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Review

Phytochemically Rich Food-System By-Products in Ruminant Diets: Nutritional and Health Benefits from Animals to Humans within a Circular Bioeconomy

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Abstract

Food-system by-products (FSBP), including agricultural by-products, agro-industrial co-products, and food-processing residues, represent an underused source of nutrients and plant secondary compounds with significant potential in ruminant feeding systems. This review synthesized 96 peer-reviewed studies published between 2000 and 2025 on phytochemically rich FSBP in ruminant diets, focusing on composition, rumen fermentation, animal health and performance, product quality, and environmental outcomes. Across the studies, many FSBP were enriched in polyphenols, tannins, and other bioactive phytochemicals that can function as natural plant extracts in ruminant diets. When appropriately incorporated into feedlot and other high-concentrate systems, FSBP can modulate rumen fermentation, improve nitrogen use efficiency, attenuate oxidative and inflammatory stress, and exert antimicrobial, antiparasitic, and anthelmintic properties, thereby supporting immune function, animal health, and productive performance. These same health-related properties may also be reflected in animal products such as milk and meat. In particular, polyphenol-rich FSBP can modify fatty acid profiles, enhance antioxidant capacity, and increase the abundance and

diversity of bioactive metabolites in these products, with potential implications for human nutrition and related health benefits. Emerging evidence supports biologically plausible biochemical linkages from plants, through animals, to humans, through which these functional properties may propagate along the food chain. Effective use of FSBP requires careful matching of fiber, protein, and phytochemical characteristics to ration composition, calibration of inclusion levels to avoid adverse effects on intake or digestibility, and processing methods such as drying, ensiling, or fermentation to stabilize composition and, in some cases, enhance bioavailability of key compounds. In intensive ruminant systems, these strategies may also reduce reliance on selected synthetic production inputs, mitigate methane and nitrogen emissions, improve life-cycle resource efficiency, and reduce competition for human-edible feed ingredients. Overall, phytochemically rich FSBP represent a promising pathway to enhance ruminant health and product quality, and to deliver downstream nutritional and health-related benefits while valorizing food-chain residues within a circular bioeconomy.

Keywords

Bioactive compounds; tannins; antioxidant activity; feedlot cattle; gut microbiota; meat quality; milk composition; metabolomics; methane mitigation

1. Introduction

Growing global demand for animal-source foods is intensifying pressure on limited land, water, and feed resources [1]. Food systems generate large volumes of residues and co-products from processing fruits, vegetables, grains, oilseeds, coffee, tea, herbs, and spices. Food-system by-products include agricultural by-products, agro-industrial co-products, and food-processing residues. Agricultural by-products originate at the farm stage. Food processing residues arise during the conversion of crops into foods. Agro-industrial co-products are generated from industrial extraction or fermentation processes. This sequence creates a waste-to-resource pathway across the food system that can be intercepted before disposal. Many products are treated as waste or low-value feedstuffs despite containing nutrients and plant secondary compounds (PSCs). Correddu et al. [1] synthesized evidence showing that olive- and grape-chain residues, citrus by-products, and coffee-derived matrices are widely available examples with both nutrient value and PSC bioactivity. Despite this availability, many materials remain underutilized or are disposed of at environmental cost, forfeiting nutritional and phytochemical value and creating avoidable waste burdens [2]. They also contribute to the food-waste component of climate change.

Ruminants provide a practical pathway to valorize these streams before disposal. Rumen microbial fermentation enables the conversion of fiber-rich, human-inedible substrates into meat and milk [3, 4]. Sharma et al. [5] reported that crop residues provide a long-standing precedent for this upcycling capacity. Conventional agro-industrial by-products such as beet pulp and citrus pulp further demonstrate successful feed integration at scale [6]. Meat and milk also provide a direct link to human nutrition because diet-driven changes in rumen metabolism and systemic partitioning can be reflected in the biochemical composition of animal-derived foods consumed by humans [7].

Interest in food-system by-products, therefore, extends beyond nutrient substitution. Many by-products supply fermentable fiber, residual protein, and energy, while also containing bioactive phytochemicals, including polyphenols, phenolic alcohols, flavonoids, tocopherols, and other antioxidant compounds [3]. Olive-chain residues, grape pomace, citrus pulp, and coffee cherry pulp often concentrate these compounds because processing retains peels, skins, seeds, and pulp fractions rich in secondary metabolites. Variation in PSC profiles and macronutrient structure helps explain why fermentation shifts and downstream responses differ across by-products. A functional grouping of phytochemically rich by-products helps interpret this heterogeneity and organize mechanistic expectations (Figure 1). Polyphenol- and tannin-rich, protein-binding matrices include olive pomace and winery by-products such as grape pomace [8]. Pectin-rich, rapidly fermentable fiber matrices include citrus residues and sugar beet pulp [9]. Lipid-containing matrices include nut-derived residues, such as hazelnut skin [10]. High-volume fermentation-derived co-products include brewer's spent grain and distillers' type residues. Dose-limited alkaloid-phytochemical matrices include coffee residues, where inclusion must be calibrated. Standardized tannin sources, including chestnut- and quebracho-derived extracts, are also used in some studies to isolate dose-dependent effects and clarify mechanisms [11, 12]. This framing emphasizes that responses depend on PSC class, matrix structure, processing, and inclusion level rather than by-product origin alone.

Evidence from well-studied regions illustrates feasibility. Bionda et al. identified olive-derived by-products, such as olive cake, pâté, and spray-dried olive mill wastewater, as suitable for incorporation into diets for dairy cows, sheep, goats, and beef cattle across Mediterranean and related agro-ecological regions [13, 14]. Multiple feeding trials with grape pomace, citrus pulp, and coffee cherry pulp across Europe, the Middle East, and tropical regions similarly indicate that these by-products can support performance and enhance aspects of meat and milk quality when included at appropriate levels [15, 16]. Studies with grape pomace show that anthocyanin- and proanthocyanidin-rich winery residues can improve oxidative stability and fatty acid profiles of meat and milk while exhibiting antioxidant, anti-inflammatory, and antimicrobial activity [17, 18]. Citrus peel and dehydrated orange pulp, which supply flavanones and vitamin C, enhance plasma antioxidant status, inhibit food-borne microbes, and increase the antioxidant capacity of cheeses in dairy goats [19-21]. Olive by-product studies report that olive cake and olive mill wastewater, characterized by hydroxytyrosol, tyrosol, and related phenolics, can improve the oxidative stability of milk, cheese, and meat while exerting antioxidant, cardioprotective, and antimicrobial effects [6, 22, 23]. Coffee and tannin-supplements have antiparasitic and anthelmintic activity, including reduced gastrointestinal nematode burdens and modulation of immune and oxidative markers in small ruminants [24].

Mechanistic synthesis across matrices indicates consistent pathways. Phytochemically rich by-products can modulate rumen fermentation and microbial communities, improve nitrogen utilization and epithelial integrity, and influence oxidative and inflammatory status, with downstream effects on immune function, parasite load, metabolic homeostasis, and the hygiene, composition, and shelf life of meat and milk [25-27]. Microbiome analyses show that olive by-products can selectively shift rumen microbial communities and fermentation pathways, linking animal-level responses to reduced methane production and increased nutrient efficiency [28]. Ecological and economic assessments also suggest that replacing conventional feeds with locally available by-products can reduce feed costs, improve resource efficiency, and align livestock systems with circular bioeconomy principles [15].

Despite these promising mechanisms and system-level opportunities, important limitations remain in the current evidence base. Studies consistently show substantial variability in by-product composition and processing methods, the presence of antinutritional factors, limited long-term animal trials, and a strong geographic concentration of research in Mediterranean countries and a few emerging regions. In addition, evidence for human health benefits remains largely indirect, relying primarily on improvements in meat and milk composition and *in vitro* antioxidant indicators rather than on direct clinical or metabolic outcomes. Fleming et al. [29] showed that beef from cattle finished on phytochemically diverse pastures altered postprandial plasma profiles of key lipophilic metabolites in human consumers compared with beef from animals raised on standard pastures. These findings provide emerging evidence that forage phytochemical diversity can influence consumer metabolism and support the plausibility of plant-animal-human biochemical linkages. Although comparable evidence is not yet available for phytochemically rich food-system by-products, this finding strengthens the biological plausibility that such by-products could also influence human metabolic responses indirectly through their effects on meat and milk composition. This review synthesizes current knowledge on phytochemically rich food-system by-products in ruminant diets, focusing on their nutritional and phytochemical characteristics; effects on ruminant performance, health, and rumen function; transfer of bioactive compounds to meat and milk; and implications for human nutrition, as well as environmental and economic dimensions within a circular bioeconomy. A conceptual overview of these plant-animal-human and circular bioeconomy linkages is shown in Figure 1.

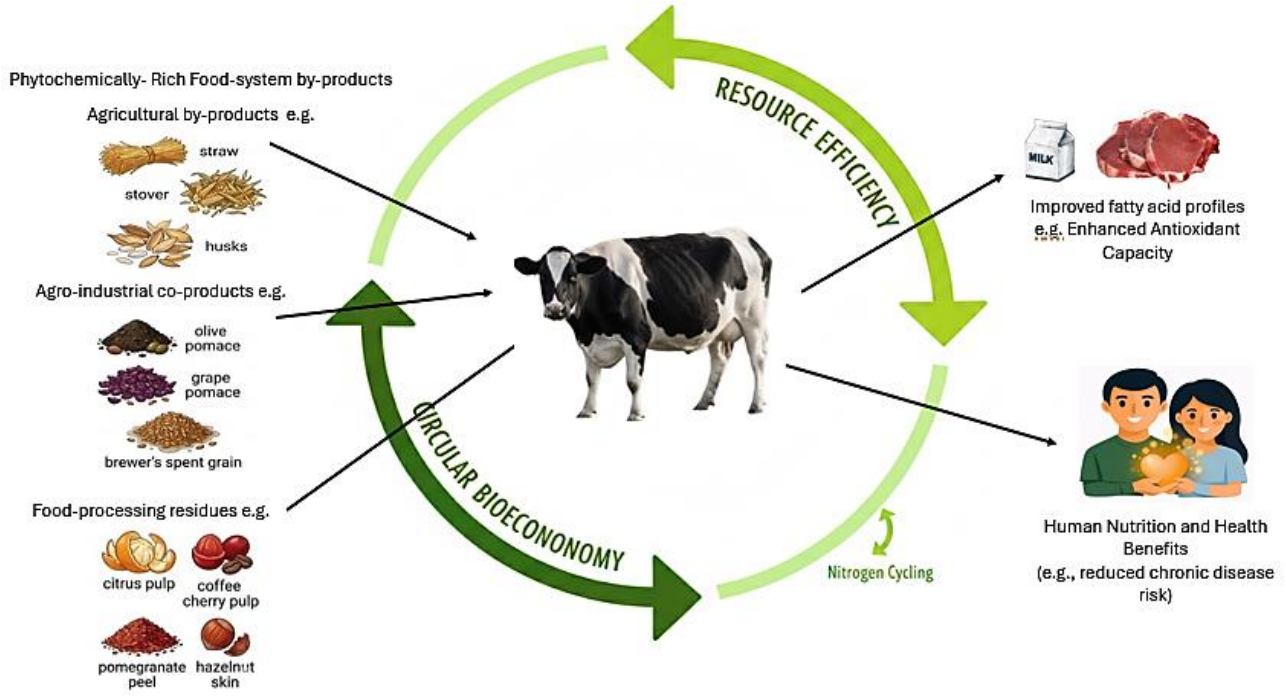

Figure 1 Conceptual representation of phytochemically rich food-system by-products fed to ruminants and potential pathways linking rumen modulation and metabolic health to improved meat and milk quality, human nutritional benefits, and circular bioeconomy outcomes such as resource efficiency and nitrogen cycling.

2. Methodology

This review was conducted as a structured narrative synthesis of peer-reviewed literature examining phytochemically rich food-system by-products as sources of nutrients and plant secondary compounds (PSCs) in ruminant diets, with emphasis on rumen fermentation, animal performance, product composition, and environmental sustainability. While olive cake, grape pomace, citrus pulp, and coffee cherry pulp are among the most extensively studied examples and therefore receive particular attention, the review also considers broader categories of agro-industrial co-products known to contain PSCs, including tomato pomace, oilseed meals, brewer's spent grain, and selected fruit and herbal residues when supported by ruminant-specific evidence.

Literature research was conducted using Scopus, Web of Science, PubMed, and CAB Abstracts as primary bibliographic databases, covering publications from 2000 to March 2025. Google Scholar was used as a supplementary tool to identify recently published studies and to perform forward and backward citation tracking of key articles. Reference lists of relevant primary studies and review papers were manually screened to ensure comprehensive coverage. Search terms combined by-product descriptors with PSC-related terms (e.g., plant secondary compounds, polyphenols, tannins, flavonoids, phenolic acids, saponins, terpenes) and outcome-related terms (e.g., rumen fermentation, nitrogen use efficiency, methane, milk fatty acids, meat quality, oxidative stability, life cycle assessment).

Studies were included if they involved ruminant species and reported chemical or phytochemical characterization, rumen fermentation responses, animal performance outcomes, transfer of bioactive compounds into milk or meat, or environmental and techno-economic assessments. *In vitro* studies were included when directly relevant to rumen fermentation or PSC bioactivity, and when they had clear implications for *in vivo* systems. Non-peer-reviewed sources, studies lacking compositional or animal-response data, and publications focused exclusively on non-ruminant species were excluded. In total, 96 peer-reviewed articles met the inclusion criteria and were evaluated in this synthesis. Given heterogeneity in PSC profiles, processing methods, inclusion levels, analytical techniques, and experimental design, findings were synthesized qualitatively rather than through formal meta-analysis.

3. Discussion

3.1 Nutritional and Phytochemical Characteristics of Food-System By-Products

Agricultural by-products and food processing residues including grape pomace and wine industry wastes, coffee pulp, citrus peels and extracts, olive pomace and olive tree leaves, and diverse fruit and vegetable residues consistently function as dual-purpose feed resources in ruminant systems, supplying both nutrients and concentrated plant secondary compounds (PSCs) [28, 30, 31]. These matrices typically contain moderate to high levels of structural carbohydrates (NDF and ADF), variable crude protein, and, in some cases, residual lipids that contribute unsaturated fatty acids, together with bioactive compounds such as polyphenols, condensed and hydrolyzable tannins, saponins, flavanones, phenolic acids, and essential oils [31, 32]. The concentration of extractable PSCs (as reported across studies using differing extraction methods) varies substantially among matrices, ranging from 2-6% in coffee pulp to 10-18% in hazelnut skin and 8-15% in milk thistle cake (Table 1). When present, this lipid fraction contributes unsaturated fatty acids that may

independently influence rumen biohydrogenation and, in some contexts, methane yield via lipid-associated hydrogen sinks and altered microbial routing. Crude protein content also differs markedly, with milk thistle cake providing 15-25% CP compared with 6-10% in citrus residues, indicating distinct functional roles as protein supplements versus primarily fermentable fiber or phytochemical sources (Table 1).

In contrast, conventional concentrate feeds (e.g., cereal grains) generally have low PSC density and function primarily as energy sources rather than modulators of rumen microbial ecology. Fermentation-derived co-products such as brewer's spent grain and distillers dried grains are additional high-volume food-system residues characterized by moderate to high neutral detergent fiber (45-60%) and elevated crude protein (18-30%) (Table 1), but comparatively lower phenolic density than fruit-derived matrices; thus, they function primarily as fermentable fiber and protein sources rather than concentrated PSC carriers. These compositional contrasts underscore that food-system by-products differ not only in phytochemical density but also in macronutrient architecture, which interacts with PSC effects to determine rumen and systemic responses (Figure 2).

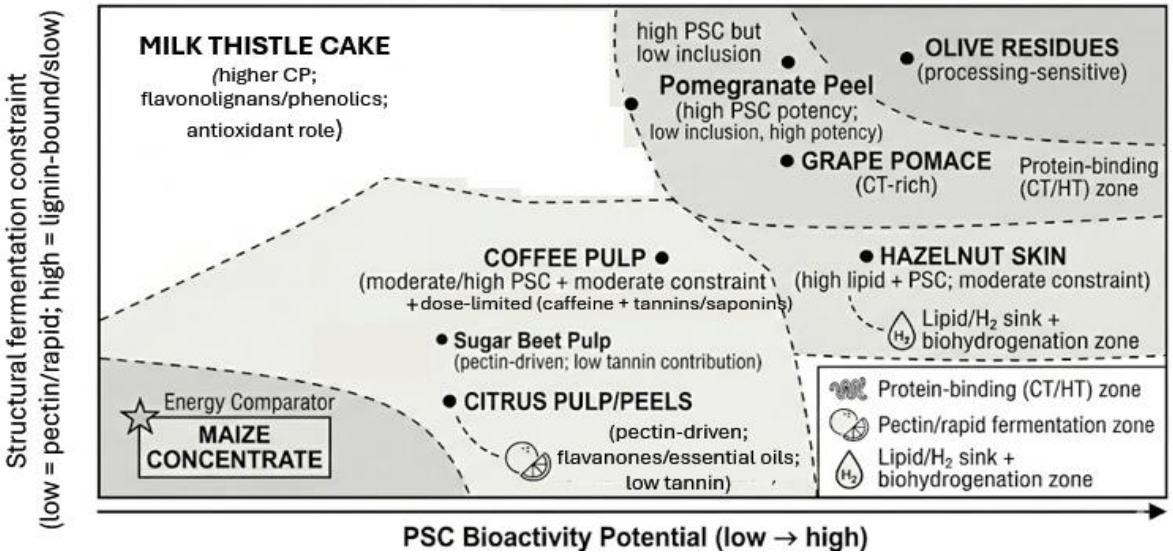

Figure 2 Conceptual mapping of Table 1 food-system by-products by PSC bioactivity potential and structural fermentation constraint. Feeds are positioned along gradients of PSC bioactivity potential (low → high) and structural fermentation constraint (low = pectin-rich/rapid fermentation; high = lignin/fiber-bound/slow fermentation) to illustrate three dominant mechanistic archetypes: (i) protein-binding matrices enriched in condensed or hydrolysable tannins (CT/HT; olive residues, grape pomace, pomegranate peel), (ii) pectin-driven rapid fermentation matrices with relatively low tannin contribution (citrus pulp/peels; sugar beet pulp), and (iii) lipid/H_2-sink matrices with potential to influence biohydrogenation (hazelnut skin). Coffee pulp is shown as a dose-limited intermediate matrix (caffeine + tannins/saponins), while milk thistle cake is positioned as a higher-CP, phenolic/flavonolignan-rich supplement with antioxidant functionality. Maize concentrate is included as a low-PSC energy comparator. Note: dashed regions are conceptual (not to scale) and summarize typical profiles reported in Table 1; placement may shift with cultivar, processing (drying, fractionation, extraction), and storage.

Mechanistically, PSC-rich residues influence rumen ecology through tannin-mediated protein binding that moderates ruminal degradation, saponin-driven protozoal suppression, and selective antimicrobial effects of polyphenols and essential oils. Reported outcomes include reduced methane emissions, lower protozoal abundance, shifts in volatile fatty acid profiles toward propionate, and improved nitrogen utilization efficiency [22, 30, 33, 34]. However, many methane and fermentation responses derive from controlled *in vitro* systems, and *in vivo* results vary with inclusion level, basal diet composition, species, adaptation period, and analytical approach [30]. Extract-based interventions deliver more concentrated and standardized phytochemical exposure than whole-matrix by-products, limiting direct comparability across studies and practical feeding conditions. These mechanistic patterns are reflected across specific matrices. Olive residues are characterized by phenolic alcohols and secoiridoids, such as hydroxytyrosol and oleuropein, compounds associated with rumen modulation and the transfer of antioxidants into milk [28, 35] (Figure 2). Grape pomace and related winery residues are particularly rich in condensed tannins, proanthocyanidins, anthocyanins, and phenolic acid compounds [33, 36]. These compounds are frequently linked with altered fermentation profiles and improved oxidative stability of animal products [37-40], although responses remain dependent on source composition and processing method. Citrus residues provide flavanones, including hesperidin and naringin, as well as essential oils and pectin. Dairy studies using lipidomic and microbiome metabolomics approaches indicate improvements in milk quality traits and metabolite signatures [41-43]. Similarly, sugar beet pulp, a residue of sugar extraction, is characterized by high pectin and low lignin content and promotes rapid propionate formation in the rumen without substantial tannin contribution [44, 45]. Its fermentation profile contrasts with tannin-dominant matrices. Alamgir [46] and Loncke et al. [47] highlighted that shifts in volatile fatty acid proportions may arise from differences in carbohydrate structure rather than from secondary metabolite concentration.

Table 1 Typical nutritional composition (%DM basis) of selected phytochemically rich food system by-products compared with a cereal-based concentrate.

By-product	Source	NDF (%)	CP (%)	EE (%)	Dominant Phytochemical Classes	References
Olive (cake, pomace, leaves)	Olive oil industry residues	45-65	8-14	8-15	Hydroxytyrosol, oleuropein, total phenolics	[13, 14, 22, 23, 28, 33]
Grape (pomace, marc)	Winery residues	35-55	11-18	5-12	Condensed tannins, anthocyanins, phenolic acids	[15-18, 34-39]
Citrus pulp peel extract	Citrus processing residues	20-30	6-10	3-8	Flavanones (hesperidin, naringin), essential oils	[15, 16, 19-21, 40-42]
Coffee cherry pulp	Coffee processing residue	40-55	12-18	2-6	Tannins, saponins, chlorogenic acids, caffeine	[24, 32]
Pomegranate peel	Fruit processing residue	30-50	6-12	2-5	Ellagitannins, polyphenols	[47, 48]
Hazelnut skin	Nut processing residue	30-45	10-16	10-18	Tannins, unsaturated fatty acids	[49-51]
Milk thistle cake	Oil extraction residue	25-40	15-25	8-15	Flavonolignans, phenolics	[52, 53]
Maize grain concentrate	Conventional cereal feed	8-12	8-10	3-5	Low phytochemical density	[54, 55]

All values are reported on a dry matter basis (% DM basis). Neutral detergent fiber (NDF), crude protein (CP), and ether extract (EE) are expressed as percentage of dry matter. Ranges reflect variability across studies included in the structured literature search (Section 3) due to cultivar, geographic origin, processing technology, extraction method, and storage conditions.

Coffee cherry pulp contains tannins, saponins, chlorogenic acids, and caffeine and demonstrates clear dose-dependent effects, with moderate inclusion improving protozoal suppression and nitrogen retention, while excessive inclusion can depress digestibility [34]. Protozoal suppression in ruminants aims to enhance nitrogen utilization and reduce methane emissions, as protozoa often reduce microbial protein efficiency and contribute to methanogenesis. Carob pods (Ceratonia siliqua), widely utilized in Mediterranean feeding systems, similarly contain condensed tannins and soluble carbohydrates and function as intermediate matrices linking forage-derived tannin systems with agro-industrial residues. Their inclusion has been associated with moderated ruminal protein degradation and improved oxidative stability of animal products under controlled inclusion levels [24]. Beyond these core matrices, multi-by-product feeding strategies combining grape, pomegranate, olive, and tomato residues have improved milk fatty acid profiles without reducing milk yield [48]. Extract-based studies show ellagitannin-rich pomegranate peel modify fermentation kinetics [56], proanthocyanidin-rich pine bark extracts suppress methane *in vitro* [49, 57], hazelnut skin influence dairy product volatiles and lamb proteomic responses [50-52], and milk thistle cake functioning as a dietary antioxidant under oxidative challenge [53, 58] (Figure 2). Concentrated tannin extracts derived from chestnut and quebracho represent standardized phytochemical matrices with high condensed or hydrolysable tannin density but minimal structural nutrients [59, 60]. Unlike whole-matrix by-products, these extracts provide targeted ruminal protein-binding capacity and are often used experimentally to isolate dose-dependent tannin effects.

Despite these mechanistic similarities, compositional variability is inherent across categories. PSC concentration and nutrient profile shift with plant species, cultivar, agro-ecological conditions, extraction technology, drying method, and storage duration [61]. Seasonal availability and preservation strategies, including ensiling, drying, pelleting, or spray drying, further influence nutrient stability and bioactive retention, and inadequate processing can reduce feed value [62-65]. Differences in pressing, centrifugation, destoning, solvent extraction, and refining procedures alter fiber structure, lipid retention, and phenolic density. These factors underscore the need for batch-specific analysis and cautious extrapolation across production regions and processing systems.

3.2 Animal-Level Benefits: Rumen Function, Performance, and Health

3.2.1 Processing Effects on Rumen Fermentation

Ruminants convert agro-processing by-products and food-system by-products into microbial protein and metabolizable energy. However, rumen responses depend on chemical composition, phytochemical class, inclusion level, and processing method rather than supply-chain origin. Materials rich in lignocellulose and phenolics alter rumen fermentation differently from pectin-rich substrates. Inclusion of grape pomace at 10-20% of dietary dry matter (DM) reduces ruminal ammonia concentrations by 15-30% and methane yields by 5-20% *in vivo* [66, 67]. In contrast, citrus pulp at similar inclusion levels primarily increases propionate proportion by approximately 5-10 mol/100 mol volatile fatty acids (VFA) without consistently reducing methane [68]. These responses indicate that fermentation shifts are driven by compounds rather than categories (Figure 3).

Processing further modifies both nutrient availability and phytochemical activity. Partially destoned olive cake contains 10-20% less lignin than crude pomace and improves neutral detergent fiber digestibility by 5-12% in small ruminants [69, 70]. High-temperature drying can reduce total phenolic concentration by 15-40%, altering antioxidant capacity and microbial modulation [62, 69].

Fractionation of grape pomace produces seed-rich materials containing >6-8% condensed tannins compared with <3% in skin-rich fractions, and seed-dominant fractions suppress ruminal ammonia more strongly but may reduce fiber digestibility when inclusion exceeds 15% DM [71]. Thus, processing modifies phytochemical density and biological response (Figure 3).

Phytochemical structure determines biological mechanism. Condensed tannins form reversible tannin-protein complexes at ruminal pH, reducing ruminal degradable protein and shifting nitrogen excretion from urine toward feces [15]. Moderate inclusion at approximately 2-4% of diet DM has reduced urinary nitrogen by 20-40% and blood urea nitrogen by 15-30% [72]. Hydrolysable tannins exert broader antimicrobial effects and have reduced methane by 10-15% at inclusion levels below 5% DM [73]. However, digestibility declines when hydrolysable tannins exceed tolerable thresholds, indicating a narrower safety margin [74]. These contrasts illustrate that phytochemical class defines both efficacy and tolerance range.

Food-system by-products also follow distinct fermentation pathways depending on carbohydrate structure. Citrus pulp increases total VFA production through rapid pectin fermentation. When effective fiber is insufficient, high inclusion may suppress acetate formation and reduce fiber digestibility [75]. Brewer's spent grain (BSG) and tomato pomace provide fermentable fiber and moderate levels of phenolic compounds. *In vitro* screening studies often rank these substrates among the lower methane producers; for example, brewer's spent grains produce about 12.8% CH_4 in total gas [76]. Tomato (and related vegetable) wastes also modify rumen fermentation and microbial communities in batch and continuous cultures [77]. However, *in vivo* feeding trials replacing conventional protein with brewers' spent grains report similar enteric CH_4 yields across treatments, indicating context-dependent responses rather than a consistent percent reduction [78]. These contrasts demonstrate that methane mitigation is not an inherent property of by-products but depends on phytochemical density and interaction with the basal diet.

Dose-response patterns are nonlinear. Beneficial fermentation shifts are commonly observed at 5-15% dietary DM for most materials and below 5% for ellagitannin-rich matrices [15, 28]. Inclusion above 15-20% DM may reduce intake and apparent digestibility [14]. Extract-based interventions often report methane suppression exceeding 20% *in vitro* [79, 80], yet *in vivo* reductions are typically 5-15% due to microbial adaptation and intake regulation [15, 28]. Processing variability further complicates Interpretation. Differences in oil extraction efficiency, drying temperature, storage duration, and fractionation alter lignin concentration, lipid oxidation, and phenolic composition [81, 82]. Many studies report total phenolics without detailed phytochemical profiling, limiting comparability. Contaminant screening is also inconsistent. Fewer than 50% of feeding trials explicitly evaluate mycotoxins, pesticide residues, or heavy metals [83]. Overall, fermentation responses are compound-specific, processing-dependent, and dose-sensitive (Figure 3). Reported methane reductions range from 0-20%, nitrogen-use efficiency improvements from 15-40%, and digestibility responses vary with inclusion level [84, 85]. Standardized phytochemical characterization and controlled dose-response evaluation remain necessary for consistent Interpretation. These fermentation and nitrogen-partitioning shifts provide the mechanistic basis through which phytochemically rich by-products can influence animal performance, physiological biomarkers, and health-related outcomes, as described next in Section 3.2.2.

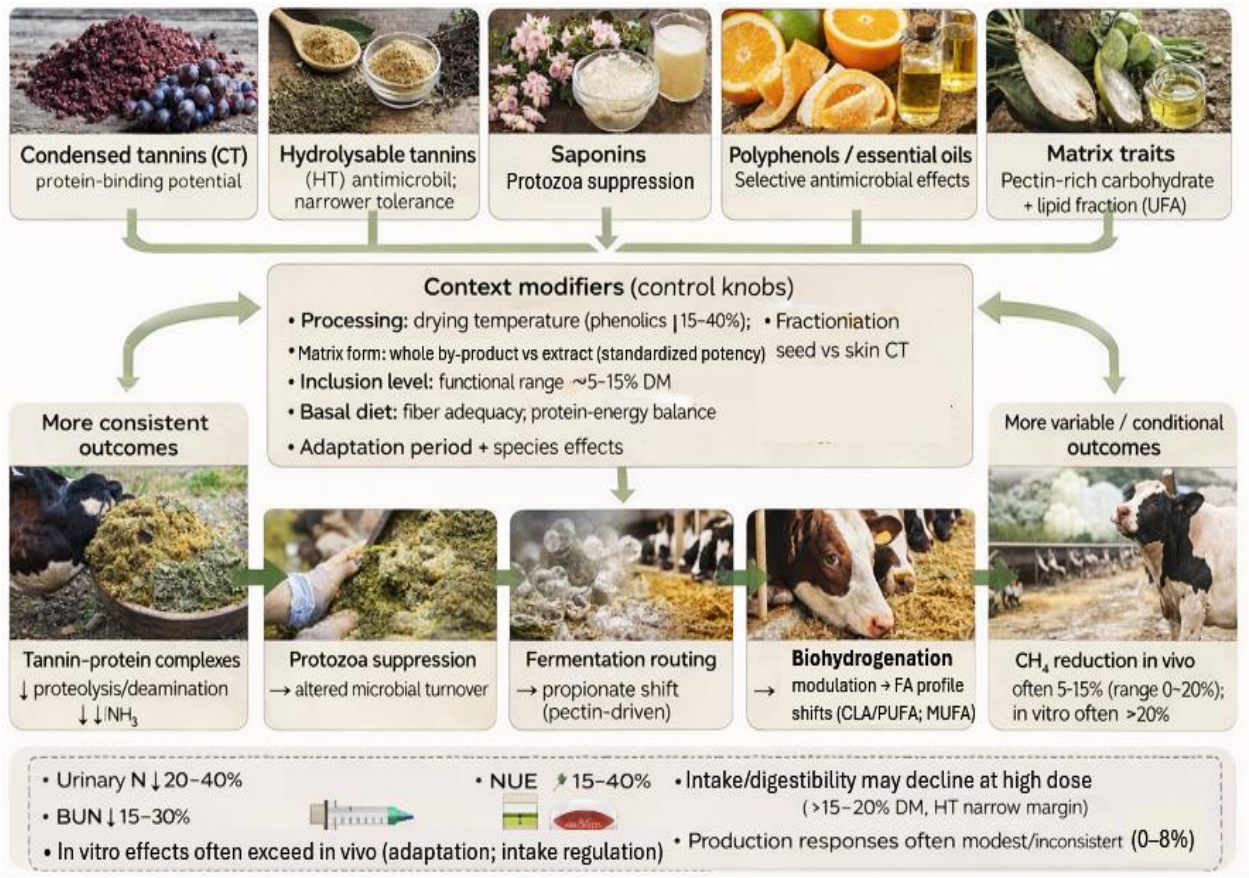

Figure 3 Mechanism context framework linking PSC class, processing, and inclusion to rumen and animal outcomes. The figure synthesizes how plant secondary compound (PSC) classes (condensed tannins, hydrolysable tannins, saponins, and polyphenols/essential oils) and matrix traits (pectin-rich carbohydrate and lipid fraction) interact with key context modifiers—processing, matrix form (whole by-product vs extract), inclusion level, basal diet, and adaptation/species effects to shape rumen mechanisms and downstream responses. Mechanistic pathways include tannin-protein complex formation that reduces proteolysis/deamination and ruminal NH_3, protozoa suppression that alters microbial turnover, fermentation routing toward propionate (notably for pectin-rich matrices), and biohydrogenation modulation influencing fatty-acid profiles (CLA/PUFA; MUFA). Outcomes are partitioned by consistency: nitrogen partitioning and efficiency responses (urinary N and blood urea nitrogen reductions; NUE improvements) are frequently reported, whereas methane mitigation is more conditional, with *in vivo* CH_4 reductions commonly 5-15% (range 0-20%) and *in vitro* effects often exceeding *in vivo* due to adaptation and intake regulation. High inclusion levels (>15-20% DM) may reduce intake and digestibility, and production responses are typically modest or inconsistent.

3.2.2 Translation of Rumen Modulation into Performance and Health Responses

The rumen fermentation shifts described in Section 3.2.1 alter the supply of metabolizable energy, amino acid availability, and systemic metabolic regulation by altering ruminal NH_3-N, VFA profiles, and microbial protein synthesis, thereby influencing nitrogen retention, tissue accretion,

milk yield, and physiological biomarkers. Moderate inclusion of agro-processing by-products and food-system by-products, typically 5-15% of dietary dry matter and occasionally up to 20% depending on matrix characteristics, generally maintains milk production, average daily gain, and carcass traits [26, 31, 86-89]. However, maintenance of production does not necessarily indicate improved biological efficiency. Instead, responses are determined by phytochemical structure, inclusion level, and dietary balance rather than material origin.

This distinction becomes evident in nitrogen metabolism. Condensed tannins reduce ruminal degradable protein through reversible tannin-protein binding. As a result, ruminal NH_3-N and blood urea nitrogen decline, and nitrogen excretion shifts from urine toward feces [4, 25]. Reported reductions in blood urea nitrogen range from 15-30%, and urinary nitrogen decreases from 20-40% under moderate inclusion. These responses indicate improved post-ruminal amino acid supply and greater nitrogen-use efficiency. In contrast, improvements in milk yield or average daily gain are often limited (0-8%) and inconsistent across studies [26]. Thus, metabolic responses appear more consistent than productive responses. A similar pattern is observed with pectin-rich food-system by-products. These matrices increase propionate proportion and glucogenic supply when effective fiber is maintained [90, 91]. Yet inclusion above 15-20% dietary dry matter, particularly for tannin-rich matrices, may reduce intake and fiber digestibility, offsetting potential metabolic benefits [92]. Productive responses are therefore dose-dependent and strongly influenced by dietary context.

The influence of phytochemicals extends beyond nutrient partitioning to oxidative and immune regulation. Phenolic compounds such as hydroxytyrosol and tyrosol reduce plasma malondialdehyde and TBARS and increase total antioxidant capacity in dairy and small ruminants [93-95]. Concurrent increases in glutathione peroxidase and superoxide dismutase activity indicate improved redox balance. Nevertheless, enhanced antioxidant status does not automatically translate into reduced morbidity or improved long-term health. Modulation of cytokine expression and reductions in matrix metalloproteinase-9 suggest regulated inflammatory signaling rather than generalized immune stimulation [94, 96]. In parallel, condensed tannin-containing materials reduce fecal egg counts and improve packed cell volume in small ruminants [15, 23], reflecting both anthelmintic activity and improved protein nutrition. Saponin-containing matrices reduce protozoal abundance and alter microbial turnover [30, 34], although excessive concentrations may impair epithelial integrity. Flavonolignan-rich residues demonstrate hepatoprotective effects during oxidative challenge [92], but supporting evidence remains largely short-term.

Collectively, these observations indicate that performance and health responses arise from compound-specific modulation of rumen fermentation, nitrogen metabolism, oxidative balance, and immune regulation. Although improvements in nitrogen-use efficiency and oxidative biomarkers are consistently reported, translation into sustained productivity, reproductive performance, or lifetime health remains insufficiently evaluated, particularly given the short duration and biomarker-centered endpoints of most trials, as evaluated in Section 3.2.3. Importantly, these animal-level shifts, especially in nitrogen partitioning, redox status, and lipid metabolism, also provide the mechanistic basis for changes in milk and meat composition discussed in Section 3.3.

3.2.3 Strengths and Limitations of Evidence on Rumen and Animal-Level Responses

The fermentation and animal-level responses described above are biologically plausible and supported by multiple controlled feeding trials. However, the strength and consistency of the evidence remain variable. While modulation of ruminal NH_3-N, volatile fatty acid profiles, nitrogen partitioning, oxidative biomarkers, and fecal egg counts is frequently reported [22, 23, 30, 34], translation of these changes into sustained improvements in productivity or long-term health outcomes is less consistent. Interpretation, therefore, requires consideration of study design, processing heterogeneity, dose-response uncertainty, and outcome selection. A primary limitation is the short experimental duration. Many trials last 4-12 weeks; these experimental periods are sufficient to detect changes in ruminal NH_3-N, volatile fatty acid profiles, blood urea nitrogen, oxidative status, and parasite indicators [97]. However, these indicators are not sufficient to evaluate long-term microbial adaptation, reproductive performance, disease incidence, or lifetime productivity. Adaptation of rumen microbiota to condensed tannins and other phenolics has been documented, and early fermentation responses may attenuate over time [98].

In contrast, long-term grazing systems incorporating tannin-containing forages have shown more stable nitrogen partitioning and parasite resilience under field conditions, suggesting that duration and ecological context influence the persistence of effects [99-101]. Experimental design further constrains inference. Sample sizes are often small, and graded inclusion levels are rarely tested. Most studies compare a control diet with a single inclusion rate. This approach does not define biological breakpoints or optimal inclusion thresholds. Nonlinear responses are likely but seldom modeled systematically.

Beyond fermentation metrics, plant secondary compounds demonstrate broader biological activity in grazing and supplementation systems. Ruminants grazing condensed tannin-containing forages have exhibited reduced methane intensity, lower urinary nitrogen excretion, reduced fecal egg counts, and improved packed cell volume, reflecting metabolic and anthelmintic effects under field conditions [102, 103]. Controlled supplementation with chestnut and quebracho tannins, pomegranate peel extracts, pine bark extracts, and flavonolignan-rich matrices has shown reductions in ruminal ammonia, modulation of volatile fatty acid profiles, increased antioxidant enzyme activity, decreased malondialdehyde, altered cytokine expression, and hepatoprotective responses [104, 105]. These findings indicate antioxidant, immunomodulatory, antiparasitic, anthelmintic, and metabolic regulatory properties that extend beyond simple nutrient substitution. However, most evidence derives from short-term trials and intermediate biomarkers rather than long-term production or health endpoints. In some cases, improved oxidative biomarkers did not correspond with measurable increases in milk yield or average daily gain [106, 107], indicating that physiological modulation does not uniformly translate into productive advantage. Thus, biological activity is evident, but the magnitude and durability of response remain conditional.

Processing variability introduces additional uncertainty. Agro-processing by-products such as olive cake and grape pomace differ in oil extraction efficiency, drying temperature, seed-to-skin ratio, and storage duration. These factors alter lignin concentration, lipid oxidation, and phenolic content [108]. Phenolic reductions of 15-40% following high-temperature drying have been reported [28]. Seed-dominant grape pomace fractions may contain >6-8% condensed tannins, whereas skin-dominant fractions contain <3% [29, 33, 71]. Similar variability in citrus pulp is observed depending on thendustrial processing method [109]. Many studies report total phenolics

without detailed phytochemical profiling, limiting comparability across experiments [110]. Translation from fermentation modulation to productive performance remains inconsistent. Nitrogen-use efficiency improvements of 15-40% are frequently reported [4, 25], yet increases in milk yield or average daily gain are often modest (0-8%) or absent [13]. Inclusion above 15-20% dietary dry matter may reduce intake or fiber digestibility [15, 25]. While extract-based studies sometimes report methane suppression exceeding 20% *in vitro* [111], *in vivo* reductions are typically 5-15% due to microbial adaptation and intake regulation [112]. These contrasts emphasize that reported benefits depend strongly on phytochemical density, matrix form, and basal diet context.

Safety assessment is also inconsistently addressed. Fewer than 50% of feeding trials explicitly screen for mycotoxins, pesticide residues, or heavy metals [113]. Tannins may impair mineral absorption at excessive concentrations, and saponins may disrupt microbial membranes when inclusion thresholds are exceeded [114]. Controlled mineral balance studies and long-term toxicological evaluations remain limited. Despite these limitations, the documented biological properties of plant secondary compounds provide a conceptual framework for strategic utilization. Agro-processing industries generate phenolic- and tannin-rich residues that could be stabilized, fractionated, and standardized for use as feed supplements or extract-based additives. Under controlled phytochemical concentrations, defined inclusion levels, and contaminant screening, locally processed by-products may provide biological functionality comparable to that of forage-derived secondary compounds. However, equivalence cannot be assumed without standardized compositional profiling, defined dose-response evaluation, long-term performance validation, and regulatory oversight. Overall, current evidence supports compound-specific effects of agro-processing and food-system by-products on rumen fermentation, nitrogen metabolism, oxidative balance, and parasite dynamics [113, 115]. However, heterogeneity in processing methods, limited dose-response evaluation, short study duration, and inconsistent productive responses reduce confidence in universal application. Moreover, methodological harmonization and long-term validation remain necessary before sustained productivity and health benefits can be conclusively established.

3.3 Translational Implications of Phytochemically Rich By-Products to Human Health Benefits

Across dairy and meat systems, these phytochemical-driven metabolic shifts are reflected in measurable changes in milk and meat composition, particularly the fatty acid profile and oxidative stability. Yet, the magnitude and biological relevance of these effects depend strongly on dose, matrix, processing method, and species. Olive chain residues such as olive cake, olive pomace, and olive mill wastewater generally increase monounsaturated fatty acids, particularly oleic acid, and enhance vaccenic and rumenic acids in milk and cheese, with reported reductions in atherogenic and thrombogenic indices often ranging between 15% and 35% under moderate inclusion levels [27, 31]. Grape pomace supplementation in dairy cows, sheep, goats, and finishing cattle typically elevates conjugated linoleic acid and total polyunsaturated fatty acids by 20% to 50% while reducing lipid oxidation in meat during refrigerated storage by 20% to 40%, as reflected in lower TBARS or malondialdehyde concentrations [15, 31, 116]. Citrus pulp and dehydrated orange residues tend to maintain milk yield while modestly increasing polyunsaturated fatty acids and antioxidant capacity of dairy products [117-120]. Coffee pulp supplementation in lambs has been associated with improved oxidative stability and altered fatty acid composition of meat, although inclusion levels

must remain limited due to caffeine and tannin content [121, 122]. Pomegranate peel, despite being used at substantially lower dietary inclusion rates, has demonstrated reductions in methane losses and shifts in milk fatty acid profile alongside improved antioxidant and immune markers in dairy cows, though responses are nonlinear and sensitive to tannin concentration [92, 123-125].

These compositional modifications are mechanistically linked to rumen microbial modulation and systemic metabolic regulation. Fleming et al. [29] provide experimental confirmation of a plant-to-animal-to-human biochemical continuum, demonstrating that phytochemical diversity in cattle forage directly influences human metabolomic responses following consumption of beef. In their double-masked, randomized, crossover clinical trial, cattle grazing phytochemically diverse pasture systems produced beef with elevated gamma-tocopherol and eicosapentaenoic acid concentrations, and these compounds were subsequently detected at higher levels in human plasma three to five hours postprandially. Importantly, this study did not merely show compositional variation in meat; it established a measurable trophic transfer of metabolic effects from forage to animal tissue and ultimately to human systemic biomarkers. The findings indicate that ruminants biotransform plant secondary compounds into bioactive metabolites, such as rumenic and vaccenic acids and phenolic derivatives, thereby integrating phytochemical diversity into animal-derived foods and influencing human metabolic profiles.

Direct evidence of phytochemical metabolite detection in milk and cheese further strengthens this mechanistic Interpretation. Hydroxytyrosol, tyrosol, and grape-derived phenolic metabolites have been identified in dairy matrices, albeit at low concentrations, representing a small fraction of ingested compounds [126-129]. Citrus-derived flavonoid metabolites have also been reported in milk, demonstrating that certain phenolics survive ruminal transformation, undergo absorption and hepatic conjugation, and are subsequently secreted via the mammary gland [130-133]. However, Fonte et al. [134] and Gou et al. [135] reported that transfer efficiency is highly variable and influenced by chemical structure, rumen microbial degradation, conjugation pathways, basal diet composition, and analytical detection limits. Polymeric tannins and large ellagitannins are extensively metabolized in the rumen, and only smaller phenolic acids or metabolites appear in circulation, resulting in relatively modest concentrations in milk and meat [136-139]. Species differences contribute to heterogeneity in outcomes, with goats and sheep sometimes exhibiting more pronounced shifts under comparable inclusion levels [10, 11, 19].

While the direction of compositional change generally aligns with dietary recommendations favoring reduced saturated fatty acids and increased monounsaturated and omega-3 fatty acids, caution remains necessary when extrapolating to long-term human health outcomes. Most available studies are short-term feeding trials lasting four to twelve weeks and rely primarily on compositional endpoints and oxidative markers rather than long-term functional health outcomes. Even in the Fleming et al. [29] trial, metabolomic responses were measured in the acute postprandial window, and sustained clinical implications remain to be determined. Controlled long-term animal studies, combined with rigorously designed human intervention trials, are necessary to determine whether phytochemically mediated modifications of animal-derived foods translate into consistent, clinically meaningful health benefits. Whether phytochemically rich food system by-products can mediate similar plant-to-animal-to-human biochemical effects depends on their capacity to modulate rumen microbial metabolism and alter subsequent systemic nutrient partitioning, thereby measurably influencing the biochemical composition of animal-derived foods and ultimately contributing to improved human health. Importantly, the same animal-level shifts in

methane yield and nitrogen partitioning that underpin product changes also scale to farm-level environmental performance and cost structure, motivating the circular bioeconomy perspective in Section 3.4 (Figure 4).

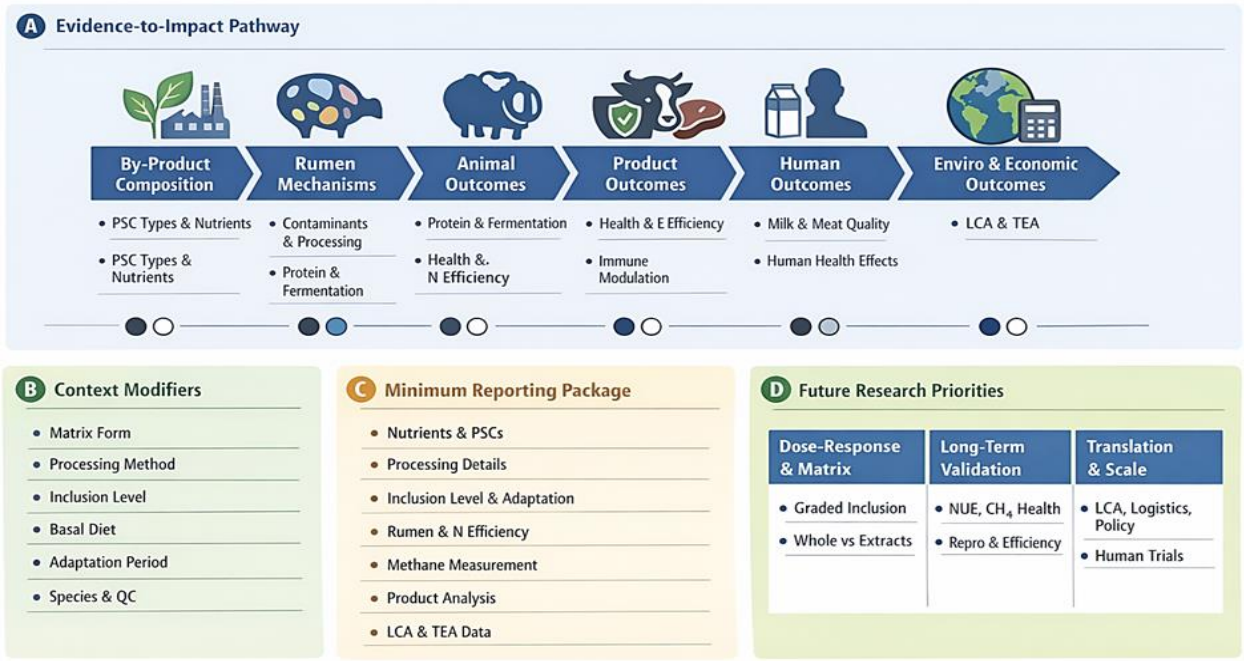

Figure 4 Evidence-to-impact translation framework and research priorities for phytochemically rich food-system by-products in ruminant diets. Panel A summarizes the mechanistic pathway linking by-product composition and processing to rumen modulation, animal outcomes, product composition, and downstream human-health and environmental implications. Evidence strength is indicated using three levels, high, moderate/conditional, and limited, reflecting consistency across studies and sensitivity to context. Panel B highlights key modifiers that drive heterogeneity in outcomes, including matrix form, processing, inclusion level, basal diet, adaptation, species, and quality-control constraints. Panel C lists a minimum reporting and measurement package to improve cross-study comparability, including nutrient and PSC characterization, contaminant screening, rumen and nitrogen-use efficiency metrics, methane measurement context, product endpoints, and life cycle and techno-economic assumptions. Panel D identifies priority research workstreams to advance translation and scalable implementation within circular bioeconomy transitions, including dose-response evaluation, long-term integrated trials, and region-specific LCA/TEA coupled with human intervention research.

3.4 Environmental and Economic Dimensions in a Circular Bioeconomy

Beyond animal- and product-level effects, phytochemically rich food-system by-products have important implications for whole-farm environmental performance and economic viability (Figure 4). Approximately twenty studies have evaluated ecological and economic outcomes when conventional feeds are partially replaced with materials containing plant secondary compounds, particularly condensed and hydrolysable tannins [3, 140]. When these by-products displace human-

edible concentrate feeds (e.g., cereals and protein meals), reductions in greenhouse gas (GHG) emissions, land occupation, and freshwater demand are frequently reported. Economic analyses commonly show 5-20% reductions in feed costs under moderate inclusion levels, particularly in regions where residues are locally available, and transport distances are minimized [61-64]. Cost savings arise from reduced reliance on imported concentrates and improved nitrogen-use efficiency [141], which can lower fertilizer demand and manure management costs [142, 143]. Fermentation-derived co-products, such as brewers' spent grain and distillers' grains, also illustrate the importance of allocation assumptions in life-cycle assessment frameworks. When treated as low-burden co-products of brewing or bioethanol production, their inclusion may reduce feed-related emission intensity relative to primary cereal cultivation. However, changes in nitrogen excretion patterns and manure emissions must be incorporated into full-system analyses to avoid overestimating mitigation benefits [144]. Economic performance also depends on residue price stability, seasonal availability, storage requirements, preservation method (drying, ensiling, pelleting), and infrastructure capacity [145]. Excessive processing intensity or long-distance transport can offset both economic and environmental gains by increasing fossil fuel inputs.

Animal-level methane responses reflect modulation of rumen microbial activity. Condensed tannins reduce methanogenic archaea activity and redirect hydrogen toward propionate formation [146] while hydrolysable tannins exert broader antimicrobial effects. Although in vitro reductions may exceed 20%, *in vivo* methane reductions typically range from 5-20% under moderate inclusion, [145, 147, 148]. Nitrogen pathways provide additional environmental leverage. Tannin-protein complex formation reduces ruminal degradable protein and shifts nitrogen excretion from urine toward feces, decreasing urinary nitrogen by 20-40% and blood urea nitrogen by 15-30% [149]. Because urinary nitrogen is the principal precursor of soil N_2O emissions in grazing systems [150-152], improved nitrogen retention can reduce environmentally labile nitrogen pools. Grazing legumes containing condensed tannins reduced methane intensity from 222 to 162 g CH_4 per kg body weight gain and lowered urinary nitrogen relative to non-tannin controls [153], while pasture supplementation with chestnut and quebracho tannins reduced blood urea nitrogen by 28% [141]. These responses indicate that environmental and economic benefits may occur concurrently when nitrogen retention improves feed conversion efficiency and reduces nutrient losses. Mechanistic simulation provides further insight into interactions among dose, allocation, and productivity. Using the MINDY model, Gregorini and Villalba [154] simulated 25 grazing scenarios incorporating tannin-containing legumes (0.05-0.20 of forage allocation) under varying allocation frequencies. Methane production and urinary nitrogen excretion increased with legume proportion due to greater dry matter intake and animal performance; however, methane yield relative to production decreased under strategic weekly allocation, and environmental costs per unit of production were lowest at 0.15-0.20 inclusion regardless of frequency. These findings demonstrate that environmental efficiency must be evaluated relative to production output rather than solely on absolute methane values. Strategic allocation that enhances productivity can reduce emission intensity and improve economic returns per unit of land and forage resources.

Whole-system Interpretation requires life cycle assessment (LCA), which integrates CH_4, N_2O, and CO_2 across defined system boundaries, including feed production, fertilizer manufacture, manure management, energy use, transport, and soil carbon dynamics. Emissions are expressed as CO_2 equivalents per functional unit (e.g., kg milk or kg carcass). Whole-farm LCA modeling in Canadian beef systems estimated a baseline emission intensity of approximately 22 kg CO_2e per kg carcass,

with enteric methane accounting for3% of total emissions and the cow-calf phase accounting for nearly 80% of system-wide GHG output [155]. Interventions targeting breeding herds reduced GHG intensity by up to 8% individually and approximately 20% when combined, whereas feedlot-focused strategies achieved reductions of <4% [155, 156]. Methane reductions measured via SF_6 or modeled through emission factors do not necessarily translate into equivalent CO_2e reductions under LCA because manure emissions, soil carbon dynamics, and feed substitution effects may offset gains. Similarly, lipid-rich or co-product diets may reduce enteric methane but alter the distribution of manure nitrogen. Environmental and economic benefits are therefore highly dependent on system boundaries, allocation assumptions, market conditions, and temporal scale. Robust Interpretation requires integrated accounting of methane, nitrous oxide, carbon dioxide, productivity response, input substitution, and cost structure rather than reliance on single emission metrics.

3.5 Future Research

Overall, current evidence supports the potential of phytochemically rich by-products to enhance circularity in ruminant systems by reducing waste, substituting human-edible feeds, improving nitrogen-use efficiency, and contributing to nutritionally improved animal products (Figure 4). However, these benefits require validation through region-specific life-cycle and techno-economic analyses that integrate methane emissions, nitrogen partitioning, land-use implications, processing energy demands, and supply-chain logistics to avoid unintended environmental trade-offs. The evidence base remains geographically and methodologically uneven. Most studies originate from Mediterranean and temperate systems, with limited representation from sub-Saharan Africa, South Asia, and parts of Latin America, where by-product composition, infrastructure, and preservation constraints differ. Trials are often short-term, use small sample sizes, and focus on single production phases, limiting inference regarding microbial adaptation, reproductive efficiency, immune resilience, mineral balance, and lifetime productivity. Standardized phytochemical characterization and harmonized analytical methods are necessary to establish clearer dose-response relationships across matrices.

Mechanistic and translational gaps also persist. Nonlinear dose-response thresholds for tannins, saponins, and mixed phytochemical matrices require systematic evaluation under both confined and grazing conditions. Comparative studies should assess whole-matrix residues versus standardized extract-based supplements at equivalent phytochemical doses to distinguish concentration effects from matrix interactions. Integration of rumen microbiome sequencing, metabolomics, immune biomarkers, and systemic metabolic profiling will strengthen causal inference linking rumen modulation to production, environmental outputs, and product composition. Concurrent use of controlled methane measurement techniques and nitrogen-use efficiency assessments is required to improve environmental resolution under practical feeding systems. Translational research must extend beyond acute metabolomic responses to long-term human clinical endpoints, evaluating whether compositional changes in milk and meat derived from phytochemically supplemented animals translate into sustained cardiometabolic or inflammatory benefits. Finally, implementation must be explicitly framed within circular bioeconomy strategies. Region-specific techno-economic assessments should account for seasonal availability, competing industrial uses, preservation infrastructure, contaminant screening, and regulatory frameworks. Standardized quality control addressing mycotoxins, pesticide residues, heavy metals, and

phytochemical stability is essential for scalable adoption. Integrating nutritional science, environmental modeling, industrial processing optimization, and supply-chain analysis will determine where phytochemically rich by-products most effectively enhance resilient circular food systems while safeguarding animal performance and human health.

4. Conclusions

Phytochemically rich food-system by-products comprise a broad and expanding resource base across diverse agro-food supply chains, extending well beyond a few emblematic matrices. When appropriately characterized and incorporated into ruminant diets, these materials can be used while generally maintaining milk and meat yields and improving key quality traits. Across studies, PSC-containing by-products frequently enhance fatty acid profiles, increase antioxidant capacity and oxidative stability of dairy and meat products, and modulate rumen fermentation, nitrogen utilization, and rumen microbiota in ways consistent with improved nutrient efficiency and potential methane and nitrogen mitigation. In addition to production outcomes, reported responses support multiple animal-health domains, including attenuation of oxidative and inflammatory stress, immunomodulatory effects, antimicrobial activity, and gastrointestinal parasite control, with antiparasitic and anthelmintic potential under calibrated inclusion levels. At farm and supply-chain scales, substituting conventional concentrates with locally available co-products can reduce waste, displace human-edible feeds, lower feed costs, and strengthen resource-use efficiency within circular bioeconomy transitions. Still, the net benefit depends on region-specific logistics, processing energy, and market context as captured by life cycle and techno-economic assessments. These benefits remain context-dependent and require cautious implementation. Composition varies widely among and within by-product streams, antinutritional factors and contaminants may be present, and preservation, logistics, and safety constraints can limit practical adoption. Short-term trials and selected regions still dominate evidence. At the same time, robust life-cycle assessment and techno-economic analysis remain limited for many by-product streams and are needed to quantify trade-offs among emissions, land and water use, transport, processing, and costs. Human health benefits arising from altered meat and milk composition should be regarded as plausible and mechanistically supported but not clinically demonstrated. Progress will depend on standardized compositional reporting, batch-specific quality control, optimized processing and inclusion strategies, and region-specific nutritional, environmental, and economic evaluation to determine where phytochemically rich by-products most effectively advance open, scalable circular-bioeconomy pathways while improving environmental efficiency, animal health, product quality, and potential human nutritional and health value.

Author Contributions

Bashiri Iddy Muzzo: Conceptualization, methodology, literature search, data curation, formal analysis, validation, visualization, writing—original draft, writing—review and editing. Frederick D. Provenza: Validation, supervision, writing—review and editing, and intellectual contribution to the interpretation and refinement of the manuscript.

Competing Interests

The author declared that there are no competing interests.

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