



## Review

# Fermentation of legumes as a strategy to enhance nutritional and sensory properties and modulate gut microbiome and human health

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## ARTICLE INFO

## Keywords:

Pulse  
Gut microbiome  
Sustainability  
Fermented foods  
Fermented legumes  
Host health

## ABSTRACT

Legumes represent a valuable and vegetable source of proteins and fiber with a very low environmental footprint production, therefore, both dietary guidelines and international agencies suggest increasing their production and consumption. Despite their favorable nutritional composition, they also naturally contain antinutritional factors such as phytic acid, that limit the absorption of micronutrients. This, coupled with the lower bioavailability of proteins as compared with meat, diminishes the biological and economic value of legumes. However, recent studies have shed a light on the power of fermentation to improve the protein profile of pulse and neutralize antinutritional compounds. In this review, we explore the benefits of legumes fermentation in depth, focusing on the role of microorganisms in enhancing the nutritional and sensory enhancement of legumes. Furthermore, we describe the properties and the microorganisms involved in the production of several craft-based fermented legumes typically consumed by non-Westernized populations, particularly delving into their effects on the gut microbiome and on the human health.

## 1. Introduction

Legumes hold a central place in global dietary patterns since they are rich in proteins (20–45%), complex carbohydrates (6–62%), dietary fiber (5–37%), healthy fats (1–6%), and important micronutrients such as calcium, potassium, phosphorus, copper, iron, and zinc (Amarowicz, 2020; Maphosa & Jideani, 2017). Additionally, legumes are also rich in bioactive compounds such as oligosaccharides and antioxidants (including polyphenols), which position them as promising ingredients for functional foods (Clemente & Olias, 2017). Nevertheless, the broader acceptability and utilization of legumes are still limited. A key limiting factor is the presence of anti-nutritional factors (ANFs) such as phytic acid, tannins, trypsin inhibitors, hemagglutinins, and non-digestible oligosaccharides, that bind with micronutrients (e.g., minerals including iron, copper and zinc) and reduce their bioavailability (Jeyakumar & Lawrence, 2022; Samtiya et al., 2020). In addition, legumes show sensory constraints linked to off-flavors, commonly described as beany, earthy, grassy, or metallic (Fischer et al., 2022; Malcolmson et al., 2014). Furthermore, legume proteins offer less desirable techno-functional properties compared with the animal counterpart, which can limit their utilization in food formulation

(Elzerman et al., 2011; Kyriakopoulou et al., 2021). To address these challenges, various processing methods, such as soaking, germination, fermentation, cooking, and enzymatic treatments, are employed to enhance digestibility, reduce ANFs, and improve sensory attributes (Gu et al., 2022). Among these, fermentation, an ancient biotransformation technique, stands out as a sustainable solution for improving nutritional, functional and sensorial properties of legumes. Indeed, microbial activity during fermentation may increase micronutrient bioavailability, reducing ANFs, lead to the production of health-promoting metabolites (e.g., vitamins) and to changes in protein structure, that increase the digestibility (Akanni & Adebo, 2024; Samtiya et al., 2020). Besides this, the interaction between fermented legumes and the gut microbiome is gaining increasing attention. Accordingly, this review aims to provide a comprehensive and critical assessment of the biochemical and functional transformations occurring in fermented legumes. Furthermore, we synthesized emerging evidence on the impact of legume-based fermented foods on the gut microbiome, highlighting their potential to modulate microbial composition and functionality. These interactions offer novel insights into the role of fermented legumes as functional foods with implications for host metabolic and immune health, thus reinforcing their relevance in novel dietary strategies aimed at

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<https://doi.org/10.1016/j.foodres.2026.119704>

Received 28 December 2025; Received in revised form 6 June 2026; Accepted 9 June 2026

Available online 10 June 2026

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promoting host-microbe symbiosis.

## 2. Traditional fermented legume foods

Fermentation of legumes is an important strategy to improve the nutritional and sensory characteristics of a wide range of products, many of which hold a significant place in the culinary heritage of Asian, African, and Latin American populations. Major fermented legumes include tempeh, natto, miso, dawadawa, and idli, each representing a staple food or culinary delicacy in its respective regions.

While the mechanisms underlying the ability of fermentation to increase legumes digestibility and availability of nutrients are detailed in the next section, here we describe some of the most consumed traditional fermented legumes, the main processing steps, the microorganisms involved and the fermentation outcomes on human health and gut microbiome modulation.

### 2.1. Tempeh

Tempeh is an ancient Indonesian fermented food produced primarily from soybeans and serves as both a dietary staple and as a valuable product with considerable cultural heritage. In tempeh production, the fermentation of whole soybean is performed by *Rhizopus oligosporus* and *R. microspores*, that create dense three-dimensional mycelial networks connecting the soybean particles as well as inducing enzymatic hydrolysis of macromolecules. As a result of the yeasts' proteolytic activity, the seeds are transformed into a protein-rich cake enriched in free amino acids (with increased bioavailability), showing desirable characteristic flavor and texture. Besides Fungi, *Lactobacillus* spp. are frequently co-present during fermentation, contributing to acidification, providing mild probiotic effects, and potentially promoting positive gastrointestinal benefits associated with tempeh consumption (Harahap et al., 2025; Kurniasih et al., 2021; Kusuma et al., 2021). The final product is rich in protein, typically ranging 36%–42% of dry matter, and in B-complex vitamins, calcium, iron, and dietary fiber (Huang et al., 2019).

Interestingly, fermentation not only improves the overall nutritional profile of soybean biomass, but also decreases anti-nutrients and enhances the levels of bioactive molecules (Huang et al., 2019; Pangastuti et al., 2019). In particular, soy fermentation into tempeh improves the bioavailability of soy isoflavones, that have documented health-promoting activities (Tan et al., 2023). Moreover, some studies have highlighted that microbial catabolism of soy proteins may reduce their allergenic potential, making tempeh potentially better accepted by individuals sensitive to soy allergens compared with non-fermented products such as tofu (Ahnan-Winarno et al., 2021). Furthermore, the antioxidant capacity of tempeh, primarily resulting from its enrichment in phenolic compounds, is significantly enhanced through fermentation, providing additional evidence for its classification as a health-promoting fermented food (Tsalissavrina et al., 2023).

### 2.2. Natto

Natto is a traditional Japanese fermented soybean food product that lies in a central position in Japanese food culture. Natto is traditionally produced by fermenting steamed soybeans with *Bacillus subtilis* var. *natto*, whose metabolic activity generates the distinctive viscous texture and strong aroma following 24-h fermentation at 40 °C (Harahap et al., 2025; Hashimoto et al., 2023).

During fermentation, *B. subtilis* var. *natto* enzymatically degrades soy proteins, while also enhancing the bioavailability of major nutrients, such as isoflavones, known for their cardioprotective and antioxidant properties (Chen et al., 2018). Moreover, nattokinase, a serine protease produced by *B. subtilis* var. *natto* with notable fibrinolytic activity, has been shown to support cardiovascular function through fibrin clot degradation, potentially reducing the risk of thrombosis (Chen et al., 2018; Wu et al., 2023). Another feature of natto is its high content of

vitamin K2 (menaquinone-7), an essential nutrient in bone metabolism and cardiovascular health. Vitamin K2 in natto is particularly bioavailable and supports bone mineralization, consequently preventing osteoporosis, while also potentially exerting anti-inflammatory and antioxidant effects (Wang et al., 2023; Zhang et al., 2024).

### 2.3. Miso

Another Japanese fermented soybean product is miso, produced through a multi-step fermentation process in which soybeans are soaked, steamed, and inoculated with *Aspergillus oryzae*, a filamentous mold responsible for producing *koji*, an enzymatically active starter essential for fermentation (Nagao et al., 2024). The *koji* is further mixed with cooked soybeans, salt, and in some cases with other grains such as rice or barley. The mixture is packed into fermentation containers, often traditional wooden barrels, and left to ferment under controlled conditions for a period ranging from several months to multiple years, in order to shape the distinctive sensory characteristics and bioactive content of the final product.

During fermentation, a diverse consortium of microorganisms mediates the conversion of raw substrates into the complex matrix of miso. *A. oryzae*, *B. subtilis*, *Lactobacillus* spp. and yeasts play critical roles in flavor development, biochemical modification, and nutritional enhancement (Negrete-Romero et al., 2021). For example, *B. subtilis* produces bioactive peptides with potential in hypertension treatment due to angiotensin-converting enzyme (ACE) inhibitory activity (Nagao et al., 2024). In addition, lactic acid bacteria (LAB) provide probiotic benefits, supporting gastrointestinal health through gut microbiome modulation and mucosal immunity enhancement (Negrete-Romero et al., 2021). Current research identifies short-chain pyroglutamyl peptides in miso, which have demonstrated anti-obesity effects in experimental models by reducing fat accumulation and modulating lipid metabolism (Sato & Kyoto University, 2022; Shirako et al., 2020). Moreover, fermentation enhances the bioavailability of micronutrients such as B vitamins and minerals, thus improving the nutritional quality of miso beyond its role as a flavoring ingredient in food preparations (Negrete-Romero et al., 2021).

### 2.4. Idli

Idli is a traditional fermented food made of rice (*Oryza sativa*) and a typical bean cultivated in Southern Asia (black gram, that is *Vigna mungo*) commonly consumed in India. The production includes soaking of parboiled rice and beans for some hours, followed by stone-grinding into a smooth batter (Sarma & Gupta, 2022). The spontaneous fermentation typically takes place overnight at room temperature (8–12 °C), when the batter undergoes extensive biochemical and microbiological transformations (Sarma & Gupta, 2022). Fermentation is driven by LAB, such as *Lactococcus lactis*, *Leuconostoc mesenteroides*, and *Lactobacillus* spp. (Mandhanja et al., 2019; Sarma & Gupta, 2022). Yeasts such as *Saccharomyces cerevisiae* and *Hansenula anomala* simultaneously increase, releasing carbon dioxide required for leavening, and contribute additional metabolic functions (Sarma & Gupta, 2022).

### 2.5. Dawadawa

Fermented legumes are widespread also in Africa. Dawadawa is a traditional African condiment, particularly prominent in Nigeria and other West African countries. It is produced from the seed of the African locust bean tree (*Parkia biglobosa*), a *Fabaceae* family leguminous plant. Dawadawa serves as a major vegetable protein source, particularly important in areas where animal protein sources are limited or economically inaccessible (Masters & Kelly, 2024). Dawadawa is produced by harvesting, dehulling, and boiling locust bean seeds, followed by spontaneous fermentation under predominantly alkaline conditions. Spontaneous fermentation is driven by *Bacillus* spp., particularly

*B. subtilis*, which dominates the microbial population and plays a key role in transforming the substrate (Akanni et al., 2018). During fermentation, *B. subtilis* hydrolyzes seed protein into smaller peptides and free amino acids, consequently enhancing dawadawa nutritional quality (Akanni et al., 2018). In parallel, the fermentation process leads to the production of a variety of volatile compounds responsible for the distinct aroma and flavor (Akanni et al., 2018; Shahidah et al., 2019).

### 3. Impact of fermentation on macronutrient composition and digestibility

Pulses such as chickpeas, lentils, peas, and beans have been widely documented as good sources of protein, with contents ranging from 15% to 45% of dry matter, depending on species and cultivar (Bera et al., 2023; Surma et al., 2022). Besides protein, they also contain carbohydrates and lipids. Legumes fermentation has been extensively shown to enhance the nutritional quality of legume proteins by modifying their amino acid profile and increasing digestibility. However, fermentation has also effect on others macro- and micronutrients present in pulses (Fig. 1), depending on the main species involved and on their metabolic potential. In the next subsections, we describe the main effects of fermentation on the macronutrients of legumes, further highlighting differences that are linked to the microbial species involved.

#### 3.1. Fermentation of legumes proteins

Several microbial groups might be involved in the metabolism of pulse proteins, including LAB, that are part of the indigenous microbiota of pulse (Cichońska & Ziarno, 2021), and that are often selected during spontaneous fermentation. Several species harbor complex proteolytic systems potentially active on pulse proteins, although exact mechanisms and hydrolytic patterns have not been clarified so far (Du et al., 2024). For example, Curiel et al. (Curiel et al., 2015) demonstrated that controlled fermentation using *Lactiplantibacillus plantarum* C48 and *Levilactobacillus brevis* AM7 elevated levels of free amino acids in regular beans, chickpea, grass pea, lentil, and peas. Similarly, red kidney beans

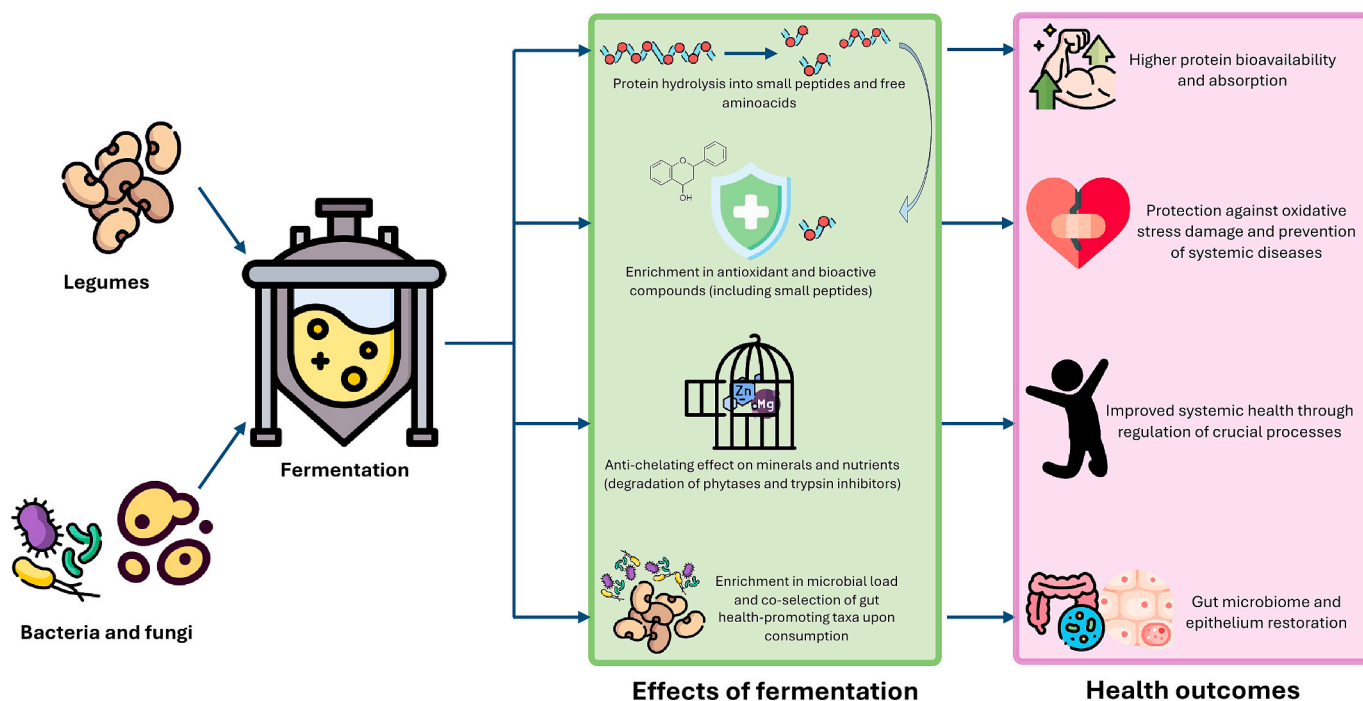
or legume flour fermentation by different LAB, including *Lactobacillus acidophilus*, *Lpb. plantarum*, *Levilactobacillus brevis*, *Bifidobacterium*, and *Streptococcus thermophilus* lowered phytates, trypsin inhibitor activity, saponins, tannins, and raffinose oligosaccharides, and increased free amino acids (De Pasquale et al., 2020; Worku & Sahu, 2017).

In addition to LAB, some fungal species show a relevant proteolytic potential. Indeed, fermentation of chickpeas with the fungus *Cordyceps militaris* raised protein digestibility by 4.4% in vitro due to protein unfolding and enhanced susceptibility to human proteases (Xiao et al., 2015). In another research study, a 10% enhancement in digestibility was achieved in African yam bean fermented by *S. cerevisiae*, as proteolysis enhanced free amino acid bioaccessibility, and reduced levels of anti-nutritional compounds (Chinma et al., 2020). Similarly, in the study of Espinosa-Páez et al. (Espinosa-Páez et al., 2017a), fermentation of kidney beans with *Pleurotus ostreatus* was shown to improve protein digestibility, reduce tannin content, and enhance the levels of several essential amino acids. In a fermented beverage of soybean using *B. subtilis* BSNK-5, lysine, phenylalanine, isoleucine, and leucine levels increased up to threefold (Gao et al., 2020).

Finally, Reyes-Moreno et al. (Reyes-Moreno et al., 2004) showed enhanced digestibility in chickpea tempeh flour due to protein hydrolysis along with simultaneous breakdown of inhibitor compounds such as tannins and phytic acid.

#### 3.2. Fermentation of legumes carbohydrates

Beyond the strong effect on the protein quality and bioavailability of legumes, fermentation also significantly impacts other macronutrients, including carbohydrates. Carbohydrates act as the main energy source for fermentative microorganisms and undergo hydrolysis and catabolism. Importantly, legumes are notably rich in certain fermentable carbohydrates, particularly oligosaccharides such as raffinose, stachyose, and verbascose (Gasiński et al., 2022). These compounds, commonly classified as FODMAPs (fermentable oligo-, di-, monosaccharides and polyols), are frequently associated with gastrointestinal symptoms, including bloating and discomfort (Syed & Iswara, 2025). Fermentation



**Fig. 1.** Main microbial activities involved in legumes fermentations and their potential health outcomes. The figure illustrates the key microbial-mediated mechanisms occurring during legumes fermentation (green box), and the associated health outcomes linked to each mechanism (pink box). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by *Lpb. plantarum*, *S. thermophilus* and *Levilactobacillus brevis* (Cichońska & Ziarno, 2021) has been shown to significantly reduce the content of FODMAPs in legumes through the activity of microbial invertases and  $\alpha$ -galactosidases (Nyyssölä et al., 2020), improving digestibility and gastrointestinal tolerance (Gänzle, 2020).

Conversely, an increase in carbohydrate levels following fermentation has been reported in some studies, such as in black beans (Odion-Owase et al., 2018) and pigeon peas (Espinosa-Páez et al., 2017b). This effect is attributed to the enzymatic conversion of resistant starch into more readily assimilable forms, thus enhancing the overall carbohydrate content.

### 3.3. Fermentation of legumes lipids

Fermentation introduces significant changes in the lipid profiles of legumes. It is a general occurrence that there is reduction in the content of lipids due to the catalytic activity of microbial lipases, that release glycerol and free fatty acids, which subsequently serve as source of both carbon and energy for fermenting microorganisms. This lipolytic effect and the resulting breakdown of lipids have been documented in fermented pigeon peas (Adebowale & Maliki, 2011), cowpea (Difo et al., 2014), as well as in soybeans (Obadina et al., 2013). However, an increased lipid content after fermentation has been reported in other studies. Indeed, elevated levels of lipids were observed in chickpea (Xiao et al., 2018), lupin (Olukomaiya et al., 2020), and significantly in cowpea (Prinyawiwatkul et al., 1996). This apparent inconsistency is justified by several factors, with microbial groups involved in the fermentation being the most relevant. Indeed, lipids increase upon fermentation has been attributed to the biosynthesis of fatty compounds from microbial activity by oleaginous yeasts, frequently isolated from fermented legumes (Bardhan et al., 2020). Similarly, the breakdown of microbial cell membranes during fermentation might release lipids. In addition, lipolysis can lead to the release of simple fatty acids, contributing to both nutritional and sensory quality of legumes (Cichońska & Ziarno, 2021). Overall, fermentation induces changes in the three macronutrients, improving protein quality and bioavailability, reducing anti-nutritional factors, and modifying carbohydrate and lipid fractions through complex enzymatic transformations. Beyond its influence on total energy bioavailability and glycemic response, it also enhances the sensory and functional qualities of the final fermented products. These effects position fermentation as a strategic tool for optimizing both the nutritional and metabolic health benefits of fermented legume-based foods.

### 4. Techno-functional properties of fermented legume products

The improvement of techno-functional properties in fermented legume-based ingredients is essential for their use in developing new food products such as plant-based milk, meat substitutes, and protein-enriched beverages. These functional properties include solubility, water-holding capacity, oil-holding capacity, emulsifying capacity, foam capacity, as well as swelling capacity, which are parameters defining the textural and processing behavior of legume-derived food matrices (Goldstein & Reifen, 2022). Hydration property enhancement due to fermentation is primarily due to microbial proteolysis, which modifies the protein structure by unmasking hydrophilic residues, hence increasing water binding capacity. Xiao et al. (Xiao et al., 2015) have shown that fermentation of chickpea powder with *Cordyceps militaris* SN-18 induces an increase in surface activity through intrinsic proteolytic activity, exposing both hydrophilic and hydrophobic regions of the proteins. Studies have further demonstrated that the solubility and emulsifying capacity of legume proteins can be enhanced by fermentation. Schlegel et al. (Schlegel et al., 2021) have reported that fermentation of pea and lupin protein isolates using *Lactobacillus* spp. significantly increases protein solubility, a key functional parameter for beverage applications. In addition, fermentation of chickpeas, pigeon

peas, and soybean using *R. oligosporus* has significantly enhanced both emulsifying capacity and emulsion stability (Toor et al., 2022). These functional improvements are likely associated with the breakdown of protein aggregates, accompanied by alterations in surface charge and hydrophobicity. Similarly, fermentation further influences starch functionality, as the semi-crystalline structure of legume starch granules undergoes significant changes in swelling behavior. This alteration primarily results from partial hydrolysis through microbial amylases that degrade starch molecules into lower-reactivity compounds such as dextrans and oligosaccharides (Li et al., 2022; Toor et al., 2022). Empirical evidence has indicated that fermented legumes such as chickpeas, pigeon peas, and soybeans exhibit larger swelling capacity, reflecting augmented hydration functionality. From a technological perspective, the increased swelling capacity enhances product texture and mouthfeel properties. This is especially desirable in high-moisture or gluten-free food processing, where achieving desirable structure and mouthfeel is challenging (Ozola et al., 2012). By enhancing these critical functional properties, fermentation significantly broadens the application of legumes in various food applications, in the development of next-generation and sustainable food products. Upon overcoming technical limitations, the food industry might take advantage of fermentation-mediated techno-functional properties, and some applications have been tested already. Indeed, emulsifying and water-holding capacities, together with production of exopolysaccharides, have efficiently improved the creaminess and texture of protein-based yogurt-like products (Montemurro et al., 2021). Similarly, legume fermentation by *B. subtilis* to produce meat-like plant-based foods has effectively improved texture (Fernández-Varela et al., 2024), opening new paths towards fine-tuning of fermentation for the production of accurate meat surrogates.

### 5. Sensory quality and consumer acceptability

The improvement of techno-functional properties of fermented legume-based ingredients should be complemented by efforts to make the products appealing and acceptable to consumers. Interestingly, among the most well-documented advantages of legume fermentation is its capacity to enhance sensory quality, a factor that plays a pivotal role in shaping consumer acceptance and overall product appeal. Legumes are known to have undesirable organoleptic traits such as beany, grassy, earthy, and bitter flavors. These sensory qualities are primarily attributed to volatile compounds such as hexanal, (E)-2-nonenal, and (E,E)-2,4-decadienal, which are generated through lipid oxidation and contribute to off-flavors in legume-based products (Nedele et al., 2021). Fermentation has been shown to significantly reduce off-flavors, while promoting the development of desirable aroma and flavor compounds, including umami, nutty, and savory notes. For example, fermentation of a soy beverage by the fungus *Lycoperdon pyriforme* has significantly lowered the green odor intensity through the reduction of the levels of aldehydes, such as hexanal and its derivatives (Nedele et al., 2021). In another study, fermentation of pea proteins with LAB and the yeasts *Kluyveromyces marxianus*, and *Torulaspora delbrueckii* reduced nonanal and butanal, associated with grassy and musty odor (El Youssef et al., 2020).

In addition, protein hydrolysis into peptides and amino acids is at the core of the development of savory and umami flavors. Spaccasassi et al. (Spaccasassi et al., 2024) reported that fermentation with *Limosilactobacillus fermentum*, *L. lactis*, and *Lactocaseibacillus rhamnosus* not only reduced bitterness but also contributed to the overall flavor profile of a pea protein beverage through the development of umami and salty flavors. Finally, it is worth highlighting that the improvement of flavor profiles and the reduction of off-flavors by fermentation are not consistent across all food products. The results are largely dependent on the type of substrate, the selected microbial strains, and the specific fermentation parameters (Senanayake et al., 2023). For instance, the release of butyric and isobutyric acids in chickpea flour fermentation led



to pleasant “butter-like” aroma in sourdough bread (Nouska et al., 2023). Conversely, the fermentation of bean water extract with three different LAB strains resulted in the formation of undesirable off-odors, which were most likely the result of volatile sulfur compounds biosynthesis (Demarinis et al., 2022). The complex interaction among microbial strains, substrate composition, and processing conditions governs whether the fermentation enhances or compromises flavor. Consequently, careful selection of microbial consortia and parameters of fermentation remains essential to consistently achieve desired sensory outcomes in legume-based fermented products.

However, while analytical investigation of fermented legumes might provide relevant outcomes in terms of reduction of off-odors and selection of potentially pleasant flavors, consumers acceptance must be eventually assessed to determine market viability. Different strategies are available to describe specific attributes of a food and quantify consumers acceptance and perception, including descriptive analysis by trained panels and administration of structured surveys or hedonic scales to wide and heterogeneous sample size representative of specific populations, respectively. Interestingly, recent consumer acceptance studies have shown that these evaluation tools are crucial to understand how non-sensory attributes (e.g., information regarding health benefits or sustainability) contribute to define the overall liking (García-Barón et al., 2025). Also, harnessing these tools has been useful to statistically confirm that Asian populations are more willing to accept and consume sustainable protein-rich foods compared to Western populations (Jakobsen et al., 2026), thus reflecting cultural differences that are strongly linked with dietary habits and culinary heritage. Therefore, although showing some limitations and technical issues (e.g., the need to recruit large sample sizes for consumers acceptance studies), these tools might effectively help in assessing the acceptance of fermented legumes in Western populations, and might contribute to drive the optimization of fermentations.

## 6. Enhancement of antioxidant capacity, micronutrient bioavailability and bioactive compounds production

Beyond enhancing macronutrient digestibility and sensory quality, legume fermentation considerably improves the functional properties and antioxidant activity of legumes through the production of diverse bioactive molecules and inactivation of ANFs. LAB, molds, and yeasts, produce a diverse pattern of health-promoting metabolites such as glutathione, vitamins (e.g., folate and other B-group vitamins), short-chain fatty acids (SCFAs), exopolysaccharides (EPS), and bioactive peptides (BAPs) with antioxidant, anti-inflammatory, and antimicrobial effects (Khubber et al., 2022; Zhao et al., 2021). LAB strains such as *Levilactobacillus brevis*, *Limosilactobacillus fermentum*, and *Lpb. plantarum* have been demonstrated to significantly improve antioxidant content. These microbes can biotransform phenolic acids - including tannins - through reduction and enzyme-mediated decarboxylation, leading to greater release of more bioavailable molecules with enhanced antioxidant potential (Filannino et al., 2015). This may be responsible for the mitigation of the oxidative stress and the inflammatory response. Notably, fermentation of chickpea flour resulted in a 7.8-fold increase in soluble antioxidant capacity compared with the unfermented matrix, with the most pronounced effects observed in samples fermented with *Lpb. plantarum* 299v, *Enterococcus faecium* E6, *Lactocaseibacillus casei* LBC491, and *L. mesenteroides* OM94 (Chiacchio et al., 2025). Moreover, enhanced levels of calcium, magnesium, iron, and zinc have been documented in fermented lentils, faba beans, and in fermented soybean products (Dhull et al., 2020; Rekha & Vijayalakshmi, 2010; Xu et al., 2024). This mineral enhancement is primarily driven by the enzymatic activity of fermenting microorganisms, which degrade phytates through expression of phytases (i.e., myo-inositol hexakisphosphate phosphohydrolase; Sharma et al., 2020) and promote mineral solubilization. Other ANFs reportedly abundant in legumes are trypsin inhibitors, that limit the absorption of proteins. However, fermentation has been

highlighted as a sustainable, cost-effective method to deactivate trypsin inhibitors. Indeed, trypsin inhibitors inactivation by *Bacillus* spp., *Lactobacillus* spp. and *Rhizobium* spp. has been observed in several traditional legume-based traditional fermented foods (Avilés-Gaxiola et al., 2018) through the expression of trypsin-like enzymes out-competing for active sites (Pham et al., 2023). Furthermore, microbes can biosynthesize vitamins such as B2 (riboflavin), B9 (folate), and B12 (cobalamin), as well as vitamin K. These biosynthetic potentials have been demonstrated particularly in some fermented products such as natto and lupin tempeh, contributing to the greater micronutrient content of fermented legumes (Chamlagain et al., 2018; Tarvainen et al., 2019). In addition to the broad spectrum of bioactive compounds generated during fermentation, mounting interest has been directed towards the specific activity of BAPs, increasingly recognized for their capacity to modulate metabolic pathways. The importance of BAPs is highlighted by recent findings that provide clear evidence of the significant anti-diabetic and anti-hypertensive potential of fermented legume matrices. Indeed, Chiacchio et al. (Chiacchio et al., 2025) reported that *Enterococcus hirae* C2a was the strain producing the highest concentration of BAPs with dual inhibitory activity against dipeptidyl peptidase-IV (DPP-IV) and angiotensin-converting enzyme (ACE) in fermented chickpea flour, both key targets in managing type 2 diabetes and hypertension. Similarly, fermentation of green lentils and yellow peas has been associated with a marked increase in DPP-IV inhibition, suggesting a broader applicability of legume-based fermented matrices in the development of functional foods with glycemic control potential (Di Stefano et al., 2019).

## 7. Effects of fermented legumes on gut microbiome and host health

Fermented legumes are increasingly recognized as functional foods capable of influencing the gut microbiome and impacting systemic health (Leeuwendaal et al., 2022). Products like tempeh, miso, and various fermented bean preparations retain the intrinsic prebiotic properties of legumes along with bioactive metabolites generated during fermentation. This dual action is thought to influence both gut microbial composition and certain physiological functions in the host (Teoh et al., 2024; Fig. 1).

We searched PubMed (<https://pubmed.ncbi.nlm.nih.gov/>; accessed in May 2025) using the query “(pulses OR legumes) AND (Gut microbiome OR Gut microbiota OR microbiome) AND (tempeh OR soy OR bean OR soybean OR fermented bean OR lentil OR pea OR chickpea OR natto OR miso)”, resulting in 903 studies filtered by year (from 2014 to 2025). Abstracts were manually screened in order to select in vitro, animal or human studies investigating the effects of fermented legumes on the gut microbiome and host health, resulting in a total of 14 studies (Table 1). Although several studies have pointed to the functional benefits of fermented legumes, there is still a notable lack of controlled human studies specifically investigating the effects of various fermented legumes on gut microbiome composition and activity. As a result, much of the available evidence is primarily extrapolated from in vitro models and animal studies. Nonetheless, emerging evidence suggests that fermented legumes could play a role in modulating gut microbiome and, by extension, systemic health.

Multiple studies have reported increases LAB, *Bifidobacterium*, and *Akkermansia muciniphila* upon increased consumption of fermented legumes. Although the increase of LAB might be linked to the direct intake of microorganisms from the fermented food, the selection of *A. muciniphila* is noteworthy, as this species is well known for its roles in immune modulation, SCFA production, and improved gut barrier function (Smolinska et al., 2025). Consistently, fermented soybean products such as Chungkookjang, Doenjang, fermented black soybean and kidney bean fermented broth have been associated with increased *A. muciniphila*, *Ruminococcaceae*, and *Lachnospiraceae* in the gut microbiome in rat and mice models. These taxa are well known for their roles

Table 1

In vitro, animal, and human studies investigating the effects of fermented legume products on gut microbiome and host health.

| Fermented legume                                                                                                                                                         | Study model                                                       | Brief diet description                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Control                                                                                    | Gut microbiome analysis method                                                                    | Variation in gut microbiome detected                                                                                                                                                                                                                                                                                                                                       | Observed health effects                                                                                                                                                                                                                                                   | Reference                |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|
| Doenjang (traditional Korean soybean paste)                                                                                                                              | ANIMAL - C57BL/6 J mice                                           | Mice were divided into two groups: standard diet with 5% freeze-dried doenjang (treatment group, DJ) or without it (control group, NC), administered for 7 days                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   | Mice fed a standard AIN-93G diet (NC)                                                      | 16S rRNA                                                                                          | <p>↓ <i>Bacillota</i> and ↑ <i>Bacteroidota</i> in DJ group compared to NC group</p> <p>↓ <i>Ruminococcaceae</i>, <i>Lachnospiraceae</i>, <i>Enterobacteriaceae</i>, <i>Clostridium_g7_f</i>, <i>Rikenellaceae</i> in DJ group compared to NC group</p> <p>↑ <i>Odoribacter_f</i>, <i>Lactobacillaceae</i>, <i>Porphyromonadaceae</i> in DJ group compared to NC group</p> | <p>↓ plasma and fecal LPS in DJ group compared to NC group</p> <p>↑ occludin expression in DJ group compared to NC group</p> <p>↓ TNF-α, β-glucuronidase in DJ group compared to NC group</p> <p>↑ IL-10 (anti-inflammatory balance) in DJ group compared to NC group</p> | (Jang et al., 2014)      |
| Tempeh                                                                                                                                                                   | HUMAN                                                             | Participants were assigned to consume 100 g of tempeh per day for 28 days                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         | Participants consumed 200 g of soymilk daily                                               | 16S rRNA                                                                                          | <p>↑ <i>Bifidobacterium</i> and <i>Akkermansia muciniphila</i> in intervention group compared to control</p>                                                                                                                                                                                                                                                               | Not reported                                                                                                                                                                                                                                                              | (Stephanie et al., 2018) |
| Fermented soybean meal (FSBM) fermented by <i>Lactiplantibacillus plantarum</i> (PTCC1058), <i>Bacillus subtilis</i> (PTCC1156) and <i>Aspergillus oryzae</i> (PTCC5163) | ANIMAL - Japanese quail                                           | Japanese quails received 5 dietary treatments for 35 days: (1) Control – standard corn-soybean meal (SBM) diet; (2) Control + probiotic mixture (PM, 0.1%) - containing <i>L. plantarum</i> , <i>L. bulgaricus</i> , <i>L. acidophilus</i> , <i>L. rhamnosus</i> , <i>B. bifidum</i> , <i>S. thermophilus</i> , <i>E. faecium</i> , <i>A. oryzae</i> , and <i>C. pintolopesii</i> ; (3) Control + organic acid mixture (OA, 0.2%) - formic acid, ammonium formate, and ammonium propionate; (4) Control + PM + OA - combined probiotic and organic acid supplementation; (5) Fermented soybean meal (FSBM) diet - SBM completely replaced by FSBM | Japanese quails fed a standard corn-soybean meal (SBM) based diet without additives (CON)  | Culture-based quantification of LAB, coliforms, and anaerobic bacteria of crop and cecal contents | <p>↑ Lactic acid bacteria in FSBM, PM and OA groups compared to control group</p> <p>↓ Coliform in FSBM, PM and PM + OA group compared to control group</p> <p>↓ Total Anaerobic Bacteria (TAB) in FSBM, PM and PM + OA groups compared to control and OA-only groups</p>                                                                                                  | <p>↑ Villus height and VH:crypt depth (CD) ratio in duodenum and jejunum in FSBM, PM, and PM + OA groups compared to control group</p> <p>↓ serum concentration of TC, LDL-C, triglycerides, VLDL-C in FSBM, PM, PM + OA group compared to control and OA-only groups</p> | (Jazi et al., 2018)      |
| Chungkookjang (Soy) fermented by <i>Bacillus subtilis</i> (BS) or <i>Bacillus amyloliquefaciens</i> (BA)                                                                 | ANIMAL - male partially pancreatectomized (Px) Spague Dawley rats | Px rats were randomly divided into 5 dietary groups based on protein source: Px-control (casein), CSB (unfermented cooked soybeans), BS (Chungkookjang fermented by <i>Bacillus subtilis</i> ), BA (Chungkookjang fermented by <i>Bacillus amyloliquefaciens</i> ), and positive control (casein + metformin). Each group received its respective diet daily for 8 weeks                                                                                                                                                                                                                                                                          | Px rats fed casein (Px-control) or casein with metformin (positive control)                | 16S rRNA                                                                                          | <p>↑ <i>Bacillales</i>, <i>Lactobacillales</i>, <i>Verrucomicrobiales</i> in BA and BS compared to the Px-control</p> <p>↑ <i>Akkermansia muciniphila</i> in BA and BS compared to the Px-control group</p> <p>↓ <i>Enterobacteriales</i> in BA and BS compared to the Px-control group</p>                                                                                | <p>↑ (prevent the decrease) in the villi area and the number of goblet cells in the intestinal tissues in the BA group</p> <p>↑ glucose regulation and ↓ in insulin resistance in BA group</p>                                                                            | (Jeong et al., 2020)     |
| Tempeh (fermented soybean)                                                                                                                                               | ANIMAL - zebrafish                                                | Animals were randomly divided into four groups: (1) blank group fed normal food; (2) control group fed normal food with tempeh fermented by <i>R. oryzae</i> (BCRC 31837); (3) MHU 001 group fed                                                                                                                                                                                                                                                                                                                                                                                                                                                  | Fish fed normal food + tempeh ( <i>R. oryzae</i> , BCRC 31837)<br><br>Fish fed normal food | 16S rRNA                                                                                          | <p>↓ <i>Pseudomonadota</i> in MHU 001 group compared to control group</p> <p>↑ <i>Actinomyces</i> in MHU 001 group compared to control group</p>                                                                                                                                                                                                                           | <p>↑ BDNF (brain-derived neurotrophic factor) in the brain of fish in MHU 001 group compared to control group</p>                                                                                                                                                         | (Chen et al., 2021)      |

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Table 1 (continued)

| Fermented legume                                                                                                        | Study model             | Brief diet description                                                                                                                                                                                                                                                                                                                                                                                  | Control                                                                               | Gut microbiome analysis method | Variation in gut microbiome detected                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Observed health effects                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 | Reference           |
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|                                                                                                                         |                         | normal food with tempeh fermented by an unknown strain; (4) MHU 002 group fed normal food with tempeh fermented by another unknown strain. Treatment lasted 2 weeks                                                                                                                                                                                                                                     |                                                                                       |                                | <p>↑ <i>Bacillota</i> in MHU 001 group compared to blank group</p> <p>↓ <i>Escherichia coli</i> in MHU 001 group compared to MHU 002 group and control group</p> <p>↑ <i>Streptococcus</i> and <i>Lactobacillus</i> spp. in MHU 001 group compare to blank group</p> <p>↓ <i>Vibrio</i> and <i>Plesiomonas</i> in MHU 001 group compared to blank group</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     | <p>↑ upregulation in the brain of serotonin-related genes (tph1b, tph2, slc6a4a) in MHU 001 group compared to blank group</p> <p>↑ upregulation in the brain of serotonin-related genes (tph1b, tph2) in MHU 002 group compared to blank group</p> <p>↑ upregulation in the brain of serotonin-related genes (tph2) in control group compared to blank group</p> <p>↓ downregulation in the gut of serotonin-related genes (tph1a, tph1b, tph2, slc6a4a, and mao) in groups consuming tempeh (control, MHU 001 and MHU 002) compared to blank group</p> |                     |
| Kidney bean fermented broth (KBF) with yeast, <i>Lactiplantibacillus plantarum</i> and <i>Lactobacillus acidophilus</i> | ANIMAL - Wistar rat     | Obese rats were assigned to consume high fat diet + saline extract (concentration 0.9%) (MOD) or higher dose of KBF (KBF-H) or medium dose of KBF (KBF-M) or lower dose of KBF (KBF-L)                                                                                                                                                                                                                  | Rats on standard diet (CON) and obese rats on high fat diet with saline extract (MOD) | 16S rRNA                       | <p>↑ Shannon index in KBF-H compared to MOD group</p> <p>↓ Simpson index in KBF-H compared to MOD group</p> <p>↓ <i>Bacillota</i> in all KBF groups compared to MOD group</p> <p>↑ <i>Bacteroidota</i> in all KBF groups compared to MOD group</p> <p>↑ <i>Muribaculaceae</i>, <i>Allobaculum</i>, <i>Romboutsia</i>, <i>Ruminococcaceae</i>, <i>Lachnospiraceae</i> in KBF-H group compared to MOD group</p> <p>↑ <i>Clostridia</i> UCG-014, <i>Ruminococcaceae</i>, <i>Lachnospiraceae</i>, <i>Saccharimonas</i> in KBF-H group compared to MOD group</p> <p>↑ <i>Verrucomicrobiota</i> in LEM, LEF, HEM, HEF groups compared to both young and elderly controls</p> <p>↑ <i>Bacillus</i>, <i>Coriobacteriaceae</i>, <i>Parvibacterin</i> LEM, LEF, HEM, HEF compared to both young and elderly controls</p> <p>↓ <i>Ruminococcus_1</i> in HEM compared to elderly male control mice (EM)</p> | <p>↓ TC, TG, LDL-C levels in KBF-H group compared to MOD group</p> <p>↓ ALT and AST activities in KBF-H and KBF-M groups compared to MOD group</p> <p>↑ pathways of alanine, aspartate, glutamate, histidine metabolism in KBF-L group compared to MOD group</p> <p>↓ weight organs in KBF-H group compared to MOD group</p>                                                                                                                                                                                                                            | (Pang et al., 2022) |
| Fermented black soybean and adlay (FBA) with <i>B. subtilis natto</i>                                                   | ANIMAL - C57BL/6 J mice | Mice were divided into 8 groups: young control males (YM), young control females (YF), aged control males (EM), aged control females (EF), aged males with low-dose FBA (2% diet) (LEM), aged females with low-dose FBA (2% diet) (LEF), aged males with high-dose FBA (6% diet) (HEM), and aged females with high-dose FBA (6% diet) (HEF). Each group received its respective diet daily for 14 weeks | Young and aged control mice did not receive FBA                                       | 16S rRNA                       | <p>↑ <i>Bacillus</i>, <i>Coriobacteriaceae</i>, <i>Parvibacterin</i> LEM, LEF, HEM, HEF compared to both young and elderly controls</p> <p>↓ <i>Ruminococcus_1</i> in HEM compared to elderly male control mice (EM)</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        | <p>↓ expression of GLB1 and p16<sup>INK4A</sup> in LEM, LEF, HEM, HEF groups compared to elderly control</p> <p>↓ MDA (Malondialdehyde) in LEM, LEF, HEM, HEF groups compared to elderly control (lower hepatic oxidative stress)</p> <p>↑ hepatic SOD level in HEM and HEF groups compared to elderly control</p>                                                                                                                                                                                                                                      | (Koh et al., 2023)  |

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Table 1 (continued)

| Fermented legume                                            | Study model            | Brief diet description                                                                                                                                                                                                                                                                                       | Control                               | Gut microbiome analysis method | Variation in gut microbiome detected                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         | Observed health effects                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Reference                |
|-------------------------------------------------------------|------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------|--------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|
|                                                             |                        |                                                                                                                                                                                                                                                                                                              |                                       |                                |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              | restored structure in HFD + Natto group compared to HFD group                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |                          |
|                                                             |                        |                                                                                                                                                                                                                                                                                                              |                                       |                                |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              | ↓ O-propanoylcarnitine, butyryl-L-carnitine, L-histidine, L-tryptophan, L-methionine, L-phenylalanine, glycyl-tyrosine (Gly-Tyr), glycyl-L-leucine, glycocholic acid and dihydrofolic acid in HFD+ Natto group compared to HFD group<br>↑ xanthine, hypoxanthine, uracil, pantothenic acid and 8,11,14-icosatrienoic acid HFD+ Natto group compared to HFD group<br>↓ abdominal adipose tissue weight in L-PN, M-PN, H-PN and nattokinase groups compared to HFD group<br>↓ HDL-C, LDL-C, T-CHO and TG in the H-PN groups compared to control group<br>↑ Restoration of colonic crypt depth and goblet cell number in H-PN groups compared to HFD group<br>↓ (inhibition of protein expression) of CD36 and FATP4 in H-PN groups compared to HFD group<br>↑ (Improvement) of lipid-related metabolic pathways ( $\alpha$ -linolenic acid, linoleic acid, palmitic acid, docosahexaenoic acid and arachidonic acid) in H-PN groups compared to HFD group<br>↓ glucose levels after glucose challenge (iPGTT) in intervention groups compared to control group<br>↑ insulin sensitivity in intervention group compared to control group<br>↑ soleus muscle weights and grip strength in intervention group compared to control group<br>↓ expression of genes related to inflammation (Tnf $\alpha$ and Ccl2) and genes related to muscle atrophy (Trim63 and Fbxo32), in the soleus |                          |
| Peanut-Natto (peanut fermented by <i>B. subtilis</i> natto) | ANIMAL - BALB/C mice   | Mice were randomly divided into six groups: (1) basic feed (control), (2) high-fat diet (HFD), (3) HFD + 10 g/100 mL peanut-natto (L-PN), (4) HFD + 100 g/100 mL peanut-natto (M-PN), (5) HFD + 200 g/100 mL peanut-natto (H-PN), and (6) HFD + 10,000 FU/100 mL nattokinase<br><br>Treatment lasted 6 weeks | Mice feed with a basic diet           | 16S rRNA                       | ↓ Shannon, Simpson and Chao 1 index ( $\alpha$ -diversity) in HFD group compared to control group<br><br>↑ (restored) $\alpha$ -diversity in L-PN, M-PN, H-PN and nattokinase groups compared to HFD group<br><br>↑ (restored) Proteobacteria, Actinomycetota and Deferribacteres as well as the B/F ratio in L-PN, M-PN, H-PN and nattokinase groups compared with those in the HFD group<br><br>↑ Predictive functional pathway increased of amino acid, carbohydrates, lipids, terpenoids and polyketide metabolisms in L-PN, M-PN, H-PN groups compared to control group |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | (Cao et al., 2024)       |
| Barley miso (fermented soybean food)                        | ANIMAL - C57BL/6J mice | Mice were randomly divided into two groups: a control group fed a high-fat/high-sucrose diet (HFHSD) and an intervention group fed HFHSD supplemented with 0.9% barley miso dissolved in water<br><br>Treatment lasted 12 weeks                                                                              | Mice fed a High-Fat/High-Sucrose Diet | Shotgun metagenomics           | ↑ <i>Prevotellaceae</i> , <i>Christensenellaceae</i> , <i>Dehalobacterium</i> , <i>Desulfibacter</i> , <i>Deferribacteraceae</i> , <i>Gemmatimonadaceae</i> in intervention groups compared to control group<br><br>↓ <i>Microbacteriaceae</i> , <i>Lactobacillaceae</i> in intervention group compared to control group<br><br>↑ SCFAs (acetic, propionic and butanoic acids) in feces, serum and soleus muscle of mice in intervention group compared to control group                                                                                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    | (Hashimoto et al., 2024) |

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Table 1 (continued)

| Fermented legume                                                                                                                                                      | Study model                                          | Brief diet description                                                                                                                                                                                                                                                                                                                                                                    | Control                                                                                                                                      | Gut microbiome analysis method | Variation in gut microbiome detected                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 | Observed health effects                                                        | Reference                  |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------|----------------------------|
| Fermented lentil flour with <i>Pleurotus ostreatus</i> (FL-F), fermented lentil gel (FL-G), fermented lentil bread (FL-B), and fermented quinoa-lentil bread (FQL-B). | IN VITRO - static in vitro colonic fermentation      | Before in vitro colonic fermentation, all substrates (FL-F, FL-G, FL-B, FQL-B) underwent simulated gastrointestinal digestion, yielding a solid undigested fraction (assumed to retain dietary fiber and resistant starch). For each assay, 0.5 g of the solid undigested fraction and 10% of the corresponding supernatant (bioaccessible fraction) were added to each fermentation vial | Unfermetend lentil flour (UL-F), Unfermented lentil gel (UL-G), Unfermented lentil bread (UL-B), Unfermented quinoa and lentil bread (UQL-B) | 16S rRNA                       | <p>↑ <i>Bacteroidota</i> after FL-F colonic fermentation</p> <p>↓ <i>Bacillota</i> after FL-F colonic fermentation</p> <p>↑ <i>Eubacterium</i> and <i>Roseburia</i> after FL-F, FL-G and FL- B colonic fermentations</p> <p>↓ <i>Asteroleplasma</i> after FL-F, FL-G and FL-B colonic fermentations</p> <p>↑ <i>Parabacteroides</i> after FL-F, FL-G and FL-B colonic fermentations</p> <p>↓ <i>Alistipes</i> after FL-F, FL-G, FL-B colonic fermentations</p> <p>↓ <i>Odoribacter</i> after FL-G and FL-B colonic fermentations</p> | muscle of mice in intervention group compared di control group<br>NOT REPORTED | (Gomez-Gomez et al., 2025) |
| Soybean fermentation broth (S-FB) (fermented by lactic acid bacteria)                                                                                                 | ANIMAL - loach ( <i>Misgurnus anguillicaudatus</i> ) | <p>Loach were injected with 100 μL of LPS and divided into two groups: control group fed a standard diet with clean water, and intervention group fed a standard diet with soybean fermentation broth (S-FB)</p> <p>Treatment lasted 1 day</p>                                                                                                                                            | Loach fed a standard diet with clean water                                                                                                   | 16S rRNA                       | <p>↑ <i>Lactobacillus</i> spp. and <i>Muribaculaceae</i> in intervention group compared to control group</p> <p>↓ <i>Aeromonas</i> and <i>Shewanella</i> in intervention group compared to control group</p> <p>↓ Shannon Index in intervention group compared to control group</p> <p>↑ pathways related to starch and sucrose metabolism, bacterial chemotaxis, flagellar assembly in intervention group compared to control group</p>                                                                                             | NOT REPORTED                                                                   | (Chu et al., 2025)         |

in butyrate production and for supporting epithelial integrity (Ahrens et al., 2021; He et al., 2023). In the same vein, other studies reported a reduction in pro-inflammatory bacteria belonging to the phylum Proteobacteria, particularly the order Enterobacteriales (Jang et al., 2014) and, more specifically, members of the *Enterobacteriaceae* family (such as *Escherichia coli*; Chen et al., 2021). Moreover, the consumption of fermented legumes has been associated with a decrease in pathogenic microorganisms, including *Vibrio* and *Plesiomonas* in zebrafish fed with tempeh (Chen et al., 2021), and *Aeromonas* in loach fed with soybean fermentation broth (S-FB; Chu et al., 2025). Fermented kidney bean broth has been shown to influence both microbial diversity and gut microbiome composition in wistar rat, including an increase in *Muribaculaceae*, *Allobaculum* (Pang et al., 2022). These genera are often associated with SCFA biosynthesis and improved metabolic profiles (Balakrishnan et al., 2021; Zhu et al., 2024). Similarly, lentil-based fermented products (e.g., flour, bread, gel) led to increase in the butyrate producers *Eubacterium*, *Roseburia*, and *Parabacteroides* during in vitro fermentation (Gomez-Gomez et al., 2025). In another study, fermented peanut-natto has been shown to reverse gut microbiome imbalances induced by a high-fat diet (HFD) in mice, including the expansion of Proteobacteria and Deferribacteres. It also restored microbial diversity and improved Bacteroidota/Bacillota ratio, that is considered a marker of a healthy gut microbiome (Cao et al., 2024; Jasirwan et al., 2021).

The overall trends in microbiota changes upon fermented legumes consumption have been accompanied by measurable health improvements. Several studies have demonstrated reductions in circulating lipids, including total cholesterol (TC), LDL-C and triglycerides (TG). For instance, fermented kidney bean broth (KBF), natto, and peanut-natto have all significantly lowered TC, TG and LDL-C levels in HFD-fed animals (Cao et al., 2024; Pang et al., 2022; Shang et al., 2024). Particularly, KBF at high doses also has reduced ALT (Alanine Aminotransferase) and AST (Aspartate Aminotransferase), liver enzymes indicative of hepatic stress, while modulating amino acid metabolism pathways involved in nitrogen balance and gluconeogenesis (Pang et al., 2022). In addition, natto consumption has been associated with a reduction in fasting glucose and better glucose tolerance, suggesting potential benefits for glycemic control (Shang et al., 2024). Furthermore, fermented black soybean and adlay (a cereal grain native to Southeast Asia) have not only altered the microbiota of aged mice, boosting *Akkermansia* and *Lachnospirillum*, but also lowered malondialdehyde, a marker of oxidative stress, and boosted the expression of aging suppression genes (p16INK4A, GLB1), suggesting that these types of food might modulate systemic aging pathways (Koh et al., 2023). Other fermented legumes such as Doenjang, a traditional Korean soybean paste, have improved intestinal barrier function by increasing occludin expression, leading to a decrease in plasma and fecal lipopolysaccharide levels, a pro-inflammatory endotoxin translocated from the gut lumen (Jang et al., 2014). Interestingly, Chungkookjang, another traditional Korean soybean product fermented with *B. amyloliquefaciens* or *B. subtilis*, has been shown to enhance insulin sensitivity and to prevent reduction in villi surface area and goblet cell numbers in rats, both structural features essential to gut mucosal defense (Jeong et al., 2020), thus improving the gut barrier and epithelial function. Accordingly, mice fed a high-fat/high-sucrose diet (HFHSD) supplemented with barley miso showed increased levels of health-associated *Prevotellaceae* and *Christensenellaceae*, as well as downregulated inflammatory (TNF- $\alpha$ ) and atrophy-related genes (Trim63, Fbxo32) in skeletal muscle (Hashimoto et al., 2024). Notably, even in non-mammalian models, like zebrafish, tempeh fermented with different microbial strains modulated gut and brain serotonin-related gene expression, highlighting potential in the gut-brain axis modulation (Chen et al., 2021).

The only human trial reviewed, involving the consumption of 100 g/day of tempeh, revealed an enrichment of *Bifidobacterium* and *A. muciniphila*, but without reported clinical outcomes (Stephanie et al., 2018).

Taken together, this body of evidence suggests that the consumption of fermented legumes consistently led to the increase in gut microbial diversity and modulated gut microbiome composition, promoting SCFA-producing and beneficial taxa, while supporting improvement in metabolic health, such as lipid metabolism, glycemic control, oxidative stress reduction, and modulation of inflammation. Interestingly, the studies not only show the modulatory potential of fermented legumes on gut microbiome by selecting for health-promoting taxa (e.g., *A. muciniphila* and members of the *Lachnospiraceae*), but also how this translates into improved gut barrier and epithelial function through improved expression of occludins and higher villus height, coupled by lower concentration of pro-inflammatory cytokines and by related synthetic pathways.

It should be pointed out that the predominance of animal studies, along with heterogeneity of products investigated and methodological approaches, limit direct translation of the effects to humans, harmonization of results, and harden to systematically compare the health outcomes of different fermented legumes. Despite this, the recurring patterns observed in both microbial shifts and health-related outcomes point to a promising role of fermented legumes in the dietary prevention of metabolic and inflammatory conditions.

## 8. Final remarks and future perspectives

Fermentation is an efficient method to enhance the nutritional, functional, and sensory properties of legumes, and, simultaneously, generate bioactive compounds that can modulate gut microbiome and health. Several preclinical results highlight consistent patterns in beneficial modulation of gut microbiome, as well as on the host health, positioning fermented legumes as potential functional foods. However, despite these favorable results, current evidence is largely limited to in vitro and animal studies. Randomized clinical trials, as well as longitudinal studies would be necessary to validate and transpose these results to humans, and to assess the modulatory impact of fermented legumes consumption on gut microbiome and systemic health over the long period. Moreover, it has to be pointed out that the results observed are strongly dependent on the fermentation process parameters, the type of substrate and its composition and the microbial strains used. Lastly, long-term effects of fermented legumes consumption on the gut microbiome and on host physiology remain still not sufficiently established. Future work should focus on rigorously designed, large-scale clinical trials to validate the health outcomes observed in preclinical models and to establish the dose-response relationships, supporting the development of nutritional recommendations for promoting metabolic health and sustainable nutrition.

## CRedit authorship contribution statement

**Roberto Marotta:** Writing – original draft, Investigation, Data curation. **Francesca De Filippis:** Writing – review & editing, Supervision, Conceptualization. **Vincenzo Valentino:** Writing – original draft, Visualization. **Danilo Ercolini:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

## Acknowledgments

This project was funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.3 - Call for Tender No. 341 of 15 March 2022 of the Italian Ministry of University and Research funded by the European Union - NextGenerationEU; Project

code PE00000003, Concession Decree No. 1550 of 11 October 2022 adopted by the Italian Ministry of University and Research, Project title “ON Foods - Research and Innovation Network on Food and Nutrition Sustainability, Safety and Security - Working ON Foods.”

## Data availability

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

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