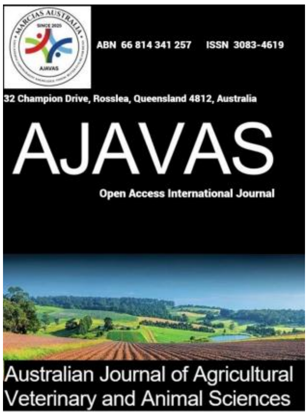
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Review Article

Fermented diets influence broiler intestinal microbiota

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ABSTRACT: *The intestinal microbiota plays a critical role in broiler health, nutrient metabolism, immune function, and overall productivity. Its composition is influenced by multiple factors, with diet being the primary driver alongside genetics, digesta passage rate, and rearing environment. Amid growing restrictions on antimicrobial growth promoters and increasing emphasis on sustainable production, fermented diets have emerged as a viable nutritional strategy in broiler nutrition. Furthermore, fermentation serves as a valuable tool for valorizing agricultural by-products and developing alternative broiler feed ingredients. Research has shown that fermented feed enhances growth performance, improves gut health, and beneficially modulates the intestinal microbiota, and hence microbiome. This review synthesizes current research on how fermented feeds, including fermented cereals, brans, legumes, pulses, pomaces, and complete rations, influence the composition, diversity, and functional dynamics of the broiler intestinal microbiota. We discuss the chicken gastrointestinal tract, microbiota, fermentation of broiler feed, the mechanisms through which fermented diets interact with the gastrointestinal environment, emphasizing their role in improving gut barrier integrity, immune responses, and nutrient absorption. By integrating recent findings, this paper highlights the potential of fermented feeds as a viable, microbiome-targeted intervention to support sustainable broiler production while addressing contemporary challenges in poultry health and nutrition.*

Keywords: broiler chicken; fermented feed; gut health, intestinal microbiome; Antimicrobial growth promoter alternatives

Highlights

- A balanced microbial community stimulates the bird's immune system and enhances host nutrient metabolism
- Fermented feed ingredients in broiler diets contribute to microbial shifts, improved nutrient absorption, stronger disease resistance, and enhanced overall growth performance
- Future research should focus on refining strategies for an effective integration of fermented feeds into diets for a healthy broiler intestinal microbiome

1.0 INTRODUCTION

Optimising gut health is paramount for sustainable and efficient broiler production (Kogut, 2019; Pan and Yu, 2014). The gut microbiota plays a critical role in broiler health (Sun et al., 2022a), nutrient metabolism (Aruwa and Sabiu, 2024), immune function (Wickramasuriya et al., 2022), and overall productivity (Fathima et al., 2022; Gao et al., 2024). As diet is the primary environmental driver shaping this microbial community, specific feed components exert profound selective pressures that determine its structure and function, thereby influencing host health (Pan and Yu, 2014). Consequently, dietary strategies to modulate the microbiota are a central focus of modern nutritional research (Kogut, 2019; Predescu et al., 2024)

Common feed ingredients used in broiler nutrition, including whole cereal grains, oilseeds, and their by-products, contain antinutritional factors (ANFs), such as tannins, saponins, phytates, gossypol, trypsin inhibitors, and non-starch polysaccharides, which impair nutrient digestibility and absorption in the avian GIT (Abbas., 2020; Samtiya et al., 2020; Nalluri and Karri, 2021). Furthermore, these compounds can induce gut inflammation and compromise intestinal integrity, exacerbating the constant challenge posed by enteric pathogens such as *Salmonella* and *Clostridium perfringens* in intensive production systems (Pan and Yu, 2014). Intensive poultry production faces the persistent challenge of enteric pathogens such as *Salmonella* and *Clostridium perfringens*, creating a critical need to move beyond traditional antibiotic growth promoters (Fancher et al., 2020). This has spurred a continuous search for safe and effective feed additives or processing methods that enhance gut health and bird performance (Salim et al., 2018; Fancher et al., 2020; Muneeb et al., 2024). Amid growing restrictions on AGPs and an increasing emphasis on sustainable production, fermented diets have emerged as a particularly promising nutritional strategy in modern broiler nutrition (Rahman et al., 2022; Pewan et al., 2025).

Feed fermentation, a traditional bioprocessing is being re-evaluated with modern science (Nan et al., 2022; Mao et al., 2023; Dastar et al., 2025; Hodzi et al., 2025; Katu et al., 2025). Fermentation enhances broiler feed quality by breaking down complex compounds, making nutrients more digestible and increasing their bioavailability for absorption by intestinal epithelial cells (Haryati Supriyati et al., 2015). A primary benefit is the significant reduction in the concentration of ANF (Sokrab et al., 2014; Predescu et al., 2024; Cardoso Dal Pont et al., 2020). Feed fermentation also elevates concentrations of beneficial components, including probiotics (Soren et al., 2024; Hodzi et al., 2025; Katu et al., 2025). Additionally, fermented feed acts as a direct source of health-promoting metabolites, including short-chain fatty acids (SCFAs), which regulate intestinal blood flow, stimulate enterocyte growth and proliferation, modulate mucin production, and influence local immune responses (Liu et al., 2023). The production of SCFAs lowers the luminal pH, creating an environment that selectively inhibits acid-sensitive pathogenic and spoilage microorganisms while favoring acid-tolerant commensals, particularly *Lactobacillus* species (Guo et al., 2021). Thus, fermented feed primarily influences the poultry gut microbiota by directly introducing beneficial microorganisms and metabolites, which suppress pathogens and improve the gut environment for health-promoting bacteria (Guo et al., 2021; Pan and Yu, 2014; Kang et al., 2025).

While promising, the effects of fermented feed on the broiler gut microbiome are complex and can vary. A comprehensive synthesis of current knowledge on how fermented diets specifically reshape the broiler intestinal microbiota is needed. This article explores the current scientific evidence on how fermented diets (fermented cereals, brans, seed meals, fruit pomaces, legumes, pulses or complete feeds) shape the composition, diversity, and functional capacity of the broiler intestinal microbiome. We analyze the interplay between fermented diets, the avian gastrointestinal tract, and the gut microbiota. By synthesizing recent research findings, this review aims to provide a clear understanding of the potential of fermented feeds as a microbiome-targeted nutritional strategy, offering insights for researchers, nutritionists, and producers seeking to advance sustainable poultry production.

2.0 Broiler GIT morphology

The gastrointestinal tract (GIT) of the broiler chicken is a specialized and highly efficient system. Morphologically, it consists of the oesophagus, crop, proventriculus, gizzard, small intestine (duodenum, jejunum, and ileum), caeca, and large intestine (Figure 1). Notably shorter than the mammalian digestive system, it processes feed rapidly, with a rapid feed transit time of approximately 3.5 hours or less (Wilkinson et al., 2016). The ceca are the critical exception to this fast passage and serve as a fermentation chamber with a much slower turnover, making them the primary habitat for a dense and highly diverse microbial community (Maki et al, 2019; Katu et al., 2025). Other segments of the broiler GIT, including the esophagus, crop, proventriculus, and gizzard, small intestine and large intestine, also host distinct microbial communities (Figure 1). These microorganisms play essential roles in supporting the growth, health, immunity, and productive performance of broilers.

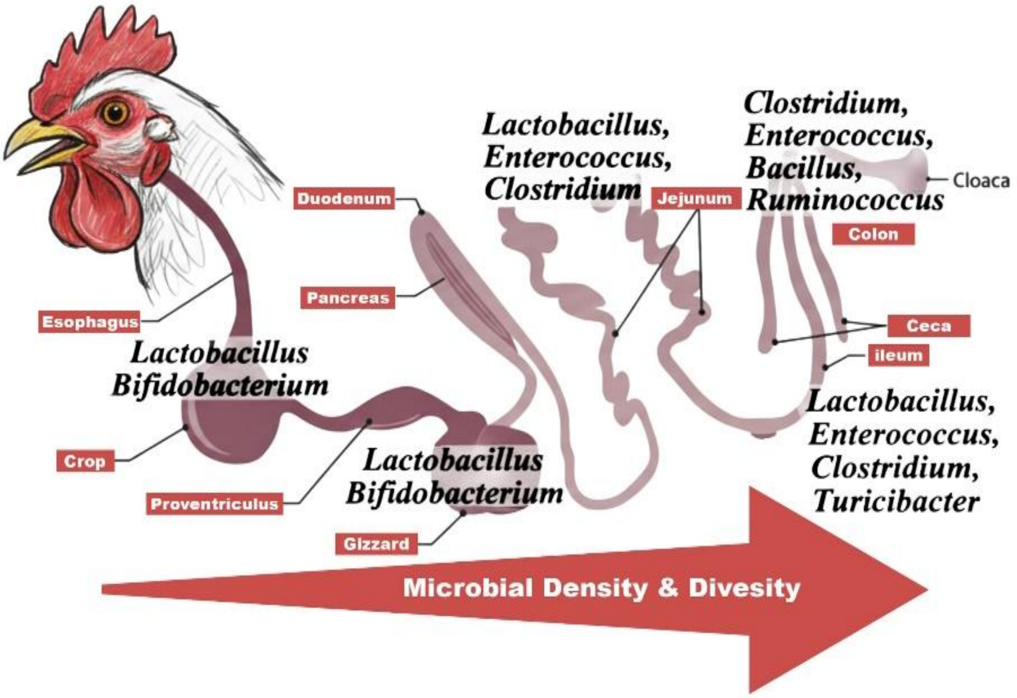

Figure 1. The broiler GIT and its predominant microbial residents

The gut mucosa lines the inner surface of the avian GIT, as shown in Figure 2.

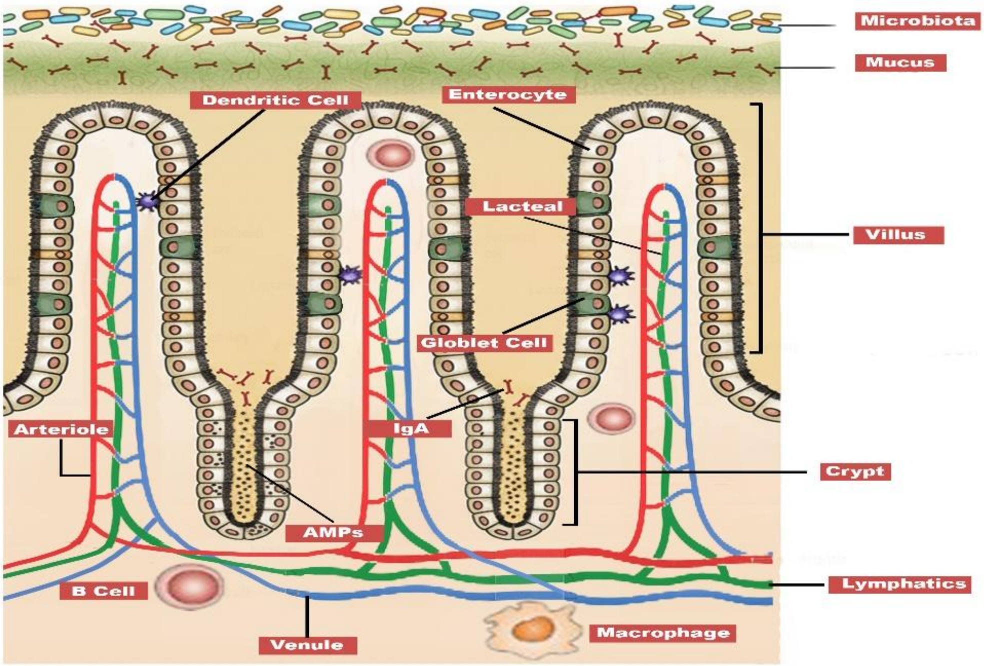

Figure 2. The broiler intestinal morphology showing microbial biofilm, mucus layer and intestinal integrity

This mucosa acts as both a physical and immunological barrier, primarily composed of a gel-like mucus layer secreted by goblet cells, a biofilm of microorganisms, their metabolites, and secretory immunoglobulin A (sIgA) (Pelaseyed et al., 2014; Alemao et al., 2021). The mucus itself is structured in two strata: an outer, loose layer that harbors the gut microbiota, and an inner, compact layer that is largely impervious to bacteria, serving as the first line of defense against infection (Pelaseyed et al., 2014; Jia et al., 2019). *In vitro* studies have shown that chicken intestinal mucus reduces *C. jejuni* virulence through inhibiting its adhesion and invasion of epithelial cells (Byrne et al., 2007; Alemka et al., 2010).

The mucus layer is anchored to a central, single-cell layer of specialized epithelial cells. Intestinal epithelial cells produce antimicrobial peptides like β-defensins, which disrupt the membranes of pathogens (Jia et al., 2019). The epithelial cells are bound together by tight junction proteins (ETJP), that regulate the passage of ions and molecules through the paracellular pathway (Awad et al., 2017). The epithelial layer is supported by the underlying lamina propria, a layer rich in immune cells, connective tissue, and blood vessels, (Vielmuth, 2021). Cellular components of the innate immune system, such as macrophages and heterophils, reside in the lamina propria and are recruited to sites of infection to eliminate invaders via phagocytosis (Chen et al., 2022). Nutrients and other compounds cross this epithelial barrier via two principal routes. The transcellular pathway moves large, antigenic, or lipophilic substances through the epithelial cells via transporters, endocytosis, or diffusion (Hansen et al., 2024). Conversely, the paracellular pathway allows small ions and hydrophilic molecules (<600 Da) to pass between cells, a process tightly regulated by the tight junctions (Wu et al., 2023; Hansen et al., 2024). The small intestine is chiefly responsible for the digestion and absorption of nutrients (El Sabry and Yalcin, 2023). Digestion and nutrient absorption occur at the level of the intestinal villi and crypts. The morphological health of this surface is gauged by villus height (VH), crypt depth (CD), and their ratio (VH/CD), where longer villi and shallower crypts indicate a greater surface area for absorption and are directly linked to enhanced growth performance (Katu et al., 2025). Ultimately, broiler intestinal health is a broad and dynamic concept reliant on the intricate interplay of three core components, which are nutrition, intestinal morphology, and the gut microbiota (Wickramasuriya et al., 2022; Ducatelle et al., 2023). These elements work in concert to maintain the functional and defensive balance of the GIT lumen, ensuring efficient nutrient movement from the lumen into systemic circulation and directly underpinning overall performance.

3.0 Microbiota and microbiome

The terms microbiota and microbiome are distinct, though often erroneously used as synonyms. The microbiota refers specifically to the community of living microorganisms, including bacteria, fungi, viruses, and protozoa, that inhabit a defined environment such as the intestine (Berg et al., 2020). In the context of poultry, the phrase "intestinal microbiota" typically denotes the bacterial population, which represents the dominant and functionally most significant component (Bailey, 2011; Maki et al., 2019; Wickramasuriya et al., 2022). Synonyms such as communal bacteria or gut microbiota are also appropriate. In contrast, the microbiome is a broader, functional organ. It encompasses not only the microbiota (the organisms themselves) but also their collective genetic material (genes and genomes), their metabolic products, and their dynamic interactions with the host environment (Berg et al., 2020). Thus, analyzing the microbiome is inherently more complex than cataloging the microbiota alone, as it involves understanding the system's functional potential and activity.

4.0 Broiler intestinal microbiome

Advances in DNA sequencing, from initial Sanger methods to modern next-generation sequencing (NGS), have enabled a comprehensive characterization of the poultry intestinal microbiome (Pan and Yu, 2014). This ecosystem is remarkably biodiverse, hosting at least 500 bacterial phylotypes or an estimated one million bacterial genes, a genetic repertoire 40 to 50 times larger than the chicken genome itself (Kogut, 2019). Crucially, over 90-95% of these microbes, particularly within the cecum, are unculturable in the laboratory (Sergeant et al., 2014; Kogut, 2019) and are thus accessible only through molecular biological approaches like 16S rRNA gene sequencing (Deng et al., 2025). While 13 bacterial phyla have been identified, the community is overwhelmingly dominated (>90%) by three: Firmicutes, Bacteroidetes, and Proteobacteria (Wei et al., 2013). The *Lactobacillus* spp. is the most dominant genus in the ileum and jejunum, comprising over 99% of bacteria (Yeoman et al., 2012; Kogut et al., 2019). The distribution of gut microbiota varies by section as shown in Figure 1. The crop exhibits the greatest diversity of *Lactobacillus*, while the cecum is the most densely colonized region (10^{10} to 10^{12} CFU/g) and hosts the highest overall bacterial diversity (Abbas et al., 2007; Jian et al., 2025). Katu et al. (2025) reported that cecal microbiota is dominated by two major phyla, which are Gram-positive Firmicutes (including families such as Ruminococcaceae and Lachnospiraceae) and Gram-negative Bacteroidetes (including *Rikenellaceae* and *Bacteroidaceae*). Ultimately, the composition of this intricate microbiome is shaped by a combination of genetic, age-related, dietary, and environmental factors, including digesta passage rate and rearing conditions (Maki et al., 2019; Sun et al., 2015; da Silva et al., 2024).

Pathogenic gut microbiota detrimentally impact the avian host through direct competition for nutrients, such as energy and protein, in the small intestine and gizzard (Fathima et al., 2022). Additionally, intestinal pathogens compromise host physiology by generating toxic metabolites and degrading bile acids, leading to suppressed growth and reduced fat digestibility (Pan and Yu, 2014). Conversely, commensal bacteria help maintain gut function, modulate the immune system, digest nutrients, and support overall intestinal homeostasis (Pan and Yu, 2014; Maki et al., 2019; da Silva et al., 2024). A healthy gut microbiome is composed of high abundance of commensals such as Firmicutes (e.g., *Lactobacillus* spp) and Bifidobacteria, alongside low levels of pathogenic bacteria such as *E. coli*, *Salmonella*, *Clostridium* spp and Bacteroides (Suriano et al., 2022; Sun et al., 2022). This balanced microbial community stimulates the bird's immune system and contributes to host nutrient metabolism. In the presence of a healthy microbiota, the intestinal lining responds by increasing both mucin production and epithelial cell turnover (da Silva et al., 2024). These mechanisms lubricate the gastrointestinal tract and prevent microbial invasion of the host epithelium.

5.0 Microbiota colonisation and succession

Microbial colonization of the chick gastrointestinal tract begins immediately after hatch and progresses in a predictable, staged manner, culminating in a stable, complex community by approximately 15–22 days of age, as shown in Figure 3. Starting from a largely sterile state, the tract is rapidly inoculated by microorganisms from the environment, including the incubator, feed, water, and handling (Proszkowiec-Weglarz et al., 2022). Within the first three days post-hatch, facultative anaerobes such as *Streptococcus* and *Escherichia* rapidly establish, lowering the gut's redox potential by consuming oxygen and creating conditions suitable for obligate anaerobes (Maki et al., 2019). These pioneering communities are subsequently displaced by anaerobic members of the Firmicutes phylum, including *Ruminococcus* and Lachnospiraceae. By day 10, the appearance of slower-growing anaerobes like *Romboutsia* spp. signifies a shift towards greater diversity and evenness, with age being the primary driver of compositional change (Jurburg et al., 2019).

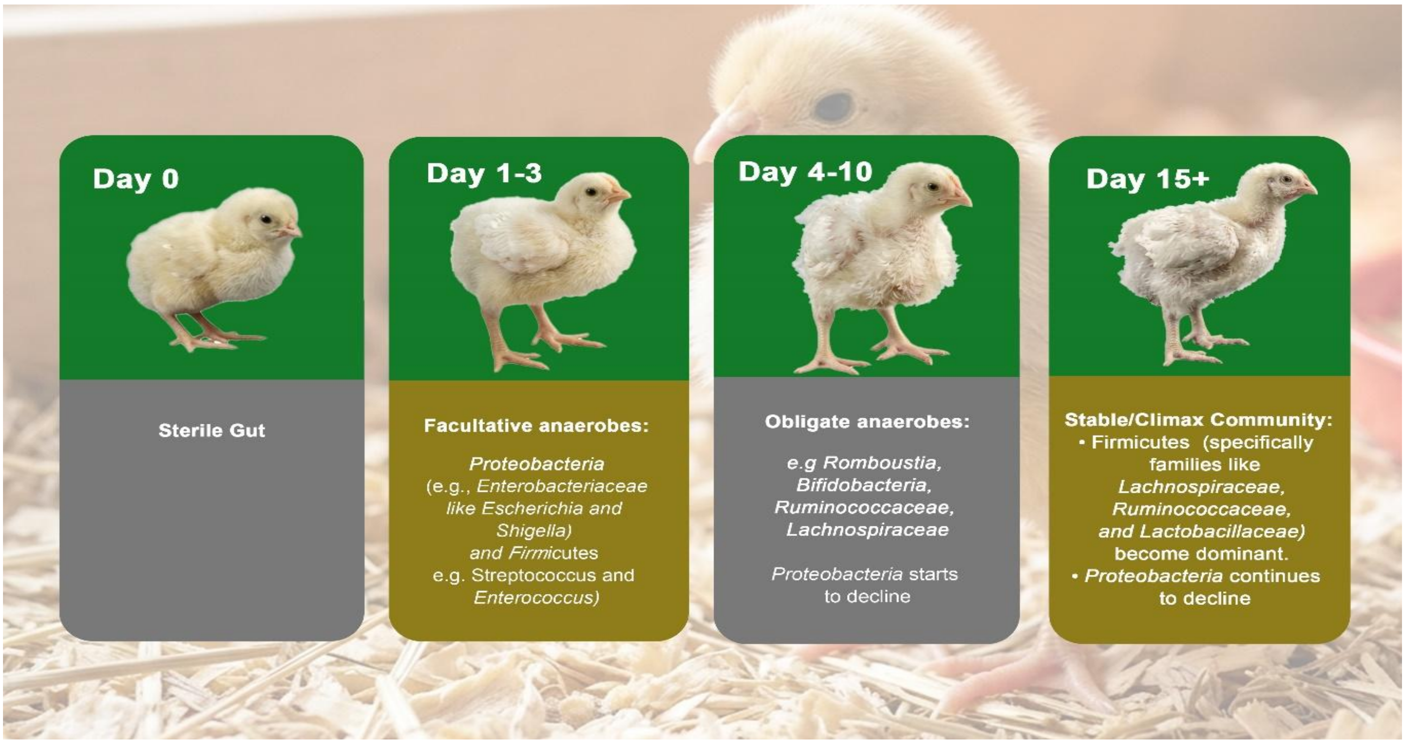

Figure 3. Microbial colonization and succession in the broiler GIT

Colonization patterns further vary by gut segment as shown in Figure 1. Low-pH regions (crop, proventriculus, gizzard) are typically dominated by *Lactobacillus*, whereas the small intestine hosts sparser populations of genera such as Lactobacillus, *Escherichia*, *Enterococcus*, and *Clostridium* (da Silva et al., 2014).

The process culminates in a stable "climax community," most developed within the ceca, which becomes dominated by the phyla Firmicutes, including *Clostridium*, *Enterococcus*, *Bacillus*, and *Ruminococcus* (da Silva et al., 2014; Maki et al., 2019). This mature, metabolically specialized microbiota is essential for host digestion, immune maturation, and pathogen resistance. Delays in microbiota succession impair the beneficial role of commensal gut microbes, heightening the susceptibility of chicks to enteric diseases such as necrotic enteritis (Pan and Yu, 2014; Maki et al., 2019). This imbalance, termed dysbiosis, triggers inflammation and disrupts digestive and immune functions, ultimately resulting in significant production losses (Teirlynck et al., 2011; Maki et al., 2019). To address this, the poultry industry employs competitive exclusion strategies. A study by Angelakis and Raoult, (2010) showed that intragastrically administering *Lactobacillus spp* microbial cultures to day-old chicks helps rapidly establish a higher weight gain, healthy and protective gut microbiome.

6.0 Microbial-microbe interactions in the avian GIT

Bacterial populations coordinate their behavior through quorum sensing, a cell-to-cell communication system mediated by secreted chemical signals called auto-inducers (Rattray et al., 2022). This mechanism regulates collective behaviors, including virulence and biofilm formation, and facilitates interspecies and even host-bacteria communication (Coolahan and Whalen, 2025). As in other microbial communities, different members of the gut microbiome interact in various ways, including competition, cooperation, and antagonism. Competition for nutrients and attachment sites is common among bacterial populations in the avian GIT. Beneficial species (e.g., *Lactobacillus*, *Bifidobacteria*) occupy adhesion sites (due to their ability to adhere to and metabolize mucin), forming a biofilm which blocks the attachment and colonization by pathogenic bacteria such as *Salmonella* and *Clostridium* spp, a phenomenon known as "competitive exclusion" (Zhao, and Maynard, 2022; Peña et al., 2025). For instance, Svetoch et al. (2011) have shown that *Lactobacillus salivarius* strains isolated from the chicken gastrointestinal tract secrete bacteriocins active against pathogens like *Salmonella*, *Enteritidis,* and *Campylobacter jejuni.*

The production of bacteriostatic and bactericidal substances by gut microbes represents another key form of microbial interaction. Beneficial bacteria break down carbohydrates to produce SCFA such as lactic acid, acetic acid and butyric acid (Peng et al., 2024; Teng et al., 2023). These reduce the intestinal pH, making the environment hostile for pathogenic bacteria (Ali et al., 2022). *In vitro* studies have demonstrated that lactic acid bacteria ferment carbohydrates to produce lactic acid, which inhibits the growth of pathogens such as *E. coli, Salmonella, Typhimurium*, and *C. perfringens* (Hinton et al., 1992; Murry et al., 2004; Pan and Yu, 2014). Furthermore, an *in vivo* study demonstrated a negative correlation between SCFA concentrations and the abundance of the *Enterobacteriaceae* family in the ceca of broilers (van Der Wielen et al., 2000).

Certain bacteria produce microbial peptides, known as bacteriocins, which can selectively inhibit the growth of competing bacteria. For example, strains of *Lactobacillus salivarius* isolated from the chicken gastrointestinal tract produce bacteriocins active against both Gram-negative and Gram-positive bacteria, including *Salmonella Enteritidis* and *Campylobacter jejuni* (Stern et al., 2006; Svetoch et al., 2011; Pan and Yu, 2014). Similarly, Teo and Tan, (2005), and Shin et al. (2008) demonstrated that bacteriocins from broiler chicken isolates of Enterococcus faecium, *Pediococcus pentosaceus*, and *Bacillus subtilis* inhibit *Clostridium perfringens* and *Listeria monocytogenes*. The ability to produce bacteriocins is a key trait in probiotic selection, as it directly targets common pathogens. Horizontal gene transfer (HGT) also occurs among avian gut microbiota (Goldenfeld and Woese, 2007). Notably, this process includes the exchange of virulence genes between poultry enteric pathogens, which can directly enhance the pathogenicity of the recipient bacteria (Johnson et al., 2010). Predominant commensal gut microorganisms often possess specific traits such as bacteriocin production or mucin utilization which enable them to outcompete pathogens and thrive in the GIT (Pan and Yu, 2014). Pathogens can acquire these advantageous traits, through horizontal gene transfer (van Reenen and Dicks, 2011; Juhas, 2015; Oladeinde et al., 2021). This can enhance a pathogen's competitiveness and survival.

7.0 Interactions between gut microbiome and host

A complex web of bidirectional interactions exists between the poultry host and its intestinal microbiome. This symbiotic relationship is fundamentally characterized by a mutual exchange of nutrients and by the profound regulatory effects of the microbiota on the host's intestinal development, physiological processes, and immune system maturation (Aruwa and Sabiu, 2024; Wickramasuriya et al., 2022; Fathima et al., 2022; Gao et al., 2024). The positive interactions with the avian host come mainly from beneficial bacteria such as *Firmicutes* (e.g *Lactobacillus* spp) and *Bifidobacterium*.

7.1. Nutritional interactions

Most readily digestible dietary carbohydrates are digested and absorbed by the host in the proximal gut, leaving indigestible polysaccharides, oligosaccharides, and residual sugars for bacterial fermentation in the distal regions. Intestinal bacteria hydrolyze these complex carbohydrates into simple sugars, which are then fermented to produce short-chain fatty acids (SCFAs), primarily acetate, propionate, and butyrate (Ali et al., 2022). SCFA production increases as young birds develop. In broilers, cecal acetate, propionate, and butyrate are undetectable at one day old (van der Wielen et al., 2000). These SCFAs are absorbed across the cecal epithelium via passive diffusion and enter various host metabolic pathways. Butyrate, in particular, serves as a crucial energy source for intestinal epithelial cells (Zhang et al., 2025; Yuan et al., 2025). Beyond energy provision, SCFAs regulate intestinal blood flow, stimulate enterocyte growth and proliferation, modulate mucin production, and influence local immune responses (Liu et al., 2023.

Gut bacteria contribute to host nitrogen metabolism by catabolizing uric acid (from urine that retrograde-peristalsis moves into the ceca) into ammonia, which the host can use for amino acid synthesis (Hajra et al., 2024; Moniaci, 2017). While some dietary nitrogen is incorporated into bacterial protein, this resource is largely lost in feces because most bacterial digestion occurs in the ceca, which cannot absorb protein (Pan and Yu, 2014; Moniaci, 2017). However, chickens can access this bacterial protein through coprophagy, which is possible when they are housed on hard floors (Pan and Yu, 2014). The poultry gut microbiome also synthesizes vitamins, notably B vitamins (Uebanso et al., 2020), but like bacterial protein, most of these are excreted unless reclaimed through coprophagy; this is evidenced by the higher vitamin requirements of cage-housed birds. In a reciprocal relationship, the host provides nutrients to the microbiota, primarily in the form of mucins secreted by gut cells, which serve as a carbon, nitrogen, and energy source for commensal bacteria such as *Bacteroides* and *Bifidobacterium* and *Akkermansia muciniphila* (Corfield, 2018; Suriano et al., 2022). While mucin degradation is well-documented in other species, these bacterial groups are also present in poultry, suggesting a similar metabolic relationship likely exists.

7.2. Effects of microbiome on broiler intestinal morphology and physiology

The gut microbiome significantly influences broiler intestinal development and structure. Research using germ-free (GF) models has demonstrated that GF chickens possess a smaller intestinal mass with thinner intestinal walls compared to conventionally raised birds (Furuse and Okumura, 1994; Gabriel and Mallet, 2006). This developmental stimulation is partly attributed to microbially produced short-chain fatty acids (SCFAs), which promote enterocyte growth and proliferation (Le Blay et al., 2000; Blottière et al., 2003). Supporting this mechanism, studies show that broilers fed fermentable carbohydrates, which enhance microbial SCFA production, exhibit increased gut weight (Muramatsu et al., 1993).

Beyond development, the microbiome critically shapes intestinal morphology (Bayer et al., 2021). Birds with a depleted or absent microbiota, such as GF models, display shorter villi and shallower crypts (Gabriel et al., 2006). Supplementing the diet with probiotic species like *Lactobacillus acidophilus*, *Bacillus subtilis*, and *Saccharomyces cerevisiae* has been shown to improve duodenal villus architecture and increase the ileal villus height-to-crypt depth ratio (Chae et al., 2012; Hernández-Coronado et al., 2025). However, pathogenic disruptions can severely damage this morphology by causing necrotic enteritis. For example, infections with *Eimeria* spp. or *C. perfringens* cause significant reductions in villus height and the villus height-to-crypt depth ratio (Golder et al., 2011; Goo et al., 2023). Furthermore, the microbiome modulates intestinal function, as evidenced by the higher activity of key digestive enzymes like intestinal alkaline phosphatase in conventional birds compared to their GF counterparts (Palmer et al., 1983).

7.3. Microbiome and avian host immunity

The gut microbiome is recognized as a key determinant of health and functions as an integral immune “organ” in chickens (Kogut and Santin, 2020; Sun et al., 2022). To establish an infection, enteric pathogens must first adhere to and breach the intestinal epithelial barrier. In healthy birds, this process is actively impeded by the resident commensal bacteria. These microbial communities densely colonize the intestinal mucosa, forming a protective biofilm (Katu et al., 2025; da Silva et al., 2024). This layer of dense and complex microbial communities can effectively block the attachment and subsequent colonization by most invading enteric pathogens. Some commensal bacteria in the gut, such as *Lactobacillus salivarius* produce bacteriocins, to inhibit the growth of competing microbes selectively (Maki et al., 2019; Svetoch et al., 2011; Predescu et al., 2024).

Beyond this physical barrier, the gut microbiome interacts with the host's innate immune system to shape subsequent adaptive immune responses (Kogut et al., 2020). For example, administration of a probiotic containing *Lactobacillus acidophilus*, *Bifidobacterium bifidum*, and *Streptococcus faecalis* has been shown to increase systemic antibody responses to sheep red blood cells, elevate intestinal IgG against tetanus toxoid, and boost serum IgG and IgM reactive to both tetanus toxoid and *Clostridium perfringens* α-toxin (Pan and Yu, 2014). The precise mechanism remains unclear, but it is hypothesized that probiotics may stimulate the production of Th2 cytokines such as IL-4 and IL-10, thereby promoting antibody-mediated immunity (Kang and Im, 2015). The gut microbiome also significantly influences cell-mediated immunity. Research using germ-free, conventional, and gnotobiotic chickens has demonstrated that the complexity of the enteric microbiome profoundly affects the gut T cell repertoire (Mwangi et al., 2010). Furthermore, different *Lactobacillus* species can induce distinct cytokine expression in T cells in chicken cecal tonsils, contributing to intestinal immune homeostasis (Brismin et al., 2012). It is important to emphasize that immune modulation is not solely the function of administered probiotics or reactions to specific pathogens. The native community of commensal bacteria is also a major immunoregulatory agent. Future research must focus on identifying which commensal species are immunologically significant and elucidating their specific mechanisms of action to fully harness their potential for enhancing poultry health.

7.4. Interactions between gut microbiome and avian diet

Diet stands as the primary environmental driver shaping the intestinal microbiome in poultry, with specific feed components exerting profound and selective pressures on microbial community structure, function, and, consequently, host health. The journey of feed through the gastrointestinal tract activates a cascade of microbial interactions. Diets rich in viscous, non-starch polysaccharides (NSPs), such as those derived from wheat, barley, or rye, increase digesta viscosity, slow intestinal transit, and reduce nutrient digestibility (Pan and Yu, 2014). This altered luminal environment creates an ideal niche for the proliferation of *Clostridium perfringens*, directly predisposing birds to necrotic enteritis. In contrast, corn-based diets, lower in these NSPs, do not trigger the same pathogenic bloom. Beyond pathogen dynamics, the carbohydrate profile fundamentally shapes the commensal landscape; for instance, a standard corn-soybean ration favors *Lactobacillus agilis* type R5, while a wheat middlings-based diet favours the type R1.

The influence of protein is equally significant. The source matters: while soybean meal is a staple, using fermented cottonseed meal as a protein alternative has been shown to increase beneficial lactobacilli and decrease coliforms in the broiler cecum. Conversely, diets high in animal protein, such as fishmeal, enrich the hindgut with undigested protein, providing a substrate that favors *C. perfringens* and elevates necrotic enteritis risk (Drew and Syed, 2004).

Furthermore, the dietary fat source modulates this ecosystem; broilers fed animal fat (lard/ tallow) harbor greater ileal *C. perfringens* populations than those fed soy oil, demonstrating that lipid composition is a key microbial determinant (Knarreborg et al., 2002; Pan and Yu, 2014). Strategically, the poultry industry employs feed additives to directly modulate this complex community toward a healthier state. Enzymes like xylanase and β-glucanase are being used to break down NSPs, and create conditions that favor beneficial *lactic acid* bacteria over adversaries like *E. coli* (Pan and Yu, 2014; Kim et al., 2025). Some interventions operate on a subtler level, interfering with bacterial communication. The use of fermented feed, for example, can exert a profound and targeted influence on the gut microbial ecosystem, delivering a consortium of beneficial effects.

8. The dawn of fermented feed ingredients in broiler nutrition

The adoption of fermented feed ingredients marks a paradigm shift in broiler nutrition. This modern application of an ancient technique is a strategic biotechnological response to the converging demands for antibiotic-free meat, enhanced feed safety, and sustainable production. Its primary drivers are the industry's search for effective antibiotic alternatives, the need to improve feed efficiency, and the opportunity to upcycle agricultural waste.

In response to global restrictions on in-feed antimicrobial growth promoters, the poultry industry has prioritized the search for effective, natural alternatives to sustain gut health and productivity (Salim et al., 2018; Rahman et al., 2022). Fermented feed has risen as a leading solution in this endeavor. This process not only fosters a favorable intestinal environment but also directly introduces beneficial microorganisms, such as *Lactobacillus* and *Bifidobacterium*, into the gastrointestinal tract (Predescu et al., 2024). These microbes benefit the avian host through positive nutritional contributions and by supporting intestinal development, physiological function, and immune system maturation (Sun et al., 2022; da Silva et al., 2024; Predescu et al., 2024). Another key driver to fermented feedstuffs is the enhancement of feed efficiency and value. Feed ingredients of plant origin contain tannins, phytic acid, and protease inhibitors (Abbas, 2020; Tadele, 2015; Erdaw and Beyene, 2018). These disrupt nutrient digestion, absorption and bioavailability in broilers (Akande et al., 2010; Tadele et al., 2015; Zhang et al., 2022; Bloot et al., 2023; Diribi and Fromsa 2025). Fermentation with fungal or bacterial microbes produces specialized enzymes such as tannases, phytases, cellulases and xylanases which breakdown the ANF, thereby enhancing nutrient availability to broilers, hence feed efficiency and value (Motta et al., 2013; Sokrab et al., 2014; Predescu et al., 2024; Hodzi et al., 2025).

In alignment with SDG 12, there is a growing focus on upcycling industrial waste to mitigate its environmental impact, which has led to innovations like the fermentation of these materials for livestock nutrition (Mnisi et al., 2022; Bibi et al., 2023; He and Cui., 2025). The fermentation process serves as a transformative biotechnology, converting low-value by-products such as fruit pomaces, cereal brans, and vegetable residues into high-quality, nutritious feed components (Wang et al., 2017; Mnisi et al., 2022; Katu et al., 2025). This practice not only diverts organic matter from landfills, reducing greenhouse gas emissions and pollution, but also establishes a circular economy within the agri-food sector. It adds tangible value to side streams, enhancing resource efficiency and creating a more sustainable and resilient production model.

The use of fermented feed in broiler nutrition is not merely an additive but a systemic upgrade, significantly improving growth performance metrics like feed conversion ratio and average daily gain (Gungor et al., 2021a; Cheng et al., 2022; Predescu et al., 2024; Hodzi et al., 2025; Dastar et al., 2025; Katu et al., 2025). Beyond mere growth, it elevates meat quality by positively influencing attributes such as fatty acid profiles and reducing cholesterol (Cao et al., 2012; Sun et al., 2022; Kim and Kang, 2016; Ding et al., 2021). Crucially, fermented feed acts directly on the gastrointestinal system, promoting optimal gut morphology through increased villus height and a healthier villus-to-crypt ratio (Qu et al., 2025; Xu et al., 2025; Katu et al., 2025; Gungor et al., 2021a). This structural improvement fosters a more robust gut barrier. Simultaneously, it beneficially modulates the gut microbiota, enriching populations of beneficial bacteria (e.g., *Lactobacillus*) while suppressing pathogenic ones (Gungor et al., 2021a; Li et al., 2020; Predescu et al., 2024; Katu et al., 2025) which collectively strengthens overall gut health, immune function, and nutrient absorption.

9. Fermenting broiler feeds

9.1. The process

The industry employs several core techniques to ferment feed ingredients, primarily liquid state fermentation (LSF), solid-state fermentation (SSF), and ensiling (Predescu et al., 2024). Liquid fermentation yields a nutrient-dense slurry rich in organic acids and live microbes, while SSF offers practical advantages like greater product stability, lower energy consumption, and reduced wastewater (Chen, 2013; Xu et al., 2023). Ensiling typically utilizes fresh, moist plant materials that naturally support vigorous microbial activity. A critical principle across all methods is the use of defined starter cultures, such as *Bacillus* strains or *Aspergillus niger*, to ensure a consistent and safe process, as spontaneous fermentation risks the growth of undesirable pathogens. *Aspergillus niger*, is valued for its production of a broad spectrum of enzymes including hemicellulases, hydrolases, pectinases, proteases, amylases, lipases, and tannases (Pinto et al., 2021, Katu et al., 2025), while various *Bacillus* strains, are favoured for their spore-forming ability which ensures survival through feed processing and the harsh gastrointestinal tract environment (Ramlucken et al., 2020; Bahaddad et al., 2023; Katu et al., 2025). For efficacy, research suggests a target concentration of live microorganisms in the final fermented biomass between 10^5 and 10^9 colony-forming units per gram (CFU/g) (Dai et al., 2020). During fermentation process, the composition of raw materials, the formulation of the starter culture, and the specific conditions of temperature, humidity, and duration during the fermentation itself should be meticulously controlled (Peng et al., 2022; Hodzi et al., 2025). Strict post-production quality control is equally vital to maintain the feed's safety and efficacy.

9.2. The outcomes

Fermented feed offers a diverse array of benefits as previously shown in Figure 3. The benefits are linked to improved gut microbiota, which is responsible for maintaining overall intestinal homeostasis. Fermentation enhances broiler feed quality by breaking down complex compounds, making nutrients more digestible and increasing their bioavailability for absorption by intestinal epithelial cells (Haryati Supriyati et al., 2015). A primary benefit is the significant reduction of anti-nutritional factors (ANFs) like tannins, phytates, and gossypol, which otherwise compromise gut integrity by inducing inflammation and mucosal damage (Sokrab et al., 2014; Predescu et al., 2024; Cardoso Dal Pont et al., 2020). Many ingredients common in broiler nutrition, including whole cereal grains, oilseeds, and their by-products, contain antinutritional factors (ANFs), such as tannins, saponins, phytates, gossypol, trypsin inhibitors, and non-starch polysaccharides (Abbas., 2020; Samtiya et al., 2020; Nalluri and Karri, 2021). These compounds adversely affect the bioavailability of nutrients across various feed components. Tannins, for example, form stable complexes with both dietary proteins and digestive enzymes like trypsin and amylase, directly blocking the breakdown and assimilation of proteins and carbohydrates (Akande et al., 2010). Similarly, phytic acid acts as a potent chelator, binding essential minerals such as calcium, zinc, and iron into insoluble salts that are indigestible to the bird, while also interfering with starch metabolism (Tadele et al., 2015; Zhang et al., 2022; Bloot et al., 2023). Protease inhibitors present another barrier by competitively and irreversibly binding to the active sites of protein-digesting enzymes, effectively halting the crucial process of protein digestion and amino acid release (Tadele, 2015; Akande et al., 2010; Diribi and Fromsa 2025). The microbial fermentation process serves as a powerful form of "external pre-digestion" that systematically dismantles these complex compounds, facilitating efficient nutrient digestion and absorption (Haryati Supriyati et al., 2015; Katu et al., 2025).

Microbial fermentation reduces the fiber (including cellulose, hemicellulose, pectin, and lignin) content of plant cereals and cereal by-products, significantly improving feed digestibility and palatability. This is particularly important for monogastric animals like pigs and poultry, which lack the enzymes that degrade these polysaccharides. Fermentation of rice bran with rumen microbes significantly reduced crude fiber and acid detergent fiber by 13% and 7%, respectively (Debi et al., 2022). Enzyme pre-treatment can also be done before microbial fermentation to enhance the outcomes. For instance, Zhu et al. (2021) demonstrated that pretreating rapeseed meal (RSM) with fiber-degrading enzymes (cellulase and pectinase) prior to fermentation with a mixed culture of lactobacilli (*Limosilactobacillus reuteri, Lactiplantibacillus plantarum*, and *Lactobacillus johnsonii*) significantly reduces crude fiber content. The enzymatic activity of *Bacillus* species, notably *B. amyloliquefaciens*, is essential for fiber breakdown (Katu et al., 2025). By producing enzymes such as α-amylases, β-glucanases, and proteases, they convert complex fibers into simple sugars and other metabolites, thereby improving the nutritional value of fiber-rich materials (Priest et al., 1987).

Concomitantly, the process elevates concentrations of beneficial components, including probiotics (Soren et al., 2024; Hodzi et al., 2025; Katu et al., 2025). Probiotics enhance commensal community in the GIT, which have protective effects through two primary modes of action. The first is metabolic antagonism, driven by the continual conversion of carbohydrates into short chain fatty acids (SCFAs), which sustains a low-pH barrier inimical to many harmful microbes (Guo et al., 2021). The second is direct microbial warfare; these beneficial bacteria synthesize and secrete a battery of antimicrobial compounds, including specialized bacteriocins, which can selectively target and inhibit intestinal pathogens (Pan and Yu, 2014; Predescu et al., 2024). This combination of environmental modification and targeted inhibition allows the commensal microbiome to effectively limit colonization by invaders, thereby enhancing intestinal health and resilience. Additionally, fermented feed acts as a direct source of health-promoting metabolites, including short-chain fatty acids (SCFAs) and essential vitamins synthesized by beneficial fermentative bacteria (Katu et al., 2025). SCFAs also aid in extending feed shelf life by inhibiting spoilage molds and bacteria (Katu et al., 2025). SCFAs will result in reduced luminal pH, which selectively inhibits acid-sensitive pathogenic and spoilage microorganisms while favoring acid-tolerant commensals, particularly *Lactobacillus* species (Guo et al., 2021). SCFAs, particularly butyrate, serves as a crucial energy source for intestinal epithelial cells (Zhang et al., 2025; Yuan et al., 2025). SCFAs also regulate intestinal blood flow, stimulate enterocyte growth and proliferation, modulate mucin production, and influence local immune responses (Liu et al., 2023.

The combined effects of reduced ANFs, increased nutrient availability, and direct microbial benefits translate to improved intestinal morphology, microbiota and function. Fermented feed primarily influences the poultry gut microbiota by directly introducing beneficial microorganisms and metabolites, thereby suppressing pathogens and improving the gut environment for health-promoting bacteria (Guo et al., 2021; Pan and Yu, 2014; Kang et al., 2025). This foundational gut health directly drives superior broiler growth performance, evidenced by enhanced feed intake, increased body weight gain, and more efficient feed conversion (Soren et al., 2024; Predescu et al., 2024).

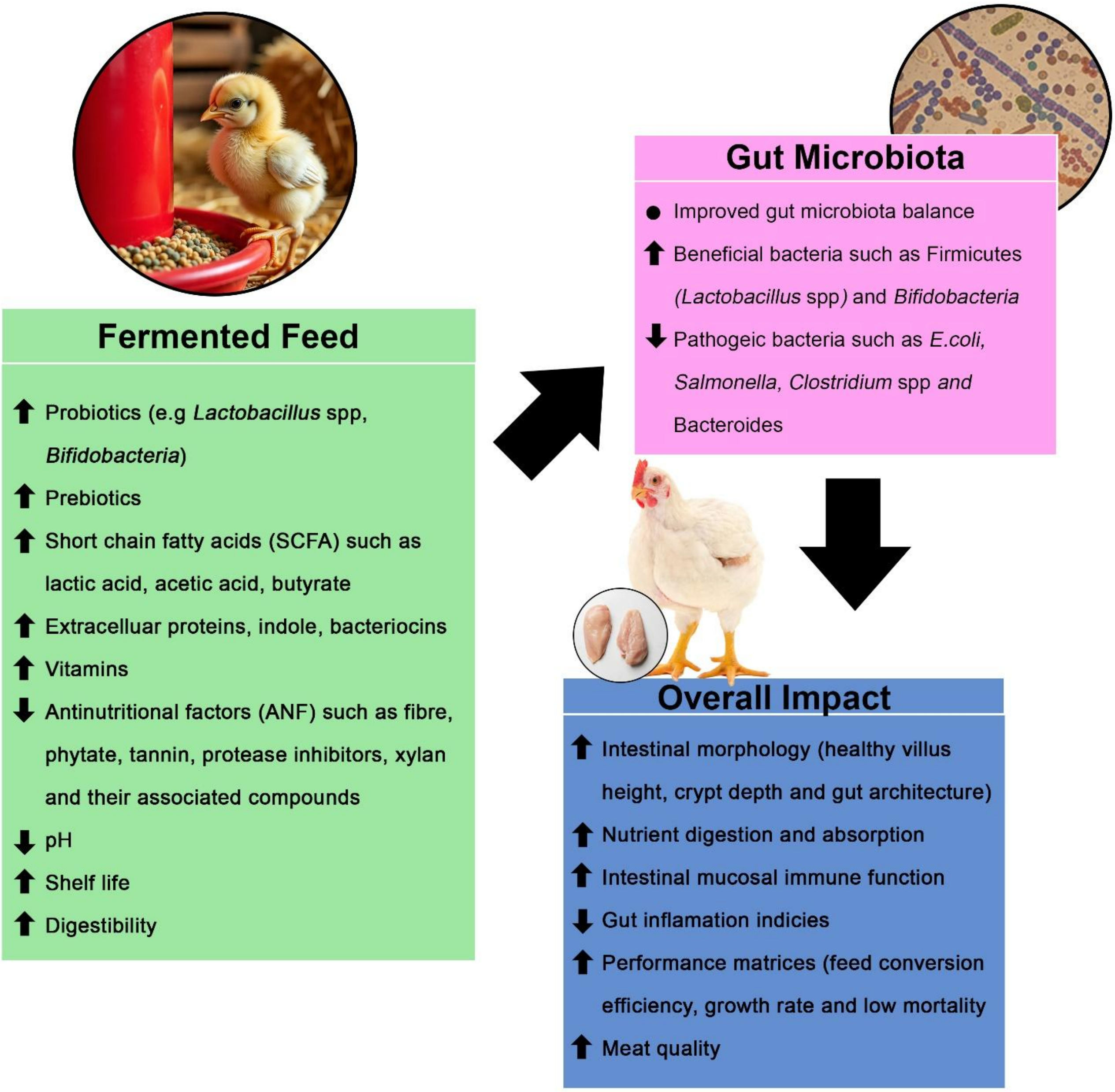

Figure 4. Fermented feed improves overall broiler growth performance and product quality

10. Scientific evidence showing effects of fermented feeds on broiler intestinal microbiome

Although fermented feed has been widely studied for its impacts on growth, health, and product quality, its influence on the broiler gut microbiome has received limited attention, resulting in inconsistent conclusions. A growing body of evidence, however, confirms that fermented feeds can significantly modulate microbial communities in the broiler gut. As summarized in Table 1, studies employing various fermentation agents, conditions, and inclusion levels have demonstrated these effects.

Table 1. Fermented feedstuffs commonly used in broiler diets and their effects on gut microbiome

Feedstuff		**Fermentation type and microbes used**	**Effect on gut microbiota**	**References**
Legumes	Soybean	• *Bacillus amyloliquefaciens*, *Lactobacillus acidophilus*, and *Saccharomyces cerevisiae*. • 37 °C for 24 h • SSF	25% inclusion: • Increased the abundance of the genera *Lachnospiraceae, Lachnoclostridium, Gastranaerophilales*, and *Lactobacillus* • Decreased the abundance of *Escherichia-Shigella* and *Clostridiales*	Li et al., 2020
Cereals	Corn, soybean, and wheat, 6:2:2 (w:w:w)	• *Lactobacillus casei* (C37M41) • SSF	3kg/ton inclusion: • Increased the abundance of beneficial microorganisms like *Lactobacillaceae* family • Decreased the abundance of pathogenic microorganisms (phylum *Delsulfobacterota* and class *Desulfovibriona* and *Negativicutes*)	Peng et al., 2022
	Wheat	• *Lactobacillus plantarum* (KCTC 1048) • 36 °C, 4 h • LSF	10g/kg inclusion: Increased the *Lactobacillus* spp Did not alter the ileal *E. coli* and total bacteria count	Kim and Kang, 2016
	Corn, soybean and wheat bran, 6:2:2 (*w:w:w*)	*Bacillus* spp., *Lactobacillus* spp., *Saccharomyces cerevisiae*	Increased good bacteria like *Parasutterella, Butyricicoccus* and *Erysipelotrichaceae*	Liu et al., 2021
		• *Laetiporus sulphureus* • SSF	5% inclusion elevated the family Lactobacillaceae and suppressed the phylum Proteobacteria's population	Lin and Lee 2020
Brans	Wheat Bran	• *Bacillus amyloliquefaciens* and *Saccharomyces Cerevisiae* • SSF	10% inclusion resulted in significantly higher illeal lactic acid bacteria (LAB) counts	Teng et al., 2017

Seed Meals	Rice bran	• *Lactobacillus plantarum* KCTC 1048 *Saccharomyces cerevisiae* KCTC 1217 and *Bacillus subtilis* ATCC 21332 • SSF	10 g/kg did not significantly alter the cecal *Lactobacillus*, *Escherichia coli* and *Salmonella* counts in broilers.	Kang et al., 2015
	Cottonseed	• *Bacillus subtilis* ST-141 and *Saccharomycetes* N5 • 7 d • LSF	17.9% increased the cecal Lactobacilli counts	Wang et al., 2017
	Palm seed kernel	• *Paenibacillus polymyxya ATCC 842* • 9d • SSF	15% inclusion fermented palm kernel cake: • Increased lactic acid bacteria (5.56 CFU/g) • Decreased the Enterobacteriaceae (4.03 CFU/g)	Alshelmani et al., 2016; Alshelmani et al., 2021
	Rapeseed	• *Lactobacillus acidophilus* (PTCC 1643), *Bacillus subtilis* (PTCC 1156), and *Aspergillus niger* (PTCC 5010) • SSF	Fermented rapeseed meal: • Significantly increased the LAB population in the crop • Reduced the illeal coliform counts	Dastar et al., 2025
	Grape seed	• *Saccharomyces cerevisiae* • LSF	4% and 6% inclusion: • Increased the Shannon and Simpson indices of intestinal microbiota • Increased the relative abundance of Firmicutes • Reduced the relative abundance of Bacteroidetes in the cecum	Nan et al., 2022
Leaf meals	Dandelion		500 and 1000 mg/kg inclusion: • Decreased the observed species, Shannon, Chao1, and Ace indexes. Decreased the abundance of Bacteroidota, Bacteroides, and Alistipes • Significantly decreased the abundance of Verrucomicrobiota • Increased the relative abundance of Firmicutes	Mao et al., 2023
	Banana peels		Inclusion of up to 15% in finisher diets decreased the ileal coliform population	Sugiharto et al, 2019

Fruit pomaces	Grape	• *Saccharomyces cerevisiae* • 48 h at 30°C	2, 4, and 6% inclusion levels: Increased the abundance of Firmicutes • Reduced the relative abundance of bacteroidetes • Altered cecal microbiota composition	Nan et al., 2022
		• *Aspergillus niger* • 7d at 30 °C • SSF	15 g/kg inclusion reduced the cecal *Clostridium perfringens* count	Gungor et al., 2021a
	Pomegranate	• *Aspergillus niger* (ATCC 9142) • 7d at 30 °C • SSF	5 and 10 g/kg inclusion decreased the cecal *Clostridium perfringens* count.	Gungor et al., 2021b
	Sour cherry	• *Aspergillus niger* • 7d at 30°C • SSF	Dietary 1% inclusion level: • Increased cecal *Lactobacillus* spp. counts.	Gungor and Erner, 2020
Vegetable pomaces	Tomato pomace	• *Aspergillus niger* • SSF	10 g/kg inclusion did not alter cecal *Lactobacillus* spp., *Enterococcus* spp., *E. coli*, *C. jejuni*, *S. aureus*, and *C. perfringens* counts	Gungor et al., 2024

In one study, fermented rapeseed meal (RSM) increased cecal and colonic *Lactobacilli* counts compared to both control diets and unfermented RSM (Dastar et al., 2025). Similarly, a 25% inclusion of fermented soybean meal (FSBM) elevated cecal abundances of beneficial genera such as *Lachnospiraceae*, *Lachnoclostridium*, *Gastranaerophilales*, and *Lactobacillus*, while reducing populations of *Escherichia-Shigella* and *Clostridiales* (Li et al., 2020). This pattern indicates that fermented feed can reshape the gut microbiome by promoting commensal bacteria and suppressing pathogenic species. Furthermore, a study using fermented wheat bran at 5% inclusion increased the family *Lactobacillaceae* and suppressed the phylum *Proteobacteria* (Lin and Lee 2020). Likewise, a diet containing a blend of fermented brans (maize bran, wheat bran, and soybean bran) enhanced the abundance of beneficial bacteria, including genus *Parasutterella*, *Butyricicoccus*, and *Erysipelotrichaceae* (Liu et al., 2021). In contrast, Kang et al. (2015) reported that the inclusion of 10 g/kg fermented rice bran did not significantly alter the cecal populations of Lactobacillus, Escherichia coli, and *Salmonella*. This, however, is a low inclusion level relative to other studies and may have been insufficient to induce a measurable change.

This principle of microbiota modulation also applies to fermented seed meals and seed kernels. It was reported that 17.9% inclusion of fermented cottonseed meal significantly increased cecal Lactobacilli counts in broilers (Wang et al., 2017). Similarly, fermented rapeseed meal (FRSM) significantly increased the LAB population in the crop, while reducing coliform counts in the ileum (Dastar et al., 2025). Additionally, Nan et al. (2022) reported that 4 % and 6% inclusion of grapeseed meal increased the Shannon and Simpson indices of intestinal microbiota. The same study also showed a reduction in the relative cecal abundance of *Bacteroidetes.* In a separate study by Alshelmani et al. (2016), they showed that a 15% inclusion of fermented palm kernel cake significantly increased lactic acid bacteria and decreased the Enterobacteriaceae. The consistency in findings regarding microbiota modulation by fermented seed meals and seed kernels demonstrates that this intervention is a reliable strategy for enhancing the gut microbiome in broilers.

As part of the valorization of industrial waste into broiler feed, fruit pomace has also been shown to alter the broiler intestinal microbiome. A study by Gungor et al. (2021a) demonstrated that 15 g/kg inclusion of fermented grape pomace (FTP) reduced the cecal *Clostridium perfringens* count in broilers. Fermented banana (Sugiharto *et al*., 2019), Pomegranate (Gungor *et al*., 2021b), and sour cherry (Gungor and Erner, 2020) all altered broiler gut microbiota.

Hodzi et al. (2025) also summarized the impacts of fermented fruit pomaces on the intestinal microbiota of broiler chickens. Fermented tomato pomace (FTP) did not alter cecal Lactobacillus spp., Enterococcus spp., *E. coli*, *C. jejuni*, *S. aureus*, and *C. perfringens* counts at 10 g/kg inclusion (Gungor et al., 2024), likely due to a low inclusion level. In contrast, Mao et al. (2023) showed that even minimal inclusions (0.5 and 1g/kg) of fermented dandelion (FD) induced significant microbial changes by increasing the abundance of Firmicutes while reducing the abundance of *Verrucomicrobiot*a. The same inclusion level also decreased alpha-diversity indices (observed species, Shannon, Chao1, and ACE) and lowered the abundance of *Bacteroidota*, *Bacteroides*, and *Alistipes*. This discrepancy suggests that the observed difference in microbial modulation is driven not solely by inclusion level but also by the inherent bioactive potency of the specific fermented ingredient.

11. Conclusion

Fermented feed components, including prebiotics and short-chain fatty acids, modulate specific microbial populations to foster a balanced intestinal microbiota in broilers. Achieving optimal feed quality and safety requires a tailored fermentation process, informed by substrate characteristics, careful selection of fermentation microorganisms and conditions, as well as routine nutritional assessments. Collectively, the reviewed literature demonstrates that fermented feed beneficially alters the broiler intestinal microbiota. This modulation consistently enhances the abundance of beneficial bacteria, such as *Lactobacillus* spp., while suppressing potentially harmful populations, including *Clostridia* spp. The resulting microbial shifts contribute to improved nutrient absorption, stronger disease resistance, and enhanced overall growth performance. Discrepancies in reported outcomes can often be attributed to variations in inclusion levels and the intrinsic properties of the fermented substrate. Future research should therefore focus on refining strategies for the effective integration of fermented feeds into broiler diets. This necessitates a deeper investigation into how the type and composition of the raw material, alongside the specific microorganisms used in fermentation, influence the final physiological and microbial outcomes in broiler production.

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