

## Probiotic *Bacillus* as fermentation agents: Status, potential insights, and future perspectives

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### ARTICLE INFO

#### Keywords:

Probiotic *Bacillus*  
Fermented food  
Fermentation agents  
Microorganisms  
Beneficial metabolites  
Contribution

### ABSTRACT

Probiotic *Bacillus* strains can solve the problems of single flavor and long fermentation time of fermented products caused by the lack of certain functional genes and insufficient metabolism ability of fermenter strains (*Lactobacillus* and *Bifidobacterium*) at the present stage. There is a lack of systematic evaluation and review of probiotic *Bacillus* as food fermentation agents. In this paper, it is observed that probiotic *Bacillus* strains are involved to varying degrees in liquid-state, semi-solid state, and solid-state fermentation and are widely present in solid-state fermented foods. Probiotic *Bacillus* strains not only produce abundant proteases and lipases, but also effective antifungal lipopeptides and extracellular polymers, thus enhancing the flavor, nutritional value and safety of fermented foods. *Bacillus* with probiotic qualities is an underutilized group of probiotic food fermentation agents, which give a potential for the development of fermentation technology in the food business and the integration of ancient traditional fermentation techniques.

### Introduction

Fermented foods, with a history spanning thousands of years, constitute a unique and integral part of global culinary cultures (Mukherjee, Breselge, Dimidi, Marco, & Cotter, 2023). Fermentation serves as an effective means for both food production and preservation. Fermented food is obtained after microbial reproduction and metabolism of raw food materials under natural conditions or through the addition of microbial agents. It has a high nutritional value and a unique flavor, is safe, and has high long-term preservation potential (Estruch & Lamuela-Raventós, 2023; Zhang, et al., 2023). During the fermentation process, various microorganisms change the chemical makeup of raw materials, improving the nutritional content of fermented food and providing customers with health advantages (Ashagrie et al., 2023; Louw, Lele, Ye, Edwards, & Wolfe, 2023). Based on differences in fermentation processes, fermentation can be broadly categorized into liquid-state fermentation, semi-solid fermentation, and solid-state fermentation. Examples of typical liquid-state fermented foods include fermented dairy products (Tian, Xiong, Yu, Chen, & Lou, 2023) and fermented fruit juice beverages (Zhang, et al., 2023). Semi-solid fermented foods encompass fermented vegetable products (Torres, Verón,

Contreras, & Isla, 2020) and fermented fruit products (Li, Chen, et al. 2023). Solid-state fermented foods predominantly include fermented cereal and legume products (Lingua et al., 2022; Xie et al., 2019), fermented tea products, and fermented meat products (Ojha, Kerry, Duffy, Beresford, & Tiwari, 2015).

Probiotics play an important function in the fermentation process of food, producing taste components and ensuring the quality and safety of fermented foods (Zhang, et al., 2023). Currently, the exploration and research of probiotic strains is predominantly focused on *Lactobacillus* and *Bifidobacterium*, which are globally recognized probiotic genera (Gaur & Gänzle, 2023; Li, Chen, et al. 2023). There are also relevant studies on bacteria such as *Staphylococcus* and *Streptococcus*, as well as yeast and fungi such as black mold (Guidi, Legras, Galeote, & Sicard, 2023; Jans et al., 2017; Khusro & Aarti, 2022). However, in traditional fermented foods, the natural fermentation process benefits from the huge macrogenome and metabolome of a complex microbiota. This leads to the formation of unique qualities and rich flavors, a process that is not accomplished by solely lactic acid bacteria or a few specific strains (Rodzi & Lee, 2021). The use of a single fermentation agent often results in long fermentation times and inferior flavors. The development of different composite fermentation strains is a trend in the industrialized

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<https://doi.org/10.1016/j.fochx.2024.101465>

Received 26 March 2024; Received in revised form 9 May 2024; Accepted 10 May 2024

Available online 15 May 2024

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production of fermented foods. It is important for the construction of quality and flavor in fermented foods, as well as safety regulation (Luo et al., 2023). Therefore, in-depth and continuous exploration of probiotic strains with good fermentation performance is necessary for the industrialized development of traditional fermented foods (Saarela, 2019). See (Fig. 1).

In addition to the popular probiotic strains mentioned above, most *Bacillus* spp. exhibit probiotic activity. In recent years, a variety of probiotic *Bacillus* strains, including *Bacillus coagulans*, *Bacillus licheniformis*, *Bacillus subtilis*, *Bacillus velezensis* and *Bacillus clausii*, have been tested in vitro and in vivo for possible probiotic activities. Probiotic *Bacillus* strains have been shown to produce a variety of enzymes, including cellulases, amylases, proteases and lipases. Furthermore, they can produce antimicrobial metabolites, such as bacteriocins and peptides, which hinder the growth and reproduction of dangerous bacteria (Soares et al., 2023; Zhao, Yu, & Yan, 2023). Probiotic *Bacillus* strains can solve the problems of single flavor and long fermentation time of fermented products caused by the lack of certain functional genes and insufficient metabolism ability of fermenter strains (*Lactobacillus* and *Bifidobacterium*) at the present stage, and also have great potential in improving the safety of fermented products (Shan et al., 2023). Although a great number of relevant studies have reported the presence of *Bacillus* spp. in fermented foods, their importance in sustaining human and animal health has been acknowledged. Probiotic *Bacillus* strains, in contrast to lactic acid bacteria, have received less attention in the fermented food sector and are not widely popular among producers and consumers. (Elshaghabee, Rokana, Gulhane, Sharma, & Panwar, 2017; Tamang, Watanabe, & Holzapfel, 2016). Therefore, to promote probiotic *Bacillus* strains as food fermentation agents, it is critical to understand the distribution of probiotic *Bacillus* in various fermented foods, elucidate the potential and benefits of probiotic *Bacillus* strains as fermentation agents, and determine their primary contribution to fermented foods.

In the present paper, we examine the distribution of probiotic *Bacillus* in the microbial composition of traditional natural fermented foods that have a long history of safe consumption, as well as recent advances in the research of the probiotic qualities of *Bacillus* as fermentation agents. Furthermore, the development prospects of probiotic *Bacillus* in the modernization of the fermentation industry, as well as the challenges of fermented food production, are examined in order to provide a reference for future research on next-generation food fermentation

agents.

## Current status of research on probiotic *Bacillus* in fermented foods

### The position of probiotic *Bacillus* in the microbial composition of fermented foods

#### Liquid-state fermented foods

Liquid-state fermented foods mainly include fermented dairy products and fermented fruit juice. Liquid-state fermented foods are commonly produced by single fermentation or co-fermentation of *Lactobacillus*, *Bifidobacterium*, and some yeasts (Ilango & Antony, 2021). In addition, the presence of probiotic *Bacillus* spp. has been documented in a limited number of naturally occurring liquid-state fermented foods, as indicated in Table 1.

Fermentation processes can change the enzymatic activity of raw materials and the metabolic activity of microbes, influencing the nutritional and bioactive qualities of the food matrix, which can have good impacts on human health (Mukherjee et al., 2023). Many scientific research have established that fermented dairy products have antihypertensive properties, improve systemic immunity, and reduce cholesterol and blood pressure. They can also be a rich source of bioactive peptides generated during protein hydrolysis, with various potential health advantages for the endocrine, digestive, cardiovascular, immunological, and neurological systems (Companys et al., 2020). It is worth mentioning that Thai Milk kefir, a stirred and fermented milk, has anti-inflammatory, immunomodulatory, antimicrobial, antiproliferative, antimutagenic, and anticarcinogenic properties and has the potential to become a functional food. To date, many studies have been published on different bacteria and yeasts isolated from kefir from different parts of the world (Urdaneta et al., 2007). Vijitra & Sirirat (Vijitra & Sirirat, 2016) found only *Bacillus* spp. in the microbial composition of Thai Milk kefir, mainly *B. amyloliquefaciens*, which and produce extracellular polysaccharides on glucose, lactose, and sucrose. In Egypt, Kishk is usually made by combining strained yogurt with milled dry wheat (cracked and gluten-free steamed grain wheat) and allowing it to ferment at room temperature for varied amounts of time. The milk is fermented, and the resulting paste is dried to a moisture content of 10 %–13 % before grinding into powder. The substance is preserved in the form of dried brown balls with a rough surface and a firm feel. The

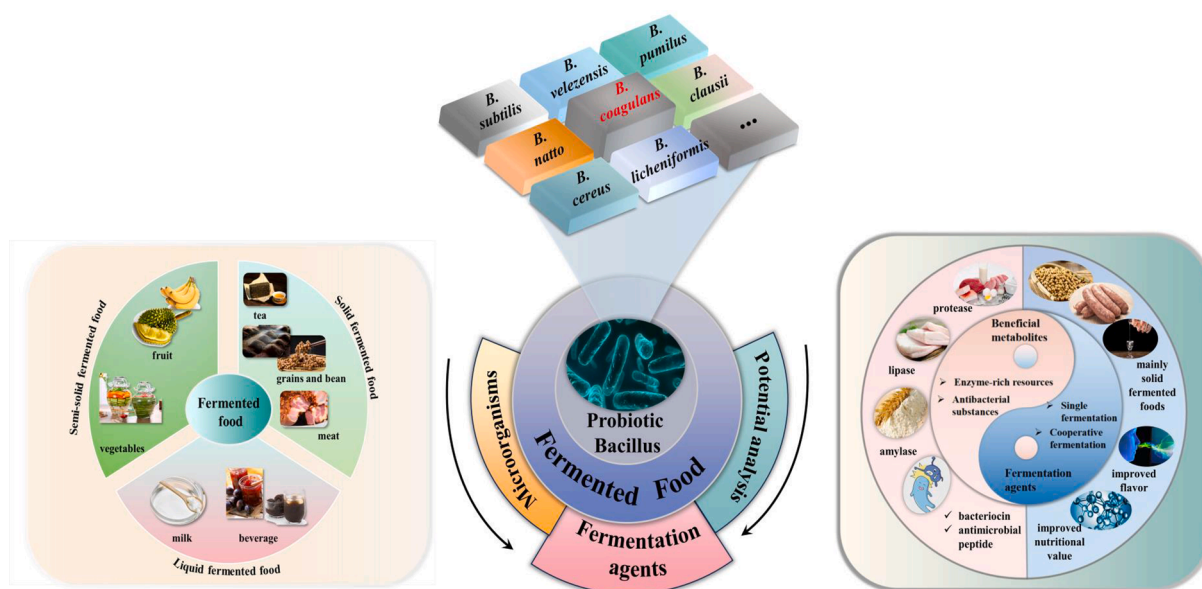


Fig. 1. Overview of probiotic *Bacillus* strains as next-generation Fermentation Agents.

**Table 1**  
Analysis of the composition of probiotic *Bacillus* in the microbiome of traditional fermented foods.

Species	Product category	Product name/ Country	Raw material	Identified Probiotic <i>Bacillus</i> strain(s)	Reference
Liquid-state fermented food	Fermented dairy products	Thai milk kefir/ Thailand	Milk, water	<i>B. amyloliquefaciens</i> SD-32, <i>Bacillus</i> sp. LB15, <i>Bacillus</i> sp. LD12AP, <i>Bacillus</i> sp. C87, and <i>B. methylotrophicus</i>	(Vijitra & Sirirat, 2016)
		Kishk/Egypt Dahi/Pakistan	Wheat, milk Milk	<i>B.subtilis</i> <i>B.cereus</i> , <i>B. licheniformis</i> , <i>B. mycoides</i> and <i>B. subtilis</i>	(Blandino et al., 2003) (Khan et al., 2023)
	Fermented fruit juice	Rhizome juice of zingiber officinale/Korea	Zingiber officinale	<i>B.fungorum</i> and <i>B. subtilis</i>	(Blandino et al., 2003)
		Tepache and garapiña/ Mexico	Pineapple	<i>B.mexicanus</i> and <i>B. subtilis</i>	(Karina et al., 2021)
Semi-solid fermented odfo	Fermented vegetable products	Fermented coconut water/Southeast Asia	Fresh coconut water	<i>B. velezensis</i> FCW2	(Raj et al., 2023)
		Fermented red dragon fruit drink/Malaysia	Fresh red dragon fruits(Hylocereus polyrhizus)	<i>B.tequilensis</i> and <i>B. subtilis</i>	(Lim et al., 2023)
		Kimchi/Korea	Mustard leaf	<i>B. inaquosorum</i>	(Kook et al., 2019)
		Gochujang/Korea	Chili powder, glutinous rice powder, soy porridge with salt, flavorings, for instance, shallots and garlic, as well as sweetener in the form of sugar syrup	<i>B. velezensis</i>	(Jang et al., 2011)
		Fermented brine pickle/ West coastal districts of India	Mangos, cabbages, Chili powder, fish sauce	<i>B. Licheniformis</i> KT921419, <i>B. amyloliquefaciens</i> KT921420, <i>B. subtilis</i> KT921421, <i>B. methylotrophicus</i> KT921422, <i>B. safensis</i> KT921423and <i>B. licheniformis</i> KT921424	(Ragul et al., 2020)
		Soibum/ India	Bamboo shoot	<i>B.subtilis</i> , <i>B. licheniformis</i> , <i>B. coagulans</i> , <i>B. cereus</i> , <i>B. pumilus</i>	(Tamang et al., 2017)
		Rhujuk/ Bastanga, india	Bamboo shoot	<i>B.subtilis</i> and <i>B. licheniformis</i>	(Jamir & Deb, 2021)
		Agbelima/ West Africa	Cassava	<i>B.subtilis</i> , <i>B. licheniformis</i> , and <i>B. pumilus</i>	(Obilie et al., 2003)
		Tape/ Indonesia	Cassava	<i>B.subtilis</i> , <i>B. amyloliquefacie</i> and <i>B.thuringiensis</i>	(Barus et al., 2013)
		Torshi/ Iran	Green pepper, Green cabbage, Red Cabbage, Cauliflower, Carrot, garlic, Celery and Persian shallot	<i>B. safensis</i> 437F, <i>B. atrophaeus</i> 1630F and <i>B. amyloliquefaciens</i> 1020G	(Talebi et al., 2018)
Solid-state fermented food	Fermented fruit products	Ntoba Mbodi/ Congo	Cassava leaves	<i>B.subtilis</i> , <i>B. licheniformis</i> , <i>B. amyloliquefaciens</i> , <i>B. pumilus</i> , <i>B. sphaericus</i> and <i>B. xylanilyticus</i>	(Mbozo et al., 2017)
		Fermented pickle/ China	Cabbage and NaCl	<i>Bacillariophyta</i>	(Sun et al., 2022)
	Fermented cereal and legume products	Pickles/ Egypt	Fruits and vegetables, NaCl	<i>B.acidicola</i> BPS4, <i>B. amyloliquefaciens</i> BPS20, <i>B.mycoides</i> BPS33 <i>B.valezensis</i> M4S1B1, <i>B. safensis</i> M5S2B8 and <i>Bacillus</i> sp. M7S2B9	(Enan & E.F., M., Abdel-Halim, & Tartour, E. , 2014) (Maheshwari et al., 2019)
		Daqu/ China	Grains (wheat, rice, sorghum, and barley)	<i>B.subtilis</i> , <i>B.amyloliquefaciens</i> , <i>B. velezensis</i> and <i>B.licheniformis</i>	(Zhu et al., 2023)
		wheat Qu/ China	Wheat	<i>Bacillus</i>	(Peng et al., 2023)
		Soy sauce/ Korean	Soybean	<i>B.amyloliquefaciens</i>	(Lee et al., 2017)
Koji/ China	Soybeans, wheat flour	<i>B. amyloliquefaciens</i> , <i>B. subtilis</i> , <i>B.licheniformis</i> , <i>B. methylotrophicus</i> , <i>B.aerius</i> , <i>B. halmapalus</i> , <i>B. flexus</i> , <i>B.thuringiensis</i> and <i>B. coagulans</i>	(Zhang, Xiong, et al. 2023)		
	Natto/ Japan	Soybean	<i>B. subtilis</i> , <i>B. natto</i>	(Dong et al., 2020)	
Tungrymbai and bekaang/ India	Soybean	<i>B. licheniformis</i> , <i>B. pumilus</i> <i>B.subtilis</i> and <i>B. coagulans</i>	(Chettri & Tamang, 2015)		

(continued on next page)

Table 1 (continued)

Species	Product category	Product name/ Country	Raw material	Identified Probiotic Bacillus strain(s)	Reference
		Cheonggukjang/ Korean	Soybean	<i>B.thermoamylovorans</i> , <i>B.licheniformis</i> , <i>B.glycinifermentans</i> , <i>B.subtilis</i> , <i>B.paralicheniformi</i>	(Tamang et al., 2022)
	Fermented tea products	Doenjang-meju, Korean Post-fermented tea/ China	Soybean Fresh leaves or mature shoots of tea plants ( <i>Camellia sinensis</i> var. <i>sinensis</i> )	<i>B.velezensis</i> <i>B.subtilis</i> DTM01, <i>B.licheniformis</i> DTM06, <i>B.laterosporus</i> DTM03, <i>B.coagulans</i> DTM02, <i>B.pumilus</i> DTM04	(Han et al., 2023) (Zhao, Lou, et al. 2021)
	Fermented meat products	Fu brick tea/ China Androlla and Botillo / Spanish Salame di Senise/ Southern Italian Pla-ra/ Thailand	Pu-erh tea pork, salt Pork, senise, wild fennel, garlic and salt Marine fish, salt, rice bran	<i>B.subtilis</i> <i>B.amyloliquefaciens</i> SA35 and <i>B.subtilis</i> SB07 <i>B.subtilis</i> tr53, tr50 and trf22	(Li et al., 2022) (Cachaldora et al., 2014) (Baruzzi et al., 2005)
		Fermented cassava fish/ Benin	Cassava fish	<i>B.subtilis</i> , <i>B.licheniformis</i> , <i>B.megaterium</i> , <i>B.mycoides</i> , and <i>B.cereus</i>	(Thongsomboon et al., 2023) (Anihouvi et al., 2007)
		Fish Sauce/ China	Fish (sardine, anchovy, and menhaden, among others) and sea salt	<i>B.subtilis</i> , <i>B.amyloliquefaciens</i> , <i>B.aryabhatai</i> , <i>B.vallismortis</i> , <i>B.cereus</i> , <i>B.megaterium</i> , <i>B.tequilensis</i> , <i>B.licheniformis</i> , <i>B.marisflavi</i> , <i>B.methylotrophicus</i> , <i>B.vietnamensis</i>	(Xiao et al., 2014)
		Utonga-kupsu, Hentak and Ngar/ North-East India	Esomus danricus, Puntius sophore, Amblypharyngodon mola, Channa punctata, Mystus vittatus, Puntius sophore, etc.	<i>B.subtilis</i>	(Singh, Mandal, Lalnumawii, & Kumar, 2018)
		Ngari/ Manipur in India	Sun-dried small cyprinid fish Puntius sophore Ham.	<i>B.indicus</i>	(Devi et al., 2015)
		Ka-pi / Thai	Shrimp	<i>salacetus</i> spp. <i>Bacillus</i> species	(Nakamura et al., 2022; Yiamsombut et al., 2021)

bacteria responsible for fermentation include *Lactobacillus plantarum*, *Lactobacillus casei*, *B. subtilis*, and *Saccharomyces cerevisiae* (Blandino, Al-Aseeri, Pandiella, Cantero, & Webb, 2003). Dahi is a popular fermented dairy product in Pakistan. It is made by bringing room temperature boiled or buffalo milk to room temperature, adding artisanal cultures (obtained by a reverse tilting technique), and then letting it sit for at least one night (sometimes up to four days, depending on the season) until a curdled product forms. Strains of *Lactococcus lactis*, *Lactobacillus casei*, *Streptococcus thermophilus*, and *Lactobacillus bulgaricus*, as well as probiotic *Bacillus* species such *B. cereus*, *B. licheniformis*, *B. mycoides*, and *B. subtilis*, are among the fermentation microorganisms found in Dahi (Khan, Bashir, & Imran, 2023).

Fermented juices, obtained by fermentation of fresh fruits with bacterial strains, have a unique flavor and high nutritional value (Zhang, Hong, et al. 2023). In recent years, studies on probiotic *Bacillus* spp. in fermented fruit juices have been conducted. *Bacillus fungorum*, *B. subtilis*, and others isolated from the juice of *Zingiber officinale* rhizome in Korea were recognized as potential probiotics (Sathiyaseelan, Saravanakumar, Han, Naveen, & Wang, 2022). Garapiña, a traditional Mexican fermented juice, is made from pineapple pulp and rind, whereas tepache is usually made from pineapple rind only; however, it can be made from other fruits such as apple, orange, and guava as well. The drink is produced by inducing fermentation of pineapple peel and brown sugar in water, which does not require pre-inoculation. The ingredients are placed in wooden barrels called “tepacheras,” where the pineapple peel and pulp ferment spontaneously for three days. Afterwards, a sweet, refreshing, and pleasant drink is obtained, thanks to microorganisms such as *Weissella confusa*, *B. graveolens*, *B. mexicanus*, and *B. subtilis*

(Karina et al., 2021). Fermented coconut water, a functional beverage fermented with beneficial microorganisms from fresh coconut water, is consumed in a variety of regions, particularly Southeast Asia, due to its refreshing taste and potential health benefits. It contains fewer calories and sugar, making it a healthier alternative to soft drinks and sugary beverages. Raj et al. (Raj, Suryavanshi, Kandaswamy, Ramasamy, & James, 2023) investigated the probiotic potential of *B. velezensis* FCW2 isolated from spontaneously fermented coconut water using in vitro and genomic characterisation. Lim et al. (Lim et al., 2023) used molecular methods to determine the variety of local microorganisms involved in the spontaneous fermentation of red dragon fruit drink. From the fermented red dragon fruit drink, twenty bacterial cultures were discovered, primarily *Klebsiella pneumonia*, *Klebsiella pneumonia*, *Brevibacillus parabravis*, *B. tequilensis* and *B. subtilis*.

#### Semi-solid fermented foods

Semi-solid fermented foods, such as pickled vegetables and fruits, represent a typical food category with a long history of consumption worldwide. Indeed, varied individuals from various cultures are drawn to these foods because of their appealing sensory qualities, high nutritional value, and long shelf life. The extensive history of fermentation, with many products originating from natural fermentation processes, makes it an intriguing source for isolating novel probiotic strains. The discovery and identification of *Bacillus* strains with significant probiotic potential will enhance their contributions to the food industry (Behera, Sheikha, Hammami, & Kumar, 2020).

Kimchi is a traditional fermented Korean food made through the fermentation of vegetables. Due to its delightful taste and beneficial



effects on human health, it has become a globally popular food. Kook et al. (Kook, Lee, Jeong, & Kim, 2019) isolated *B. licheniformis* BioE-BL11 and *Enterococcus faecium* LMD18 from Kimchi. These strains produced a substantial amount of extracellular polysaccharides. Additionally, Jang et al. (Jang, Kim, Park, & Park, 2011) conducted a microbial community analysis of Gochujang, another traditional Korean fermented food. They identified a total of 31 microorganisms, with *B. velezensis* accounting for 29 % of the population, making it the predominant microbe in Gochujang.

*B. licheniformis* KT921419, *B. amyloliquefaciens* KT921420 and *B. subtilis* KT921421 were identified from the traditional fermented brine mango pickle in the western coastal region of India. They have substantial antioxidant, antidiabetic, and antityrosinase activities. These strains can serve as novel fermentation agents or co-cultures imparting health benefits in food systems. Furthermore, the lengthy history of pickle consumption attests to the safety of these strains, and their additional health-promoting properties make them an ideal candidate for marketing pickles as healthy and functional foods (Ragul, Kandasamy, Devi, & Shetty, 2020). Soibum is an ethnic fermented bamboo shoot dish from Manipur, India. Thin slices of immature shoots are packed securely in an enclosure, sealed with a polyethylene film on top, and pressed with an appropriate weight. During fermentation, the bottom of the fermentation chamber is punctured to drain acidic fermentation juice, which is permitted to ferment for 6–12 months. Fermentation's microbial population includes lactic acid bacteria such as *Lactobacillus plantarum*, *Lactobacillus brevis*, *Lactobacillus coryniformis*, and *Lactobacillus delbrueckii*, as well as *Bacillus* spp. including *B. subtilis*, *B. licheniformis*, *B. coagulans*, *B. cereus* and *B. pumilus* (Tamang, Holzapfel, Shin, & Felis, 2017). Rujuk, an indigenous fermented cuisine from Nagaland, India, has been discovered to have *Bacillus* spp. as the main bacterium in majority of the foods based on a combination of morphological and genetic investigations. Agbelima is an African sour-dough product. It is mainly made from heap-fermented cassava roots to reduce the rubbery texture of the subsequently produced flour (Jamir & Deb, 2021). Obilie et al. (Obilie, Tano-Debrah, & Amoa-Awua, 2003) demonstrated that several fungi and *Bacillus* spp. isolated from heap-fermented cassava roots were able to break down cassava tissues. Tape is a traditional cassava fermented dish in Indonesia, and its quality is dictated by the microorganisms engaged in the fermentation process, with the amylase-producing *Bacillus* spp. (*B. subtilis*, *B. amyloliquefaciens* and *B. thuringiensis*) dictating the quality of cassava (Barus, Kristani, & Yulandi, 2013).

Torshi, a pickled vegetable condiment from the Middle East. Typically, it is made by households rather than industries, and there are hundreds of recipes depending on local traditions. Torshi is produced in eastern Iran using a variety of vegetables, including green peppers, green kale, red kale, cauliflower, carrots, garlic, celery, and Persian green onions, which are pickled in salted vinegar for several weeks. Three novel *Bacillus* strains, *B. safensis* 437F, *B. atrophaeus* 1630F, and *B. amyloliquefaciens* 1020G, were identified as promising probiotics (Talebi, Makhdoui, Bahreini, Matin, & Moradi, 2018).

Popular fermented food from the Republic of the Congo called Ntoba Mbodi is a major source of protein for the diets of the local populace. It is made by gathering cassava leaves, letting them wither for 2–3 days, and then cleaning, chopping, washing, dividing, and wrapping the leaves in huge leaves like papaya or Senegalese plant leaves. The combination is then allowed to ferment at room temperature for two to four days. *Bacillus* species, such as *B. subtilis*, *B. licheniformis*, *B. amyloliquefaciens*, *B. pumilus*, *B. cereus*, and *B. xylosoxus*, are the main microbes that cause fermentation in these mixes. *B. subtilis* is typically described as the dominating species (Mbozo et al., 2017).

Fermented pickle is a Chinese traditional fermented food. To produce fermented pickle, vegetables are immersed in a salt solution and undergo lactic acid fermentation. Pickles fermented by *Lactobacillus* not only have a delicious taste and high nutritional value, but also offer digestive assistance and potential benefits in preventing atherosclerosis.

Lactic acid bacteria are the major microorganisms in pickles and play an important role in taste creation (Sun et al., 2022). Additionally, several research imply that non-lactic acid bacteria also play a major role in flavor generation during the vegetable fermentation. Throughout the natural fermentation and storage of pickles, there is a diverse microbial community, and the complex succession of microbial colonies and diverse metabolic pathways significantly influences flavor formation. *Bacillus* and *Streptococcus* bacteria play a role in flavor creation throughout this process. Enan and colleagues (Enan & E.F., M., Abdel-Halim, & Tartour, E., 2014) recovered 61 strains of bacteria from Egyptian pickles and discovered *Lactobacillus plantarum* LPS10, *B. acidicola* BPS4, *B. amyloliquefaciens* BPS20, and *B. mycooides* BPS33 as possible probiotic strains.

Panchamirtham is a traditional fermented fruit mixture (banana, jaggery, seedless dates, sugar candy, honey, cardamom, and ghee) which is widely consumed in the southern regions of India. This traditional fruit mixture is rich in dietary fiber, vitamins, proteins, and minerals. Panchamirtham contributes to resistance against infectious pathogens in the body and serves as a potent antioxidant, providing a source of minerals, vitamins, and carbohydrates. Maheshwari et al. (Maheshwari et al., 2019) conducted 16S rRNA sequencing and evaluated the microbiota in Panchamirtham, identifying *Bacillus* spp. with probiotic potential such as *B. safensis* M5S2B8 and *B. velezensis* M4S1B1.

#### Solid-state fermented foods

Solid-state fermented foods encompass a variety of types, including cereal- and legume-based fermented products, fermented tea products, and fermented meat products. Extensive research data indicate that these fermented foods, often produced in open environments, have a diverse and complex microbial composition. In addition to common *Lactobacillus*, the types and quantities of probiotic *Bacillus* strains in these foods are diverse and intricate (Li, Zheng, et al. 2023).

Typical representatives of cereal and soybean fermented products include Chinese liquor (Baijiu) and soy sauce, which probiotic *Bacillus* strains are detected more frequently and play crucial role in the fermentation process, contributing substantially to the quality and flavor of the products. Chinese liquor, with its rich history and cultural significance, has gained widespread popularity globally. In recent years, its market dominance has grown, with a total production of 7,156,000 kiloliters and a profit of 170.194 billion yuan in 2021. Chinese liquor has emerged as a vital business that contributes to local economic development. Brewing techniques in each region are always evolving and improving, resulting in distinct microbiological ecosystems and flavor variations. Despite regional differences, the production of Daqu (a large fermentation starter) has consistently been a core process in Chinese liquor production. The Chinese liquor industry has been based on the principle of "First make Daqu, then brew" for thousands of years (Pan, Qiu, Lv, & Li, 2023; Zhang, Hou, et al. 2023). According to research, barley malt can introduce microorganisms for stacked fermentation while also providing taste ingredients for the liquor. Typical raw materials used are barley, wheat, and pea, which are high in starch and protein.

These macromolecules are degraded by a variety of enzymes, including amylases, glucoamylases, and proteases (typically acidic proteases), which provide nutrients and substrates for microbial growth and taste metabolism. Esterase is also an important enzyme involved in the creation and hydrolysis of volatile esters, which are essential for flavor development. These enzymes are primarily produced by microbes such as *Aspergillus*, *Rhizopus*, *Bacillus* spp., *Lactobacillus* and *Saccharomyces cerevisiae*. Related studies found that *Bacillus* was also the dominant genus of Daqu (Peng et al., 2023; Zhu et al., 2023). The fermentation process is driven by the functional microbiota, which also effects the flavor and end result. Soy sauce, a dark and salty condiment, is produced through the fermentation of cooked soybeans and roasted grains. It is a fundamental component in Chinese, Japanese, and other Asian cuisines, gaining popularity in Western cuisines as well. Soy sauce

is often produced by soaking soybeans in water, heating them, and blending them with roasted wheat flour. The mixture is then injected with *Aspergillus oryzae* or *Aspergillus sojae* and cultured for 2–3 days at 25–30 °C to produce koji. The koji is then mixed with a high-concentration salt solution to achieve a final salt concentration of 22 %–23 %, and left to ferment at room temperature for 6–12 months. China produces approximately 5 million tons of soy sauce annually, accounting for over 50 % of the world's production. The main microorganisms involved in soy sauce fermentation are *Bacillus* spp., such as *B. licheniformis*, *B. velezensis*, *B. amyloliquefaciens*, *B. methylotrophicus*, *B. aerius*, *B. halmapalus*, *B. flexus* and *B. thuringiensis* (Lee et al., 2017; Zhang, Xiong, et al. 2023).

Additionally, probiotic *Bacillus* spp. is the main bacteria in many viscous fermented foods in Asian. Natto, typically made from soybeans fermented by *B. subtilis* and *B. natto*, is a traditional Japanese fermented food. Natto has a golden color and a distinctive aroma and forms a white, transparent bacterial film on the surface. When stirred, it exhibits long and slimy strands (Dong et al., 2020). In India's Meghalaya state, tungrymbai and bekgang is a naturally fermented soybean sticky food consumed as a side dish. The microbial species include *B. thermoamylovorans*, as well as *B. licheniformis*, *B. glycinifermentans*, *B. subtilis* and *B. paralicheniformis* (Chettri & Tamang, 2015). Cheonggukjang, a traditional fermented soybean food from Korea, is produced by fermenting steamed soybeans with natural microbial cultures. The main microbes in Cheonggukjang are *B. thermoamylovorans* and *B. licheniformis* (Tamang et al., 2022). Doenjang, another ancient fermented soybean dish from Korea, has been taken for millennia as both a protein source and a flavor, comparable to miso in Japan and tempeh in Indonesia. Traditionally, Doenjang is made by mixing and fermenting brine with moldy cooked soybeans, in which naturally transported bacteria destroy soy proteins and produce a variety of nutritious chemicals. *Bacillus* is believed to be dominant in soybean paste, and the probiotic *Bacillus* spp. involved in its fermentation are *B. licheniformis* and *B. subtilis* (Han, Baek, Chun, & Jeon, 2023).

Post-fermented tea (also known as black tea) is a distinctive Chinese tea product created from the tea plant's fresh leaves or mature buds. The manufacturing process consists mostly of enzyme inactivation, rolling, heap fermentation, steaming, and drying. Yunnan Pu-erh Tea, Hubei Qingzhuang Tea, Hunan Fuzhuan Brick Tea, and Guangxi Liubao Tea are the four most well-known post-fermented teas, which have received widespread attention from tea consumers in Hong Kong, Macau, mainland China, Southeast Asia, and other countries for their unique flavor quality and health benefits (Zhu et al., 2020). During the heap fermentation stage, tea is turned over on a weekly basis, and the fermentation is ended when the tea blocks turn reddish-brown and no longer taste bitter. This natural solid-state fermentation process involves a number of events, including degradation, oxidation, condensation, structural alteration, methylation, and glycosylation. Previous research has shown that the concentrations of catechin derivatives, flavonoids and their glycosides, phenolic acids, alkaloids, and terpenoids fluctuated dramatically during solid state fermentation. The post-fermentation process takes place in a very complex microecosystem involving bacteria and fungi (Lin et al., 2021). Antagonism between microorganisms in this microecosystem has piqued interest, and the potential antifungal capacity of *Bacillus* strains in particular has been extensively researched due to their ability to produce a wide range of potent compounds that inhibit fungal growth and mycotoxin production. *Bacillus* spp., including *B. subtilis*, *B. licheniformis*, *B. laterosporus*, and *B. coagulans*, produce tiny antifungal peptides with molecular weights of  $\leq 10$  kDa (Li et al., 2022; Zhao, Wang, Zhao, & Yan, 2021).

Typically, fermentation can occur spontaneously due to natural microbial contamination of the raw materials. Fermentation is an ancient technique of preserving food, and the complicated microbial makeup during fermentation provides distinctive aromas, textures, and nutritional value to meat products (Cruxen, et al., 2019). Fermented meat products include pork, beef, lamb, and fish, as well as river shrimp.

Fermented meat products are classified into two types: those produced from whole or sliced meat (cubes and jerky) and those prepared with minced meat. Lactic acid bacteria are the most common microbes involved in meat fermentation, followed by coagulase-negative *Staphylococcus*, *Micrococcus*, and *Bacillus* spp., such as *B. subtilis*, *B. mycooides*, *B. lentus*, and *B. amyloliquefaciens*. Fermented fish and fish products are part of many people's diets worldwide. According to tradition, they are eaten as major dishes, side dishes, and sauces. Several bacterial and yeast species have been identified in fermented and traditionally cured fish items around the world, including probiotic *Bacillus* spp., mainly *B. subtilis*, and *B. amyloliquefaciens*. Cachaldora et al. (Cachaldora, Fonseca, Gómez, Franco, & Carballo, 2014) investigated the growth and metabolic properties of 19 *Bacillus* species isolated from Androlla and Botillo sausages, discovering that *B. amyloliquefaciens* SA35 (isolated from Androlla) and *B. subtilis* SB07 (isolated from Botillo) could hydrolyze myoplasmic proteins and myosin, as well as have lipolytic activity (very high activity in SB07 and high activity in SA35). Both strains showed low levels of decarboxylase activity. These findings imply that *Bacillus* strains may have a role in the maturation and development of sensory qualities in these sausages. The results of the technological properties of *Bacillus* strains (*B. subtilis* tr53, tr50 and trf22) isolated from the southern Italian sausage "Salame di Senise" by Baruzzi et al. (Baruzzi, Matarante, Caputo, & Morea, 2005) showed that *B. subtilis* strains always present in meat curing can contribute to the development of texture and organoleptic properties. Strains that are constantly present in meat curing could influence the texture and organoleptic properties of sausages.

Fermented fish products are consumed in many nations throughout the world. According to tradition, they are eaten as main courses, side dishes, and as condiments. Several species of bacteria and yeasts have been documented to be present in fermented and traditionally cured fish products across the globe (Belleggia & Osimani, 2023), including probiotic *Bacillus* species mainly *B. subtilis*, *B. licheniformis*, *B. megaterium*, *B. mycooides* and *B. cereus*. Traditional Thai salt-fermented freshwater fish (Pla-ra) is a popular cuisine produced and consumed throughout Thailand. The Thai Food and Drug Administration has authorized a local fermenter, a combination of *B. subtilis* UD6-2 and *Virgibacillus halodenitrificans* NCF-2, as an acceptable food culture for Pla-ra fermentation (Thongsomboon et al., 2023). Anihouvi et al. (Anihouvi, Sakyi-Dawson, Ayernor, & Hounhouigan, 2007) investigated the microbial alterations that occurred during the spontaneous fermentation of cassava fish and discovered that the fermented fish's microbial community included a diverse variety of Gram-positive bacteria (92.7 %) and Gram-negative bacteria (7.3 %). *Bacillus* spp. (48.7 %), *Staphylococcus* spp. (27.3 %), and *Micrococcus* spp. (9.4 %) were the most common halophilic gram-positive bacteria. All *Bacillus* species discovered started the fermentation, however only *B. subtilis*, *B. licheniformis* and *B. megaterium* survived until the end of the fermentation process. Xiao; et al. (Xiao, Zhao, Wu, Lin, Zhang, & Gao, 2014) isolated fifty-five protease-producing bacteria from ten fermented fish sauce samples and identified them using the 16S rDNA gene sequences. BLAST examination of the 16S rDNA sequences revealed that forty-six strains belonged to *Bacillus* spp. Ngari is the most popular fermented fish product in Northeast India, made exclusively from sun-dried tiny carp *Puntius sophore* Ham, also known locally as phabou. It is generated by natural fermentation for up to a year and is used as an aperitif and flavor enhancer in a variety of culinary dishes due to its exceptional organoleptic features.

A total of 210 bacteria isolated from the samples were identified using ARDRA-based grouping and 16S rRNA gene sequence similarity analysis. The dominating bacteria were *Staphylococcus cohnii* (38.0 %), *Tetragenococcus halophilus* (16.8 %), a new phylotype linked to *Lactobacillus pobuzihii* (7.2 %), *Enterococcus faecium* (7.2 %), *B. indicus* (6.3 %), and *Staphylococcus carnosus* (3.8 %) (Devi, Deka, & Jeyaram, 2015). Kapi, a traditional fermented shrimp paste from Thailand, is commonly used as a condiment. Small shrimp (*Acetes vulgaris*) and krill (*Mesopodopsis orientalis*) are commonly used as components, along with sea

salt in a 5:1 ratio. After drying and grinding, the mixture is stored in jars at room temperature for many months, or until the characteristic perfume emerges. Traditional fermented foods are deemed healthy due to their long history of consumption, but they have not been examined for hygienic and microbiological safety. When their microbiota was examined using 16S rRNA gene amplicon sequencing, *Bacillus* spp. were discovered (Nakamura et al., 2022; Yiamsombut, Kanchanasin, Phongsopitanun, Kuncharoen, Savarajara, Shi, Wu, Ma, & Tanasupawat, 2021).

#### Commercially available probiotic *Bacillus* spore products

*Bacillus* strains are widely distributed in the natural environment, including soil, air, fermented foods, and the human intestinal tract. Probiotic *Bacillus* spores are resistant to harsh environmental conditions, which allows them to survive in situations when other vegetative bacteria could die off (Gao et al., 2023). The ability of probiotic *Bacillus* spores to germinate, grow, and regenerate in the gastrointestinal tract has been demonstrated (Fig. 2). Spores of probiotic *Bacillus* spp. have been demonstrated to momentarily coexist as commensal organisms within the host, and it is thought that the spores of these species germinate or persist in the small intestine, where they regulate intestinal conditions. Many items containing *Bacillus* spores are sold as “novel foods” or dietary supplements with the promise of improving user health and reestablishing the intestinal tract’s natural microbiota (Zhao et al., 2023). *Bacillus* spore products are primarily used as growth promoters and feed additives in animal and aquaculture farming (Ramlucken et al., 2020). This review primarily focuses on human applications of spore products formed by probiotic *Bacillus*, providing a brief summary of the major *Bacillus* spp. used in commercial products (Table 2). Most commercial *Bacillus* probiotics include *B. coagulans*, *B. subtilis*, *B. polyfermenticus*, *B. clausii*, *B. cereus*, *B. pumilus*, and *B. licheniformis*. Interestingly, the fact that many *Bacillus* spore products are licensed as human pharmaceutical supplements confirms that these *B. coagulans* are safe for consumption.

#### Beneficial metabolites

#### Enzyme-rich resources

Food fermentation is a biochemical process based on the metabolism and action of microorganisms, in which certain components are transformed into other compounds, thus changing the form, taste, and aroma

of the food product. *Bacillus* spp. has the ability to produce high amounts of protease, lipase, and amylase, which play a vital role in food fermentation, improving not only the quality and taste of food, but also the nutritional value.

Currently, *Bacillus* species represent the primary bacterial source of proteases, exhibiting the ability to generate elevated quantities of both alkaline and neutral proteolytic enzymes, each with unique characteristics. Proteases produced by *Bacillus* and their applications in food are summarized in Table 3. Sanjukta et al. (Sanjukta, Rai, Muhammed, Jeyaram, & Talukdar, 2015) hydrolyzed soy protein using *B. subtilis* MTCC5480 and *B. subtilis* MTCC1747 proteases, and the released peptides and free amino acids presented strong antioxidant properties. Zhao et al. (Zhao et al., 2012) showed that the cold-adapted collagenolytic protease MCP-01 secreted by *B. subtilis* BEM01 had a stronger tenderizing effect on meat samples than papain, and meat tenderization at low temperatures was more conducive to maintaining the freshness and quality of meat. Sorapukdee et al. (Sorapukdee, Sumpavapol, Benjakul, & Tangwatcharin, 2020) found that the proteases secreted by *B. subtilis* B13 and *B. siamensis* S6 efficiently hydrolyzed bovine Achilles tendon collagen and that these two *Bacillus* proteases had higher hydrolytic activity on elastin and beef intramyocardial collagen and lower hydrolytic activity of beef myofibrillar proteins than papain and pineapple protease. *B. licheniformis* LBA46 protease can be used to hydrolyze pea protein to prepare pea protein peptides. The hydrolysis conditions of pea protein were optimized using response surface methods, and the best conditions were determined to be a pH of 10 and an enzyme concentration of 100 U/mL. The hydrolysis product has a strong 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging ability, oxygen radical absorbance, and ferric ion reducing/antioxidant power, indicating some application potential (Aguilar & d. S., Castro, R. J. S. d., & Sato, H. H., 2020). Yang et al. (Yang et al., 2016) found that the extracellular proteases secreted by *B. licheniformis* CGMCC 0635 were able to improve the nutritional properties of peanut proteolytic digests, such as the levels of crude protein, organic acids, acid-soluble oligopeptides, and minerals, and to enhance the antioxidant properties, amino acid balance, and in vitro digestibility. Thermolysin, secreted by *B. thermophilus*, digested rice bran and produced peptides with antihypertensive properties (Shobako et al., 2018). Song et al. (Song et al., 2021) heterologously expressed and purified *B. cereus* CMCC 63303 collagenase and applied it to the hydrolysis of bovine bone collagen to prepare collagen peptides.

Lipases are very essential commercial enzymes that catalyze the hydrolysis of triglycerides to glycerol and free fatty acids, laying the

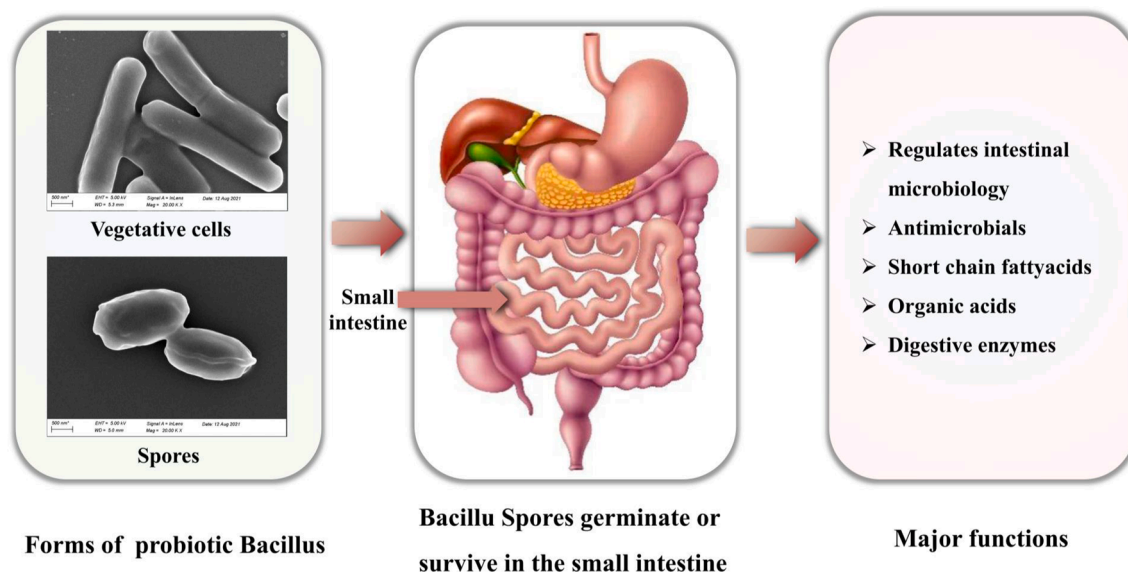


Fig. 2. Schematic diagram of the forms of probiotic bacillus used and their functions on the human body.



**Table 2**  
Probiotic *Bacillus* spores in commercial products.

Product	Manufacturer	Comments	References
Primal Defense	Garden of life, USA	Combination of 12 probiotics, one of which includes <i>B. subtilis</i> DE-111	(Gallart, Sanseverino, & Winger, 2020)
MegaSporeBiotic	Microbiome Labs, USA	<i>B. indicus</i> , <i>B. subtilis</i> , <i>B. coagulans</i> , <i>B. licheniformis</i> , <i>B. clausii</i>	(Elshaghabe et al., 2017)
Biosubtyl	Biophar Company, Nha Trang, Vietnam	Sachet (1 g) carrying $10^6$ – $10^7$ of <i>B. pumilus</i> spores mixed with tapioca. Product labelled as <i>B. subtilis</i>	(Duc, Hong, Barbosa, Henriques, & Cutting, 2004; Soares et al., 2023)
Bispan	Binex Co. Ltd, Busan, Korea	Tablet carrying spores ( $1.7 \times 10^7$ ) of <i>B. polyfermenticus</i> SCD <sup>d</sup>	(Paik, Park, & Park, 2005)
Domuvar	BioProgress SpA, Anagni, Italy	Vial carrying $1 \times 10^9$ spores of <i>B. clausii</i> in suspension, labelled as carrying <i>B. subtilis</i>	(Cutting, 2011; Lee, Kim, & Paik, 2019)
Flora-Balance	Flora-Balance, Montana, USA	Capsules labelled as carrying <i>Bacillus laterosporus</i> BODD but containing <i>Brevobacillus laterosporus</i> BOD	(Sanders, Morelli, & Tompkins, 2003)
Lactospore	Sabinsa Corp., Piscataway, NJ, USA	Labelled as carrying <i>Lactobacillus sporogenes</i> but contains <i>B. coagulans</i> $6$ – $15 \times 10^9$ g <sup>-1</sup>	(David, Katy, & Judith, 2010)
Medilac	Hanmi Pharmaceutical Co. Ltd., Beijing, China	<i>B. subtilis</i> strain R0179 (at 108 g l) in combination with <i>Enterococcus faecium</i>	(Hong, Duc, & Cutting, 2005)
Natur's First Food	Nature s First Law, San Diego, CA, USA	42 species listed as probiotics including: <i>B. subtilis</i> , <i>B. polymyxa</i> , <i>B. pumilus</i> and <i>B. laterosporus</i>	(Sanders et al., 2003)
Neolactoflorene	Newpharma S.r.L., Milan, Italy	<i>L. acidophilus</i> , <i>B. bifidum</i> and <i>L. sporogenes</i> . <i>L. sporogenes</i> at $3.3 \times 10^5$ CFU/g whose valid name is <i>B. coagulans</i> is mislabelled and is a strain of <i>B. subtilis</i>	(Fasoli et al., 2003)
Subtyl	Mekophar, Pharmaceutical Factory No. 24, Ho Chi Minh City, Vietnam	Capsule carrying $10^6$ – $10^7$ spores of a <i>B. cereus</i> species termed <i>B. cereus</i> var vietnami. Product labelled as carrying <i>B. subtilis</i>	(Soares et al., 2023)

groundwork for the production of taste compounds during food fermentation. Elemosho et al. (Elemosho, Antonius, & Maggy, 2021) reported successful extracellular expression of thermophilic lipase (T1.2RQ), a new industrially desirable heat-stable lipolytic enzyme with outstanding hydrolytic and ester-exchange activity, in *B. subtilis* WB800. Disha Sharma et al. optimized the key growth parameters to enhance the extracellular lipase yield produced by *B. alkalophilus* KS4 3.54-fold. Nguyen et al. (Nguyen et al., 2024) cloned the lipase gene *estA* from *B. subtilis* KM-BS and optimized it for effective heterologous protein production in *Escherichia coli* BL21 (DE3) cells. The ability of this pure recombinant lipase to hydrolyze waste cooking oil was biochemically

characterized.

Amylases are extracellular enzymes that randomly hydrolyze starch molecules to yield a variety of products, including dextrans and progressively smaller polymers made up of glucose units. Trabelsi et al. (Trabelsi, Mabrouk, Kriaa, Ameri, Sahnoun, Mezghani, & Bejar, 2019) found that Amy586 secreted by *B. subtilis* strain US586 improves bread textural parameters by decreasing bread hardness and increasing cohesion and elasticity values. Du et al. (Du et al., 2018) isolated and characterized a new  $\alpha$ -amylase generated by *B. amyloliquefaciens* BH072, which showed high hydrolysis rates of maize, wheat, and potato starch and hydrolyzed soluble starch to glucose, maltose, maltotriose, and maltotetraose.

#### Antibacterial substances

Bacteriocins are proteins generated by bacteria that serve as antimicrobial agents, primarily inhibiting the growth of closely related bacteria. Bacteriocin production is a good trait of probiotic strains, which are inherently non-toxic and have excellent bacteriostatic action against food spoilage bacteria and human infections. A number of *Bacillus* species produce bacteriocins which have a significant inhibitory effect on pathogenic or endogenous infections by conditionally pathogenic bacteria, some notable examples of which are listed in Table 3.

*B. subtilis* is thought to be one of the most efficient “antibiotic-producing” species in the *Bacillus* genus, with antibiotic production accounting for 4 %–5% of its genome. In total, 66 antibiotics have been identified in different strains of *B. subtilis*, suggesting that this species has important biotechnological potential. For example, Subtilisin A produced by *B. subtilis* had the strongest inhibitory effect on *Rhizopus*, followed by *Listeria monocytogenes* and other bacterial strains (Epparti, Eligar, Sattur, & Halami, 2022). Iturin A produced by *B. subtilis* R0179 has a significant inhibitory effect on the growth of *Candida* (Zhao, Lou, Shui, Zhang, Hu, Zhang, Li, Wu, & Li, 2021). Mejuicin, a novel bacteriocin, has a bactericidal effect on the trophoblasts and sporoblasts of *B. cereus* (Lee & Chang, 2018). Amicoumacin A generated by *B. subtilis* is an antibiotic with anti-inflammatory effects that can be used to treat *Helicobacter pylori* infection (Zhao et al., 2016). *B. natto* produces surfactin, which may prevent the growth of *Candida albicans* in the digestive system (Jakab et al., 2022). Similarly, Abdullah et al. (Abdullah et al., 2018) investigated the production of a broad-spectrum lipopeptide (a bacitracin-like peptide compound) from *B. megaterium*, which is highly effective against both Gram-positive and Gram-negative bacterial pathogens. Saising et al. (Saising et al., 2012) demonstrated that Gallidermin suppressed not only the growth of *Staphylococcus* in a dose-dependent manner but also effectively prevented biofilm formation. *B. licheniformis* ATCC 14580 developed a dipeptide antibiotic called Lichenicidin, which was effective against *L. monocytogenes*, methicillin-resistant *Staphylococcus aureus*, and vancomycin-resistant *E. faecium* (Begley, Cotter, Hill, & Ross, 2009). *Clostridium beijerinckii* ATCC 25752 produces Circularin A, which is active against *Clostridium tyrobutyricum*, a bacteria that causes cheese deterioration. (Kawai, Kemperman, Kok, & Saito, 2004).

#### Probiotic *Bacillus* as fermentation agents

With the in-depth and extensive research on *Bacillus probioticus*, it is slowly being used as fermentation agent in single fermentation or co-fermentation with *Lactobacillus*, and the latest results are shown in Table 4. The probiotic *Bacillus* spp. used for food fermentation include *B. subtilis*, *B. coagulans*, *B. velezensis*, *B. amyloliquefaciens*, *B. pseudomycolides*, *B. natto*, *B. licheniformis*, *B. brevis*, and *B. cereus*. It is exciting that the use of probiotic *Bacillus* strains in fermented foods imparts a richer flavor and texture to the products, increases the nutritional value of the products, improves the safety of the products and degradation rate of the products to a certain extent, shortens the fermentation time, and provides a new way to reduce salt levels in fermented foods. Of these, *B. coagulans* has been reported to be safe by the



**Table 3**  
Beneficial metabolites produced by probiotic *Bacillus*.

Product type	Probiotics <i>Bacillus</i> species	Beneficial metabolite	Effectiveness	References	
Enzymes	<i>B. subtilis</i> MTCC5480 <i>B. subtilis</i> MTCC1747	Fibrinolytic enzyme and proteolytic enzyme	Soybean fermented with possible proteolytic <i>B. subtilis</i> strains had higher antioxidant capabilities due to increased peptides and polyphenols.	(Sanjukta et al., 2015)	
	<i>B. subtilis</i> BEM01	Cold-adapted collagenolytic protease MCP-01	MCP-01 significantly reduces beef shear when applied at 4 °C, preserving meat's bright color and moisture. Unlike commercially available papain and bromelain, MCP-01 is highly selective for collagen degradation at 4 °C.	(Zhao et al., 2012)	
	<i>B. subtilis</i> B13 <i>B. siamensis</i> S6	Serine proteases and some metalloproteases	In contrast to papain and bromelain, these collagenolytic proteases showed strong hydrolysis toward collagen and elastin as well as beef intramuscular collagen with low beef myofibrillar protein degradation.	(Sorapukdee et al., 2020)	
	<i>B. subtilis</i>	<i>B. subtilis</i> protease powder (CTC E-essentials MT-70 N)	<i>B. subtilis</i> protease can be used as a meat tenderizer instead of current commercial tenderizers that contain plant-derived proteases.	(Burerros, Dizon, Israel, Abanto, & Tambalo, 2020)	
	<i>B. licheniformis</i> LBA46	Alkaline protease LBA	<i>B. licheniformis</i> pea protein hydrolysate exhibits significant DPPH radical rate, oxygen radical uptake and iron ion reducing antioxidant capacity.	(Aguilar & d. S., Castro, R. J. S. d., & Sato, H. H., 2020)	
	<i>B. licheni formis</i> CGMCC0635	Extracellular	It improves the crude protein, organic acids, acid-soluble oligopeptides and other actives, minerals and antioxidant properties, amino acid balance and in vitro digestibility in peanut protein, and enhances the nutritional and functional properties of peanuts.	(Yang et al., 2016)	
	<i>B. thermophilus</i>	Thermolysin	The antihypertensive activity of protease-digested rice bran in a spontaneously hypertensive rat (SHR) paradigm.	(Shobako et al., 2018)	
	<i>B. cereus</i> CMCC63303	Collagen enzyme	Under ideal conditions (110.0 µg/mL collagenase concentration, 35 °C, pH 8.0, and 6.0 h), collagenase demonstrated hydrolytic activity.	(Song et al., 2021)	
	<i>B. subtilis</i> WB800	Geobacillus stearothermophilus lipase (T1.2RQ)	Excellent hydrolytic and transesterification activity.	(Elemosho et al., 2021)	
	<i>B. subtilis</i> KM-BS	Lipase EstA	EstA, a recombinant lipase, demonstrated strong activity (49.67 U/mL), as well as high heat and pH stability.	(Nguyen et al., 2024)	
	<i>B. pumilus</i> V1, <i>B. pumilus</i> V7, and <i>B. subtilis</i> V8 <i>B. subtilis</i> strain US586	Extracellular lipase Acid-stable alpha-amylases	The bacterial cultures <i>B. pumilus</i> V1, <i>B. pumilus</i> V7, and <i>B. subtilis</i> V8 produced 27.8, 25.2, and 16.6 µg/mL of lipase respectively. Adding pure amylolytic extract from the newly identified <i>B. subtilis</i> strain US586 to weak local flour enhances dough rheological properties and bread quality.	(Kandasamy et al., 2021) (Trabelsi et al., 2019)	
	<i>B. amyloliquefaciens</i> BH072	α-amylase	The reported α-amylase enzyme has a specific activity of 2162.42 U/mg and a molecular mass of approximately 68 kDa.	(Du et al., 2018)	
	Antimicrobial substances	<i>B. subtilis</i> SC3.7	Subtilosin A	The strongest zone of inhibition was reported against <i>K. rhizophila</i> , followed by <i>L. monocytogenes</i> and other bacterial species.	(Epparti et al., 2022)
		<i>B. subtilis</i> R0179	Iturin A	It significantly inhibits the growth of <i>Candida</i> species.	(Zhao, Wang, et al. 2021)
<i>B. subtilis</i> N7		Mejucin ( a novel bacteriocin )	Mejucin have bactericidal effects on both vegetative and spore cells of <i>B. cereus</i> .	(Lee & Chang, 2018)	
<i>B. subtilis</i> NT-6		Antimicrobial peptide AMPNT-6	AMPNT-6 proved effective in controlling biofilms on various contact surfaces by lowering adhesion and/or eliminating biofilm.	(Deng et al., 2017)	
<i>B. subtilis</i>		Amicoumacin A	It has been shown to be antagonistic against Enterobacteriaceae species, as well as to inhibit <i>Helicobacter pylori</i> .	(Zhao et al., 2016)	
<i>B. natto</i> <i>B. megaterium</i>		Surfactin A bacitracin like peptide compound	It may inhibit the growth of <i>Candida albicans</i> in the digestive tract. It has exhibited potential broad spectrum antimicrobial activity.	(Jakab et al., 2022) (Abdullah et al., 2018)	
<i>B. clausii</i>		Gallidermin	Gallidermin suppresses staphylococci growth in a dose-dependent manner while also effectively preventing biofilm formation by <i>Staphylococcus aureus</i> and <i>Staphylococcus epidermidis</i> .	(Saising et al., 2012)	
<i>B. licheniformis</i> ATCC 14580		Lichenicidins	Lichenicidin is a two-peptide lantibiotic with antibacterial activity against all <i>Listeria monocytogenes</i> , methicillin-resistant <i>Staphylococcus aureus</i> , and vancomycin-resistant Enterococcus strains tested.	(Begley et al., 2009)	
<i>Clostridium beijerinckii</i> ATCC25752		Circularin A	<i>Clostridium beijerinckii</i> ATCC25752 produces Circularin A, which is active against <i>Clostridium tyrobutyricum</i> , a recognized cheese-spoilage bacterium.	(Kawai et al., 2004)	

US Food and Drug Administration and the European Union Food Safety Authority, and it is on the GRAS and QPS lists. In addition, genome sequencing has been reported to provide information about the overall characteristics of the bacteria, which can better demonstrate its safety as a food supplement. The genome of *B. coagulans* GBI-30 was sequenced and was found to be free of any deleterious genes.

A large number of Probiotic *Bacillus* strains have been isolated from traditional natural fermented foods. Probiotic *Bacillus* strains have long been used by consumers in the form of fermented foods, but it has been

neglected and its role in human health and food fermentation has not been emphasized. *Bacillus* is an understudied bacterial genus, which is commonly found in many fermented foods, especially solid-state fermented foods. Certain probiotic *Bacillus* species generate large amounts of lipases and proteases, as well as extracellular polymeric compounds and strong antifungal lipopeptides that are uncommon in other significant food fermenters, such as *Lactobacillus*, *Acetobacter*, or *Propionibacterium*. Further research into the probiotic properties of *Bacillus* spp. will support their development into next-generation fermentation

**Table 4**  
Probiotic *Bacillus* as food fermentation agents.

Species	Fermentation mode	Food	Contribution	References
<i>B. subtilis</i> WX-17	Single fermentation	Probiotic beverage	Essential amino acids and short-chain fatty acids were dramatically increased. Total phenolic content and antioxidant content (measured by DPPH radical scavenging activity) rose by 6.32 and 1.55, respectively.	(Mok, Tan, Lyu, & Chen, 2020)
<i>B. subtilis</i> LK-1	Single fermentation	Dark tea	New flavor substances such as geranyl isovalerate are produced after fermentation, and the floral and fruit aroma of dark tea improved with fermentation.	(Xiao et al., 2023)
<i>B. subtilis</i> lwo	Single fermentation	Chickpeas	The proteolysis and the antioxidative properties of chickpeas were improved by solid-state fermentation.	(Li & Wang, 2021)
<i>B. subtilis</i> Y61	Single fermentation	Sichuan paocai	The inoculated fermentation of <i>B. subtilis</i> Y61 can improve the quality and safety of SCP while also shortening fermentation time.	(Yang et al., 2020)
<i>B. coagulans</i>	Single fermentation	Tender Coconut Water	The synthesis of exopolysaccharides by <i>B. coagulans</i> during fermentation resulted in a considerable increase in the soluble solids content and viscosity of the fermented coconut water.	(Gangwar, Bhardwaj, & Sharma, 2018)
<i>B. coagulans</i> VHProbi C08	Single fermentation	Plant-based drink	Plant-based drink fermented by VHProbi C08 has great antibacterial and antioxidant activities.	(Shudong et al., 2022)
<i>B. velezensis</i> CS1.10S	Single fermentation	Soy sauce	CS1.10S is salt tolerant and improves the taste and aroma of soy sauce.	(Bai et al., 2023)
<i>B. clausii</i>	Single fermentation	Spent coffee grounds (SCG)	Peptides with strong bioactive potential are more abundant in fermented SCG and can be used to treat diabetes, hypertension, and oxidative stress.	(Ramírez, Pineda-Hidalgo, & Rochín-Medina, 2021)
<i>B. natto</i>	Single fermentation	Peanuts	The method reduced more than 77.3 % of the IgE reactivity in peanut protein preparations.	(Pi et al., 2021)
<i>B. natto</i>	Single fermentation	Rosa roxburghii pomace	<i>B. natto</i> helps to produce high-quality dietary fiber from Rosa roxburghii pomace.	(Chu et al., 2019)
<i>B. coagulans</i> MTCC 5856 and <i>Streptococcus thermophilus</i>	Cooperative fermentation	Fermented dairy	<i>B. coagulans</i> coupled with <i>S. thermophilus</i> produce a dairy product of improved quality, and the product has a high antioxidant activity enhancing its therapeutic value.	(Lavrentev et al., 2021)
<i>Enterococcus</i> , <i>Lactobacillus</i> , <i>Bacillus</i> , and <i>Leuconostoc</i>	Cooperative fermentation	Amaranth doughs	Fermentation of amaranth with <i>LAB</i> and <i>Bacillus</i> spp. allowed the release of protein hydrolysates with antioxidant, antihypertensive, and antimicrobial activity.	(Cruz-Casas et al., 2023)
<i>B. amyloliquefaciens</i> MK063714 and <i>Candida versatilis</i> MK063708	Cooperative fermentation	Horse bean	Combination of <i>B. amyloliquefaciens</i> and <i>C. versatilis</i> could obtain more extensive aroma profiles, especially for the enrichment of miso-like and fruity flavors.	(Lu, Yang, Yang, Chi, & He, 2021)
<i>B. amyloliquefaciens</i> HZ-12, <i>Escherichia coli</i> DH5 $\alpha$	Cooperative fermentation	Soybean	The lycopene yield of <i>B. amyloliquefaciens</i> HZ-12/pHYcrtEIB was further increased.	(Zou et al., 2022)
<i>Saccharomyces cerevisiae</i> and <i>B. licheniformis</i>	Cooperative fermentation	Jujube wine	Co-fermentation enhances the flavor of jujube wine, as evidenced by substantial differences in color, taste, amino acids, organic acids, and aroma ( $p < 0.05$ ). Co-fermented jujube wine also has superior color quality.	(Zhao et al., 2022)
<i>B. subtilis</i> and <i>B. coagulans</i>	Cooperative fermentation	Soybean residue	<i>B. subtilis</i> R0179 and <i>B. coagulans</i> 123 reduced undesirable green and beany flavours in okara.	(Keong, Toh, Lu, & Liu, 2023)
<i>Aspergillus oryzae</i> and <i>B. subtilis</i>	Cooperative fermentation	Gochujang meju	Acid protease has high activity and free amino acid content.	(Kim, Han, & Kim, 2010)
<i>B. cereus</i> DM423 and <i>L. plantarum</i> HH-LP56	Cooperative fermentation	Pork	<i>B. cereus</i> DM423 can promote flavor formation in fermented sausages	(Shan et al., 2023)

agents for the production of many new and improved fermented foods.

## Opportunities and challenges

### Opportunities

As consumer habits evolve and interest in food and health grows, there is an increasing demand for healthier and more practical food options. Traditional fermented foods, primarily produced at home or in small-scale settings, face the challenge of modernized manufacturing techniques in traditional food enterprises. The integration of ancient traditional fermentation processes with modern technologies poses new challenges and opportunities for the food industry. In particular, the exploration and enrichment of microbial resources, coupled with the development of diverse microbial fermentation agents, are crucial tasks. Probiotic *Bacillus* strains, with their potential to become next-generation probiotic fermentation agents, play a key role in meeting this demand.

Many probiotic *Bacillus* strains can be isolated from traditional naturally fermented foods, especially solid-state fermented products. However, research on their role as fermenting agents in food

fermentation is limited and not comprehensive. Some probiotic *Bacillus* strains possess excellent probiotic characteristics that remain underexplored. Once characterized, these strains can be used for co-fermentation with the now common probiotics (*L. plantarum*, *L. lactis*) to make food products with a better flavor and higher nutritional value. Simultaneously, the spores produced by *Bacillus probioticus* provide a new nutritional enhancer for heat-treated probiotic products due to their heat resistance, which can be of interest to food companies and consumers. The longstanding presence of probiotic *Bacillus* strains in traditional fermented foods, coupled with existing reports on their probiotic properties and fermentation performance, paves the way for further comprehensive research and exploration of their potential as fermentation agents.

Furthermore, with the advancement of scientific and technological capabilities, the refinement of omics technologies such as genomics, proteomics, and metabolomics has allowed us to gain a deeper understanding of organisms. This enhanced understanding includes the fundamental composition and evolutionary patterns of living organisms. Through genomic analysis at the gene level, we can predict and analyze functional genes, gene clusters related to the synthesis of bioactive

metabolites, resistance genes, and independent factors. These advancements in omics technologies propel the research and development of probiotic *Bacillus* strains, enabling a more comprehensive exploration of their capabilities and potential.

### Challenges

The presence of probiotic *Bacillus* spp. in most traditional natural fermented foods confirms that probiotic *Bacillus* strains have a long application history. However, several *Bacillus* spp. provide dangers, including the formation of toxic metabolites and toxins, the transmission of antibiotic resistance genes, the generation of excess amines, and infection. Therefore, the use of probiotic *Bacillus* strains as food fermentation agents must be adequately investigated with more detailed phenotypic and genotypic safety assessments to ensure that it is safe.

Probiotic *Bacillus* strains, being novel fermentation agents in the development of new fermented foods, introduce new and unknown components, leading to public caution. Thermophilic *Bacillus* spp. and their metabolites represent a new category of food components. To promote consumer health, operators must provide extensive information on the new food product prior to manufacture and sale, while complying to regulations and processes unique to each country and region. The procedures for approving the market entry of new foods vary by location, and there is a lack of globally unified regulatory standards for the assessment and oversight of new foods. In order to address this, it is crucial for regulatory bodies worldwide to establish consistent standards for the evaluation and regulation of new foods to ensure consumer safety.

### Conclusion

This article provides an overview of the presence of probiotic *Bacillus* strains in the microbial composition of liquid, semi-solid and solid fermented foods, and probiotic *Bacillus* strains widely exist in solid fermented foods. Furthermore, the statistics of probiotic *Bacillus* products currently on the market, and the production of enzymes and antibiotics by probiotic *Bacillus* strains are conducted to illustrate their edible safety and fermentation feasibility. Finally, a statistical analysis is performed on the research on single fermentation and mixed fermentation of probiotic *Bacillus* strains as food fermentation agents. Excitingly, the use of probiotic *Bacillus* strains in food fermentation enhances the flavor and texture of the product, increases the nutritional value, and improves the safety. Additionally, it contributes to the metabolism of raw food material, shortens fermentation times, provides a new avenue for salt reduction in fermented foods, and offers novel approaches for modernizing manufacturing techniques in traditional food enterprises. The integration of modern and ancient traditional fermentation processes has been made possible through the utilization of probiotic *Bacillus* strains, paving the way for innovative developments in the fermented food industry.

Based on this, we can focus on the following research directions in the future: (1) Further explore the resources of probiotic microorganisms in traditional natural fermented foods, and use more accurate microbial diversity characterization technology (such as the third generation sequencing technology, etc) to make the safety and probiotic properties of probiotic *Bacillus* strains more clear. (2) Combined use of multi-omics technologies such as genomics, proteomics and metabolomics to further explore the pathways of probiotic *Bacillus* on microbial composition and complex flora material metabolism in the traditional natural fermented food process, and clarify the positive contribution of probiotic bacteria in the food fermentation process. (3) Explore the flavor substance formation mechanism of probiotic *Bacillus* collaborative fermentation in traditional fermented foods, and achieve intelligent and precise control of the brewing process of traditional fermented foods to produce better-quality and more delicious foods.

### CRediT authorship contribution statement

**Shijie Liu:** Writing – review & editing, Writing – original draft, Investigation. **Lijun Zhao:** Writing – review & editing, Formal analysis. **Miaoyun Li:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Yaodi Zhu:** Writing – review & editing. **Dong Liang:** Supervision. **Yangyang Ma:** Supervision. **Lingxia Sun:** Supervision. **Gaiming Zhao:** Supervision. **Qiancheng Tu:** Supervision.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

### Acknowledgments

This research was supported by the Major science and technology projects in Henan province (221100110500, 231100110400), the Science and Technology Innovation Team of Henan Universities (22IRTSTHN021), the joint fund of Henan province (scientific and technological research) (232103810023), the Science and Technology of Henan Province (232102110136) and the National Modern Agriculture (beef yak) Industrial Technology System Construction Special (CARS-37).

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