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Review

# The duality of filamentous fungi: Beneficial uses and risks in the food industry

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ABSTRACT

Filamentous fungi are ubiquitous microorganisms, comprising approximately 150,000 documented species, although global estimates suggest a total diversity of 11 million species. The role of filamentous fungi in the food supply chain is complex, balancing production benefits with risks of contamination and health concerns. These fungi have both positive and negative impacts on the food industry, reflecting their duality. Historically, fungi have played a key role in the production of antibiotics, such as penicillin, and have revolutionized food production, particularly cheese manufacturing, by contributing to the development of new sensory traits. Currently, filamentous fungi are extensively used in food production for biomass, protein, acid, enzyme, pigment, and biopolymer production, and the commercialization of fungal cultures has been well established. However, research into new fungal strains for food applications continues to emerge. However, filamentous fungi are a major cause of spoilage in the food industry. Due to their reproductive characteristics, they can contaminate food and lead to mold growth, causing flavors and odor. A significant concern is mycotoxin-producing fungi, as the ingestion of mycotoxins has been linked to adverse health effects. Despite ongoing studies, the mechanisms behind mycotoxin production remain incompletely understood. This review aims to explore both the positive and negative aspects of filamentous fungi in the food industry, highlighting the current challenges in their commercialization and the potential negative impacts they have on food safety and quality.

## 1. Introduction

Filamentous fungi play an essential role in the environment, acting as primary agents of organic matter decomposition and contributing essential components to the ecosystem for microbial communities. Additionally, they facilitate nutrient absorption in plants (Research Features, 2017). In food production, filamentous fungi are being increasingly utilized, particularly in the large-scale synthesis of

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ingredients, such as organic acids, pigments, biopolymers, proteins, and enzymes, as well as in the production of specific food products (Huq et al., 2022; Siddiqui, 2016). Similar to bacterial cultures and their by products, fungal cultures and their derivatives can obtain Generally Recognized as Safe (GRAS) or Qualified Presumption of Safety (QPS) status (Singh & Gaur, 2021). Several filamentous fungi, including *Aspergillus, Penicillium, Fusarium, Mucor, Trichoderma, Rhizopus, Monascus,* and *Talaromyces* spp., are used in food production, either directly as food or as components of food products (Takahashi et al., 2020). Numerous fungal-derived products are commercially available for food applications (Table 1).

Despite the widespread commercialization of fungi and their byproducts in a continually expanding market, certain factors must be considered. Studies have suggested that the global reduction in crop yields may be linked to the spread of fungal pathogens into previously unexplored geographic regions (Meyer et al., 2020). Additionally, the ongoing search for new fungicides is contributing to the rise of antifungal resistance, exacerbating clinical fungal infections worldwide (Meyer et al., 2020). Lind et al. (2018) identified important genes associated with the pathogenicity of *Aspergillus fumigatus*. Notably, the presence of the *brlA* gene, which regulates secondary metabolism in this fungus, is controlled by *laeA*, a major regulator of this metabolic pathway. This regulatory network drives secondary metabolism and plays a direct role in cellular processes linked to the virulence of *A. fumigatus* (Lind et al., 2018). *A. fumigatus* is commonly found in the air and soil and has also been historically isolated from food (Melo dos Santos et al., 2003; Egbuta et al., 2015; Nieminen et al., 2002), but its role in aspergillosis, a clinical disease and its increasing resistance to antifungal treatments have been confirmed (Lestrade et al., 2018).

**Table 1**
Commercial fungal derived products available for food applications.

| Fungi product | Company | Food application | Website |
|---|---|---|---|
| ClearIQ™ Natural Flavor | Myco Technology™ | Flavor/ Ingredient | https://www.mycoiq.com/ |
| Honey Truffle Sweet Protein | Myco Technology™ | Protein/ Ingredient | https://www.mycoiq.com/ |
| Quorn Meatless ChiQin Patties | Quorn | Vegan Protein (Burguer) | https://www.quorn.us/products/meatless-burgers |
| Mycelium | Mycovation | Ingredient/ Protein snacks application | https://www.mycovation.asia/ |
| ProteVin™ | NextFerm | Vegan Protein | https://nextferm.com/protevin/ |
| BakeZime® | Dsm-firmenich | Glucose oxidase/ Enzyme/ Ingredient | https://www.dsm-firmenich.com/en/home.html |
| Tolerase® | Dsm-firmenich | Lactase Enzyme/ Ingredient | https://www.dsm-firmenich.com/en/home.html |
| Plant Based Meal | More Foods | Vegan Protein | https://www.more-foods.co/ |
| Chy-Max® | CHR Hansen | Enzyme/ Ingredient for cheese production | https://www.chr-hansen.com/ |
| Portabella Mushroom Jerk | Savory Wild | Flavor/ Ingredient | https://savorywild.com/ |
| MonascusRed® | Biotech | Colorant/ Ingredient | https://biotech.uplb.edu.ph/technologies/monascus-red-colorant/ |
| Red+ | Michroma | Colorant/ Ingredient | https://www.michroma.co/our-ingredients |
| My®BACON | My Forest Foods | Whole cut meat analogues | https://myforestfoods.com/mybacon |
| Citric acid | Tate&Lyle | Acidulant/ Ingredient | https://www.tateandlyle.com/ |
| Mixed mushrooms with Porcini | Nova Funghi | Protein/ ready-to-eat product | https://novafunghi.it/ |
| Promyc® S110 | Naplasol | Mycoprotein | https://www.promyc.com/products |
| Choozit® LYO Cheese cultures | Danisco | *Penicillium roquefort*/ Cheese Production | https://www.iff.com/food-beverage/dairy/ |

Another important aspect related to filamentous fungi is their impact on food spoilage. This represents a significant challenge for the processing industry, as spoilage agents are undesirable and can lead to several problems, including visible mold growth and flavor and odor productions (Garnier et al., 2017). Recent studies have also highlighted the increasing occurrence of biofilm production by fungi, which can be difficult to remove, especially considering that spores can be disseminated throughout the industrial environment (Miranda et al., 2022). Although studies on fungal biofilm formation have been limited in recent years, it is essential to emphasize the relevance of this topic. A recent study explored the adaptation of methods typically used for bacteria and yeasts to assess fungal biofilm formation, aiming to identify reproducible and reliable methodologies for evaluating fungal performance and biofilm development (Kulišová et al., 2023).

In the food industry, quality control management systems, such as Good Manufacturing Practices (GMP), Hazard Analysis and Critical Control Points (HACCP), and other quality systems must be robust and effective to prevent contamination by pathogenic and spoilage microorganisms, including both bacteria and filamentous fungi (Garnier et al., 2017) Recently, several studies have explored the antifungal activity of bacteria as a potential biocontrol strategy for fungal contaminants in the food industry (Souza et al., 2023; Taroub et al., 2019; Zhao et al., 2022). This approach offers an alternative to traditional chemical preservatives, to which fungi are increasingly developing resistance mechanisms. Furthermore, this aligns with the growing “clean label” trend, which seeks to reduce the use of chemical preservatives in food processing (Guimarães et al., 2018; Ma et al., 2019; Simões et al., 2023; Souza et al., 2023; Taroub et al., 2019; Zhao et al., 2022).

The ability of filamentous fungi to produce mycotoxins in food must also be addressed. Mycotoxins such as ochratoxins, aflatoxins (B1, B2, G1, G2, $M_{1,}$ and $M_2$), patulin, fumonisins, zearalenone, trichothecenes, alternariol, deoxynivalenol and enniatin B represent a significant public health concern. These toxins cause a range of diseases, such as carcinomas, impaired renal function, genotoxic, cytotoxic, DNA damage, and reproductive toxicity. The main symptoms of exposure include apathy, vomiting, and food rejection (Hamad et al., 2022). Recent studies have identified and quantified mycotoxins in food products, such as fruit, cereal, tea, and dairy products (Carraturo et al., 2018; Ji et al., 2022; Rodríguez-Cañás et al., 2023).

Considering the significant role that fungi play in the food chain, this review aims to explore the pathways through which fungi impact the food industry. The dual nature of fungi's effects are explored, focusing on their beneficial effect in food applications and providing an overview of fungal cultures for food production in the market,

and their detrimental effects, such as spoilage and safety concerns, as mycotoxin producers in food production. This review also examines the implications of fungal contamination on food safety and quality at all stages of food production, from a farm-to-fork perspective.

## 2. Biotechnological properties of filamentous fungi

The use of filamentous fungi in production is not a recent development. The earliest documented applications of filamentous fungi in history date back to the 18th century, particularly in the production of cheeses, such as Roquefort and Camembert (Labbe & Serres, 2009; Ropars et al., 2017). Initially, these cheeses were not produced through deliberate inoculation but became colonized due to accidental contamination by spores naturally present in the environment. Once the beneficial effects of these fungi in cheese production were discovered, several types, including those found on spoiled bread, were isolated and intentionally introduced during cheese production (Labbe & Serres, 2009; Ropars et al., 2017).

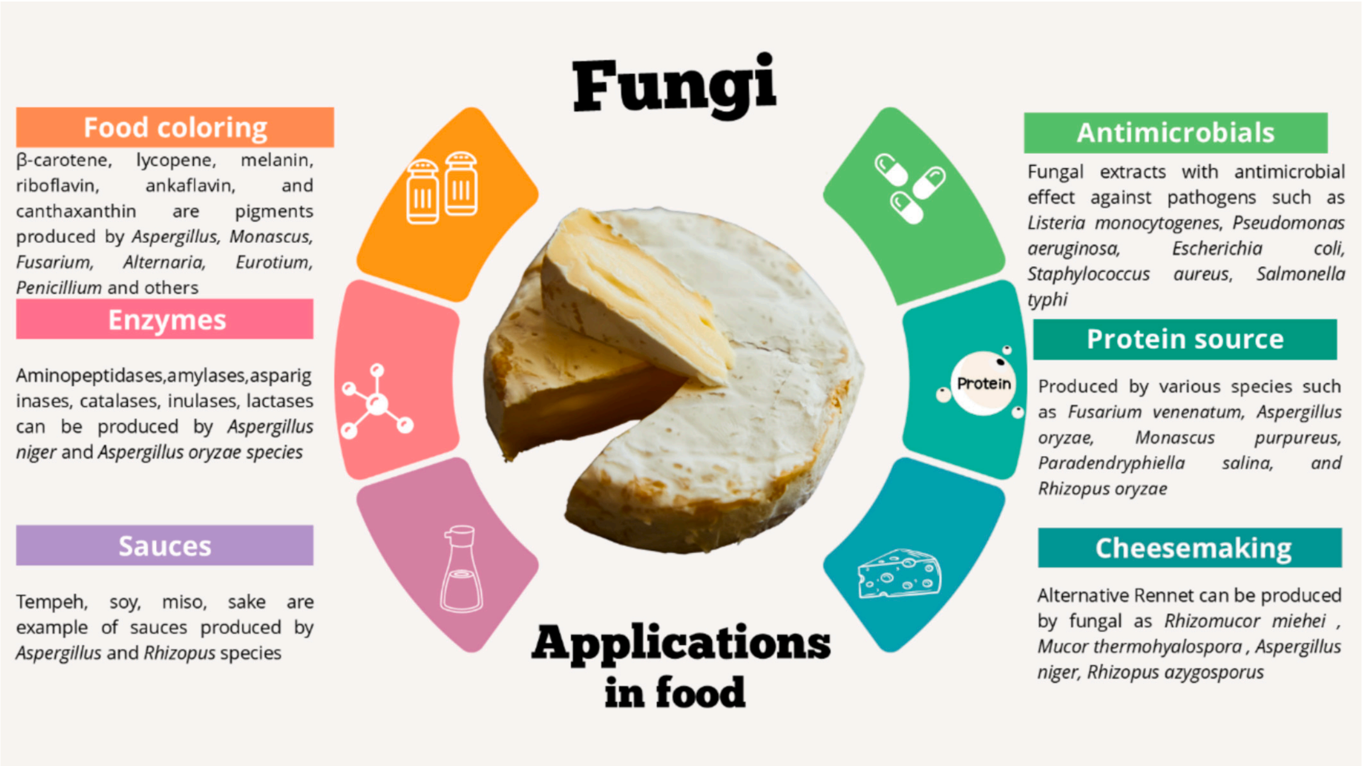
Over time, the use of filamentous fungi spread globally and became key ingredients in producing various cheeses, rather than Roquefort and Camembert, as Brie, St. Nectaire and Reblochon, significantly enhancing their value (Ropars et al., 2020). During this time, the technological application of filamentous fungi expanded in food production, covering a relevant financial market worldwide. Currently, fungi are exploited across diverse foods, such as cheese, beverages, fermented foods, sauces, and essential ingredients that are used in the food industry such as enzymes, pigment, protein, and antimicrobials (Fig. 1) (Kaya et al., 2024; Niego et al., 2023; Tu et al., 2025).

Regarding the potential of fungi for protein production in the food industry, one widely known product is Quorn™, produced by Marlow Foods, which has been on the market for over 30 years. This product is made from *Fusarium venenatum*, although other fungal species, such as *Aspergillus oryzae*, *Monascus purpureus*, *Paradendryphiella salina,* and *Rhizopus oryzae,* are also used (Mapook et al., 2022; Souza Filho et al., 2018). The market for fungal-derived proteins alone is expected to reach a value of USD 69.6 billion in 2025, with a growing trend worldwide (Global Market Insights, 2025). A comprehensive review of several fungal-derived protein products can be found in Mapook et al. (2022). In addition to serving as a protein source, fungi also produce a variety of enzymes with relevant applications in the food industry, including aminopeptidases, amylases, apariginases, catalases, inulases, lactases, and triacylglycerol lipases, which are produced by strains of *Aspergillus niger* and *A. oryzae* (Sidiqui, 2016).

A significant historical development in the use of filamentous fungi took place in Asian countries, particularly China, Japan, and Korea, where edible fungi were first discovered. Today, these fungi play a crucial role in the large-scale production of traditional fermented foods and beverages. For example, filamentous fungi are widely used in the production of soy sauce, miso, and sake fermentation, with *A. oryzae* being the predominant species involved (Hyde et al., 2019). Similarly, in Indonesia, fungus-fermented products are relevant to local cuisine, with *Rhizopus oligosporus* being the dominant species used in soybean fermentation to produce "tempeh", which is a widely consumed product, known for its distinctive flavor and nutritional properties, undergoing a fermentation process that typically lasts around two days (Nout & Kiers, 2005). In addition, filamentous fungi also participate in the fermentation of dark green tea in several Chinese provinces, where their succession and metabolic activities significantly influence the tea's flavor profile. *Aspergillus* is often the dominant genus in the fermentation process, contributing to the production of key flavor compounds, such as catechins and amino acids, through its metabolic activities (Hu et al., 2021).

Pigments have several applications in the areas of health, textiles, and the food industry (ATCC, 2022). For over a century, researchers have investigated fungi that produce pigments through secondary metabolism, focusing on optimizing large-scale production. Qiu et al. (2010) explored the ability of endophytic fungi to synthesize red pigments, while a more recent study examined the potential of *Aspergillus ustus* to synthesize brown and bright pigments (Zhou et al., 2023). In another study, Gong et al. (2022) evaluated the efficiency of red pigment production by an isolated strain of *Talaromyces aurantiacus* under various conditions and utilizing different favorable substrates. Furthermore, they conclusively demonstrated the antioxidant potential of the pigment produced. Furthermore, Chen et al. (2020) evaluated the ability of *Monascus* to produce yellow and orange pigments under extreme conditions, such as high-salt stress, and reported a notable capacity for pigment production under these conditions. Many other genera are also capable of producing pigments suitable for application in food products, such as *Monascus*, *Eurotium*, *Fusarium*, *Penicillium*, *Alternaria*, *Talaromyces*, *Ashbya*, *Blakeslea, Epicoccum, Paecilomyces* and others (Dufossé et al., 2014).

The American Type Culture Collection (ATCC), a leading organization of cell culture development and supply, maintains a collection of more than 180 fungal strains with demonstrated potential for pigment production. These strains can be used for scientific research and commercial applications under proper licensing (ATCC, 2022). Lagashetti



**Food coloring**

β-carotene, lycopene, melanin, riboflavin, ankaflavin, and canthaxanthin are pigments produced by *Aspergillus, Monascus, Fusarium, Alternaria, Eurotium, Penicillium* and others

**Enzymes**

Aminopeptidases,amylases,aspariginases, catalases, inulases, lactases can be produced by *Aspergillus niger* and *Aspergillus oryzae species*

**Sauces**

Tempeh, soy, miso, sake are example of sauces produced by *Aspergillus* and *Rhizopus* species

**Antimicrobials**

Fungal extracts with antimicrobial effect against pathogens such as *Listeria monocytogenes, Pseudomonas aeruginosa, Escherichia coli, Staphylococcus aureus, Salmonella typhi*

**Protein source**

Produced by various species such as *Fusarium venenatum, Aspergillus oryzae, Monascus purpureus, Paradendryphiella salina,* and *Rhizopus oryzae*

**Cheesemaking**

Alternative Rennet can be produced by fungal as *Rhizomucor miehei* , *Mucor thermohyalospora* , *Aspergillus niger, Rhizopus azygosporus*

**Fig. 1.** Functional roles of fungi in food applications.

et al. (2019) and Kalra et al. (2020) highlighted the essential role of fungi in pigment production, noting that fungal-derived pigments are already widely used in the food industry. These include beta-carotene, lycopene, melanin, riboflavin, ankaflavin, and canthaxanthin, and others already available on the market (Kalra et al., 2020; Rousta et al., 2021).

Filamentous fungi are also recognized as promising sources of bioactive compounds, particularly protein hydrolysates such as bioactive peptides, which can act as physiological modulators. Depending on their residual chemical structure and amino acid sequence, these peptides may exhibit antioxidant, antimicrobial, antithrombotic, hypocholesterolemic, and antihypertensive properties. Examples of bioactive peptides produced by filamentous fungi include Dipeptidyl Peptidase-IV (DPP-IV) inhibitory peptides, as well as peptides containing leucine, valine, lysine, arginine, isoleucine, proline, histidine, tyrosine, tryptophan, methionine, cysteine, glycine, glutamic acid, glutamine, serine, and tyrosine (Rousta et al., 2024).

In addition to peptides, other bioactive compounds synthesized by various fungal species include ergosterol, chitin and chitosan, β-glucans, and fructooligosaccharides. Multiple fungal genera have been associated with the production of these bioactive metabolites, such as *Aspergillus*, *Rhizopus*, *Monascus*, *Fusarium*, *Neurospora*, *Mucor*, *Scopulariopsis*, *Aureobasidium*, *Acremonium*, and *Trichoderma* (Rousta et al., 2024).

Species such as *Aspergillus niger* and *A. oryzae* are widely used in fermentation processes. For instance, a study conducted by Magro et al. (2019) reported the use of these species for the production of phenolic compounds, along with in vitro evaluations of antidiabetic and antioxidant activity. Furthermore, the production of L-carnitine has been explored in species including *A. oryzae*, *Neurospora intermedia*, *Rhizopus oligosporus*, and *Rhizopus oryzae*, as described by Rousta et al. (2021). L-carnitine is a quaternary ammonium that plays an important role in energy metabolism. It functions as a transport molecule across the mitochondrial membrane, facilitating the transfer of long-chain fatty acids for subsequent β-oxidation. The consumption of L-carnitine has been associated with nutraceutical benefits (Walter et al., 2000; Rousta, 2021).

Fermentation products derived from filamentous fungi, such as *A. oryzae* have also been explored for their antimicrobial properties, having potential applications in the food industry. Since *A. oryzae* has already been granted GRAS status, its use in food production is particularly promising. Tu et al. (2025) evaluated the antimicrobial potential of extracts fermented by *A. oryzae* against *Listeria monocytogenes*, showing effective inhibition in both in vitro and in situ tests using a milk matrix. *Penicillium chrysogenum* has also been employed as an antimicrobial agent, as its crude extract has demonstrated inhibitory activity against pathogenic bacteria, such as *Staphylococcus* and *Pseudomonas aeruginosa*, with minimum inhibitory concentrations (MIC) of 12.5 and 25 mg/mL, respectively (Adeoyo & Adewumi, 2024). Similarly, Sharaf et al. (2022) reported antimicrobial activity from crude extracts of fungal species such as *Aspergillus nidulans*, *Aspergillus fumigatus*, and *Aspergillus flavus* against a range of pathogenic microorganisms, including *Staphylococcus aureus*, *Bacillus cereus*, *Bacillus subtilis*, *Escherichia coli*, *Salmonella typhimurium*, *P. aeruginosa*, *Klebsiella pneumoniae*, and *Candida albicans*. Other fungal genera have also been investigated for their antimicrobial potential against pathogenic bacteria. These include *Alternaria*, *Engyodontium*, *Fusarium*, *Acremonium*, *Cladosporium*, *Trichoderma*, and *Periconia* (Jakubczyk & Dussart, 2020).

Another compound that can be produced on a large scale by filamentous fungi is chitosan, as the fungal cell wall itself is composed of this polysaccharide. Chitosan has applications in the food industry, such as antimicrobial agents and coating materials (Huq et al., 2022). Similar to bacteria, filamentous fungi can synthesize organic acids with potential of industrial applications in the food industry, including lactic, citric, succinic, aspartic, fumaric, itaconic, malic, and glucaric acid. *Aspergillus* and *Rhizopus* spp. are commonly used for this purpose, with *A. niger* being the most extensively used species (Porro & Branduardi, 2017).

Rennet is another biotechnological product that can be derived from filamentous fungi for use in food production. Traditionally, rennet for cheese manufacturing has been sourced from animals, particularly calves. However, fungal-derived rennet is a cost-effective and sustainable alternative that caters to specific consumer groups, such as vegetarians. Several fungal rennet products are already commercially available, including Fromase® XL, derived from *Rhizomucor miehei* and produced by the DSM company, and Chy-Max® derived from *A. niger*. and produced by the CHR Hansen company. Additionally, studies such as that by Chinmayee et al. (2019), have explored new fungal strains belonging to *Mucor thermohyalospora* and *R. azygosporus*, which have demonstrated high yields in solid-state fermentation (SSF). These strains may provide more efficient enzymatic activity while maintaining the compositional characteristics of cheeses (Chinmayee et al., 2019).

Fungal mycelia have also been utilized as flavor and color modifiers in fermented foods, including blue cheese, red mold rice, soy sauce, green tea and tempeh (Hu et al., 2021; Mapook et al., 2022). Filamentous fungi are known to produce flavor compounds, such as methyl ketones, vanillin, β-carotene, benzaldehyde, umami amino acids, and various organic acids with a special focus on sensory applications (Kinsella et al., 1976; Lesage-Meessen et al., 2002; Lv et al., 2024; Zhang et al., 2013; Zorn et al., 2003). Given the extensive applications of filamentous fungi in the food industry, understanding the mechanisms underlying metabolite production is essential. This knowledge enables industries to develop optimization strategies that enhance production efficiency while ensuring sustainability, practicality and food safety.

### 2.1. *Biosynthesis pathways for industrially relevant fungal metabolites*

Fungal metabolism is known for its high versatility. As discussed in the previous section of this review, filamentous fungi produce a wide range of compounds that are relevant to the food industry. However, the complexity of fungal metabolism continues to present challenges for comprehensive understanding. In recent years, significant advancements in DNA sequencing of filamentous fungi, as well as improvements in the accuracy of fungal taxonomy databases, have enabled more in-depth studies on species of interest for food production and genetic engineering for large-scale production. Both the primary and secondary metabolism of fungi are generally utilized to generate compounds of interest for the food industry. Further details on the general metabolism of fungi are presented by Keller (2019) and Cairns et al. (2019).

Primary metabolism involves the biosynthesis of molecules essential for the growth, development, and maintenance of the fungal cells. These molecules are also important in secondary metabolism, acting as a source of monomeric building blocks (Chroumpi et al., 2020). Organic acid production, a key aspect of primary metabolism, is one of the most significant processes in the food industry. These compounds are used in several applications, such as acidulants, flavoring agents, buffers, preservatives, and technological additives (Copetti, 2019).

Citric acid, predominantly produced by *A. niger,* is the most widely used in food, pharmaceuticals, and several other industries, and it holds a substantial global market value (Cairns et al., 2019). *A. niger* produces citric acid through the fermentation of glucose or sucrose, with both the cytosol and mitochondria serving as sites for this process (Copetti, 2019). Citric acid biosynthesis is an intermediate of the Krebs cycle, in which, during glycolysis, one molecule of D-glucose is converted into two molecules of pyruvate. One pyruvate enters the mitochondrion and is converted to acetyl-CoA, while the other contributes to the tricarboxylic acid (TCA) cycle. Malate produced in this process is transported into the mitochondrion via the malate–citrate antiporter (CTP) and subsequently converted into citrate through TCA cycle activity. Citrate is then exported to the cytosol via counter transport with malate, leading to cytosolic citrate accumulation. The rise in intracellular malate levels, observed in organisms such as *A. niger*, appears to precede and stimulate citrate accumulation, highlighting malate's regulatory role. This pathway has a theoretical maximum yield of 1 mol of citrate per mol of glucose when pyruvate is derived from glycolysis (Chroumpi et al., 2020). The distinction between primary and secondary metabolism is often blurred, as several primary metabolites can exhibit specific features typically associated with secondary metabolism. Historically, secondary metabolism has represented a major turning point due to the biological relevance of many secondary metabolites. These compounds display diverse bioactivities and have significant applications in human health (e.g., pharmaceuticals and cosmetics), agriculture (e.g., biopesticides and plant defense agents), and the food industry (e.g., functional ingredients and additives) (Bills & Gloer, 2016).

In secondary metabolism, metabolites are usually produced during the stationary phase, and the genes that regulate their biosynthesis are often clustered together. These metabolites are commonly low-molecular-weight compounds, including metal chelators, hormones, pigments, antioxidants, and antimicrobials. They are chemically and metabolically derived from four main classes: non-ribosomal peptides, terpenes, polyketides and alkaloids (Keller et al., 2005). Multiple regulatory mechanisms are involved in the production of these compounds, and certain aspects of these mechanisms are not yet fully understood (Cairns et al., 2019).

In the context of evolutionary taxonomy, particularly with regard to phylogenetic interpretations, a key feature of fungal secondary metabolism is the diversification of biosynthetic gene clusters across fungal lineages. This diversification is driven by several factors, including horizontal gene transfer, gene duplication, and the differential expression of regulatory genes involved in metabolic processes. For example, certain metabolites such as pigments and other bioactive compounds are classified as secondary metabolites. Their production can be optimized through a detailed understanding of the corresponding biosynthetic pathways and the genes involved in their synthesis. Furthermore, the application of specific stimuli and the optimization of growth conditions are essential strategies to enhance the production of these metabolites (Bills & Gloer, 2016).

Extracellular proteins typically contain an N-terminal signal peptide (15–36 amino acids) that directs them to the secretory pathway. Translation of the corresponding mRNA begins on cytosolic ribosomes. As the signal peptide emerges from the ribosome, it is recognized by the signal recognition particle (SRP), which temporarily halts translation and facilitates the targeting of the ribosome–nascent chain complex to the endoplasmic reticulum (ER) membrane. Translation then resumes, and the growing polypeptide is translocated into the ER lumen, where it undergoes initial folding and post-translational modifications (Lübeck & Lübeck, 2022). Nearly mature proteins are subsequently transported in secretory vesicles through the Golgi apparatus and delivered to the cytoplasmic membrane, where they are secreted. A defining characteristic of filamentous fungi, in contrast to yeasts, is their polarized hyphal growth, with protein secretion occurring predominantly at the hyphal tip (Lübeck & Lübeck, 2022). Like bacteria, filamentous fungi require specific nutrients for growth and compound production. Nutrients source of nitrogen, carbon, phosphate, and certain mineral salts are vital for metabolite production (Sharif et al., 2021; Soccol et al., 2017). Consequently, research focuses on manipulating cultivation conditions, including intrinsic and extrinsic factors, such as temperature, nutrient availability, oxygen levels, pH, water content, and redox potential, to optimize metabolite production on both laboratory and industrial scales.

In the food industry, fungal fermentation can be carried out through two processes: submerged fermentation (SmF) and SSF. In SmF, the process occurs in a liquid medium that contains all the necessary nutrients for fungal growth (Sharif et al., 2021). One of the key advantages of SmF is its capacity for large-scale processing, rapid scalability, reduced fermentation duration, minimal labor requirements, and ease of parameter control (Strong et al., 2022). Cao et al. (2024) utilized almond hull extract as a nutrient source in the SmF process, to enhance the production of biomass of *Aspergillus awamori* in batches with passive aeration. When combined with other nutrients and compared to the potato dextrose broth medium, there was a 19.59 % increase in protein production of the biomass, and a reduction in fat content, demonstrating that the nutrients provided to fungi impact the final contents of the biomass, such as protein, fat and ash contents.

In a recent study by Tiwari et al. (2025), SmF cultivation was applied with variations in the liquid medium, using corn steep liquor and defatted soya flour to enhance the production of mycelium and improve the nutritional composition of the edible mushroom *Agaricus bisporus*. Although these by-products are not commonly used for submerged cultivation of fungi, a growing trend toward using by-products and adopting more sustainable strategies has been observed.

Conversely, SSF is a process carried out on an insoluble substrate that serves as both physical support and a nutrient source, without the presence of a free-flowing liquid. In contrast to SmF, SSF requires less water, presents a lower risk of contamination, a greater use of food industrial by-products and lower energy requirements (Verduzco-Oliva & Gutierrez-Uribe, 2020; Strong et al., 2022;). Açaí biomass, a significant agro-food by-product in Brazil, has gained attention for its use in SSF by fungi. Açaí, a palm native to the Amazon, is economically valuable due to its pulp, but it also produces large quantities of waste that are now being repurposed for innovative applications. Lima et al. (2021) demonstrated that açaí seeds enhanced β-mannanase production by *Penicillium citrinum*, highlighting the potential to generate valuable enzymes from waste materials.

Novelli et al. (2016) conducted a comparative study on protease production via SSF using *Aspergillus oryzae, A. flavipes, and Penicillium roquefortii* strains employing various agro-industrial substrates (e.g., agro-industrial waste, soybean, and wheat bran). Distinct biochemical differences were observed among the enzymes produced by the different strains. All exhibited thermal stability up to 50 °C and activity across a broad pH range; however, *A. flavipes* showed an optimal activity temperature of 90 °C, while *P. roquefortii* exhibited optimal activity at 50 °C. The lyophilized protease from *A. oryzae* achieved a yield of 1251 U/g (∼155,010 U/kg of substrate). Although the yields for *A. flavipes* and *P. roquefortii* were not reported in U/g, their enzyme production levels were comparable to those observed for *A. oryzae*. These findings underscore the critical influence of both process parameters and strain selection on enzymatic production efficiency and biochemical properties.

Thus, it is important to emphasize that fungal metabolism is inherently complex and exhibits specificities in each biosynthetic process relevant to the food industry. Conversely, it is known that this metabolism can be modulated in different ways that contribute to the spoilage of several food matrices. Therefore, within this largely unexplored domain, it is crucial to elucidate the environmental factors, particularly those related to food production, and to identify which fungal species may be beneficial or detrimental within the food chain, in order to address the duality challenge highlighted in this review.

## 3. Spoilage fungi in the food industry

Food spoilage, loss, and waste are major global concerns, particularly for food safety and security (FAO, 2019). According to the latest Food Waste Index Report from the United Nations (UNEP), the rate of food waste has increased, totaling 1.05 billion tons of food waste—equivalent to 132 kg per capita—representing almost one-fifth of all food available to consumers. This alarming fact contradicts the United Nations Sustainable Development Goals (SDGs), which aim to halve the per capita global food waste, confirming that this goal remains a significant global challenge (UNEP, 2024).

Food spoilage occurs through chemical, physical, and microbiological changes. Bacteria and fungi are the primary agents responsible for microbial spoilage. In general, in the food industry, filamentous fungi, including species of *Aspergillus*, *Penicillium*, *Fusarium*, *Cladosporium*, *Alternaria*, *Mucor*, *Rhizopus*, *Trichoderma*, and others are frequently associated with food degradation, contributing to significant economic losses, quality deterioration, and product recalls (Pitt & Hocking, 2009).

The presence of these fungi demands careful monitoring and control to ensure food safety. Conventional counting methods often classify yeasts and molds together, limiting the resolution required for accurate detection of specific spoilage organisms. In addition, limitations in species-level identification techniques can hinder effective risk assessment, especially when spoilage is caused by toxigenic fungi (Snyder et al., 2024). Several of these species can produce hazardous mycotoxins, such as aflatoxins, ochratoxins, fumonisins, zearalenone, patulin, and citrinin, which may compromise consumer health and further affect the sensory and structural integrity of food products (Pattono et al., 2013; Ráduly et al., 2020).Filamentous fungi are ubiquitous and common contaminants of food, including raw items, such as fruit, vegetables, animal-derived products, and their processed forms (Parussolo et al., 2019; Ráduly et al., 2020). Grains and their products, processed beverages, nuts, teas, and meat products are also associated with fungal spoilage (Gong et al., 2024). In recent years, plant-based meat analogs have experienced significant growth in the market. The market was valued at USD 14,552.69 million in 2024 and is projected to reach USD 20,858.97 million by 2033, reflecting a promising outlook with a compound annual growth rate (CAGR) of 12.75 % over the forecast period. However, even these newer products are susceptible to fungal contamination (Global Market Statistics, 2025).

Li et al. (2024) investigated spoilage dynamics in pea-based meat analogues and compared these with the profiles observed in ground beef. The study found that *Geotrichum* species were predominant in the plant-based products, where they caused significant deterioration in aroma, flavor, color, and texture. In ground beef, a different fungal community was identified, primarily composed of *Cladosporium* species, which are associated with surface discoloration and the appearance of black spots due to mycelial development. This comparison clarifies that the objective was to assess differences both in spoilage characteristics and in the composition of fungal communities between plant-based and animal-based products. Including quantitative data, such as changes in volatile compounds or measurable losses in textural integrity, would provide further insight into the specific impact of *Geotrichum* species during storage. In general, the food production environment constitutes a potential source of contamination, as fungal spores can be aerosolized and dispersed throughout the processing facility (Parussolo et al., 2019).

The impact of fungal contamination can lead to visible and invisible defects in the final product. The most visible defect is fungal growth with the noticeable presence of a thallus, which eventually leads to rotting (Pitt & Hocking, 2009). Black, white, green, pink, and/or yellow spots are commonly associated with fungal development. This often results in elimination, whether at the industrial or consumer level. Some “invisible” defects include gas production, off-flavors, and texture changes (Pinches & Apps, 2007). Recently, compounds with atypical odors, identified as 1-hydroxyoctan-3-one and octane-1,3-diol, were detected in wines contaminated by fungi (Ployon et al., 2025). Several types of volatile organic compounds, particularly C8-alcohol/ketone and terpene, induce mushroom and/or earthy odors in a wide range of food products (Gong et al., 2024).

Regarding dairy products, several studies have covered contamination situations in different types of products, such as cheese, yogurt, butter, cream, and milk (Anelli et al., 2019; Garnier et al., 2017; Kure et al., 2004; Pattono et al., 2013). Many *Penicillium*, *Aspergillus*, *Acremonium*, *Cladosporium*, *Fusarium*, *Nigrospora*, *Mucor*, *Phaeosphaeria*, *Riopa*, and *Trichoderma* spp. are commonly found in dairy environments and products with the potential to cause spoilage (Anelli et al., 2019; Garnier et al., 2017; Pitt & Hocking, 2009; Souza et al., 2022). Due to the growth capabilities of certain spoilage fungi such as some species of *Penicillium* (e.g., *Penicillium charlesii*, *Penicillium fellutanum*, *Penicillium adametzioides*, and *Penicillium antarcticum*) at low pH values and storage temperatures below 10 °C, they can easily contaminate fermented dairy products, producing enzymes that modify the product’s sensory characteristics. Additionally, they can cause visible color changes and excessive mustiness (Garnier et al., 2017; Pitt & Hocking, 2009).

Fungal contamination in cereal grains can occur at any stage of the process, whether during harvest or processing. The negative effects of fungal contamination include loss of germination potential of the grains, yield losses, and changes in the color and production of odorous compounds (Almeida et al., 2024). In bread production, the primary concern related to fungal contamination is the presence of a visible mold. These products often provide ideal conditions for fungal growth, particularly when preservatives are not incorporated. However, even with preservatives, fungal contamination remains a risk due to mycotoxin production, which is further addressed in this review, or resistance development. Additional defects associated with bread include the overproduction of alcohol compounds and the emergence of undesirable odors (Garcia et al., 2019).

Spoilage of fruits and vegetables results from a combination of internal and external factors. Internal factors include physiological processes such as natural ripening, senescence, and the progressive decline in intrinsic resistance mechanisms, including the production of phenolic compounds and the activation of wound-healing responses (Alegbeleye et al., 2022; Moss, 2008). Despite these natural defenses, fruits and vegetables remain susceptible to fungal contamination. External factors, however, play a more decisive role in postharvest spoilage. Mechanical injuries occurring during harvesting or handling provide direct entry points for fungal pathogens. These injuries also accelerate ripening and senescence, further reducing resistance to infection. In addition, inadequate storage and transportation conditions, particularly high humidity and temperature fluctuations, create environments that promote fungal growth and sporulation. Fungal species demonstrate considerable adaptability to these conditions, and some genera exhibit marked specialization in colonizing postharvest produce. Among the most frequently isolated fungi from spoiled fruits and vegetables are *Alternaria*, *Fusarium*, *Botrytis cinerea*, *Rhizopus*, *Penicillium*, *Cladosporium*, and *Aspergillus* (Tournas & Katsoudas, 2005; Al-Najada & Gherbawy, 2015; Hasan & Zanuddin, 2018; Saleh & Al-Thani, 2019).

Overall, the ecological dynamics of fungal growth in foods are modulated by a suite of physicochemical parameters that determine the suitability of a substrate for fungal spoilage. Key determinants include water activity (aw), pH, temperature, gas composition, physical consistency, nutrient profile, solute effects, and the presence of preservatives. Water activity, in particular, is a pivotal factor, as it defines the thermodynamic availability of water necessary for fungal metabolism. Xerophilic fungi, such as *Xeromyces bisporus*, are capable of germinating and growing at aw values as low as 0.62 in fructose based environments, representing one of the lowest known thresholds among food-associated microorganisms (Pitt & Hocking, 2022).

*Penicillium expansum* is capable of growth across a moderately wide pH range (approximately 3.5–7.0) and water activity levels typical of fruit surfaces (aw >0.90). The pathogenicity of this fungus and its production of the mycotoxin patulin are significantly affected by the surrounding pH, showing increased toxin synthesis under acidic conditions. These physiological adaptations enable *P. expansum* to effectively colonize fruit substrates, other food products and contribute to spoilage (Jimdjio et al., 2021).

Additionally, similar to bacteria, fungi are increasingly exhibiting traits of resistance to preservatives commonly used in the food industry, which can facilitate the spread of fungi potentially adapted to adverse conditions, thereby enabling their dissemination. Wang et al. (2025) identified dipicolinic acid synthase, relevant components of bacterial spores, in *Paecilomyces* and some strains of *Aspergillus* and *Penicillium*, indicating that this compound may be associated with enhanced resistance to heat, salt content, and pH variations, which are conditions commonly used in the food industry.

Heat resistance significantly influences fungal survival through processing, particularly in acidic food products. The ascospore-forming *Paecilomyces variotii* (formerly *Byssochlamys spectabilis*) can survive pasteurization, with D-values equal to or greater than 10 min at 90 °C. This resistance is attributed to cytoplasmic vitrification by trehalose and mannitol matrices, which stabilizes internal structures under thermal stress (Pitt & Hocking, 2022). These resistance mechanisms illustrate the importance of applying multiple preservation strategies in parallel, combining reduced water activity, low pH, thermal processing, and chemical preservatives to control fungal spoilage effectively.

Another extremely important point related to the emergence and predominance of filamentous fungi as spoilage agents in food is associated with climate projections. It is expected to substantially alter fungal global geographic distributions over the years. Considering the dual role of filamentous fungi within the food chain, as both ecological allies and potential contaminants, climate change may profoundly disrupt their functional balance in ecosystems. Environmental fungi perform essential ecological functions by decomposing organic matter, forming mycorrhizal associations that support plant development, and establishing mutualistic relationships with various insect species (Case et al., 2025).

Global climate change, characterized by rising average temperatures and increasingly frequent extreme weather events such as droughts, floods, wildfires, and storms, has been shown to significantly affect fungal community dynamics and their ecological interactions (Case et al., 2025; Seidel et al., 2024). These disturbances may select for more adaptable and virulent fungal strains, with higher temperatures promoting heat tolerance close to human body temperature and increasing zoonotic risks. Additionally, shifts in humidity and ecosystems alter fungal distributions, enabling new fungal disease outbreaks in different regions and hosts (Fisher et al., 2020; Casadevall, Kontoyiannis and Robert, 2021). Therefore, these shifts underscore the urgent need to reassess current control strategies and anticipate emerging risks in a changing environment.

### *3.1. Mycotoxins: A significant public health concern*

Mycotoxins are low-molecular-weight metabolites produced by the secondary metabolism of filamentous fungi and pose a potential hazard to humans and animals (El-Sayed et al., 2022; Ji et al., 2022). The main food contaminated by fungi, and associated with potential risks, are cereals, including corn, wheat, soybean, sorghum, peanut, and their by-products. Additionally, the consumption of animal-derived products such as milk, butter, and meat, which may contain mycotoxin residues or metabolites represents a public concern (Table 2) (El-Sayed et al., 2022).

Among the filamentous fungi known to produce mycotoxins, three genera *Aspergillus*, *Penicillium*, and *Fusarium*, are the most prominent in food contamination. Although *Trichoderma*, *Trichothecium*, and *Alternaria* are less frequently related to mycotoxin contamination in food, they also remain important (Adeyeye, 2016; Reddy et al., 2010). The mycotoxins produced by these fungi can cause mycotoxicosis, with a range of adverse reactions, which, depending on their toxicity, may include teratogenic, mutagenic, hemorrhagic, estrogenic, hepatotoxic, nephrotoxic, immunosuppressive, endocrine, and carcinogenic effects (Agriopoulou et al., 2020). Although more than 400 mycotoxins have been reported in the literature, six classes are considered the most significant to public health: aflatoxins, ochratoxins, fumonisins, trichothecenes, zearalenone, and patulin (Agriopoulou et al., 2020; El-Sayed et al., 2022).

Aflatoxin is one of the most hazardous mycotoxins. It is produced by *Aspergillus* spp., mainly by *Aspergillus flavus* and *A. parasiticus* (Massomo, 2020) and has been classified as a Group 1 carcinogen in humans and animals, due to its toxic and mutagenic effects (Jallow et al., 2021; Shabeer et al., 2022). Food contamination by aflatoxin can occur at different stages of the food chain and is influenced by multiple intrinsic factors, such as temperature, water activity, pH, and nutrient composition (Jallow et al., 2021; Shabeer et al., 2022).

Ochratoxin is another important mycotoxin that is a risk to both human and animal health. It is produced by *Aspergillus* and *Penicillium* spp., particularly *A. ochraceus*, *A. carbonarius*, *A. niger*, and *P. verrucosum*. Contamination can occur both pre- and postharvest, enabling these microorganisms to spread into food and animal feed (Ganesan et al., 2022). Similar to aflatoxins, ochratoxins are found in a wide range of food products (Table 2), and their consumption has been linked to neurotoxicity and carcinogenic effects (Ganesan et al., 2022; Kumar et al., 2020).

**Table 2**
Occurrence of mycotoxins in different food matrices.

| Mycotoxin | Type | Food | Reference |
|---|---|---|---|
| Aflatoxin | M1 | Milk and infant milk food | (Rastogi et al., 2004) |
| | B1 | Dry fruit | (Awan et al., 2022) |
| | B1 | Luncheon and hot dog meat | (Algahtani et al., 2020) |
| | – | Maize | (Akello et al., 2021) |
| | – | Rice | (Makun, Dutton, Njobeh, Mwanza, & Kabiru, 2011) |
| Citrin | – | Vegetable foodstuffs | (Ostry, Malir, & Ruprich, 2013) |
| | – | Red yeast rice | (Liao, Chen, Lin, Chiueh, & Shih, 2014) |
| | – | Broiler Chicks | (Roberts & Mora, 1978) |
| Fumonisin | B1 | Corn | (Wang et al., 2008) |
| | B1 and B2 | Rice | (Makun, Dutton, Njobeh, Mwanza, & Kabiru, 2011) |
| Ochratoxin | A | Rice | (Makun, Dutton, Njobeh, Mwanza, & Kabiru, 2011) |
| | | Semi-hard cheeses | (Pattono et al., 2013) |
| | | Coffee | (Taniwaki, Pitt, Teixeira, & Iamanaka, 2003) |
| | | Dry-cured ham | (Delfino et al., 2022) |
| | | Dry fruits | (Iamanaka et al., 2005) |
| Patulin | – | Tomato products and apple juice | (Cunha et al., 2014) |
| | – | Semi-hard cheeses | (Pattono et al., 2013) |
| | – | Fruits products | (Ji et al., 2017) |
| | – | Dry cured ham | (Rodríguez et al., 2012) |
| Zearalenone | – | Hen's eggs | (Osaili et al., 2022) |
| | – | Rice | (Makun, Dutton, Njobeh, Mwanza, & Kabiru, 2011) |

Fumonisins are mycotoxins produced by several *Fusarium* spp., with *Fusarium verticillioides* and *Fusarium proliferatum* being the most significant contributors to food contamination, particularly in cereals and cereal-based products (Reddy et al., 2010). Fumonisins have hazardous effects, including neurotoxicity, pulmonary toxicity, immunotoxicity, and carcinogenicity (Yang et al., 2024).

Trichothecenes are also produced by *Fusarium* spp.; however, several other genera, such as *Myrothecium*, *Spicellum*, *Stachybotrys*, *Cephalosporium*, *Trichoderma*, and *Trichothecium*, can also synthesize these compounds (McCormick et al., 2011). Similar to other mycotoxins, trichothecene production occurs under specific environmental conditions that favor fungal growth. Recent studies have suggested that mycotoxin production is higher in tropical and subtropical regions due to the elevated humidity and temperature conditions (Nichea et al., 2022; Polak-śliwińska & Paszczyk, 2021). Considering that this group comprises more than 200 toxins, their effects on humans and animals are diverse. Trichotecenes are quickly absorbed by the body, affecting hematologic and progenitor cell systems, the immune system, skin, kidneys, liver, and gastrointestinal tract (McCormick et al., 2011; Polak-śliwińska & Paszczyk, 2021).

Zearalenone is another mycotoxin produced by *Fusarium* spp., mainly *F. graminearum* and *F. culmorum* (Mahato et al., 2021). The effects of this mycotoxin on the human body are dependent on individual conditions, such as immune status. After ingestion, its effects can vary, including teratogenic, carcinogenic, estrogenic, neurotoxic, and immunosuppressive outcomes (Mahato et al., 2021; Ropejko & Twarużek, 2021).

Although *Fusarium* spp. are major producers of mycotoxins affecting cereals and related products, other fungal genera also contribute to mycotoxin contamination in different food matrices. Notably, *Penicillium*, *Aspergillus*, and *Byssochlamys* spp. synthesize patulin, a mycotoxin predominantly found in moldy fruit, vegetables, and their byproducts (Mahato et al., 2021b; Notardonato et al., 2021). Patulin has been associated with carcinogenic effects, but no conclusive scientific evidence has confirmed this relationship (Notardonato et al., 2021).

Considering the increasing number and diversity of newly discovered mycotoxins, many of which pose potential risks to human health, the need for effective control measures has grown significantly. From a legislative perspective, regulatory agencies continuously update regulations to enhance the monitoring of various emerging mycotoxins. Since 2006, the European Commission (EC) of the European Union (EU) has actively monitored and regulated several mycotoxins in food, including aflatoxins (AFB1, B2, G1, G2, and M1), fumonisins (FB1 and FB2), deoxynivalenol (DON), ochratoxin A (OTA), patulin (PAT), and zearalenone (ZEN) (EC, 2006). In 2013, the EU recommended the monitoring of T-2 and HT-2 mycotoxins in cereals and related products (EC, 2013). More recently, in 2022, regulatory standards were established for alternariol (AOH), alternariol methyl ether (AME), and tenuazonic acid (TeA) in foods, such as cereal-based products, legumes, and nuts (EC, 2022).

In the United States, the Food and Drug Administration (FDA) updated its compliance program in 2024 to include mycotoxins, such as zearalenone and T-2 and HT-2 toxins (FDA, 2024). Previously, the program focused on evaluating mycotoxins, such as aflatoxins (B1, B2, G1, G2), deoxynivalenol, fumonisins (B1, B2, B3), and ochratoxin A. Although many mycotoxins are already monitored and regulated, several others may still be present in food without regulatory oversight, posing challenges for the food supply chain. For instance, sterigmatocystin (STE) and emodin (EMO) produced by *Aspergillus*, enniatins (ENNs), beauvericin (BEA), moniliformin (MON), fusaproliferin (FP), fusaric acid (FA), culmorin (CUL), and butenolide (BUT) produced by *Fusarium*, mycophenolic acid (MPA), produced by *Penicillium*, and alternariol (AOH), alternariol mono-methyl ether (AME), and tenuazonic acid (TeA) produced by *Alternaria* are currently unregulated mycotoxins (Gruber-Dorninger et al., 2017; Rossi et al., 2020). It is expected that monitoring practices will continue to evolve with advancements in analytical methodologies, detection, and quantification techniques.

Although often underestimated, studies on mycotoxins have the potential to provide a deeper understanding of their effects as well as the mechanisms underlying their production. Consequently, the adoption of key strategies to minimize and mitigate mycotoxin production should be increasingly optimized alongside the development of effective and efficient techniques for their identification and quantification, which may contribute to the control of these metabolites.

### 3.2. *Strategies for the mitigation of fungal and mycotoxin contamination*

The ubiquitous presence of fungi in water, soil, and air renders food contamination a persistent and intrinsic challenge within both the agricultural and food industry sectors. In this context, the adoption of comprehensive and scientifically grounded strategies for the control and mitigation of fungal growth and mycotoxin accumulation is essential across the entire food supply chain. To achieve effective outcomes, these strategies must be systematically implemented at each critical stage of the chain. The initial and perhaps most complex point of intervention lies in source prevention, which encompasses pre-harvest practices and soil management. This stage demands careful attention to agronomic conditions, crop rotation, and ecological variables that influence fungal proliferation.

Crop rotation is a widely used preventive measure, as fungal species often rely on specific hosts for their development (Matumba et al., 2021). Drakopoulos et al. (2021) found that intercropping wheat with maize effectively reduced mycotoxin levels in wheat without compromising yield. In addition to preventive strategies such as crop rotation, the fungal mitigation strategies typically rely on the use of fungicides. However, the widespread application of fungicides contradicts global sustainability principles and may also contribute to the emergence of fungicide-resistant fungal strains. For example, in the European Union, five major health and environmental agencies—EFSA (European Food Safety Authority), ECDC (European Centre for Disease Prevention and Control), ECHA (European Chemicals Agency), EEA (European Environment Agency), and EMA (European Medicines Agency)—have conducted studies demonstrating that azole-based fungicides, the most commonly used compounds in agriculture, and their residues in food products, may pose risks to human health (EMA, 2025).

The primary recommendations emphasize a globally coordinated One Health approach involving human health, veterinary medicine, agriculture, food production, and environmental sciences. Key actions include stricter fungicide approval criteria addressing resistance and pathogenicity, strengthening good agricultural and manufacturing practices, and advancing research on antifungal agents. Additionally, further exploration of innovative and sustainable strategies is essential to combat antifungal resistance and emerging pathogenic fungal strains (EMA, 2025).

Increased spore dispersal combined with the selection of fungicide-resistant strains undermines food security by reducing crop yields and necessitating greater reliance on chemical pesticides, which in turn pose additional environmental risks. Alongside, advancements in the medical field have led to increasingly regulated and diversified strategies to combat fungal pathogens, including antivirulence therapies, biofilm disruption, immunomodulation, and novel antifungal agents. These developments, while primarily targeting human health, offer a comparative framework that highlights the urgent need for equally robust control strategies in agriculture. The World Health Organization reports that 43 antifungal agents are currently in clinical or preclinical development, with *Aspergillus fumigatus* identified as a critical priority pathogen due to its high pathogenicity. These medical advances underscore the necessity of integrated, cross-sectoral approaches to mitigate fungal threats, particularly in food systems where prevention and control remain fragmented and underregulated (WHO, 2025).

Subsequently, proper handling during harvest and the application of effective post-harvest storage practices play a crucial role in minimizing the risk of fungal colonization and subsequent mycotoxin production. Postharvest contamination of grains by mycotoxins is primarily driven by mechanical damage, infestation of insect, harvest timing, inadequate drying, and poor handling and storage infrastructure. Critical environmental parameters such as temperature and moisture content strongly influence fungal proliferation and mycotoxin synthesis. As well reviewed by Neme & Mohammed, 2017, effective postharvest mitigation strategies include rapid and uniform drying, pest management, proper packaging and transport, and controlled storage conditions. Additionally, the application of natural or chemical preservatives and physical methods such as irradiation and others can further reduce contamination. Processing steps such as cleaning, sorting, milling, fermentation, roasting, extrusion, and nixtamalization have also been shown to lower mycotoxin levels.

As food progresses through the supply chain, targeted strategies during processing and distribution become equally critical. Given that each food product is subject to specific processing technologies and unit operations, which often involve high levels of complexity and multiple processing stages, mitigation approaches must be tailored to the characteristics of each matrix. Thus, fungi-related food deterioration is a major challenge in the industry. Modern practices, along with preventive and control approaches, are used in combination to reduce the incidence of these fungi in industrial facilities (Garnier et al., 2017). Among the preventive practices, air filtration, aseptic packaging, hygiene protocols, microbiological control, humidity and shelf-life management, as well as the implementation of Good Manufacturing Practices (GMP), can be highlighted. Control strategies, on the other hand, involve the use of additives, chemical preservatives, modified atmosphere packaging, high-pressure processing (HPP), thermal treatments, refrigeration, fermentation, and biopreservation. Prevention methods aim to avoid contamination or recontamination during product processing, while control methods focus on slowing or inhibiting microbial growth (Fig. 2). However, when control and prevention methods are not applied effectively, fungal development may deteriorate food quality and lead to fungi dissemination, which may occur both in the processing plant and in the final product (Rahman, 2020).

Given these challenges, when choosing the most appropriate preventive and control methods, different factors must be considered. These include the product characteristics that need to be maintained (composition and water activity), preservation of microorganisms of interest, and manufacturing, sanitation, and storage conditions (Garnier et al, 2017). Consumer perception and acceptance of preservation methods and their impact on hygiene and safety are also important considerations (Garnier et al., 2017; Rahman, 2020). Thus, among the emerging methods used to combat fungi-caused food deterioration, technology-based means have increased as industries aim to reduce the use of chemical preservatives—a development that has attracted considerable interest in the market.

Thus, emerging strategies for the mitigation of fungi and their mycotoxins have been increasingly explored and which can be used at any stage of the food chain and have been widely used, mainly in the processing stages, including physical methods, biopreservation techniques, and the development of novel antifungal products. Among the physical methods, notable examples include ionizing and non-ionizing irradiation (IR), high-pressure processing (HPP), pulsed electric fields (PEF), pulsed light (PL), and cold plasma (CP). Biopreservation approaches involve the utilization of bacteria, yeasts, and even microbial consortia. Regarding the development of new antifungal compounds, attention has been given to the production of salts, natural compounds, bio-based films, peptides, and antibodies (Sánchez-Torres, 2024).

Conventional food processing methods, including thermal treatments, are usually ineffective at inactivating mycotoxins, as these compounds exhibit high stability under typical industrial processing conditions (Bullerman & Bianchini, 2007; Piotrowska, 2021). In fact, the optimal approach would not rely on alternative solutions to mitigate mycotoxins; rather, the primary mitigation strategy should focus on controlling fungal growth itself, as effectively inhibiting the fungus prevents mycotoxin production. However, in instances where mycotoxins have already been produced and persist within the food chain, their removal or neutralization becomes a critical objective.

One effective strategy for mitigating mycotoxin production early in the food supply chain is the implementation of robust monitoring systems and rapid diagnostic techniques that facilitate improved agricultural management. Mallmann et al. (2020) assessed the presence of mycotoxins in corn using near infrared spectroscopy and concluded that such early and rapid diagnostic approaches are instrumental in enabling the adoption of proactive measures to reduce mycotoxin-related risks at any stage of the food supply chain. Given the importance of mitigating filamentous fungi and mycotoxins, most emerging treatments remain insufficient when applied in isolation, highlighting the need for integrated, multi-step approaches aligned with the United Nations (UN) 2030 Sustainable Development Goals (UNEP, 2024).

Applying the emergent method HPP to control and remove fungal and mycotoxins in food, Kalagatur et al. (2018) verified a reduction of 96.73 % in the level of deoxynivalenol and 97.04 % in the level of ZEN in maize grains. HPP can reduce the fungal population, therefore reducing mycotoxin levels. CP has also been used to remove mycotoxin-producing fungi and mycotoxins. Zhao et al. (2024) evaluated the effect of such a technique on *A. niger* spores and found a reduction of 4.47 log CFU/mL and a consequent reduction in aflatoxin production. In situ studies have also been carried out, such as the one conducted by Soulier et al. (2024), who reported a positive effect of dual-frequency CP on bread wheat. They observed a 1.5 log reduction in grains and a degradation of over 90 % of the deoxynivalenol mycotoxin content after just 5 min of CP exposure. Antifungal activity has also been demonstrated through non-thermal techniques such as Intense Pulsed Light (IPL), achieving significant removal rates of up to 90 % for biofilms formed by *A. niger* and *Penicillium glaucum*, and up to 99 % for planktonic cells (Li et al., 2023).

Strategies such as biopreservation and the development of naturally derived antifungal compounds have gained increasing prominence as sustainable alternatives for fungal control (Souza et al., 2023).

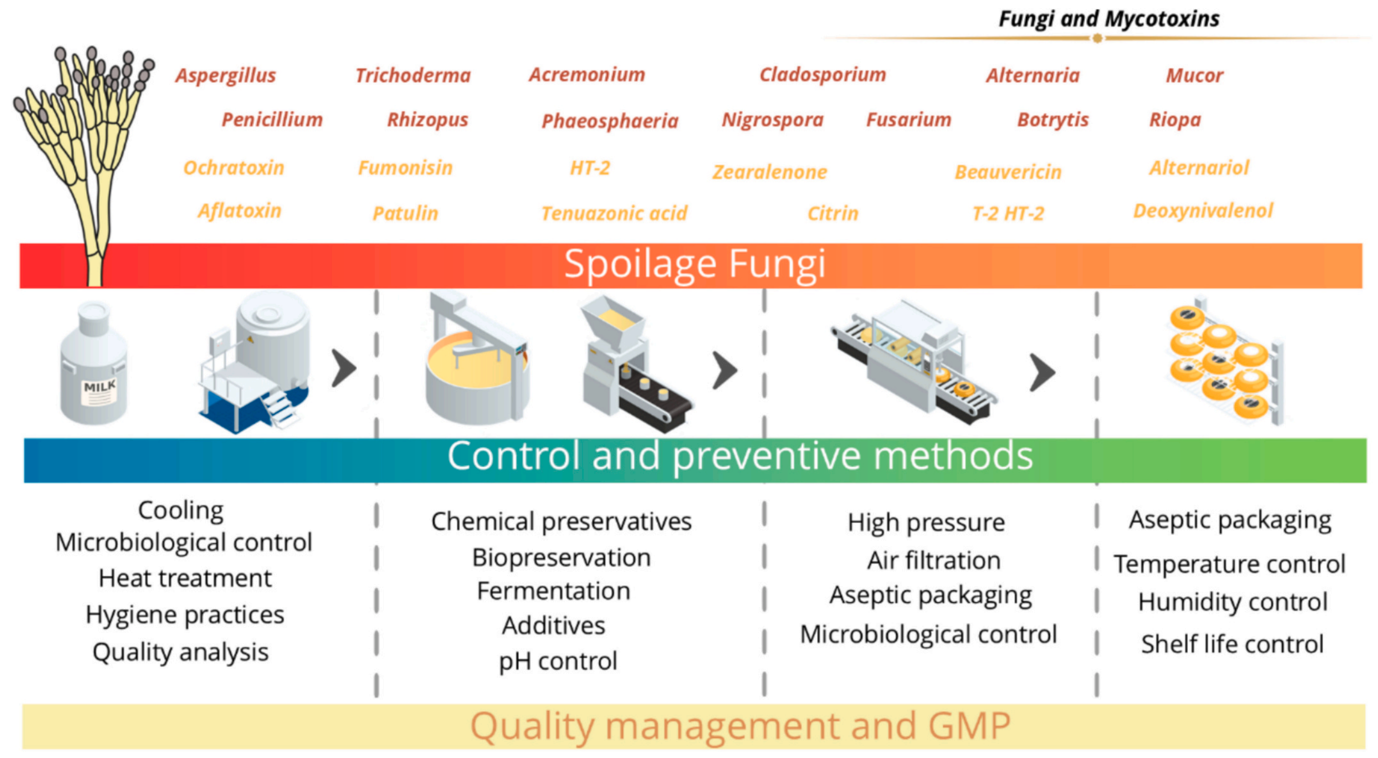


**Fig. 2.** Control and preventive strategies in food production to reduce or inhibit the growth of spoilage fungi.

Complementing these approaches, omics technologies leveraging high-throughput sequencing have become indispensable for unraveling complex pathogenic mechanisms, metabolic pathways, and fungal genomics. This molecular-level insight is crucial for overcoming key challenges in the agri-food sector, particularly in managing the intricate interactions between fungi and food systems. In parallel, the removal of mycotoxins has been explored through enzymatic and microbiological methods; however, these techniques currently face limitations in scalability and efficacy. Among biological agents, lactic acid bacteria (LAB) stand out due to their demonstrated capacity to reduce mycotoxin concentrations via transformation and adsorption. This functionality is largely attributed to their structurally complex cell walls, composed of peptidoglycan, teichoic acids, lipoteichoic acids, and exopolysaccharides, which facilitate effective adhesion and binding to mycotoxins and other macromolecules (Wafula et al., 2022; Zhou et al., 2017).

LAB species, such as *Lactobacillus*, *Enterococcus*, and *Streptococcus*, produce exopolysaccharides that contribute to fungal and mycotoxin mitigation. The peptidoglycan layer contains disaccharides that, when modified, affect the bacteria's ability to bind toxins. Detoxification mechanisms involve the interaction of cell wall proteins and exopolysaccharides with mycotoxins, especially after enzymatic treatment, which enhances binding. Positive surface charges, along with calcium and magnesium ions, play a significant role in this binding (Murtaza et al., 2023).

Studies have suggested that the mycotoxin-binding properties of LAB are highly strain-specific and determined by multiple factors, such as cell density, pH value, viability, temperature, and mycotoxin concentration (Nasrollahzadeh et al., 2022; Wafula et al., 2022). Murtaza et al. (2024) demonstrated that the *Lactobacillus consortium* LBC-4 effectively removed 88.7 and 89 % of zearalenone (ZEN) in an in vitro model, generating fewer toxic derivatives and exhibiting enhanced adsorption following heat treatment. Structural changes were confirmed by scanning electron microscopy and Fourier transform infrared analysis. The mechanisms of ZEN removal were elucidated, highlighting the roles of the LAB cell wall, viable cells, and culture supernatants (Murtaza et al., 2024). Similarly, Simões et al. (2023) tested strains of *Lacticaseibacillus* spp., *Levilactobacillus* spp., and *Lactiplantibacillus* spp. isolated from naturally fermented Brazilian table olives and observed significant reductions in the production of aflatoxin, ochratoxin A, and patulin, with adsorption rates up to 51, 33, and 24 %, respectively. Additionally, Mateo et al. (2022) observed reductions in aflatoxins ranging from 19.0 % for aflatoxin B1 to 60.8 % for aflatoxin B2, while ochratoxin A reduction varied from 7.3 to 100 %, depending on the strains and temperatures tested. In this context, the LAB strains with the highest anti-aflatoxin activity were *Pediococcus pentosaceus* and *Leuconostoc mesenteroides* subsp. *dextranicum*, while the strains with the highest anti-ochratoxin A activity were *Leuconostoc paracasei* subsp. *paracasei* and L. *mesenteroides* subsp. *dextranicum*.

In situ studies have consistently demonstrated the potential of LAB in mycotoxin detoxification across various food matrices. Mischler et al. (2024) achieved up to 90 % zearalenone reduction in contaminated grains using *Levilactobacillus brevis* and *Bacillus* spp., while Nahle et al. (2022) observed significant aflatoxin M1 and ochratoxin A removal in Ultra High Temperature (UHT) milk and grape juice through *Lactobacillus rhamnosus* biofilms. Similarly, Bovo et al. (2013) found that heat-killed cells of L. *rhamnosus*, *L. delbrueckii* subsp. *bulgaricus*, and *Bifidobacterium lactis* removed over 33 % of AFM1 in phosphate-buffered saline, with Bi. lactis exhibiting the highest efficiency in UHT skim milk at 4 °C. Further expanding on LAB applications, *Lactobacillus* sp. RM1, isolated from traditional Egyptian fermented milk, demonstrated antifungal properties, inhibiting aflatoxin B1 and ochratoxin A production and suppressing *Aspergillus parasiticus* growth on wheat grains (Shehata et al., 2019). These findings reinforce the potential of LAB and its metabolites as natural preservatives, contributing to food safety and an extended shelf life.

Despite the implementation of various conventional and emerging techniques at different stages of the food supply chain, the mitigation of filamentous fungi across all links remains a significant challenge. Interventions applied early in the food supply chain, particularly during the pre- and post-harvest phases, play a critical role in reducing the initial fungal load and limiting conditions favorable to mycotoxin synthesis. As food moves through processing, storage, and distribution, the adoption of tailored mitigation strategies becomes increasingly crucial. Accordingly, effective control at each stage not only enhances the overall efficacy of fungal management but also contributes to the safety, quality, and sustainability of the entire food system.

Moreover, regulatory oversight is essential to ensure the effectiveness and consistency of mitigation measures. Competent authorities are responsible not only for enforcing food safety standards and conducting routine inspections but also for adopting continuous improvement strategies within monitoring and control systems, in coordination with other sectors and industries. Coordinated regulatory supervision is, therefore, indispensable for protecting public health and ensuring food safety throughout the production and distribution process.

## 4. Challenges of duality

The presence of fungi in the food industry represents a duality. As previously discussed, fungi can be utilized in different ways, such as to produce new products or to change the sensorial characteristics of conventional food. However, the same microorganism can also contribute to food spoilage and mycotoxin production. One example is *Penicillium roqueforti*, a filamentous fungus widely used in cheese making and known for producing several desirable compounds in cheese, such as acetic, butyric, caprylic, and caproic acid (López-Díaz et al., 2023; Vallone et al., 2014). However, *P. roqueforti* is also considered a common spoilage agent in foods, such as fruit, bread, and refrigerated products, due to its ability to tolerate cold temperatures, low oxygen concentrations, alkaline preservatives, and weak acids (Ropars et al., 2017).

Another important aspect related to these fungi is their ability to produce mycotoxins, roquefortine C, PR-toxin, patulin, penicillic acid, mycophenolic acid, and isofumigaclavine A and B (Vallone et al., 2014). Their toxicity is low, but they are highly unstable. Therefore, it is essential to protect cheeses against fungal contamination. This is particularly important because many cheese production processes do not rely on the use of defined fungal starter cultures. Instead, they allow the natural colonization of environmental fungi during ripening. As a result, any strain that has not been properly characterized and approved for commercial application should be considered unsuitable for intentional use in food production (López-Díaz et al., 2023; Singh & Gaur, 2021). The potential use of fungal strains in food products, such as cheese, requires careful evaluation prior to any commercial application. This is because, despite possible technological or protective benefits, each strain must be proven safe. Safety assessments typically include testing for the ability to produce mycotoxins, toxicological screening, and genomic analyses to ensure the absence of genes associated with toxin biosynthesis. Only strains that meet these strict safety standards can be considered suitable for use in the food industry (Singh & Gaur, 2021).

*Mucor* is a ubiquitous microorganism commonly associated with the spoilage of dairy products, particularly cheese, as well as meat and fruit. It can cause off-flavors, anomalous textures, and discoloration (Morin-Sardin et al., 2016; Yegin et al., 2011). Despite these disadvantages, *Mucor* has recently been explored for its potential in enzyme production for cheesemaking. Bensmail et al. (2020) investigated the potential of certain species in Camembert cheese production and isolated 20 fungal strains from soil, of which 1 demonstrated a strong ability to coagulate milk. This microorganism, identified as *Mucor circinelloides*, exhibited a coagulation capacity comparable to that of vegan rennet. In a sensory panel evaluation, assessors found that cheese produced with *M.*

*circinelloides* was similar to the conventional version, suggesting that the produced enzyme acts as a viable alternative to traditional rennet.

*Monascus* fungi are widely recognized for red pigment production, which is used as a colorant in the food industry. This beneficial property is already commercially exploited, as shown in Table 1. The pigments produced by *Monascus ruber* have been reported to exhibit antimicrobial activity against pathogenic bacteria, such as *Staphylococcus aureus* and *Escherichia coli*, as demonstrated by Vendruscolo et al. (2014). Additionally, these pigments may possess other biological functions, including antioxidant and anti-inflammatory properties (Qin et al., 2023). However, *Monascus ruber* has been identified as causing spoilage in table olives (Panagou et al., 2002). This duality highlights the need for caution, as certain *Monascus* spp. can produce the mycotoxin citrinin, raising concerns about the biotechnological aspects of pigment production.

Recent studies have aimed to address this challenge through genetic engineering and clustered regularly interspaced short palindromic repeat (CRISPR)/Cas technologies, focusing on understanding and manipulating metabolic pathways to optimize pigment production while minimizing or eliminating citrinin biosynthesis. Zhang et al. (2025) demonstrated that targeted gene editing using CRISPR/Cas9 can effectively knock out or repress key genes involved in citrinin biosynthesis, thereby reducing toxin levels without compromising pigment yield. These strategies offer a promising approach to mitigate the safety concerns associated with *Monascus*-derived products by decoupling pigment production from citrinin formation.

Several *Fusarium* spp. are recognized for their biotechnological potential, particularly in the cultivation of biomass known as mycoproteins, offering a sustainable alternative with diverse applications in various food products (Cheriaparambil & Grossmann, 2025). This includes derived products, such as triacylglycerol lipases from *Fusarium oxysporum*, which have received GRAS status for use in the production of baked goods, and fungal proteins obtained from *Fusarium* sp. mycelia (FDA, 2016; FDA, 2021). *Fusarium oxysporum* is also known as a significant plant pathogen, with specificity for over 150 plant host species. Bananas are frequently attacked by *Fusarium oxysporum* f. sp. *cubense*, which produces beauvericin. These compounds not only cause physical crop damage but also pose a risk to human health when ingested (Li et al., 2013).

*Aspergillus niger* is a common black mold found in several types of foods, such as fruit, corn, and nuts (Li et al., 2020). It is a fungus found in air, water, and soil and can develop fast, depending on the food characteristics (Fendiyanto & Dwi Satrio, 2020; Li et al., 2020). In addition to causing food spoilage, there is growing concern regarding the production of the mycotoxins fumonisin and ochratoxin A, which pose significant public health risks (Li et al., 2020). However, similar to the other microorganisms presented, biotechnological studies have been evaluating this organism for the production of important compounds for the food industry, such as citric acid (Xue et al., 2021), amylase (Bellaouchi et al., 2021), cellulase (Bellaouchi et al., 2021; Siva et al., 2022), and lipase (Bellaouchi et al., 2021; Xiang et al., 2021). These show that a single microorganism can perform a variety of functions, maximizing its potential and not only negatively affecting society. To ensure their safe commercialization, fungal strains must obtain GRAS or QPS status (Singh & Gaur, 2021).

Although fungi are commercially available and studies on metabolism are gaining increasing attention, the European Food Safety Authority (EFSA) has excluded filamentous fungi from QPS evaluations. Despite the growing knowledge of their metabolites, this decision was based on information regarding their toxicology, which remains limited. Among the most recent notifications (12 filamentous fungi) submitted, none have been evaluated by this authority to date (EFSA, 2020; EFSA, 2025).

Another important characteristic of fungi is their ability to produce biofilms. Biofilms are microbial communities formed by the adhesion of microorganisms to the surface, followed by exopolysaccharide production. This matrix acts as a protective barrier, enhancing the microorganism's resistance to environmental stress and antimicrobial agents (Miranda et al., 2022). In the food industry, biofilms are often associated with negative impacts, as they cause blockages in processing pipelines and contribute to product contamination when biofilm fragments detach from surfaces (Becerril et al., 2023; Miranda et al., 2022). However, in certain areas of food production, biofilm formation can be beneficial, particularly in fermentation processes. For instance, in a study on fumaric acid production, Sebastian et al. (2021) observed a 40 % increase in fumaric acid yield when *Rhizopus oryzae* was immobilized on polystyrene foam beads compared to free mycelial fermentation. In addition to improving fermentation efficiency, such techniques can facilitate fungal reuse and simplify fungal mycelium recovery, streamlining the overall process.

All aspects of the duality of filamentous fungi can be linked to the One Health approach, which seeks to sustainably balance human, animal, and environmental health. Within this framework, antimicrobial resistance and food safety must be addressed comprehensively to integrate ecosystems and promote global health. Therefore, advancing research on fungal resistance is crucial. Currently, the most extensively studied aspects of antifungal resistance are related to antifungals commonly used in agriculture and clinical medicine, primarily azole and triazole compounds (Fisher et al., 2022).

Research on antimicrobial resistance has advanced significantly more in bacteria, mainly due to the biological differences between bacterial (prokaryotic) and fungal (eukaryotic) pathogens. Additionally, for a long time, fungi have not been regarded as a major public health threat (Fisher et al., 2022). For example, the resistance of *A. fumigatus* to triazoles in clinical settings has already been reported (Denning et al., 2011). Recently, more in-depth analyses of high-quality nuclear genomes, genome-wide association studies, and closed circular mitogenomes have been conducted to elucidate the pathways involved in the acquisition of resistance in fungi, such as *A. fumigatus*. A key aspect of understanding this process may be linked to mitochondrial functions, which confer resistance to azoles (Delbaje et al., 2025). However, substantial studies utilizing self-definition tools and extrapolating to other fungi and their mechanisms require further investigation. This is particularly important for gaining a comprehensive understanding of competence in acquiring and transmitting resistance and pathogenicity.

In the food industry, studies have been conducted to understand fungal resistance to sanitizers and chemical preservatives traditionally used in the food supply chain. Bernardi et al. (2018) evaluated the efficacy of commercial sanitizers, such as sodium hypochlorite, biguanide, peracetic acid, benzalkonium chloride, and quaternary ammonium compounds, against several fungi, including *Aspergillus*, *Penicillium*, and *Cladosporium*. Despite being recommended for use in the food industry, the authors found that certain sanitizers, such as biguanide, exhibited limited efficacy against the evaluated filamentous fungi. The most effective antifungal sanitizer was sodium hypochlorite. Peracetic acid was ineffective at the lowest recommended concentrations for most species except *Cladosporium cladosporioides*. However, it was effective at the highest concentration against all tested species, with Aspergillus *brasiliensis* being the only species resistant to intermediate concentrations.

The efficacy of a sanitizer can be influenced by various factors including its concentration, recommended usage, temperature, and contact time (Visconti et al., 2022). Furthermore, the diversity of fungi present within an industrial environment must be considered as different species and genera may prevail in different regions. Additionally, emerging fungal strains that are increasingly resistant may exhibit insensitivity to traditionally used sanitizers. These studies are relevant for developing more effective strategies to prevent the spread of undesirable fungi throughout the industry. Such strategies can also support biotechnological processes involving filamentous fungi by minimizing contamination from other fungi that may affect these processes.

In summary, the realm of fungi remains largely unexplored. Compared to bacteria, this gap is evident. A search in the National Center for Biotechnology Information (NCBI) revealed 105,601,236 nucleotide sequences related to bacteria, while only 22,567 sequences were associated with fungi (NCBI, 2024). This disparity highlights the significant gap in our understanding of fungi. Despite their commercial and biotechnological importance, much more research is needed to optimize their use and ensure the safety of fungi and their derived products in the marketplace. Additionally, future studies should focus on addressing issues related to spoilage fungi and mycotoxin production—both of which are major concerns for the food industry and public health.

## CRediT authorship contribution statement

**Luana Virgínia SOUZA:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Raiane Rodrigues da SILVA:** Writing – review & editing, Writing – original draft, Visualization. **Valéria Quintana CAVICCHIOLI:** Writing – review & editing, Writing – original draft, Visualization. **Rafaela de Melo TAVARES:** Writing – review & editing, Visualization. **Cinzia Lucia RANDAZZO:** Writing – review & editing, Visualization, Conceptualization. **Cinzia CAGGIA:** Writing – review & editing, Visualization, Conceptualization. **Antonio Fernandes de CARVALHO:** Writing – review & editing, Visualization, Resources, Conceptualization. **Luís Augusto NERO:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors 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

No data was used for the research described in the article.

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