

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 (CH₄) 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 CH₄ inhibitors, oils and fats, oilseeds, electron sinks, and tanniferous forages, decreased absolute CH₄ emissions by on average -21% (range -12 to -35%) and CH₄ emissions per unit of product (CH₄I; 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 CH₄I 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 CH₄ 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 scenario¹. 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 (CH₄) emissions from enteric fermentation by ruminant livestock contribute 30% of the global anthropogenic CH₄ emissions². As CH₄ is a powerful but short-lived GHG, decreasing global CH₄ 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 Strategy³ 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 2030⁴. 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 CH₄ emissions from animal production by -24 to -47% by 2050 relative to 2010⁶, while simultaneously increasing the production of animal-sourced food to meet the projected 68% increase in demand between 2010 and 2050⁷. Reaching these apparently conflicting twin goals will require effective enteric CH₄ mitigation strategies that, at a minimum, do not compromise animal productivity or have other unacceptable tradeoffs⁸ and, ideally, increase animal-sourced food production. Strategies that increase animal production and reduce product-based CH₄ emissions (i.e., emission intensity variables CH₄I_G and CH₄I_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 countries¹¹. 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 CH₄ emissions^{8,12,13}.

However, thus far studies either only investigated the quantitative effects of a single mitigation strategy or only compared CH₄ yield (CH₄Y; CH₄ per unit of feed intake) between multiple mitigation strategies. Nonetheless, CH₄Y is only one measure and other important CH₄ emission and animal performance metrics must be considered to determine the effectiveness and feasibility of mitigation strategies. Important CH₄ emission metrics include daily CH₄ emissions, CH₄Y, CH₄-energy conversion factor [Y_m ; CH₄ 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 Change¹⁴], CH₄I_G, and CH₄I_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 CH₄ mitigation strategies published in peer-reviewed journals by examining their quantitative effects on the aforementioned CH₄ emission and animal performance metrics. There is an urgent requirement for strategies that can effectively mitigate both absolute and product-based CH₄ emissions without negatively affecting animal productivity or that can effectively mitigate product-based CH₄ 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 CH₄ emissions; the remaining 35 strategies decreased daily CH₄ emissions and CH₄Y 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 CH₄ emissions, if they significantly (adjusted $P < 0.05$) decreased daily CH₄ emissions, CH₄Y, and CH₄I_G or CH₄I_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 CH₄ emissions if they significantly decreased CH₄Y and CH₄I_G or CH₄I_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 CH₄ and animal performance metrics as well as their relevance for confinement or grazing systems are presented in Fig. 2. As CH₄Y was highly correlated with Y_m (adjusted $R^2 = 0.83$; Supplementary Fig. 1) and more data were available for CH₄Y than for Y_m (Supplementary Fig. 2), only results for CH₄Y are presented and discussed here. All other strategies that were not classified as effective but had a significant effect on CH₄, CH₄Y, Y_m, CH₄I_G or CH₄I_M are presented in Supplementary Fig. 3 to 5. The CH₄ 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 carcinogen¹⁵. 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-CH₄ emitting animals and improving animal health. Modeling studies have shown that strategies that improve animal health can significantly increase animal productivity and reduce emission intensity¹⁶. In the subsequent text, the effects of mitigation strategies on CH₄ 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 CH₄ emissions

Rumen manipulation by feeding CH₄ inhibitors effectively decreased daily CH₄ 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 archaea¹⁷. Its supplementation decreased daily CH₄ emissions (-39%, -29 to -47%, 11), CH₄Y (-37%, -26 to -46%, 12), and CH₄I_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 cattle¹⁸ or fiber digestibility in early-lactation dairy cows¹⁹ and decreased daily CH₄ emissions throughout a 15-week experiment²⁰. A recent meta-analysis showed that 3-NOP decreases daily CH₄ 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 content²¹. 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 conditions²³. Supplementation of 3-NOP increased milk fat content in dairy cattle¹⁹ and feed efficiency in feedlot cattle²⁴, 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 CH₄ inhibitor strategy is supplementation with seaweed (e.g. *Asparagopsis taxiformis*), which can decrease daily CH₄ emissions by up to 80%²⁵. However, more research is warranted on dietary inclusion levels, effects on animal feed intake and production²⁶, the implications and safety of feeding bromoform²⁷, its main active compound²⁸, 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 seaweed²⁹ before it can be recommended as a mitigation strategy.

Dietary inclusion of oil and fat decreased daily CH₄ emissions (-20%, -15 to -24%, 63) and CH₄Y (-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 CH₄I_G (-22%, -8 to -35%, 6) and CH₄I_M (-12%, -6 to -18%, 24); however, possible effects on manure CH₄ emissions due to decreased fiber digestibility need to be evaluated¹⁴. Of the subcategories included here, only dietary inclusion of predominantly vegetable oils effectively decreased daily CH₄ 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 CH₄Y (between -9 to -14%), feed intake (-6%) and increased milk yield (+4%)^{13,30}. Oil inclusion reportedly decreases daily CH₄ emissions in a dose-response manner³⁰ 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 oil³³. Vegetable oils that effectively decreased daily CH₄ 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 CH₄ emissions likely varies by region and country, because oil and meat and milk prices vary considerably therein. Studies in China³⁴, France³⁵, or the Netherlands³⁶ found that dietary inclusion of oils, for the purpose of mitigating enteric CH₄ 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 CH₄ 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 CH₄ emissions (-20%, -15 to -24%, 26), CH₄Y (-14%, -8 to -20%, 18), and CH₄IM (-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 oils³⁷. In addition, similar to oil inclusion possible effects on manure CH₄ emissions due to decreased fiber digestibility need to be evaluated. Oilseeds that effectively decreased daily CH₄ 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 rumen³⁸, decreased daily CH₄ emissions (-17%, -14 to -20%, 54) and CH₄Y (-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 CH₄IG (-12%, -2

to -20%, 3) and CH₄I_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 CH₄ emissions (-15%)³⁹. Nitrate has also been shown to decrease daily CH₄ emissions and CH₄Y in a dose-response manner with no loss of effectiveness over and effectively decreased CH₄ over the long-term^{40,41}. Similar to 3-NOP, nitrate was more effective in decreasing daily CH₄ emissions and CH₄Y in dairy than in beef cattle³⁹. 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 acclimatized⁴². 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 fed⁴³. Simultaneous sulfate supplementation has been shown to help protect cattle against nitrate toxicity⁴⁰. Nitrate supplementation may increase enteric and possibly manure nitrous oxide emissions⁴⁴. Studies in France³⁵ and the Netherlands³⁶ found that nitrate supplementation was not cost-effective.

Dietary inclusion of tanniferous forages decreased daily CH₄ emissions (-12%, -7 to -16%, 42) and CH₄Y (-10%, -6 to -14%, 39) without affecting feed intake or animal production and consequently decreased CH₄I_M (-18%, -8 to -26%, 7). However, it also decreased fiber digestibility (-7%, -2 to -12%, 21), which could potentially increase manure CH₄ emissions¹⁴. *Sericea lespedeza* (*Lespedeza cuneata*) decreased daily CH₄ emissions (-32%, -24 to -39%, 5) without affecting feed intake in goats and it has been effective in decreasing daily CH₄ emissions throughout a 12-week experiment⁴⁵. Other tanniferous forages that may potentially decrease daily CH₄ 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 intake⁴⁶. 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 manure⁴⁷. The cost-effectiveness of their supplementation still needs to be evaluated. Among the identified effective strategies to decrease absolute and product-based CH₄ 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 CH₄ emissions are attributed to grazing systems⁴⁸.

Strategies that decrease product-based CH₄ emissions

Decreasing dietary forage-to-concentrate ratio decreased CH₄Y (-13%, -10 to -16%, 69) without increasing daily CH₄ 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, CH₄I_G (-9%, -3 to -15%, 16) and CH₄I_M (-9%, -4 to -14%, 19) were decreased. The reduction in CH₄Y was most likely the result of a shift in rumen fermentation patterns and a decrease in rumen pH, which inhibits methanogens³⁸.

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 cattle⁴⁹. 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 CH₄ emissions (+18%, +14 to +22%, 42), but decreased CH₄Y (-8%, -4 to -12%, 31). Fiber digestibility was decreased (-7%, -2 to -12%, 18), likely due to increased rumen passage rates⁵⁰. Increasing feed intake resulted in increased weight gain (+162%, +38 to +398%, 7) and milk yield (+17%, +10 to +25%, 8) and decreased CH₄I_M (-17%, -9 to -23%, 5). No data were available for CH₄I_G. Similar to our data, a recent study showed that increasing the level of feeding decreased CH₄Y, while increasing daily CH₄⁵¹. Increasing feed intake to improve animal productivity significantly decreases CH₄I_G and CH₄I_M^{8,52} and the overall carbon footprint of animal-sourced food⁵³ when diet composition remains unchanged. This strategy directs energy for CH₄ towards animal production⁵¹ 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 CH₄Y and increasing feed intake⁸. Potential effects of this practice on manure CH₄ 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 forage⁵⁴.

Decreasing grass maturity decreased CH₄Y (-4%, -1 to -8%, 8) but not daily CH₄ emissions. It did not affect feed intake but increased milk yield (+9%, +1 to +18%, 6) and thus decreased CH₄I_M (-13%, -7 to -18%, 6). Furthermore, decreasing grass maturity improved fiber digestibility (+15%, +9 to +21%, 9), which can potentially decrease manure CH₄ emissions¹⁴. 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 excretion⁵⁵. 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 linseed³⁶.

CONCLUSION

Effective strategies that reduced daily and product-based CH₄ emissions without negatively affecting animal production decreased daily CH₄ 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 CH₄ emissions and increased animal production decreased product-based CH₄ 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 CH₄ mitigation need to be investigated. Of the effective strategies that decrease absolute and product-based CH₄ 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 CH₄ 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 CH₄ 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, MitiGate¹³, 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 CH₄ 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 ≤ 10 days) or measurement technique (e.g. the ‘sniffer technique’ that is based on the CH₄-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 CH₄ 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 CH₄ emission metric and two of the remaining CH₄ 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, CH₄I_M included daily CH₄ 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 CH₄I_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 CH₄ emissions (92%), feed intake (84%), and CH₄Y (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%), CH₄I_M (21%), or CH₄I_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 CH₄, CH₄Y, Y_m, CH₄I_G, CH₄I_M, feed intake, weight gain for growing animals, milk yield, and fiber digestibility) using a log ratio of means, namely $\log(\text{Treatment}/\text{Control})$, 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, $[(\text{Treatment}-\text{Control})/\text{SE}_{\text{Diff}}]$, due to the presence of negative growth rate responses in two treatment mean comparisons⁵⁹. 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 error⁶⁰ (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 $0.05 \leq \text{adjusted } P \leq 0.10$ was considered as a trend.

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FIGURES AND TABLES

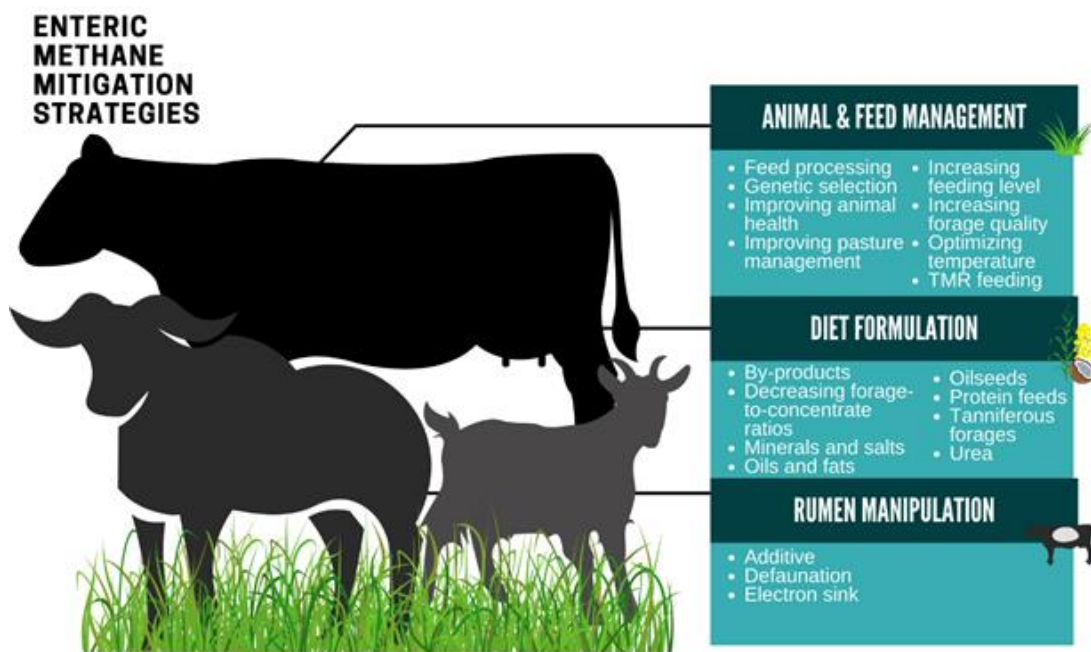


Figure 1. Studied enteric methane mitigation strategies. For a complete list of strategies, see supplementary Table S2.

A

MITIGATION STRATEGY		POTENTIAL EMISSIONS REDUCTION				RELEVANT PRODUCTION SYSTEM		
Absolute & Product-Based Reductions	1 CH ₄ INHIBITORS	Daily CH ₄ -35% CH ₄ Y -34%	CH ₄ I _G No Data CH ₄ I _M -32%					
	2 OILS & FATS	Daily CH ₄ -19% CH ₄ Y -15%	CH ₄ I _G -22% CH ₄ I _M -12%					
	3 OILSEEDS	Daily CH ₄ -20% CH ₄ Y -14%	CH ₄ I _G No Effect CH ₄ I _M -12%		 Lactating only			
	4 ELECTRON SINKS	Daily CH ₄ -17% CH ₄ Y -15%	CH ₄ I _G -12% CH ₄ I _M -13%					
	5 TANNIFEROUS FORAGES	Daily CH ₄ -12% CH ₄ Y -10%	CH ₄ I _G No Data CH ₄ I _M -18%	 				
Product-Based Reductions	6 DECREASING DIETARY FORAGE-TO-CONCENTRATE RATIO	CH ₄ I _G -9% CH ₄ I _M -9%						
	7 INCREASING FEEDING LEVEL	CH ₄ I _G No Data CH ₄ I _M -17%	 					
	8 DECREASING GRASS MATURITY	CH ₄ I _G No Data CH ₄ I _M -13%	 	 Lactating only				

LEGEND

SYSTEM

 CONFINED

 GRAZING

ANIMAL SPECIES

 CATTLE

 SHEEP

 SMALL RUMINANTS

 OTHER RUMINANTS

B

	MITIGATION STRATEGY	Relative Treatment Effect on Animal Performance			
		INTAKE	DIGESTIBILITY	GAIN	MILK
Absolute & Product-Based Reductions	1 CH ₄ INHIBITORS	No Effect	No Effect	No Effect	No Effect
	2 OILS & FATS	-6%	-4%	No Effect	No Effect
	3 OILSEEDS	No Effect	-8%	-13%	No Effect
	4 ELECTRON SINKS	-2%	No Effect	No Effect	+3%
	5 TANNIFEROUS FORAGES	No Effect	-7%	No Effect	No Effect
Product-Based Reductions	6 DECREASING DIETARY FORAGE-TO-CONCENTRATE RATIO	+9%	No Effect	+21%	+17%
	7 INCREASING FEEDING LEVEL	+58%	-7%	+162%	+17%
	8 DECREASING GRASS MATURITY	No Effect	+15%	No Data	+9%

Figure 2. Effective mitigation strategies and their effect on methane (CH₄) emission (a) and animal performance metrics (b). Daily CH₄ = daily CH₄ emission (g animal⁻¹ day⁻¹); CH₄Y = CH₄ yield (CH₄ g per kg of dry matter intake), CH₄I_G = CH₄ emission intensity for weight gain (g CH₄ per kg of weight gain for growing animals), CH₄I_M = CH₄ emission intensity for milk (CH₄ 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

SUPPLEMENTARY TABLES

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

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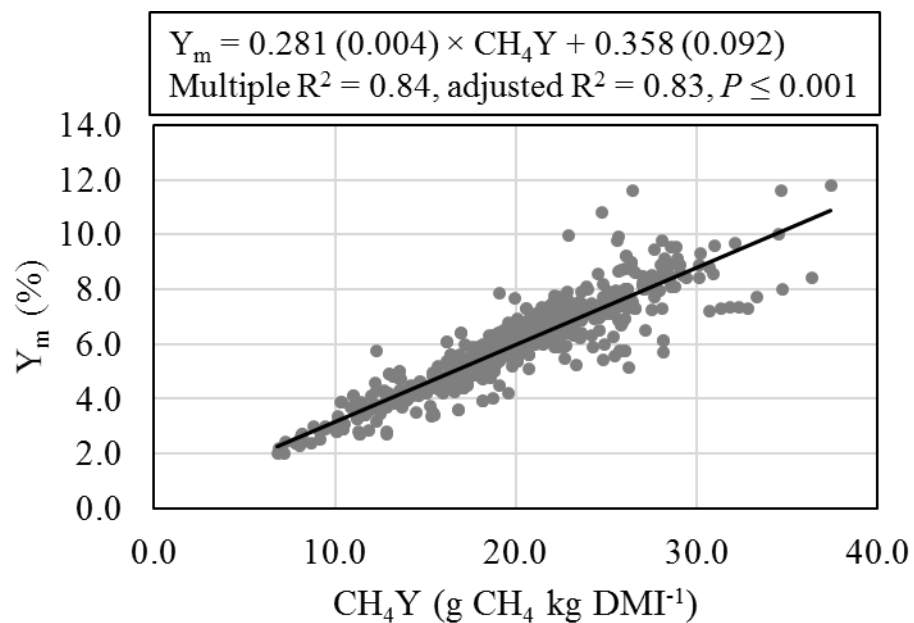
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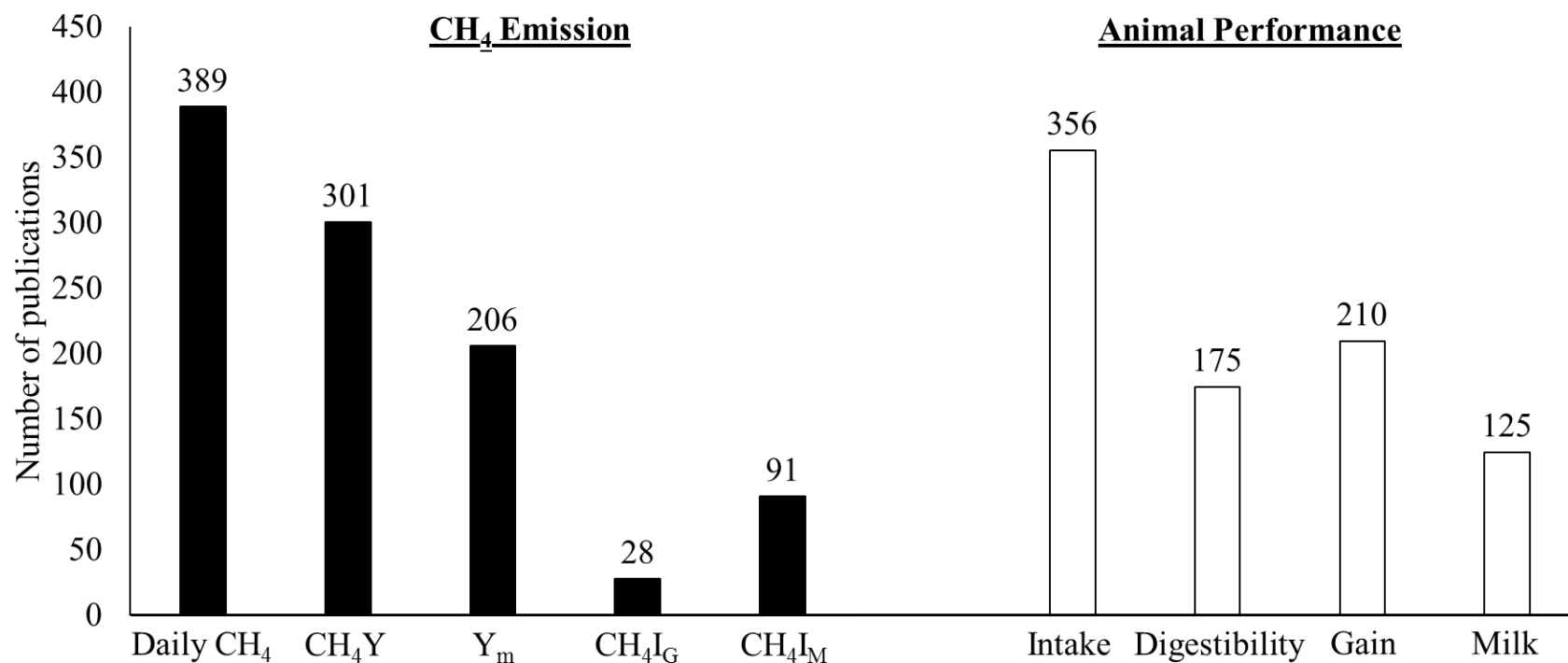
Supplementary Table 2. Mitigation strategies (categories and subcategories) included in this meta-analysis.

Animal and feed management	Diet formulation	Rumen manipulation
Feed processing Forage processing Urea-treated straw Grain processing Genetic Selection Low residual feed intake Low CH₄ emitter Improving health Improving pasture management Grazing plus supplementation Grazing plus concentrate Improved pasture Increased Nitrogen fertilization Legume-grass vs. grass only pastures Reduced pre-grazing herbage mass Increasing feeding level Increasing forage quality Decreasing grass maturity Increasing corn silage maturity Optimizing temperature Total mixed ration feeding Total mixed ration vs. grazing	By-products Fiber sources Soybean hulls Glycerol Lipid sources Extruded canola Extruded linseed Protein sources Distiller's dried grains with solubles Soybean meal Pulp sources Citrus pulps Decreasing forage-to-concentrate ratio Barley Corn Minerals and Salts Oils and fats Canola oil Coconut oil Linseed oil Oil blends Rumen protected fat Sunflower oil Tallow Oilseeds Canola seed Cottonseed Linseed Sunflower seed Increasing protein Tannifores forages Lespedeza Leucaena Lotus Sainfoin Urea	Additives Amino acids CH₄ inhibitors 3-nitrooxypropanol Bromochloromethane Enzymes Galactooligosaccharides Ionophores Monensin Organic acids Carboxylic acids Long chain fatty acids Unsaturated fatty acids Docosahexaenoic acid Probiotics Bacteria <i>Lactobacillus</i> <i>Propionibacterium</i> Yeasts <i>Saccharomyces</i> Secondary plant compounds Essential oils Essential oil blends Garlic Oregano Flavonoids Phenols Saponins Saponaria Tea saponin Yucca saponin Tannins Condensed tannins <i>Acacia</i> <i>Quebracho</i> 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 .		

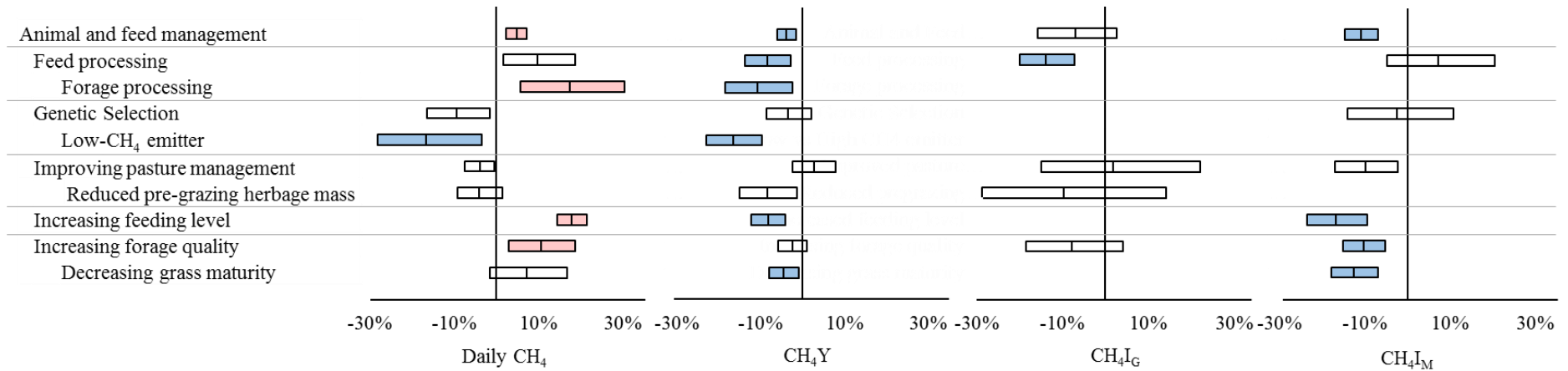
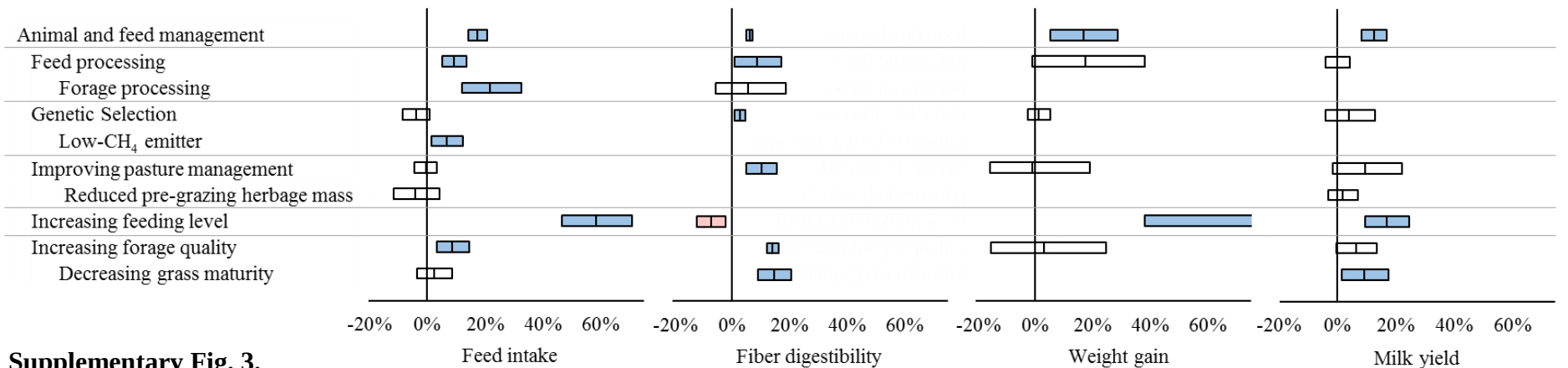
SUPPLEMENTARY FIGURES



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) $\times$ 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.



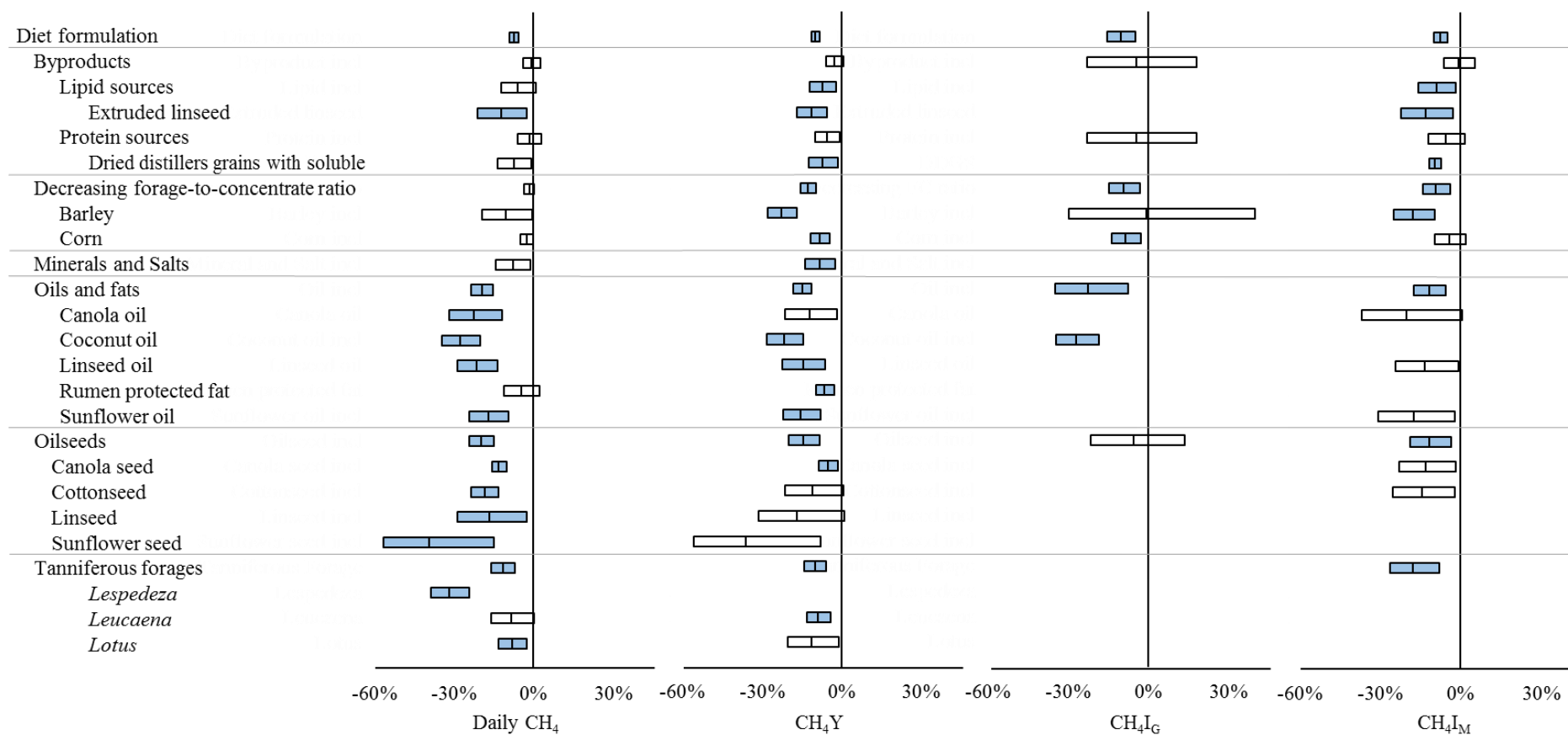
Supplementary Fig 2. Number of publications that reported methane (CH₄) emission and animal performance variables of the 425 studies that were analyzed in the current meta-analysis. Methane emission variables included in the analysis were: Daily CH₄ = daily CH₄ emission (g d⁻¹), CH₄Y = CH₄ yield (CH₄ per unit of feed dry matter intake, g kg⁻¹), Y_m = CH₄ conversion factor (CH₄ energy (MJ) per gross energy intake (MJ) × 100, %), CH₄I_G = CH₄ intensity for weight gain (CH₄ per unit of weight gain of growing animals, g kg⁻¹), CH₄I_M = CH₄ intensity for milk (CH₄ 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.**

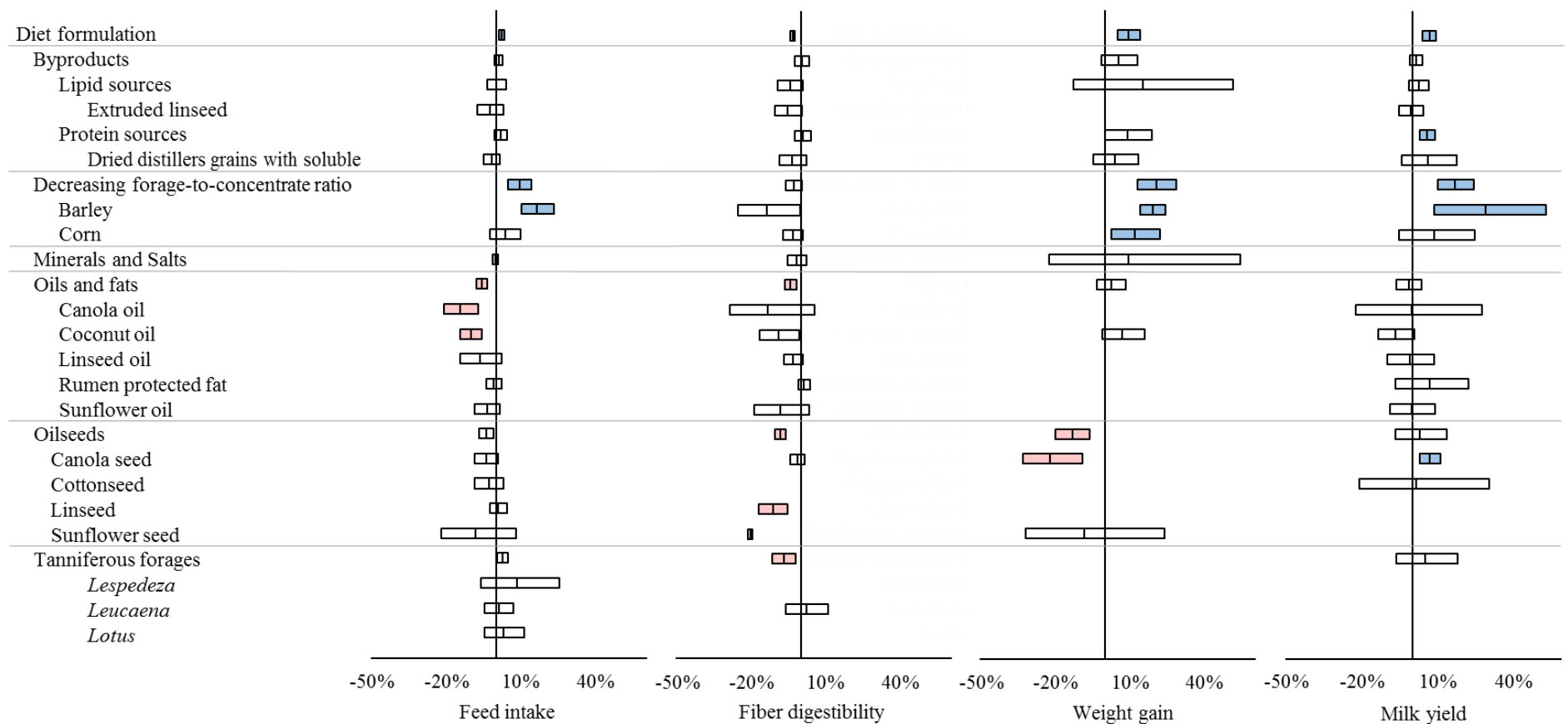
Relative treatment effects and 95% confidence intervals of (a) Daily CH₄ = daily CH₄ emission (g d⁻¹); CH₄Y = CH₄ yield (CH₄ per unit of feed dry matter intake, g kg⁻¹); CH₄I_G = CH₄ emission intensity for weight gain (CH₄ per unit of weight gain of growing animals, g kg⁻¹); and CH₄I_M = CH₄ emission intensity for milk (CH₄ 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 CH₄, CH₄Y, or Y_m = methane conversion factor [CH₄ 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

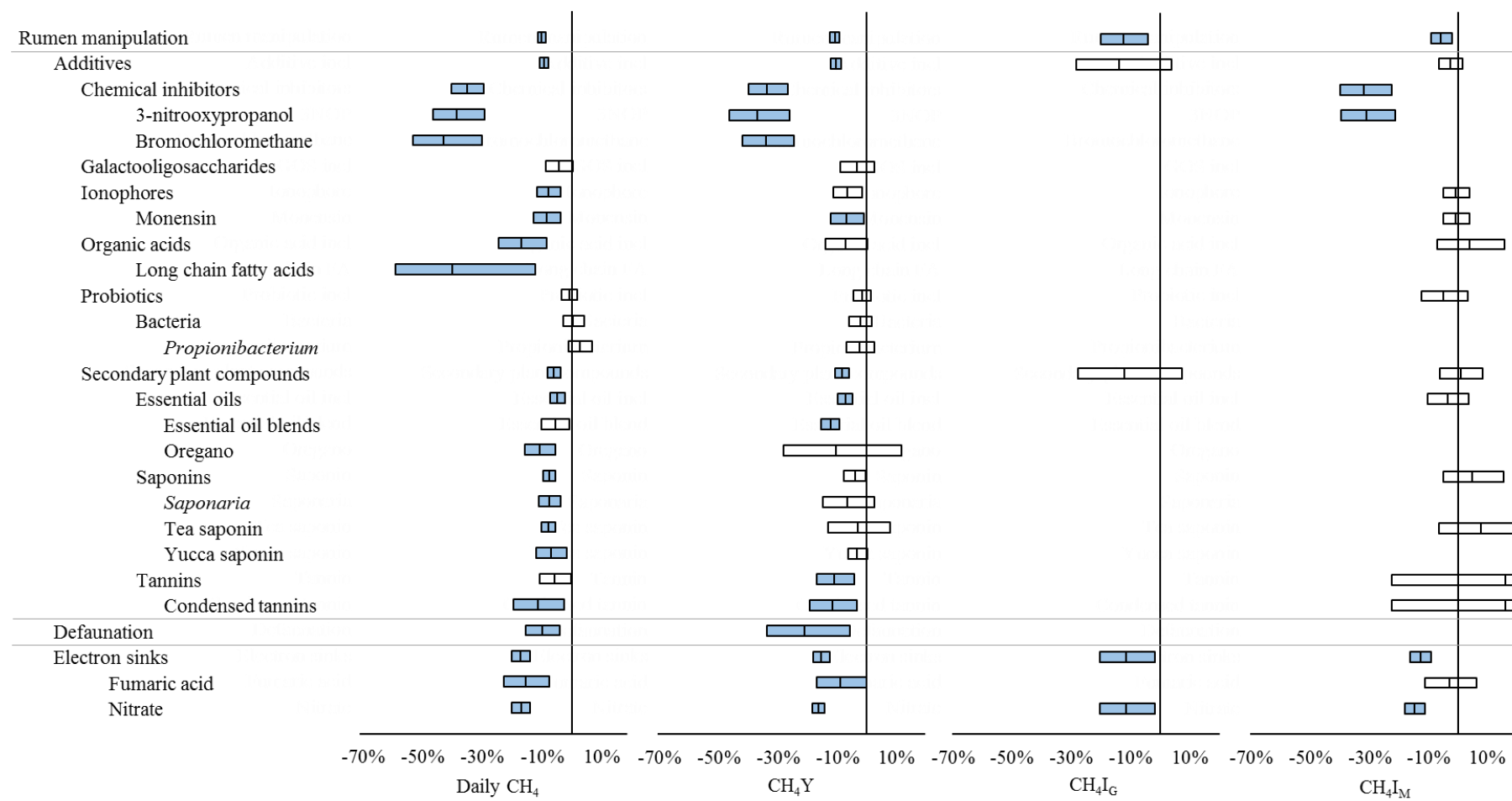


b

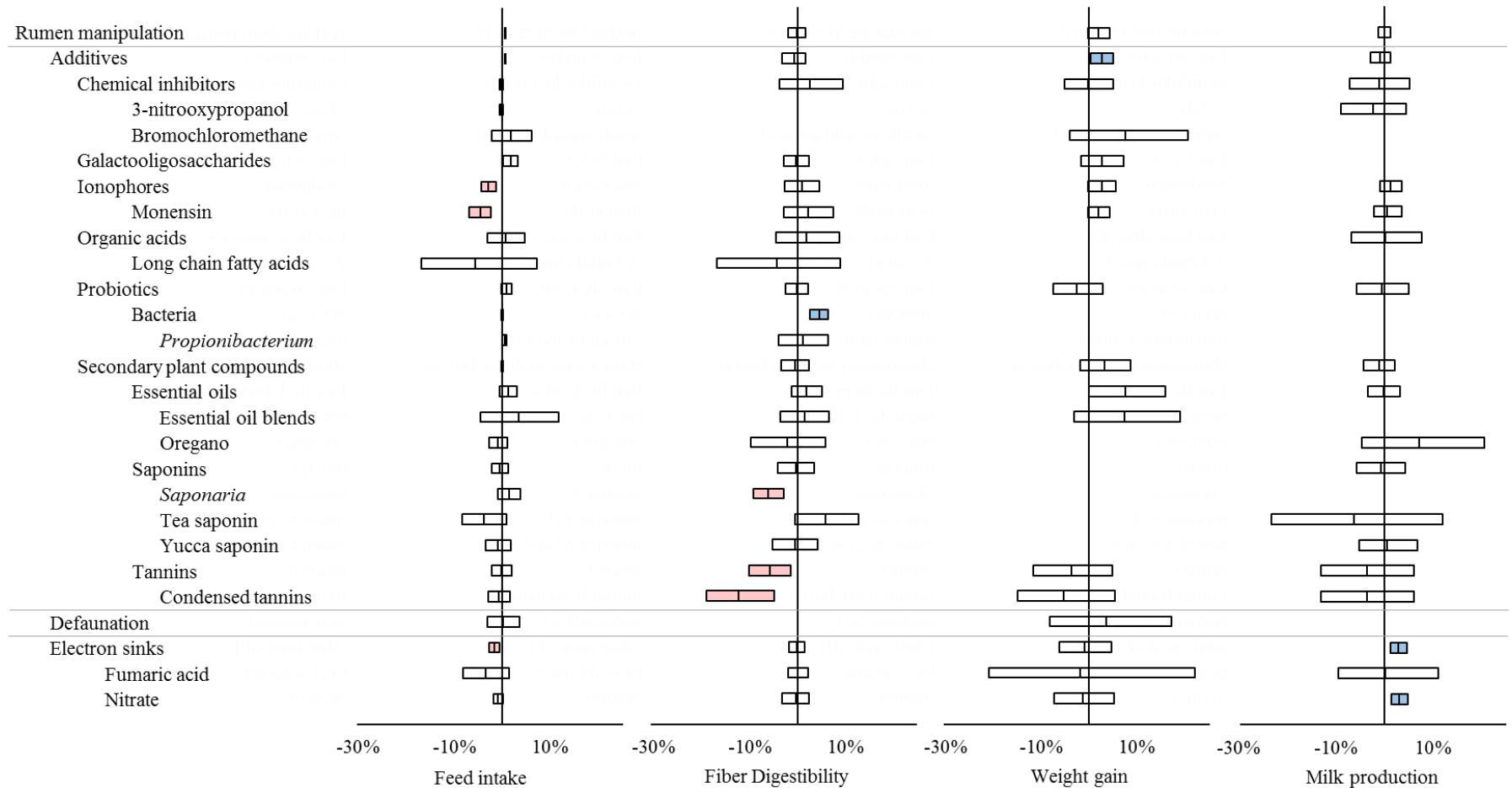


Supplementary Fig 4. Relative treatment effects and 95% confidence intervals of (a) Daily CH_4 = daily CH_4 emission (g d^{-1}); CH_4Y = CH_4 yield (CH_4 per unit of feed dry matter intake, g kg^{-1}); CH_4I_G = CH_4 emission intensity for weight gain (CH_4 per unit of weight gain of growing animals, 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



b



Supplementary Fig 5. Relative treatment effects and 95% confidence intervals of (a) Daily CH₄ = daily CH₄ emission (g d⁻¹); CH₄Y = CH₄ yield (CH₄ per unit of feed dry matter intake, g kg⁻¹); CH₄I_G = CH₄ emission intensity for weight gain (CH₄ per unit of weight gain of growing animals, g kg⁻¹); and CH₄I_M = CH₄ emission intensity for milk (CH₄ 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%.