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Synergetic action between the rumen microbiota and bovine health

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ABSTRACT

Host-rumen-microbe interactions are essential components of many physiological processes, and therefore can affect ruminant health. Classical knowledge of rumen microbiology is based on culture-dependent methodologies, which only account for 10–20% of the rumen bacterial communities. While, the advancement in DNA sequencing and bioinformatics platforms provide novel approaches to investigate the composition and dynamics of the rumen microbiota. Recent studies demonstrated that the ruminal ecosystem is highly diverse and harbors numerous microbial communities. The composition of these microbial communities are affected by various environmental factors such as nutrition and different management strategies. Disturbance in the microbial ecology of the rumen is associated with the development of various diseases. Despite the flow of recent rumen-based studies, rumen microbiota is still not fully characterized. This review provides an overview of recent efforts to characterize rumen microbiota and its potential role in rumen health and disease. Moreover, the recent effects of dietary interventions and probiotics on rumen microbiota are discussed.

1. Introduction

The bovine gastrointestinal tract is a complex ecosystem that is responsible for overall ruminant health [1]. The resident microbial populations in the rumen and their potential roles have been the focus of extensive research in recent years. Advances in culture-independent high-throughput sequencing technology have provided new opportunities for improved phylogenetic analysis and detailed characterization of gastrointestinal microbiota [2] [3] [4]. The bovine gastrointestinal tract, including the rumen, was thought to be sterile at birth but is rapidly colonized by bacteria from the surrounding environment within the first 24 h of life [5].

Evolution of the rumen ecosystem occurs in the following precise sequence: ruminal papillae growth [6], increase in the fermentation carbohydrate and proteins [7], promotion of enzyme activity [8] and modulation of microbial colonization [9]. Inadequate development of the rumen results in poor absorption and less nutrient digestion, whereas, complete rumen maturation facilitates feed digestion and increases animal productivity. Development of the rumen microbiota are influenced by various host factors including sex, age, host genetics [10], feeding strategy [11] and environmental exposures [12]. Despite the differences in gut physiology among different species, the cattle gastrointestinal microbiome is assumed to be relevant to those of other mammals [13] [14]. Recent metagenomics studies implicate the gut microbiota as a microbial organ that influences host phenotype and genotype [15] [16]. Therefore, an increased understanding of gut microbial diversity and microbiome-host interactions would provide reference values for homeostatic communities and help to develop effective feeding strategies [17].

This review provides an overview of recent researches accomplished to characterize the bovine gastrointestinal microbial communities and its potential role in bovine health and disease. Additionally, recent hypotheses regarding the effects of dietary intervention and probiotics supplementation on the bovine rumen microbiome are also discussed.

2. Genomic tools for the characterization of rumen microbial communities

The characterization of the composition and structure of rumen microbial populations has relied on traditional culture-based

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approaches [18]. These approaches focus on easily cultured microbes [19], and only detect 11% of the rumen bacterial population [20]. Considering the vast diversity and complexity of rumen ecosystems, culture-based approaches are not suitable to fully understand changes in microbial community composition and structure [21].

For efficient characterization of the composition of rumen microbiotas, the usefulness of high-throughput sequencing technologies for understanding the potential role of microbial ecology throughout the gastrointestinal tract has been highlighted [3]. For comparative genomic studies, the 16S rRNA is the most frequently targeted gene to investigate microbial ecosystems because this gene is present in all prokaryotes and can be used for high-throughput data generation [22]. The current use of the 16S rRNA gene has revealed the complexity of gastrointestinal ecosystem [23] and established correlations between imbalances of gastrointestinal microbiota and their host health [24].

Several molecular based-techniques are used to assess the rumen microbial population, including RNA dot blot hybridization, flow cytometry [25], fluorescent in situ hybridization (FISH) [26] and quantitative real-time PCR assays [27]. Amongst these technologies, qPCR and FISH are the most widely used because it provides information about the specific site of luminal and mucosal population [26]. Fingerprinting techniques [28], restriction fragment length polymorphism analysis [29], denaturing gradient gel electrophoresis [30], and automatic ribosomal intergenic spacer analysis have also been used to characterize the complex populations at multiple gut locations [31]. These techniques are employed to identify the differences and similarities in community structure but do not provide direct sequence information [32].

With advancement in high-throughput sequencing technologies, thousands of sequences can now be produced and analyzed within a few hours [33] [34] [35] [36]. Most high-throughput sequencing studies conducted to date are based on 454 pyrosequencing [37] and the Illumina platform (San Diego, CA, USA) [33] [38] [39]. Other high-throughput sequencing platforms that can be used includes Ion Torent, SOLid and SMRT system [40]. To further characterize metagenome functional potential, metabolic profiles (metabolomics), gene expression (metatranscriptomics) and protein products (metaproteomics) should be assessed [41]. Application of these advanced techniques to animal breeding and production might serve as the cornerstone for the next-generation phenotyping required for the improvement of trait selection programs [42]. Until now, the application of metatranscriptomics to study the active functional metagenome in rumen microbiome is limited [43] [44]. Although these techniques are complex and have provided conflicting information, further advancements in this field are expected.

3. Phylogenetic diversity of rumen microbial communities

The bovine rumen acts as a type of anaerobic fermentation chamber in which rumen microbial communities synergistically interact with one another [45]. The bovine rumen harbors diverse and complex populations of bacteria (up to 10^{11} viable cells/mL), ciliate protozoa (10^4–10^7 cell/mL), anaerobic fungi (10^3–10^5 zoospores/mL), bacteriophages (10^7–10^9 particles/mL) and methanogens (10^6 cells/mL) [21]. Within this complex and diverse ecosystems, bacterial populations are constitute the predominant community that responsible for the digestion and transformation of plant fiber to short-chain volatile fatty acids (VFAs), proteins and gasses [9]. VFAs are absorbed across the rumen epithelium and serve as the primary carbon and energy sources supporting animal maintenance and growth [46]. The produced gases are used by archaea to generate methane, which is implicated in global warming and contributes to eliminating the inhibitory effect of gases on the fermentation process [47].

Traditionally, classical knowledge of the rumen microbial communities allowed the major bacterial species providing the primary nutritional sources and carrying out the primary fermentation processes to be characterized [48]. Recently, advances in genomic deep-sequencing platforms have provided beneficial and comprehensive coverage of rumen microbial ecosystems, which has allowed us to distinguish the predominant core microbiota and increased our potential to characterize functionally important uncultured microbial populations [49].

Most of the rumen sequences available in GenBank up-to-date indicate that the predominant phyla present in the rumen are *Firmicutes* and *Bacteroidetes*, in addition to a variety of anaerobic protozoa, archaea, and fungi [50]. The prevalence of the *Firmicutes* and *Bacteroidetes* phyla highlights their important roles in the rumen [51]. Each of these phyla exhibits a specific role in plant cell wall deconstruction. For example, the degradation capacity of *Firmicutes* is largely circumscribed to the cell surface, whereas, the degradation of *Bacteroidetes* is largely periplasmic or intracellular [52].

Most of the *Firmicutes* sequences are assigned to classes *Clostridia*, *Bacilli,* and *Erysipelotrichi*. Within class *Clostridia*, the predominant families include *Lachnospiraceae, Ruminococcaceae,* and *Veillonellaceae*. The predominant genera include *Butyrivibrio, Acetivibrio, Ruminococcus, Succiniclasticum, Pseudobutyrivibrio,* and *Mogibacterium*. In addition to the predominant genera, several genera are rarely reported in the rumen, including *Syntrophococcus Lachnobacterium, Oribacterium, Roseburia, Moryella, Papillibacter* and *Dialster* [50]. Within class *Bacilli,* the predominant genera were represented by the lactic acid-producing bacteria such as *Streptococcus* and *Carnobacterium* [50].

Within phylum *Bacteroidetes*, most sequences are assigned to classes *Bacteroidia* and *Sphingobacteria*, with *Prevotella* representing the predominant bacterial genus, potentially accounting for 60–70% of the observed sequence diversity [53]. The ruminal *Prevotella* are important for protein degradation and starch utilization in the rumen [54]. The most abundant bacterial taxa identified in the rumen samples in selected gastrointestinal microbiome studies are presented in Table 1.

In addition to the dominant bacterial species, the predominant ruminal archaeal sequences belonged to phylum *Euryarchaeota*, and more than 90% of archaeal sequences are represented by methane-producing genera such as *Methanobrevibacter* [50]. The predominant genera of protozoa that have been identified are *Dasytricha, Entodinium, Eudiplodinium, Ostracodinium, Diploplastron, Diplodinium, Epidinium, Polyplastron* and *Ophryoscolex* [55]. The predominant functionally important fungal genera are *Neocallimastix, Piromyces, Anaeromyces, Caecomyces, Orpinomyces* and *Cyllamyces* [18].

4. Potential role of the rumen microbial populations in bovine health

The rumen ecosystem harbors sophisticated microbial communities that play a vital role in gastrointestinal health. Host-microbe relationships are described as competitive, cooperative or combinatorial [56], all of which provide functional and metabolic capabilities that are relevant to host health and well-being [57]. The rumen microbiota can be correctly considered a metabolic organ with protective, immunological, developmental and nutritional functions [58] [59]. The protective mechanisms of the gastrointestinal tract result from the interaction between the resident microbial populations and the multilayer mucosal epithelium, which can restrict the permeability of large molecules [60] [61]. Rumen microbial equilibrium is achieved through the combination of different activities including; a constant supply of immunoglobulins [62], Toll-like receptors activity [63], peptidoglycan recognition proteins [63], pattern recognition receptors [64], and antimicrobial peptide defensins [63]. Establishing a stable commensal microbiota holds vast potential for the prevention of gastrointestinal infection, resulting in improved animal production [65] and improvements in efficiency and animal welfare [66]. Gut microbial communities also play an important role in shaping and maturation of the host immune system [67] [68]. The resident gut microbiota could influences drug metabolic activities and toxicity [69], dietary calorific bioavailability [60] [70], improve response to epithelial cell injury [71] [13],

Table 1
The most abundant bacterial taxa in rumen samples of selected gastrointestinal microbiome studies.

Citation	16 s rRNA Region	Sequencing platform	Most abundant bacterial taxa
[9]	V1−V3	454 pyrosequencing	*Prevotella, Oscillibacter, Coprococcus, unclassified Ruminococcaceae*, and *Butyrivibrio* were abundant in liquid fraction. While in solid fraction, *Butyrivibrio* and *Blautia* were significantly overrepresented.
[123]	V1− V3	454 GS-FLX Titanium	*Prevotella, Fibrobacter, Anaerovorax, Succinivibrio, Ruminococcus* and *Succiniclasticum* were the most abundant.
[5]	V3−V5	454 pyrosequencing	In 14-day old calves, the predominant genera were *Prevotella, Bacteroides, Oscillibacter, Paraprevotella, Butyricimonas*, and *Pelistega*. In 42 old calves, the abundant genera were *Bacteroides, Porphyromonas, Prevotella, Butyricimonas* and *Coprococcus*. In 12-month-old calves fed a hay diet, *Prevotella, Butyrivirbio, Treponema, Acetivibrio, Sporobacter, Coprococcus* and *Fibrobacter* were the most abundant.
[5]	V3− V5	454 GS-FLX Titanium pyrosequencing	*Prevotella, Succiniclasticum, Fibrobacter, Ruminococcus,* and *Treponema* were dominant. Exogenous butyrate infusion resulted in a drastic reduction in *Prevotella* and significant increase in the *Treponema, Ruminobacter*.
[54]	V2− V3	454 pyrosequencing	*Prevotella, Bacteriodes,clostridium, eubacterium, Blautia* and *Butyrivibrio* were the most abundant.
[124]	V3−V5	454 pyrosequencing	*Butyrivibrio, Fibrobacter, Oscillibacter, Paraprevotella, Prevotella, Ruminococcus, Succinivibrio,* and *Treponema,* accounted for 67.6% of 1 sequence reads.
[125]	V2 −V3	454 pyrosequencing	*Prevotella, Eubacterium, Dialister, Lactobacillus,* and *Clostridia* were the most abundant.
[126]	V4	Illumina Miseq	At prepartum (*Prevotella, Ruminococcaceae, Bacteroidales* and *Lachnospiraceae)* were dominant. While, at postpartum (*Prevotella, Ruminococcaceae, Ruminococcus, Bacteroidales* and Lachnospiraceae) were dominant.
[8]	V3−V4	454 pyrosequencing	The predominant bacterial genera were *Prevotella, Bacteroides, Streptococcus, Fusobacterium* and *Granulicatella.*
[127]		454 pyrosequencing	*Prevotella, Selenomonas, Psuedobutyrivibrio, Streptococcus* and *Fibrobacter* were the most abundant.
[3]	V1−V3	Illumina MiSeq	*Prevotella, Dialister, Succiniclasticum, Ruminococcus, Butyrvibrio* and *Mitsuokella* were the most abundant.
[128]	V1−V3	Illumina MiSeq	*Prevotella* was the most abundant in all samples. For the first half of lactation, *Ruminococcus* were less abundant than at the second half of lactation.
[129]	V1−V2	454 pyrosequencing and Ion Torrent (PGM)	*Prevotella* was representing the single most abundant genus in both sequencing platforms. Comparisons between both platforms at the genus level revealed differences in few genera such as *Prevotella, Ruminococcus, Succiniclasticum* and *Treponema.*
[130]	V3−V4	Illumina MiSeq	The predominant bacterial genera were *Clostridium, Prevotella, Butyrivibrio, Turicibacter, Ruminococcus, Succiniclasticum, Desulfobulbus, Mogibacterium*. Ruminal content had a greater percentage of *Prevotella, Saccharofermentans, Succiniclasticum* and *Ruminococcus*. While, ruminal epithelium presented a higher abundance of *Butyrivibrio, Mogibacterium, Treponema, Syntrophococcus, Howardella, Campylobacter, Desulfovibrio* and *Desulfobulbus.*
[131]	V4	Illumina Miseq	*Prevotella, Succinivibrio* and *Sharpea* were dominant. *Prevotella* remained stable in the rumen despite weaning strategy. Conversely, *Succinivibrio* was the most abundant in pre-weaned calves but declined following weaning.
[132]	V1−V3 and V1−V8	Illumina Miseq	*Prevotella* was the most abundant in V1−V3 and V1−V8 amplicons. The relative abundance of *Succinivibrionaceae*, *Paraprevotellaceae*, *Succiniclasticum* and *Succinivibrio* showed significance difference differences between V1−V8 and V1−V3 amplicons.
[92]		Ion Torrent	*Prevotella, Bacteroides, Parabacteroides* and *Paludibacter* were dominant. *Prevotella* decreased from lactation first to lactation third. While, *Bacteroides, Butyrivibrio, Lachnoclostridium, Eubacterium* and *Ruminococcus* increased.

and post-surgical recovery [72]. Therefore, disturbance of this complex ecosystem could have major consequences on host health.

5. Role of rumen microbiota alterations in disease

Despite the key function of the gastrointestinal microbiota in sustaining overall health (nutritional, physiological, and immunological), recent discoveries indicate that alterations in the gastrointestinal microbial ecosystem play a large role in many intestinal and extra intestinal disorders [18]. Understanding the potential roles of the homeostatic rumen microbial population in both health and disease is important for the identification of biomarkers for gastrointestinal diseases and the development of new therapeutic approaches. In human medicine, disruption of the gut microbiota or dysbiosis is linked to processes involved in several diseases, such as obesity, insulin resistance [73], inflammatory bowel diseases [74], circulatory disease [75], multiple sclerosis [76], central nervous system and atopic disorders [77]. Additionally, dysbiosis of the gastrointestinal microbiota plays an important role in the metabolic and immunological capacities of the host [78]. Although several studies have examined the potential function of the gut microbiota in human health and disease, studies that focus on ruminants are limited. Most digestive disorders that occur in ruminants, such as ruminal bloat and acute and subacute ruminal acidosis (SARA), are associated with disturbance of the composition and function of the rumen microbiota [79].

Ruminal acidosis is a subset of acute digestive disorders characterized by intermittent depression of rumen pH for prolonged periods due to VFA accumulation [80] [81]. Unlike acute lactic acidosis, SARA is a more chronic condition and is not conjoined with agglomeration of lactic acid in the rumen [82]. The collateral effects of SARA includes epithelial damage in the ruminal mucosa [83], decreased milk production [84], reduced fiber degradation, laminitis [85], and decreased dry matter intake [86]. The severity of these conditions has also been linked to instability of the microbial flora [87], and decreases in the absorptive capability of the ruminal epithelium, resulting in an impaired rumen ecosystem [24]. Alterations in the ruminal microbiotas have been declared to potentially play a role in ruminal acidosis [24] [88] [89]. The most common bacterial taxa detected in SARA are *Lactobacillus*, *Streptococcus*, *Succiniclasticum* and *Clostridium* [89]. Studies performed on feedlot cattle and dairy cows that are gradually adapted to a high-grain diets indicate that SARA is significantly associated with disruption of the microbial community structure [20]. The majority of these studies have revealed decreases in proportions of *Fibrobacter succinogenes* and *Butyrivibrio fibrisolvens* and increseses in the proportion of *Proteobacteria, Megasphaera elsdenii*, *Streptococcus bovis, Selenomonas ruminantium,* and *Prevotella bryantii*.

Frothy bloat is one of the primary causes of morbidity and mortality in feedlot cattle [90]. The onset of bloat and its effect on rumen microbial communities are variable among animals and can be attributed to the rate of fermentation and ruminal gas production [91]. A previous study identified distinct microbial populations between bloated and non-bloated calves, with increases in the relative abundance of *Clostridium, Eubacterium* and *Butyrivibrio* and decreases in the relative abundance of the *Prevotella* and *Ruminococcus* in bloated cattle [92]. The alterations in the rumen microbiota associated with selected gastrointestinal diseases are depicted in Table 2. These rumen microbiota

Table 2
Changes in the rumen microbiota associated with selected gastrointestinal disease.

Citation	Condition	16 s rRNA region and sequencing platform	Study implication
[120]	Sub-acute ruminal acidosis	V1−V3 (454pyrosequencing platform)	The predominant genera in acidotic group were *Lachnospiraceae,* unclassified *Bacteroidales* and unclassified *Ruminococcaceae.* During acidosis, the level *of Ruminococcus, Atopobium*, unclassified *Clostridiales* and *Bifidobacterium* were increased. While, *Prevotella, Treponema, Anaeroplasma, Papillibacter, Acinetobacter,* and unclassified *Lentisphaerae* were decreased.
[24]	Acidotic challenge	V1−V3 (454 pyrosequencing)	Comparison of the microbial profiles of clinical vs. subclinical acidotic heifers showed increases in the relative abundances of *Acetitomaculum, Lactobacillus, Prevotella,* and *Streptococcus* in subclinical acidotic challenge.
[133]	Induced ruminal acidosis	V1−V3 (454 pyrosequencing platform)	The most abundant bacterial genera during acidotic challenge were *Atopobium, Desulfocurvus, Fervidicola, Eubacterium cellulosolvens incertae sedis, Lactobacillus, Olsenella, RC39, Roseburia, Sharpea, Solobacterium, Succiniclasticum*, and *Succinivibrio*. Conversely, the acidotic challenge resulted in decrease relative abundance of *Azonexus, Butyrivibrio fibrisolvens, Carboxydibrachium, Eubacterium brachy, Fervidicola, Fusobacterium, Clostridium viride incertae sedis, Marvinbryantia, RC1-13, RF21, RF38, RFN8-YE57, Ruminococcus group 1* and *Saccharofermentans.*
[89]	Induced Subacute ruminal acidosis	V4 (MiSeq Illumina platform)	In solid fraction: the relative abundance *of Streptococcus, Succiniclasticum, Clostridium, YRC22, Psuedobutyrivibrio, Anaerostipes,* and *Shuttleworthia* were increased on day 6 in SARA. In liquid fraction, the relative abundance of *Streptococcus, Lactobacillus, S24-7*, as well as *Prevotella* and *YCR22*, were increased on day 6 in SARA.
[88]	Severe subacute ruminal acidosis	Primer sets for essential ruminal taxa were Synthesized. (quantitative real-time PCR platform)	Under severe SARA conditions *Prevotella, Lactobacillus, Megasphaera elsdenii,* and *Entodinium* spp. were most abundant, whereas *Ruminobacter amylophilus* was less abundant.
[92]	Wheat induced frothy bloat	V1−V2 (454 pyrosequencing platform)	During bloat, the level of *Bacteroides, Parabacteroides, Clostridium, Eubacterium* and *Butyrivibrio* were increased. While, the level of *Prevotella, Ruminococcus, Slackia, Atopobium, Eggerthella, Olsenell, Bifidobacterium,Collinsella,Gordonibacter* and *Cryptobacterium* were decreased.
[134]	Subacute Ruminal Acidosis	Illumina sequencing of theV4region	SARA resulted in decrease richness, diversity, and stability of bacterial communities and resulted in distinctly different microbiota in the rumen. Only the relative abundance of *Firmicutes* in the rumen was increased by the SARA challenge.

alterations further support the theory that the microbial dysbiosis relates to the overall bovine health and encourage further research to better understand this complex ecosystem.

6. Impacts of dietary intervention on rumen microbiota

Numerous attempts have been made to optimize rumen functions by altering ruminal microbiotas through different dietary interventions [50]. A deeper understanding of the interactions between diets and the microbial composition could modulate the barrier function of the gastrointestinal tract and, thus, influence intestinal function [83]. Most ruminant feed stuffs are consisting of complex polymeric constituents that enhance cooperation between rumen microbial populations. Researchers have identified that there is no single organism is responsible for the complete degradation of the feed stuffs, and that a complex rumen microbial consortia is required for the catabolism of the complex polymeric constituents in the diet [18]. The effect of different types of feeding systems on the structure and diversity of the rumen microbial ecosystem has been widely investigated using next-generation sequencing [24] with primary attention to the diet composition (Table 3).

In a previous study of Pitta et al. [23], in which the composition and diversity of rumen bacteria were examined in response to a shift of the diet from Bermuda grass hay to grazing wheat, significant differences in the phylogenetic composition were found between the liquid and solid fractions and between the two different diets, with greater relative abundance of *Prevotella* being observed in wheat-fed cattle. Members of *Prevotella* have the capacity to degrade proteins, and their presence in the rumen across a variety of diets indicates the substantial metabolic diversity of this genus [93]. More recently, the impact of different dietary interventions on rumen microbiota-host relationship in livestock production was demonstrated by the importance of a highly fibrous diet and the associated host–microbe symbiosis in improving production efficiency and growth performance [94].

The high energy requirements of intensive livestock production systems requires feeding high-grain diets to provide nutrients [95]. DNA-based sequencing technology recently demonstrated the adverse effects of high-grain diets on the structure and function of the rumen microbiota, in turn affecting animal health and production [96]. The ruminant gastrointestinal tract varies in its susceptibility to these adverse effects of high-grain feeding. Moreover, different types of grain diets and grain-processing techniques have different effects on gut health. The inclusion of grain in cattle diets increases the starch content of the digesta and the production of organic acids such as VFAs and lactic acid in the rumen [97] [89].

Although the fat content in ruminant feeds is generally very low (5%), lipids additions plays a crucial roles in improving the energetic values of ruminant diets, modulate rumen function, and mitigate methane emissions particularly in intensive farming systems [98]. Recently, the negative effect of unsaturated fatty acid on the microbial composition and diversity have been reported. A pioneer study showed that the addition of fat to ruminant diets, decreases ruminal cellulose degradation and VFA concentration, and alter the ruminal microbiota composition [98]. As a result, dietary supplements such as yeasts, probiotics, prebiotics and direct-fed microbials might be useful in attenuating the adverse effects of a high-grain diet and, thus, improving animal health and productivity [79].

7. Effects of probiotic supplementation on rumen microbiota

Probiotics traditionally defined as direct-fed microbials (live beneficial microorganisms), are commonly used as feed additives and act as alternatives to sub-therapeutic antibiotics to provide health benefits and to prevent bacterial infections [99]. During the past few decades, the use and effects of probiotics in livestock production have become well established, providing opportunities for the investigation of their relevant roles in the modulation of dysbiosis of the resident microbial populations [100].

While the response of the probiotics are higly variable, the inclusion of some probiotics strain in bovine feeding programs improves rumen ecosystem through direct production of digestive enzymes, and promoting the growth and function of beneficial microbiota, which leads to a stable microbial ecosystem [101]. Some probiotics strains have the potential to produce metabolites, like rumen acetogens and antimicrobial compounds which stimulate the growth, and inhibit potential

Table 3
Selected gastrointestinal metagenomics studies that have studied the impacts of dietary intervention on rumen microbial populations.

Citation	Diet	16 s rRNA Region	Sequencing platform	Rumen microbiome changes
[118]	Dried distillers grain (DDG)		FLX amplicon pyrosequencing	For 50% DDG, *Prevotella* and *Bacteroides* increased whereas *Succinivibrio* decreased compared with 0% DDG.
[135]	Pasture and total mixed ration (TMR)	V1−V2	454 pyrosequencing	In pasture samples, the relative abundance of *Fibrobacteraceae Prevotellaceae, Veillonelaceae,* and *Lachnospiraceae* were increased.
[136]	Diets Containing Citrus Pulp Pellets		FLX amplicon pyrosequencing	Increased Firmicutes, *Butyrivibrio* and *Carnobacterium, Bacilli* and decline in the population of *Dialister* and *Catonella.*
[137]	Starch diet	V3 −V4	454 FLX Titanium	Dietary starch increased *Prevotella, Barnesiella, Oribacterium* and *Olsenella* and decreased *Ruminococcaceae incertae sedis, Oscillibacter, Fastidiosipila,* and *Bifidobacterium.*
[24]	Transition from Forage to Concentrate	V1−V3	454 pyrosequencing	*Ruminococcus* and *Fibrobacter*, *Succinogenes* accounted for a large percentage in the mixed forage diet and contributed the least to the high grain diet whereas *Selenomonas* and *Megasphaera* accounted for the smallest proportion of the bacterial population in heifers fed forage.
[138]	High fiber diet and High starch diet.	V3−V4	454 pyrosequencing	In high fiber diet, *Lachnospiraceae, Ruminococcaceae* and *Fibrobacteraceae* were increased. In high starch diet, Prevotellaceae and Flavobacteriaceae bacteria were increased.
[45]	Bermudagrass Pastures	V4−V6	454 pyrosequencing	Increased *Prevotellaceae, Bacteroidales*, and *Ruminococcacea*. While *Lachnospiraceae, Bacteroidaceae, Spirochaetaceae*, as well as four unidentified families, were not affected.
[139]	High-forage diet (dry and green roughage)		Ion torrent PGM	A-Dry roughage; In liquid fraction (increased *Prevotellaceae Fibrobacteraceae, Ruminococcaceae,* and *Porphyromonadaceae*). In solid fraction (increased *Prevotellaceae Ruminococcaceae, Fibrobacteraceae,* and *Porphyromonadaceae).* B− Green roughage: In liquid fraction (increased *Prevotellaceae Fibrobacteraceae*, *Ruminococcaceae,* and *Porphyromonadaceae*). In solid fraction (increased *Prevotellaceae Ruminococcaceae, Lachnospiraceae*, and *Fibrobacteraceae*).
[140]	Wheat pasture	V1−V3	Titanium pyrosequencing	Increased *clostridium, Oscillospira, Moryella* and *Mogibacterium* in the fiber fraction. While *Prevotella* increased in the liquid fraction.
[141]	Forage/concentrate diet with different forage sources; Cornstalk (CS) Leymus chinensis (LC) Alfalfa hay (AH).	V3−V6	Pyrosequencing	AH feeding increased relative abundance of *Prevotella* and *Selenomonas* compared with the CS diet, while CS feeding increased *Anaerotruncus, Papillibacter, Thermoactimoyces, Bacillus* and *Streptomyces* compared with the LC or AH diet.
[142]	Flax and echium oil	V6−V8	454 pyrosequencing	Increased *Butyrivibrio, Howardella, Oribacterium, Pseudobutyrivibrio* and *Roseburia* post flax feeding. Increased *Succinovibrio* and *Roseburia* post echium feeding.
[143]	Ryegrass (GRA) diets	V1−V2	Ion Torrent	Increased the abundance of *Bacteroidetes,* particularly (*Prevotellaceae* and *Marinilabiliaceae*) as well as the phyla *Tenericutes* (*Anaeroplasmataceae*).
[97]	High grain diet: 60 g/day of fumarate-malate organic acid, (O) and 100 g/day of polyphenol-essential oil (P).	V4	MiSeq platform	The O and P treatments showed a significant increase in *Christenenellaceae abundance* and a decline of *Prevotella brevis.* Additionally, P treatment enhanced the abundance of many taxa belonging to *Bacteroidetes, Firmicutes,* and *Tenericutes*. P dietary treatment also showed increased *Bacteroidales, BS11, Paludibacter, YRC22, CF231, Butyrivibrio, Christensenellaceae, Mycoplasmataceae,* and *RFN20*. The opposite occurred for *WCHB1-25*.
[37]	Fresh perennial ryegrass (PRG)	V6−V8	454 pyrosequencing	*Butyrivibrio, Prevotella, Fibrobacter* and *Olsenella* did not change significantly over time. While, *Pseudobutyrivibrio, Selenomonas,* and *Ruminococcus* change significantly over time.
[144]	Isoflavone-Enriched Feed	V3−V4	Illumina MiSeq	Increased *Prevotella, Fibrobacteraceae*, and unclassified *Burkholderiales.*
[145]	Total mixed rations containing either corn silage (CS) or grass silage (GS) as forage.		Real-time quantitative (q) PCR	CS Increased *Fibrobacter succinogenes* in solids. While, GS increased numbers of *Fibrobacter succinogenes* and *Selenomonas ruminantium* in the liquid fraction as well as the numbers of *Ruminobacter amylophilus, Prevotella bryantii* and *ruminococci* in both fractions.
[146]	Ensiled mulberry leaves (EML) and Sun-dried mulberry (SDM)	V4	Illumina MiSeq	The predominant genera *Prevotella,Ruminococcus, Butyrivibrio,* and *Succiniclasticum.* Increased *Fibrobacter* in the SDM group and *Treponema* decreased in the EML group.
[147]	Sunflower and Marine Oils		T-RFLP and qPCR Analysis	Supplementation with oils decreased the numbers of *Butyrivibrio, protozoa, methanogens, Selenomonas ruminantium* and *Streptococcus bovis.*
[148]	Mineral salts	Bacterial and archaeal 16S ribosomal RNA	Illumina MiSeq platform	The response of rumen microbiota to mineral salt differed mainly in terms of predominant propionate-producing bacteria. Mineral salt intake triggered a shift from predominant *Succiniclasticum* to *Prevotella* and *Prevotellaceae* in adults, but a similar effect was not observed in heifers, which simply maintained propionate homeostasis.

(*continued on next page*)

Table 3 (*continued*)

Citation	Diet	16 s rRNA Region	Sequencing platform	Rumen microbiome changes
[149]	Monensin and a blend of essential oils (BEO)	bacterial or archaeal 16S rRNA genes	Illumina MiSeq Sequencing	BEO treatment had no effect on the rumen microbiota, whereas monensin decreased bacterial diversity. Monensin caused a significant decrease in the relative abundance of 23 bacterial species, all belonging to the phyla *Bacteroidetes* and *Firmicutes*. Ten bacterial operational taxonomic units belonging to the phyla *Actinobacteria, Bacteroidetes, Cyanobacteria*, and *Firmicutes* increased in relative abundance due to the monensin treatment.
[150]	Tasco (air-dried Ascophyllum nodosum)	Partial bacterial and archaeal 16S rRNA genes	Illumina MiSeq platform	Tasco effectively reduced pathogenic *E. coli* but had only minimal impacts on rumen fermentation.
[151]	Olive oil pomace (OOP)	V3–V4	Illumina MiSeq platform	OOP had no effect on the overall rumen microbial composition. However, significant differences, between control and OOP groups, were found for six bacterial taxa. In particular, rumen microbiota from animals fed OOPs showed a reduction in *Anaerovibrio*, which is a lipase-producing bacterium.
[152]	Combined garlic essential oil and linseed oil.	Bacterial (V3–V4) and archaeal 16S rRNA genes	Illumina HiSeq platform	This study demonstrates that a long-term early-life dietary intervention induced modifications in the composition of the rumen bacterial community that persisted after the intervention ceased with little effect on archaeal and protozoal communities.

pathogens [102]. It has been well established that some probiotics can help the establishment of crucial microbial populations (*Prevotella, Eubacterium Bacteroides,* and *Clostridium*) in rumen by removing the oxygen from the surrounding environment [102].

Based on previous studies in ruminant, probiotics play an important role in improving feed efficiency, enhancement of feed conversion ratio, and increasing weight gain and milk production [103] [104]. Probiotics helps in regulation of the intestinal microbial homeostasis [105], reduce the frequency of neonatal diarrhea [106], regulate ruminal pH [107], stimulate immunity [101] [108]. Probiotics impact the immune system through multi-cellular signaling pathway and induce production of local and systemic cytokines such as interleukin 18, interleukin 12, TLR2 and tumor necrosis factor alpha [104]. Probiotics may also contribute to overgrowth of certain microbial populations while inhibiting the growth of others potentially pathogenic bacteria through their interactions with host-microbial populations [108].

The most widely used veterinary probiotic supplements in ruminants include *Lactobacillus* and *Saccharomyces*, *Bacillus, Bifidobacterium, Enterococcus, Propionibacterium, Megasphaeraelsdenii and Prevotellabryanti* species [108] [109]. The response of the host to probiotics is highly dependent upon probiotics strain, age, breed and other dietary traits [110]. Table 4 summarizes selected research studies on the impact of probiotics on rumen microbial composition and function. Although yeasts, bacteria and fungi may be adopted as probiotics, the bacterial strains, especially the lactic acid bacteria, are primarily used as probiotics, because of the awareness that they are beneficial members of the gastrointestinal microbiota [111]. Lactic acid bacteria incorporate a group of Gram-positive, non-motile, anaerobic rods, non-spore-forming bacteria. The use of lactic acid bacteria and direct-fed microbes as probiotics in ruminants has been observed to reduces the abundance of pathogenic *E. coli* [112], improve dry matter intake [104], reduce frequency of diarrhea [113], and enhances immune protection during infection through secretion of bacteriocin and modulate host microbial ecosystem [114]. Several strains of *Lactobacillus* are used as growth promoters in calves, instead of antibiotics, thus counteracting the negative effects of widespread antibiotic use and subsequently reducing antimicrobial resistance and unnecessary treatments [113]. Although production of antimicrobial compounds may be the principal mechanism for antimicrobial activity of probiotics, there are further mechanisms such as attachment to epithelial cells, competition for nutrients, and modulation of the immune system [111]. In general, antimicrobial compounds produced by lactic acid bacteria can be divided into bacteriocins (high molecular mass) and non-bacteriocins (low molecular mass) antimicrobial substances [115]. Amongst these antimicrobial substances produced by lactic acid bacteria, the most important one are the organic acids, especially lactic and acetic acids, that responsible for beneficial impact of these strains in the gastrointestinal ecosystem through colonization of beneficial microbiota and diminishing pathogenic populations [111].

Live yeast (*Saccharomyces cerevisiae*) is one of the widely used and efficient probiotics used in livestock producing system because of its varieties of function in establishing and balancing the rumen ecosystem [104]. Recently, the probiotic effects of *Saccharomyces* species have been assessed. The use of *Saccharomyces cerevisiae* fermentation products as feed additives stimulate growth of lactic acid bacteria, influences milk production [116], VFAs concentrations and ruminal pH [117], which can benefit various types of rumen microbial population [118] [119] [120], and improve rumen metabolism [104]. In early life, *Saccharomyces cerevisiae* interventions showed marked improvement in ruminal morphology, possibly because of an increase in *Butyrivibrio* and a decrease in *Prevotella* richness in the rumen fluid, which results in an increase in butyrate and VFAs production [121]. *Saccharomyces cerevisiae* has also been investigated as a probiotic to increase fiber digestion in the rumen [122]. Supplementation with *Saccharomyces* may indirectly promote microbial fiber degradation by stabilizing ruminal pH and increasing dry matter intake [11]. Because of varying results

Table 4
Selected research studies that have studied the impact of probiotics on gastrointestinal microbial composition and functions in ruminant.

Citation	Probiotic strain	Host	Observation
[153]	*Yarrowia lipolytica* (non-pathogenic yeast)	Dairy calves	Calved fed this strain had higher count of *Entodinimorphida, Holotricha* and total bacteria in reticulorumen with no effect on PH and concentration of total volatile fatty acid.
[110]	*Saccharomyces cerevisiae*	Dairy cows	*S. Cerevisiae* could modulate the rumen microbial balance and has enhancing effect on milk production and milk fat contents in lactating cows.
[154]	*Megasphaera elsdenii*	Dairy calves	The results of this study suggest that a single administration of the *M. elsdenii* probiotic may not affect the rumen establishment of the organism.
[155]	*Lactobacillus casei* and *Lactobacillus plantarum*	Dairy cows	The probiotics supplementation significantly increases the rumen fermentative bacteria (*Bacteroides, Roseburia, Ruminococcus, Clostridium, Coprococcus* and *Dorea*) and beneficial bacteria (*Faecalibacterium prausnitzii*) Further, the probiotics supplementation significantly increased the milk production and the contents of milk immunoglobulin G, lactoferrin, lysozyme and lactoperoxidase.
[102]	*Saccharomyces cerevisiae*	Lactating cows	Improve gastrointestinal tract microbial balance and improve milk and its fat contents.
[156]	*Lactobacillus plantarum* and *Bacillus subtilis*	Dairy calves	This study concluded that, the oral administration of the probiotics affected the rumen bacterial community and decreased numbers of cellulolytic bacteria.
[157]	*Lactobacillus reuteri*	Beef cattle	*L. reuteri* exerted an antimicrobial activity against the rumen endogenous microbiota.
[158]	*Saccharomyces cerevisiae*	Buffalo bulls	The results indicated that yeast culture increased significantly the mean protozoal count and the total bacterial count.
[159]	*Ruminococcus flavefaciens*	Dairy cow	The result of this study showed that the presence of probiotics or a change in the concentrate to forage ratio in the diet did not succeed in establishing the new strain in the rumen.

among studies, the effects of probiotics on the microbiota composition have not been conclusively determined, but some studies show promising results. Therefore, further studies are required to fully understand the effects of probiotics and other direct-fed microbial supplements on the restoration of the microbiome to a healthy state.

8. Future directions and conclusions

Recent advances in rumen microbiome research is exciting and has redefined our ability to describe the rumen microbiota and its functions. We can now distinguish the locations of specific microbes, determine the population diversity and explore the relationships between the microbiome and the host [16]. With the continuous advancement in sequence-based technologies and in-depth characterization of the phylogenetic and functional capacity of rumen microbiome, more effective strategies will raise to modulate rumen microbiome through dietary manipulations and the administration of prebiotics and antibiotics. Furthermore, the application of metatranscriptomics, metaproteomics, and metabolomics-based studies is required for a better understanding of the role of host-microbe interactions in health and disease, allowing less reduce inappropriate antibiotic use, which in turn will reduce the antimicrobial resistance, and ensure the production of quality products to meet global demands.

Conflicts of interest

The author declares no conflict of interest.

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