et al., 2024). Currently, BSG is used mainly as low-quality animal feed, but its short shelf life and high production volume mean that large amounts are instead managed through landfilling or incineration, both of which pose significant environmental challenges (Parchami et al., 2023). Rich in hemicellulose, cellulose, protein, lignin, and phenolic compounds, BSG holds significant potential for biorefinery applications (Qazanfarzadeh et al., 2023).

3.2. *Agro-industrial wastes and residues*

3.2.1. *Crop residues*

Cereal crops such as wheat, rice, and corn account for a major share of global crop residues, annually producing over 650 million tons of wheat straw and 70 million tons of corn husks (Deshwal et al., 2021). With global grain production projected to exceed 2.9 billion metric tons in 2025, the accumulation of cereal residues is expected to rise significantly, posing both a challenge and an opportunity for valorization (Food and Agriculture Organization of the United Nations, 2024; Statista, 2025a). Cereal residues are utilized for multiple purposes, including livestock feed (≈19 %), domestic fuel in resource-limited areas, soil carbon and nitrogen enrichment, and erosion control. However, about 10 % of these residues are still burned in the fields, causing air pollution, nutrient loss, and potential pest problems. Current utilization practices are often not economically optimal and may have negative environmental and health impacts (Jafarzadeh et al., 2025). Cereal straws are rich in cellulose, hemicellulose, lignin, and essential nutrients, and can be considered as promising substrates for fungal fermentation (Ying et al., 2024). Despite their recalcitrance, fungi, particularly white rot species, excel at lignin degradation, enhancing substrate accessibility. For instance, *Trichoderma* has been shown to accelerate rice straw decomposition (Organo et al., 2022).

Similarly, corn stover (stalks, leaves, and cobs left after harvesting) is a high-potential lignocellulosic feedstock, containing 35 % cellulose, 20 % glucuronoarabinoxylan, and 12 % lignin. Certain fungi, such as *Ustilago maydis*, can utilize corn stover as a sole nutrient source, relying on its sugar content for growth (Robertz et al., 2024).

Cereal bran, a byproduct of milling, is another abundant resource for fungal cultivation that is composed of hemicelluloses, starch, polyphenols, and proteins. Rice bran alone contributes 5–15 kg per 100 kg of milled rice (Kayalvizhi and Jacob, 2025). Currently, rice bran is mainly used as animal feed, leading to a loss of valuable nutrients. To enhance its utilization, processing methods such as fermentation, irradiation, and extrusion are increasingly applied to improve its sensory and nutritional qualities (Wu et al., 2024). Besides, it can be a potential feedstock for mycelium-based biomaterials (Sisti et al., 2021).

3.2.2. *Legume and oilseed residues*

The legume and oilseed industries generate large volumes of nutrient-rich residues, including oilseed cakes, soybean processing byproducts, and legume husks. These residues are primarily utilized as an animal feed supplement, although incorporation levels are limited by antinutritional factors and high fiber content. In practice, it is also commonly applied as compost or fertilizer, while alternative routes include its use for energy production or the extraction of protein isolates/concentrates. Given its nutritional composition, oilseed cake also provides a suitable substrate for various biotechnological processes (Purohit et al., 2023; Sousa et al., 2023b). Fungal bioprocessing can enhance nutrient availability, bioactivity, and protein quality, expanding their potential in food, feed, and industrial applications.

In 2025, global oilseed production is projected to reach 679.37 million metric tons, generating 387.43 million metric tons of protein-rich oilseed cakes (USDA, 2025). These residues contain carbon, proteins, and bioactive compounds, making them promising substrates for enzyme production, bioactive extraction, and fungal mycelium-based materials.

However, some oilseed cakes contain anti-nutritional factors that restrict their direct use. For instance, cottonseed cake contains gossypol, a toxic compound, which can be reduced through fungal fermentation using *Candida tropicalis* and *Saccharomyces cerevisiae*, improving lysine content and feed quality (Mageshwaran et al., 2023). Similarly, fermenting flaxseed, mustard, and rice bran meal with *Aspergillus* species increases protein and antioxidant content (Dutta et al., 2023). Additionally, oilseed cakes such as rapeseed and sunflower have been fermented with *Rhizopus oryzae*, *Aspergillus ibericus*, and *Aspergillus niger* to produce enzyme-rich extracts with high antioxidant potential (Sousa et al., 2023a).

Soybean is a major legume and oilseed crop that generates okara, an insoluble byproduct of tofu, soymilk, and soy nut production, at a ratio of 1.1–1.2 kg per 1 kg of processed soybean (Asghar et al., 2023; Canaan et al., 2022). Despite being nutritionally comparable to soy products, containing 50 % carbohydrates, 20–30 % protein, and 10–20 % fat, okara is often used as animal feed or otherwise discarded as waste (Devanthi et al., 2024). Its high organic content makes it an ideal substrate for fungal fermentation, enabling applications in enzyme production, mycoprotein synthesis, and bioethanol production.

In addition to oilseeds, legume husks and pods remain underutilized, despite their high cellulose, hemicellulose, and lignin content (Emenike et al., 2024). Fungal fermentation of common bean pods using *Trametes versicolor* has been shown to enhance laccase enzyme production, while green bean peels fermented with *Penicillium commune* have been used to produce tannase, which improves beverage quality by reducing tannins and increasing reducing sugars (Caroca et al., 2022; Mostafa, 2024).

3.2.3. *Sugarcane bagasse*

Sugarcane bagasse is the fibrous residue from sugarcane juice extraction. Global sugarcane production exceeded 2 billion metric tons in 2023 (Statista, 2025). From each ton of processed sugarcane, 270 kg of bagasse is generated (Toscano Miranda et al., 2021) which generally contains 26–50 % cellulose, 24–34 % hemicellulose, and 10–26 % lignin (Mili et al., 2025). Sugarcane bagasse is mainly combusted in sugar mills for cogeneration of steam and electricity, but production often exceeds energy needs. The surplus is typically stored which causes dust, land use, and fire risks or inefficiently burnt for disposal (Matsueda and Antunes, 2024).

Fungal fermentation enables the bioconversion of bagasse into high-value products, including biofertilizers, ethanol, and industrial enzymes (Prajapati et al., 2020). *Aspergillus niger*, for example, has been used in submerged fermentation, where sugarcane bagasse combined with soybean meal resulted in xylanase and protease production. Enzyme yields varied across different systems, with bubble column reactors achieving the highest activities, 60.5 U/mL for xylanase and over 7 U/mL for protease (Valladares-Diestra et al., 2021).

4. Applications

4.1. Mycoproteins

The demand for animal protein is projected to reach nearly 470 million tons by 2050 (Lynch et al., 2018) with average meat consumption per capita to rise from 40 kg to 52 kg per year by 2050 (Lumsden et al., 2024). This growing pressure on global protein supply necessitates the development of sustainable and scalable alternatives. One such solution is mycoprotein, a protein-rich food derived from filamentous fungal biomass, offering a nutritious and environmentally promising substitute for meat (Majumder et al., 2024).

The origins of mycoprotein date back to the post-World War II era, when global food insecurity prompted research into single-cell proteins, exploring microorganisms such as fungi and bacteria as alternative protein sources for human consumption and development of meat analogues (Wood and Tavan, 2022). Mycoprotein emerged as one of the most successful outcomes of these efforts, particularly through the industrial production of Quorn™ by Marlow Foods in the UK, starting in 1981. Since then, the growing market for meat alternatives has spurred interest in fungal-based protein products.

Nutritionally, mycoprotein is recognized as a high-quality, “complete protein’’, providing all nine essential amino acids. It exhibits a protein digestibility-corrected amino acid score (PDCAAS) of 0.996, comparable to that of eggs and milk (100 %) and surpassing beef (92 %) (Derbyshire, 2022; Linder, 2024). Its essential amino acid content (21.1 g/100 g) exceeds that of lean beef (14.8 g/100 g) and skinless chicken (14.1 g/100 g) (Derbyshire, 2022). Beyond protein, mycoprotein contains β-glucans (dietary fiber), lipids, B vitamins, and essential minerals such as zinc, selenium, and iron, with higher sodium and iron levels than red meat, and also provides vitamin D (Derbyshire and Ayoob, 2019; Linder, 2024).

In addition to its nutritional profile, mycoprotein has been linked to several health benefits, including improved immune responses, enhanced lipid metabolism, and potential impacts on longevity (Lee et al., 2024). However, assessments of its environmental sustainability have yielded conflicting results. Some studies report greenhouse gas (GHG) emission reductions of up to 81 % when mycoprotein replaces conventional meat in the diet (Bakman et al., 2024; Shahid et al., 2024), while others emphasize the high energy demand of the fermentation process and reliance on refined carbon sources, such as glucose or other sugars, offset these environmental gains (Smetana et al., 2023). Fig. 3 provides a schematic overview of the current state of fungal mycoproteins.

Mycoproteins are among the most advanced fungal-derived foods, exhibiting a combination of high nutritional value and demonstrated consumer acceptance. However, their primary challenges include the reliance on refined substrates and energy-intensive fermentation (Akinsemolu and Onyeaka, 2025). Future advancements in this field hinge on the integration of low-cost by-products and the enhancement of process efficiency as well as further consumer acceptance.

Efforts are currently focused on improving the sustainability of mycoprotein production, particularly through the use of alternative, low-cost carbon feedstocks such as industrial side streams and food processing residues. These substrates could reduce both production costs and environmental impact, making mycoprotein a more viable component of the future circular bioeconomy. Table 2 summarizes recent advances in alternative feedstocks for mycoprotein production.

To ensure consumer safety, it is important to distinguish between established food-grade mycoprotein processes and emerging approaches that use industrial side streams or residues as substrates. Commercial products such as Quorn™ are manufactured under hazard analysis and

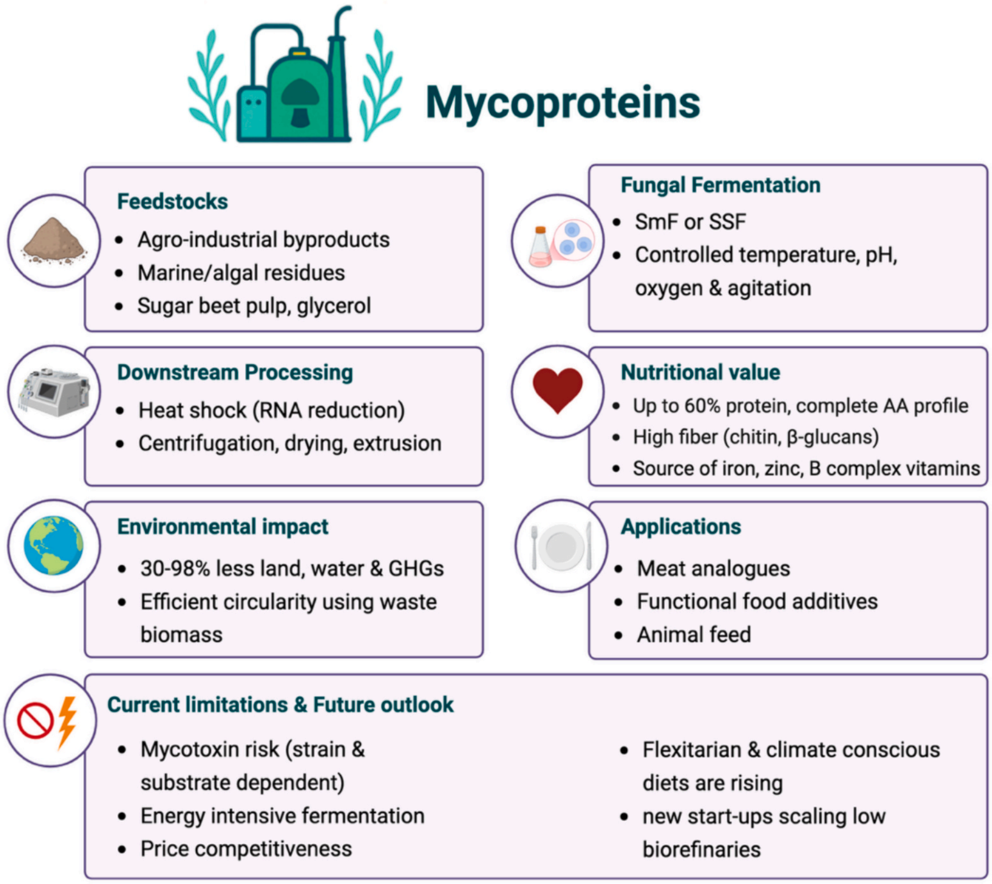

Fig. 3. Schematic overview of fungal mycoprotein production and its different aspects.

Table 2
Advances in alternative feedstocks for mycoprotein production.

Fermentation mode	Substrate	Fungal species	Key parameters	Key Findings	References
SmF	Sea water	*Fusarium venenatum*	At 28 °C	Seawater fermentation increased iron (2.2 mg/100 g wet weight) and calcium (27.9 mg/100 g wet weight) while keeping sodium within safe limits, with no plasticizers or heavy metals detected. A unique metabolite (dihydroorotic acid) was identified as a biomarker, and safety tests showed no adverse effects. The method saves ~ 50 % freshwater without reducing biomass yield.	(Yang et al., 2024)
SmF	Sugarcane molasses and corn steep liquor (CSL)	*Rhizopus microsporus* var. *oligosporus*	In 14 L airloop pilot bioreactors at 25 °C, pH 5.5 for 96 h	Achieved 38.3 g/L biomass with 70 % crude protein (≈52.15 g protein ton^{-1}h^{-1}). Process is scalable, low-energy, and cost-effective, exploiting agro-industrial by-products. Supports potential application of *R. microsporus* mycoprotein for animal feed and possibly human food.	(Furlan et al., 2024)
SmF	Date waste	*Fusarium venenatum*	3 L stirred tank bioreactor at 28 °C, pH 5.6 for 72 h	Produced 55 % protein in dried biomass with fibrous, meat-like texture. No DON/ZON toxins detected after 3 weeks; fumonisin genes present but not expressed in short-term fermentation. Prick tests showed no allergic reactions. Heavy metals detected: Pb (659 µg/kg, >EU meat limit), As (162 µg/kg), Cd (31 µg/kg), Hg (ND). Balanced essential amino acids profile, UFA/SFA ratio ~ 2:1, and mineral content (Ca, Fe, Mg, Zn) similar to those recommended for daily use	(Hashempour-Baltork et al., 2020)
SmF	By products from tomato, potato, carrot.	*Cordyceps militaris, Ganoderma resinaceum, Lentinula edodes, Pleurotus eryngii* and *Pleurotus ostreatus*	Using insect-based liquid media	Submerged fermentation on agro-by-products enabled high yields; *P. eryngii* on black soldier fly exuviae hit 23.1 g/L biomass with 51 % protein. Antioxidant metrics peaked at total phenolic content (TPC: 586.4 mg gallic acid equivalents [GAE] per 100 g dry weight, in *P. ostreatus*) and ferric reducing antioxidant Power (FRAP: 15.14 mmol trolox equivalents [TE] per 100 g dry weight, in *L. edodes*). First report of insect-exuviae liquid media for mushroom SmF, highlighting efficient valorization of insect/vegetable side-streams for protein-rich mycoprotein.	(Ferrero et al., 2024)
SmF	Seaweed and seaweed waste	*Paradendryphiella salina*	at 25 °C, pH 5.5 for 8 days with 200 rpm agitation	Fermentation increased protein (~141 % and ~ 131 %) and amino acids (+73.5 %). Carbohydrates reduced by 35–38 %; alginate dropped by 1.5-fold and cellulose by 2.9-fold. Fermented biomass showed the highest phenolic content (+181 %) and antioxidant activity (+86 %), enhancing nutritional and functional value.	(Salgado et al., 2021)
SmF	Pea-processing byproduct	*Neurospora intermedia, Aspergillus oryzae* var. *oryzae, Fusarium venenatum* and *Rhizopus oryzae*	250 mL Erlenmeyer flasks at 35 °C, pH 5.5 for 8 days with 150 rpm agitation	*A. oryzae* produced 0.26 g protein/g byproduct, yielding ~ 680 kg fungal biomass and ~ 38 % extra protein per ton of pea-processing residues. This is the first demonstration of pea-industry byproducts as substrates for vegan mycoprotein production	(Souza Filho et al., 2018)
SSF	Pea protein extract	*Penicillium limosum*	50 L fermenter	A safe, protein-rich strain of *P. limosum* was isolated and blended with pea protein isolate to produce high-moisture meat analogues (HMMA). At 5 % inclusion, mycoprotein improved viscosity, chewiness, fibrous texture, and protein digestibility (68.7 %), while increasing oil absorption and slightly reducing water absorption capacity; higher levels weakened texture and digestibility.	(Zhang et al., 2024b)

critical control points (HACCP) protocols, which require strict monitoring of mycotoxins, allergens, and trace metals to comply with food safety regulations. In contrast, side-stream-based processes may introduce additional risks due to the variability and potential contamination of raw materials. Therefore, pretreatments such as thermal or enzymatic processing, detoxification steps, or separation of inhibitory compounds are often necessary to ensure substrate safety and quality. Integrating these safety considerations will be critical for translating side-stream valorization into food-grade mycoprotein production.

4.2. Enzymes

The global industrial enzyme market is projected to grow from USD 7.9 billion in 2024 to USD 11.2 billion by 2029, at a compound annual growth rate (CAGR) of 7.2 % (MARKETS AND MARKETS, 2023). Fungal enzymes are a major driver of this growth due to their high yields, ease of extraction, and diverse catalytic capabilities (Das et al., 2024).

Among fungi, *Aspergillus niger* is particularly prominent, producing commercially relevant enzymes such as amylase, lactase, cellulase, pectinase, glucose oxidase, and acid protease, widely used in the food, fermentation, and pharmaceutical industries (Zhang et al., 2025). Optimizing media composition and physicochemical conditions is critical to enhancing enzyme yields and reducing production costs (Bhattacharya et al., 2024).

Both SSF and SmF are employed for fungal enzyme production. However, SSF is often preferred for filamentous fungi, as it more closely mimics their natural habitat and can enhance enzyme productivity (Corrêa et al., 2024). Lignocellulosic residues are frequently used as substrates to produce lignocellulose-degrading enzymes, including cellulases (e.g., endoglucanase, β-glucosidase), hemicellulases (e.g., xylanase), and lignin-modifying enzymes, all of which are relevant to sectors such as biofuels, paper, textiles, food, and animal feed (Andriani et al., 2020; Bhattacharya et al., 2024).

In addition to cellulolytic enzymes, fungi synthesize other industrially important enzymes: pectinases, used in juice and wine clarification (Mukhopadhyay et al., 2024); amylases, essential in glucose syrup production and baking (Silva et al., 2025); proteases, applied in food processing, leather, detergents, and pharmaceuticals (Moussi et al., 2025); lipases, with roles in biodiesel production, flavor enhancement, and cleaning agents (Kumar et al., 2023).

Multiple fungal genera such as *Trichoderma*, *Penicillium*, *Aspergillus*, *Phanerochaete*, *Fusarium*, and *Trametes* are noted for their capacity to degrade both crystalline and amorphous cellulose (Leong et al., 2021). Meanwhile, protease production has been reported from *Aspergillus*, *Penicillium*, *Rhizopus*, *Mucor*, *Humicola*, *Thermoascus*, and *Thermomyces* (Moussi et al., 2025).

For example, SSF using wheat bran and grape pomace with *Trametes villosa* and *Trichoderma asperellum* yielded high levels of β-glucosidase (218.91 U/gds), xylanase (170.28 U/gds), β-xylosidase (19.39 U/gds), and laccase (16.5 U/gds) (Corrêa et al., 2024). Another study using *Trichoderma reesei* MTCC 4876 on a waste sorghum grass–cottonseed oil cake medium in a 6-L SSF-packed bed reactor reported significant production of cellulase (20.64 ± 0.36 FPU/g-ds) and xylanase (16,186 ± 912 IU/g-ds). These enzymes improved apple juice clarity by reducing turbidity and viscosity while increasing sugar release (Bhattacharya et al., 2024). Fig. 4 illustrates fungal enzymes diversity and their various applications.

A wide range of filamentous fungi and agro-industrial substrates have shown potential for cost-effective enzyme production, offering scalable solutions for various biorefinery and industrial processes. A summary of some recent studies on fungal strains, fermentation conditions, enzyme yields, and substrates is presented in Table 3.

Overall, fungal fermentation represents one of the most promising strategies for sustainable enzyme production, with cellulases, hemicellulases, proteases, lipases, and pectinases emerging as the most commercially relevant product streams due to their wide application in food, feed, detergents, textiles, pharmaceuticals, and biofuels. SSF on agro-industrial residues offers a cost-effective approach, aligning with

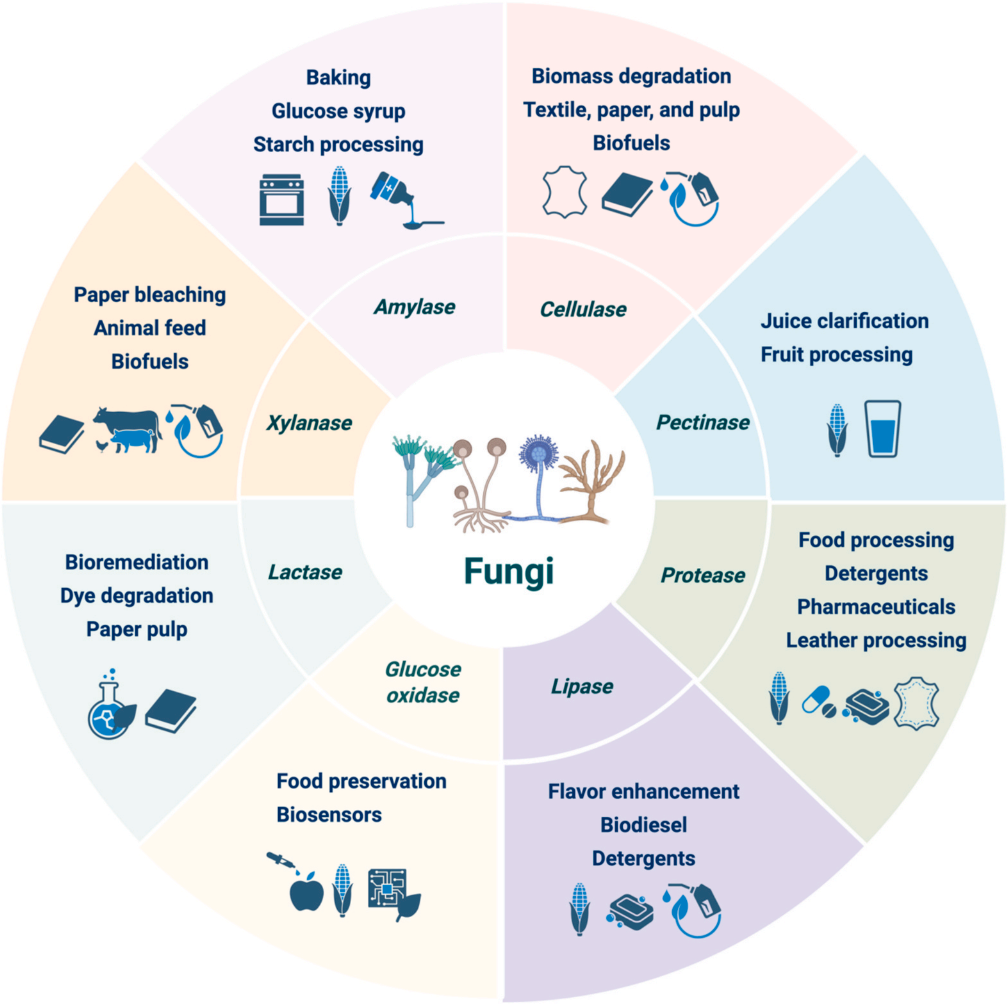

Fig. 4. Diversity of fungal derived enzymes and their fields of applications.

Table 3
Summary of recent studies on production of fungal enzymes using alternative feedstocks.

Enzyme	Fungus species	Fermentation condition	Substrate	Enzyme activity	Reference
Lipase	*Aspergillus niger*	SSF	*C. inophyllum* oil cake and coconut oil cake	127.5 U/g substrate	(Al-Khattaf et al., 2024)
Cellulase Xylanase	*Aspergillus terreus*	SSF (30 °C for 8 days, pH 7)	Moistened rice straw	16.466U/ mg protein 407.959 U/mg protein	(Hassan et al., 2024)
Aspartic protease	*Mucor racemosus*	Rotating drum-type SSF (flow rate of 1 L/min, 20 °C for 5 days)	Wheat bran, sugar beet, and barley	35 U/ mg	(Qasim et al., 2025)
Lipase	*Penicillium polonicum*	SSF (55 % moisture, 27 °C for 96 h)	Sunflower seed cake and rice husk	29.3 U/g	(Carvalho et al., 2024)
Glucoamylase	*Aspergillus fumigatus*	SSF (30 °C for 7 days)	Mixed food waste	2.9 U/ml	(Das et al., 2024).
Pectinase	*Aspergillus terreus*	SmF (pH 6.0, 28 °C for 72 h)	Sweet lime peel and yeast extract	450 U/mg	(Mukhopadhyay et al., 2024)
Protease	*Aspergillus candidus*	SSF (PH 9, 24 °C for 8 days, 53 % moisture content)	Wheat bran	3076.92 U/mL	(Moussi et al., 2025)
Amylases	*Pleurotus pulmonarius*	SSF (PH 9, 28 °C for 3 days)	Cocoa waste, husks, and cocoa bean peel	83.90 U/gds.	(Silva et al., 2025)
Glucoamylase α-amylase	*Aspergillus clavatus*	SmF (PH 6.5, 25 °C for 72 h)	Starch, yeast extract, peptone, sodium phosphate buffer.	4.5 U/mL 6.5–55 U/mL	(Mendonça et al., 2023)
Pectinase	*Aspergillus niger*	SmF (28 °C on a rotary shaker for 7 days)	Apple juice	~27 U/mL	(Wagh et al., 2022)
		SSF (28 °C for 5 to 7 days)	Dried orange peel, banana peel and rice bran	36.39 U/mL	

circular bioeconomy principles while reducing substrate and waste disposal costs. Nonetheless, several technical bottlenecks remain, including the heterogeneity and recalcitrance of lignocellulosic feedstocks, challenges in scaling up SSF due to heat, aeration, and moisture transfer limitations, and the high costs of downstream recovery and purification to meet industrial enzyme quality standards (Borkertas et al., 2025; Mansour et al., 2016).

4.3. Biopolymers and biochemicals

Fungi are prolific producers of a wide range of biopolymers and biochemicals, including polysaccharides, biosurfactants, and small bioactive molecules, many of which have applications in the pharmaceutical, food, cosmetic, and environmental sectors (Ali et al., 2024; Wadhwa et al., 2024). These compounds are often synthesized using low-cost agro-industrial residues, positioning fungi as key contributors to their sustainable bioproduction.

Fungal polysaccharides, particularly β-glucans, have gained increasing interest due to their nutritional, immunomodulatory, and antioxidant properties (Pan et al., 2025a). Chitin is also widely distributed in fungi, occurring in *Ascomycetes*, *Basidiomycetes*, and *Phycomycetes*. These biopolymers can be obtained from fruiting bodies, spores, or fermentation processes, including SmF, which yields both intra- and extracellular polysaccharides (Abdeshahian et al., 2021).

Fungal fermentation has been shown as a sustainable approach for converting agro-industrial lignocellulosic waste into high-value biochemicals and biopolymers, offering a viable alternative to petrochemical-based production. In this regard, the *Aspergillus* strains (e.g. A. *oryzae*, A. *terreus* and A. *tubingensis*) have been employed in SmF and SSF to produce itaconic and fumaric acids from acid- or enzymatically pretreated wheat bran and corn cobs (Jimenez-Quero et al., 2017, 2016; Jiménez-Quero et al., 2020). Fungi also produce biosurfactants, a class of amphiphilic molecules with applications in bioremediation, food processing, cosmetics, and pharmaceuticals due to their emulsifying, foaming, and dispersing properties (Mahmoud et al., 2024). Structurally, they consist of hydrophobic (e.g., fatty acids) and hydrophilic (e.g., carbohydrates, amino acids, phosphate groups) moieties. Various fungi, including *Trichoderma* spp., *Fusarium fujikuroi*, *Aspergillus niger*, and *Penicillium chrysogenum*, have shown the ability to produce biosurfactants using low-cost substrates such as agricultural and industrial waste (Asgher et al., 2020; Mahmoud et al., 2024). For instance, *A. niger* produced biosurfactants during SSF on banana stalk powder, yielding up to 5.5 g/L with an emulsification index of 62.3 % after optimization (Asgher et al., 2020). Other feedstocks such as crude oil sludge (Othman et al., 2022), waste cooking oil (Fernandes et al., 2023), and black cumin cake (Ciurko et al., 2023) have also been successfully used to produce biosurfactants with environmental and industrial applications.

In addition to biopolymers, fungi synthesize and release a diverse array of low-molecular-weight bioactive compounds such as alkaloids, polyketides, terpenoids, meroterpenoids, and peptides, many of which are used in pharmaceuticals, agrochemicals, and cosmetics (Pan et al., 2025b; Ramadan et al., 2024). These compounds are often produced *via* fungal enzymatic transformation of complex feedstocks. For instance, fungal pretreatment of oil palm empty fruit bunches using *Serpula lacrymans* facilitated lignin depolymerization, enabling the release of phenolic compounds such as vanillin, with an extraction yield of 3.48 μg/g after 42 days (Guo et al., 2025). This treatment also enhanced biomethane potential during subsequent anaerobic digestion, demonstrating both biochemical and bioenergy co-benefits.

Pretreatment strategies are often needed to improve biochemical yields, particularly when dealing with recalcitrant lignocellulosic substrates. A recent study applied fungal delignification using *A. niger* and white rot fungi, followed by mild acid hydrolysis, to improve sugar availability for xylitol production from detoxified de-oiled rice bran. This sequential method achieved a final concentration of 23.56 g/L xylitol with a yield of 0.48 g/g xylose after 96 h of fermentation using *Pichia fermentans* (Kayalvizhi and Jacob, 2025). Table 4 provides a summary on fungal-derived compounds, their sources, and production conditions.

In general, fungi represent a versatile platform for sustainable bioproduction, with the most promising product streams including polysaccharides (notably β-glucans), biosurfactants, and low-molecular-weight bioactive compounds for applications in food, pharmaceuticals, cosmetics, and environmental remediation. The use of agro-industrial side streams as low-cost substrates offers a sustainable route to scale-up, but broader commercialization still faces several technical bottlenecks. Among these are the high production costs, particularly in downstream processing, which can account for up to 60 % of total costs, as well as purification and recovery methods that remain inefficient and resource intensive (Luft et al., 2020).

Table 4
Recent advances on fungal derived biopolymers and biochemicals using alternative feedstocks.

Biochemicals	Fungus species	Fermentation condition	Substrate	Yield	Reference
Perylenequinone derivative	*Alternaria alstroemeriae*	SmF (28 °C for 14 days)	Rice and water as substrate	NA	(Li et al., 2025b)
Diketopiperazines (versicoines)	*Aspergillus puulaauensis*	SmF (25 °C for 16 days)	Rice and distilled artificial seawater.	NA	(Wu et al., 2025)
Prenyl quinone compounds	*Panus lecomtei*	SmF (40 °C for 7 days, *200* r/min)	Yeast extract, Magnesium sulfate heptahydrate, water	NA	(Wang et al., 2025)
Vanillic acid Nomilin glucoside Trimethoxybenzaldehyde Phenol glucuronide	*Trichoderma asperellum*	SSF (22 °C for 12 days in darkness)	Fruit waste (orange, apple, banana, kiwi) and wood sawdust	0.45 1.12 2.89 1.80 (mg/100 g)	(Bulgari et al., 2024)
ε-poly-L-lysine	*Streptomyces albulus*	SmF (10 % v/v inoculum, 5-L, pH 6.8, 30 °C, aeration of 0.5 vvm)	Cassava starch as substitute for glucose in medium (glucose, yeast extract, nitrogen, and inorganic salts)	27.56 g/L.	(Li et al., 2024b)
Methyl ferulate and oleic acid	*Aspergillus pseudodeflectus*	SSF (pH 7.0, 30 °C for 10 days)	Wheat bran and sodium nitrate	0.18 g/1g substrate	(Ramadan et al., 2024)
Phenolic compounds	*Aspergillus niger*	SSF (pH 5.5, 30 °C for 2 days)	*Flourensia cernua*	43.440 mg GAE/g	(Usme-Duque et al., 2025)
Chlorogenic acid	*Aspergillus oryzae and Aspergillus niger*	SSF (30 °C for 8–13 days, forced aeration flow rate 0.5 L/min, moisturizing pulse of 30 mL/d)	Spent coffee ground	76.1 mg/g substrate	(Arancibia-Díaz et al., 2025)

4.4. *Feed and compost applications*

To address food security challenges, future animal feed ingredients must not compete with resources intended for human consumption, especially given the rapid growth of the global population and the increasing scarcity of food supplies. A prime example is fish meal, which is predominantly sourced from wild-caught fish, a resource with limited availability (Péron et al., 2010).

Industrial waste biomass holds considerable promise as a feedstock for ruminants or as compost. However, depending on its composition, a pretreatment process may be necessary to enhance its suitability (Chaurasia et al., 2025). Such pretreatment could involve reducing lignin content or mitigating heavy metal contamination and toxicity concerns. Biological pretreatments, particularly those utilizing fungi, offer a sustainable, low-energy solution (Rasmussen et al., 2010). Specifically, white rot fungi have been shown to effectively degrade lignin while preserving the carbohydrate content, making the biomass suitable for ruminant consumption (González et al., 2021; Martens et al., 2023; Van Kuijk et al., 2015). This biological method presents a distinct advantage over chemical treatments, such as alkali or urea, which have significant drawbacks. In this case of fungal pretreatment, SSF is particularly advantageous due to its simplicity, cost-effectiveness, and minimal effluent production, making it the preferred choice of fermentation (Duong et al., 2024; Pallín et al., 2024; Van Kuijk et al., 2015).

The application and impacts of fungal-based feed derived from food and agricultural waste has been explored across the aquaculture and poultry sectors, including for fish, chickens and broilers (Bergman et al., 2024; Hamza and Gunyar, 2022; Khan et al., 2024a; Onomu and Okuthe, 2024; Zantioti et al., 2025). Such biomass provides essential amino acids and fats that rival those found in fish meal or soybeans. Different studies indicate improvements in both the nutritional profile of the fungal biomass and the digestion efficiency for ruminants (Khan et al., 2024b; Rulli et al., 2021; Sufyan et al., 2024). Fungal feed from *Aspergillus oryzae* as supplement increases nutrient digestion and boosts milk production yield in dairy cows (Cantet et al., 2025). Furthermore, SSF of BSG using the edible fungus *Pleurotus ostreatus* has enhanced its nutritional profile as animal feed, resulting in a 49.5 % increase in protein content, a tenfold rise in β-glucans, and an 11.4 % reduction in cellulose, thereby improving digestibility (Eliopoulos et al., 2022). Yet, variability in waste biomass composition, risks of contaminants, and the absence of standardized large-scale processing protocols pose critical limitations. Future efforts must focus on safety assessments, and techno-economic optimization to enable reliable industrial deployment. Table 5 presents some recent studies on utilization of fungal fermentation strategies for producing feed.

5. Life cycle and techno economic assessments

Recent techno economic assessments (TEAs) consistently highlight fungal valorization as one of the most economically attractive routes for converting agro-industrial residues into high-value outputs, especially lignocellulolytic enzymes. For instance, a TEA of laccase production *via* SSF on perennial biomass estimated a minimum selling price of USD 0.05 per kilo-unit (kU) at small scales (~230 Mg/year), emphasizing the cost benefits of using low-cost feedstocks and simpler downstream recovery processes (Rahic et al., 2025). Similarly, TEA of cellulolytic enzyme production from coffee husk using *Trichoderma reesei* compared liquid and powder formulations at an annual scale of 1,893 tons. The analysis showed that the liquid enzyme product was the most favorable option, achieving a net present value of USD 32.96 million, while also meeting industrial specifications for enzyme concentration and moisture content (Coral-Velasco et al., 2024). Recent life cycle assessment (LCA) also reinforce both the opportunities and challenges of positioning fungal-derived proteins within future sustainable diets. (Fernández-López et al., 2024) highlighted that substrate choice and pretreatment steps dominate the environmental footprint, while electricity demand consistently emerged as the critical hotspot across fungal fermentation systems. However, methodological inconsistencies, particularly in defining system boundaries when organic waste streams are employed, continue to complicate robust comparisons, and nutritional quality (e.g., amino acid content) remains insufficiently integrated into impact assessments.

6. Challenges, limitations and next frontiers in fungal biorefinery applications

Fungal-based biorefineries are gaining traction in response to global sustainability, health and ethical concerns. Their long-term success and viability hinges on addressing a series of technical, regulatory and socioeconomic challenges and limitations. This section outlines the most pressing aspects which is also summarized in a schematic overview in Fig. 5.

6.1. *Feedstock composition and logistics*

One major challenge is the inconsistent composition of the waste

Table 5
Recent advances on feed production using fungi and alternative substrates.

Fermentation mode	Substrate	Fungi	Key findings	References
SmF	Sugarcane vinasse from bioethanol industry	*Aspergillus* sp. *V1*	Fungal biomass met the nutritional standards for fish feed with safe aflatoxin levels. No adverse effects in fish feeding trials.	(Del Gobbo et al., 2023)
SSF	Wheat straw	*P. ostreatus*	Reduced lignin content, increased crude protein (46 %), improved intake, digestibility and cow milk yield	(Sufyan et al., 2024)
SmF	Wheat straw and food waste	*Trametes versicolor* and *Pleurotus ostreatus*	Reduced lignin content up to 48 %. Enriched essential amino acids, and improved nitrogen profile, improving energy and protein value	(Sun et al., 2023)
SmF	Green alga *Ulva rigida*	*Trichoderma reesei*	Methionine content, a limiting amino acid increased 4 times. The protein digestibility of the fungal biomass increased from 71 % to 94 %	(Brain-Isasi et al., 2021)
SSF	Agro residues (groundnut shells, pigeon pea husk, wheat bran)	Endophytic fungi isolated from C. *paniculatus* leaves and twigs	Phytate and tannins content significantly reduced in processed waste. Therefore, processed waste can be used up to 20 % for the commercial poultry diet without any adverse effects.	(Patil et al., 2020)
SSF	Agro-industrial residue of faba bean	*Aspergillus niger*	Improved body weight gain, feed conversion, antioxidant status and immune responses.	(Al-Gheffari et al., 2024)
NA	Sulphite stillage from bioethanol production side streams grown on lignocellulosic waste	*P. variotii*	*P. variotii* replaced 20 % of crude protein in diets for Atlantic salmon. This dietary inclusion increased nutrient utilization efficiency, improved gut health and exhibited immune-modulatory capacity in the intestine of salmon. It also reduced GHG emissions and dissolved waste output.	(Hooft et al., 2025)

derived and side stream feedstocks, which often varies due to seasonality, processing methods, or source heterogeneity (Khatami et al., 2021; Mou et al., 2024). Such fluctuations can significantly affect fungal growth, enzyme activity, and overall process performance, requiring adaptive strategies or additional processing steps to ensure stable product quality (Novy et al., 2021). In addition, logistics for collection, transportation, and storage impose extra costs, especially at industrial scale. One potential solution is the integration of fungal bioprocesses within existing industrial settings, such as food processing, or biofuel facilities, where waste streams are generated on-site. This not only reduces logistical burdens but also supports the development of multi-stream biorefineries. However, this transition demands further infrastructure upgrades and financial investment, and supportive policy frameworks.

In recent years, several successful pilot and demonstration scale implementations have been supported by Horizon Europe and CBE_JU funding programs, underscoring the feasibility of fungal biorefineries. For instance, Fl'Our Planet (GA ID: 190144130) has established a scalable SSF platform (100 T/y capacity), converting fruit and vegetable side streams into high value functional food ingredients. Other projects, including PROLIFIC (under GA No 790157), FUNGUSCHAIN (under GA No 720720), MY-FI (GA ID: 101000719) and Smart protein (under GA No 862957), have demonstrated the valorization of various side streams into mycoprotein, dietary fibers, bioplastics, materials, antimicrobial and antioxidant compounds.

6.2. *Product safety and health concerns*

When using waste-derived substrates, toxins such as mycotoxins and cyanotoxins may form during fermentation, requiring additional safety measures and downstream processing to ensure product safety, particularly for food and feed applications. Additionally, in food applications, products like mycoproteins may contain high nucleic acid levels, which have been linked to kidney stone formation (Gundupalli et al., 2024; Sillman et al., 2019). Furthermore, long-term health impacts of fungal-based foods, such as their effects on glycemic index, immune function,

Fig. 5. Current limitations and next frontiers of fungal based biorefineries.

and metabolic health, shall be further studied.

Nevertheless, fungal proteins pose lower allergenic risks in comparison to other alternative proteins such as insect proteins and soy, while the reported adverse reactions remain limited in comparison. In this regard, the allergenic risks of fungal protein, particularly mycoprotein, have been extensively evaluated and found to be very low compared with common food allergens. Following its “GRAS” approval in the United States, only a handful of confirmed allergic cases have been reported since its introduction, with large-scale reviews concluding that adverse reactions occur at extremely low frequencies around 1 in 9 million packages sold. Most reported reactions are gastrointestinal and largely attributed to the high fiber content of mycoprotein rather than true IgE-mediated allergy (Finnigan et al., 2019; Miller and Dwyer, 2001).

6.3. *Emerging feedstocks*

Algal residues, both micro- and macroalgae offer a promising substrate for fungal fermentation, as they are abundant, fast growing, non-dependent on freshwater, and rich in nutrients and have low allergenicity (Bora et al., 2024; Fabris et al., 2020; Kaur et al., 2025). Future work should explore proteins and other high-value compounds derived from fungi-algae processes, including bioactives, enzymes, and materials. One major challenge in utilizing algal biomass lies in its high moisture content, making it perishable and prone to microbial spoilage (Lytou et al., 2021). Fungal metabolism can stabilize the algal biomass, enhance its shelf life and reduce the need for energy intensive drying. Moreover, fermentation of algal residues has shown to improve organoleptic properties, reducing undesirable tastes and odors and enriching biomass in proteins and essential amino acids (Bonilla Loaiza et al., 2022; Sarıtaş et al., 2024). The resulting fermented biomass can be tailored for various applications. Several Horizon EU-funded projects, including CIRCALGAE (GA ID:101060607) and ProFuture (GA ID:862980) are exploring the integration of algal bioprocesses to develop ingredients for food, feed and cosmetics, increasing the industrial relevance of these synergies.

Another potential feedstock is biofuel production residues. Bioethanol production from corn generates distillers dried grains with solubles (DDGS) as a major byproduct, with global ethanol production reaching 35.53 billion gallons in 2024. On average, 100 kg of corn in dry mill biorefineries produces 27 kg of DDGS, which is rich in proteins up to 31 % and 8–12 % lipids, making it a promising substrate for fungal fermentation (Renewable Fuels Association, 2022; Veljković et al., 2018). DDGS has been successfully used to produce organic acids and hydrolytic enzymes. For instance, *Rhizomucor miehei* fermentation of DDGS generated dry fermented solids (DFS) with lipase activity, which catalyzed esterification of oleic acid and ethanol, achieving conversion rates of 72 % and 80 % in tray and fixed-bed reactors, respectively (Aguieiras et al., 2024).

6.4. *Research and technological innovation*

To fully exploit the potential of side stream and waste-derived substrates, especially for food applications, multi-omics tools such as metagenomic sequencing and metabolic profiling, can be applied to map microbial communities and fermentation pathways. As shown by (Maini Rekdal et al., 2024), this integrative analysis can elucidate key interactions and improve process efficiency and product quality. For example, transcriptomic and metabolomic integration has already been used in *Aspergillus* species to reveal condition-dependent activation of cryptic biosynthetic gene clusters (BGCs), while proteomics validated the presence of key enzymes, linking gene expression to metabolite production (Prakash et al., 2025).

Moreover, the application of artificial intelligence (AI) in fungal fermentation is a highly promising yet underutilized field. AI-driven models can support process optimization, strain selection, and feedstock matching, particularly when working with heterogeneous and variable side streams. For example, the Circular Bio-Based Europe (CBE) founded ZEST project (GA ID:101157382) is currently trying to integrate AI-based monitoring in process optimization and zero-waste production systems for fungal fermentation proteins with applications in food, feed and cosmetics. Additionally, AlphaFold-based protein structure prediction has been applied to fungal enzymes, such as cytochrome P450s in *Aspergillus*, where AI-driven modeling of enzyme–substrate interactions helped identify pathway bottlenecks and guided fermentation optimization strategies (Prakash et al., 2025). Similarly, AI and machine learning were applied to optimize SmF of *Aspergillus terreus* for L-asparaginase production, an enzyme with applications in cancer therapy and food processing (Baskar et al., 2025).

When combined with omics tools, AI could enable even more resilient and adaptive fermentation systems, aligned with circular bioeconomy principles.

6.5. *Consumer perception and market integration*

Despite environmental benefits, the acceptance of alternative proteins and generally products derived from waste streams still faces consumer skepticism. Consumer acceptance ultimately depends on sensory attributes and price competitiveness, which often outweigh sustainability arguments. Neophobia and the "waste-derived" stigma remain major barriers, particularly for food and cosmetic applications (Altintzoglou et al., 2021; Giacalone and Jaeger, 2023; Lin et al., 2025). However, flexitarian and climate-conscious consumer segments are rapidly growing, offering new opportunities for fungal derived products. Addressing concerns around safety, quality, and transparency through clear labeling through positive framing, storytelling, and co-creation strategies (Coderoni and Perito, 2020), education and communication strategies, and regulatory support is crucial for their market adoption. Ultimately, aligning product development with consumer expectations in terms of taste, convenience, and affordability will be key to their market integration (Drewnowski and Monsivais, 2020).

6.6. *Prioritization of challenges*

Among these challenges, ensuring feedstock consistency and product safety remains the most urgent, as they directly affect process reliability and consumer trust. By contrast, advances in AI-driven optimization, omics integration, and improved bioreactor design appear more solvable in the short to medium term, supported by ongoing EU-funded projects. In the longer run, achieving market acceptance and regulatory harmonization will be essential to unlock the full potential of fungal biorefineries in food, feed, and biomaterials.

7. Conclusions

Fungal fermentation offers a powerful and sustainable platform for trasforming industrial and agricultural residues into high-value biomolecules, bridging waste valorization with renewable biomanufacturing. Its versatility and scalability position fungi as a key catalyst in advancing circular bioeconomy principles through efficient resource recovery and low-carbon production.

Fungal fermentation stands at the crossroads of biotechnology, food innovation and environmental stewardship. By coupling process optimization with the intelligent use of diverse side streams, it can drive global sustainability; reducing waste, closing nutrient cycles and generating renewable sources of protein, enzymes and biochemicals. The continued evolution of fungal biorefineries, guided by interdisciplinary innovation and industrial collaboration, will be crucial to shaping resilient and resource-efficient bioeconomy that truly feeds, fuels and sustains the future.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the writing preparation of this work, the authors used GPT-4o in order to improve the language and readability of the manuscript. After using this tool, the authors have reviewed and edited the content as needed and take full responsibility of the content of the published article.

CRediT authorship contribution statement

Kasra Khatami: Writing – review & editing, Writing – original draft, Visualization, Project administration, Conceptualization. **Zeinab Qazanfarzadeh:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Amparo Jiménez-Quero:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Amparo Jimenez Quero reports financial support was provided by European Commission. Amparo Jimenez Quero reports financial support was provided by Swedish Research Council Formas. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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Further reading

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