



# Soil and ruminant gut microbiomes in diverse pasture systems and regenerative agriculture: a review

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## Abstract

Pasture systems strongly influence microbiome diversity in both soils and grazing ruminants, and their interactions through interconnected microbial exchange pathways. In temperate regions, grazed pasture systems are predominantly composed of perennial ryegrass-white clover, representing standard systems under contemporary management. However, sustainable alternatives such as regenerative agriculture, which emphasise diverse pasture species, are gaining attention. Diverse pastures, due to their varied root structures and nutritional composition, exert more pronounced effects on soil and ruminant microbiomes than standard swards. This review synthesises current knowledge on soil and ruminant gut microbiome responses to diverse pasture systems. Diverse swards enhance soil organic carbon and microbial abundance, while their varied nutrient profiles and bioactive compounds, together with ingested soil microbes during grazing, contribute to a more diverse and stable gut microbiome, potentially strengthening soil–gut microbial interactions. However, few omics-based studies have explored microbiome responses to pasture management, and none have simultaneously investigated soil and ruminant gut microbiomes under regenerative management. This review highlights these gaps and proposes future research directions, including integrated multi-omics approaches, to advance understanding of soil–gut microbiome dynamics, interactions, and functional roles within pasture-based agroecosystems.

**Keywords** Diverse pastures · Regenerative management · Ruminant gut microbiome · Soil microbiome

## Introduction

Grazed pasture systems in temperate climates predominantly rely on standard pastures, comprising perennial ryegrass (*Lolium perenne* L.) alone or in combination with white clover (*Trifolium repens* L.) (Gilliland et al. 2007; Grelet et al. 2021). Standard pastoral farming is characterised by practices such as high stocking densities, short rotational grazing intervals, and the regular use of synthetic fertilisers and agrochemicals to maintain productivity and control pests and weeds, representing contemporary management (Jerrentrup et al. 2020). Standard pastures provide an abundant, high-quality feed for grazing ruminants and enhance soil fertility through nitrogen-fixing bacteria (e Castro et al. 2016). Although utilising a limited number of plant species can simplify grazing management (Chapman et al. 1996), it may result in lower dry matter (DM) yield (Norton et al. 2016). Additionally, the high crude protein concentration of a perennial ryegrass-white clover pasture may increase

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urinary nitrogen (N) excretion in grazing ruminants, leading to greater N losses from pastoral systems (Cheng et al. 2016).

To mitigate these challenges, alternative forages such as plantain (*Plantago lanceolata* L.) and chicory (*Cichorium intybus* L.) have been incorporated alongside perennial ryegrass and white clover (Nguyen et al. 2022; Woodward et al. 2013). These forages can reduce urinary N excretion without negatively affecting milk production (Nguyen et al. 2022; Totty et al. 2013), although their DM yield can be inconsistent over time (Moorhead and Piggot 2009; Sanderson et al. 2003; Tozer et al. 2011).

Regenerative agriculture is a sustainable farming approach that aims to improve soil health, enhance the nutritional quality of plants and animals, and minimise the use of chemical inputs (Grelet et al. 2021; Schreefel et al. 2020). Regenerative agriculture encompasses multiple practices, such as introducing diverse pastures, rotational grazing, reduced chemical inputs, no-till farming with residue retention, integrated pest management, application of biostimulants and carbon-rich amendments, and balancing of minerals and trace elements (Grelet et al. 2021). Merfield (2019) highlighted that the use of diverse pasture systems, no-till farming with residue retention, and rotational grazing are the key practices of regenerative management.

Diverse pasture systems incorporate a range of grasses, legumes, and herbs, to improve both above ground and below ground biodiversity (Hermans et al. 2023). These diverse pastures have shown the ability to increase DM production over standard pastures, particularly during drier seasons (Nobilly et al. 2012; Nölke et al. 2021; Woodward et al. 2013). Additionally, diverse pastures help to reduce nitrate leaching by limiting urinary N excretion from grazing ruminants (Totty et al. 2013; Woodward et al. 2012).

Diverse pastures also improve soil organic carbon (SOC) inputs through varied root systems, exudates, litter, and decomposition (Wilson et al. 2018), which stimulates microbial populations in the rhizosphere (Montealegre et al. 2002) and enhances microbial necromass, a major contributor to SOC (Li et al. 2024). Increased soil microbial diversity supports soil structure, nutrient cycling, and organic matter decomposition, promoting overall soil fertility (Brown et al. 2020). Ruminant grazing patterns further influence the soil microbiome in diverse pastures, with grazing type, intensity, and season affecting microbial dynamics and network complexity, whereas overgrazing can reduce microbial abundance (Camuy-Vélez et al. 2024; Ford et al. 2013; Ma et al. 2022; Xun et al. 2018; Yang et al. 2019a; Zhang et al. 2023).

Diverse pastures combined with rotational grazing can modulate the gut microbiome of grazing ruminants (Distel et al. 2020; Mueller-Harvey 2006; Niderkorn et al. 2012). A more diverse diet provides nutrients and bioactive

compounds that support a stable and diverse gut microbiome, enhancing ruminant performance (Berca et al. 2021; Song et al. 2020; Zanon et al. 2022).

Despite increasing interest in microbiome research, soil and gut microbial communities are rarely studied together. Soil and gut microbiomes are interconnected through microbial exchange pathways within pasture systems (Attwood et al. 2019; Cheong et al. 2025). As ruminants graze, they ingest plant material colonised by soil microbes, which pass through the digestive tract and are subsequently returned to the soil via faeces (Jamieson et al. 2002). This microbial cycling underpins the health and productivity of soils, pastures, and grazing ruminants (Attwood et al. 2019).

Omics-based microbiome studies targeting microbial DNA, RNA, proteins, and metabolites provide insights into the abundance, diversity, functional capacity, and interactions of microbial communities across environments. Previous work has typically focused on either soil or gut microbiomes under pasture management systems, but no studies have simultaneously examined both microbiomes within diverse pasture systems under regenerative management. This review therefore synthesises existing evidence and proposes a multi-omics framework, combining metagenomics (DNA-based) and metatranscriptomics (RNA-based) to quantify soil–gut microbial linkages and their functional roles across pasture management systems, with particular emphasis on diverse pastures and regenerative agriculture.

## Grazed pasture systems

Grazed pastures that are dominated by one or two highly productive species are widely adopted in intensive pastoral farming systems worldwide (Caradus et al. 2023). These systems underpin livestock production including dairy, sheep, and beef industries in regions such as New Zealand, Australia, Europe, and the Americas (Clewett et al. 2021; Faria et al. 2025; Markiewicz-Keszycka et al. 2023). Temperate climates provide ideal conditions for the establishment and persistence of these pasture swards (Delaby et al. 2020).

## Standard pasture systems under contemporary management

In temperate grazing systems, perennial ryegrass–white clover swards remain the dominant pasture base maintain through contemporary management practices to sustain productivity (Fairweather et al. 2009; Gilliland et al. 2007; Grelet et al. 2021; Jerrentrup et al. 2020). These pastures support the nutritional requirements of grazing animals by

providing abundant, high-quality forage (Hills et al. 2015). White clover further contributes to soil fertility through biological nitrogen fixation in symbiosis with N-fixing bacteria (e Castro et al. 2016). Management of these systems is relatively straightforward due to the use of well-adapted species suited to lower temperatures and moist climates (Chapman et al. 1996). However, their reliance on a narrow range of grasses and legumes can limit overall biodiversity, reducing habitat availability for beneficial insects, soil fauna, and decomposer communities (Delaby et al. 2020).

The restricted range of shallow rooted plant species in standard pasture systems limits the variety of organic inputs available to the soil (Bolinder et al. 2002). This leads to a reduction in soil microbial diversity (Singh and Mukerji 2006), which further hinders nutrient cycling efficiency (Knops et al. 2002). Furthermore, low root biomass in the soil (within the top 10 cm) can contribute to soil compaction and reduce porosity, thereby negatively effecting water infiltration and retention (Lu et al. 2020). Limited plant diversity can also reduce the resistance of a pasture systems to environmental stresses, such as drought or disease, ultimately leading to lower DM production (Ribeiro Filho et al. 2005). High crude protein content and solubility of perennial ryegrass-white clover pastures result in a large proportion of dietary N being excreted in the urine of grazing animals (Box et al. 2017). Nitrate derived from the breakdown of urea in urine through microbial processes in the soil can leach into groundwater or be emitted into the atmosphere as nitrous oxide (N<sub>2</sub>O) (Sakadevan and Nguyen 2017), a potent greenhouse gas and significant environmental concern (Di et al. 2010). For example, a single urine patch from a dairy cow in New Zealand can result in N loading up to 1000 kg N/ha, substantially contributing to nitrate leaching (Sakadevan and Nguyen 2017). Similarly, Selbie et al. (2014) reported peak N<sub>2</sub>O emissions of 110 g N<sub>2</sub>O-N ha/day from a single urine patch.

### Incorporating forages into standard pastures

Incorporating herbaceous forage species such as chicory and plantain into standard perennial ryegrass-white clover pastures improves N utilisation and reduces urinary N excretion in ruminants due to their high concentrations of water-soluble carbohydrates, elevated water content, and bioactive compounds (Minnée et al. 2017, 2019; Peterson et al. 2022). Minnée et al. (2017) reported that higher water-soluble carbohydrate content in chicory and plantain (14%) compared with perennial ryegrass (7%) providing readily available energy for rumen microbes and enhancing N utilisation. A meta-analysis by Nguyen et al. (2022) demonstrated a negative relationship between the proportion of plantain in

cattle diets and urinary N concentration. The deep-rooting systems of these herbs also allow efficient uptake of N from urine patches, reducing N losses through leaching or gaseous emissions (Vibart et al. 2016). Additionally, plantain contains biologically active compounds such as aucubin and verbascoside, which may act as biological nitrification inhibitors in the soil (Al-Mamun et al. 2008; Peterson et al. 2022). Chicory can also influence the mineral content and nutrient uptake of pasture mixtures. Belesky et al. (2001) in the USA showed that chicory often contains greater levels of essential minerals than grasses and legumes. They further noted that mineral uptake of chicory is influenced by sward composition, N input, and management practices. Both chicory and plantain can produce similar or greater DM yield than ryegrass-white clover swards, particularly during warmer seasons due to their deep root systems (McNally et al. 2015; Pembleton 2015).

The effects of chicory and plantain on urinary N concentration and DM yield have been widely studied in grazing experiments under temperate conditions. In New Zealand, urinary N concentration in ruminants has been shown to decrease by 13–75% as the proportion of plantain in the diet increases, compared with standard pastures (Box et al. 2017; Edwards et al. 2015; Minnée et al. 2020; Navarrete et al. 2022; Nkomboni et al. 2021). This reduction is largely attributable to diuresis, driven by the approximately 30% greater water content of plantain (Minnée et al. 2019), which results in total water intakes 10–20 L cow/day greater than cattle offered perennial ryegrass-white clover diets (Dodd et al. 2019; Minnée et al. 2020). A recent review provides a comprehensive synthesis of plantain's effects on urinary N excretion, soil N transformations, and N leaching in New Zealand grazing systems (Pinxterhuis et al. 2024). Therefore, in this review, these findings are summarised only briefly to highlight the effects of these forages on urinary N concentration in comparison with perennial ryegrass-white clover standard swards. Nobilly et al. (2012) reported that including chicory and plantain increased DM yield by over 10% compared to standard pastures. Moorhead and Piggot (2009) found that a plantain mix with ryegrass and white clover produced up to 6 t DM/ha in the first year, although yields declined to 1.2 t DM/ha by the third year, highlighting persistence challenges. Sanderson et al. (2003) observed that chicory swards were substantially reduced over time, while plantain did not survive beyond the second year of the study. These findings are consistent with the meta-analysis by Komainda et al. (2025), which underscores the difficulty of obtaining reliable persistence data in temperate regions due to the short duration of many experimental studies.

## Regenerative agriculture

Regenerative agriculture builds on sustainable farming principles by focusing on restoring soil health, enhancing biodiversity, and improving ecosystem resilience while maintaining productivity (Grelet et al. 2021; Schreefel et al. 2020). However, regenerative management has not yet been widely adopted or studied, with only a small, but growing number of farmers using this approach. Limited awareness and concerns about the economic risks associated with transitioning from contemporary to regenerative practices are significant barriers to its widespread implementation (Grigorieva et al. 2023). However, Grelet and Lang (2021) highlighted that regenerative management is not directly opposed to contemporary management, as there is significant overlap in practices between two systems, which reduces the economic risk of adoption.

Incorporation of diverse plant species, long-duration rotational grazing, and no-till farming combined with residue retention are considered key practices of regenerative management (Merfield 2019). Other regenerative agriculture practices include minimal use of synthetic fertilisers, integrated pest management, application of bio-stimulants and carbon-rich amendments, and mineral balancing and trace elements. Among these, the integration of diverse pastures with rotational grazing is particularly notable for its synergistic benefits (Giller et al. 2021; Grelet et al. 2021; Merfield 2019).

## Diverse pasture systems

Diverse pasture systems are generally defined as pastures containing at least five species, including grasses, legumes, and herbs (Woodward et al. 2013) (Table 1).

Diverse pastures often enhance DM production compared with standard pastures, because different plant species utilise resources more efficiently, and the presence of legumes contributes N to support growth, while the sward is more resilient to environmental stress (Li et al. 2015). For example, in New Zealand, diverse pastures under rotational grazing produced about 10% more DM annually than standard ryegrass-white clover swards, with particularly notable increases during summer (Nobilly et al. 2012). Similarly, multi-species mixtures including perennial ryegrass, white clover, chicory, plantain and lucerne (*Medicago sativa* L.) have shown similar or greater yield gains in subsequent years (Woodward et al. 2013).

Grazing on diverse pastures, which contain species such as chicory, plantain, and lucerne, supports reductions in urinary N excretion, providing additional environmental benefits (Edwards et al. 2015; Totty et al. 2013; Woodward et al. 2012). These benefits are largely attributed to the high-water

content, elevated water-soluble carbohydrate levels, and bioactive compounds of the herbs, which enhance rumen N utilisation and increase urine volume (Minnée et al. 2017, 2019; Peterson et al. 2022).

## Soil organic carbon and microbial dynamics under diverse pastures

A variety of plants in diverse pastures can capture carbon (C) from the atmosphere during photosynthesis and transfer it

**Table 1** Commonly used species in diverse pasture swards growing in temperate regions

Pasture species	Description
Perennial Ryegrass ( <i>Lolium perenne</i> L.)	Perennial grass with rapid establishment, high yield, strong grazing preference and high forage nutritive value.
White Clover ( <i>Trifolium repens</i> L.)	Legume commonly grown with grasses to improve nitrogen fixation and overall forage quality.
Red clover ( <i>Trifolium pratense</i> L.)	Legume providing nitrogen fixation and high forage nutritive value in pasture mixtures.
Crimson clover ( <i>Trifolium incarnatum</i> L.)	Legume used as a cover crop or in temporary pasture mixes.
Balansa clover ( <i>Trifolium michelianum</i> Savi)	Legume that performs well in low pH soils and moderate fertility conditions.
Persian clover ( <i>Trifolium resupinatum</i> L.)	Fast-growing legume suitable for short-term pastures and rotational grazing.
Chicory ( <i>Cichorium intybus</i> L.)	Deep-rooted herb with high mineral content, drought tolerance, and summer productivity.
Plantain ( <i>Plantago lanceolata</i> L.)	Broad-leaved herb containing secondary metabolites aucubin, catalpol, and verbascoside, high mineral content.
Cocksfoot ( <i>Dactylis glomerata</i> L.)	Robust grass providing good ground cover, drought tolerance, and summer growth.
Timothy ( <i>Phleum pratense</i> L.)	Cool seasons grass suitable for wetter climates, maintains pasture persistence.
Tall Fescue ( <i>Festuca arundinacea</i> Schreb.)	Deep-rooted bunchgrass, tolerant of intensive grazing, persists under diverse conditions.
Meadow Fescue ( <i>Festuca pratense</i> Huds.)	Perennial grass with high digestibility.
Phalaris ( <i>Phalaris aquatica</i> L.)	Persistent perennial grass performing well under moderate fertility.
Vetch ( <i>Vicia villosa</i> Roth)	Legume commonly used as a cover crop or green manure to improve soil fertility.
Lucerne ( <i>Medicago sativa</i> L.)	Deep-rooted perennial legume with high protein content, commonly referred to as alfalfa
Prairie grass ( <i>Bromus catharticus</i> Vahl, syn. <i>Bromus willdenowii</i> Kunth)	Cool seasons grass suitable for dairy pastures, adaptable and highly nutritious.

Sources: Bryant et al. (2017); Charlton and Belgrave (1992); Charlton and Stewart (1999); Peterson et al. (2022); Rowarth et al. (2020); Weber et al. (2025)

into the soil as SOC through root exudates, litter deposition and decomposition of plant material (Wilson et al. 2018). Soil organic carbon serves as a vital energy source for soil microorganisms, stimulating their activity, enhancing several soil properties, and facilitating the breakdown of organic materials (Bhattacharyya et al. 2022). Bacteria and fungi are the primary decomposers of organic material and contribute significantly to SOC through their necromass (Li et al. 2024). Microbial necromass is particularly high in diverse plant communities, where varied roots, exudates, and litter inputs promote greater microbial abundance (Zak et al. 2003).

Plant species richness is considered a key driver of SOC accumulation (Whitehead et al. 2018). Both controlled and field studies have reported that increasing plant diversity generally enhances SOC storage, depending on management type and site conditions (Lange et al. 2015; Yang et al. 2019b). For example, in the USA, Skinner and Dell (2016) reported that over 9 years, 5-species mixtures under rotational grazing accumulated 1.8 Mg C/ha/yr, compared to 0.5 Mg C/ha/yr in 2-species mixtures (Table 2). Similarly, Alemu et al. (2019) found that a 12-species pasture under continuous grazing in Canada had the highest SOC stock (31 Mg C/ha). In New Zealand, McNally et al. (2015) reported an increase in root mass C of approximately 1203 kg C/ha in moderately diverse 6-species cut pastures (Table 2). Long-term studies further support these findings showing that diverse pastures stored more SOC than pure stands of the same species over time (Fornara and Tilman 2008; Yang et al. 2019b). However, not all studies report consistent positive effects of diversity on SOC. In some cutting experiments, SOC accumulation did not increase or even declined with higher species richness (Bonin et al. 2014; Skinner et al. 2006) (Table 2).

Greater SOC and higher root biomass under diverse pastures, along with enhanced exudate production, support the development of a more diverse microbial community within the rhizosphere (Liang et al. 2017). The biochemical diversity of root exudates can promote beneficial microbes, enhancing plant growth through hormone production and pathogen suppression (Abeysingha and Weeraratne 2010; Kowalchuk et al. 2002; Scherer-Lorenzen et al. 2003; Sturz and Christie 2003). These microbes play a crucial role in improving soil structure over time by promoting soil particle aggregation (Gupta et al. 2022; Zhang et al. 2022), which facilitates greater root penetration, enabling plants to access nutrients and moisture deeper within the soil profile (Bronick and Lal 2005). Consequently, this supports healthier plant growth and greater DM yields, reduces reliance on synthetic fertilisers and contributes to long-term soil fertility (Brown et al. 2020; Hermans et al. 2023). (Fig. 1).

The soil microbiome under diverse pasture systems is shaped by ruminant grazing patterns, as shown in several omics studies conducted in temperate regions (Ford et al. 2013; Yang et al. 2019a). For example, Yang et al. (2019a) reported that continuous cattle grazing in pasture systems in the USA increased bacterial diversity by over 18% compared to ungrazed lands during the spring-summer period (Table 3). Similarly, Ford et al. (2013) found that gram-negative bacterial phospholipid fatty acids (PLFAs) markers were more abundant in ruminant-grazed pasture units (33%) than in ungrazed units (31%) during spring-summer in the UK (Table 3). However, the effects of grazing intensity on soil microbial diversity appear to be variable across regions and seasons. In China, Xun et al. (2018) observed that overgrazing during summer reduced bacterial (5%) and fungal (14%) abundance, and Yao et al. (2025) reported that soil bacterial diversity decreased by 3.3% under moderate grazing and by 7.2% under higher grazing intensities compared to ungrazed conditions during spring to autumn (Table 3). In contrast, Mhuireach et al. (2022) reported that archaeal and bacterial richness remained relatively stable across different grazing intensities in the USA, although microbial community composition varied significantly between grazing types from summer to autumn (Table 3). Similarly, Ma et al. (2022) demonstrated that seasonal grazing from spring to summer in temperate grasslands of China increased fungal diversity by 30%, while late summer grazing enhanced soil archaeal abundance by 12% compared to ungrazed plots. Zhang et al. (2023) also found that moderate grazing in China improved bacterial diversity by 7% relative to non-grazed conditions during summer. Grazing intensity also affects protists and microbial network interactions within the soil microbiome. Camuy-Vélez et al. (2024) in the USA, showed that increased grazing intensity led to greater protist diversity and revealed strong associations between protist, bacteria, and fungi, highlighting their intricate interactions within the soil microbiome during spring to autumn. Predatory protist abundance increased under grazing, whereas arbuscular mycorrhizal fungi declined. Microbial network complexity also increased with grazing intensity, with fungal taxa playing a central role in network structure. Collectively, these studies illustrate that grazing patterns modify microbial interactions, leading to changes in diversity and network complexity.

### Ruminant gut microbiome under diverse pastures

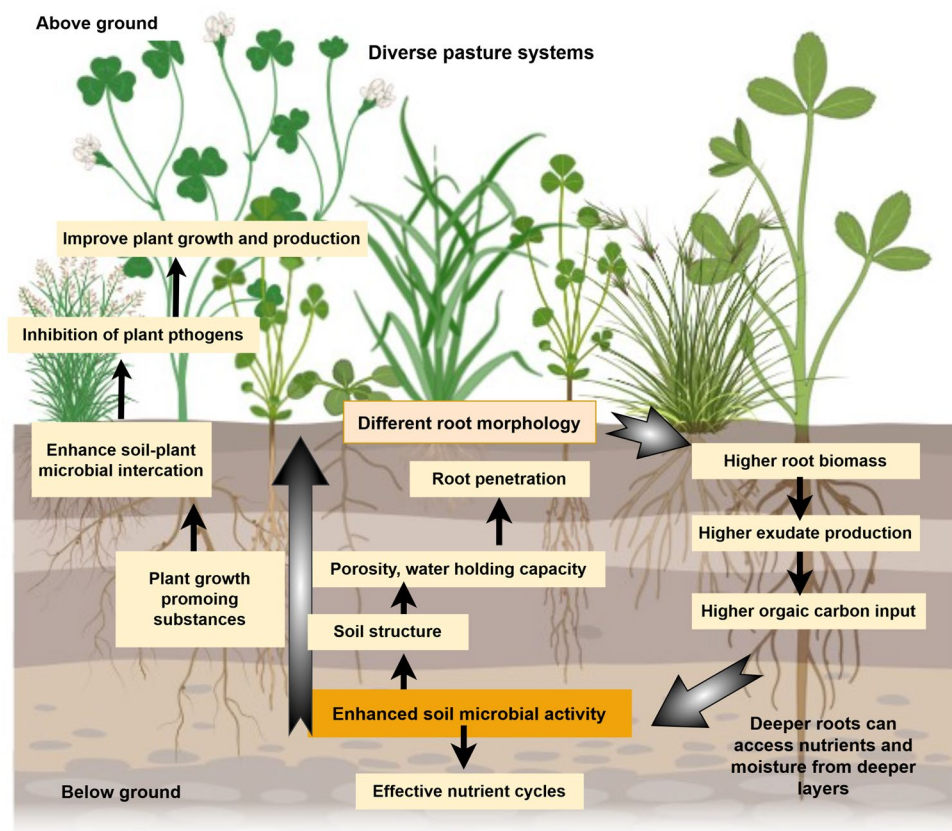
The gut microbiome forms a complex community that colonises various parts of the ruminant digestive tract, including the rumen, reticulum, omasum, abomasum, small intestine, caecum, and large intestine (Barathan et al.

**Table 2** Field experiments in relation to pasture diversity and associated changes in soil organic carbon in grasslands

Country	Study objective	Duration (years)	No. of sown species	Experimental details	Management Type	SOC measurement/indicator	Key Findings	SOC effect <sup>a</sup>	Reference
USA	Evaluate production and C sequestration of grazed pastures	9	5	Rotational grazing (5 events/yr)	Rotational grazing (5 events/yr)	SOC accumulation (Mg C/ha/yr)	5-species mixture accumulated 1.8 Mg C/ha/yr vs. 0.5 Mg C/ha/yr in 2-species pastures	+	Skinner and Dell (2016)
	Determine persistence and yield of complex forage mixtures; effect of photosynthetic inputs	4	11	Cut/mowed (1–3 cuts/yr)	Cut/mowed (1–3 cuts/yr)	SOC change	SOC decreased in 11-species mixture	-	Skinner et al. (2006)
	Evaluate management of perennial warm season grasses for grazing and soil C	5	10	Grazed + Mowed (moderate rotational grazing 2/yr; canopy 60 → 16 cm; post-graze mowing to 30 cm)	Grazed + Mowed (moderate rotational grazing 2/yr; canopy 60 → 16 cm; post-graze mowing to 30 cm)	SOC stock	No significant effect of species composition or management	0	Bonin et al. (2014)
Canada	Plant diversity effects on soil C storage	22	16	Non-grazed, annual cutting	Non-grazed, annual cutting	Annual SOC accumulation (Mg C/ha/yr)	16-species pastures: 0.54 Mg C/ha/yr (first 13 yrs) → 0.71 Mg C/ha/yr (afterwards); higher than 1–8 species	+	Yang et al. (2019b)
	Long-term effects of plant functional diversity on SOC	12	16	Annual cutting	Annual cutting	Net SOC accumulation (g C/m <sup>2</sup> /yr)	16-species plots: 69.5 ± 8.86 g C/m <sup>2</sup> /yr; significantly higher than 1–8 species plots	+	Fomara and Tilman (2008)
	Effect of forage mixtures and grazing management on productivity and SOC	9	12	Continuous and deferred rotational grazing	Continuous and deferred rotational grazing	SOC stock (Mg C/ha)	12-species mixture under continuous grazing had highest SOC (31 Mg C/ha)	+	Alemu et al. (2019)
New Zealand	Quantify root structure and nutrient dynamics in moderately diverse pasture	2	6	Cut (4 cuts/yr)	Cut (4 cuts/yr)	root mass C to soil (kg C/ha)	Moderately diverse 6-species pasture increased soil C input (~1203 kg C/ha)	+	McNally et al. (2015)

<sup>a</sup> Soil C changes in response to elevated plant diversity are indicated as (+)=increase or improvement; (-)=decrease; (0)=no change

**Fig. 1** Hypothesized mechanism of the plant-soil rhizosphere under diverse pastures. Diverse root morphologies increase root biomass and exudate production, stimulating soil microbial activity and nutrient cycling. Enhanced microbial activity improves soil structure, water retention, and produces growth-promoting substances that support beneficial plant-microbe interactions and suppress pathogens. Deeper roots access subsoil nutrients and moisture. These above and below ground interactions synergistically enhance soil health, sustaining long-term pasture productivity and fertility



2024; Clemmons et al. 2019). They play a pivotal role in the digestion of cellulose and other complex carbohydrates, converting them into nutrients and energy through fermentation (Arshad et al. 2021; Malmuthuge and Guan 2016).

The rumen hosts a diverse community, primarily composed of bacteria (>50%), along with methanogenic archaea (~2–4%), protozoa (~2%), and fungi (~2%), and a small fraction consists of viruses, bacteriophages, and unclassified microbes (Mizrahi and Jami 2018; Nagaraja 2016). The dominant bacteria phyla are Firmicutes and Bacteroidetes (Fernando et al. 2010; McCann et al. 2016). Petri et al. (2013) reported that these phyla accounted for 43.2% and 32.8%, respectively of the known bacterial abundance in the rumen. Methanogenic archaea from the phylum Euryarchaeota are key contributors to enteric methane emissions, a potent greenhouse gas produced during dietary fermentation (Palangi et al. 2024). Some studies in China indicated that the reticulum and omasum are dominated by Firmicutes, including genera such as *Butyrivibrio*, *Ruminococcus*, *Clostridium*, and *Succiniclaticum*, while Euryarchaeota are represented by *Methanobrevibacter* (Xue et al. 2018; Zeng et al. 2017). The abomasum is enriched with Proteobacteria and Tenericutes, whereas Proteobacteria and Firmicutes dominate the small and large intestines (Mao et al. 2015; Xue et al. 2018).

Pasture diversity can influence gut microbiome composition through ingestion of plant-associated and soil microbes during grazing and exposure to a wider range of plant secondary metabolites and fibre types. Diverse pastures, with varied root systems, enhance soil microbial diversity, and ingested microbes may transiently colonise the gut, creating soil-gut microbial interactions that improve fermentation efficiency and nutrient absorption (Attwood et al. 2019; Arshad et al. 2021; Scherer-Lorenzen et al. 2003; Woodward et al. 2013). A more diverse and functionally enriched gut microbiome can increase fibre degradation, optimise volatile fatty acid (VFA) production, and improve nitrogen utilisation, which collectively enhance energy supply for milk synthesis and animal growth (Chen et al. 2022; Xu et al. 2025). Shifts in microbial composition and fermentation pathways influence hydrogen flow in the rumen, reducing its availability for methanogenesis and potentially lowering enteric methane emissions (Martinez-Fernandez et al. 2016). These interactions extend beyond grazing, as animals return 70–90% of ingested nutrients to the soil via dung and urine, with excreta composition shaped by diet and gut microbiome diversity (Negash 2022). Thus, diverse pastures influence soil nutrient cycling, greenhouse gas emissions, and animal performance through both plant traits and microbiome-mediated feedback loops.

**Table 3** Ruminant grazing impacts on soil microbial communities under diverse pastures

Study objective	Key findings	Pasture species under grazing	Reference
Difference in soil microbiome after 13 years of grazing	Inverse Simpson index diversity was higher in grazed lands (155) than in ungrazed lands (130)	Dominant species: Common bermudagrass Other species not specified	Yang et al. (2019a)
Impact of grazing intensity on soil decomposer communities	Gram-negative bacterial PLFAs were more abundant (33%) in grazed pasture units compared to ungrazed units (31%) Total PLFA concentrations were 50% higher in grazed areas	Browntop, Red fescue, Lady's bedstraw, Sand sedge, Sheep's fescue	Ford et al. (2013)
Influence of grazing management on microbial structure and antibiotic resistance	Similar microbial richness across grazing treatments Microbial community differentiation associated with grazing intensity	Annual ryegrass, Perennial ryegrass, White clover, Dandelion, Plantain, Chicory	Mhui-reach (2022)
Impact of grazing intensity on soil microbial diversity and SOC turnover	Overgrazing reduced bacterial (5%) and fungal abundance (14%)	Chinese ryegrass, Baikal needlegrass, Tough sedge, Lady's bedstraw, Spleenwort bupleurum, Siberian fescue	Xun et al. (2018)
Seasonal grazing effects on microbial richness in temperate grasslands	No effect on bacterial diversity Fungal diversity was 30% higher in seasonal grazing plots than in non-grazed plots	Krylov's feather grass, Chinese ryegrass, Squareseed cleistogenes	Ma et al. (2022)
Grazing effects on microbial biomass and diversity	Moderate grazing increased bacterial diversity by 7% compared to non-grazed plots	Dominant species: Chinese ryegrass Other species not specified	Zhang et al. (2023)
Grazing intensity and microbial network complexity	Higher grazing intensity increased protist diversity and microbial network complexity	Dominant species: Prairie grasses Other species not specified	Camuy-Vélez et al. (2024)
Effects of grazing management, climate, edaphic properties, and plant-microbial communities	Soil bacterial diversity decreased by 3.3% under moderate grazing and by 7.2% under heavy grazing compared to no grazing	Mixed temperate grassland species Specific names not provided	Yao et al. (2025)

Diverse pastures have been hypothesised to reduce enteric methane emissions by altering gut microbiome fermentation and methanogenesis pathways. However, evidence under grazing conditions is mixed. A recent meta-analysis by Komainda et al. (2025) evaluated all available grazing studies ( $n=16$ ) comparing diverse and standard pastures and found no consistent difference in methane emissions primarily because methane-mitigating species such as tannin-rich plants were present only in small proportions. Nevertheless, other grazing studies outside this meta-analysis suggest that functional diversity can play a role when species with bioactive compounds are present. For example, Gere et al. (2024) reported a 29% reduction in daily methane emissions and a 36% reduction in methane yield in beef steers grazing a cover crop mixture of vetch (*Vicia sativa* L.), Italian ryegrass (*Lolium multiflorum* Lam.), and forage radish (*Raphanus sativus* L.) compared with those on lucerne + tall fescue (*Festuca arundinacea* Schreb.) pastures. Such reductions are often linked to the presence of condensed tannins, which bind to dietary proteins and carbohydrates, decreasing their ruminal degradation and reducing hydrogen availability for methanogenesis (Kolesnik et al. 2024). These findings suggest that methane mitigation depends not merely on species richness but on the inclusion of plants with traits such as condensed tannins or secondary metabolites that influence hydrogen availability for methanogenesis.

Evidence for the effects of pasture diversity on milk yield under grazing conditions is also mixed. Although gut microbiome shifts are hypothesised to contribute, direct evidence linking microbiome changes to milk yield is limited. In the same meta-analysis, Komainda et al. (2025) found no consistent difference in milk yield between diverse and standard pastures in grazing-only trials, suggesting that species composition and functional traits may be more influential than species richness alone. Similarly, McCarthy et al. (2020) reported no effect of pasture diversity in grazing trials but observed higher milk yield when controlled feeding trials were included.

Some grazing experiments, however, have reported higher milk yield when species such as chicory, plantain and lucerne were included in pasture mixtures, compared with standard perennial ryegrass-white clover swards (Bryant et al. 2018; Dodd et al. 2019; Jonker et al. 2018; Loza et al. 2021; Roca-Fernández et al. 2016; Woodward et al. 2013). For example, in New Zealand, mixed pastures containing prairie grass (*Bromus catharticus* Vahl, syn. *Bromus willdenowii* Kunth), chicory, plantain, and lucerne increased first-year milk yield relative to perennial ryegrass-white clover (9.6 vs. 8.1 kg/cow/day) (Woodward et al. 2013).

Similar increases in milk yield from diverse pastures have been reported in other New Zealand and European studies.

In contrast, other experiments reported that cows grazing monocultures produced similar or slightly higher milk yields than mixed pastures. For example, Box et al. (2017) observed that plantain monoculture yielded slightly more milk (16.4 L/cow/day) than a 50:50 mixture of perennial ryegrass-white clover and plantain (16.3 L/cow/day) and perennial ryegrass-white clover alone (14.3 L/cow/day). Additional studies have reported no or negative effect of pasture diversity on milk yield (Bryant et al. 2017; Carmona-Flores et al. 2020; Soder et al. 2006).

Seasonal conditions, lactation stage, and grazing management further influence milk yield, potentially through diet-driven changes in nutrient utilisation and fermentation (Chapman et al. 2008; Pembleton et al. 2016). For example, chicory+white clover increased summer milk yield in Australia compared with ryegrass-white clover (18.8 vs. 9.8 L/cow/day) (Chapman et al. 2008), and perennial ryegrass+white clover+plantain mixtures consistently outperformed simpler pastures across lactation stages in New Zealand (Pembleton et al. 2016).

Collectively, these variable responses may reflect differences in species composition, functional traits, seasonal forage quality, lactation stage, and grazing management, as well as indirect effects mediated through gut microbiome shifts that influence milk production. However, none of the grazing studies cited here measured rumen or gut microbiomes directly, so microbiome-related mechanisms remain hypothetical, inferred from known effects of diet composition and plant secondary metabolites on rumen fermentation, volatile fatty acid profiles, and nitrogen utilisation (Chen et al. 2022; Scherer-Lorenzen et al. 2003; Xu et al. 2025).

Grazing on diverse pastures enhances sheep performance, with higher ewe live weight gain, improved body condition and increased milk production reported on chicory-plantain-clover swards compared with standard ryegrass-white clover pastures (Corner-Thomas et al. 2020; Hutton et al. 2011; Kenyon et al. 2010). These responses are hypothesised to be mediated in part by a more functionally enriched gut microbiome, although microbiome dynamics were not measured in these studies.

## Insight into the research gap and future perspectives

There is increasing scientific interest in understanding the dynamics of microbiomes under different pasture management systems. However, few omics-based studies have examined either soil or gut microbiomes under

pasture systems, and research simultaneously addressing their dynamics and interactions in diverse pastures under regenerative agriculture remains limited. Future omics-driven studies should compare regenerative and contemporary management across both diverse and standard pastures using field scale DNA-based metagenomics to assess how these management practices influence the composition, abundance, and diversity of soil and gut microbiomes over time. Moreover, soil-gut microbial interactions may occur through shared microbial taxa, and investigating microbial gene expression using RNA-based metatranscriptomics under comparative pasture management systems could provide insights into the functional roles of the microbiomes and its contributions to both soil and ruminants. In addition to DNA- and RNA-based approaches, integrated multi-omics combined with advanced techniques such as stable isotope probing (SIP) could be applied to trace C, N, and micronutrient fluxes between soil and ruminant gut microbiomes, thereby elucidating how pasture diversity and management regulate microbial functions and soil-animal interactions.

## Glossary

Alpha diversity	A measure of the diversity within a single sample, reflecting species richness and evenness.
Bacterial and fungal abundance	The quantity or biomass of bacteria and fungi present in a given sample, often assessed using molecular or biochemical methods.
Beta diversity	A metric that quantifies the variation in microbial community composition between different samples or environments.
Diverse pasture systems	Pastures containing multiple plant functional groups, typically at least five species of grasses, legumes, and herbs, designed to increase above- and belowground biodiversity.
Enteric methane emissions	Methane produced in the digestive tract of ruminants during microbial fermentation of feed, primarily in the rumen, and released via eructation
Inverse simpson index	A diversity index that reflects the probability that two randomly selected individuals belong to different species, emphasizing dominant species.

Metagenomic studies	Analytical approaches that sequence genetic material directly from environmental samples to characterize the collective genomes of microbial communities.	Standard pastures (contemporary management)	Pastures dominated by one or two highly productive species, typically perennial ryegrass with or without white clover, managed with relatively high stocking rates, short grazing intervals, and regular synthetic inputs.
Metatranscriptomics	The study of all active gene transcripts (RNA) in a microbial community, used to understand functional activity and microbial responses to environmental conditions.	Total phospholipid fatty acid (PLFA) markers	Biomolecular indicators used to estimate the biomass and community composition of microorganisms in environmental samples by analysing fatty acids from cell membranes.
Microbial necromass	The residual organic matter derived from dead microbial cells that contributes to the formation and stabilisation of soil organic carbon.		
Multi-omics approaches	Integrated analytical frameworks that combine two or more omics techniques (such as metagenomics, metatranscriptomics, metaproteomics, or metabolomics) to investigate microbial community composition, function, and interactions.		
Regenerative agriculture	A farming approach that aims to restore soil health, enhance biodiversity, and improve ecosystem resilience through practices such as diverse pastures, rotational grazing, reduced chemical inputs, and minimal soil disturbance.		
Ruminant gut microbiome	The complex community of microorganisms inhabiting the ruminant digestive tract, including bacteria, archaea, protozoa, and fungi, which drive fermentation, nutrient utilisation, and metabolite production.		
Soil organic carbon (SOC)	The carbon stored in soil organic matter, derived from plant residues, root exudates, and microbial necromass, which underpins soil structure, fertility, and microbial activity.		
Stable isotope probing (SIP)	A technique that uses isotopically labelled substrates (e.g. $^{13}\text{C}$ or $^{15}\text{N}$ ) to link microbial identity with function by tracing the assimilation of labelled elements into microbial biomass, DNA, RNA, or metabolites.		

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## Declarations

**Competing interests** The authors declare that they have no competing interests.

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