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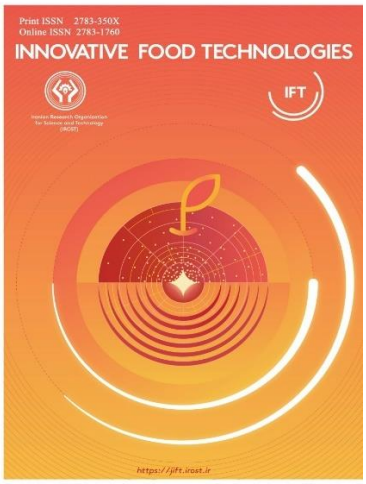

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A Review of Probiotic-Enhanced Bioavailability of Vitamins, Minerals, and Phenolic Metabolites in Food Matrices

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Abstract

Functional foods containing probiotics have gained considerable attention due to their ability to improve the nutritional quality and health-promoting effects of food products. Probiotics, which are live microorganisms that confer health benefits when consumed in sufficient amounts, can enhance the bioavailability of nutrients through diverse mechanisms. Recent studies indicate that certain probiotic strains can produce essential vitamins, including B-complex vitamins and vitamin K, facilitate mineral absorption by lowering intestinal pH and breaking down antinutritional compounds such as phytates, and convert complex phenolic compounds into more bioactive and readily absorbable forms. These processes are driven by enzymatic activities, shifts in gut microbial populations, and the generation of short-chain fatty acids. This review examines the metabolic pathways involved in vitamin synthesis, mineral solubilization, and phenolic compound transformation by probiotics, providing updated insights into their nutritional and functional potential. Incorporating selected probiotic strains into food products represents a promising strategy to combat nutrient deficiencies and support health, while understanding the underlying molecular mechanisms and optimizing strain selection are essential for developing next-generation functional foods with superior nutritional and therapeutic properties.

Keywords: Bioavailability, Vitamins, Minerals, Phenolic compounds, Probiotics.

1. Introduction

Functional foods have attracted growing attention among consumers due to their ability to promote health and reduce the risk of certain diseases by establishing a beneficial link between diet and overall well-being. These foods can be enhanced through the incorporation of probiotics, prebiotics, or synbiotics, providing bioactive components that support health in both humans and animals (Beikzadeh et al., 2016; Beikzadeh et al., 2025; Bermúdez-Humarán et al., 2024; Stanton et al., 2005) Beyond measuring nutrient content, it is essential to consider their bioavailability to fully understand their health impact. Probiotics, particularly lactic acid bacteria, are known to improve the absorption and utilization of nutrients such as vitamins, minerals, and phenolic compounds, while also stimulating the immune system ((Bermúdez-Humarán et al., 2024; Chiang & Pan, 2012; Salva et al., 2011)

Vitamins, including folate and cobalamin, are vital for maintaining human health, with deficiencies linked to cardiovascular diseases, cognitive disorders, Alzheimer's disease, and certain cancers (Gisondi et al., 2007). Minerals, as essential inorganic elements distributed throughout tissues and fluids, play critical roles in numerous biochemical and physiological processes (Eruvbetine, 2003; Özcan, 2004). In many developing regions, insufficient intake of micronutrients remains a major public health concern. For instance, iron deficiency can impair cognitive performance, reduce physical work capacity, weaken immunity, and increase pregnancy complications ((Batra & Seth, 2002).

Phenolic compounds, which constitute a significant class of plant secondary metabolites, have attracted attention due to their health-promoting properties. They exhibit diverse biological activities, including antioxidant, anticarcinogenic, antimutagenic, and anti-inflammatory effects (Karakaya, 2004; Parr & Bolwell, 2000). However, the bioavailability of polyphenols can be limited by structural factors such as polymerization and glycosylation, meaning that only a portion of these compounds is effectively absorbed and exerts physiological effects (Hamidpour et al., 2017; Manini, 2015; Tomas et al., 2025)

This review focuses on the role of probiotics in influencing nutrient metabolism, particularly their effects on vitamin and mineral bioavailability, as well as the production and transformation of phenolic metabolites.

Although several review articles have examined the role of probiotics in the production of vitamins, enhancement of mineral absorption, or metabolism of phenolic compounds separately, a comprehensive review integrating these three aspects and their underlying mechanisms in food matrices is still lacking. Therefore, this review aims to provide an integrated and up-to-date overview of the mechanisms by which probiotics improve the bioavailability of vitamins, minerals, and phenolic compounds, while highlighting recent advances, current challenges, and future research directions.

Unlike previous reviews that have primarily focused on individual aspects such as vitamin biosynthesis, mineral absorption, or phenolic metabolism, the present review provides an integrated and comparative overview of probiotic-mediated enhancement of nutrient bioavailability across multiple nutrient classes. Furthermore, it critically discusses the underlying mechanisms, food matrix effects, current limitations, and emerging future directions, thereby providing a broader perspective for the development of next-generation functional foods.

2. Mechanisms of probiotic-mediated enhancement of nutrient bioavailability

Probiotics enhance nutrient bioavailability through multiple complementary mechanisms involving microbial metabolism, enzymatic activities, and modulation of the intestinal environment. One of the principal mechanisms is the de novo biosynthesis of vitamins,

particularly B-group vitamins, by selected probiotic strains belonging to the genera Lactobacillus and Bifidobacterium. These microorganisms can synthesize vitamins during food fermentation or within the gastrointestinal tract, thereby increasing the nutritional value and bioavailability of foods (Bedani et al., 2024; Bermúdez-Humarán et al., 2024).

Another important mechanism is the production of extracellular enzymes, including phytases, esterases, and glycosidases. Phytase hydrolyzes phytic acid, an antinutritional factor that chelates essential minerals such as iron, zinc, calcium, and magnesium, thereby enhancing their intestinal absorption. Similarly, glycosidases and esterases catalyze the conversion of complex phenolic compounds into smaller and more bioaccessible metabolites with higher biological activity (Anwer & Wei, 2024; Tomas et al., 2025).

In addition, probiotic fermentation stimulates the production of short-chain fatty acids (SCFAs), including acetate, propionate, and butyrate. These metabolites lower intestinal pH, improve mineral solubility, strengthen epithelial barrier integrity, and promote nutrient transport across the intestinal mucosa. Probiotics also contribute to maintaining gut microbial homeostasis, suppressing pathogenic microorganisms, and modulating intestinal permeability, all of which collectively facilitate nutrient absorption(Bedani et al., 2024; Bermúdez-Humarán et al., 2024).

Overall, the enhancement of nutrient bioavailability by probiotics results from the synergistic effects of microbial vitamin biosynthesis, degradation of antinutritional compounds, enzymatic biotransformation of dietary constituents, SCFA production, and modulation of the gut microbiota. These mechanisms support the application of probiotics as promising functional ingredients for improving human nutrition and developing next-generation functional foods (Bermúdez-Humarán et al., 2024; Tomas et al., 2025).

Host-microbe interactions play a pivotal role in determining nutrient bioavailability beyond microbial nutrient synthesis. Probiotic microorganisms interact with intestinal epithelial cells, immune cells, and the resident gut microbiota to improve nutrient absorption and utilization. These interactions enhance epithelial barrier integrity by strengthening tight junction proteins, reduce intestinal inflammation, and promote the expression of nutrient transporters involved in the uptake of vitamins and minerals. Furthermore, probiotic-derived short-chain fatty acids (SCFAs), particularly butyrate, acetate, and propionate, lower intestinal pH, increase mineral solubility, and provide energy for colonocytes, thereby improving intestinal function and nutrient absorption. The modulation of gut microbial composition also suppresses pathogenic microorganisms and creates a favorable intestinal environment for efficient nutrient utilization. Collectively, these host–microbe interactions represent key biological mechanisms through which probiotics enhance nutrient bioavailability beyond their capacity for nutrient biosynthesis (Bermúdez-Humarán et al., 2024; Tomas et al., 2025).

2.1. Role of food matrices in probiotic-mediated nutrient bioavailability

Food matrices play a fundamental role in determining the survival, metabolic activity, and functionality of probiotic microorganisms, thereby directly influencing nutrient bioavailability. The physicochemical characteristics of different food matrices, including pH, water activity, protein and fat content, dietary fiber, and the presence of antinutritional factors, affect both probiotic viability and microbial metabolism during fermentation. Dairy products generally provide a favorable environment for probiotic survival because of their buffering capacity and nutrient-rich composition, whereas cereal- and plant-based matrices often contain dietary fibers and phytochemicals that may act as prebiotic substrates but also include phytic acid and other compounds that can reduce mineral bioavailability(Beikzadeh et al., 2017). Furthermore, the interaction between probiotic strains and food components determines the efficiency of vitamin

biosynthesis, phytate degradation, mineral solubilization, and phenolic biotransformation. These interactions are highly matrix-dependent and may explain the considerable variability observed among different studies. Therefore, selecting an appropriate food matrix is as important as selecting an effective probiotic strain for developing functional foods with enhanced nutrient bioavailability(Bermúdez-Humarán et al., 2024; Tomas et al., 2025)

3. Production of vitamins

Vitamins can be classified into two main categories: water-soluble and fat-soluble. Water-soluble vitamins include the B-complex group (thiamine, riboflavin, niacin, pantothenic acid, pyridoxine, folic acid, cobalamin), vitamin C, and biotin, while fat-soluble vitamins comprise A, D, E, and K. Fat-soluble vitamins mainly contribute to cell membrane structure, whereas water-soluble vitamins function as coenzymes and carriers for various chemical groups in metabolic reactions (Basu & Dickerson, 1996). Although probiotics require certain vitamins for growth, many strains possess the ability to produce specific B-complex vitamins and vitamin K. This capability can be harnessed to naturally fortify fermented foods (Anwer & Wei, 2024; Massaro et al., 2025; Quinn, 2020; Snell, 1993). Several lactic acid bacteria, including *Lactobacillus plantarum*, *L. fermentum*, *L. rhamnosus*, and *Bifidobacterium adolescentis*, have been reported to synthesize B-group vitamins during fermentation.

Recent studies (Bermúdez-Humarán et al., 2024) suggest that probiotics not only generate vitamins but also enhance their absorption in the host. This effect is achieved through modulation of the gut microbiota and production of short-chain fatty acids (SCFAs), which can improve intestinal uptake of micronutrients. It is important to note that vitamin production varies among probiotic strains and can be influenced by factors such as the fermentation substrate, pH, and co-culturing with other beneficial microorganisms, all of which affect the overall yield. The major mechanisms underlying probiotic-mediated enhancement of nutrient bioavailability are schematically illustrated in Figure 1.

3.1. Thiamine (Vitamin B1)

Thiamine, also known as vitamin B1, acts as a cofactor for several enzymes involved in energy metabolism and plays a vital role in maintaining neurological health (Bedani et al., 2024; Fattal-Valevski, 2011). Its dietary requirement for healthy adults is generally between 1.0 and 1.5 mg per day, depending on caloric intake (Nutrients et al., 2000). Thiamine is naturally found in foods such as whole grains, cereals, bread, legumes, nuts, brown rice, and meats. Insufficient thiamine intake can lead to clinical conditions including dry and wet beriberi, peripheral neuropathy, lactic acidosis, and Wernicke–Korsakoff syndrome.

Several probiotic and non-probiotic bacterial strains have demonstrated the ability to produce thiamine. Notable examples include *Lactobacillus sanfranciscensis*, *L. reuteri* ATCC 55730, *L. plantarum* WCFS1, *Bifidobacterium bifidum*, *L. rhamnosus*, *Streptococcus thermophilus* ST5, *L. helveticus* R0052, and *B. longum* R0175 (Champagne et al., 2010; LeBlanc et al., 2017; Saulnier et al., 2011; Vogel et al., 2011).

Interestingly, *L. plantarum* WCFS1 is also capable of producing thiamine despite missing several genes typically associated with this pathway. This strain possesses orthologous genes, such as MoaD and MoeE, which may compensate for missing reactions and support thiamine biosynthesis (Magnúsdóttir et al., 2015).

Experimental studies have confirmed the impact of probiotics on thiamine content in fermented foods. For instance, (Hou et al., 2000) reported that after 48 hours of milk fermentation, thiamine levels increased from 0.33 mg/100 mL to 0.38 mg/100 mL with *B. infantis* and to 0.37 mg/100 mL with *B. longum*. Similarly, (Fabian et al., 2008) observed that consuming probiotic or

conventional yogurt daily for two weeks elevated plasma levels of vitamins B1 and B2 in healthy women. Additionally, (Yang & Zhang, 2009) found that fermentation of *Ganoderma lucidum* enhanced both thiamine and niacin content, highlighting the role of microbial metabolism in vitamin enrichment.

Although most studies consistently report that probiotic fermentation enhances thiamine content, the extent of vitamin B1 production varies considerably among probiotic strains and food matrices. These differences are largely attributed to strain-specific metabolic pathways, substrate composition, fermentation conditions, and interactions with the resident microbiota. Recent evidence also suggests that the ability of probiotics to improve vitamin bioavailability depends not only on microbial biosynthesis but also on modulation of gut microbial ecology and the production of short-chain fatty acids, which facilitate intestinal nutrient absorption (Batta et al., 2024; Bermúdez-Humarán et al., 2024). Furthermore, the limited number of comparative studies conducted under standardized experimental conditions makes it difficult to identify the most efficient probiotic strains for vitamin B1 biofortification. Therefore, future investigations should employ harmonized methodologies and directly compare probiotic strains across different food matrices to improve the translational potential of these findings (Bedani et al., 2024; Bermúdez-Humarán et al., 2024).

3.2 Riboflavin (Vitamin B2)

Riboflavin (vitamin B2) is an essential nutrient that serves as a precursor for coenzymes vital to human metabolism (Bedani et al., 2024; Dricot et al., 2024). The recommended daily intake is approximately 1.3 mg for men and 1.1 mg for women (Nutrients et al., 2000). Riboflavin is converted in the body into flavin mononucleotide (FMN) and flavin adenine dinucleotide (FAD), which act as coenzymes for flavoproteins involved in electron transport and other metabolic reactions (Massey, 2000).

Humans obtain riboflavin through dietary sources as well as microbial production by gut microbiota. Various bacteria, including *Bacillus subtilis*, *Escherichia coli*, *Lactococcus lactis*, *Lactobacillus plantarum*, *Leuconostoc mesenteroides*, and *Propionibacterium freudenreichii*, and some fungi, such as *Ashbya gossypii*, *Candida famata*, and *Eremothecium* (Ascomycetes), are capable of riboflavin synthesis ((Bacher et al., 2000; Burgess et al., 2006; Ibrahim et al., 2015).

In microbial biosynthesis, guanosine-5′-triphosphate (GTP) and ribulose-5-phosphate act as primary precursors. The enzyme encoded by the *ribA* gene in *B. subtilis* and *E. coli* converts GTP to 2,5-diamino-6-(ribosylamino)-4(3H)-pyrimidinone-5′-phosphate, which is further processed into riboflavin. Subsequently, *ribC* in *B. subtilis* and *ribF* in *E. coli* convert riboflavin into FMN and FAD, supporting redox reactions and overall metabolic regulation (Mack et al., 1998).

In lactic acid bacteria (LAB), a rib operon containing four genes (*ribH*, *ribA*, *ribB*, and *ribG*) orchestrates riboflavin production (Ibrahim et al., 2015). These genes encode enzymes that sequentially convert nucleotide precursors into riboflavin and its active coenzymes, maintaining cellular redox balance.

Regulatory mechanisms differ between bacterial types: Gram-positive bacteria mainly use transcriptional attenuation, whereas Gram-negative bacteria control riboflavin synthesis at the translation initiation stage (Bermúdez-Humarán et al., 2024; Hübenthal & Mack, 2025). These variations reflect the evolutionary diversity in riboflavin biosynthesis among microbial species.

Thakur and Tomar, 2015 reported that *Lactobacillus fermentum* KTLF1 and *L. plantarum* produced riboflavin at concentrations of approximately 2.36 mg/L and 2.13 mg/L, respectively, when cultured in MRS medium (Thakur & Tomar, 2015). Similarly, Guru & Viswanathan, 2013 observed that *L. acidophilus* generated higher levels of riboflavin compared to *Lactococcus lactis*, suggesting that whey serves as a more effective fermentation substrate than skim milk for maximizing vitamin B2 production (Guru & Viswanathan, 2013). Del Valle et al. (2014) evaluated 179 lactic acid bacteria (LAB) strains for their ability to increase riboflavin content in soymilk (Del Valle et al., 2014). Supporting these findings, Arena et al. (2014) reported overproduction of riboflavin in selected *Lactobacillus plantarum* and *L. fermentum* strains(Arena et al., 2014). Furthermore, Da Silva et al. (2016) demonstrated that LAB strains can simultaneously synthesize multiple B vitamins during milk fermentation, achieving an average of 138 ng/mL of total folate and 364 ng/mL of riboflavin in vitamin-free media (Da Silva et al., 2016). Del Valle et al. (2014) conducted a screening of 179 LAB isolates and found that only 42 strains were capable of growing after four successive passages in riboflavin-free media. From these, five high-performing strains-*L. fermentum* CRL 220 and CRL 345, *L. plantarum* CRL 725, *Streptococcus thermophilus* CRL 417, and *L. paracasei* subsp. *paracasei* CRL 76—were selected for soymilk fortification due to their superior riboflavin-producing capacity (Del Valle et al., 2014).In the current study, *L. plantarum* CECT 8328 and *L. fermentum* CECT 8448 exhibited substantially enhanced riboflavin production, generating 3.4-fold and 2.2-fold higher levels, respectively, compared to their non-roseoflavin-resistant counterparts. These results highlight the potential of probiotic LAB strains as effective natural biofactories for vitamin B2 enrichment in fermented food products(Massaro et al., 2025).

Although numerous studies have confirmed the ability of lactic acid bacteria to synthesize riboflavin, considerable variability exists in vitamin B2 production among different probiotic strains. Lactobacillus plantarum and L. fermentum generally exhibit superior riboflavin-producing capacities; however, their performance is strongly influenced by the fermentation substrate, environmental conditions, and genetic background of the strains. Moreover, most available studies have focused on in vitro fermentation models, while clinical evidence demonstrating enhanced riboflavin bioavailability in humans remains limited. Future studies should therefore emphasize standardized comparative evaluations and well-designed human intervention trials to establish the translational significance of riboflavin-producing probiotics (Bermúdez-Humarán et al., 2024; Dricot et al., 2024).

3.3. Niacin (Vitamin B3)

Niacin, also known as vitamin B3, is an essential nutrient that serves as a precursor for coenzymes crucial to human metabolism. The recommended daily intake is approximately 41 mg for men and 27 mg for women. Niacin is converted into nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP), which are key coenzymes involved in multiple oxidation–reduction reactions, facilitating the transfer of electrons and protons within cells. Although niacin can be synthesized from the essential amino acid L-tryptophan, this endogenous pathway is relatively inefficient and heavily influenced by dietary protein intake. Among water-soluble vitamins, niacin is highly stable, resisting heat, oxygen, and oxidative conditions, but it can be degraded under extreme acidic or alkaline environments. Several studies have shown that probiotic fermentation can enhance niacin content in foods. For example, Tolouie et al. (2013) reported that probiotic yogurt contained higher levels of niacin compared to conventional yogurt (Tolouie & Toloun, 2013). Similarly, Rekha (2010) observed a significant increase in vitamin B3 during the fermentation of soymilk by probiotic strains,

indicating that microbial activity plays an important role in niacin biosynthesis and enrichment in fermented food products (Rekha, 2010).

3.4. Pantothenic Acid (Vitamin B5)

Pantothenic acid (PA), commonly referred to as vitamin B5, is a crucial nutrient that forms part of coenzyme A (CoA) and the acyl carrier protein (ACP), both essential for a wide range of cellular metabolic processes. Present in all living cells, pantothenic acid plays a central role in energy metabolism (Bedani et al., 2024). The recommended daily intake for adults is generally between 5 and 20 mg. Among the isomers of pantothenic acid, only the D-form exhibits biological activity. Functionally, pantothenic acid participates in numerous biochemical reactions, particularly those involved in energy release from carbohydrates, fatty acids, and amino acids. It is widely available in foods such as meat, kidneys, egg yolk, fruits, vegetables, and yeast, providing both animal- and plant-based dietary sources. Microbial production of pantothenic acid has been observed for nearly a century. Early research indicated that PA levels increase during fermentation and food ripening, largely due to de novo synthesis by microorganisms (Pilevar et al., 2022; Ragaller et al., 2011). These observations emphasize the potential of microbial metabolism to naturally enhance vitamin B5 content in fermented foods, suggesting probiotics and fermentation systems as effective strategies for nutritional fortification.

3.5. Pyridoxine (Vitamin B6)

Pyridoxine, commonly known as vitamin B6, serves as a critical cofactor for numerous enzymes, especially those involved in amino acid metabolism (Bedani et al., 2024). Its active form, pyridoxal-5′-phosphate (PLP), functions as a coenzyme in various enzymatic reactions including transamination, decarboxylation, and racemization. Vitamin B6 exists in three interconvertible forms (pyridoxal, pyridoxine, and pyridoxamine) differentiated by the C-4 substituent on the pyridine ring. This vitamin is broadly distributed in both plant- and animal-derived foods, though its levels can vary depending on processing and storage conditions. In a mixed diet, approximately 75% of vitamin B6 is bioavailable (Tarr et al., 1981). The recommended daily intake for adults is around 2 mg/day, while the tolerable upper intake limit is set at 100 mg/day. Vitamin B6 can be synthesized by a wide range of organisms, including bacteria, archaea, fungi, plants, and Plasmodium species. Two main biosynthetic pathways have been identified: the 1-deoxy-D-xylulose-5-phosphate (DXP)-dependent pathway and the DXP-independent pathway. The DXP-dependent pathway, initially characterized in *Escherichia coli*, involves seven enzymatic reactions divided into two branches. In the long branch, erythrose-4-phosphate is converted into 3-hydroxy-1-aminoacetone phosphate via the actions of erythrose-4-phosphate dehydrogenase (Epd), phosphoerythronate dehydrogenase (PdxB), 3-phosphoserine aminotransferase (SerC), and phosphohydroxy-L-threonine dehydrogenase (PdxA), using glutamate as a co-substrate. In the short branch, DXP synthase (Dxs) catalyzes the formation of DXP from pyruvate and glyceraldehyde-3-phosphate. Condensation of 3-hydroxy-1-aminoacetone phosphate with DXP is mediated by PNP synthase (PdxJ) to produce pyridoxine-5′-phosphate (PNP), which is subsequently oxidized by PNP oxidase (PdxH) to form the active PLP coenzyme (di Salvo et al., 2003). The DXP-independent pathway, identified later in fungi, plants, archaea, and Gram-positive bacteria such as *Bacillus subtilis*, relies on the PLP synthase enzyme complex, composed of PdxS and PdxT subunits. In *B. subtilis*, this complex synthesizes PLP directly from glutamine and either ribose-5-phosphate or ribulose-5-phosphate, combined with glyceraldehyde-3-phosphate or dihydroxyacetone phosphate (Strohmeier et al., 2006). Both biosynthetic pathways of vitamin B6 are closely linked with central metabolic networks, including glycolysis, the pentose phosphate pathway, and nitrogen metabolism, highlighting the

essential role of pyridoxal phosphate in cellular biochemical processes. The presence of two evolutionarily distinct mechanisms for synthesizing the same coenzyme emphasizes the biological significance and evolutionary conservation of PLP biosynthesis across diverse life forms (Bermúdez-Humarán et al., 2024; Fitzpatrick et al., 2010).

Several studies have explored the enhancement of vitamin B6 production through microbial engineering. For instance, soy fermentation using *Streptococcus thermophilus* ST5, *Lactobacillus helveticus* R0052, or *Bifidobacterium longum* R0175 showed minor increases in thiamine and pyridoxine levels, though these changes were not statistically significant (Champagne et al., 2010)). In another approach, overexpressing the *pdxST* genes from *Bacillus subtilis* in *E. coli* via a plasmid led to production of up to 61 mg/L of B6 vitamers (Quinn, 2020).

3.6. Folate (Vitamin B9)

Folate, also referred to as vitamin B9, comprises a group of biologically active compounds related to folic acid. The recommended daily intake for folate is estimated to be between 170 and 300 µg per day (Bedani et al., 2024; Kariluoto et al., 2006). Folate is essential for the synthesis of purines, pyrimidines, and certain amino acids, thereby supporting DNA replication and cell growth (Kariluoto et al., 2006). Natural dietary sources of folate include milk and other dairy products, although heat treatments such as pasteurization can significantly reduce their folate content. Whole-grain foods also provide folate, and fermentation processes—such as sourdough preparation using yeasts—can enhance folate levels, although some loss occurs during subsequent cooking or baking (Kariluoto et al., 2006; Kariluoto et al., 2004). This has spurred interest in using folate-producing probiotic strains to naturally fortify fermented foods (Scott & Roessner, 2007).

Several microorganisms are capable of de novo folate synthesis, including bacterial species such as *Lactococcus lactis*, *Bacillus subtilis*, *Lactobacillus plantarum*, *Bifidobacterium longum*, *L. acidophilus*, *L. bulgaricus*, and *Streptococcus thermophilus*, as well as yeasts like *Candida milleri*, *Saccharomyces cerevisiae*, and *Torulaspora delbrueckii* (Kariluoto et al., 2006; Lin & Young, 2000)The stability of folate in fermented dairy products may vary during storage. For example, after two weeks at refrigeration temperature, folate content decreased by approximately 27% in milk fermented with *L. bulgaricus* 449 and by about 8% in milk containing *L. acidophilus* ATCC 4356. Optimal folate production by lactic acid bacteria (LAB) generally occurs at 37 °C over 6 hours in reconstituted milk; however, LAB can both produce and consume folate, and at lower temperatures (e.g., 4 °C), consumption may exceed synthesis (Lin & Young, 2000).

Crittenden et al. (2003) demonstrated that *Streptococcus thermophilus* could increase folate levels in skim milk nearly fourfold (Crittenden et al., 2003), whereas Sybesma et al. (2003) highlighted that pH strongly affects folate biosynthetic activity (Sybesma, Starrenburg, Tijsseling, et al., 2003). Conversely, some studies reported that certain *Lactobacillus* starter cultures did not significantly modify folate concentrations in fermented milk (Crittenden et al., 2003). Additional studies have shown that both *Lactobacillus helveticus* MTCC 5463 (a probiotic strain) and *Lactobacillus rhamnosus* MTCC 5462 (a non-probiotic strain) can elevate folate levels in fermented milk, whether applied individually or together (Crittenden et al., 2002; Goswami, 2012). Furthermore, co-fermentation of *Saccharomyces cerevisiae* ALKO 743 with *Candida milleri* CBS 8195 in a water–flour mixture resulted in the highest folate production, indicating a synergistic interaction between the two yeast species (Kariluoto et al., 2006; MIRZA et al., 2022).

While *Lactobacillus bulgaricus* has been reported to produce folate under certain conditions (Kariluoto et al., 2006; Lin & Young, 2000), earlier studies suggested that this species primarily consumes folate rather than synthesizing it. Similarly, most *Lactobacillus* species lack the capacity for folate biosynthesis, with *Lactobacillus plantarum* being a notable exception (Sybesma, Starrenburg, Tijsseling, et al., 2003). Variations in folate production among studies are likely due to differences in strain-specific metabolism, growth conditions, and the composition of the culture medium (Kariluoto et al., 2006). For example, higher pH values and supplementation with p-aminobenzoic acid (pABA) enhance folate synthesis, whereas addition of tyrosine can inhibit it (Sybesma, Starrenburg, Tijsseling, et al., 2003).

In addition to folate, certain *Lactobacillus reuteri* strains are capable of producing cobalamin (vitamin B12). Specifically, *L. reuteri* CRL1098 synthesizes cobalamin, while *L. reuteri* JCM1112 can generate both folate and cobalamin, with an approximate folate-to-cobalamin mass ratio of 170:1 (Santos et al., 2008).

Folate biosynthesis begins with the attachment of a pteridine molecule to p-aminobenzoic acid (pABA) (Burgess et al., 2009). The production of dihydrofolate requires glutamate and pABA as essential precursors. In *Lactococcus lactis* and *Bacillus subtilis*, formation of the pyrophosphate ester from 6-hydroxymethylneopterin is catalyzed by a bifunctional enzyme and FolK, respectively (Perkins & Pero, 2001). Additionally, in *Lactococcus lactis*, the presence of pabBC genes along with pABA further promotes folate synthesis (Wegkamp et al., 2007)

Folate biosynthesis generally proceeds through the transformation of GTP into tetrahydrofolate (THF) via two key reactions (McConkey et al., 2004):

The condensation of p-aminobenzoic acid (pABA) with 2-amino-4-hydroxy-6-hydroxymethyl-7,8-dihydropteridine, forming dihydropteroate.

- The subsequent reaction of dihydropteroate with glutamate, resulting in the production of dihydrofolate.
- The enzymes PabA, PabB, and PabC are critical for synthesizing pABA. Studies have confirmed that *Lactococcus lactis* contains these pab genes along with several folate biosynthesis genes, including folA, folB, folKE, folP, ylgG, and folC, as identified in the *L. lactis* MG1363 strain (Wegkamp et al., 2007).

Folate production profiles differ among lactic acid bacteria species. For instance, *Lactococcus lactis* predominantly generates 5,10-methenyl-THF and 10-formyl-THF, whereas *Streptococcus thermophilus* mainly produces 5,10-methenyl-THF and 5-formyl-THF (Sybesma, Starrenburg, Kleerebezem, et al., 2003).

In food analysis, folate content is commonly measured by quantifying tetrahydrofolate, 5-methyltetrahydrofolate, and 5-formyltetrahydrofolate. Among these forms, THF plays a central role in DNA synthesis, while 5-methyltetrahydrofolate serves as the primary storage form of folate in humans and is abundant in vegetables, fruits, and dairy products (Lin & Young, 2000).

The available evidence indicates that probiotic-mediated folate production is highly strain-dependent and cannot be generalized across all lactic acid bacteria. While Lactobacillus plantarum, Lactococcus lactis, and selected Streptococcus thermophilus strains have demonstrated promising folate-producing capacities, other strains may consume rather than synthesize folate. These inconsistencies emphasize the importance of strain selection, fermentation parameters, and food matrix characteristics. Furthermore, despite encouraging in vitro findings, robust human clinical evidence confirming improved folate bioavailability remains insufficient. Future research should integrate metabolomic and microbiome-based

approaches to better understand strain-specific folate metabolism and its nutritional implications (Bermúdez-Humarán et al., 2024; Dehghani et al., 2025).

3.7. Cobalamin (Vitamin B_{12})

Cobalamin, commonly known as vitamin B_{12}, It primarily exists in two biologically active forms: methylcobalamin and adenosylcobalamin, both of which act as essential cofactors in enzymatic reactions. These forms are among the most structurally complex vitamins known (Martens et al., 2002). During industrial production, the methyl or adenosyl groups are replaced with a cyano group to form cyanocobalamin, the form most frequently used commercially (Raux et al., 2000).The detailed structures of cobalamin have been extensively characterized. Structurally, cobalamin contains a central cobalt atom within a corrin ring, composed of three main components: cobinamide, 5,6-dimethylbenzimidazole (DMB), and the linkage connecting cobinamide and DMB (Warren et al., 2002; Jeter et al., 1984).

In natural sources, vitamin B_{12} is found in foods containing cobalamin-producing bacteria, in tissues of animals that consume such foods, and within the gut microbiota of animals (Basu & Dickerson, 1996; Dehghani et al., 2025). The recommended daily intake for humans is approximately 1–2 µg/day.

The biosynthesis of adenosylcobalamin occurs via two distinct pathways, depending on oxygen availability: an aerobic pathway that requires oxygen and an anaerobic pathway that does not (Roessner and Scott, 2006). Various bacterial species have been identified as cobalamin producers, including lactic acid bacteria, *Salmonella typhimurium*, *Bradyrhizobium japonicum*, *Pseudomonas denitrificans*, *Klebsiella pneumoniae*, *Propionibacterium freudenreichii*, *Nocardia* spp., *Bacillus megaterium*, *Citrobacter freundii*, and *Streptococcus sanguinis* (Santos et al., 2008). However, many lactic acid bacteria cannot synthesize cobalamin de novo (Deguchi & Morishita, 1992). Certain probiotic strains, such as *Lactobacillus reuteri* CRL1098, are capable of producing B_{12} independently, highlighting their potential use in fortified fermented foods (Taranto et al., 2003)

Cobalamin production in *L. reuteri* is influenced by the culture medium and availability of substrates. The presence of glycerol, which acts as a hydrogen acceptor, and the absence of specific amino acids like cysteine, enhance B_{12} biosynthesis (Daniel et al., 1998). For example, supplementing the medium with glycerol increased B_{12} output by approximately fivefold in *L. reuteri* 8 (Santos, 2008). The bacterium requires eight amino acids—alanine, aspartate, cysteine, glycine, isoleucine, proline, lysine, and serine—with glycerol supplementation increasing glycine demand. Interestingly, removing certain amino acids (aspartate, glycine, alanine, lysine) can also boost cobalamin production even without glycerol.

Mechanistically, glycerol is converted into 3-hydroxypropionaldehyde via the enzyme glycerol dehydratase, which depends on 5′-deoxyadenosylcobalamin (AdoCbl). This intermediate is further reduced to 1,3-propanediol by 1,3-propanediol:NAD oxidoreductase. *L. reuteri* synthesizes AdoCbl to facilitate glycerol metabolism and possesses all necessary genes for cobalamin biosynthesis (Daniel et al., 1998; Santos, 2008). The CRL1098 strain expresses cob genes encoding key enzymes such as CobA, CbiJ, and CbiK, essential for B_{12} production (Taranto et al., 2003). However, under anaerobic conditions, *Lactobacillus reuteri* can produce pseudo-vitamin B_{12}, a form that is biologically inactive in humans. The primary distinction between cobalamin and pseudo-vitamin B_{12} lies in the α-ligand of the molecule: in cobalamin, 5,6-dimethylbenzimidazole (DMB) is attached to the C-1 position of ribose via an α-glycosidic bond, whereas in pseudo-vitamin B_{12}, adenine replaces DMB due to the absence of oxygen and incomplete conversion of riboflavin to DMB (Taga & Walker, 2008).

To enhance the production of active cobalamin and reduce pseudo-vitamin B_{12} formation, Mohammed et al. (2014) demonstrated that the addition of δ-aminolevulinic acid (ALA) at the initial stage of the biosynthetic pathway, along with the overexpression of *hemA* and *hemL* genes, significantly improves cobalamin synthesis (Mohammed et al., 2014). Furthermore, supplementation with DMB under aerobic conditions promotes the generation of biologically active B_{12}. In strictly anaerobic bacteria, the conversion of adenosyl-GDP- cobinamide to active cobalamin requires substitution with α-ribazole, which consists of DMB linked to ribose (Escalante-Semerena, 2007; Ibrahim et al., 2015).

3.8. Vitamin K

Vitamin K is a crucial fat-soluble vitamin present in several dietary forms. In plants, it predominantly exists as phylloquinone, while in bacteria and animals, it is mainly found as menaquinones (MKs) (Bedani et al., 2024; Conly & Stein, 1992). This vitamin is essential for the post-translational modification of proteins, including the generation of γ-carboxyglutamic acid residues, which are critical for calcium binding and proper blood clotting.The recommended daily intake of vitamin K is roughly 1 μg per kg of body (Morishita et al., 1999).

Bacteria produce menaquinones through two separate biochemical pathways. In lactic acid bacteria (LAB), commonly used in industrial fermentation, the naphthoquinone ring is synthesized from chorismate, a product of the shikimate pathway, via enzymes encoded by the men genes. The isoprenoid side chain is synthesized independently and then linked to the naphthoquinone ring to form demethylmenaquinone (DMK), which is subsequently methylated to generate the final menaquinone structure. The structure and diversity of MKs are influenced by bacterial species and growth conditions. Modifications often include demethylation of the naphthoquinone ring, partial saturation of the isoprenoid chain, and conversion between MK and DMK. Typically, Gram-positive bacteria mainly produce MKs, whereas Gram-negative bacteria can generate MKs, DMKs, and ubiquinones (Collins & Jones, 1981).

Within LAB, strains such as Leuconostoc lactis YIT 3001, Lactococcus lactis ssp. cremoris YIT 2007, 2011, 2012, and L. lactis ssp. lactis YIT 2016, 2027 have been identified as potent menaquinone producers (Morishita et al., 1999). The most abundant menaquinone types in LAB, *Bacillus*, and some anaerobic bacteria are MK-7 to MK-10 (Ramotar et al., 1984). Kim et al. (2011) reported that *Lactobacillus fermentum* LC272 produced vitamin K_2 at 184.94 μg/L in Rogosa medium and 63.93 μg/L in reconstituted skim milk, highlighting its potential for K_2-enriched fermented products (Kim et al., 2011). Moreover, Enterobacter agglomerans, Serratia marcescens, and Enterococcus faecium, isolated from neonatal gut flora, were also capable of synthesizing various MK forms (Cooke et al., 2006). In another study, *Bacillus subtilis* strains from traditional Japanese natto produced vitamin K_2, reaching a maximum of 35 mg/L after 4 days of fermentation. The dominant producer of vitamins by probiotic bacteria in presented in Table 1.

Insert Table 1

4. The effects on minerals:

Minerals are vital nutrients required for maintaining overall health and supporting a variety of physiological processes. They are essential for the proper functioning of bones, muscles, heart, and brain, and they also play a key role in the production of enzymes and hormones (Anaya et al., 2025; Balch, 2006; Mondal et al., 2024; Napiórkowska-Baran et al., 2025). Certain probiotic bacteria produce phytase enzymes, which break down phytate, a compound that binds minerals and reduces their absorption. By hydrolyzing phytate in cereals and legumes, these microorganisms improve the bioavailability of essential minerals, including calcium, iron, zinc,

and magnesium. Clinical evidence suggests that probiotics such as *Lactobacillus plantarum* and *Lactobacillus reuteri* can increase serum ferritin levels and enhance bone mineral density in humans.

Minerals are commonly classified into major (macro) minerals and trace (micro) minerals. Major minerals include calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), chloride (Cl), phosphorus (P), and sulfur (S), whereas trace minerals consist of iodine (I), zinc (Zn), selenium (Se), iron (Fe), manganese (Mn), copper (Cu), cobalt (Co), molybdenum (Mo), fluoride (F), chromium (Cr), and boron (B) (McClure, 2008). The body requires macro-minerals in amounts exceeding 100 mg/day, while trace minerals are needed in quantities below 100 mg/day (Hamidpour et al., 2017; Manini, 2015).

Many minerals serve structural and functional roles in the body. For example, calcium, phosphorus, and fluoride are important components of teeth, whereas calcium, magnesium, manganese, phosphorus, boron, and fluoride contribute to bone structure. Trace minerals such as copper, iron, manganese, magnesium, selenium, and zinc act as cofactors in enzymatic reactions, while major minerals including calcium, magnesium, phosphorus, sodium, and potassium are involved in nerve impulse transmission. Additionally, trace elements support processes such as red blood cell formation (Co, I, Fe), glucose metabolism (Cr), and antioxidant defense (Mo). Major minerals like calcium and potassium play a role in blood pressure regulation, and several minerals, including Ca, Mg, Cu, Se, and Zn, are crucial for immune function, whereas others like Cr and Mn contribute to neurological activity (Gharibzahedi & Jafari, 2017).

Mechanisms of Mineral Bioavailability Enhancement by Bacteria

Bacteria enhance the bioavailability of minerals through several mechanisms, including:

- Increasing mineral solubility by producing short-chain fatty acids (SCFAs).
- Hydrolyzing phytate via bacterial phytase enzymes.

Reducing intestinal inflammation, which indirectly supports improved bone mineral density. The major mechanisms involved in probiotic-mediated enhancement of mineral bioavailability are illustrated in Figure 2.

- Breaking glycosidic bonds in dietary compounds using enzymes produced by *Lactobacillus* and *Bifidobacterium* species.

Together, these actions promote greater absorption of both macro- and micro-minerals, ultimately improving nutritional status and overall health (Hamidpour et al., 2017; Manini, 2015). Effective probiotic bacteria on minerals in a variety of food products in presented in Table 2.

Insert Table 2

Multiple studies have demonstrated that mineral bioavailability can be substantially increased through probiotics, prebiotics, and fermentation processes. For example, Proulx and Reddy (2007) showed that adding small amounts of lactic acid to unfermented maize products enhanced iron absorption (Proulx & Reddy, 2007), while Sundberg (2011) emphasized the positive effect of probiotic and prebiotic supplementation on iron bioavailability (Sundberg, 2011).

Experimental and clinical research further indicates that diets enriched with probiotics improve absorption of calcium, phosphorus, and zinc (Abd El-Gawad et al., 2014). Rekha and Vijayalakshmi (2010) found that fermenting soymilk with lactic acid bacteria (LAB) and the yeast *Saccharomyces boulardii* increased the bioavailability of iron, calcium, magnesium, and zinc (Rekha, 2010). In addition, Darío Pérez-Conesa et al. (2006) evaluated infant formulas supplemented with probiotics (*Bifidobacterium bifidum* and *Bifidobacterium longum*), prebiotics,

or synbiotics, observing enhanced absorption of calcium, magnesium, and phosphorus in rat models. Probiotics, mainly lactic acid-producing bacteria from *Lactobacillus* and *Bifidobacterium* genera, can modulate gut microbiota composition and metabolic activity, further supporting nutrient absorption (Dehghani et al., 2025; Pérez-Conesa et al., 2006). Recent evidence highlights that lactic acid produced by probiotics facilitates the uptake of trace minerals and proteins, particularly in plant-based diets. Infant formulas enriched with probiotics or prebiotics have been shown to significantly improve Ca, Mg, and P bioavailability in rats. Additionally, Manini et al. (2015) reported that LAB strains isolated from wheat bran sourdough with phytate-degrading capabilities can be effectively used to increase mineral bioavailability in food products (Manini, 2015).

The enhancement of mineral bioavailability by probiotics is mediated through several complementary mechanisms. Organic acid production decreases intestinal pH, thereby increasing the solubility of minerals such as iron, calcium, and zinc. In addition, phytase-producing probiotic strains hydrolyze phytic acid, reducing its mineral-chelating activity and improving mineral absorption. Probiotics may also strengthen intestinal barrier function and modulate the gut microbiota, creating a favorable environment for mineral transport and utilization. These mechanisms act synergistically and are influenced by strain characteristics, fermentation conditions, and food matrix composition (Bermúdez-Humarán et al., 2024; Dehghani et al., 2025).

Although substantial evidence supports the beneficial role of probiotics in improving mineral bioavailability, the magnitude of these effects differs according to probiotic strain, mineral type, dietary matrix, and host-related factors. Current evidence suggests that phytase production, organic acid synthesis, and modulation of intestinal microbiota collectively contribute to enhanced mineral absorption; however, the relative contribution of each mechanism remains incompletely understood. Moreover, most mechanistic studies have been performed in animal models or in vitro systems, highlighting the need for well-controlled human clinical trials to validate these findings and identify the most effective probiotic strains for mineral biofortification (Anwer & Wei, 2024; Bermúdez-Humarán et al., 2024).

In addition to phytase-mediated phytate degradation, probiotics improve mineral bioavailability through the production of organic acids and short-chain fatty acids, which reduce intestinal pH and increase mineral solubility. The extent of these effects depends on probiotic strain, food matrix composition, fermentation conditions, and host physiological characteristics. Therefore, optimization of these factors is essential to maximize mineral absorption in functional foods (Anwer & Wei, 2024; Bermúdez-Humarán et al., 2024).

5. The effects on phenolic metabolites

Phenolic compounds, a broad group of plant-derived bioactive molecules, play a significant role in human health. Variations in the C-ring structure of these compounds generate major flavonoid subclasses, including flavonols, flavones, flavanones, flavanols, isoflavones, and anthocyanidins. These phenolics are abundant in plant-based foods and contribute to sensory characteristics such as flavor, astringency, and color. Common methods for extracting bioactive compounds from natural sources include solid–liquid extraction, supercritical fluid extraction, high-pressure processing, microwave-assisted extraction, and ultrasound-assisted extraction (Cortazar et al., 2005; Markom et al., 2007; Wang & Weller, 2006). Recently, fermentation-based techniques have gained popularity as an alternative for producing and enriching phenolic compounds, providing high-quality extracts with potent bioactivity while avoiding the potential toxicity of

organic solvents. Phenolic compounds demonstrate a wide spectrum of health benefits, including cardiovascular protection, antioxidant activity, anti-mutagenic, anti-allergenic, anti-inflammatory, and antimicrobial effects (Dudonné et al., 2015; Méndez-Galarraga et al., 2025; Parvathy et al., 2009). The major pathways involved in probiotic-mediated biotransformation of phenolic compounds and the subsequent enhancement of their bioavailability are illustrated in Figure 3.

Probiotics can biotransform phenolic compounds into more absorbable forms through microbial enzymes such as β-glucosidases and esterases, often producing aglycone derivatives with improved bioavailability and bioactivity. Moreover, combining probiotics with phenolic-rich prebiotics (e.g., grape seed extract, green tea catechins) has been shown to synergistically enhance gut microbiota diversity and function, potentially improving phenolic metabolism(Méndez-Galarraga et al., 2025). The bioavailability of phenolic compounds refers to the proportion of an ingested dose that reaches systemic circulation. While the plasma concentration of individual phenolics rarely exceeds 1 μM after consuming 10-100 mg, the total plasma phenolic content—including metabolites formed by colonic microbiota and tissue metabolism—is generally higher (Scalbert and Williamson, 2000). Overall, phenolic bioavailability is limited, with urinary excretion ranging from 0.3% for anthocyanins to 43% for isoflavones such as daidzin (Manach et al., 2005). The gut microbiota influences polyphenol bioavailability by modifying aglycones, glycosides, and conjugates such as O-glucuronides and O-sulfates (Kaprasob et al., 2017; Shen et al., 2018; Vamanu & Gatea, 2020). The dominant producer of phenolic metabolite by probiotic bacteria n presented in Table 3.

Insert Table 3

Several studies highlight the role of probiotics in improving phenolic bioavailability. For instance, *Lactobacillus johnsonii* LA1, *L. reuteri* SD2112, and *L. acidophilus* LA-5 increased free phenolic acid levels in whole grain barley and oat groat flours. Similarly, co-supplementation of cranberry with *Bacillus subtilis* CU1 enhanced phenolic absorption, likely by promoting the growth of phenolic-degrading bacteria in the gut (Dudonné et al., 2015). Microencapsulated probiotics such as *Bifidobacterium longum* R0175 have also been shown to increase flavanone bioavailability in orange juice (Pereira-Caro et al., 2015). Furthermore, lactic acid fermentation has been reported to improve flavonoid bioavailability, demonstrating the potential of fermentation to enhance the dietary intake of phenolic compounds (Zhao & Shah, 2016). Probiotic-mediated enhancement of phenolic bioavailability mainly depends on microbial enzymatic activities, including β-glucosidases, esterases, and phenolic acid decarboxylases, which convert complex polyphenols into smaller bioactive metabolites with improved intestinal absorption. The efficiency of these reactions is influenced by probiotic strain, substrate composition, and interactions with the gut microbiota. Consequently, the biological activity of phenolic compounds is determined not only by their initial concentration but also by microbial biotransformation occurring during fermentation and within the gastrointestinal tract (Kaprasob et al., 2017; Tomas et al., 2025; Zhao & Shah, 2016).

The effectiveness of probiotics in enhancing phenolic bioavailability is influenced by multiple factors, including the chemical structure of phenolic compounds, the food matrix, and the enzymatic capabilities of individual probiotic strains. Although numerous studies have demonstrated increased production of bioactive phenolic metabolites following fermentation, significant differences remain among microbial species and fermentation systems. Furthermore,

most available evidence originates from experimental studies, whereas clinical validation of the health benefits associated with probiotic-mediated phenolic biotransformation is still limited. Future investigations should combine metabolomics, gut microbiome profiling, and controlled human intervention studies to better elucidate the relationship between probiotic metabolism and phenolic bioavailability (Bermúdez-Humarán et al., 2024; Tomas et al., 2025).

Probiotic-mediated biotransformation of phenolic compounds is strongly influenced by microbial enzymatic activity, particularly β-glucosidases and esterases, as well as interactions with the food matrix. These enzymatic reactions increase the release of bioactive aglycones and low-molecular-weight phenolic metabolites with enhanced intestinal absorption and antioxidant activity. Nevertheless, significant strain-dependent variability exists, highlighting the need for comparative investigations under standardized experimental conditions (Bermúdez-Humarán et al., 2024; Kaprasob et al., 2017).

6. Factors influencing probiotic-mediated nutrient bioavailability

In addition to probiotic strain selection, several technological and environmental factors play critical roles in determining nutrient bioavailability. Fermentation conditions, including pH, temperature, fermentation time, oxygen availability, and substrate composition, strongly influence microbial growth, metabolic activity, and the synthesis of bioactive compounds. Optimizing these parameters is essential for maximizing vitamin production, phytase activity, and phenolic biotransformation.The composition of the food matrix also affects probiotic survival and functionality by providing nutrients, buffering capacity, and bioactive substrates while influencing the release and stability of micronutrients. Furthermore, co-culture strategies, involving combinations of probiotic bacteria with other beneficial microorganisms, may enhance metabolic interactions and improve nutrient production compared with monocultures.

Advances in food processing technologies, including controlled fermentation, high-pressure processing, and novel drying techniques, can further improve probiotic stability and nutrient retention. In addition, microencapsulation has emerged as an effective approach to protect probiotic cells during food processing, storage, and gastrointestinal transit, thereby enhancing their viability and functional performance.

Future research should integrate these technological approaches with strain selection to maximize probiotic-mediated nutrient bioavailability and facilitate the development of next-generation functional foods (Anwer & Wei, 2024; Bermúdez-Humarán et al., 2024). Summary of probiotic-mediated biotransformation of phenolic compounds and their health implications in presented in Table 4.

Insert Table 4

7. Conclusion and Future perspectives

This study emphasizes the capability of probiotic bacteria to be purposefully employed for the synthesis of bioactive and complex molecules, thereby improving the nutritional value of foods. By carefully choosing specific probiotic strains, fermented products can be naturally enriched with essential vitamins, offering an efficient strategy to enhance nutritional content and develop innovative vitamin-fortified functional foods. In addition, probiotics with high phytase activity can break down phytic acid during fermentation, which enhances the bioavailability of vital minerals and helps prevent deficiencies. The ability of probiotic strains to increase the absorption and effectiveness of phenolic compounds provides added nutritional and protective benefits,

while also supporting the natural preservation of foods through the generation of bioactive metabolites.

Despite the substantial progress achieved in understanding probiotic-mediated enhancement of nutrient bioavailability, several important knowledge gaps remain. Most available evidence is derived from in vitro experiments and animal studies, whereas well-designed human clinical trials remain limited. Furthermore, considerable variability exists among probiotic strains, food matrices, fermentation conditions, and host-related factors, making direct comparisons across studies challenging. Future research should focus on standardized experimental protocols, strain-specific mechanisms, and the integration of multi-omics technologies to better elucidate host–microbe interactions. In addition, emerging approaches such as engineered probiotics, artificial intelligence-assisted strain selection, postbiotics, and personalized nutrition offer promising opportunities for developing next-generation functional foods with enhanced nutritional value. Addressing these challenges will facilitate the translation of current scientific knowledge into practical dietary and industrial applications.

Recent advances in microbiome science and food biotechnology have opened new opportunities for improving nutrient bioavailability through next-generation probiotic approaches. One promising strategy is the development of engineered probiotics, in which targeted genetic modifications enhance microbial capabilities for vitamin biosynthesis, phytase production, and phenolic compound biotransformation. These engineered strains may provide more efficient and targeted nutritional interventions than conventional probiotics.

Another emerging area is the application of artificial intelligence (AI) and machine learning for probiotic strain discovery and selection. AI-based predictive models can integrate genomic, metabolomic, and phenotypic data to identify probiotic strains with superior functional properties, thereby accelerating the development of precision functional foods (Anwer & Wei, 2024)

In addition, increasing attention has been directed toward postbiotics, defined as preparations of inanimate microorganisms and/or their metabolites that confer health benefits to the host. Compared with live probiotics, postbiotics offer improved stability, safety, and shelf life while retaining many beneficial biological activities, making them attractive ingredients for functional food development (Salminen et al., 2021).

Finally, personalized nutrition represents an important future direction. Advances in gut microbiome profiling, metabolomics, and multi-omics technologies may enable the selection of probiotic interventions tailored to an individual's microbial composition, dietary habits, and health status. Such personalized strategies have the potential to maximize nutrient bioavailability and optimize health outcomes (Bermúdez-Humarán et al., 2024).

Overall, integrating synthetic biology, artificial intelligence, postbiotic technologies, and precision nutrition is expected to drive the next generation of probiotic-based functional foods and nutritional interventions.

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Table 1. The dominant producer of vitamins by probiotic bacteria

Vitamins	**Organisms**	**The dominant producer**	**Reference**
Thiamine	*B. infantis CCRC 14633 & B. longum B6*	-	(Hou et al., 2000)
Riboflavin	*Lactobacillus*, *streptococcus*, *Pediococcus*, and *Leuconostoc*. *Lactobacillus*	*Lactobacillus fermentum*	(Jayashree et al., 2010)
Riboflavin	*L. lactis* subsp. *cremoris* MG1363	-	(Burgess et al., 2009)

Cobalamin	*Lactobacillus reuteri* CRL1098	-	(Taranto et al., 2003)
Riboflavin-Folate	*Lactobacillus plantarum, Lactococcus lactis, Streptococcus thermophiles, Lactobacillus rhamnosus*	*Lac.lactis, Lb. plantarum*	(Ibrahim et al., 2014)
Riboflavin-Folate	*Lactobacillus plantarum, Streptococcus thermophilus*	-	(Ibrahim et al., 2015)
Folate	*Bifidobacterium longum* B6 and ATCC 15708, *Lactobacillus acidophilus* N1 and ATCC 4356, *Lactobacillus delbrueckii* ssp. *bulgaricus* 448 and 449, and *Streptococcus thermophilus* MC and 573	*Bifidobacterium longum* B6	(Lin & Young, 2000)
Folate	*Lactobacillus bulgaricus, Streptococcus thermophilus*, probiotic lactobacilli, *bifidobacteria, Enterococcus faecium*	*Streptococcus thermophilus*	(Crittenden et al., 2003)
Folate	*Candida milleri* CBS 8195, *Saccharomyces cerevisiae* TS 146, and *Torulaspora delbrueckii* TS 207, *Saccharomyces cerevisiae* ALKO 743	*Saccharomyces cerevisiae* ALKO 743 and *Candida milleri* CBS 8195	(Kariluoto et al., 2006)
Folate	*Lactococcus, Lactobacillus, Streptococcus* & *Leuconostoc*	*Lactococcus lactis*	(Sybesma, Starrenburg, Kleerebezem, et al., 2003)
Vitamin k	*Lactococcus, Lactobacillus, Enterococcus, Leuconostoc and Streptococcus*	-	(O'Connor et al., 2005)
Vitamin k	*Enterobacter agglomerans, Serratia marcescens and Enterococcus faecium*	-	(Cooke et al., 2006)
Menaquinones	*Lactococcus cremoris, Lactococcus lactis Leuconostoc lactis*	-	(Morishita et al., 1999)
B-group vitamins	*Lactobacillus acidophilus, Lactobacillus casei, Lactobacillus plantarum, Leuconostoc mesenteroides*, and *Bifidobacterium longum*	*Lb. acidophilus, Lb. casei*	(Kaprasob et al., 2018)
B1, Biotin, Pantothenic acid, B3, B6, B12, B9, B2	Various *Lactobacillus and Bifidobacterium* spp.	-	(Batta et al., 2024)
B9, B2, B12, B1, B6	Food-related lactic acid bacteria (LAB) and human gut commensals	Strain-dependent	(Bermúdez-Humarán et al., 2024)
(B1-B12)	Gut bacteria community cross-feeding	-	(Bedani et al.,

			2024)
B2, especially for women's health	Riboflavin-producing *Lactobacillus* strains	-	(Dricot et al., 2024)
K (MK-4 to MK-9)	*Lactobacillus, Bifidobacterium, Bacillus* (e.g., *B. subtilis natto*)	-	(Smajdor et al., 2023)
K2 via fermentation	*Lactococcus lactis* ssp. cremoris MG1363 engineered strains	-	(Bøe & Holo, 2020)

Table 2. Effective probiotic bacteria on minerals in a variety of food products

Mineral	**Organisms**	**product**	**Reference**
Selenium	*Lactobacillus sp., Bifidobacter sp., Streptococcus thermofilus*	yogurt	(Eszenyi et al., 2011)
Calcium, phosphorus, Zinc	*Bifidobacteria*	milk and soymilk yoghurts	(Abd El-Gawad et al., 2014)
Selenium and Zinc	*L. buchneri Lb26, B. lactis Bb1*		(Mogna et al., 2012)
Calcium	*L. acidophilus ATCC 4962, ATCC33200, ATCC 4356, ATCC 4461, L. casei ASCC 290, L. plantarum ASCC 276,* and *L. fermentum VRI-003*	calcium-fortified soymilk	(Tang et al., 2007)
Iron	*Lactobacillus acidofillus*		(Natanzi et al., 2017)
Calcium, Iron, Zinc, Selenium (review)	Various *Lactobacillus* spp., *Bifidobacterium* spp.	(general, gut interaction)	(Bielik & Kolisek, 2021)
Calcium (post-menopausal / T2D)	Multistrain probiotics (*L. plantarum, L. acidophilus, B. infantis, B. lactis*)	Clinical trials in humans	(Bermúdez-Humarán et al., 2024)
Calcium, Zinc, Iron (children)	Same multistrain combination	Pediatric pilot trial	(Bermúdez-Humarán et al., 2024)
Mineral-enriched Postbiotics (Se, Zn)	Mineral-enriched probiotic/postbiotic preparations (LAB)	(general/preclinical models)	(Dinu et al., 2022)
Micronutrient status (Ca, Zn, Fe, B12, folate)	Probiotic supplementation in healthy humans	Clinical trials (systematic review)	(Barkhidarian et al., 2021)
Iron & Calcium absorption (animal feeding)	Probiotics in broiler feeds	Animal model (chickens)	(Bermúdez-Humarán et al., 2024)

Table 3. The dominant producer of phenolic metabolite by probiotic bacteria

Phenolic metabolite	Organisms	References
kaempferol-glucoside	*Lactobacillus paracasei* A221	(Shimojo et al., 2018)
phenolic	*Bacillus subtilis* CU1	(Dudonné et al., 2015)
(poly)phenols	*B. longum* R0175	(Pereira-Caro et al., 2015)
Phenolic compounds	*Lactobacillus acidophilus*	(Shen et al., 2018)
flavonol glucosides	*Lactobacillus plantarum S1*	(Bisakowski et al., 2007)
Phenolic metabolites	*Lactobacillus plantarum*, *L. casei* and *L. acidophilus*	(Kaprasob et al., 2017)
flavan-3-ol derived metabolites	Newly identified *L. plantarum* strains (12 strains with enhanced production capabilities)	(Pulido-Mateos et al., 2024)
Phenolic acids from flavonoids/amino acids	Gut microbiota in general (producing phenolic acids from dietary substrates)	(Kiriyama et al., 2024)
Variability in (poly)phenol metabolism ("metabotypes")	Gut microbiota-generally including *Lactobacillus, Bifidobacterium, Gordonibacter, Ruminococcus* spp.	(Luo & Wang, 2025)
Flavonoid-gut microbiota interactions (prebiotic/duplibiotic effects)	General gut microbiota, including *Akkermansia muciniphila* (not necessarily probiotic)	(Rodríguez-Daza et al., 2021)

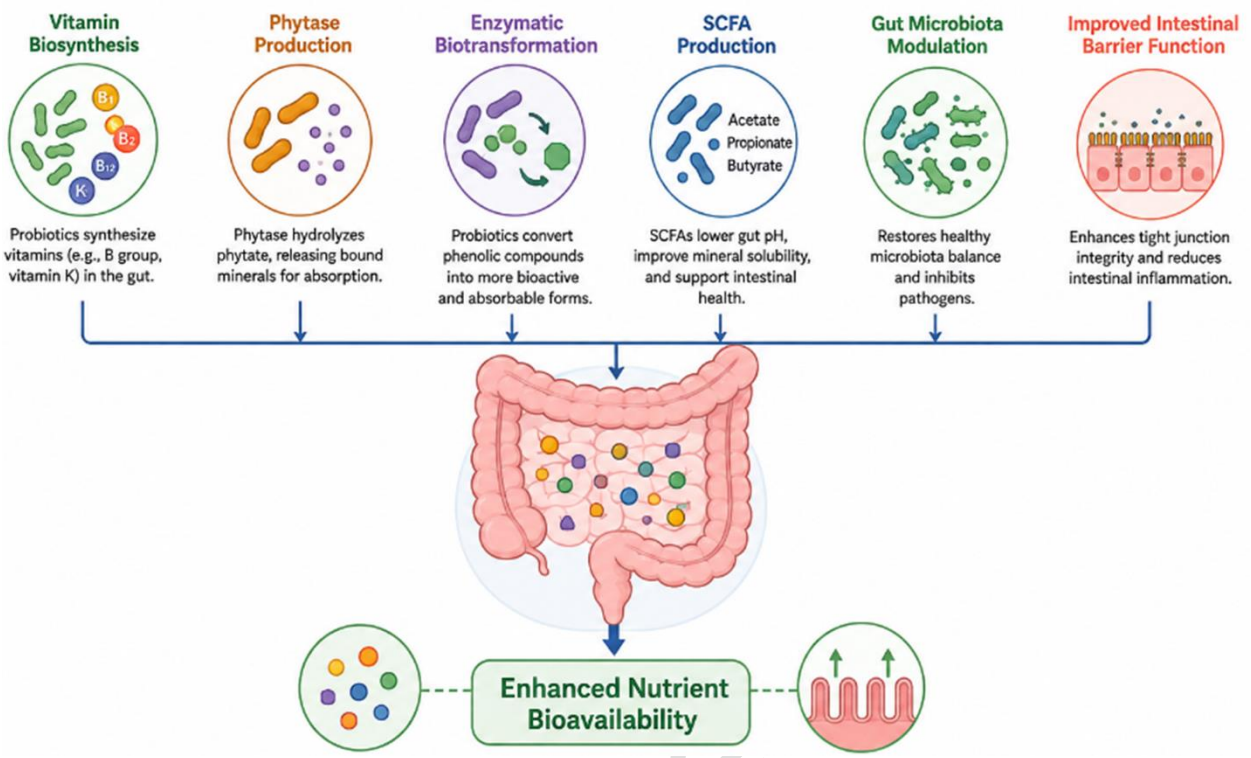

Figure 1. Mechanisms of probiotic-mediated enhancement of nutrient bioavailability

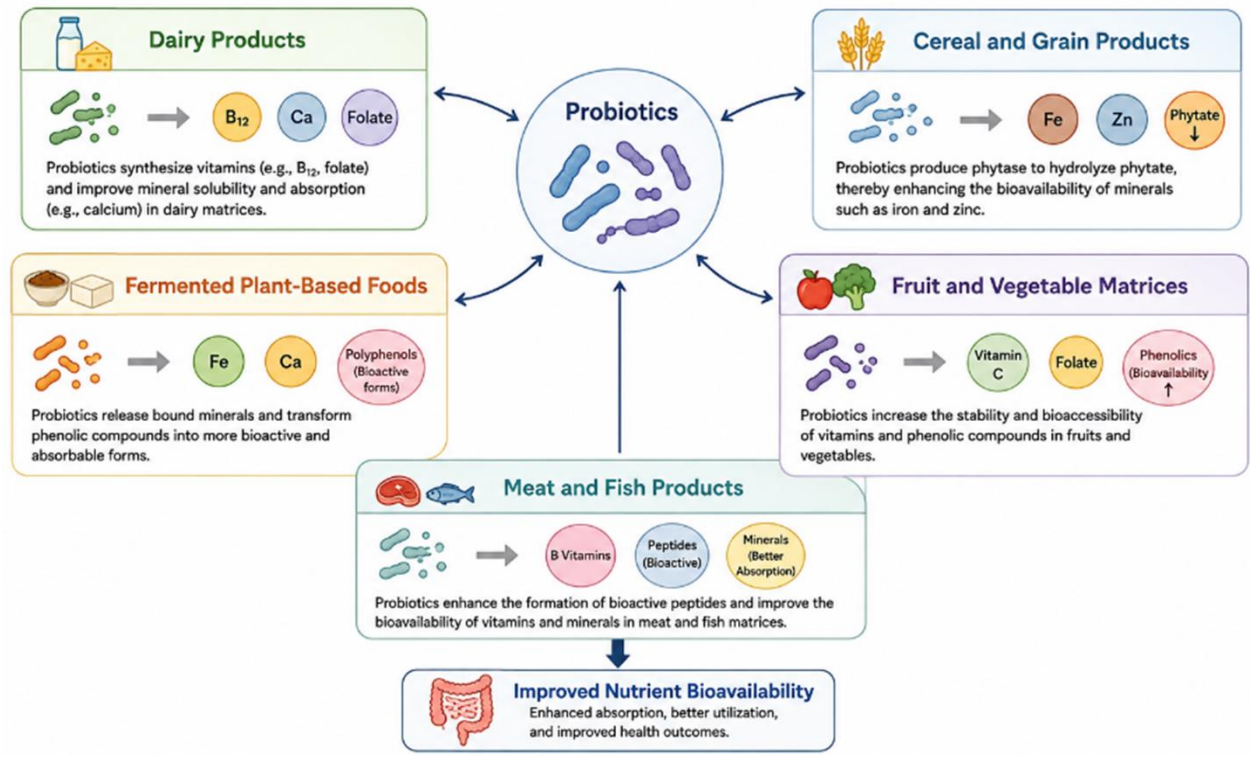

Figure 2. Effects of probiotics on vitamins, minerals and phenolic compounds and their bioavailability.

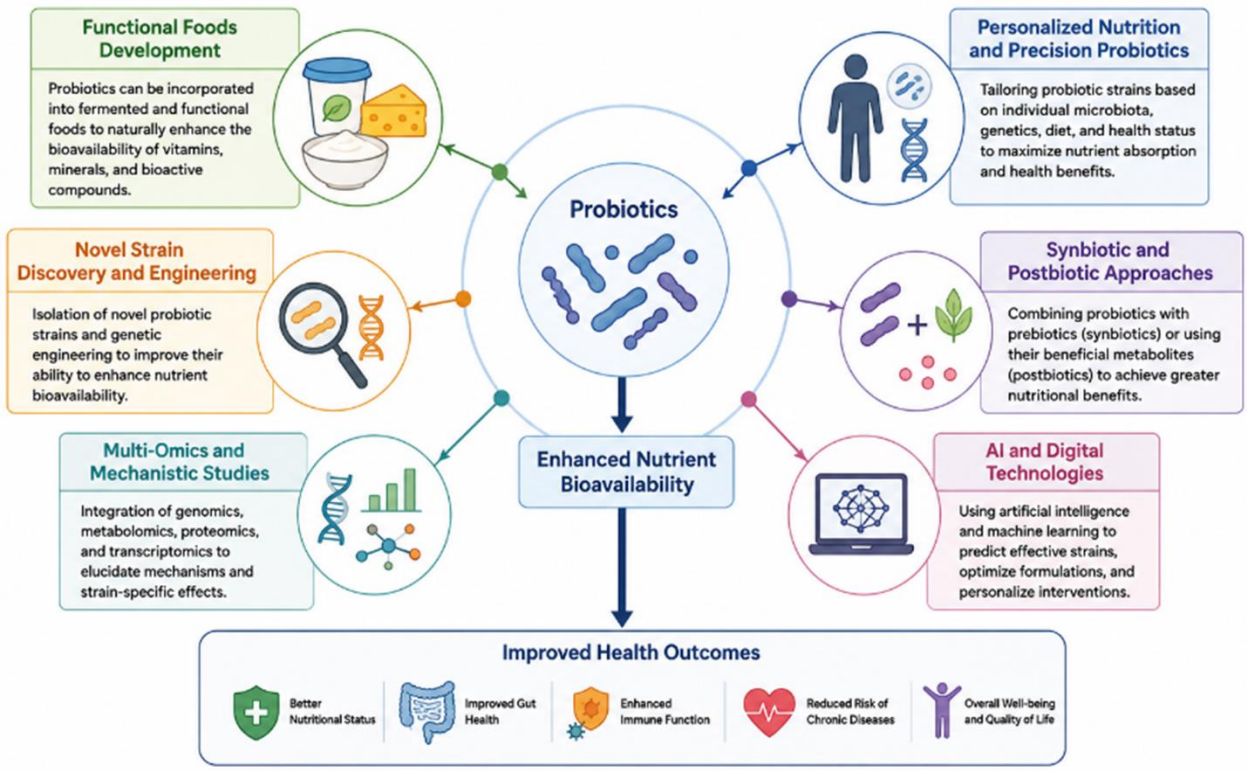

Figure 3. Future perspectives of probiotics in functional foods.

Table 4. Summary of probiotic-mediated biotransformation of phenolic compounds and their health implications

Phenolic compound	Probiotic strain(s)	Biotransformation mechanism	Main outcome	Reference
Flavanones (hesperidin, eriocitrin)	Lactobacillus plantarum, L. acidophilus, Bifidobacterium bifidum	β-Glucosidase-mediated deglycosylation	Increased release of aglycones and enhanced antioxidant activity	(Pereira-Caro et al., 2015; Zhao & Shah, 2016)
Isoflavones	Lactobacillus acidophilus LA-5, Bifidobacterium longum R0175	Hydrolysis of glycosidic bonds	Increased bioavailability and biological activity of isoflavone aglycones	(Zhao & Shah, 2016)
Phenolic acids	Lactobacillus	Esterase and	Increased release	(Dudonné et al.,

	johnsonii LA1, L. reuteri SD2112	phenolic acid metabolism	of free phenolic acids	2015)
Polyphenols from plant-based foods	Lactic acid bacteria (LAB)	Enzymatic biotransformation during fermentation	Enhanced bioaccessibility and antioxidant capacity	(Kaprasob et al., 2017; Vamanu & Gatea, 2020)
Dietary phenolics	Lactobacillus spp., Bifidobacterium spp.	Gut microbial metabolism	Formation of low-molecular-weight metabolites with improved intestinal absorption	(Dudonné et al., 2015; Pereira-Caro et al., 2015)