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Review

Biosurfactants Produced by Yeasts: Environmental Roles and Biotechnological Applications

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Abstract

Biosurfactants are amphipathic compounds produced by various microorganisms, including fungi and yeasts, with those produced by the latter being of particular interest as they are considered microorganisms of low or no sanitary risk. This article presents an analysis of the available information regarding the role these compounds play within the ecological habitat where yeasts inhabit, as well as their potential biotechnological applications in commercial areas. Some of the biological roles that biosurfactants play for their producing microorganisms are unknown and can be highly diverse, depending on the adaptive needs microorganisms have to survive the environmental conditions prevalent in their habitat. However, some of these roles that have been reported are related to nutrient availability, cellular communication, and competition, as well as surface colonization. The structures of biosurfactant molecules produced by yeasts are highly diverse, and so far, have been reported as sophorolipids, carbohydrate–protein–lipid complexes, carbohydrate–protein polymers, mixtures of lactones, and mannosylerythritol lipids. In addition to their properties as surfactants and/or emulsifiers, many of these molecules have also been reported to possess biological activities, including antimicrobial, antifungal, antitumoral, antioxidant, antiadhesive, antiviral, ultraviolet (UV)-protectant, anti-aging agent, moisturizing, and enzyme-activator/inhibitor properties. By understanding the functions that biosurfactants perform in nature, novel and efficient methods for their production can be proposed, as well as new applications in areas such as pharmaceuticals, food, and cosmetics. The latter is of particular interest due to the growing biosurfactant market and the processes that demand greater knowledge about their production, biological, and environmental interactions for their management and disposal.

Keywords: biosurfactants; yeast; natural role; biotechnology

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1. Introduction

Yeasts are microorganisms widely distributed on the planet, capable of growing in different types of terrestrial and aquatic environments, in symbiosis with plants and animals, and in food products [1]. It has also been reported that some species are capable of populating environments with extreme conditions, such as pH, temperature, water activity, and nutrient limitation, among others. The survival of yeasts in this variety of environments has been related to abiotic and biotic factors; among the latter, their ability to adapt stands

out, thanks to the production of compounds such as antioxidants, exopolysaccharides, antibiotics, and biosurfactants [2].

Biosurfactants are produced by diverse types of microorganisms and are characterized as amphipathic molecules with interfacial activity, capable of reducing the interfacial and surface tension of liquids. Biosurfactants have been characterized by superior properties compared to synthetic surfactants, including their stability at high salinity, temperature, and pH values; the formation of stable emulsions, low toxicity, and improved biodegradability [3]. Biosurfactants produced by yeasts are more valued than those produced by bacteria due to their GRAS (Generally Recognized As Safe) status, especially when their production is required for applications in areas such as pharmaceuticals, cosmetics, or food. Some of the yeast genera reported as biosurfactant producers are *Candida*, *Yarrowia*, *Torulopsis*, *Pseudozyma*, *Kurtzmanomyces*, *Debaryomyces*, *Saccharomyces*, *Kluyveromyces*, *Rhodotorula*, *Wickerhamomyces*, *Galactomyces*, *Geotrichum*, *Apiotrichum*, *Pichia*, *Rhynchosporium* [1,4–7].

Bioprospecting has been a pivotal tool in the discovery of biosurfactants with remarkable properties, such as stability under extreme conditions or their production utilizing renewable feedstocks like agro-industrial and food industry waste [3,8]. The identification of their metabolites has contributed to the understanding of the roles these compounds play for the yeast that produced them in their ecological context. This information facilitates the identification of factors that promote the production of those metabolites under controlled laboratory conditions, as well as their mechanisms of action in diverse applications. Still, despite their significance, the biological roles of biosurfactants in the yeasts that produce them and in their native environments remain largely underexplored, often being limited to a few roles already characterized for other microorganisms. It is not easy to generalize the role biosurfactants play on the survival of yeast in their natural environment, given their diverse chemical nature [9].

On the other hand, the application of yeast biosurfactants is intrinsically linked to their molecular structure, which in turn is dependent on the yeast's origin. For instance, many biosurfactants exhibiting outstanding properties regarding resistance to extreme conditions and product stability have been reported to originate from yeasts isolated from extreme environments, both terrestrial and marine.

This chapter describes some of the strategies used in bioprospecting the yeast biosurfactants that were applied to diverse ecosystems, from Antarctic soil to marine sediments. Also, the biological roles of the yeast biosurfactants were analyzed in the context of the ecological habitats from which they were isolated. Moreover, the available information about their discovered biotechnological applications and considerations for their production has been reviewed.

2. Bioprospecting for Biosurfactant-Producing Yeasts

Bioprospecting is defined as the process of exploring biological diversity in search of biotechnological products, directly utilizing microorganisms, plants, and higher organisms, and/or their metabolites or derivatives, which can range from genetic material to metabolites, enzymes, and novel strains. It focuses on the development of new products with therapeutic applications and on the conservation of diversity. Bioprospecting is guided by the evolutionary and ecological development of selected species, as these exhibit adaptations that confer survival advantages for their ecological habitats [10–12]. Bioprospecting involves the identification, evaluation, and exploitation of diversity for commercial purposes, needing strategies that encompass both cultivable and culture-independent approaches, as well as in silico methods where microbial genome sequences are analyzed to explore novel genes and metabolic pathways [10,11,13].

Generally, bioprospecting comprises four stages: sample collection, cultivation and characterization, metabolite selection, and product development. However, additional stages may be incorporated depending on the specific research objective (Figure 1). For instance, during bioprospecting, it is crucial to employ specific monitoring methods for strain selection that aid in confirming the production of the metabolite of interest, in this case, biosurfactants. These techniques include the use of the drop collapse test, the emulsification index, and surface tension measurements, which are more extensively described in Satpute et al. [14]. It is important that during the bioprospecting process, diverse monitoring methods are selected for simultaneous application. These methods should be based on the distinct properties exhibited by biosurfactants, ensuring their complementarity, as the analytical approach of their properties will vary depending on their molecular structure type. Specifically, for effective surfactants, tests assessing their capacity to reduce surface tension are crucial, whereas for potent emulsifiers, tests corresponding to this specific property must be conducted.

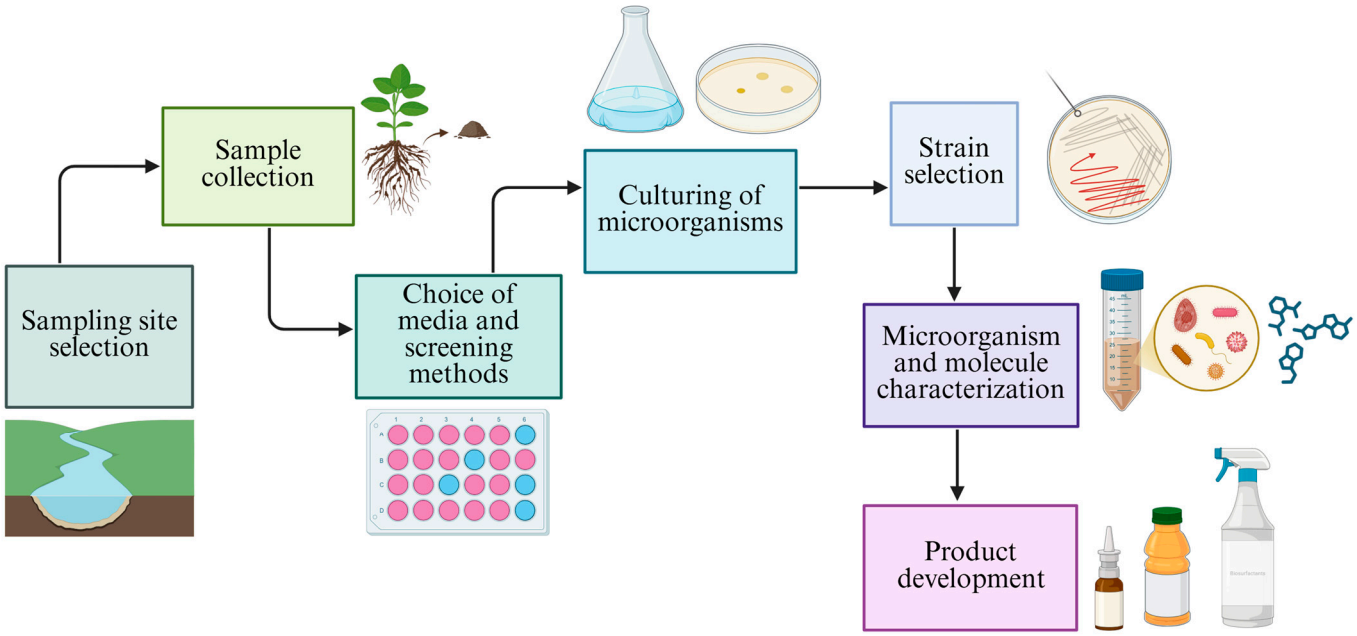

Figure 1. Bioprospecting stages (Created in https://BioRender.com).

It is important to highlight that while there is a larger volume of research on biosurfactant-producing bacteria and their respective biosurfactants, there is a growing necessity to explore a broader spectrum of microbial diversity [10]. Especially for yeasts, given their low health risk and classification as GRAS organisms, this underscores the relevance of the bioprospecting and strain selection methodologies previously indicated in the text for identifying novel and valuable producers.

Yeasts are recognized as ecological regulators due to their widespread distribution and antagonistic mechanisms. Specifically, they can exhibit antagonistic activity by competing for nutrients and are also capable of producing secondary metabolites, such as antimicrobials, thereby controlling the population of microorganisms within their ecological habitats. Furthermore, they possess multiple mechanisms for adapting to stress conditions, employing these as survival strategies [7]. Some yeasts produce toxins that impact cellular translation and transcription, thereby inhibiting the growth of specific antagonistic microorganisms. Notably, among these mechanisms is the capacity of some yeasts to produce biosurfactants, which can be utilized as biological control agents against pathogenic fungi and bacteria [15,16]. For instance, *Geotrichum candidum*, *Galactomyces pseudocandidum*, and

Candida tropicalis are examples of biosurfactant-producing yeasts that have been isolated from the rhizosphere of healthy crops, suggesting their beneficial presence for plants [6].

Many yeast species readily adapt to extreme conditions of salinity, pH, pressure, and temperature, making them targets of increasing interest for their use in the biosynthesis of industrially applicable metabolites. Moreover, understanding the physiological and metabolic adaptations that enable them to thrive in extreme habitats is of significant interest. The isolation of wild yeast from extreme environments is crucial for biotechnology, since only 1% of yeast species have been discovered. Protocols such as the Nagoya Protocol must be followed for access to genetic resources. Molecular identification of yeasts is primarily conducted through the amplification of 18S rRNA gene sequences and the internal transcribed spacer (ITS), leading to the isolation and classification of over 2000 yeast species. Consequently, genome sequencing and the application of metagenomics are key tools for exploring the diversity and adaptations of these yeasts, and collaboration among microbiology, ecology, and molecular biology can accelerate the discovery of novel biotechnological strategies [6,9,17–19].

It has also been reported that some of the habitats colonized by biosurfactant-producing microorganisms are cold climates, where the average temperature hovers around 5 °C. Notably, it is estimated that approximately 50% of microorganisms in polar soils are known to produce biosurfactants, including yeasts [20]. Biosurfactants synthesized under low-temperature conditions are particularly appealing because they retain their surfactant and emulsifying properties even in such environments. Also, their production at low temperatures offers a significant advantage for energy-efficient production systems [20,21]. As an example, the Antarctic yeasts *Naganishia adeliensis* and *Candida glaebosa*. The biosurfactant from *Naganishia adeliensis* demonstrated an emulsification index of approximately 60% when grown on an alternative carbon source, specifically a sugarcane hemicellulose hydrolysate, within just 72 h of cultivation. Additionally, it could maintain its activity at temperatures ranging from 0 to 4 °C but not exceeding 40 °C [22]. In contrast, the biosurfactant from *Candida glaebosa* achieved emulsification indices of up to 30% [23].

Many species of fungi and yeasts have been reported to possess extraordinary capabilities for thriving under extreme conditions, for instance, surviving pH values ranging from 2.5 to 11, high temperatures up to 60 °C, and salt concentrations up to 4 M. Beyond these resilient capacities, they have also been described as exhibiting broad metabolic diversity, enabling them to utilize various nutrient types. For example, regarding carbon sources, they can metabolize complex polymers like hemicellulose into simple sugars, such as glucose, rendering them attractive for cultivation using renewable nutrient sources like agro-industrial waste [24].

Yeasts are widely distributed in various habitats, including marine environments, where they have also been explored as biosurfactant producers, including contaminated sites [19,25]. An example is the marine yeast *Cyberlindnera saturnus*, which produces the biosurfactant cybersan and has been isolated from marine sediments contaminated with hydrocarbons. This yeast exhibits significant antimicrobial activity (proven by in vitro assays) against clinical strains of *E. coli* and *S. aureus*, demonstrating growth inhibition at a concentration of 200 μg/mL [19].

Marine fungi and yeasts have been understudied for biosurfactant production, although molecules with unique properties have been obtained, with glycolipids and glycoproteins being reported. It is important to highlight that, due to climate change-induced environmental deterioration, oceans are expected to experience some of the most significant losses in biodiversity, which is a compelling reason to invest resources in the bioprospecting of biosurfactant-producing fungi and yeast in this habitat. Once isolated and scaled to production stages, these microorganisms offer various advantages, such as their ability

to withstand wide ranges of extreme values of temperatures, pH, and salinity. Also, high salinity resistance provides an advantage from a sterility perspective, as many potential contaminating microorganisms will not grow under those conditions [14]. One such marine environment from which biosurfactant-producing yeasts have been isolated is that of zoanthids, from which strains of *Yarrowia lipolytica* have been recovered. The biosurfactants produced by those strains have demonstrated the capacity to form stable emulsions of up to 61%, even at temperatures of 120 °C and pH ranges between 2 and 10, in addition to being able to metabolize hydrocarbons such as kerosene [26]. Among other halophilic biosurfactant-producing yeasts are *Rhodotorula mucilaginosa* and *Debaryomyces hansenii*, whose sophorolipid-type biosurfactants exhibit interesting antimicrobial activities (proven by in vitro assays) against both Gram-positive and Gram-negative pathogenic bacteria [27].

It is important to consider that the demand for bioprospecting is steadily increasing due to its significant contribution to the development of novel products, the establishment of innovative processes, the sustainable exploitation of biological resources, and the conservation of biodiversity [11].

3. Relationship Between Structural Diversity and Biological Role

The specific type of biosurfactant molecule depends on factors such as the synthesizing microorganisms, the carbon source used, and whether it is hydrophilic or lipophilic [4]. The structure of biosurfactants produced by yeasts is highly diverse, including molecules from the glycolipid family, such as sophorolipids, as well as carbohydrate–protein–fatty acid complexes and polymeric forms like liposan [28].

Biosurfactants are commonly classified in several ways, depending on their structure, charge, or molecular weight. Within this latter classification, high- and low-molecular-weight biosurfactants are included. Low-molecular-weight biosurfactants include lipopeptides and glycolipids, which are characterized by their ability to reduce surface tension efficiently [11,29].

The biological role of biosurfactants is not fully understood, but in some cases, it has been observed to have a relationship with their structure (Figure 2). The case is similar to antibiotics, which are generally known as secondary metabolites and, in some instances, are not essential for cell viability but are crucial for surface colonization processes, providing a competitive advantage against other microorganisms. Some authors have suggested that the use of biosurfactants could be beneficial in treating certain pathogenic microorganisms that have already developed resistance to existing antibiotics [28,30].

Some microorganisms are known to produce extracellular biosurfactants, while others produce membrane-anchored ones. The primary biological function of the first one is recognized to be the emulsification of hydrophobic compounds typically utilized by the microorganism as a carbon source, whereas the second latter is known to contribute to the transport of compounds across the cell membrane [31]. It has been reported that membranal biosurfactants are predominant over extracellular ones, achieving a yield of up to 900 mg/L with an emulsifying capacity of approximately 61%, which suggests that these microorganisms primarily employ the transport of hydrocarbons across the membrane [26]. Consequently, the use of biosurfactant-producing microorganisms in environmental decontamination processes for oil spills proves to be an effective approach for bioremediation of contaminated sites.

As previously mentioned, in terms of their molecular weight, biosurfactants can be classified as low and high-molecular-weight. The first ones are identified as those capable of mobilizing or solubilizing hydrophobic compounds like hydrocarbons, while the second latter ones are known for their ability to emulsify these compounds. In general, microbial biosurfactants have the physiological function of facilitating the contact of microorganisms

with hydrophobic substrates, especially for those capable of metabolizing them [12,32]. In the case of yeasts, it has been reported that their cell wall possesses lipophilic channels containing hydrophobic polymers that exhibit high affinity for the same kind of substrates, thereby enabling these cells to anchor more easily and consume them as carbon and energy sources. For extracellular biosurfactants, their physiological function lies in modifying hydrophobic substrates through their emulsification or partial solubilization, allowing for their transport and subsequent consumption [32].

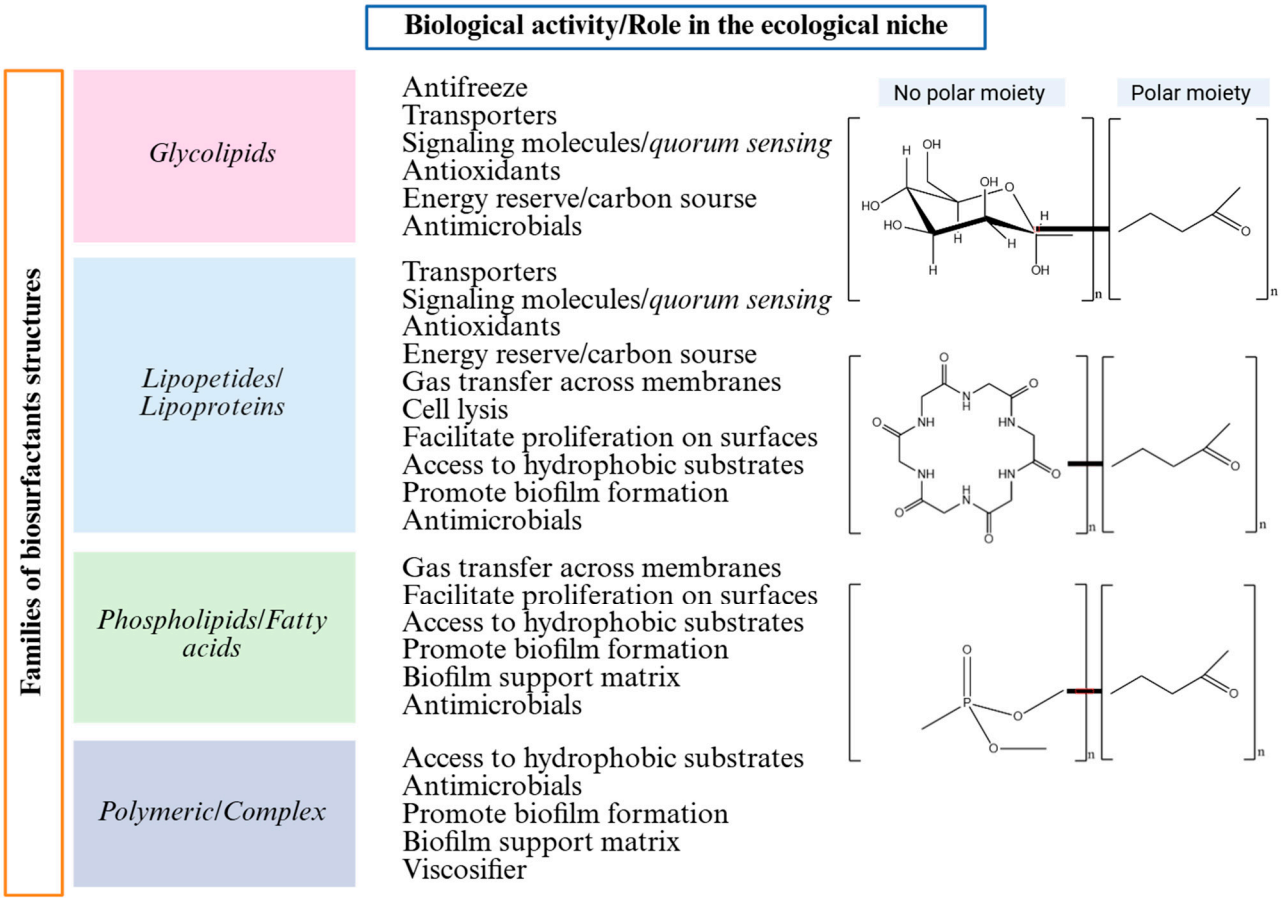

Figure 2. Families of reported structures and the biological role attributed to them (Created in https://BioRender.com).

Regarding structural diversity, over 2000 structures produced by various microorganisms, including fungi and yeasts, have been reported. High-molecular-weight biosurfactants include polysaccharides and proteins, while low-molecular-weight biosurfactants comprise glycolipids, fatty acids, lipopeptides, and lipoamino acids. The hydrophobic moiety of biosurfactants typically consists of fatty acid residues with 8 to 18 carbon chains, which may or may not contain unsaturations. Depending on their charge, they can also be classified as anionic and non-ionic [33]. Biosurfactants with biological activities such as antimicrobial, anti-adhesive, and antioxidant, typically possess complex structures that are selectively capable of inhibiting target molecules [24,34].

3.1. Glycolipids and Glycoproteins

Glycolipids have been reported to play a physiological role in the cells that produce them as protein stabilizers, mediators in cell recognition, and participants in membrane formation [30]. Glycolipids are among the most commercially relevant biosurfactants due to their production at high concentrations and their properties as low-molecular-weight

compounds. Still, the mechanisms of regulation, biosynthesis, and transport are poorly understood [35].

Biosurfactants such as glycolipids are produced as secondary metabolites, meaning they are not essential for cell viability. For several microorganisms, glycolipids can play a significant role in colonizing different types of habitats, especially those with antimicrobial activity, as they can inhibit microorganisms that may compete for nutrients. It has also been reported that, by acting as signaling molecules, they can coordinate cellular communication and enable the aggregation and transport of microbial communities to form biofilms. Furthermore, some molecules have been reported to activate the immune response in mammalian cells, as well as to act as protectors against free radicals, thereby exhibiting antioxidant activity. Some other biosurfactants, such as sophorolipids, can function as carbon reserves that can be consumed in times of nutrient scarcity [36]. The functions of antimicrobial agents, carbon source reserve, and transport system for hydrophobic substrates have also been confirmed by the catabolic pathway of biosurfactants, as these components can be utilized by both producing microorganisms and those that can consume them in the environment where they are released [37]. The antimicrobial activity of some sophorolipids has been related to the sugar moiety of the biosurfactant molecule [38]. Some biosurfactants function like triglycerides, serving as energy reserves for yeasts, as with mannosylerythritol lipids (MELs) and other glycolipids [39].

Among the glycolipids produced by yeasts, mannosylerythritol lipids (MELs) stand out. These biosurfactants have garnered increasing interest due to their low toxicity [40] and biodegradability, making them sought after for pharmaceutical and cosmetic applications. MELs are non-ionic, low-molecular-weight glycolipid biosurfactants [1,39,41]. They are produced by yeasts of the genera *Ustilago*, *Moesziomyces*, and *Pseudozyma* [9,40,42]. These biosurfactants have been reported to possess antimicrobial properties (proven by in vitro assays), antioxidant activity, and the ability to protect cells from UV radiation damage and reduce signs of aging [40,41,43]. It has been reported that the antibiotic action of some MELs targets the lipid bilayer of cell membranes, destabilizing them. Direct penetration into the membrane layer and variation in the extracellular solute concentration are two reported mechanisms, and they are highly effective against Gram-positive and Gram-negative bacteria [30,40]. The structure of MELs is central for their activity, with carbon chain length and degree of acetylation being determinant factors in their antimicrobial action [1,30,42]. Some authors have reported prebiotic properties for certain biosurfactants, such as MELs [43,44].

An important aspect in the characterization of biosurfactant molecules is their ability to self-assemble into various structures, which is a hierarchical process dependent on both concentration and temperature. The particles formed from these assemblies can be employed for different types of compound encapsulation [30]. This aggregation capacity of MELs is associated with the presence of acetylated groups [42]. The lipidic chain length of biosurfactants has been linked to the carbon source. However, the size of this molecular portion does not influence the Critical Micelle Concentration (CMC) value or the reduction in surface tension, as reported for MELs biosurfactants [20]. On the other hand, in cold environments, biosurfactants play an important role for microorganisms as they are utilized for solubilization and to facilitate access to scarce nutrients, especially those of a hydrophobic nature. It has been reported that MEL-type biosurfactants produced by the yeast *Moesziomyces antarcticus* play a significant role in the microorganism's survival under extreme low-temperature conditions, as they possess the capacity to act as an ice crystal anti-aggregant and reduce the freezing point [20].

Some glycoproteins can affect cell permeability, exhibiting activity as toxins against phytopathogenic fungi and other pathogenic microorganisms inhabiting the same eco-

logical habitat as the yeasts that produce them, thereby inhibiting or controlling their growth [15].

3.2. Lipopeptides

Lipopeptides are another type of biosurfactant molecule that plays a distinct role depending on the needs of the microorganisms that produce them. It has been reported that they can promote gas exchange across cell membranes, modify the viscosity of the cellular microenvironments, facilitate cell motility, enhance access to substrates, and support growth on surfaces (biofilm formation), among other activities (Figure 2) [28]. In the context of promoting biofilm formation, this is associated with the high degree of virulence and antifungal resistance that some pathogenic strains of fungi and yeasts from *Cryptococcus* and *Candida* genera may possess [45,46].

Among other functions possessed by biosurfactants, biosurfactants applied in agriculture play an important role in the plant rhizosphere by facilitating the colonization of microorganisms in the roots, promoting the adhesion of beneficial bacteria, and forming rich microbial communities, whose communication is also benefited by biosurfactants through their function as *quorum-sensing* signaling molecules in biofilms [28,47]. Microbial biosurfactants also play a significant role in the ecology of degraded, contaminated, or poor soils, as they improve the bioavailability of micronutrients, such as minerals, and solubilize contaminants like hydrocarbons and pesticides, making them more accessible for bioremediation, in addition to immobilizing heavy metals [48].

4. Biosurfactant Properties and Biotechnological Applications

In the previous section, we discussed how the structure of biosurfactants is related to their biological roles, in the same way, the structure of the biosurfactant influences the properties, this is, the chemical nature of the polar head and the carbon chain length of the hydrophobic tail determine the capacity of reduce the surface tension and/or the emulsifying capacity of different oils, that is why each biosurfactant or bioemulsifier is characterized by this properties. Although the chemical structure is related to the properties, predicting them solely from the chemical composition of the biosurfactant molecule remains challenging. Therefore, characterizing its capacities and properties is necessary to understand its possible applications, as described below.

Among the properties that are required to be analyzed in biosurfactants are emulsifying activity, Critical Micelle Concentration (CMC), and reduction in surface tension. These properties enable their utilization in various biotechnological fields, as shown in Table 1. Although many of the biosurfactants reported for yeast are glycolipids, they do not share the same properties despite having a similar chemical structure (Table 1).

Microbial biosurfactants exhibit superior properties compared with synthetic surfactants. For instance, CMC values range from 1 to 2000 mg/L, effectively reducing the surface tension of water to as low as 30 mN/m, although lower values have been reported in some cases. Additionally, they demonstrate stability at high temperatures and across a pH range of 2 to 12, in addition to tolerating salt concentrations of up to 10% (Table 1) [49]. On the other hand, they are considered environmentally safe, due to their low toxicity, which allows them to be employed for the recovery of hydrocarbons in contaminated sites and hydrocarbon extraction and metal processing locations [50,51]. This is attributed to their emulsifying capacity and their ability to reduce surface tension, which facilitates the extraction or solubilization of hydrocarbons, in addition to their chelating capacity required for metal extraction.

The use of yeast biosurfactants has proven successful for this purpose, such as the crude extract (cell-free broths) from *Candida sphaerica*, which achieved up to 90% removal of

motor oil from contaminated sand, a value superior to those reported with synthetic surfactants (55–80%). Furthermore, the presence of the biosurfactant accelerated the biodegradation rate by 10 to 20% during the first 45 days of the process [52]. *Rhodotorula* sp. is another biosurfactant-producing yeast that has also been reported as a successful application case, using the microorganism along with its biosurfactants for the removal of contaminants such as hydrocarbons, vegetable oils, and nitrogen. It has reported a removal efficiency of up to 84% for ammoniacal nitrogen in leachates and removal greater than 95% for hydrocarbons in contaminated soils [53,54].

Table 1. Biosurfactant, its properties, and biotechnological applications.

Biosurfactant	Yeast	Properties	Applications	References
Glycoprotein complex with low lipid content	*Yarrowia lipolytica*	Emulsification index of 61% or greater, emulsion stability at temperatures of 90–120 °C, stability at pH 2 to 10, and salinity up to 10%. CMC of 15 mg/mL, reduction in surface tension down to 43.8 mN/m.	Enhanced hydrocarbon recovery in contaminated sites.	[26]
Sophorolipid	*Cutaneotrichosporon mucoides*	Emulsification index of up to 70% with an emulsifying activity of 3.0 EU/mL.	NR	[55]
Sophorolipid	*Metschnikowia dubei Metschnikowia shirgulensis*	Surface tension reduction between 34–35.5 mN/m, CMC between 4–5 mg/mL, emulsification index ranging from 82–89%, remaining stable even at 121 °C and 10% NaCl. It possesses antifungal activity against *F. solani* and *F. oxysporum*. It induces apoptosis in cancer cells via the generation of reactive oxygen species (ROS).	Antioxidant, anticancer, antifungal (proven by in vitro assays).	[56]
Glycolipid	*Aureobasidium thailandense*	CMC of 550 mg/L, reduction in surface tension down to 31.2 mN/m.	Hydrocarbon recovery in contaminated sites.	[57]
Anionic Glycolipid	*Geotrichum candidum, Galactomyces pseudocandidum and Candida tropicalis*	Reduction in surface tension down to 51.6 mN/m, with emulsification index between 14 and 59.6%.	NR	[6]
Cybersan (Glycolipid)	*Cyberlindnera saturnus*	Antimicrobial activity (200 µg/mL), CMC of 30 mg/mL, reduction in surface tension down to 28 mN/m. Low cytotoxicity with cell viability greater than 70%.	Antimicrobial (proved in vitro assays).	[19]
Pullusurfactants A-E (myo-inositol lipids)	*Aureobasidium pullulans*	Reduction in surface tension from 22.4–32.3 mN/m, low cytotoxicity (>50 ppm).	Pharmaceutical and cosmetic products.	[58]
Anionic Lipopeptide	*Candida lipolytica*	No toxicity in seeds and *Artemia salina*. CMC of 0.03%, with a surface tension reduction down to 25 mN/m.	Industrial and environmental applications.	[59]

Table 1. *Cont.*

Biosurfactant	Yeast	Properties	Applications	References
Mannosylerythritol lipids-B	NR	At a concentration of 31.6 mg/L, it promotes surface wettability, modifying the contact angle of the water drop. At 158 mg/L, it promotes lettuce seed germination and root growth.	Bioestimulant	[60]
Rufisan	*Candida lipolytica*	CMC of 0.03%, with a surface tension reduction down to 25 mN/m. Antimicrobial activity against *Streptococcus agalactiae* and *Streptococcus mutans* strains. Anti-adhesive activity in *Lactobacillus*, *S. epidermidis*, *E. coli*, *C. albicans*, and *P. aeruginosa* strains.	Antimicrobial and anti-adhesive (proven by in vitro assays).	[34]
Glycolipid	*Candida bombicola*	Surface tension reduction to 29–30 mN/m, CMC of 0.5%, interfacial tension of 3.5 mN/m, emulsification index between 49–58%. No toxic effects on seeds or significant cytotoxicity.	Thickener for sauces and foods.	[61]

NR: Not Reported.

Biosurfactants can be employed as substitutes for surfactants in products for agricultural use due to their biodegradability, as they perform the same function as dispersants or emulsifiers. Moreover, they have been reported to possess benefits such as seed protection, growth stimulation (including germination and secondary root development), and serving as biocontrol agents, among others. Sophorolipids from *Rhodotorula babjevae* have demonstrated efficacy against phytopathogenic fungi such as *Colletotrichum gloeosporioides*, *Fusarium verticilliodes*, *Fusarium oxysporum* f. sp. *pisi*, *Corynespora cassiicola*, and *Trichophyton rubrum* [47,62]. Regarding the capacity to promote seed germination, glycolipids produced by the yeast *Pichia occidentalis*, along with the yeast itself, have been reported to enhance germination and root growth in sorghum and millet. Meanwhile, the glycolipid MEL-B, when applied to *Lactuca sativa* L. seeds, promotes root growth, suggesting its potential use as a biostimulant. However, at concentrations equal to or greater than 316 mg/L, it exhibited a phytotoxic effect, which indicates that studies on the toxic concentration for each target organism should be expanded [60,63].

The capacity to biodegrade or be readily absorbed into the environment, along with their low toxicity (at least one order of magnitude lower than synthetic surfactants), are advantages of their use in products employed in agricultural production worldwide, thus reducing the ecological footprint generated by agrochemicals. In environmental applications, biosurfactants can be used to increase the bioavailability of contaminants. They can sequester and encapsulate hydrophobic pollutants, heavy metals, or pesticides, contributing to their degradation and removal from the environment [10,64]. It has also been reported that some biosurfactants contribute to biofilm formation, either by enhancing cell-to-cell communication or by serving as an anchoring material, which helps beneficial plant microorganisms colonize their roots, thereby improving nutrient absorption and biological control of pests [10]. For environmental applications, it is also important to consider that biosurfactants appear to exhibit no toxicity towards seeds, microorganisms, or higher organisms at the concentrations reported in existing studies [51,59]. MELs biosurfactants produced by *M. antarcticus* have shown IC_{50} values of 999.9 mg/L, compared

to values of 60.4 mg/L for the commercial hydrocarbon dispersant Corexit, making them safe for environmental applications [51].

In the pharmaceutical field, *Candida* species are among the most extensively studied for the production of biosurfactants, with applications including pharmacological therapies and immunotherapy. Regarding these types of applications, it is important to emphasize that biosurfactants must exhibit low cytotoxicity to be considered safe for humans or animals. Cybersan and pullusurfactants are low-toxicity glycolipids that have been proven to be biocompatible, as they demonstrate cell viability exceeding 70%, even at concentrations up to 50 ppm [19,58]. In addition to the importance of their applications, another advantage of biosurfactants produced by yeast is that they achieve higher concentrations than those produced by bacteria, which would facilitate their production to meet commercial demand [24].

Among the most significant biological activities attributed to yeast-derived biosurfactants are antimicrobial, anti-adhesive, antiviral, anticancer, antifungal, immunological adjuvant, and drug encapsulation systems for their controlled release [19,24,28,56,65]. Due to their capacity to form micelles, biosurfactants have been considered for the encapsulation of compounds used in pharmaceuticals, food, or cosmetics, as is the case with MELs, which can be part of liposomes [30,44]. MELs have been reported to possess the lowest CMC, ranging from 2.7–6.0 $\times$ 10^{-6} M, with the ability to reduce the surface tension of water to as low as 24.3 mN, one of the lowest values reported for microbial biosurfactants. Additionally, they exhibit an emulsifying capacity superior to that of Tween 80 (a synthetic surfactant commonly used). The biosurfactants that display these properties are produced mainly by yeasts of the genus *Pseudozyma* [1,66,67]. Considering the capacity of MELs self-assembly they display interesting properties for applications in the cosmetic field, such as: thermostability at high temperatures (up to 95 °C), formation of water-in-oil microemulsions and bicontinuous emulsions, formation of vesicles and structures for the encapsulation of liposoluble products, and some exhibit moisturizing activity similar to ceramides, restoring cell viability in models of damaged skin [67].

Some biosurfactants exhibit antioxidant properties, as is the case with sophorolipids, mannosylerythitol lipids, and lipopeptides. This antioxidant capacity would have several applications in the pharmacological, cosmetic, and food industries, as they can act as protective compounds for components sensitive to light, UV rays, high temperatures, or free radical activity, or also directly as protectors of skin cells [68]. Sophorolipids produced by yeasts of the genus *Metschnikowia* have also been reported to present antifungal, anticancer, and antioxidant activity (Table 1) [56].

Biosurfactants are also utilized in the food sector as foaming, dispersing, and thickening agents, as they contribute to enhancing the texture, extending the shelf life of products, and promoting long-term stability [61]. Additionally, they facilitate the formation of stable foams due to their ability to reduce surface tension. Their emulsifying capacity allows for the maintenance of stable emulsions during cooling and cooking processes, while also providing unique textures that enhance the sensorial properties of food products. Glycolipids are particularly interesting in food applications, such as the one produced by *Candida bombicola* [61], which has proven to be especially useful for stabilizing micro- and nanoemulsions necessary for obtaining thick sauces. In food processing, changes in pH, temperature, and salinity are commonly employed. However, the presence of biosurfactants can contribute to maintaining product stability even under these changes, as they have been reported to withstand variations in these parameters over wide ranges. The antioxidant activity is a desirable property in food additives, as it allows for the protection of their active compounds; for example, they can inhibit the auto-oxidation of edible oils, as has been demonstrated with the use of biosurfactants from *Saccharomyces cerevisiae* in

food applications [69]. Some biosurfactants also exhibit anti-adhesive activity, which means that they can reduce the ability of some cells to adhere to surfaces and form biofilms. This capacity is desirable for use in cleaning food processing surfaces to prevent pathogen adhesion and thus food contamination [70].

5. Biosurfactant Production and Product Formulations

The bioprocess developed to obtain biotechnological products generally includes five stages (Figure 3): selection of culture conditions, inoculum production, fermentation scale-up, separation/purification of the molecule of interest, and packaging. These same stages are also present in the production of biosurfactants, with the addition of specific methodologies and techniques for monitoring the cells and the molecule of interest, as well as for verifying the surfactant and/or emulsifying properties of the product at each stage of the bioprocess. Within these stages, several points can be determinant for a sustainable and commercially competitive production, such as the use of alternative or low-cost carbon and energy sources, the use of optimized fermentation systems and media, the use of metabolically optimized strains, as well as efficient extraction and purification systems [71–73]. However, the production of biosurfactants currently remains costly, from the biosynthesis process through to their separation and purification processes.

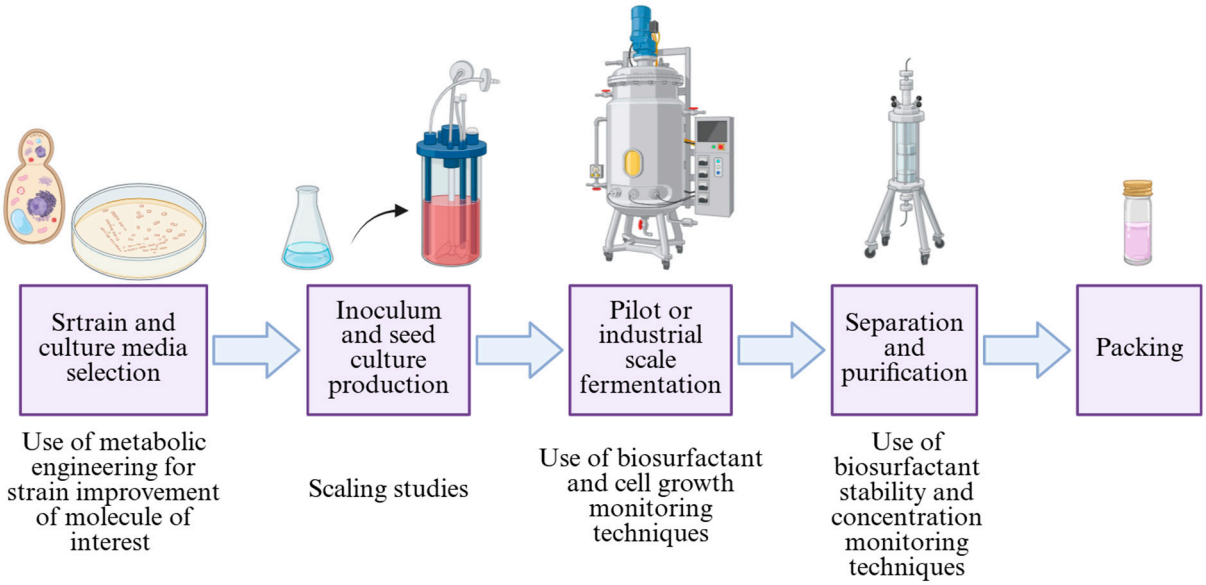

Figure 3. General steps involved in the biosurfactant production process (Created in https://BioRender.com).

During the biosynthesis of biosurfactants for some yeast strains, the cells require the presence of both a hydrophilic and a hydrophobic carbon source, as well as a restriction in nitrogen availability or a high C/N ratio [23,74,75]. It is noteworthy that the hydrophobic carbon source defines the hydrophilic moiety of the biosurfactant molecule. Nonetheless, its presence is not strictly necessary, as some microorganisms can synthesize it de novo, although at a higher energetic cost. The effect of nitrogen limitation on biosurfactant biosynthesis has been studied in greater detail in yeasts that produce sophorolipids, mannosylerythritol lipids, and cellobiose lipids, since in all three cases, this condition contributes to increasing the biosurfactant yields. These conditions are not only responsible for controlling the type of molecule produced and the yield, but they also significantly influence their properties, by yielding molecules that are more soluble in water, generating more stable emulsions, or reducing surface tension more efficiently [75,76]. Additionally, other components of the culture media were found to positively influence biosurfactant

production, as evidenced by the $ZnSO_4$ in the cellobiose lipids production, which improves the concentration produced, reporting a concentration of 4.95 g/L that is the highest titter achieved in this type of bioprocess [76].

Carbon sources that have been tested to produce biosurfactants include soluble sugars such as glucose, both mineral and vegetable oils, or combinations of them, namely, hydrophilic with hydrophobic carbon source mixtures [59]. Renewable carbon sources derived from industrial residues such as oils, bagasses, or liquors, like sugarcane hemicellulose hydrolysate, have also been evaluated [8,22,55]. Other tested residues include agro-industrial by-products such as corn steep liquor, sugarcane molasses, and olive oil mill wastewater. *Aureobasidium thailandense* can utilize olive oil wastewater (1.5% *w*/*w*) for biosurfactant biosynthesis, achieving a maximum production of up to 139 mg/mL in only 48 h and demonstrating a reduction in surface tension to 31.2 mN/m [57].

Biosurfactant production can be made sustainable by employing renewable carbon sources such as residual vegetable oils or food industry wastes. However, these residues do not always maintain the same properties of the produced biosurfactants, which could modify production yields and the molecular structure biosynthesized. Depending on the application expected for the metabolites, this can have a differential effect; for environmental or industrial applications, the purity and concentration of the molecule do not demand as much rigor as in pharmaceutical, food, or cosmetic applications. The modifications affect not only the fermentation stage but also the extraction and purification stages [31].

As part of the production process improvements, the study and modification of transport proteins for extracellular biosurfactants, as well as those involved in the transport and consumption of carbon sources, have been considered, since modifying any of these can enhance the metabolic flux that allows for a greater biosynthesis of these metabolites, for example, reaching up 3.07 g/g h with xylose as carbon source [13,35]. Likewise, modifying the capacity of yeasts to consume certain types of substrates, such as complex sugars, hydrocarbons, fatty acids, or glycerol, enables the use of unconventional media or those considered as waste streams from particular industries [35].

For any bioprocess, there are upstream, fermentation, and downstream stages, with a greater number of publications in biosurfactants focusing on the upstream and fermentation stages rather than on the downstream stage. Although it is known how to obtain good yields for many biosurfactants during their biosynthesis, there is limited knowledge regarding their extraction and purification, which hinders the scaling-up of the bioprocess to obtain concentrations that would permit sustainable commercial production, highlighting that in any bioprocess, the separation and purification stages typically represent 60 to 80% of total process cost [77,78].

The selection of purification methods for biosurfactants is based on the type of molecule produced, starting with whether they are cell membrane-anchored, intracellular, or extracellular compounds. One of the most widely used methods is liquid–liquid extraction for extracellular biosurfactants. However, the use of hydrophobic carbon sources from agro-industrial waste, such as vegetable oils, makes the purification process more complex and costly, as they share the hydrophobic nature with the fatty acid moiety of biosurfactants, as is the case for MELs [77]. Therefore, alternative methods have been suggested to increase the specificity of biosurfactant purification, including centrifugation, more specific solvent extraction, foam fractionation, acid precipitation, nanofiltration, and activated carbon filtration [78]. Nanofiltration is a novel technique that has proven effective in separating MELs, with a reported increase in purity from 66 to 93% [77]. As MELs biosurfactants, cellobiose lipids (CBLs) possess interesting properties and applications in pharmaceutics, cosmetics, and agroindustry. Chromatographic columns are commonly used in high-level purification procedures to separate compounds with similar

structures as CBLs and MELs; however, the optimization of this technique requires more investigations [79].

The production and the degree of purification of biosurfactants are closely related to their intended application. For this reason, numerous patents have been registered regarding the production, purification, formulation, and application of microbial biosurfactants, with those produced by yeasts being prominent in sectors such as agriculture, pharmaceuticals, food, cosmetics, and the oil industry. Countries like the United States, Brazil, India, and China are notable leaders in this area of patent production [80].

Although for industrial or environmental applications, the biosurfactants do not need to possess a high degree of purity, the molecule must remain homogeneously dispersed in solution to ensure effective contact with the contaminant upon application. Likewise, the formulations must remain stable over time, even under changes in pH, temperature, and salinity. Almeida et al. [81] report that a biosurfactant produced by a strain of *C. tropicalis*, formulated with potassium sorbate that homogenizes the distribution of the biosurfactant, was able to maintain the stability of food emulsions for up to 120 days and under pH changes between 5–9, temperatures ranging from 40 to 50 °C, and salinity concentration of 1–5%.

In the pharmaceutical and cosmetic fields, which are those with the most publications and have been most successful in reaching the market, it is known that biosurfactants must possess a higher degree of purity, typically around 90–95%. Therefore, some of the main challenges to overcome for quality production are reducing fermentation costs, increasing yields, and affordable separation and purification methods [36]. Yeast biosurfactants have been used in cosmetic formulation, both in their pure form and as part of crude ferment extracts. Ferments are produced from media containing plant extracts or some pure agro-industrial residues, inoculated with specific strains or consortia, which may include yeasts from the genera *Saccharomyces*, *Torulaspora*, *Brettanomyces*, *Hanseniaspora*, *Schizosaccharomyces*, *Galactomyces*, and *Candida*. These fermented extracts have been reported to exhibit various activities in skincare, including anti-wrinkle and anti-melanogenic properties (proven by in vitro assays), and moisturizing effects. It is important to highlight that these activities are not solely due to the presence of biosurfactants, as a wide variety of metabolites produced by the utilized microorganisms can be found in the ferments, ranging from proteins, fatty acids, polymers, polyphenols, cytokines, and enzymes. Biosurfactants are used in cosmetic formulations as antimicrobial agents, dispersants, texture enhancers for products, and to increase the penetration of drugs or active compounds through the skin. Sophorolipids have been employed as adjuvants in skin healing and wound treatment processes [62,76]. MELs are biosurfactants currently utilized by cosmetic companies such as TOYOMO and Nippon Fine Chemicals Co., Ltd., as part of the formulation for makeup bases, hair treatments, shampoos, conditions, soaps, and moisturizing creams, with superior benefits to synthetic surfactants [67]. Bk and Cipla are companies that also use the MELs in their formulations of a serum and a cream to prevent acne and improve skin hydration, respectively [82].

Based on the foregoing description, it can be concluded that some of the significant challenges encountered during the production of biosurfactants and their subsequent utilization in commercial formulations include:

- Strain selection and bioprospecting: Securing hyper-producing strains, preferably isolated from extreme environments, which impart the capacity to manage them under variable conditions of pH, temperature, salinity, and nutrient scarcity. Although their use is advantageous for industrial-scale conditions, the bioprospecting of these strains poses significant challenges when implementing appropriate isolation and screening methodologies.

- Use of sustainable feedstock: The utilization of media or media components derived from industrial waste streams, while promoting process sustainability, presents substantial challenges in terms of conducting precise media characterization. Furthermore, this complicates the separation of residual matter from the final products, thus increasing the cost of purification procedures.
- Fermentation strategies and bioreactor control: Achieving high biosurfactant concentrations during fermentation is hindered by a scarcity of studies on optimal cultivation strategies (e.g., batch, fed-batch, or continuous cultures) and suitable bioreactor configurations. Most operations involve submerged cultures with mechanical agitation, which introduces a significant technical challenge related to controlling the foaming generated by the biosurfactant itself. This foam phenomenon can significantly impact mass and energy transfer phenomena.
- Process scale-up: The scale-up of bioprocesses constitutes a significant hurdle when aiming to develop a process capable of handling a high volume of culture broth and achieving a high concentration of the final product without the excessive consumption of solvents.

6. Conclusions and Prospects

The biological roles of biosurfactants to date have been more described for bacteria than for yeast. However, the roles described for yeast are linked to nutrient and space competition in the environment from which the yeasts were isolated, which is enhanced thanks to their emulsifying capacity and lowering of surface tension. Thus, the biological role may be related to the specific chemical structure of the biosurfactant. Among the most frequently reported structures are glycolipids, notably MELs, which exhibit diverse activities ranging from acting as emulsifiers in food to possessing antimicrobial, antioxidant, and immunostimulant activity. Biosurfactants with proven interesting biological activities, such as MELs, are already being commercialized and utilized in pharmaceuticals and cosmetic formulations.

Currently, the changes in biosurfactant production center on improving the production yields of the strains, as well as optimizing the downstream process of separation and purification. Success in their areas, combined with the use of alternative and sustainable carbon sources, would enable a reduction in production costs in response to increasing demand for these biotechnological bioproducts.

The growing demand for biosurfactants in products such as soaps and detergents used in industrial cleaning or personal care is expected to drive the market size of biosurfactants, which was valued over USD 8 billion in 2022 and is set to represent around 5% Compound Annual Growth Rate (CAGR) from 2023 to 2032, according to Global Market Insights, Inc. [83]. Therefore, the biosurfactant market will increasingly demand a larger variety of available products, as well as guaranteeing the safety and sustainability of these products when used in any particular market. Hence, the development of new biotechnological products such as biosurfactants requires a broader bioprospecting effort to clearly understand the roles of these metabolites in the environment, a better understanding of their molecular structures, their characteristics, their interaction with other microorganisms, and their mechanisms of action. Further research is needed to determine their diverse toxicity and biodegradability. Furthermore, studies on the scaling up of their production, from fermentation to purification methods, are also required.

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Abbreviations

The following abbreviations are used in this manuscript:

CBLs	Cellobiose lipids
CMC	Critical Micelle Concentration
C/N	Carbon/nitrogen
GRAS	Generally Recognized As Safe
IC_{50}	Half Maximal Inhibitory Concentration
MELs	Mannosylerythritol lipids

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