Strategies to Mitigate Enteric Methane Emissions by Ruminants – A Way to Approach the 2.0°C Target

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ABSTRACT

Ruminant livestock enteric fermentation contributes approximately one-third of the global anthropogenic methane (CH_4) emissions and is projected to increase significantly to meet the increasing demand for animal-sourced protein. Methane, a short-lived greenhouse gas, needs to be reduced -24 to -47% by 2050 relative to 2010 to meet the 2.0°C target. This study describes the results of a comprehensive meta-analysis to determine effective mitigation strategies. The database included findings from 425 peer-reviewed studies (1963 to 2018). Mitigation strategies were classified into three main categories [animal and feed management, diet formulation, and rumen manipulation (additives and methods used to modify the rumen)] and up to five subcategories (98 total mitigation strategy combinations). A random-effects meta-analysis weighted by inverse variance was carried out (Comprehensive Meta-Analysis, V3.3.070). Five feeding strategies, namely CH_4 inhibitors, oils and fats, oilseeds, electron sinks, and tanniferous forages, decreased absolute CH_4 emissions by on average -21% (range -12 to -35%) and CH_4 emissions per unit of product (CH_4I; meat or milk) by on average -17% (range -12 to -32%) without negatively affecting animal production (weight gain or milk yield). Furthermore, three strategies, namely decreasing dietary forage-to-concentrate ratio, increasing feeding level, and decreasing grass maturity, decreased CH_4I by on average -12% (range -9 to -17%) and increased animal production by on average 45% (range 9 to 162%). The latter strategies are central to meeting the increasing demand for animal-sourced food. All strategies, but CH_4 inhibitors, can be implemented now and offer immediate approaches for combating global warming.

SIGNIFICANCE STATEMENT

Ruminant enteric fermentation is a major contributor to global anthropogenic methane emissions. The demand for animal-sourced products and associated methane emissions are projected to increase, which could prohibit reaching the 2.0°C target. This meta-analysis was undertaken to identify effective mitigation strategies to resolve this issue. We determined five strategies (the supplementation of methane inhibitors, oils and fats, oilseeds, electron sinks, and tanniferous forages) that decrease absolute and product-based methane emissions without negatively affecting animal productivity, and three strategies (decreasing dietary forage-to-concentrate ratio, increasing feeding level, and decreasing grass maturity) that decrease product-based methane emissions and increase animal productivity. All strategies, except methane inhibitors, can be adopted now and offer an immediate approach to combat global warming.

INTRODUCTION

The goal of the Paris Agreement, to limit global warming to 2.0°C above pre-industrial levels, is unlikely to be achieved if food systems continue operating on a business-as-usual scenario[1]. Thus, it is of utmost importance to determine and implement strategies that mitigate food-related greenhouse gas (GHG) emissions. Among the food-related GHG emissions, methane (CH_4) emissions from enteric fermentation by ruminant livestock contribute 30% of the global anthropogenic CH_4 emissions[2]. As CH_4 is a powerful but short-lived GHG, decreasing global CH_4 emissions is especially important for limiting global warming in the short-term. This urgency has been underlined by the European Commission, which recently published the EU Methane Strategy[3] that is essential to meet the EU's nationally determined contributions under the Paris Agreement and its 2050 climate neutrality goal.

In addition to the Paris Agreement, the international community also agreed to 17 Sustainable Development Goals (SDGs) to achieve sustainable development by 2030[4]. These include SDG 1 - no poverty, SDG 2 - no hunger, and SDG 13 - climate action. Consequently, measures to address SDG 13 (climate action) cannot countervail other SDGs, in particular SDG 2 (zero hunger). This is explicitly highlighted in article 2.1 (b) of the Paris Agreement "Increasing the ability to adapt to the adverse impacts of climate change and foster climate resilience and low greenhouse gas emissions development, in a manner that does not threaten food production"[5].

Given all this, effective mitigation strategies that comply with both SDG 13 (climate action) and SDG 2 (zero hunger) are urgently needed. Accordingly, the challenge facing food systems is the need to reduce CH_4 emissions from animal production by -24 to -47% by 2050 relative to 2010[6], while simultaneously increasing the production of animal-sourced food to meet the projected 68% increase in demand between 2010 and 2050[7]. Reaching these apparently conflicting twin goals will require effective enteric CH_4 mitigation strategies that, at a minimum, do not compromise animal productivity or have other unacceptable tradeoffs[8] and, ideally, increase animal-sourced food production. Strategies that increase animal production and reduce product-based CH_4 emissions (i.e., emission intensity variables CH_4I_G and CH_4I_M, emission per unit of weight gain or milk produced, respectively) are especially paramount in low and middle-income countries where productivity and production per animal are low[9,10]. Advocates of reducing the global ruminant population as a means to achieve climate change mitigation goals have acknowledged that this approach is particularly inappropriate for low-income countries[11]. Therefore ruminants are of major importance to achieving SDG 2 (zero hunger), as they provide food for human consumption from marginal lands and in subsistence agriculture situations.

Several reviews have determined that animal and feed management, diet formulation, and rumen manipulation strategies could significantly decrease enteric CH_4 emissions[8,12,13]. However, thus far studies either only investigated the quantitative effects of a single mitigation strategy or only compared CH_4 yield (CH_4Y; CH_4 per unit of feed intake) between multiple mitigation strategies. Nonetheless, CH_4Y is only one measure and other important CH_4 emission and animal performance metrics must be considered to determine the effectiveness and feasibility of mitigation strategies. Important CH_4 emission metrics include daily CH_4 emissions, CH_4Y, CH_4-energy conversion factor [Y_m; CH_4 energy as a proportion of gross energy intake; a component of the Tier 2 calculation for national GHG inventories recommended by the Intergovernmental Panel on Climate Change[14]], CH_4I_G, and CH_4I_M. Important animal performance metrics include feed intake, nutrient digestibility, and animal production.

The objective of this study was to conduct a comprehensive meta-analysis of enteric CH_4 mitigation strategies published in peer-reviewed journals by examining their quantitative effects on the aforementioned CH_4 emission and animal performance metrics. There is an urgent requirement for strategies that can effectively mitigate both absolute and product-based CH_4 emissions without negatively affecting animal productivity or that can effectively mitigate product-based CH_4 emissions while increasing animal-sourced food production. Our approach of identifying effective ´dual-action´ strategies ensures that both the ´climate action´ objective of SDG 13 and the ´zero hunger´ objective of SDG 2 are targeted simultaneously.

RESULTS AND DISCUSSION

The meta-analysis included 98 mitigation strategies reported in 425 peer-review journal publications (Supplementary Table 1). Mitigation strategies were classified into three main categories: animal and feed management, diet formulation, or rumen manipulation strategies. Of the strategies included, 63 did not significantly (adjusted $P \geq 0.05$) decrease daily CH_4 emissions; the remaining 35 strategies decreased daily CH_4 emissions and CH_4Y by on average -18% (ranging from -5 to -43%) and -14% (ranging from -4 to -37%), respectively. These strategies were classified as 'effective' in decreasing absolute and product-based CH_4 emissions, if they significantly (adjusted $P < 0.05$) decreased daily CH_4 emissions, CH_4Y, and CH_4I_G or CH_4I_M without decreasing animal production (weight gain of growing animals or milk yield of dairy animals) when production data were present. Strategies were also classified as 'effective' in decreasing product-based CH_4 emissions if they significantly decreased CH_4Y and CH_4I_G or CH_4I_M while significantly increasing animal production. A summary of the studied mitigation strategies is presented in Fig. 1 and the full list of the studied mitigation strategies is presented in Supplementary Tables 2.

Effective mitigation strategies in the order of efficacy and their effect on CH_4 and animal performance metrics as well as their relevance for confinement or grazing systems are presented in Fig. 2. As CH_4Y was highly correlated with Y_m (adjusted $R^2 = 0.83$; Supplementary Fig. 1) and more data were available for CH_4Y than for Y_m (Supplementary Fig. 2), only results for CH_4Y are presented and discussed here. All other strategies that were not classified as effective but had a significant effect on CH_4, CH_4Y, Y_m, CH_4I_G or CH_4I_M are presented in Supplementary Fig. 3 to 5. The CH_4 inhibitor bromochloromethane was not classified as effective, despite fulfilling the selection criteria for an effective mitigation strategy, because it is an ozone-depleting compound that is harmful to aquatic organisms and a confirmed carcinogen[15]. Furthermore, several mitigation strategies were excluded from the present evaluation or classified as ineffective because of insufficient publications and warrant further research. These include breeding low-CH_4 emitting animals and improving animal health. Modeling studies have shown that strategies that improve animal health can significantly increase animal productivity and reduce emission intensity[16]. In the subsequent text, the effects of mitigation strategies on CH_4 emissions and animal performance metrics are reported in parenthesis as mean, 95% confidence interval (CI), and number of treatment comparisons (n). Reported differences were significant (adjusted $P < 0.05$) unless indicated otherwise.

Strategies that decrease absolute and product-based CH_4 emissions

Rumen manipulation by feeding CH_4 inhibitors effectively decreased daily CH_4 emissions (mean = -35%, 95% CI = -30 to -40%, n = 23, throughout the paper). Within this category, 3-nitrooxypropanol (3-NOP) is most effective acting on methyl-coenzyme M reductase, a key enzyme of the methanogenesis pathway of archaea[17]. Its supplementation decreased daily CH_4 emissions (-39%, -29 to -47%, 11), CH_4Y (-37%, -26 to -46%, 12), and CH_4I_M (-31%, -21 to -40%, 2) without affecting feed intake or milk yield. Insufficient data were available to evaluate its effect on weight gain or fiber digestibility in this analysis. However, in recent studies, 3-NOP did not show adverse effects on weight gain of growing beef cattle[18] or fiber digestibility in early-lactation dairy cows[19] and decreased daily CH_4 emissions throughout a 15-week experiment[20]. A recent meta-analysis showed that 3-NOP decreases daily CH_4 emissions in a dose-response manner, that its mitigation effect is greater for dairy than beef cattle, and that its effectiveness decreases with increasing dietary fiber content[21]. In its current form, 3-NOP can only be used in confinement systems, because it is more effective when fed continuously within the animals' diet[20,22], but ongoing research is developing mechanisms for its application under grazing conditions[23]. Supplementation of 3-NOP increased milk fat content in dairy cattle[19] and feed efficiency in feedlot cattle[24], which may help offset its cost and stimulate adoption. A limitation of 3-NOP is that its use as a feed additive requires regulatory approval by various countries. Another CH_4 inhibitor strategy is supplementation with seaweed (e.g. *Asparagopsis taxiformis*), which can decrease daily CH_4 emissions by up to 80%[25]. However, more research is warranted on dietary inclusion levels, effects on animal feed intake and production[26], the implications and safety of feeding bromoform[27], its main active compound[28], the extremely high iodine content of *Asparagopsis* species (which limits how much can be fed in many countries), as well as the environmental effects of cultivating seaweed[29] before it can be recommended as a mitigation strategy.

Dietary inclusion of oil and fat decreased daily CH_4 emissions (-20%, -15 to -24%, 63) and CH_4Y (-15%, -11 to 18%, 52). Weight gain in growing animals or milk production in dairy animals was unaffected despite decreasing feed intake (-6%, -3 to -8%, 58) and fiber digestibility (-4%, -2 to -7%, 37). This resulted in decreased CH_4I_G (-22%, -8 to -35%, 6) and CH_4I_M (-12%, -6 to -18%, 24); however, possible effects on manure CH_4 emissions due to decreased fiber digestibility need to be evaluated[14]. Of the subcategories included here, only dietary inclusion of predominantly vegetable oils effectively decreased daily CH_4 emissions. This effect can be attributed to increased supply of non-fermentable highly digestible energy, a decreased feed intake and fiber digestibility as well as inhibition of methanogenesis by unsaturated (or medium-chain saturated) fatty acids, which are usually abundant in vegetable oils. Other meta-analyses also found that oil inclusion decreased CH_4Y (between -9 to -14%), feed intake (-6%) and increased milk yield (+4%)[13,30]. Oil inclusion reportedly decreases daily CH_4 emissions in a dose-response manner[30] and over the long-term[31,32]. The amount of oil that can be included in ruminant diets, however, is limited and inclusion level should not be at the expense of healthy rumen fermentation that may negatively impact animal health and productivity. Maximum oil inclusion levels in ruminant diets depend on the animals´ physiological stage, lipid and other nutrient composition of the basal diet, and fatty acid profile of the supplemental oil[33]. Vegetable oils that effectively decreased daily CH_4 emissions were: (1) coconut oil (-28%, -20 to -35%, 16), (2) canola oil (-22%, -12 to -32%, 4), (3) linseed oil (-22%, -14 to -29%, 14), and (4) sunflower oil (-17%, -9 to -24%, 5). The cost-effectiveness of feeding oils to decrease daily CH_4 emissions likely varies by region and country, because oil and meat and milk prices vary considerably therein. Studies in China[34], France[35], or the Netherlands[36] found that dietary inclusion of oils, for the purpose of mitigating enteric CH_4 emissions, was not cost-effective, but trade-offs by concomitant improvements in the fatty acid profile of milk and meat from a human-health perspective might help to support the implementation of certain oils and oilseeds.

Dietary inclusion of oilseeds (cracked or crushed) had similar effects on CH_4 emissions and animal performance metrics as the inclusion of oils, even though part of the oil in crushed oilseeds is rumen-protected. Oilseeds decreased daily CH_4 emissions (-20%, -15 to -24%, 26), CH_4Y (-14%, -8 to -20%, 18), and CH_4I_M (-12%, -4 to -19%, 6), tended to decrease feed intake (-4%, -1 to -7%, 25, $P = 0.06$), and decreased fiber digestibility (-8%, -6 to -11%, 13). Similar to oils, oilseeds had no effect on milk yield but decreased weight gain in growing animals (-13%, -6 to -20%, 8); thus, dietary oilseed inclusion may only be recommended for lactating dairy animals and not for growing animals. Likewise, the inclusion of oilseeds needs to be limited to not negatively impact rumen fermentation, animal health and production. However, as part of the oil in oilseeds is rumen-protected, dietary inclusion levels can be slightly higher than oils[37]. In addition, similar to oil inclusion possible effects on manure CH_4 emissions due to decreased fiber digestibility need to be evaluated. Oilseeds that effectively decreased daily CH_4 emissions were: (1) sunflower seeds (-39%, -15 to -57%, 3), (2) cottonseeds (-19%, -13 to -23%, 7), (3) linseeds (-17%, -2 to -29%, 4) and (4) canola seeds (-13%, -10 to -16%, 8).

Rumen manipulation with electron sinks, alternative electron acceptors that can redirect hydrogen from methanogenic archaea towards metabolically beneficial sinks in the rumen[38], decreased daily CH_4 emissions (-17%, -14 to -20%, 54) and CH_4Y (-15%, -13 to -18%, 51). Despite small decreases in feed intake (-2%, -1 to -3%, 49) small increases in milk yield (+3%, +1 to +5%, 13) were observed, resulting in decreased CH_4I_G (-12%, -2 to -20%, 3) and CH_4I_M (-13%, -9 to -16%, 12). Of the studied electron sinks (fumaric acid and nitrate), only nitrate was classified as effective. Another meta-analysis found similar effects of nitrate on daily CH_4 emissions (-15%)[39]. Nitrate has also been shown to decrease daily CH_4 emissions and CH_4Y in a dose-response manner with no loss of effectiveness over and effectively decreased CH_4 over the long-term[40,41]. Similar to 3-NOP, nitrate was more effective in decreasing daily CH_4 emissions and CH_4Y in dairy than in beef cattle[39]. Although nitrate can be toxic, early research on nitrate supplementation in ruminant diets reported a decrease in feed intake and no toxicity symptoms; however, toxicity can occur if animals are not properly acclimatized[42]. Acclimatization of animals to dietary nitrate is required to avoid methemoglobinemia, but rumen adaptation can be lost within three weeks if nitrate is not continuously fed[43]. Simultaneous sulfate supplementation has been shown to help protect cattle against nitrate toxicity[40]. Nitrate supplementation may increase enteric and possibly manure nitrous oxide emissions[44]. Studies in France[35] and the Netherlands[36] found that nitrate supplementation was not cost-effective.

Dietary inclusion of tanniferous forages decreased daily CH_4 emissions (-12%, -7 to -16%, 42) and CH_4Y (-10%, -6 to -14%, 39) without affecting feed intake or animal production and consequently decreased CH_4I_M (-18%, -8 to -26%, 7). However, it also decreased fiber digestibility (-7%, -2 to -12%, 21), which could potentially increase manure CH_4 emissions[14]. *Sericea lespedeza* (*Lespedeza cuneata*) decreased daily CH_4 emissions (-32%, -24 to -39%, 5) without affecting feed intake in goats and it has been effective in decreasing daily CH_4 emissions throughout a 12-week experiment[45]. Other tanniferous forages that may potentially decrease daily CH_4 emissions are *Leucaena* (-8%, 0 to -16%, 12, P = 0.10) and *Lotus* (*corniculatus* and *pedunculatus*) (-8%, -3 to -13%, 3). Although this meta-analysis did not reveal any effect on feed intake, tanniferous forages have been associated with decreased palatability and feed intake[46]. Tannins can bind to dietary protein and thus decrease protein digestion and animal production, especially when dietary protein is limiting. Nevertheless, when dietary protein is excessive or highly degradable, tannins may be beneficial, because they reduce excretion of nitrogen in urine, which decreases ammonia and nitrous oxide emissions from manure[47]. The cost-effectiveness of their supplementation still needs to be evaluated. Among the identified effective strategies to decrease absolute and product-based CH_4 emissions, dietary inclusion of tanniferous forages is the only one applicable to both confinement and grazing systems. This is important as 37% of global enteric CH_4 emissions are attributed to grazing systems[48].

Strategies that decrease product-based CH_4 emissions

Decreasing dietary forage-to-concentrate ratio decreased CH_4Y (-13%, -10 to -16%, 69) without increasing daily CH_4 emissions despite increasing feed intake (+9%, +5 to +14%, 85). The associated increase in overall feed intake did not affect fiber digestibility and led to an increase in weight gain (+21%, +13 to +29%, 32) and milk yield (+17%, +10 to +24%, 26). Consequently, CH_4I_G (-9%, -3 to -15%, 16) and CH_4I_M (-9%, -4 to -14%, 19) were decreased. The reduction in CH_4Y was most likely the result of a shift in rumen fermentation patterns and a decrease in rumen pH, which inhibits methanogens[38]. However, the supplementation of grain-based concentrate needs to be limited, because overfeeding can lead to subacute ruminal acidosis. Subacute ruminal acidosis is a nutritional disease that is associated with perturbation of rumen fermentation and decreased fiber digestibility, milk fat content, and animal health mostly found in feedlot and high-yielding dairy cattle[49]. In addition, the promotion of increased use of (food-quality) grain-based concentrate in ruminant diets will likely intensify feed-food competition. In contrast, if concentrate-rich diets are mainly based on food industry by-products, the feed food-competition may be avoided. The cost-effectiveness of this strategy will depend on forage and concentrate costs as well as associated increases in animal production and the price of animal products (meat and milk).

Increasing feeding level (+58%, +47 to +71%, 47) increased daily CH_4 emissions (+18%, +14 to +22%, 42), but decreased CH_4Y (-8%, -4 to -12%, 31). Fiber digestibility was decreased (-7%, -2 to -12%, 18), likely due to increased rumen passage rates[50]. Increasing feed intake resulted in increased weight gain (+162%, +38 to +398%, 7) and milk yield (+17%, +10 to +25%, 8) and decreased CH_4I_M (-17%, -9 to -23%, 5). No data were available for CH_4I_G. Similar to our data, a recent study showed that increasing the level of feeding decreased CH_4Y, while increasing daily CH_4[51]. Increasing feed intake to improve animal productivity significantly decreases CH_4I_G and CH_4I_M[8,52] and the overall carbon footprint of animal-sourced food[53] when diet composition remains unchanged. This strategy directs energy for CH_4 towards animal production[51] but also decreases energy requirements for maintenance relative to milk production and reduces the time to slaughter for growing animals. Increased feeding level also causes differences in digestive efficiency including microbial metabolism, particle passage and digestive kinetics, all of which contribute to the negative relationship between CH_4Y and increasing feed intake[8]. Potential effects of this practice on manure CH_4 emissions, as a result of decreased fiber digestibility, need to be evaluated. The practice is applicable to both confinement and grazing systems, but particularly the latter and especially in certain climatic regions where animals are underfed due to insufficient or low nutritive forage[54].

Decreasing grass maturity decreased CH_4Y (-4%, -1 to -8%, 8) but not daily CH_4 emissions. It did not affect feed intake but increased milk yield (+9%, +1 to +18%, 6) and thus decreased CH_4I_M (-13%, -7 to -18%, 6). Furthermore, decreasing grass maturity improved fiber digestibility (+15%, +9 to +21%, 9), which can potentially decrease manure CH_4 emissions[14]. Insufficient data were available for growing animals and thus, based on our analysis this mitigation strategy can currently only be recommended for lactating animals. The positive effect of decreasing grass maturity on milk yield is likely attributed to greater digestible energy and protein content. Increased protein content, however, can lead to increased nitrogen intake and excretion[55]. Thus, possible tradeoffs associated with direct and indirect manure nitrous oxide emissions require further evaluation. This strategy is applicable to both confinement and grazing systems. Although decreasing grass maturity increases the overall efficiency of dietary nutrient use for milk production (kg milk per unit of feed intake) and milk production, it was not deemed to be cost-effective in the Netherlands; however, it was more cost-effective than supplementation with nitrate or linseed[36].

CONCLUSION

Effective strategies that reduced daily and product-based CH_4 emissions without negatively affecting animal production decreased daily CH_4 emissions by on average -21% (range from -10 to -35%) and product-based emissions by on average -17% (range from -12 to -32%). Strategies that reduced product-based CH_4 emissions and increased animal production decreased product-based CH_4 emissions by on average -12% (range from -9 to -17%), and increased animal production by on average +45% (range from +9 to +162%). Nevertheless, future studies should continue to explore novel mitigation strategies and possible synergistic effects of combining effective mitigation strategies, e.g. 3-NOP with lipids or lipids with nitrates, to develop innovative strategies that have a large mitigation potential. In addition, possible tradeoffs and pollution swapping with upstream processes, such as GHG emissions associated with feed productions as well as manure GHG emissions that could offset gains in enteric CH_4 mitigation need to be investigated. Of the effective strategies that decrease absolute and product-based CH_4 emissions, only tanniferous forages are applicable in grazing systems, and it is of utmost importance that more strategies are developed for these systems. Strategies that mitigate enteric CH_4 emissions whilst improving animal production are of particular relevance in view of the significant role of ruminants in providing food for human consumption in low-income countries. All identified effective mitigation strategies, except for the supplementation of 3-NOP, could be implemented today. Owing to the short-lived manner of CH_4 as a GHG, any such strategy implemented today will significantly reduce the contributions of food systems to global warming by 2030, and is a way to approach the 2°C target.

Materials and Methods

Literature Search and Classification of Mitigation Strategies. The database for this meta-analysis was compiled using data obtained by searching the databases of the Commonwealth Agricultural Bureau International (CABI), the EBSCO Discovery Service, and the Web of Science from 1964 to 2018. Publications from 1964 through 2016 were searched using CABI and EBSCO Discovery Service with the search terms 'rumen' AND 'methane' and an additional four searches were completed in the EBSCO Discovery Service using the term 'rumen' in combination with 'methane', 'energy partitioning', 'energy metabolism', or 'energy balance'. Publications from 2017 through 2018 were searched using CABI and Web of Science databases. Seven searches were conducted with the search term 'methane' in combination with 'beef', 'cattle', 'dairy', 'goat', 'sheep', 'rumen', or 'ruminant' and three searches with the search term 'rumen' in combination with 'energy balance', 'energy metabolism', or 'energy partitioning'. Publications listed in an independently developed database supported by the AnimalChange project, MitiGate[13], were merged with the database created in the current analysis.
The abstracts of the publications found in the search were reviewed and, based on abstract content, publications were selected for further consideration if they included *in vivo* measurement of enteric CH_4 emissions, a clearly defined treatment and control, and multiple replications (i.e., at least four or more animals in continuous design experiments, crossover design experiments, etc.). Publications were excluded if they were not from peer-reviewed literature or if they were not in English, French, German, or Portuguese. Furthermore, publications were excluded if they were based on inappropriate study design (i.e., experimental period $\leq$ 10 days) or measurement technique (e.g. the 'sniffer technique' that is based on the CH_4-to-carbon dioxide ratio of exhaled breath[56,57]).
The completed database consisted of 650 publications. From these, only publications that had a treatment that could be assigned to one of three main mitigation categories, as described below, and reported statistical variance for at least one of the CH_4 emissions emission metrics (e.g. LSD, RSD, or SE of the mean) were included in the final analysis. WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/; accessed 30 October 2019) was used to determine absolute values for a total of nine metrics in seven publications where data were reported as figures.
Data were classified into three main mitigation categories: (1) animal and feed management, (2) diet formulation, and (3) rumen manipulation, each of which was then further classified into up to five subcategories (Supplementary Table 2). Only mitigation strategies, for which at least two publications were available for at least one CH_4 emission metric and two of the remaining CH_4 emission or animal metrics, were analyzed within a main category. Treatment effects were assessed relative to their respective control values for all responses, therefore, closely related variables and variables with

different units were included in the analysis. For example, CH_4I_M included daily CH_4 emissions per liter of milk and milk corrected for fixed energy, fat and protein, or milk solids (all milk non-water components combined) content as well as milk solids yield. Similarly, for CH_4I_G, both weight gain and carcass gain were used. Metrics for feed intake included intakes of dry matter, gross energy, organic matter, and intake expressed per unit of body weight or metabolic body weight. Digestibility (of fiber) metrics included only apparent digestibility of neutral detergent fiber. Where multiple treatments of a common treatment type were present within an experiment, those treatment means were averaged, and their respective errors pooled, such that each experiment produced a single "Treatment" and "Control" pair of response means and SDs.

The final meta-analysis included data from 425 peer-reviewed publications, of which 66% were with cattle, 31% with small ruminants (sheep and goats) and 3% with other ruminant species (buffalo, deer, and yak). The complete list of references used in the current analysis is given in Supplementary Table 1. The majority of publications reported daily CH_4 emissions (92%), feed intake (84%), and CH_4Y (71%), whereas less than half of the publications reported weight gain for all animal types (growing, lactating, and other adult animals) (49%), Y_m (48%), fiber digestibility (41%), milk yield (29%), CH_4I_M (21%), or CH_4I_G (7%) (Supplemental Fig. 2). The final analysis only included weight gain data for growing animals (106 publications), which led to the exclusion of the weight gain data of half of the publications (104) that reported weight gain data for lactating and other adult animals.

Statistical Analysis**.** A mixed model meta-analysis weighted by inverse variance was carried out considering treatment mean comparisons within publication as a random effect. Analyses were run across all ruminant species (cattle, buffalo, deer, goat, sheep, and yak) and included main mitigation strategies and their respective subcategories as potential moderator fixed effects. Analyses were conducted separately for each of the nine response variables (daily CH_4, CH_4Y, Y_m, CH_4I_G, CH_4I_M, feed intake, weight gain for growing animals, milk yield, and fiber digestibility) using a log ratio of means, namely log(Treatment/Control), in order to standardize treatment effects across multiple measures, species, and outcomes, as well as to allow the expression of treatment differences as relative percentages[58,59]. Weight gain for growing animals when consuming tanniferous plants, however, was assessed based on a standardized relative difference, [(Treatment-Control)/SE_{Diff}], due to the presence of negative growth rate responses in two treatment mean comparisons[59]. Computations were carried out using Comprehensive Meta-Analysis (V. 3.3.070; Biostat, Englewood, NJ). All analyses were adjusted for multiple comparisons using a step-down Bonferroni procedure to reduce the risk of Type I error[60] (SAS, V. 9.4; SAS Inst. Inc, Cary, NC). The effect of a mitigation strategy was considered to be significant for adjusted $P < 0.05$ and $0.05 \leq$ adjusted $P \leq 0.10$ was considered as a trend.

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FIGURES AND TABLES

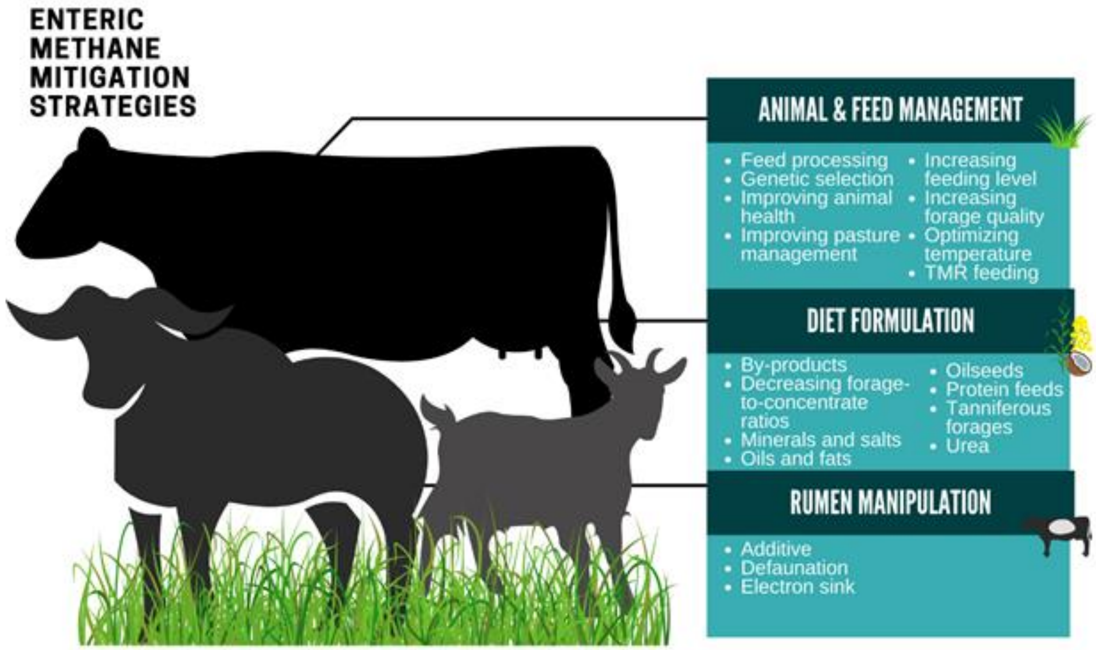
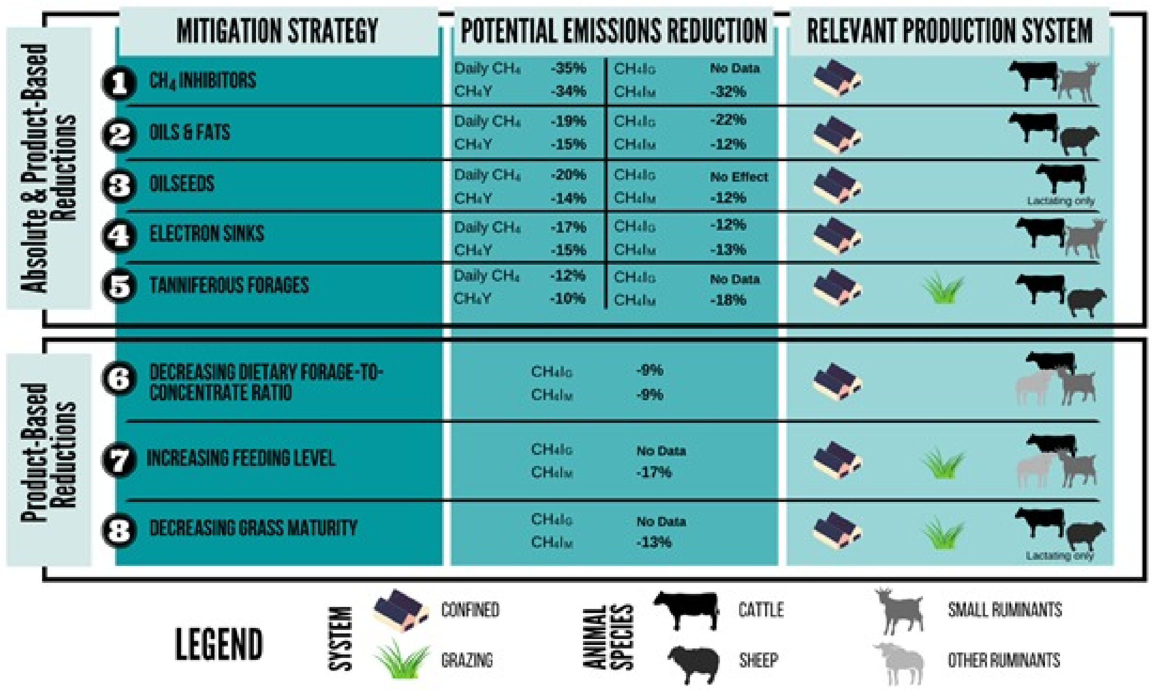


Figure 1. Studied enteric methane mitigation strategies. For a complete list of strategies, see supplementary Table S2.

A



B

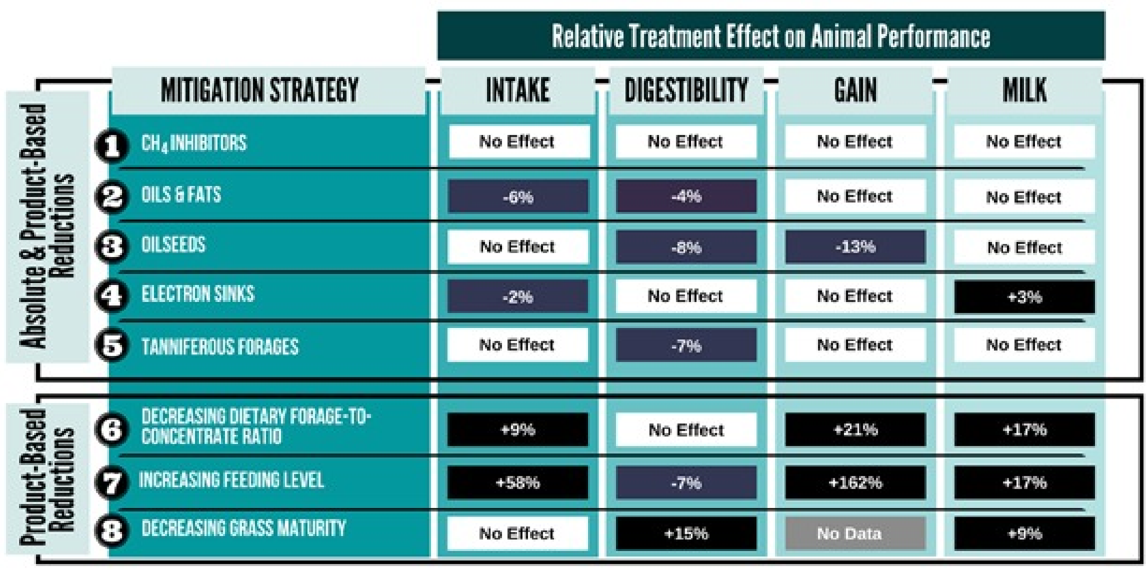


Figure 2. Effective mitigation strategies and their effect on methane (CH_4) emission (a) and animal performance metrics (b). Daily CH_4 = daily CH_4 emission (g animal^{-1} day^{-1}); CH_4Y = CH_4 yield (CH_4 g per kg of dry matter intake), CH_4I_G = CH_4 emission intensity for weight gain (g CH_4 per kg of weight gain for growing animals), CH_4I_M = CH_4 emission intensity for milk (CH_4 g per kg of milk), Intake = dry matter intake (kg d^{-1}); Digestibility = apparent digestibility of neutral detergent fiber (%); Gain = average daily gain (kg d^{-1}), Milk = milk yield (kg d^{-1}); when numeric values are shown a significant effect was observed (adjusted $P < 0.05$) and no effect when adjusted $P \geq 0.05$.

SUPPLEMENTARY INFORMATION

SUPPLEMENATARY TABLES

Supplementary Table 1. Publications included in this meta-analysis.

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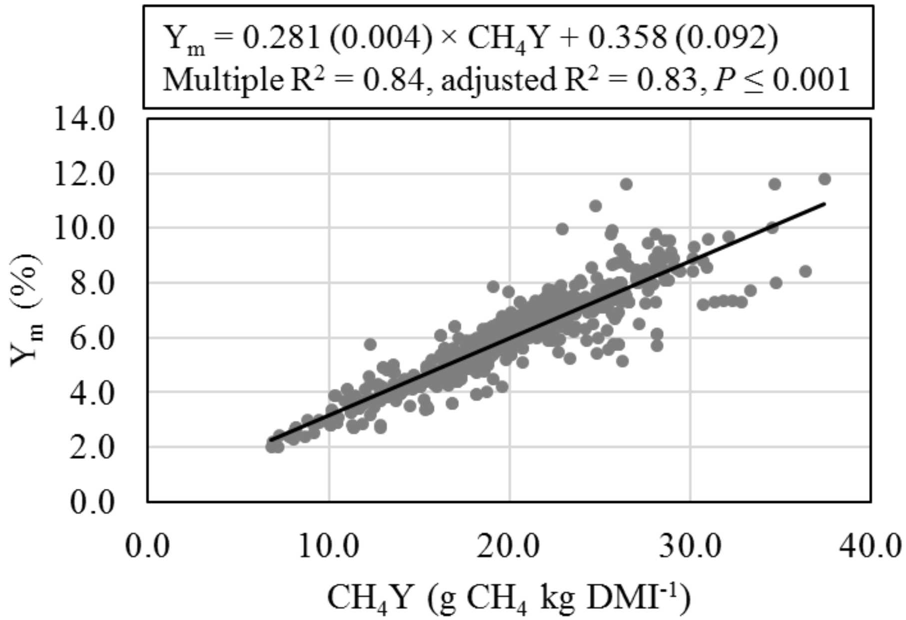
Supplementary Table 2. Mitigation strategies (categories and subcategories) included in this meta-analysis.

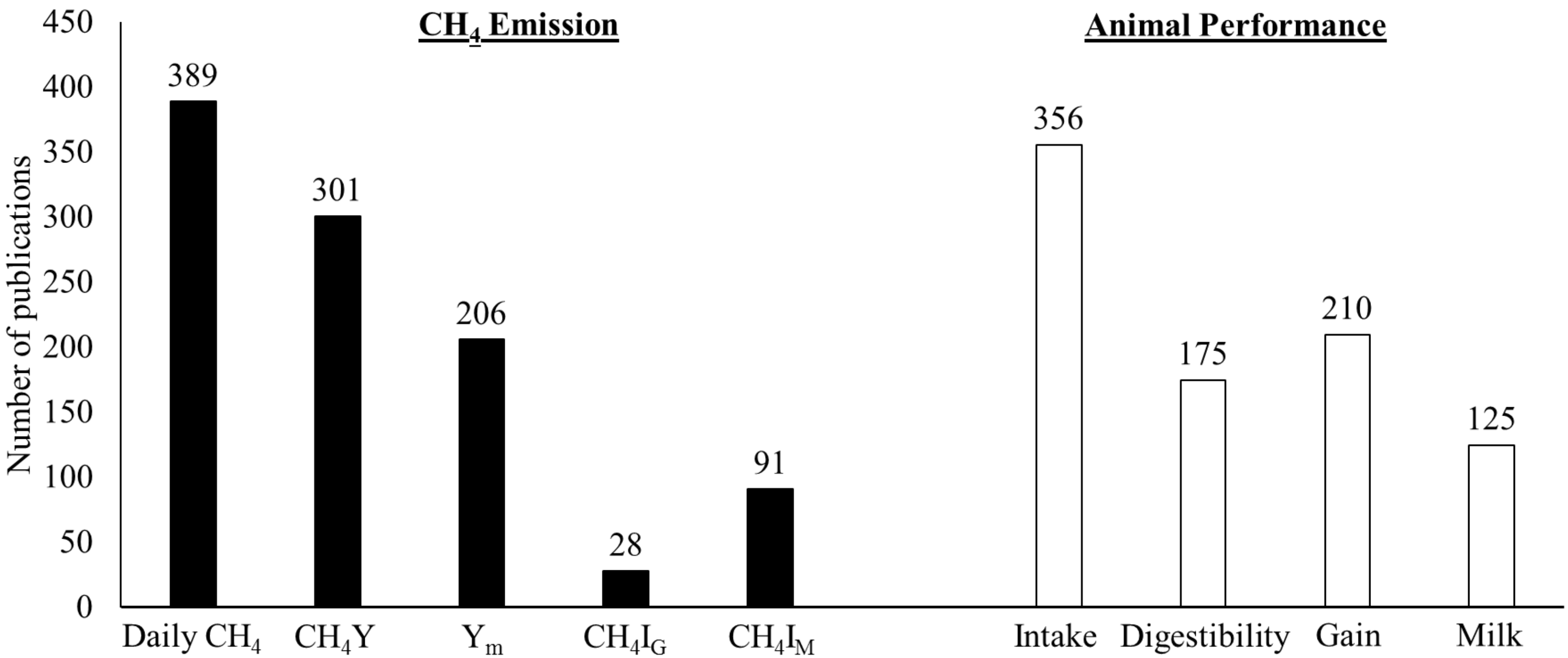
Animal and feed management	Diet formulation	Rumen manipulation
Feed processing	**By-products**	**Additives**
Forage processing	Fiber sources	Amino acids
Urea-treated straw	Soybean hulls	**CH_4 inhibitors**
Grain processing	Glycerol	**3-nitrooxypropanol**
Genetic Selection	**Lipid sources**	**Bromochloromethane**
Low residual feed intake	Extruded canola	Enzymes
Low CH_4 emitter	**Extruded linseed**	**Galactooligosaccharides**
Improving health	**Protein sources**	**Ionophores**
Improving pasture management	**Distiller´s dried grains with solubles**	**Monensin**
Grazing plus supplementation	Soybean meal	**Organic acids**
Grazing plus concentrate	Pulp sources	Carboxylic acids
Improved pasture	Citrus pulps	**Long chain fatty acids**
Increased Nitrongen fertilization	**Decreasing forage-to-concentrate ratio**	Unsaturated fatty acids
Legume-grass vs. grass only pastures	**Barley**	Docosahexaenoic acid
Reduced pre-grazing herbage mass	**Corn**	Probiotics
Increasing feeding level	**Minerals and Salts**	**Bacteria**
Increasing forage quality	**Oils and fats**	*Lactobacillus*
Decreasing grass maturity	**Canola oil**	***Propionibacterium***
Increasing corn silage maturity	**Coconut oil**	Yeasts
Optimizing temperature	**Linseed oil**	*Saccharomyces*
Total mixed ration feeding	Oil blends	**Secondary plant compounds**
Total mixed ration vs. grazing	**Rumen protected fat**	**Essential oils**
	Sunflower oil	**Essential oil blends**
	Tallow	Garlic
	Oilseeds	**Oregano**
	Canola seed	Flavonoids
	Cottonseed	Phenols
	Linseed	**Saponins**
	Sunflower seed	***Saponaria***
	Increasing protein	**Tea saponin**
	Tannifores forages	**Yucca saponin**
	Lespedeza	**Tannins**
	Leucaena	**Condensed tannins**
	Lotus	*Acacia*
	Sainfoin	*Quebracho*
	Urea	Hydrolysable tannins
		Defaunation
		Electron sinks
		Fumaric acid
		Nitrate

Strategies that decreased (adjusted $P < 0.05$) daily methane (CH_4) emission (g d^{-1}), CH_4 yield (CH_4 per unit of dry matter intake, g kg^{-1}), or CH_4 conversion factor [CH_4 energy (MJ) per gross energy intake (MJ), %] are presented in **bold**.

SUPPLEMENTARY FIGURES

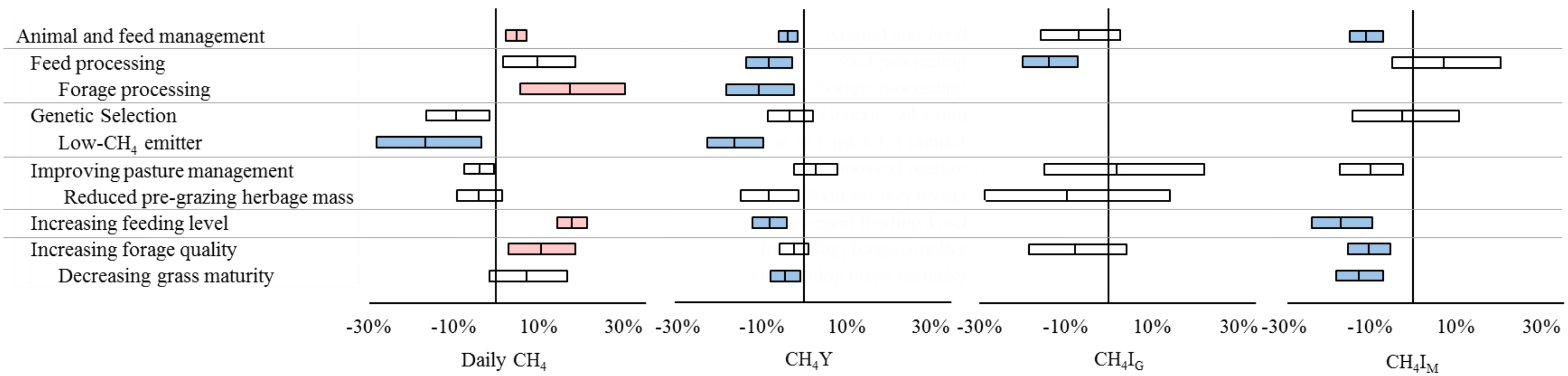


Supplementary Fig 1. Relationship between CH_4Y (CH_4 yield = CH_4 per unit of feed dry matter intake, g kg^{-1}) and Y_m (CH_4 conversion factor = CH_4 energy (MJ) per gross energy intake (MJ) × 100, %), MJ CH_4/MJ] of treatment means included in the database of this study (n = 783). Linear regression analysis was performed using the lm function in R. Standard errors are reported in parenthesis.

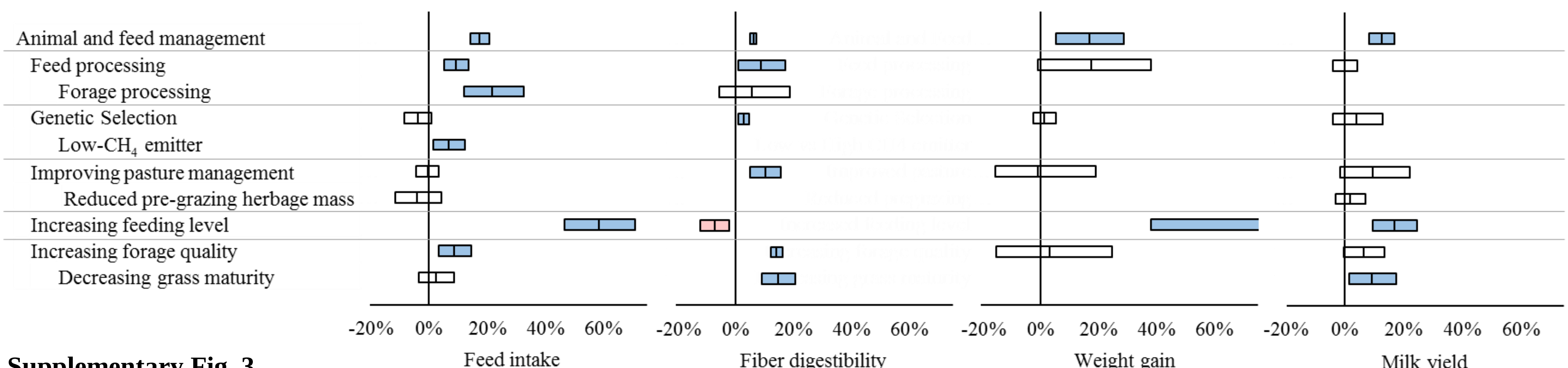


Supplementary Fig 2. Number of publications that reported methane (CH_4) emission and animal performance variables of the 425 studies that were analyzed in the current meta-analysis. Methane emission variables included in the analysis were: Daily CH_4 = daily CH_4 emission (g d^{-1}), CH_4Y = CH_4 yield (CH_4 per unit of feed dry matter intake, g kg^{-1}), Y_m = CH_4 conversion factor (CH_4 energy (MJ) per gross energy intake (MJ) × 100, %), CH_4I_G = CH_4 intensity for weight gain (CH_4 per unit of weight gain of growing animals, g kg^{-1}), CH_4I_M = CH_4 intensity for milk (CH_4 per unit of milk produced, g kg^{-1}), Intake = feed intake (dry matter intake, kg d^{-1}), Digestibility = fiber digestibility (neutral detergent fiber digestibility, %), Gain = weight gain (average daily gain, kg d^{-1}), and Milk = milk yield (kg d^{-1}).

a



b

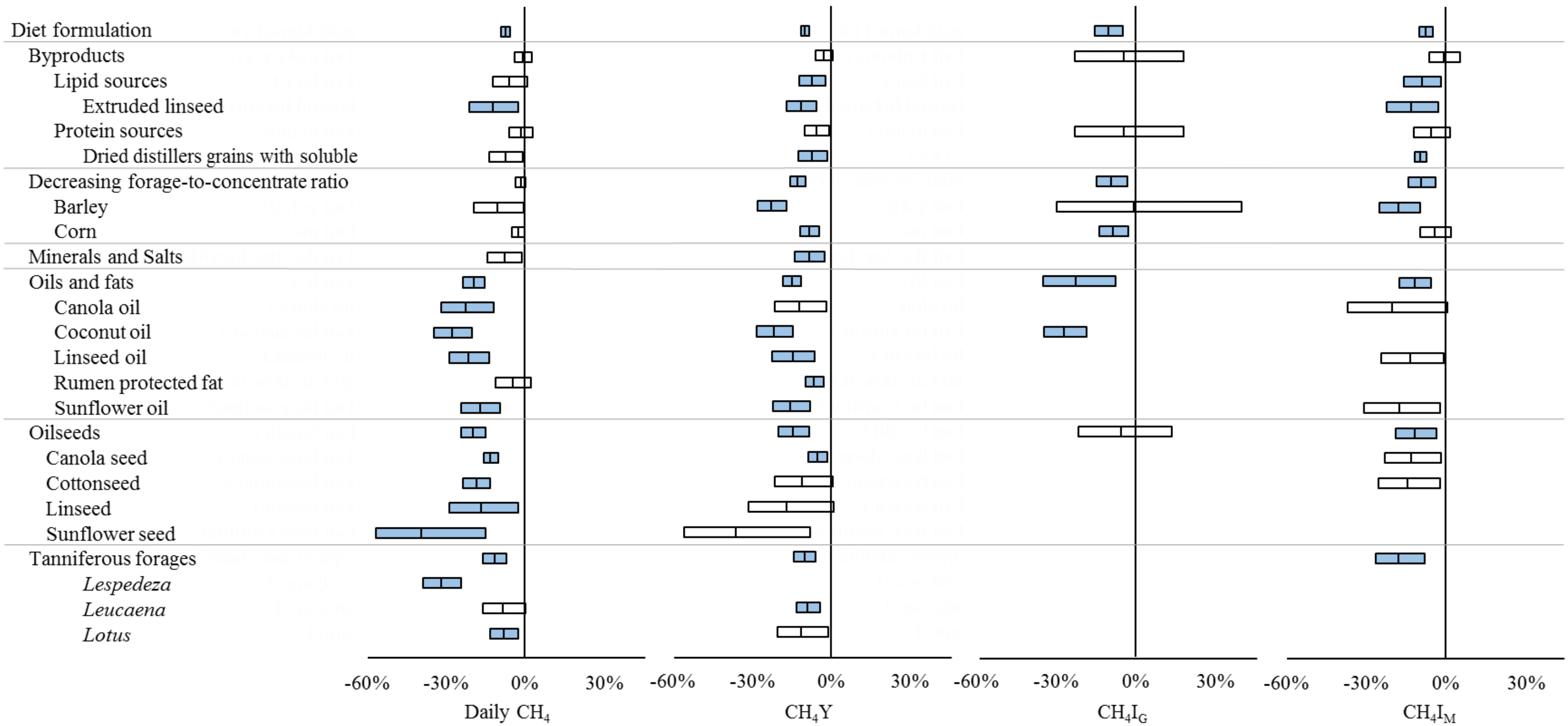


Supplementary Fig. 3.

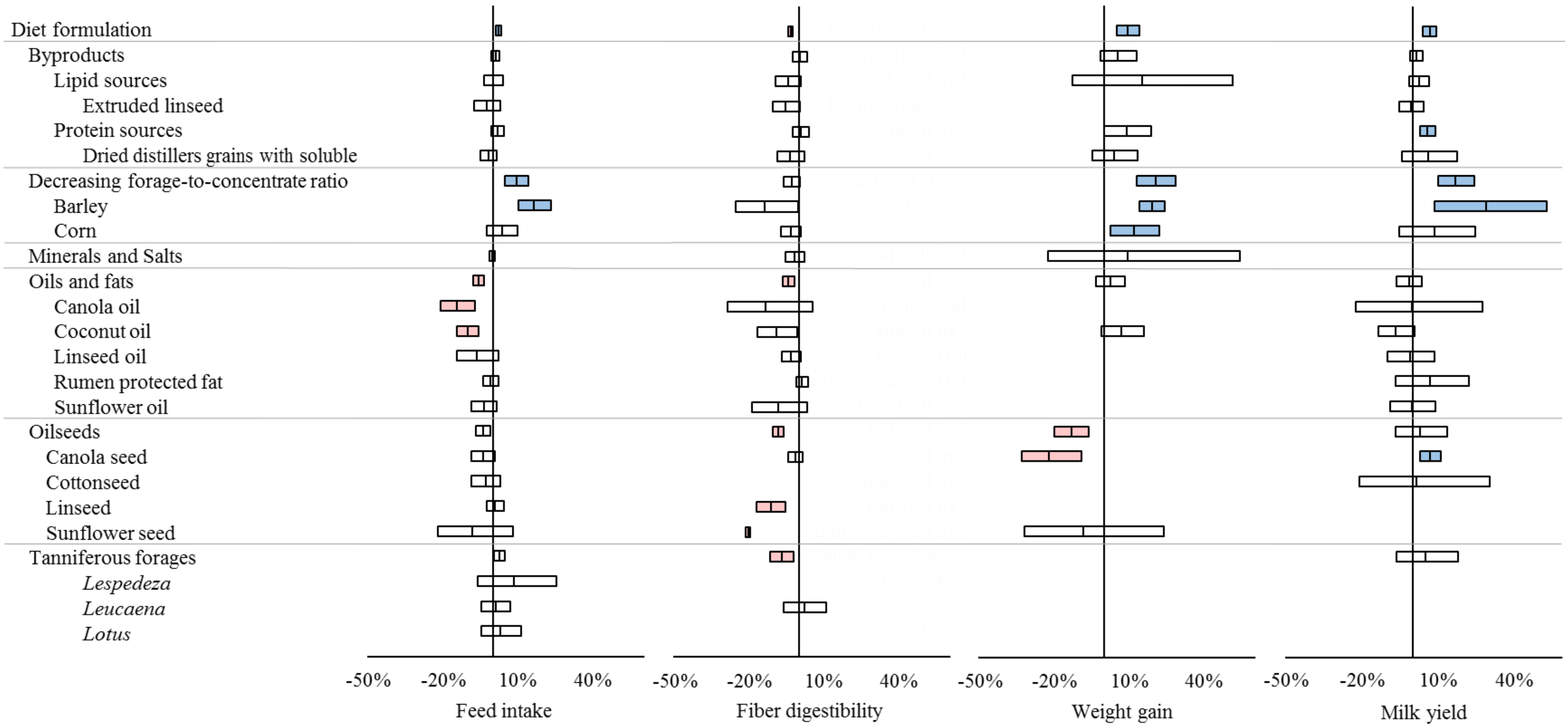
Relative treatment effects and 95% confidence intervals of (**a**) Daily CH_4 = daily CH_4 emission (g d^{-1}); CH_4Y = CH_4 yield (CH_4 per unit of feed dry matter intake, g kg^{-1}); CH_4I_G = CH_4 emission intensity for weight gain (CH_4 per unit of weight gain of growing animals, g kg^{-1}); and CH_4I_M = CH_4 emission intensity for milk (CH_4 per unit of milk produced, g kg^{-1}) and (**b**) Feed intake (dry matter intake, kg d^{-1}); weight gain (average daily gain, kg d^{-1}), milk yield (kg d^{-1}); and fiber digestibility (neutral detergent fiber digestibility, %) for animal and feed management strategies that had a significant effect (adjusted $P < 0.05$) on daily CH_4, CH_4Y, or Y_m = methane conversion factor [CH_4 energy (MJ) per gross energy intake (MJ), %]. Next higher mitigation categories were included for all significant categories (adjusted $P < 0.05$) even if they were not significant (adjusted $P \geq 0.05$)

Blue and red bars indicate significant desirable and undesirable effects (adjusted $P < 0.05$), respectively, white bars indicate lack of significant effects (adjusted $P \geq 0.05$), and no bars indicate that no data were available. The relative treatment effect of increasing feeding level on weight gain is only partially shown; its relative treatment effect was 162% and its 95% CI was 38 to 398%.

a

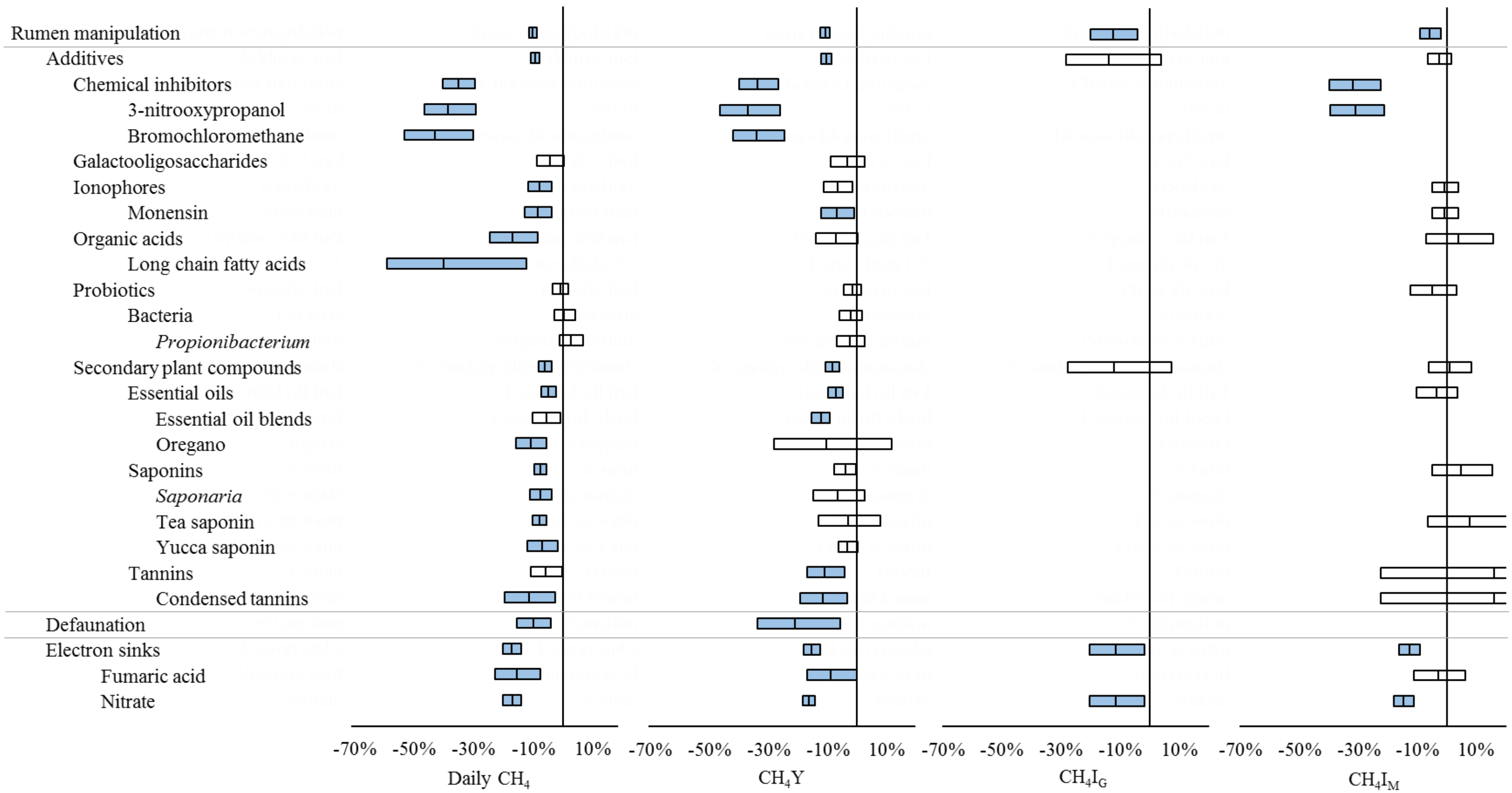

Diet formulation
Byproducts
Lipid sources
Extruded linseed
Protein sources
Dried distillers grains with soluble
Decreasing forage-to-concentrate ratio
Barley
Corn
Minerals and Salts
Oils and fats
Canola oil
Coconut oil
Linseed oil
Rumen protected fat
Sunflower oil
Oilseeds
Canola seed
Cottonseed
Linseed
Sunflower seed
Tanniferous forages
Lespedeza
Leucaena
Lotus
-60% -30% 0% 30%
Daily CH_4
CH_4Y
CH_4I_G
CH_4I_M

b



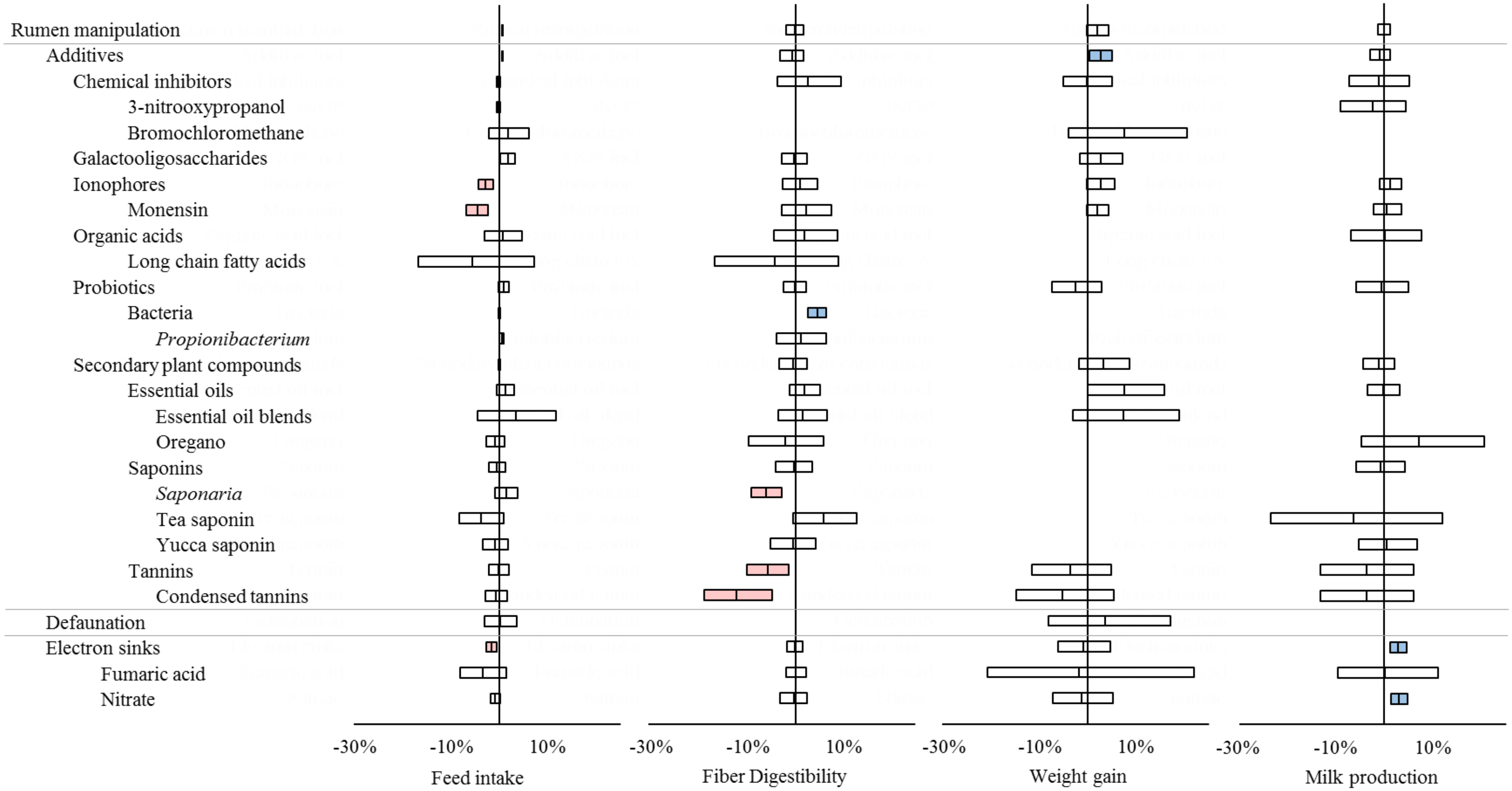
Supplementary Fig 4. Relative treatment effects and 95% confidence intervals of (**a**) Daily CH_4 = daily CH_4 emission (g d^{-1}); CH_4Y = CH_4 yield (CH_4 per unit of feed dry matter intake, g kg^{-1}); CH_4I_G = CH_4 emission intensity for weight gain (CH_4 per unit of weight gain of growing animals, g kg^{-1}); and CH_4I_M = CH_4 emission intensity for milk (CH_4 per unit of milk produced, g kg^{-1}) and (**b**) Feed intake = feed intake (dry matter intake, kg d^{-1}); weight gain (average daily gain, kg d^{-1}), milk yield (kg d^{-1}); and fiber digestibility (neutral detergent fiber digestibility, %) for diet formulation strategies that had a significant effect (adjusted $P < 0.05$) on daily CH_4, CH_4Y, or Y_m = methane conversion factor [CH_4 energy (MJ) per gross energy intake (MJ), %]. Next higher mitigation categories were included for all significant categories (adjusted $P < 0.05$) even if they were not significant (adjusted $P \geq 0.05$). Blue and red bars indicate significant desirable and undesirable effects (adjusted $P < 0.05$), respectively, white bars indicate lack of significant effects (adjusted $P \geq 0.05$), and no bars indicate that no data were available. Weight gain for tanniferous forage was not significant (not shown, because it was analyzed with standardized relative difference instead of log ratio of means that was used for the remaining analyses).

a



Rumen manipulation
Additives
Chemical inhibitors
3-nitrooxypropanol
Bromochloromethane
Galactooligosaccharides
Ionophores
Monensin
Organic acids
Long chain fatty acids
Probiotics
Bacteria
Propionibacterium
Secondary plant compounds
Essential oils
Essential oil blends
Oregano
Saponins
Saponaria
Tea saponin
Yucca saponin
Tannins
Condensed tannins
Defaunation
Electron sinks
Fumaric acid
Nitrate
-70% -50% -30% -10% 10%
Daily CH_4
CH_4Y
CH_4I_G
CH_4I_M

b



Supplementary Fig 5. Relative treatment effects and 95% confidence intervals of (**a**) Daily CH_4 = daily CH_4 emission (g d^{-1}); CH_4Y = CH_4 yield (CH_4 per unit of feed dry matter intake, g kg^{-1}); CH_4I_G = CH_4 emission intensity for weight gain (CH_4 per unit of weight gain of growing animals, g kg^{-1}); and CH_4I_M = CH_4 emission intensity for milk (CH_4 per unit of milk produced, g kg^{-1}) and (**b**) Feed intake = feed intake (dry matter intake, kg d^{-1}); Weight gain (average daily gain, kg d^{-1}), Milk production (kg d^{-1}); and Fiber digestibility (neutral detergent fiber digestibility, %) for rumen manipulation strategies that had a significant effect (adjusted $P < 0.05$) on daily CH_4, CH_4Y, or Y_m = methane conversion factor [CH_4 energy (MJ) per gross energy intake (MJ), %]. Next higher mitigation categories were included for all significant categories (adjusted $P < 0.05$) even if they were not significant (adjusted $P \geq 0.05$), and no bars indicate that no data were available. Blue and red bars indicate significant desirable and undesirable effects (adjusted $P < 0.05$), respectively, white bars indicate lack of significant effects (adjusted $P \geq 0.05$), and no bars indicate that no data were available. Weight gain for tanniferous forage was not significant (not shown, because it was analyzed with standardized relative difference instead of log ratio of means that was used for the remaining analyses). The relative treatment effect of tannin and condensed tannin on CH_4I_M is only partially shown; its relative treatment effect was for both -3.5% and its 95% CI was -15.1 to 9.5%.