Gut microbiota, metabolome and nutritional interventions in poultry
An integrated review of a defined literature set with data-validated research gaps

Bélmikrobióta, metabolom és takarmányozási beavatkozások baromfiban
Egy meghatározott szakirodalmi halmaz integrált áttekintése, adatokkal alátámasztott kutatási hiányosságokkal

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SUMMARY

The gut microbiota strongly influences performance, immunity and disease resistance in poultry. We synthesised 78 studies selected for relevance from 209 records retrieved from the Web of Science Core Collection (2018–2026) to link dietary interventions with changes in the microbiota, microbial metabolites (short-chain fatty acids, bile acids, indoles) and host outcomes. Across intervention categories, enrichment of *Lactobacillus*, *Faecalibacterium* and Bacteroidetes was consistently associated with higher caecal butyrate, better barrier integrity and lower pathogen colonisation. Coding all 209 records showed that none described a commercial-scale intervention trial, and that shotgun metagenomics (5.7%), indole metabolites (1.4%), longitudinal designs (1.0%) and receptor-level validation (3.3%) were rare. These proportions describe the analysed literature rather than the whole field and identify priorities for precision poultry nutrition research.

Keywords: poultry nutrition; gut microbiota; nutritional interventions; metabolomics; short-chain fatty acids; precision nutrition

Abbreviations: AhR, aryl hydrocarbon receptor; BCFA, branched-chain fatty acids; BSFL, black soldier fly larvae; DCA, deoxycholic acid; FCR, feed conversion ratio; FE, feed efficiency; FLHS, fatty liver haemorrhagic syndrome; FMT, faecal microbiota transplantation; FXR, farnesoid X receptor; GPR41/43, G-protein-coupled receptors 41 and 43; HDAC, histone deacetylase; HDP, host defence peptide; IAA, indole-3-acetic acid; ICOOH, indole-3-carboxylate; ILA, indole-3-lactic acid; IPA, indole-3-propionic acid; LAB, lactic acid bacteria; LCA, lithocholic acid; MAG, metagenome-assembled genome; NE, necrotic enteritis; NSP, non-starch polysaccharide; RS, resistant starch; SCFA, short-chain fatty acid; SCP, single-cell protein; TGR5, Takeda G-protein-coupled receptor 5; Trp, tryptophan; XOS, xylo-oligosaccharides

ÖSSZEFOGLALÁS

A baromfi bélmikrobiótája metabolikusan aktív „szervként” jelentősen befolyásolja a termelési eredményeket, az immunrendszer működését és a betegségekkel szembeni ellenálló képességet. Az antibiotikum-alapú hozamfokozók kivonása óta egyre nagyobb az igény arra, hogy a bélmikrobiótát takarmányozási eszközökkel befolyásoljuk. Áttekintésünk célja annak összefoglalása

volt, hogy a takarmányozási beavatkozások milyen mikrobiális és metabolikus változásokon keresztül hatnak a baromfi egészségére és teljesítményére, valamint a kutatási hiányosságok számszerűsítése. A Web of Science Core Collection adatbázisban 2026. április 28-án strukturált keresést végeztünk; a 234 találatból a 2018 és 2026 között megjelent 209 közlemény alkotta a vizsgált adathalmazt. Ezek közül relevancia alapján 78, baromfival foglalkozó tanulmányt választottunk ki a szöveges szintézishez, a kutatási hiányosságokat pedig mind a 209 közlemény előre meghatározott szempontok szerinti kódolásával számszerűsítettük. A vizsgált beavatkozások (probiotikumok, prebiotikumok és fermentálható rostok, a nem keményítő típusú poliszacharidokat [NSP] bontó enzimek, szerves savak és fitogén takarmány-kiegészítők) esetében a *Lactobacillus*, a *Faecalibacterium* és a Bacteroidetes arányának növekedése rendszeresen együtt járt a vakbelek magasabb butirátkoncentrációjával, a bélfal barrierfunkciójának javulásával és a kórokozók kisebb mértékű megtelepedésével. A közvetlen összehasonlításokban a kombinált stratégiák (pl. enzim és prebiotikum együttes alkalmazása) hatékonyabbnak bizonyultak az egyedi beavatkozásoknál. A kódolás alapján egyetlen közlemény sem számolt be üzemi léptékű (≥10 000 madár) takarmányozási kísérletről; shotgun metagenomikát a közlemények 5,7%-a, indol- és triptofánmetabolit-mérést 1,4%-a, longitudinális kísérleti elrendezést 1,0%-a, receptorszintű mechanisztikus vizsgálatot 3,3%-a, két vagy több omikai módszer együttes alkalmazását pedig 14,8%-a tartalmazta. Következtetésünk szerint a mechanisztikus ismeretek gyakorlati hasznosításához üzemi körülmények között végzett, longitudinális, több omikai szintet integráló kísérletekre van szükség. Az eredmények a vizsgált szakirodalmi halmazra vonatkoznak, és nem tekinthetők a teljes szakterületre érvényesnek.

Kulcsszavak: baromfitakarmányozás, bélmikrobióta, takarmányozási beavatkozások, metabolomika, rövid szénláncú zsírsavak, precíziós takarmányozás

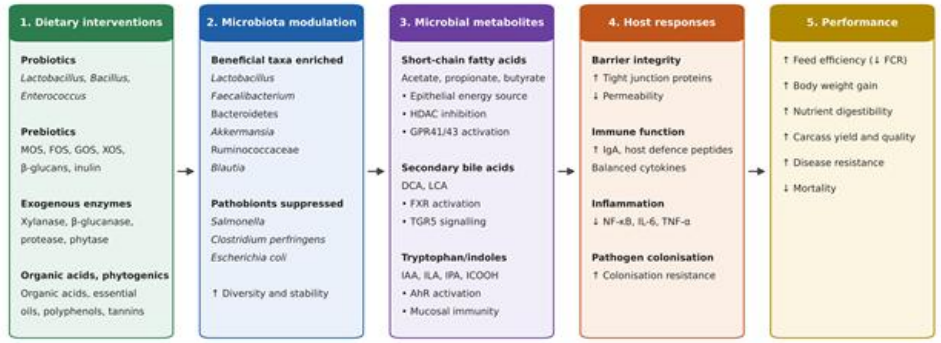
1 Introduction

The worldwide withdrawal of antibiotic growth promoters (AGPs) from poultry feed has created both a production challenge and a scientific opportunity: to understand how the intestinal microbiota can be managed nutritionally to maintain or improve performance without pharmacological support. The avian gastrointestinal tract harbours a dense, spatially compartmentalised microbial ecosystem, reaching 1010–1011 bacterial cells per gram of caecal content, whose composition and metabolic output respond strongly to diet *(Sun and Jia, 2018; Utkina et al., 2025)*.

Lee et al. (2022) argued that the microbiome and its metabolome can be deliberately targeted by nutritional management, and quantitative-genetic studies support this view. In Chinese indigenous chickens, the caecal microbiota explained 10.1% of the individual variation in body weight *(Wang et al., 2023a)*, and in a population of 705 chickens the duodenal microbiability of hepatic steatosis (m^2 = 0.26) was comparable to its heritability (h^2 = 0.25) *(Sun et al., 2024)*. The metabolome—the set of small molecules produced by microbial and host metabolism—sits at the interface between diet and physiology, yet in poultry it remains poorly characterised: in the literature set analysed here, only 33% of records included any metabolomic measurement and only about 10% combined microbiome and metabolome profiling.

Scope of this review. This is a narrative synthesis of a defined and deliberately restricted body of literature, not an exhaustive review. It is based on 78 studies selected from 209 records retrieved by a structured Web of Science search (2018–2026); the search strategy and the way studies were selected are described in Section 2. Consequently, the overviews of individual feed-additive classes (Section 4) summarise what was observed in the selected studies and do not aim to characterise each additive class comprehensively. Where background beyond the selected pool is needed (for example, the composition of the small-intestinal and caecal microbiota, or individual mechanistic studies that complement the selected evidence), additional literature is cited and is not counted among the included studies. The quantitative research gaps in Section 7 are proportions of this 209-record dataset and should be read as properties of the analysed literature rather than of the entire field.

The conceptual framework linking dietary interventions, modulation of the intestinal microbial community, microbial metabolism and host physiology is shown in Figure 1. It illustrates the sequential and interconnected pathways through which nutritional strategies reshape the microbial community, leading to the formation of bioactive metabolites that ultimately influence growth performance, immune function and intestinal health in poultry.



1. ábra. A takarmányozási beavatkozások, a bélmikrobióta módosulása, a mikrobiális metabolitok képződése és a baromfi termelési eredményei közötti összefüggések elvi kerete

Figure 1 Conceptual framework illustrating the relationship between dietary interventions, gut microbiota modulation, microbial metabolite production and host performance outcomes in poultry

2 Materials and Methods

2.1 Literature search

A structured literature search was performed in the Web of Science Core Collection on 28 April 2026. The following search string was applied to the Topic

field (title, abstract, author keywords and Keywords Plus): ("diet" OR "nutrition" OR "feeding" OR "food") AND ("microbiota" OR "microbiome" OR "flora" OR "bacteria") AND ("metabolome" OR "metabolomics" OR "metabolites" OR "biomarkers") AND ("interaction" OR "relationship" OR "effect" OR "influence") AND ("poultry" OR "chicken" OR "avian" OR "fowl"). The search returned 234 records, of which 209 were published between 2018 and 2026; restricting the results to this publication window removed 25 older records. The resulting 209 records were exported with full bibliographic information and abstracts and form the dataset used for the quantitative research-gap analysis (Sections 2.3 and 7). Because a Topic search also matches records that mention poultry only in passing, the dataset contained some records on non-poultry hosts; how these were handled is described in Section 2.2.

2.2 Study selection

The studies for the qualitative synthesis were selected purposively rather than through a formal systematic-review screening protocol. The authors assessed the titles and abstracts of all 209 records and retained the 78 studies judged most relevant to the aims of this review. Relevance was judged on three considerations: (i) the study concerned poultry (chickens, turkeys, ducks, geese, quail or pigeons) or was a review focused on poultry or on the mechanisms discussed here; (ii) it examined a dietary or nutritional intervention, or a nutritional condition; and (iii) it reported gut microbiota outcomes together with microbial metabolite, host physiological or performance outcomes. Records on non-poultry hosts (for example companion animals, rodents, fish and amphibians), which the Topic search returned because they mention poultry, and general reviews on livestock were not included. Priority was given to studies that covered several links of the diet → microbiota → metabolite → host chain and to studies providing mechanistic rather than purely compositional evidence. Because selection relied on the authors' judgement of relevance, the number of records set aside at each step was not recorded and a PRISMA flow diagram cannot be provided; this introduces a risk of selection bias, which we acknowledge in Section 7.5. The quantitative research-gap analysis (Section 7), however, was computed on all 209 records and is therefore not affected by this selection step. The included studies are listed, with their host species, in Supplementary Table S1.

2.3 Data extraction and coding of research-gap indicators

To quantify research gaps, every one of the 209 retrieved records (not only the 78 included studies) was coded as present/absent for a predefined set of indicators, using the title, abstract and, where necessary, the full text. The indicators were: host species and production type; experimental scale, with a commercial-

scale trial defined as a controlled intervention conducted in a commercial house with ≥10,000 birds; longitudinal design, defined as repeated sampling of the microbiota over time within the same experiment; microbiota method (16S rRNA amplicon sequencing, shotgun metagenomics); metabolite classes measured (SCFAs, BCFAs, bile acids, tryptophan/indole metabolites, succinate); number of omics layers (≥2 layers counted as multi-omics integration); receptor-level mechanistic validation (GPR41/43, FXR, TGR5, AhR); faecal microbiota transplantation; analysis of bacteriophages (phage–bacteria interactions); germ-free or gnotobiotic models; epigenomic outcomes; and the physiological axes investigated (gut–liver, gut–brain, gut–bone). Coding was performed by the authors. Each indicator is reported as the number and percentage of the 209 records. Severity classes were assigned a priori as critical (0–5%), major (6–15%) and moderate (16–35%).

2.4 Synthesis approach

Because the included studies differed widely in host species, intervention, dose, duration and analytical platform, a meta-analysis was not attempted, and the results were synthesised narratively. Representative interventions were tabulated (Table 1), and the strength of evidence for each was rated as strong (mechanistic data supported by more than one study), moderate (consistent findings with limited mechanistic data) or emerging (single study or indirect evidence). No formal risk-of-bias assessment was carried out; this and other limitations are discussed in Section 7.5.

3 Gut Microbiota in the Reviewed Studies: Composition, Function and Links to Performance

This section gives only a brief orientation to the avian gut microbiota as it relates to the studies included in this review. It is not a comprehensive description of the avian gut microbiome, for which readers are referred to dedicated reviews *(Shang et al., 2018; Rychlik, 2020)*.

3.1 Spatial organisation and dominant taxa

The microbiota of the avian gastrointestinal tract differs markedly along its length. The crop and the small intestine, the main site of digestion and nutrient absorption, are dominated by Lactobacillus and other aerotolerant Firmicutes and have comparatively low bacterial density and diversity. The caeca, the main fermentation chambers, harbour the densest and most diverse community. Across the poultry literature this community is dominated by Firmicutes (largely Clostridia: Lachnospiraceae and Ruminococcaceae) and Bacteroidetes, with Proteobacteria

and Actinobacteria as further consistently present core phyla and Verrucomicrobia usually at low abundance *(Shang et al., 2018; Rychlik, 2020)*. The relative abundance of each phylum varies widely with bird age, genotype, diet and housing *(Kers et al., 2018)*. Early-life events also matter: in broilers, hatching time influenced both production traits and the early development of the caecal bacteriota *(Such et al., 2023)*. The studies included in this review focused mainly on the caeca: among the included studies that named an intestinal segment in their title, caecal samples were far more common than small-intestinal ones (Supplementary Table S1). Consistent with this, *Du et al. (2020)* mapped microbial communities and SCFA concentrations along the entire intestinal tract of quail and found caecal acetate, propionate and butyrate concentrations 2- to 5-fold higher than in any other segment, confirming the caeca as the primary site of microbial fermentation.

Within the selected studies, a small group of taxa was repeatedly reported as a marker of favourable intestinal conditions: Faecalibacterium prausnitzii (butyrate producer with anti-inflammatory properties), Ruminococcaceae (degraders of dietary fibre), Bacteroides (polysaccharide degradation and bile acid transformation) and Akkermansia (mucin degradation, supporting cross-feeding of SCFA producers) *(Utkina et al., 2025; Wang et al., 2023a)*. *Utkina et al. (2025)* applied constraint-based metabolic modelling to metagenome-assembled genomes from chicken caeca and described a network of competitive and cooperative interactions in which Bacteroides acts as a primary fibre degrader, releasing oligosaccharides that are consumed by secondary SCFA producers. Such modelling offers a predictive basis for designing substrate-targeted interventions—an approach that was largely absent from the applied feeding studies in this dataset.

3.2 Associations between the gut microbiota and performance

Several of the included studies linked specific microbial features to production traits. *Sun et al. (2024)* combined host genomics, molecular phenomics and 16S rRNA sequencing of each gut segment in 705 chickens and estimated a duodenal microbiability of 0.26 for hepatic steatosis, comparable to the host heritability (h^2 = 0.25). Wang et al. (2023a) combined 16S rRNA sequencing, serum metabolomics and cytokine profiling in Chinese indigenous chickens and showed that Sphaerochaeta was associated with improved growth via bovinic acid (a conjugated linoleic acid isomer) metabolism, whereas Synergistes and an unclassified Desulfovibrionaceae genus were associated with reduced growth through induction of the pro-inflammatory cytokine IL-6. This is one of the few studies in the dataset to link specific taxa to specific metabolites and host pathways within a single experiment.

Causal evidence is scarcer still. *Elokil et al. (2022)* transplanted caecal microbiota from highly feed-efficient broilers into laying-type chicks early in life; the recipients' caecal microbiota shifted towards the donor profile and their body

weight gain increased. Only 2 of the 209 records (1.0%) used microbiota transplantation, and only 1 (0.5%) used germ-free or gnotobiotic birds, so most microbiota–performance relationships in this literature set remain correlative.

4 Nutritional Modulation of the Gut Microbiota

The following subsections group the interventions in the included studies into three broad classes. Each subsection opens with a short definition of the additive class and then summarises the evidence from the selected studies; it is not intended as a complete review of that class.

4.1 Live microbial additives: probiotics, synbiotics and bacteriophage combinations

Probiotics are live microorganisms—most commonly Bacillus, Lactobacillus and other lactic acid bacteria (LAB), and yeasts such as Saccharomyces—that confer a health benefit on the host when administered in adequate amounts. Synbiotics combine probiotics with a substrate selectively used by host microorganisms, and bacteriophages are viruses that infect specific bacterial hosts and can be used to reduce target pathogens.

Few probiotic studies characterised the mechanism of the administered strain, but those that did were informative. *Choi et al. (2021)* showed that Bacillus subtilis 29784 not only restructured the intestinal community, reducing Proteobacteria and increasing Firmicutes, but also contributed directly to gut metabolism by producing hypoxanthine and nicotinic acid. *Hoepers et al. (2024)* combined metagenomics and metabolomics to show that a blend of LAB and Saccharomyces boulardii reduced the caecal load of Salmonella Heidelberg, increased microbial diversity and shifted the caecal organic acid profile; multi-omics designs of this kind were used in only 14.8% of the 209 records.

The route and timing of administration also matter. *Brugaletta et al. (2020)* compared alternative administration programmes of a synbiotic, including early delivery, and found effects on caecal microbiota composition, blood metabolites and foot-pad dermatitis. *Choi et al. (2026)* showed in a chick model of multidrug-resistant Salmonella infection that a bacteriophage–probiotic combination restored tight junction protein expression and weight gain more effectively than either treatment alone. Phage–bacteria interactions were addressed in only 7 of the 209 records (3.3%), although phages are important regulators of SCFA-producing bacterial populations (Section 5.1).

4.2 Fermentable carbohydrates and NSP-degrading enzymes

Prebiotics are substrates that are selectively used by host microorganisms and confer a health benefit; in poultry they include oligosaccharides such as xylo-oligosaccharides (XOS), fructo- and mannan-oligosaccharides, and fermentable fibres such as resistant starch (RS). Non-starch polysaccharides (NSP)—arabinoxylans, β-glucans and related cell-wall polymers of cereal grains—are not digested by endogenous avian enzymes. Exogenous NSP-degrading enzymes (for example, xylanases and β-glucanases) are added to feed to reduce digesta viscosity and release encapsulated nutrients; they also generate oligosaccharides in situ that act as prebiotics. Because enzyme and prebiotic effects overlap mechanistically, they are discussed together here; the combination of an enzyme with its oligosaccharide product is termed a stimbiotic.

XOS were among the best-characterised prebiotics in the included studies. *Das et al. (2024)* showed that in ovo feeding of xylobiose and xylotriose increased post-hatch caecal Bifidobacterium, Lactobacillus and total SCFAs as well as plasma immunoglobulin A, directly linking substrate supply to immune endpoints. *Singh et al. (2021)* found that xylanase plus XOS increased caecal butyrate and villus height more than either additive alone, indicating synergy between enzyme and substrate. Similarly, *Wang et al. (2024)* reported that xylanase supplementation of wheat-based broiler diets increased caecal butyrate and propionate, enriched Faecalibacterium and Lactobacillus, and altered serum metabolites including histidine, consistent with in situ release of XOS acting as a prebiotic. Jonchère et al. (2025) showed that a starter stimbiotic had distinct short- and long-term effects on gut health in broilers fed wheat- and rye-based diets. *Aftab and Bedford (2018)* emphasised that responses to NSP enzymes are diet-dependent and cannot be judged from changes in metabolisable energy alone; microbiological and metabolomic endpoints now allow these broader effects to be measured.

Among fermentable fibres, RS selectively enriches Faecalibacterium and Ruminococcaceae, increases butyrate, modulates cytokines (IL-6, IL-10, TNF-α) and may improve calcium and phosphorus absorption relevant to skeletal health *(Oluseyifunmi and Olukosi, 2026)*. Their review was one of only 2 records in the dataset (1.0%) that addressed the gut–bone axis, a pathway of potential commercial importance for bone integrity in laying hens. Gum arabic at 0.25–0.50% of the diet increased caecal butyrate and mucin-2 gene expression and improved villus morphology in post-hatch broiler chicks *(Al-Baadani et al., 2024)*. *Kirn et al. (2024)* reported that peas and pea products affected the intestinal microbiota of broilers, and *Asif et al. (2026)* showed that dietary perennial ryegrass alleviated hepatic dysfunction in geese through the gut–liver axis. Only 11% of the records addressed the gut–liver axis, despite its central importance in fatty liver disorders.

4.3 Organic acids, microbial bile-acid metabolites and phytogenic additives

Organic acids are short-chain carboxylic acids (for example, formic, fumaric, propionic and butyric acids) and their salts, which act by lowering digesta pH, exerting direct antimicrobial effects and serving as energy substrates for enterocytes. Phytogenic (plant-derived) additives include herbs, spices, essential oils and purified plant compounds such as berberine, which can have antimicrobial, antioxidant and anti-inflammatory activity *(Abdelli et al., 2021)*. Microbially derived metabolites such as secondary bile acids, when supplemented directly, are discussed here as well because they were tested alongside organic acids in the included studies.

Kim et al. (2024) showed, in chicken cells and in broilers, that deoxycholic acid (DCA) and butyrate act synergistically to induce host defence peptide (HDP) synthesis and claudin-1 expression, improving survival and reducing intestinal lesions in necrotic enteritis (NE). This DCA–butyrate mechanism is supported by *Bansal et al. (2020)*, who showed that dietary DCA attenuated Clostridium perfringens-induced ileitis and restored ileal bile acids in subclinical NE, and by *Alrubaye et al. (2019)*, who reported that DCA reshaped the microbiota and reduced Campylobacter jejuni colonisation of chickens. *Adewole et al. (2021)* showed that a blend of organic acids and essential oils combined with oat fibre increased caecal butyrate and Lactobacillus abundance and improved FCR relative to bacitracin-treated controls, suggesting that fibre acts as a cofactor for the antimicrobial and fermentative effects of organic acids.

Among phytogenics, berberine undergoes bidirectional interaction with the gut microbiota: it modulates microbial composition and is in turn biotransformed into more bioavailable derivatives such as berberrubine and thalifendine *(Dehau et al., 2023). Park et al. (2022)* showed that the microbiota-derived metabolite indole-3-carboxylate (ICOOH) activated AhR in intestinal epithelial cells, increasing nutrient transporter expression and reducing pro-inflammatory cytokines in broilers challenged with Eimeria maxima; this was one of the most mechanistically complete studies in the dataset.

5 The Intestinal and Systemic Metabolome

5.1 Short-chain fatty acids

Short-chain fatty acids (SCFAs)—mainly acetate (C2), propionate (C3) and butyrate (C4)—are the predominant products of caecal fermentation and the most frequently measured microbial metabolites in the dataset (49 of 209 records; 23.4%). Butyrate regulates intestinal homeostasis by inhibiting histone deacetylases (HDACs) and activating the G-protein-coupled receptors GPR41 and GPR43; these actions support epithelial energy supply, increase expression of

tight junction proteins (ZO-1, claudin-1 and occludin), suppress NF-κB activation and stimulate HDP synthesis *(Kim et al., 2024; Bansal et al., 2020)*.

Wang et al. (2026) provided a system-level characterisation in ducks: birds with high feed efficiency (FE) had greater caecal acetate, propionate and butyrate production associated with Faecalibacterium, Ruminococcaceae and Bacteroides, higher expression of hepatic fatty acid oxidation genes and corresponding changes in serum metabolites. Notably, bacteriophages targeting SCFA-producing bacteria differed between high- and low-FE birds, pointing to a phage-mediated regulatory layer that was examined in very few records of the dataset.

Chen et al. (2023) characterised a gut–liver mechanism in chickens: high-fat-diet-induced dysbiosis reduced butyrate, which downregulated hepatic miR-204 and thereby derepressed acetyl-CoA synthetase 2 (ACSS2), promoting hepatic lipogenesis. This links caecal fermentation to fat deposition through an epigenetic intermediate. Only 5 of the 209 records (2.4%) investigated epigenetic pathways, even though SCFAs are well-established HDAC inhibitors with genome-wide effects. *Li et al. (2026)* further showed that dietary energy level modulated the caecal microbiota and thereby the amino acid composition of meat in local chickens (Section 5.4).

High-protein diets increase the flow of undigested protein to the hindgut, where its fermentation yields branched-chain fatty acids (BCFAs: isobutyrate, isovalerate) and potentially toxic products such as phenols, ammonia and p-cresol. Protein-fermentation risk was quantified in only 7 of the 209 records (3.3%), although it is a relevant safety consideration for novel protein sources such as insect meals (e.g., black soldier fly larvae, BSFL) and single-cell protein (SCP) *(Oluseyifunmi and Olukosi, 2026; Taylor-Bowden et al., 2024; Hartinger et al., 2022)*.

5.2 Bile acids: biotransformation and host signalling

Primary bile acids synthesised in the liver (in chickens predominantly chenodeoxycholic and cholic acid conjugates) are deconjugated and 7α-dehydroxylated by intestinal bacteria to form secondary bile acids such as DCA and lithocholic acid (LCA), which signal through the farnesoid X receptor (FXR), Takeda G-protein-coupled receptor 5 (TGR5) and other host receptors. Despite their documented roles in NE prevention, Campylobacter control and HDP induction *(Kim et al., 2024; Alrubaye et al., 2019; Bansal et al., 2020)*, bile acids were measured in only 14 of the 209 records (6.7%).

Zhang et al. (2026) showed that in laying hens with fatty liver haemorrhagic syndrome (FLHS), disturbance of microbial bile acid metabolism was accompanied by increased pro-inflammatory arachidonic acid metabolites, and that supplementation with Bacteroides fragilis restored bile acid homeostasis and re-

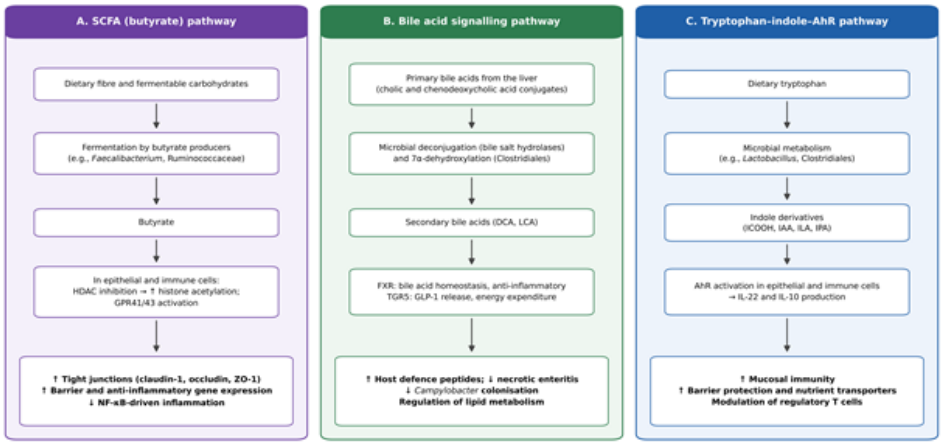
duced these metabolites. *Asif et al. (2026)* similarly linked a fibre-rich dietary intervention to improved hepatic lipid metabolism through the gut–liver axis in geese.

5.3 Tryptophan, indoles and the gut–brain axis

Tryptophan (Trp) metabolism is an important but poorly characterised interface between the microbiota and the host in poultry. Alongside the host kynurenine and serotonin pathways, intestinal bacteria—notably Lactobacillus and members of the Clostridiales—convert Trp into indole derivatives such as ICOOH, indole-3-acetic acid (IAA), indole-3-propionic acid (IPA) and indole-3-lactic acid (ILA). These indoles activate AhR signalling, stimulating IL-22 secretion, strengthening tight junctions and modulating regulatory T cells *(Park et al., 2022)*. Only 3 of the 209 records (1.4%) measured indole metabolites, and only 8 (3.8%) addressed the gut–brain axis.

Zhu et al. (2025) characterised changes in brain metabolite profiles, including serotonin-related metabolites, together with shifts in the caecal microbiota of Sansui ducks receiving phytogenic supplements. *Yang et al. (2023)* showed that Ligilactobacillus salivarius promoted growth and reduced oxidative stress in broilers through regulation of the microbiota–gut–brain axis. The practical relevance is considerable, because altered serotonergic signalling has been associated with feather pecking in laying hens, yet very few studies have investigated this relationship from a microbiota perspective.

The main metabolic pathways linking the gut microbiota to host physiology are summarised in *Figure 2*, which shows how SCFAs, bile acids and tryptophan–indole metabolites regulate gene expression, immune responses and intestinal barrier integrity.



2. ábra. A bélmikrobiótát a gazdaszervezet élettani folyamataival összekapcsoló főbb, metabolitok által közvetített mechanizmusok: SCFA-jelátvitel (HDAC-gátlás, GPR41/43-aktiválás), epesav-jelátvitel (FXR, TGR5) és triptofán–indol–AhR kölcsönhatások

Figure 2 Key metabolite-mediated mechanisms linking the gut microbiota to host physiology: SCFA signalling (HDAC inhibition, GPR41/43 activation), bile acid pathways (FXR and TGR5 signalling) and tryptophan–indole–AhR interactions

5.4 Systemic metabolomics as a performance predictor

Beauclercq et al. (2018) showed that a partial least squares model based on six serum amino acids and two butyrate derivatives explained 59% of the variation in apparent metabolisable energy in chickens, indicating that serum metabolomics can provide biomarkers of digestive efficiency. *Li et al. (2026)* identified 188 differentially abundant muscle metabolites between dietary energy groups in local chickens, with effects mediated by differences in the caecal microbiota, illustrating the complete diet → microbiota → metabolome → meat chain. *Shan et al. (2025)* used serum metabolomics to characterise, together with gut microbiota analysis, the growth-promoting mechanism of *Clostridium autoethanogenum* protein in broilers and identified differential metabolites in amino acid and energy pathways, and *Xu et al. (2025)* used integrative multi-omics and bioinformatics to analyse the effects of BaiRui YuPingFeng powder on intestinal health in broilers, exemplifying the increasingly multidimensional approaches in recent literature.

6. Host Outcomes and Comparative Summary

The mechanistic chains described above converge on four host outcome areas, whose coverage in the 209-record dataset was: feed conversion ratio (FCR) and growth performance (57 records; 27.3%), immune function (113; 54.1%), intestinal

barrier integrity (35; 16.7%) and egg and meat quality (28; 13.4%). *Table 1* summarises representative interventions from the included studies for which microbial, metabolic and host outcomes were linked directly, and *Table 2* summarises the major microbiota-derived metabolite classes.

Table 1 Representative dietary interventions, microbial shifts, key metabolites and host outcomes in the included poultry studies (2018–2026).

Beavatkozás / Intervention	Faj / Species	Mikrobiális változás / Microbial shift	Kulcsmetabolit(ok) / Key metabolite(s)	Hatás / Host outcome	Bizonyíték / Evidence
Bacillus subtilis 29784	Broiler	↑ Firmicutes; ↓ Proteobacteria	↑ Hypoxanthine, nicotinic acid; ↑ butyrate	Improved FCR; ↑ gut barrier	Strong
LAB + *S. boulardii* blend	Broiler	↑ Diversity; ↓ *Salmonella*	↑ Caecal organic acids; ↑ IgA	↓ Pathogen burden; ↑ mucosal immunity	Strong
Phage + probiotic combination	Broiler	Microbiota restored; ↓ MDR *Salmonella*	Distinct caecal metabolite profile	↑ Tight junctions; ↑ weight recovery	Emerging
L. salivarius + trans-cinnamaldehyde	Turkey	↑ *Lactobacillus*; altered bile acid flux	↑ Bile acids; ↑ amino acid metabolites	↑ Resistance to *Salmonella* colonisation	Moderate
In ovo XOS (xylobiose/xylotriose)	Broiler	↑ *Bifidobacterium*; ↑ *Lactobacillus*	↑ Caecal SCFAs; ↑ plasma IgA	↑ Post-hatch immune function	Strong
Xylanase + XOS (stimbiotic)	Broiler	↑ *Faecalibacterium*; ↑ *Lactobacillus*	↑ Butyrate, propionate	Improved FCR; ↑ villus height	Strong
Xylanase alone (wheat diet)	Broiler	↑ *Faecalibacterium*; ↑ *Lactobacillus*	↑ Butyrate, propionate; altered serum histidine	↑ Growth; ↑ nutrient digestibility	Strong
DCA + butyrate	Broiler	↑ SCFA producers; ↓ *C. perfringens*	↑ HDPs; ↑ claudin-1	↓ NE lesion scores; ↑ survival	Strong
Organic acids + essential oil + oat fibre	Broiler	↑ *Lactobacillus*; ↓ *Clostridium*	↑ Caecal butyrate and total SCFA	Improved FCR vs. bacitracin; ↑ gut barrier	Moderate
Gum arabic (prebiotic)	Broiler	↑ *Lactobacillus*; ↑ Bacteroidetes	↑ Caecal butyrate; ↑ mucin-2 mRNA	↑ Villus height; ↑ mucosal integrity	Moderate
Berberine (phytogenic)	Broiler	↑ *Blautia* (butyrate producer)	Berberrubine, thalifendine (microbial metabolites)	↑ Gut health; improved FCR	Moderate
Perennial ryegrass (fibre)	Goose	↑ *Akkermansia*; ↑ *Faecalibacterium*	↑ SCFAs; gut–liver metabolites	↓ Hepatic steatosis	Emerging
Bacteroides fragilis (probiotic)	Laying hen (FLHS)	Restored bile-acid-transforming microbiota	↓ Pro-inflammatory oxylipins; ↑ secondary bile acids	↓ Hepatic steatosis; ↓ FLHS severity	Emerging
Resistant starch (prebiotic)	Broiler/layer	↑ *Faecalibacterium*; Ruminococcaceae	↑ Caecal butyrate; modulated IL-6, IL-10	↑ Gut health; ↑ Ca/P absorption; ↑ bone	Moderate
Fermented mixed feed	Squab/broiler	↑ LAB diversity; ↑ beneficial taxa	↑ Lactic acid; ↑ organic acids	Improved FCR; ↑ villus height; ↑ antioxidant capacity	Moderate

↑ = increase; ↓ = decrease; improved FCR = lower feed conversion ratio. Evidence strength: strong (mechanistic data supported by more than one study), moderate (consistent findings with limited mechanistic data), emerging (single study or indirect evidence)

1. táblázat. A vizsgált baromfikísérletekből kiemelt takarmányozási beavatkozások, mikrobiális változások, kulcsmetabolitok és a gazdaszervezetre gyakorolt hatások (2018–2026)

Table 2 Major gut microbiota-derived metabolite classes in poultry: producers, receptors, host effects and coverage in the 209-record dataset

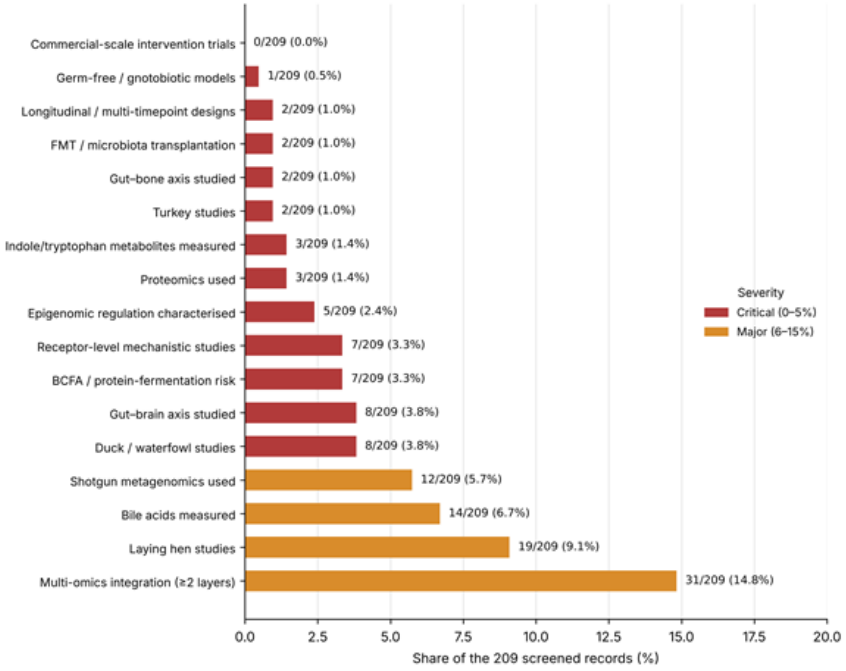
Metabolitcsoport / Metabolite class	Fő termelők / Primary producers	Receptor, jelút / Receptor, pathway	Hatás / Host effect	Közlemények / Records (n/209)
Butyrate (SCFA)	*Faecalibacterium*, *Roseburia*, Ruminococcaceae, *Blautia*	HDAC inhibition; GPR41/43	↑ Epithelial energy; ↑ tight junctions; ↑ HDP; ↓ NF-κB; epigenetic regulation	49 (23.4%)*
Propionate (SCFA)	Bacteroidetes, *Veillonella*, *Dialister*	GPR41/43; gluconeogenesis	Energy metabolism; hepatic lipid regulation; satiety signalling	49 (23.4%)*
Acetate (SCFA)	*Bifidobacterium*, *Lactobacillus*, *Bacteroides*	GPR41/43; peripheral uptake	Systemic energy substrate; anti-inflammatory	49 (23.4%)*
Deoxycholic acid (secondary bile acid)	Clostridiales (7α-dehydroxylation)	FXR; TGR5	↑ HDP synthesis; ↓ NE; ↓ *Campylobacter*; bile acid homeostasis	14 (6.7%)†
Indole-3-carboxylate and other indoles	*Lactobacillus*, Clostridiales (Trp catabolism)	AhR → IL-22	↑ Mucosal immunity; ↑ nutrient transporters; anti-coccidial	3 (1.4%)
Succinate	*Prevotella*, *Bacteroides*	SUCNR1; mitochondrial TCA cycle	Mitochondrial function; hepatic lipid metabolism	~3 (1.4%)
Isovaleric acid (BCFA)	*Bacteroides*, *Prevotella* (protein fermentation)	GPR41; immune cell signalling	↑ Intestinal IgA response *(Wang et al., 2023b)*; cytotoxic at high concentrations	7 (3.3%)
Serotonin and Trp precursors	Enterochromaffin cells (microbiota-primed)	5-HT receptors; gut–brain axis	Gut motility; stress modulation; feather pecking	9 (4.3%)‡
Epigenetic intermediates (miRNA, histone acetylation)	Microbiota-dependent (e.g., butyrate-driven)	HDAC; miR-204	Regulation of lipogenesis (ACSS2), immune and barrier genes	5 (2.4%)

Records measuring SCFAs (any of the three); †records measuring any bile acid; ‡records measuring serotonin or Trp-related metabolites, which overlaps with but is not identical to the 8 records addressing the gut–brain axis

2. táblázat. A baromfi bélmikrobiótájából származó főbb metabolitcsoportok: termelő baktériumok, receptorok, hatások és előfordulásuk a 209 közleményből álló adathalmazban

7 Research Gaps: Data-Validated from the 209-Record Dataset

The gaps below are derived from the coding of all 209 records retrieved by the search (Section 2.3). They therefore describe the analysed literature set; because the search covered one database, one time window and a defined set of terms, they should not be read as estimates for the entire poultry microbiome literature (Section 7.5). *Table 3* and *Figure 3* summarise the coded indicators.



3. ábra. Adatokkal alátámasztott kutatási hiányosságok a vizsgált szakirodalmi halmazban (209 közlemény, 2018–2026): az egyes szempontokkal foglalkozó közlemények száma és aránya súlyossági kategóriák szerint színezve (kritikus 0–5%; jelentős 6–15%). Mérsékelt kategóriába (16–35%) egyetlen szempont sem esett.

Figure 3 Data-validated research gaps in the analysed literature set (209 records, 2018–2026): number and percentage of records addressing each indicator, coloured by severity class (critical 0–5%; major 6–15%). No indicator fell in the moderate class (16–35%)

Table 3 Data-validated research gaps quantified from the 209-record dataset (2018–2026). Severity classes: critical (0–5%), major (6–15%), moderate (16–35%)

Research gap / Kutatási hiányosság	n/209	%	Severity / Súlyosság	Scientific consequence / Következmény	Priority action / Teendő
Commercial-scale (≥10,000 birds) intervention trials	0	0.0	Critical	No translation evidence in this dataset; all intervention findings from controlled pens	Multi-farm controlled trials in commercial houses
Germ-free / gnotobiotic models	1	0.5	Critical	Causality of microbiota effects on host phenotype rarely testable	Germ-free chick colonisation models for mechanistic validation
Longitudinal / multi-timepoint designs	2	1.0	Critical	Microbiota succession under intervention largely unknown	Repeated sampling at hatch, d 7, 14, 21, 35 and slaughter

Research gap / Kutatási hiányosság	n/209	%	Severity / Súlyosság	Scientific consequence / Következmény	Priority action / Teendő
FMT / microbiota transplantation	2	1.0	Critical	Causality of microbiota–performance links rarely tested directly	FMT from high-FE donors to gnotobiotic or low-FE recipients
Gut–bone axis studied	2	1.0	Critical	SCFA–bone mineralisation link largely unexplored in poultry	Bone densitometry plus caecal SCFA in RS-supplemented layers
Turkey studies	2	1.0	Critical	A major poultry sector nearly absent from microbiome–metabolome research	Species-specific intervention studies in turkeys
Indole/tryptophan metabolites measured	3	1.4	Critical	AhR-mediated mucosal immunity essentially unmeasured	Targeted LC-MS for ICOOH, IAA, IPA alongside microbiome analysis
Proteomics used	3	1.4	Critical	Host protein-level responses to the microbiota largely unstudied	Intestinal mucosa proteomics alongside microbiome analysis
Epigenomic regulation characterised	5	2.4	Critical	Genome-wide effects of butyrate as HDAC inhibitor unmeasured	Methylation (RRBS/WGBS), histone ChIP-seq, miRNA profiling of caecal epithelium
Receptor-level mechanistic studies	7	3.3	Critical	GPR41/43, FXR, TGR5, AhR roles largely assumed from mammals	Avian cell-line and in vivo receptor expression and ligand studies
BCFA / protein-fermentation risk	7	3.3	Critical	Novel proteins (insect, SCP) adopted without caecal BCFA safety data	Caecal BCFA, phenol and ammonia profiling for each novel protein
Gut–brain axis studied	8	3.8	Critical	Links of serotonin and feather pecking to the microbiome rarely measured	Paired brain and gut metabolomics in laying hen welfare studies
Duck / waterfowl studies	8	3.8	Critical	Distinct gut anatomy and production systems poorly characterised	Duck caecal microbiome–metabolome atlases
Shotgun metagenomics used	12	5.7	Major	Species-level taxonomy and functional genes unknown in most studies	Paired 16S and shotgun metagenomics in intervention studies
Bile acids measured	14	6.7	Major	Secondary bile acid axis (DCA, NE prevention, HDP) underexplored	LC-MS bile acid profiling of caecal and ileal contents
Laying hen studies	19	9.1	Major	FLHS, feather pecking and bone disorders inadequately covered	Longitudinal layer studies from pullet to late lay
Multi-omics integration (≥2 layers)	31	14.8	Major	Microbiota–metabolite causal chains cannot be built in most studies	Microbiome and metabolome co-profiling in the same animals

3. táblázat. A 209 közleményből álló adathalmaz (2018–2026) alapján számszerűsített kutatási hiányosságok. Súlyossági kategóriák: kritikus (0–5%), jelentős (6–15%), mérsékelt (16–35%)

7.1 The largest translational gap: commercial-scale intervention trials

None of the 209 records was coded as a controlled intervention trial conducted at commercial scale (≥10,000 birds). This does not mean that no microbiome research takes place on farms: observational studies of commercial flocks and analyses of farm-level factors such as housing, litter, flock age and management exist and show that these factors shape the chicken gut microbiota *(Kers et al., 2018)*; in broiler breeders, for example, prolonged litter exposure of hatching eggs reduced hatchability *(Csitári et al., 2025)*. Such studies were not deliberately excluded: the search string (Section 2.1) contained no terms for farm or commercial conditions, so on-farm studies, most of which are observational, were largely not retrieved. Within the dataset, *Zeng et al. (2025)* compared rearing systems in Lueyang blackbone chickens, but in experimental groups rather than at commercial scale. The intervention findings summarised in this review—the DCA–NE relationship, SCFA responses to stimbiotics and the phage–probiotic combinations—were obtained in experimental pens or cages with typically 6–40 birds per replicate *(Kim et al., 2024; Jonchère et al., 2025; Choi et al., 2026)*. Commercial houses holding 20,000–50,000 birds differ qualitatively: endemic pathogen pressure, ammonia accumulation, feed pelleting (which reduces the viability of some probiotics) and reused litter all influence the microbiota. Bridging this gap requires controlled trials under commercial conditions, preferably across several farms.

7.2 Indole/tryptophan and bile acid metabolites

Despite strong mechanistic evidence that AhR-activating indole metabolites modulate mucosal immunity, upregulate nutrient transporters and protect against coccidiosis *(Park et al., 2022)*, only 3 of the 209 records (1.4%) measured them. Similarly, although DCA has well-documented roles in pathogen clearance, HDP induction, NE attenuation and bile acid homeostasis *(Kim et al., 2024; Alrubaye et al., 2019; Bansal et al., 2020; Zhang et al., 2026)*, bile acids were measured in only 14 records (6.7%). For both classes the basic science exists but routine measurement does not; targeted LC-MS panels should become standard in intervention studies.

7.3 The epigenomic gap

Butyrate is one of the most potent endogenous HDAC inhibitors known, so microbial SCFA production can directly alter gene regulation in the intestinal epithelium. Nevertheless, only 5 of the 209 records (2.4%) characterised epigenetic outcomes. *Chen et al. (2023)* identified the butyrate–miR-204–ACSS2 axis as a regulator of lipogenesis in chickens, showing that epigenetic mechanisms are already operating in the systems under study. The lack of systematic methylation, ChIP-seq or miRNA profiling in microbial intervention studies is therefore a structural gap.

7.4 Multi-omics integration remains the exception

Only 31 of the 209 records (14.8%) combined two or more omics layers. Moreover, 47 records reported metabolomics without microbiome analysis and 26 reported microbiome analysis without metabolomics, indicating that the two research communities often work in parallel without integrating their data. As a result, the literature is rich in associations but weak in causal interpretation. Studies that integrated several layers—for example *Wang et al. (2022), Xu et al. (2025)* and *Asif et al. (2026)*, which combined microbiome analysis with SCFA profiling, hepatic transcriptomics and serum or hepatic metabolomics—revealed relationships that remain invisible in single-omics studies.

7.5 Limitations of this review

Several limitations affect the interpretation of this review. First, the search used a single database *(Web of Science Core Collection)*, a single search string and a fixed time window (2018–2026); the string did not include terms for specific additive classes or for farm or field conditions, so relevant studies indexed elsewhere, published earlier, or not captured by the search terms are missing; this applies in particular to on-farm studies (Section 7.1). Second, the narrative synthesis covers 78 studies selected purposively for relevance, without a formal screening protocol, and is not exhaustive; the overviews of individual additive classes and of the gut microbiota are correspondingly limited, and selection bias cannot be excluded. Third, the gap indicators were coded from all 209 retrieved records, including records on non-poultry hosts that the Topic search returned because they mention poultry, so the percentages slightly understate coverage within poultry studies proper; moreover, some indicators depend on how methods were reported in abstracts. Fourth, no formal risk-of-bias assessment or meta-analysis was performed, and the evidence-strength ratings in *Table 1* are qualitative. Finally, most included studies were conducted in experimental facilities with small groups of birds, which limits the generalisability of their results to commercial production.

8. Conclusions

This review synthesises 78 studies selected from 209 records retrieved by a structured search (2018–2026) to provide an integrated mechanistic picture of the interactions among poultry diet, gut microorganisms, metabolites and host physiology. Within the limits of this literature set (Section 7.5), and with the caveat that nearly all evidence derives from controlled experimental conditions, the following conclusions are supported:

- Butyrate is a central mechanistic link between dietary interventions and gut outcomes. Increases in caecal butyrate—whether achieved through probiotics, prebiotics, enzyme-mediated XOS release or organic acids—were consistently associated with improved barrier integrity, reduced pathogen susceptibility and improved FCR across the intervention categories examined *(Kim et al., 2024; Singh et al., 2021; Al-Baadani et al., 2024; Adewole et al., 2021)*.
- In the studies that compared them directly, combined strategies outperformed single interventions: enzyme plus prebiotic, organic acid plus fibre, and phage plus probiotic combinations gave larger responses, consistent with complementary mechanisms acting at different points of the diet–microbiota–metabolite chain *(Singh et al., 2021; Jonchère et al., 2025; Adewole et al., 2021; Choi et al., 2026)*.
- Secondary bile acids and indole metabolites are mechanistically important but rarely measured: bile acids were measured in 14 and indole metabolites in 3 of the 209 records, despite their documented roles in pathogen control, HDP induction and mucosal immunity *(Kim et al., 2024; Alrubaye et al., 2019; Park et al., 2022)*.
- Translation to commercial production is the most important gap identified in this dataset: no record described a controlled intervention trial at commercial scale, and the mechanistic findings reviewed here were generated under experimental conditions that do not fully represent commercial environments *(Lee et al., 2022; Kers et al., 2018)*.
- Multi-omics integration and longitudinal designs are needed for causal inference. With only 14.8% of records combining two or more omics layers and 1.0% using longitudinal designs, the analysed literature cannot yet establish the causal chains that precision nutrition requires *(Lee et al., 2022; Utkina et al., 2025; Xu et al., 2025)*.

The mechanistic basis described here is promising, but its practical value depends on better-designed, multi-omics, longitudinal and commercially validated research programmes that bridge the gap between mechanistic understanding and practical application

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Supplementary Material

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