*fermentation*

*Review*

# Underexplored Potential of Lactic Acid Bacteria Associated with Artisanal Cheese Making in Brazil: Challenges and Opportunities

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**Abstract:** Artisanal cheeses are prepared using traditional methods with territorial, regional and cultural linkages. In Brazil, there is a great diversity of artisanal cheeses (BAC), which have historical, socioeconomic and cultural importance. The diversity of the BAC between producing regions is due to the different compositions of raw milk, the steps involved in the process and the maturation time. The crucial step for cheese differentiation is the non-addition of starter cultures, i.e., spontaneous fermentation, which relies on the indigenous microbiota present in the raw material or from the environment. Therefore, each BAC-producing region has a characteristic endogenous microbiota, composed mainly of lactic acid bacteria (LAB). These bacteria are responsible for the technological, sensory and safety characteristics of the BAC. In this review, the biotechnological applications of the LAB isolated from different BAC were evidenced, including proteolytic, lipolytic, antimicrobial and probiotic activities. In addition, challenges and opportunities in this field are highlighted, because there are knowledge gaps related to artisanal cheese-producing regions, as well as the biotechnological potential. Thus, this review may provide new insights into the biotechnological applications of LAB and guide further research for the cheese-making process.

**Keywords:** traditional foods; fermentation; bioprospecting; biotechnology



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## 1. Introduction

Lactic acid bacteria (LAB) are a diverse group of Gram-positive bacteria that produce lactic acid as the main fermentation product of the carbohydrate metabolism. The term "LAB" is somewhat ambiguous and is often used to refer to bacteria applied in the production of fermented foods [1]. These include bacteria with high G+C (Bifidobacterium) and low G+C content (Firmicute such as *Lactobacillus*, *Lactococcus* and *Streptococcus*). They are acid-tolerant, meso-aerophilic, not mobile or spore-forming and either rod-shaped (bacilli) or spherical (cocci) [2]. The term LAB has a rather positive connotation, containing bacteria generally considered safe for human consumption, although some strains of enterococci raise concern due to the possible presence of virulence factors and the potential transfer of antibiotic resistance.

LAB are widely spread in the environment and play an important role in fermentation processes. They are employed in the production of pickles, sauerkraut, fermented meats, breads and especially dairy products [3]. Cheese making involves a process of fermentation by LAB. During this process, milk is coagulated by adding rennet or an acid. The acid may be produced by the fermentation of lactose by LAB. Artisanal cheeses are produced by indigenous LAB present in the raw material or from the environment [4]. For all processes, LAB are important for acidification and the ripening process. In addition, they produce key metabolites with antimicrobial activity, including organic acids, ethanol, hydrogen peroxide, diacetyl, $CO_2$ and bacteriocins [5,6].

In recent years, Brazilian cheeses have been recognized for their quality in several awards, both at national [7] and international [8] levels. In general, the production of Brazilian artisanal cheeses (BAC) involves the use of raw milk and an endogenous ferment consisting of the whey collected the day before, which can be named according to the region, such as "pingo" for Artisanal Minas Cheeses (AMC), the most famous in the country, or "repique" for Porungo cheese, produced in São Paulo state. BAC produced with raw milk must be ripened in accordance with specific legislation in minimum periods in order to guarantee its safety [9,10].

Several studies have demonstrated the diversity of LAB in BAC, with emphasis on *Lactobacillus, Lactococcus, Enterococcus, Weissella, Pediococcus* and *Leuconostoc* genera [11–13]. Different biotechnological applications of LAB isolated from BAC were detected, including probiotic potential [11]; diacetyl [14] and exopolysaccharides (EPS) production [14]; and antimicrobial [5], proteolytic [15] and lipolytic activities [14]. However, there is a lack of knowledge about the biotechnological potential of LAB isolated from BAC. In this review, we present the main gaps detected, indicating the under-investigated artisanal cheese-producing regions, the opportunities for biotechnological exploration, as well as the need to organize a collection of LAB typical of BAC for the purpose of biotechnological research and exploitation. With an ultimate goal, this review provides new insights into the industrial applications of LAB isolated from BAC.

## 2. Brazilian Artisanal Cheeses (BAC)

In Brazil, there is a great diversity of artisanal cheeses with historical, socioeconomic and cultural importance. In general, cheese production takes place on small farms and includes raw milk and traditional methods, which has been transmitted over hundreds of years by generations of cheesemakers [16,17]. BAC are produced in different geographic regions (Figure 1), such as Marajó cheese in the north; Coalho and Manteiga cheeses in the northeast; Caipira cheese in the central region; Colonial, Serrano, KochKäse and Käschmier in the south; and in the southeast, Artisanal Minas Cheese (AMC), Cabacinha, Parmesan-type cheeses (Alagoa, Vale do Suaçuí and Mantiqueira de Minas), Porungo and Requeijão Moreno [4].

Minas Gerais state is responsible for half of all cheese produced in the country, whose importance is reinforced by the existence of several producing regions. Among them, AMC production is responsible for 50% of the national production [4]. It is produced in the micro-regions of Araxá, Campo das Vertentes, Canastra, Cerrado, Serra do Salitre, Serro, Triângulo Mineiro and, more recently, Serras do Ibitipoca and Entre Serras (Figure 1) [18,19]. The AMC production method has even been recognized as Brazilian intangible heritage. Its production steps consist of milking, filtration, the addition of rennet and endogenous ferment, coagulation, curd cutting, draining, molding, pressing, dry salting and ripening [20]. Its quality has been reinforced by several awards; in 2021, for example, Brazil was one of the leading countries in the ranking of the most famous world cheese contest, winning 57 medals; 4 of the 5 medals in the "super gold" modality were won by cheeses produced in Minas Gerais state [21]. In addition to the socio-cultural relevance of AMC, it has economic importance, representing the main source of income for thousands of rural producer families [22].

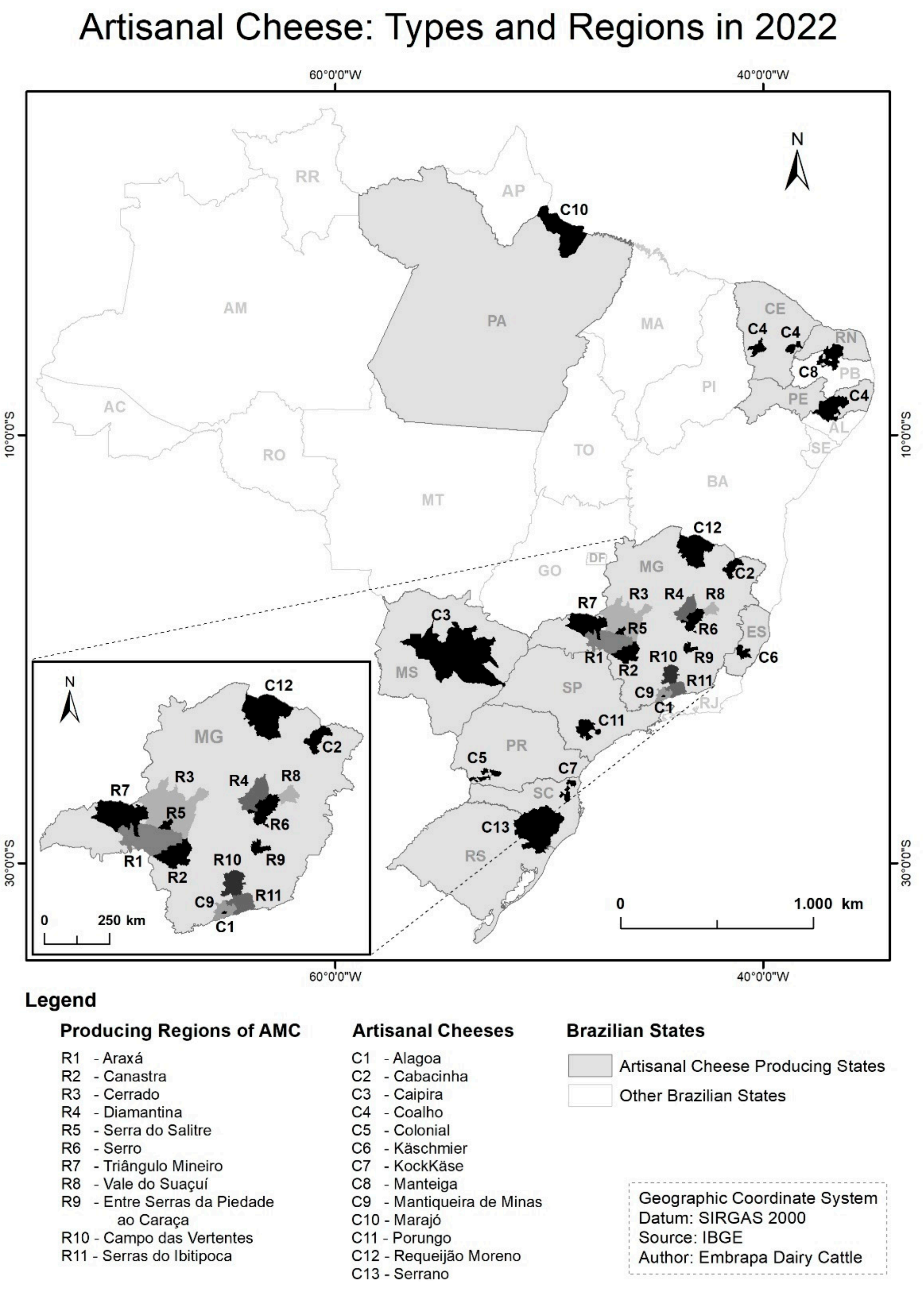


**Figure 1.** Brazilian artisanal cheeses: types and regions in 2022. In the detail at the bottom left, the producing regions of AMC and the most famous BAC are highlighted.

### 3. LAB and Food Industry

LAB produce lactic acid as the main fermentation product, generated from two fermentative metabolic pathways: homofermentative and heterofermentative. In cheese making, both LAB metabolisms are reported. Homofermentative LAB includes *Enterococcus, Lactococcus, Pediococcus, Weissella* and *Streptococcus* which produce lactic acid as an end metabolite by Pentose Phosphate or the Embden-Meyerhof-Parnas pathway. Heterofermentative LAB includes *Leuconosctoc* and *Oenococcus* which produce several other products in addition to lactic acid, such as ethanol, acetic acid and $CO_2$, from the conversion of lactose via the 6-P-gluconate/phosphoketolase pathway. Finally, *Lactobacillus* includes both homofermentative and heterofermentative species [23–25].

*Streptococcus thermophilus, Lactococcus lactis* and many lactobacilli grow in the presence of a maximum of 2% or eventually 4% of salt, in addition to tolerating environments with a low pH. LAB can also produce several types of glycolytic, lipolytic and proteolytic enzymes. These characteristics reinforce their importance for different applications in the food industry [26,27]. In addition, LAB contribute to the sensory development of various foods, especially flavor (as they produce volatile compounds) and texture (improved by the production of exopolysaccharides). The safety history of LAB contributes to the GRAS (Generally Recognized As Safe) or QPS (Qualified Assumption of Safety) status, enabling its use in food, either as starter cultures or probiotic strains [28]. For fermented foods produced from previously sanitized or pasteurized raw materials, the use of a LAB starter culture is necessary [27]. In addition, there are also non-starter LAB (NSLAB) that are especially important for cheese ripening, for example [26].

In recent years, several studies have explored the potential of LAB to be used as live vectors for in situ synthesis, i.e., the production and delivery of biomolecules at their site of use/application, without removing or transporting them to another site. This is only possible due to the GRAS status of the LAB strains. Another path consists of the direct application of compounds obtained by ex situ synthesis, which means applying the compounds in a place or environment outside their place of use or application [29]. However, in situ synthesis is advantageous as it allows the use of LAB strains instead of purified compounds, enabling the development of polyfunctional cultures, as well as reducing the costs of downstream isolation and purification steps. This strategy may also be better accepted by consumers, because purified compounds are considered food additives [30].

Recent studies have evaluated the use of in situ LAB for the synthesis of gamma-aminobutyric acid (GABA) from L-glutamate—an amino acid released during milk fermentation. This non-essential amino acid plays an important role in the central nervous system as an inhibitory neurotransmitter. Its properties include antidepressant, anxiolytic and antihypertensive activity, as well as the ability to regulate hormone secretion [6]. The production of GABA by LAB appears to be directly related to the acid stress response; thus, LAB strains able to produce GABA could be employed for functional purposes, especially in foods with reduced pH values [31]. Challenges related to the use of LAB in situ include its ability to resist certain types of stress, especially the osmotic pressure resulting from the use of salts by the food industry [32]. In this context, the isolation of LAB from artisanal cheeses aiming at its in situ application is notoriously promising, given its survival in ripened cheeses, which generally have high amounts of salt [11]. Thus, it may represent, in the near future, a promising strategy for the food industry.

Finally, the biotechnological potential of LAB also includes the encapsulation of metabolites produced ex situ by them for the controlled release or application in active packaging. Microencapsulation technology allows food-grade ingredients or bioactive components to be adequately protected and released in a controlled manner over long periods, including at specific sites [33]. The microencapsulation of LAB with probiotic properties for use in livestock, for example, has already been demonstrated [34]. As for the active packaging, antibacterial bioplastic film incorporated with purified bacteriocin from *Lactilactobacillus sakei* was able to reduce the contamination of Coalho cheese by coagulase-positive staphylococci and thermotolerant coliforms [35].

## 4. LAB Isolated from BAC

In general, BAC are produced from raw milk, which presents a pH close to neutrality, high water activity and significant nutritional value. It also has rich microbiota, mainly composed of LAB [36,37], essential for the fermentation process and, consequently, for the cheese quality and safety [38,39]. The relevant sensory characteristics of artisanal cheeses are provided by the activity of autochthonous LAB, especially related to the production of organic acids, fatty acids and amino acids, as well as peptidases and lipases [40–44].

In BAC, the most frequently reported genera of LAB are *Lactobacillus, Lactococcus, Enterococcus, Pediococcus, Leuconostoc, Streptococcus* and *Weissella* (Table 1). No data were found regarding the LAB isolated from Cabacinha, Parmesan-type cheeses, Porungo and KochKäse and Käschmier cheeses. It should also be noted that LAB also correspond to the majority group in an endogenous ferment used in the production of various types of BAC, in addition to the milking and production environment; therefore, the LAB diversity of BAC is influenced by the geographic location, climatic conditions and processing steps [15,43,44].

**Table 1.** LAB isolated from BAC produced in several producing regions.

| BAC | LAB * | References |
|---|---|---|
| *Caipira* | *Enterococcus* sp., *E. faecium*, *E. durans*, *E. faecalis*, *E. hermanniensis*, *Lactococcus*, *Lb. plantarum* subsp. *plantarum*, *Lb. paracasei* subsp. *paracasei*, *Lb. casei.* | [12,39] |
| *Coalho* | *Enterococcus* sp., *E. faecium*, *E. casseliflavus*, *E. durans*, *E. faecalis*, *E. gallinarum*, *E. italicus*, *E. hermanniensis*, *Lactobacillus* sp., *Lb. acidophilus*, *Lb. curvatus*, *Lb. fermentum*, *Lb. paracasei* subsp. *paracasei*, *Lb. plantarum* subsp. *plantarum*, Lb. rhamnosus , *Lactococcus* sp., *Lc. lactis, Lc. lactis* subsp. *lactis, Lc. garvieae, Leuconostoc* sp., *Lc. mesenteroides* subsp. *mesenteroides*, *Streptococcus* sp., *S. infantarius,* subsp. *infantarius, S. lutetiensis, S. macedonicus, S. waiu, Weisella* sp., *W. paramesenteroides* | [12,39,45–47] |
| *Colonial* | *E. faecium, E. durans, E. faecalis,, E. hermanniensis, Lactococcus* sp., *Lc. lactis, Lc. piscium, Lc. raffinolactis* group, *Lactobacillus* sp., *Lb. brevis, Lb. casei-paracasei, Leuconostoc* sp., *S. equinus-lutetiensis, S. parauberis, S. porcorum/sanguinis* | [12,39,48] |
| *Manteiga* | *E. faecium, E. durans, E. faecalis, E. hermanniensis, Lactobacillus* sp., *Lactococcus* sp., *Leuconostoc* sp., *Streptococcus* sp | [12,39] |
| *Marajó* | *E. durans, E. faecium, E. faecalis, E. gilvus, E. hermanniensis, Lactobacillus* sp., *Lactococcus* sp., *Leuconostoc* sp., *Streptococcus* sp | [12,39,49] |
| *Artisanal Minas* | *Enterococcus* spp., *E. durans, E. faecalis, E. faecium, E. gilvus, E. hermanniensis, E. raffinosus, E. rivorum, Lactobacillus* sp., *Lb. casei, Lb. paracasei* subsp. *paracasei, Lb. plantarum* subsp. *plantarum*, *Lb. paraplantarum*, Lb. rhamnosus, *Lb. hilgardii, Lb. brevis, Lb. buchneri* subsp. *buchneri, Lb. parabuchneri, Lb. acidipiscis, Lactococcus* spp., *Lc. lactis, Lc. garvieae, Leuconostoc* sp., *Ln. mesenteroides, Pediococcus* sp., *P. acidilactici, Streptococcus* sp., *S. agalactiae, S. macedonicus, S. porcorum/sanguinis, S. thermophilus, S. infantarius, W. paramesenteroides* | [39,40,44,48,50–55] |
| *Serrano* | *Enterococcus* sp., *E. faecium*, *E. durans*, E. faecalis, *E. hermanniensis. Lactobacillus* sp., *Lb. casei*, *Lb. plantarum* subsp. *plantarum*, *Lb. paracasei* subsp. *paracasei*, Lb. rhamnosus, *Lb. acidophilus*, *Lb. curvatus*, *Lb. fermentum*, *Lactococcus* sp., *Lc. lactis, Lc. piscium*, *Lc. raffinolactis*, *Leuconostoc* sp., *Ln. mesenteroides*, *Streptococcus* sp., *S. equinus-lutetiensis-infantarius, S. parauberis, S. porcorum/sanguinis.* | [39,56–58] |

* *Lactobacillus* species updated according to the reclassification [59]. *E. = Enterococcus*, *Lc. = Lactococcus*, *Lb. = Lactobacillus*, *Ln = Leuconostoc*, *S. = Streptococcus*, *P. = Pediococcus*, *W. = Weissella*.

The importance of LAB in cheese production is due to the presence of starter cultures and NSLAB. Starter cultures, mainly *Lc. lactis* and *S. thermophilus*, are responsible for converting lactose into lactic acid at a controlled rate. This process results in a gradual decrease in pH, which has a significant impact on various aspects of cheese production and ultimately determines the cheese's composition and quality. During the early stages of cheese ripening, *Lb. delbrueckii* and *Lb. helveticus* play a critical role, breaking down proteins, metabolizing lactose, producing aromatic compounds and providing substrates that can be further consumed by other microbial groups, such as NSLAB [60]. NSLAB mainly include the facultative heterofermentative *Lactobacillus* genus, followed by *Pediococcus pentosaceus* [61]. They can impact the cheese flavor and texture due to the production of compounds from the catabolism of amino acids, mainly methionine, aromatic amino acids and branched-chain amino acids, in addition to the synthesis of EPS [39,61–63]. In addition, bacteriocins, hydrogen peroxide, diacetyl and $CO_2$ are also produced by NSLAB, acting as biopreservatives and contributing to the cheese safety [5,11,64,65].

## 5. Biotechnological Potential of LAB Isolated from BAC

The self-sufficiency in inputs, the increasing demand for clean-label products and food production in the bioeconomy context have stimulated the development of research for bioprospecting microbial and bioactive compounds from different types of products, especially fermented foods [66,67]. Among them, dairy products stand out due to their recognized microbial diversity, especially LAB. In this context, artisanal cheeses have proved to be an important source for the isolation of microorganisms with biotechnological purposes [11].

Recent studies have demonstrated the potential for the industrial application of LAB, such as the production of enzymes, diacetyl, EPS, antimicrobial compounds, probiotic and prebiotic effects, among others, aimed mainly at improving food quality and safety [32,68,69]. In Brazil, research has been carried out to discover novel LAB strains isolated from BAC for industrial exploitation (Table 2). In the next sections, the main biotechnological applications of LAB identified in BAC by different studies published in recent years are discussed.

**Table 2.** Biotechnological potential of LAB isolated from BAC.

| BAC | Biotechnological Potential | References |
|---|---|---|
| *Marajó* | Antimicrobial activity against *L. monocytogenes*, *St. aureus* and *Es. coli,* lipolytic activity, proteolytic activity, acidification capacity, diacetyl production | [11,14,49,70,71] |
| *Manteiga* | Antimicrobial activity against *L. monocytogenes* and *St. aureus*, lipolytic activity, proteolytic activity, acidification capacity, diacetyl production, probiotic potential | [11,14,39,72] |
| *Coalho* | Antimicrobial activity against *Listeria* sp., *B. cereus*, *B. subtilis*, *E. faecalis*, *St. aureus*, *Es. coli*, *K. pneumoniae* and *P. aeruginosa*, lipolytic activity, proteolytic activity, acidification capacity, probiotic potential, β-galactosidase synthesis | [11,14,39,47,72–74] |
| *Serrano* | Antimicrobial activity against *L. monocytogenes*, *St.aureus*, *Es. coli*, *S. enterica* and *Penicillium*, lipolytic activity, proteolytic activity, acidification capacity, diacetyl production, probiotic potential | [11,14,39,72,75] |
| *Caipira* | Antimicrobial activity against *L. monocytogenes* and *St.aureus*, lipolytic activity, proteolytic activity, acidification capacity, diacetyl production, probiotic potential | [11,14,39,72] |
| *AMC* | Antimicrobial activity against *Listeria* sp., *Enterococcus* sp., *St. aureus*, *S.* Typhimurium and *S.* Enteritidis, lipolytic activity, proteolytic activity, acidification capacity, diacetyl production, probiotic potential, EPS production | [11,14,39,43,72,76–83] |
| *Colonial* | Antimicrobial activity against *L. monocytogenes* and *St. aureus*, lipolytic activity, proteolytic activity, acidification capacity, diacetyl production, probiotic potential | [11,14,39,72] |

*L. = Listeria, St. = Staphylococcus, Es. = Escherichia, K. = Klebsiella, P. = Pseudomonas, B. = Bacillus, S. = Salmonella.*

### *5.1. Bacteriocin Production*

Bacteriocins are proteins or peptides ribosomally synthesized by Gram-positive and -negative bacteria, with recognized antimicrobial activity (bacteriostatic, bactericidal or bacteriolytic) against taxonomically related or unrelated microorganisms [84–86]. They can be broad spectrum, inhibiting a wide variety of bacteria, or narrow spectrum, inhibiting taxonomically close bacteria [86,87]. In general, they are cationic and exhibit amphipathic properties, with the cell membrane being, in most cases, the target of their activity [88]. The first studies about the antimicrobial activity of LAB date back to the 1920s, with the discovery of colicin V; the discovery of nisin, in 1969, intensified the search for bioactive peptides synthesized by LAB, more specifically bacteriocins. Its use by the food and medical industries represents an alternative to the use of chemical additives and antibiotics, respectively, which has stimulated the interest in novel research in the area [31,89–91].

The industrial application of bacteriocins has several advantages, such as the activity against pathogens and spoilage microorganisms in foods, relative stability in different pH and temperature values, possibility of use as natural preservatives in foods and selective toxicity and inactivation by digestive proteases, with little influence on gut microbiota. Furthermore, a genetic determinant is usually encoded by plasmids, which allows facilitated genetic manipulation [92,93]. In addition, bacteriocins produced by LAB are considered GRAS, which favors their industrial application. However, the only bacteriocin approved by the Food and Drug Administration (FDA) for use as a preservative in foods is nisin, produced by *Lactococcus lactis* and commercially available as Nisaplin® [94]. Nisin can also be applied in veterinary practice, for example, in the treatment of mastitis as an alternative to conventional antibiotics [95,96]. However, the low stability and solubility of nisin at neutral pH, the hydrophobic nature and the selection of resistant bacteria reinforce the importance of studies focused on the discovery of new bacteriocins [97,98].

In this context, artisanal cheeses consist of an important source of bacteriocins [39]. A recent evaluation of the phylogenetic distribution of the LAB bacteriocin repertoire associated with artisanal cheeses reported bacteriocins not yet characterized, for example, two novel putative glycocins and one lasso peptide in the genome of some strains belonging to the *E. faecalis* species, reinforcing their relevance as a potential source [84]. Pediocins produced by four different strains of *Pediococcus pentosaceus* isolated from AMC were able to inhibit the growth of *Listeria monocytogenes*, a relevant foodborne pathogen [98]. The *Pediococcus* and *Lactobacillus* strains isolated from sheep cheese produced in southern Brazil and artisanal cheese produced in Minas Gerais state have also been identified as producing bacteriocins with anti-listeria activity [99,100]. In addition to this pathogen, *Bacillus cereus*, one of the most important causes of food poisoning, and *Pseudomonas fluorescens*, common spoilage bacteria, were inhibited by bacteriocins (not identified yet) produced by the LAB isolated from Colonial cheese produced in southern Brazil [101].

### *5.2. Acidification Capacity*

The acidification capacity is a widely studied aspect in LAB isolated from artisanal cheeses and can vary significantly depending on the strain and substrate. LAB are mainly responsible for the acidification of the raw milk, resulting in the pH decreasing and, consequently, affecting the activity of the rennet. Acidification also contributes to the solubilization of calcium phosphate, impacting the cheese texture, as well as the syneresis process, with reflections on its centesimal composition. Finally, acidification plays an important role in the microbial succession during cheese ripening, favoring the enzymatic activity of NSLAB, with desirable effects on the cheese flavor and texture [62,102,103].

Furthermore, the decreasing pH resulting from the production of organic acids can inhibit the growth of spoilage and pathogenic microorganisms. The release of short-chain weak organic acids, especially lactic, acetic, sorbic and propionic, during the fermentation process corresponds to one of the main mechanisms of biopreservation in fermented foods [104]. The increase in the lipid solubility of organic acids under conditions of high acidity interferes with the cell membrane potential, impairing the metabolic functions of undesirable microorganisms [105].

The acidification capacity of LAB isolated from BAC varied according to the microbial species and producing region; *Lacticaseibacillus paracasei* and *Levilactobacillus brevis* were more efficient in acidifying the substrate under the LAB isolated from AMC, Coalho and Caipira cheeses and presented a high acidification capacity [11], which was attributed to the type of herd feeding, differences in the cheese pressing stage, as well as the higher proportion of carbohydrate in the cheese. A low acidification capacity was observed for *Weissella* spp. isolated from BAC [71], reinforcing that acidification depends on the LAB species. It is also worth mentioning that the acidification capacity may vary according to the culture medium used for isolation; LAB isolated from M17 agar showed a greater acidification capacity than those isolated from MRS agar, which makes it difficult to compare the results of LAB isolated from different culture media [43].

### *5.3. Probiotic Potential*

According to the Food and Agriculture Organization [106], probiotics are live microorganisms that, when administered in adequate amounts, confer health benefits on the host. The term prebiotic refers to substrates that, when metabolized by the host's gut microbiota, result in health benefits. However, prebiotics can also be found in other sources, such as food, where they can stimulate the growth or activity of beneficial microorganisms [107]. The consumption of probiotics and/or prebiotics corresponds to one of the most efficient ways to maintain the balance of the intestinal microbiota (eubiosis) [108].

A probiotic strain must present some requirements, such as the ability to resist the acidic conditions, adhere to the gut environment, inhibit pathogens, modulate the immune system and confer benefits on the host's health; in addition, it does not present virulence factors. Several LAB strains meet these requirements, which make them even more relevant for application by the food industry [109]. Regarding probiotic food, it must comply with legal rules, demonstrating that viable microorganisms confer health benefits and are in a sufficient minimum number until the expiration date. If the food does not meet all these requirements, it only contains probiotics but is not considered as a probiotic food. This is mainly applied for artisanal fermented foods, in which the microbial species present, as well as their quantities, are generally not known [110].

Several probiotic LAB strains are widely used by the food industry, especially in the production of functional foods. Recent studies have demonstrated different types of benefits of probiotic LAB and their respective functional applications [111–113]. Many of these properties are related to the increasing values of proteins, minerals and vitamins in foods. In addition, the releasing of products from microbial metabolism, such as peptides, GABA, conjugated linoleic acids (CLA) and EPS, can contribute to health promotion [114]. Other benefits of probiotic LAB include the prevention of cardiovascular diseases, diarrhea, allergies, certain types of cancer and immunomodulation, among others [115].

The probiotic potential of LAB isolated from BAC has been demonstrated by different studies. Strains isolated from Colonial cheese showed high resistance to gastric acidity, with significant potential for use as a probiotic [116]. In vitro and in vivo probiotic potential was demonstrated for a *Lb. plantarum* strain isolated from AMC produced in the Canastra region, Minas Gerais state [117]. *Lb. plantarum* and *Lb. rhamnosus* isolated from the same type of cheese have already been evaluated as probiotic cultures in fermented milk [76].

Regarding the prebiotic property of compounds produced by LAB, it is generally related to the production of EPS (as will be discussed further in the next section), because it can favor the growth of probiotic strains. In cheeses, the supplementation with prebiotics can increase the populations of viable probiotic microorganisms; for example, the use of galactooligosaccharides (GOS), fructooligosaccharides (FOS) and inulin as nutraceuticals has stimulated the growth, survival and activity of probiotic strains in cheeses [118]. In artisanal cheeses, lactulose promoted the growth of lactobacilli and induced the production of short-chain fatty acids (SCFA) in Portuguese Serpa cheese [29]. SCFA contribute to health benefits, such as the regulation of energy metabolism, protection against colorectal cancer and inflammatory bowel disorders and obesity prevention [119]. At this moment, the prebiotic potential of LAB isolated from artisanal cheeses still remains unexplored in Brazil.

### 5.4. Exopolysaccharide (EPS) Production

Exopolysaccharides are biopolymers produced by microorganisms, whose composition and production yield are strain-dependent, both impacted by fermentation conditions [120,121]. *Xanthomonas campestris* and *Acetobacter xylinum* are recognized as excellent EPS-producing species; however, for industrial use, it is preferable that the producing microorganisms are GRAS, which reduces costs with purification processes. Furthermore, the application of purified EPS results in different effects on food when compared to EPS produced in situ, with better results [120].

The production of EPS by LAB has already been reported for *Lactobacillus*, *Lactococcus*, *Leuconostoc* and *Streptococcus* genera [122–124]. *Lb. rhamnosus* and *Lactobacillus kefiranofaciens* are even recognized as excellent EPS-producing species [109]. *Leuconostoc mesenteroides* and *Streptococcus salivarius* subsp. *thermophilus*, for example, have already been identified as producing species of dextran and fructan homopolysaccharides, respectively [120]. In this sense, the EPS production by LAB is especially important for the food industry, mainly for obtaining viscosity, stabilizing, emulsifying or gelling agents [109,125].

In cheeses, the production of EPS by NSLAB results in curd strengthening and the reduction of syneresis as a result of its binding with water molecules in the casein network [126]; thus, it contributes especially for the improvement in appearance and texture attributes in cheeses. In addition, EPS can minimize the harmful effects of bacteriophages during the fermentation process of dairy products, as they make the virus adsorption on the surface of the microbial cell difficult [127]. In BAC, the potential for EPS production by LAB has been little explored, with the first results indicating the AMC from Canastra, Campo das Vertentes, Serro and Cerrado, as well as Serrano cheese, as a source of LAB for this purpose [39]. These authors reinforce that obtaining EPS from the LAB of BAC constitutes a cheap, natural and sustainable strategy, with lower exploration costs, aiming at application in dairies.

In addition to the technological properties of EPS, its prebiotic effect stands out, reinforcing the relevance of the LAB (Table 2). The EPS produced by LAB favor the tolerance of probiotic strains to gut stress conditions, resulting in increased viability [109,121]. Because they can be metabolized in the gut, EPS constitute a substrate for the growth of probiotic strains, favoring the health benefits already demonstrated for this microbial group. For example, EPS produced by *Lb. plantarum* favored the growth of probiotic bacteria [128], and it also showed a bifidogenic effect, reducing the damages related to putrefactive bacteria [109].

### 5.5. Diacetyl Production

Diacetyl (2,3-butanedione) is a volatile compound produced by some LAB species during the conversion of citrate to pyruvate in the fermentation process, although it is not an exclusive feature of LAB [74,129,130]. The presence of diacetyl in certain foods is desirable, contributing to the buttery aroma and flavor [39,131]. It also presents antimicrobial activity against food pathogens, for which the mechanism of action consists of blocking the binding site of the microbial enzyme responsible for the use of arginine, affecting protein synthesis [129,132].

The production of diacetyl by *Lc. lactis* subsp. *lactis* biovar *diacetylactis* isolated from raw goat milk has already been reported [105]. In BAC, the LAB isolated from Marajó, Manteiga and AMC cheeses were able to produce diacetyl (Table 2). The *Leuconostoc* and *Streptococcus* strains isolated from Coalho cheese also showed this ability [74]. Finally, it was found that strains of *Weissella cibaria* and *Weissella paramesenteroides* isolated from cheeses produced in several regions of Brazil can produce diacetyl; *W. paramesenteroides* also stood out as an excellent producer of protease and had a high acidification capacity, desirable characteristics for cultures used in the dairy industry [71].

Interestingly, the occurrence of diacetyl-producing LAB may vary in BAC depending on the type of endogenous ferment used in the cheesemaking process. [78] evaluated the diacetyl production capacity in LAB isolated from "pingo" (the endogenous ferment used in the production of AMC) and from "rala", a kind of alternative inoculant consisting of portions of grated cheese; 66% of the "rala" isolates were able to produce diacetyl, much higher compared to the "pingo" isolates (25%). This difference can be explained by the predominance of NSLAB in the "rala" (a group that includes the main producers of diacetyl), because it is obtained from cheeses ripened for 3 to 5 days, unlike the "pingo" which consists of the whey collected from the still-fresh cheese produced on the previous day.

### 5.6. Proteolytic and Lipolytic Activities

Microbial cultures presenting proteolytic activity are widely used in the food industry, such as in the production of several types of dairy products, including cheeses and fermented milks; in the meat industry, to improve its texture, aroma and color; in the bakery industry, to break down the gluten net, improving the bread texture; in the alcoholic and non-alcoholic beverage industry, to reduce turbidity; and even in the production of animal feed [133].

In cheeses, proteolytic LAB play important roles for their quality, especially in ripened cheeses; therefore, the use of proteolytic cultures or purified enzymes is of great relevance for the cheese industry [134,135]. Proteolytic LAB strains can be used as adjunct cultures, acting on the peptide bonds of the matrix with the consequent release of amino acids and improvement in the cheese aroma, flavor and texture [70]. In addition, they can be used in the elaboration of dairy products with lower allergenic potential, reducing the risks for consumers with greater sensitivity to milk proteins [32].

*Pediococcus acidilactici* and *Weissella viridescens* proteolytic strains were isolated from ripened BAC [136], in addition to *Enterococcus* spp. isolates from AMC produced in the Campo das Vertentes, Serro and Cerrado regions, and from Coalho, Colonial, Serrano and Caipira cheeses [14]. The cheese-producing region can influence the microbial diversity of the product and, consequently, the occurrence of LAB with proteolytic activity. The LAB isolated from the AMC produced in the Campo das Vertentes region showed greater proteolytic activity than the LAB from cheeses produced in the Canastra region [43].

The contribution of LAB to the lipolysis processes in BAC is secondary, being more relevant for certain types of cheeses, such as blue cheeses (Gorgonzola and Roquefort) and cheddar [62]. However, lipases play an important role in the releasing of free fatty acids, precursors of volatile aromatic compounds that improve the sensory quality of the product [32,130]. It has been shown that BAC are good sources for the isolation of LAB with lipolytic activity, especially LAB isolated from AMC produced in the Araxá, Canastra and Serro regions, as well as from Colonial and Serrano cheeses, in addition to *Pediococcus acidilactici* isolated from Marajó cheese [11] and *Enterococcus* spp. isolated from AMC produced in the Araxá, Campo das Vertentes and Cerrado regions [14].

### 5.7. β-Galactosidase Activity

β-galactosidases are widely used for the hydrolysis of lactose by the food industry, with the aim of reducing its content in dairy products. This enzyme prevents crystallization and increased sweetness, flavor and solubility in several types of dairy products. In addition, the hydrolysis of lactose into D-glucose and D-galactose enables the development of lactose-free products, suitable for intolerant consumers, who correspond to about 70% of the world's adult population [137]. β-galactosidases are also able to catalyze transgalactosylation reactions, being successfully applied in the synthesis of lactose-based prebiotics, such as GOS, lactulose and lactosaccharose [138].

Another application of β-galactosidases that has been evaluated in recent years is the increase in safety due to the reduction in pH during the fermentation process. The glucose released from its activity can be consumed by the microbiota with the consequent production of lactic acid, increasing acidification rates, and thus contributing to the inhibition of pathogens [73]. Furthermore, β-galactosidases have also been used for the treatment of whey. Its inadequate disposal has been shown to be a serious environmental problem, especially regarding the eutrophication of rivers and water courses. In this context, the application of β-galactosidases can help to mitigate the damage resulting from the disposal of whey, in addition to allowing its reuse for the production of ingredients to be used in confectionery and bakery products [139].

To the best of our knowledge, there are no reports of the isolation of β-galactosidase-producing LAB from BAC. The production of β-galactosidase by strains of *Lacticaseibacillus casei* and *Limosilactobacillus fermentum* isolated from buffalo mozzarella has been demonstrated [140]; a strain of *Leuconostoc mesenteroides* subsp. *mesenteroides* with β–galactosidase activity, also from buffalo mozzarella, has been reported [141]. In BAC, only one study demonstrated the production of β-galactosidases in the strains of *E. durans* and *E. faecium* isolated from Coalho cheese [73].

## 6. Underexplored Biopotential and Opportunities for LAB from BAC

Brazil is one of the largest economies in the world, but it still depends on the import of inputs widely used in different industries, such as food, pharmaceuticals and biofuels, among others [142]. It is a paradox, given that the country has the greatest biodiversity on the planet and, therefore, a practically inexhaustible source for prospecting microorganisms with biotechnological potential. In this context, Brazilian fermented foods represent a relevant source of bacteria and fungi aimed at industrial exploitation; among these, BAC has stood out in recent years [11,66].

For this review, studies about LAB with biotechnological potential isolated from BAC were evaluated. Despite considerable progress in recent years, reinforced by the promising results presented here, there is still a gap to be filled by further studies. Most of the research carried out has focused mainly on the evaluation of antimicrobial activity, acidification capacity and enzyme and diacetyl production by LAB (Table 2). A few studies demonstrated the EPS production in different LAB isolated from BAC [39,71,78]. A similar situation was observed for the β-galactosidase synthesis, more specifically by LAB strains isolated from Coalho cheese [47,73]. As for prebiotics, there are no studies, so far, that have demonstrated their potential for use in LAB isolated from BAC.

In addition, most of the studies have been carried out in traditional and nationally recognized cheese-making regions, especially those involved in the production of AMC (Figure 2). Therefore, some types of cheese still lack information about their microbial diversity; for example, there are no studies of the isolation and identification of LAB isolated from Cabacinha cheeses, Parmesan-type cheeses, Porungo and KochKäse and Käschmier cheeses, produced in the south by German immigrants. It is, therefore, a niche opportunity for exploring the biotechnological potential of LAB; new insights into the genetic heritage of these traditional products can be provided from studies with cheesemakers in these regions.

Finally, it is worth to emphasize the urgent necessity to create and maintain a Brazilian collection of LAB that includes researchers from different regions in the country. Considering the continental dimension of Brazil, it is a complex and onerous effort. However, the articulation of researchers from universities and research institutions with public agents is essential to obtain human and financial resources aiming at the establishment of a national collection of LAB with scientific legitimacy and that becomes a reliable source of microorganisms for future research. We believe that this collection will have the potential to become a world reference in the cataloguing of LAB strains isolated from cheeses, with inestimable biotechnological value.

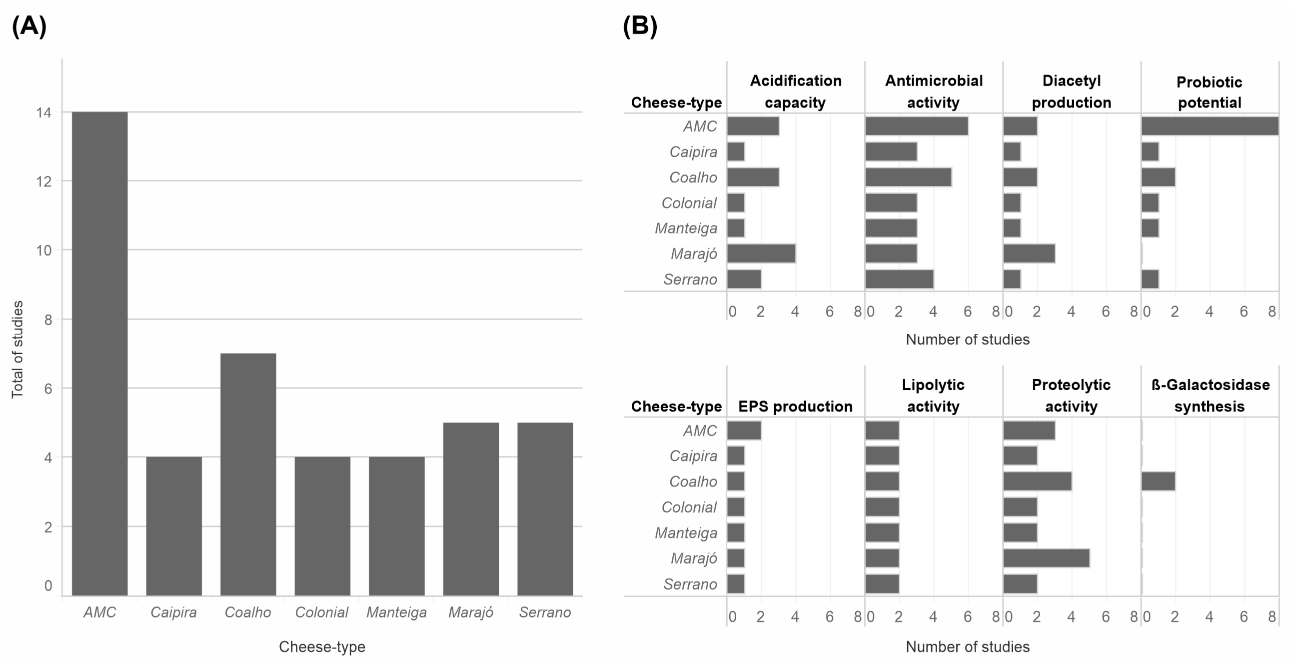


**Figure 2.** Studies about biotechnological potential from LAB isolated from BAC. (**A**) Number of studies about LAB in BAC published last 10 years; (**B**) Distribution of the studies according to biotechnological potential of LAB.

## 7. Conclusions

This review demonstrated the challenges and opportunities little explored for the application of LAB isolated from BAC. The discovery and characterization of new LAB strains isolated from BAC allow to increase the knowledge of the variety of compounds and enzymes produced by these bacteria and, consequently, expand the opportunities of applications. The use of producer strains or even isolated substances can be used for the elaboration of new functional foods, with improved sensorial and rheological characteristics, and also with greater microbiological safety.

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