

Full adoption of the most effective strategies to mitigate methane emissions by ruminants can help meet the 1.5 °C target by 2030 but not 2050

Article

Accepted Version

Arndt, C., Hristov, A. N., Price, W. J., McClelland, S. C., Pelaez, A. M., Cueva, S. F., Oh, J., Dijkstra, J., Bannink, A., Bayat, A. R., Crompton, L. A., Eugène, M. A., Enahoro, D., Kebreab, E., Kreuzer, M., McGee, M., Martin, C., Newbold, C. J., Reynolds, C. ORCID: <https://orcid.org/0000-0002-4152-1190>, Schwarm, A., Shingfield, K. J., Veneman, J. B., Yáñez-Ruiz, D. R. and Yu, Z. (2022) Full adoption of the most effective strategies to mitigate methane emissions by ruminants can help meet the 1.5 °C target by 2030 but not 2050. *Proceedings of the National Academy of Sciences of the United States of America*, 119 (20). e2111294119. ISSN 0027-8424 doi: 10.1073/pnas.2111294119 Available at <https://centaur.reading.ac.uk/103980/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1073/pnas.2111294119>

Publisher: National Academy of Sciences

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

1

2 **Main Manuscript for**

3 Full Adoption of The Most Effective Strategies to Mitigate Methane
4 Emissions by Ruminants Can Help Meet the 1.5°C Target by 2030
5 but Not 2050

6

7 Claudia Arndt^{a*}, Alexander N. Hristov^b, William J. Price^c, Shelby C. McClelland^d, Amalia M.
8 Pelaez^e, Sergio F. Cueva^b, Joonpyo Oh^b, André Bannink^e, Ali R. Bayat^f, Les A. Crompton^g, Jan
9 Dijkstra^e, Maguy A. Eugène^h, D. Enahoro^a, Ermias Kebreabⁱ, Michael Kreuzer^j, Mark McGee^k,
10 Cécile Martin^h, Charles J. Newbold^l, Christopher K. Reynolds^g, Angela Schwarm^m, Kevin J.
11 Shingfield^{f**}, Jolien B. Venemanⁿ, David R. Yáñez-Ruiz^o, and Zhongtang Yu^p.

12

13 ^aInternational Livestock Research Institute (ILRI), Nairobi 00100, Kenya; ^bThe Pennsylvania State
14 University, University Park, USA; ^cUniversity of Idaho, Moscow, USA; ^dColorado State University,
15 Fort Collins, USA; ^eWageningen University and Research, Wageningen, The
16 Netherlands; ^fNatural Resources Institute Finland, Helsinki, Finland; ^gUniversity of Reading,
17 Earley Gate, Reading, UK; ^hINRAE, UCA-VAS, UMRH Centre ARA, Saint-Genès-Champagnelle,
18 France; ⁱUniversity of California, Davis, USA; ^jETH Zurich, Zürich, Switzerland; ^kTeagasc, AGRIC,
19 Grange, Ireland; ^lSRUC, Edinburgh, United Kingdom; ^mNorwegian University of Life Sciences,

20 Aas, Norway; ⁿDe Heus Animal Nutrition, Ede, The Netherlands; ^oEstación Experimental del
21 Zaidín, CSIC, Granada, Spain; ^pThe Ohio State University, Columbus, USA.

22

23 *Claudia Arndt

24 **Email:** claudia.arndt@cgiar.org

25

26 **The author is deceased.

27

28 **Author Contributions:** C.A., A.N.H., A.M.P., A.B., L.A.C., J.D., M.A.E., E.K., and M.K. conceived
29 and designed the study, A.N.H., S.C.M., A.M.P., S.F.C., A.B., L.A.C., J.D., M.A.E., E.K., M.K.,
30 M.M., C.M., C.J.N., C.K.R., A.S., K.J.S., J.B.V., D.R.Y.-R. contributed data to the database, C.A.,
31 A.N.H., S.C.M., A.M.P., S.F.C., and J.O. collated the database. W.J.P. analyzed the data, C.A.
32 wrote the first draft with A.N.H., W.J.P., S.C.M., A.R.B., L.A.C., J.D., M.A.E., D.E., M.K., M.M.,
33 C.M., C.K.R., A.S., Z.Y. contributing to further revisions.

34 **Competing Interest Statement:** The authors declare no competing interests.

35 **Classification:** Biological Sciences/Agricultural Sciences, Physical Sciences/Sustainability
36 Science

37 **Keywords:** enteric methane, mitigation, meta-analysis.

38 **This PDF file includes:**

39 Main Text

40 Figure 1 to 3

41 Supplementary Figures

42 Supplementary Tables (Table 3 can be found in separate excel file)

43 **Abstract**

44 To meet the 1.5°C target, methane (CH₄) from ruminants must be reduced by 11 to 30% by 2030
45 and 24 to 47% by 2050 compared to 2010 levels. A meta-analysis identified strategies to
46 decrease product-based [PB; CH₄ per unit meat or milk (CH₄I)] and absolute (ABS) enteric CH₄
47 emissions while maintaining or increasing animal productivity (AP; weight gain and milk yield).
48 Next the potential of different adoption rates of one PB and/or one ABS strategy to contribute to
49 the 1.5°C target was estimated. The database included findings from 430 peer-reviewed studies,
50 which reported 98 mitigation strategies that can be classified into three categories: animal and
51 feed management, diet formulation, and rumen manipulation. A random-effects meta-analysis
52 weighted by inverse variance was carried out. Three PB strategies, namely increasing feeding
53 level, decreasing grass maturity, and decreasing dietary forage-to-concentrate ratio, decreased
54 CH₄I by on average 12% and increased AP by a median of 17%. Five ABS strategies, namely
55 CH₄ inhibitors, tanniferous forages, electron sinks, oils and fats, and oilseeds, decreased daily
56 methane by on average 21%. Globally, only 100% adoption of the most effective PB and ABS
57 strategies can meet the 1.5°C target by 2030 but not 2050, because mitigation effects are offset
58 by projected increases in CH₄ due to increasing demand. Notably, by 2030 and 2050 low- and
59 middle-income countries may not meet their contribution to the 1.5°C target for this same reason,
60 whereas high income countries could meet their contributions due to only a minor projected
61 increase in enteric CH₄ emissions.

62

63 **Significance Statement**

64 Agricultural methane emissions must be decreased by 11 to 30% of the 2010 level by 2030 and
65 by 24 to 47% by 2050 to meet the 1.5°C target. We identified three strategies to decrease
66 product-based (PB) methane emissions while increasing animal productivity (AP) and five
67 strategies to decrease absolute methane emissions (ABS) without reducing AP. Globally, 100%
68 adoption of the most effective PB and ABS strategies can meet the 1.5°C target by 2030 but not

2050, because mitigation effects are offset by projected increases in methane. On a regional level, Europe but not Africa may be able to meet their contribution to the 1.5°C target, highlighting the different challenges by high and middle- and low-income countries, respectively.

Main Text

Introduction

Global food systems contribute to 30% of the worldwide greenhouse gas (GHG) emissions¹. The goal of the Paris Agreement, to limit global warming to 1.5°C above pre-industrial levels, is unlikely to be achieved if food systems continue operating on a business-as-usual (BAU) scenario¹. Among the food-related GHG emissions, methane (CH₄) from livestock contributes 30% of the global anthropogenic CH₄ emissions², 17% of the global food system GHG emissions, and 5% of global GHG emissions^{2,3}. Eighty eight percent of the global livestock CH₄ emissions is contributed by enteric fermentation⁴.

Methane is a short-lived climate pollutant. Given its perturbation lifetime in the atmosphere of around 12.5 years, CH₄ contributes significantly to near-term global warming⁵. Its Global Warming Potential is 84 or 28, for 20- or 100-year time horizons, respectively⁵. When evaluating the contribution of global food systems to CH₄ emissions over a 20-year period instead of the commonly used 100-year time period for national GHG inventories, the contribution of CH₄ to food system GHG emissions more than doubles from 17 to 36%^{3,5}.

The realization of Nationally Determined Contributions and 2050 climate neutrality goals depends upon the reduction of CH₄ emissions. Within sectoral reductions of CH₄ emissions, technical solutions to decrease CH₄ from agricultural production, especially strategies to mitigate CH₄ from enteric fermentation by ruminant livestock are integral to meeting these climate targets, but quantitative data on mitigation potentials are scarce⁶. Based on 2010, GHG emission levels, and different mitigation scenarios to limit global warming to 1.5°C, agricultural CH₄ emissions need to be decreased by 11 to 30% by 2030 and by 24 to 47% by 2050⁷.

The global population is projected to increase by 23% between 2010 and 2030 with most of the increase occurring in low- and middle-income countries (LMIC)⁸. Ruminants contribute about half of the animal protein produced by livestock⁴. In LMIC, ruminant livestock plays a crucial role in food security⁹. Ruminants can convert human-inedible feeds like those from pastures and grain commodity by-products produced on marginal lands or from subsistence agricultural production systems into nutritionally dense human-edible foods. Ruminants also provide other benefits, such as traction and manure for fuel and fertilizer¹⁰. In addition, human population growth is generally high in LMIC, while consumption of animal-sourced food is often below recommended dietary levels and/or reliant upon ruminant meat and milk for livelihoods and nutrition security^{10,11}. Thus, from a feed-food competition perspective, ruminant production increases in LMIC should rely on human inedible feeds (i.e. forage and by-products). In contrast, in high income countries (HIC) population growth is much lower and the consumption of animal protein is often above recommended dietary levels^{9,11}.

Sustainable strategies for enteric CH₄ mitigation that align with the 1.5°C target should preferably avoid socioeconomic and environmental tradeoffs¹², and, ideally, increase production yield per unit of input. Reductions in both CH₄ emissions intensity, i.e., emissions per unit of milk and gain (CH₄I_M and CH₄I_G, respectively), and absolute CH₄ emissions are therefore needed. Strategies that reduce CH₄I and increase production per unit of input could be used to expand food production from the existing ruminant population without increasing total CH₄ emissions^{13,14,15}, and thus contribute to the 1.5°C target as well as to Sustainable Development Goals (SDGs) that are impacted by climate change. Several reviews indicate that animal and feed management, diet formulation, and rumen manipulation strategies could significantly decrease enteric CH₄ emissions^{12,16,17}. However, previous studies consisted of qualitative reviews¹², examined the quantitative effects of a single mitigation strategy^{18,19,20}, or compared CH₄ yield (CH₄Y; CH₄ per unit of feed intake) between multiple mitigation strategies¹⁷. Methane yield is only one relevant measure, and other major CH₄ emission and animal performance metrics must be considered to determine the effectiveness and feasibility of mitigation strategies. Only one recent publication examined the quantitative effects of multiple mitigation strategies on CH₄ emission and animal

performance metrics, but the analysis was limited to Latin America²¹. Important CH₄ emission metrics include daily CH₄ emissions, CH₄Y or 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 Change²²], 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 effect on the aforementioned *in-vivo* CH₄ emissions and animal performance metrics and to estimate their potential to contribute to the 1.5°C target. As outlined above, there is an urgent need for strategies that can effectively mitigate enteric CH₄ emissions without negatively affecting AP by focusing exclusively on strategies that decouple CH₄ emissions from animal production²³. Mitigation effects were quantified on global level as well as on a regional level. The African and European region were selected to represent LMIC and HIC, respectively.

Results and Discussion

The meta-analysis included 98 mitigation strategies reported in 430 peer-reviewed journal publications (Table S1). 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 by on average 18% (ranging from 5 to 43%). These strategies were classified as 'effective' in decreasing product-based CH₄ (PB strategies) if they significantly decreased CH₄I_M or CH₄I_G and CH₄Y while significantly (adjusted $P < 0.05$) increasing AP. Strategies were classified as 'effective' in decreasing absolute CH₄ emissions (ABS strategies) if they significantly decreased daily CH₄ emissions, CH₄I_M or CH₄I_G, and CH₄Y without decreasing AP (weight gain of growing animals or milk yield of lactating dairy animals) when productivity data were present.

A summary of the studied mitigation strategies is presented in Fig. 1, and the full list of the studied mitigation strategies and their effects on enteric CH₄ emission and animal performance metrics are presented in Tables S2 and S3, respectively. Effective mitigation strategies and their impact on CH₄I_M, CH₄I_G, daily CH₄, CH₄Y, as well as their relevance for different systems (feedlot, mixed, and grassland) are presented in Fig. 2 from highest to lowest efficacy in reducing CH₄I_M. 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 Fig. S1 to S3.

The meta-analysis identified three effective PB strategies, namely increasing feeding level, decreasing grass maturity, and decreasing dietary forage-to-concentrate ratio. These PB strategies decreased CH₄I by on average 12% (range 9 to 17%) and increased AP by a median of 17% (range 9 to 162%). Furthermore, there were five effective ABS strategies, namely CH₄ inhibitors, tanniferous forages, electron sinks, oils and fats, and oilseeds (only for lactating animals since oilseed supplementation significantly decreased weight gain in growing animals). These ABS strategies decreased CH₄I by on average 17% (ranging from 12 to 32%) and daily CH₄ emissions by on average 21% (ranging from 12 to 35%) without negatively affecting AP.

Several mitigation strategies were excluded from the present evaluation or classified as ineffective because of insufficient publications. These include breeding low-CH₄ emitting animals and improving animal health. However, modeling studies have shown that strategies that improve animal health may significantly increase AP and reduce CH₄I²⁴. In the subsequent section, the effects of mitigation strategies are reported in parenthesis as mean, 95% confidence interval (95% CI), and the number of treatment comparisons (n). Reported differences were significant (adjusted $P < 0.05$) unless indicated otherwise.

Strategies that decrease product-based CH₄ emissions and increase production

Increasing feeding level (mean = 58%, 95% CI = 47 to 71%, n = 47) decreased CH₄I_M (17%, 9 to 23%, 5). No data were available for CH₄I_G. Fiber digestibility was decreased (7%, 2 to 12%,

18), likely due to increased rumen passage rates²⁵. Increasing feed intake resulted in increased weight gain (162%, 38 to 398%, 7) and milk yield (17%, 10 to 25%, 8). Increasing feed intake to improve AP significantly decreases CH₄I_G and CH₄I_M^{12,26} as well as the overall carbon footprint of animal-sourced food²⁷ when diet composition remains unchanged. This strategy directs energy for CH₄ towards animal production²⁸ but also decreases energy requirements for maintenance relative to milk production and reduces the time to slaughter for growing animals. 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 feedlots, mixed, and grassland systems, but particularly the latter and especially in certain climatic regions where animals are underfed due to insufficient or low nutritive forage²⁹.

Decreasing grass maturity decreased CH₄I_M (13%, 7 to 18%, 6), did not affect feed intake but increased milk yield (9%, 1 to 18%, 6). Furthermore, it improved fiber digestibility (15%, 9 to 21%, 9), which can potentially decrease manure CH₄ emissions²². 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 excretion³⁰. Thus, possible tradeoffs associated with direct and indirect manure nitrous oxide emissions require further evaluation. This strategy is applicable to all production systems. Although decreasing grass maturity increases the overall efficiency of dietary nutrient use for milk production (kg milk per unit of feed intake), it was not deemed to be cost-effective in the Netherlands; however, it was more cost-effective than supplementation with nitrate or linseed³¹.

Decreasing dietary forage-to-concentrate ratio decreased CH₄I_M (9%, 4 to 14%, 19) and CH₄I_G (9%, 3 to 15%, 16). It increased feed intake (9%, 5 to 14%, 85), which led to an increase in weight gain (21%, 13 to 29%, 32) and milk yield (17%, 10 to 24%, 26) but did not increase absolute CH₄ emissions or reduce fiber digestibility. Reduced CH₄Y (13%, 10 to 16%, 69) was the result of increased feed intake, which most likely resulted in a shift in rumen fermentation patterns and a decrease in rumen pH, which inhibits methanogens³². 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 are mostly found in the feedlot and high-yielding dairy cattle³³. 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).

Strategies that decrease absolute CH₄ emissions

Rumen manipulation by feeding CH₄ inhibitors 3-nitrooxypropanol (3-NOP) effectively decreased CH₄I_M (31%, 21 to 40%, 2) without affecting feed intake or milk yield. 3-nitrooxypropanol acts on a key enzyme of the methanogenesis pathway that is used by methanogenesis to produce CH₄³⁴. Insufficient data were available in the database 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 cattle³⁵ or fiber digestibility in early-lactation dairy cows³⁶ and decreased daily CH₄ emissions throughout a 15-week experiment³⁷. A recent meta-analysis showed that 3-NOP decreased daily CH₄ emissions in a dose-dependent manner, that its mitigation effect was greater for dairy than beef cattle, and that its effectiveness decreased with increasing dietary fiber content¹⁸. In its current form, 3-NOP can only be used in confinement systems because it is more effective when fed continuously^{36,38}, but ongoing research is developing mechanisms for its application under grazing conditions³⁹. Supplementation of 3-NOP increased milk fat content in dairy cattle²⁹ and feed efficiency in feedlot cattle⁴⁰, 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%⁴¹. However, more research is warranted on dietary inclusion

levels, effects on animal feed intake and production⁴², the implications and safety of feeding bromoform⁴³, its main active compound⁴⁴, 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 seaweed⁴⁵ before it can be recommended as a mitigation strategy.

Dietary inclusion of tanniferous forages 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 emissions²². Daily CH₄ emissions were also decreased (12%, 7 to 16%, 42) and feed intake or animal production were unaffected. There are differences in efficacy among tannin sources. *Sericea lespedeza* (*Lespedeza cuneata*) and *Lotus* (*corniculatus* and *pedunculatus*) were determined as the most promising tanniferous forage as they significantly decreased daily CH₄ emissions (32% and 8%, respectively) without affecting feed intake. *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 experiment⁴⁶. 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 intake⁴⁷. In addition, 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 the excretion of nitrogen in urine, which decreases ammonia and nitrous oxide emissions from manure⁴⁸. The cost-effectiveness of their supplementation still needs to be evaluated. Among the identified effective ABS strategies, dietary inclusion of tanniferous forages is the only one applicable to grassland besides feedlot and mixed systems. As 37% of global enteric CH₄ emissions from ruminant livestock is attributed to grazing systems⁴, it will be important to identify other effective ABS strategies that are applicable to grassland systems.

Rumen manipulation with electron sinks decreased $\text{CH}_4\text{I}_\text{M}$ (13%, 9 to 16%, 12) and $\text{CH}_4\text{I}_\text{G}$ (12%, 2 to 20%, 3). Although they led to small decreases in feed intake (2%, 1 to 3%, 49), small increases in milk yield (3%, 1 to 5%, 13) were observed. Electron sinks accept hydrogen that would otherwise be used by methanogens for CH_4 production in the rumen³². Of the studied electron sinks (fumaric acid and nitrate), only nitrate was classified as effective. Nitrate has been shown to decrease daily CH_4 emissions and CH_4Y in a dose-dependent manner with no loss of effectiveness and effectively decreased daily CH_4 emissions over the long-term^{20,49}. Similar to 3-NOP, nitrate was more effective in decreasing daily CH_4 emissions and CH_4Y in dairy than in beef cattle²⁰. 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 acclimatized⁵⁰. Acclimatization of animals to dietary nitrate is required to avoid methemoglobinemia, a blood disorder in which too little oxygen is delivered to the cells. However, this acclimatization can be lost within three weeks when nitrate is not fed daily⁵¹. Simultaneous sulfate supplementation has been shown to help protect cattle against nitrate toxicity⁵². Nitrate supplementation may increase enteric and possibly manure nitrous oxide emissions⁵³. Studies in France⁵⁴ and the Netherlands³¹ found that nitrate supplementation was not cost-effective.

Dietary inclusion of oil and fat decreased $\text{CH}_4\text{I}_\text{M}$ (12%, 6 to 18%, 24) and $\text{CH}_4\text{I}_\text{G}$ (22%, 8 to 35%, 6); however, possible effects on manure CH_4 emissions due to decreased fiber digestibility (4%, 2 to 7%, 37) need to be evaluated²². 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 likely because of the high energy concentration of lipids compared with feeds it replaces in livestock diets. Of the subcategories included in oil and fat supplementation, 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, 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. Oil inclusion reportedly decreases daily CH₄ emissions in a dose-response manner¹⁹ and over the long-term^{55,56}. 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 productivity⁵⁷. 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 oil⁵⁸. Dietary oils and fats are by-products of oilseed production, which has been associated with nearly doubling of the GHG emissions per kg dry matter compared with other concentrate feeds (1.27 vs. 0.70 CO₂ equivalents kg dry matter⁻¹)⁵⁹. Thus, upstream emissions are likely to increase when concentrate feeds are substituted by oil and fat. However, enteric fermentation usually contributes substantially more GHG to the carbon footprint of ruminant products than feed production^{60,61} and the dietary inclusion of oil is limited. Thus, increases in upstream emissions are unlikely to offset GHG reduction through the mitigation of enteric CH₄ emissions by oils or fats. Nevertheless, exact upstream offsets of oils should be evaluated. The cost-effectiveness of feeding oils to decrease CH₄I varies by region and country, because the price of oil, as well as meat and milk, vary considerably therein. Studies in China⁶², France⁵⁴, and The Netherlands³¹ 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 adoption of certain oils and oilseeds in animal diets.

Dietary inclusion of oilseeds (cracked or crushed) had similar effects on CH₄I_M (12%, 4 to 19%, 6) compared with oils and fat. Their supplementation 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 animals and not for growing animals. Likewise, the amount of inclusion of oilseeds should be limited to avoid negative impacts on 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 that of oils⁶³. And

similar to oil inclusion, the possible impact to manure CH₄ emissions due to decreased fiber digestibility needs to be evaluated. Oilseeds that tended to decrease CH₄I_M were cottonseed (15%, 2 to 25%, 2, *P* = 0.07) and canola seed (13%, 2 to 23%, 3, *P* = 0.07).

The potential of the identified strategies to decrease enteric methane emissions

The potential of the identified strategies to decrease enteric CH₄ emissions globally, in Africa and in Europe, between 2012 and 2030 and between 2012 and 2050 was estimated using three mitigation scenarios. The year 2012 was used as the baseline instead of 2010, because projections used for demand⁶⁴ and human population⁶⁵ only had figures for 2012 and not 2010. The identified strategies in the current meta-analysis (Fig. 2) and BAU projections for per capita red meat and dairy food protein demand⁶⁴ together with FAO projections for human population growth⁶⁵ were used in the mitigation scenarios. Although international trade allows livestock products to move across regions, it was assumed that demand increases in each of the modeled regions would be met by livestock production within the same region, an assumption that suggests technological, market and policy conditions would allow each region to produce enough to meet their own livestock protein demand. A sensitivity analysis for 100%, 75%, 50%, and 25% adoption rates of mitigation measures was performed. The three mitigation scenarios were: 1) Adoption of one PB strategy, 2) Adoption of one ABS strategy, and 3) Simultaneous adoption of one PB and one ABS.

Globally, only the 100% adoption of the most effective PB and ABS strategies (increasing feeding level and inclusion of a CH₄ inhibitor, respectively) decreased enteric CH₄ emissions sufficiently (14%) to meet the 1.5°C target by 2030 (Fig. 3A) but not by 2050 (Fig. S4A). In Africa, which was chosen to represent LMIC, none of the mitigation scenarios had the potential to meet the 1.5°C target by 2030 or 2050 (Fig. 3B and Fig. S4B). Although, the 100% adoption of the most effective PB and ABS strategies was estimated to mitigate enteric CH₄ emissions by 47% and 76% between 2012 and 2030 and 2012 and 2050, respectively, the mitigation effect was offset by

estimated increases in CH₄ emissions in BAU scenario (87% and 220%, respectively; Fig. 3B and Fig. S4B).

In contrast, in Europe, which was chosen to represent HIC, projected increases in enteric CH₄ emissions between 2012 and 2030 and 2012 and 2050 without mitigation strategy were only 11% (Fig. 3C and Fig S4C). By 2030, Europe could meet the 1.5°C target under the following mitigation scenarios (Fig. 3C): 1) The simultaneous 100% and 75% adoption of one PB strategy (when assuming the average or above average mitigation potential of all PB strategies) and one ABS strategy (when assuming the average or above average mitigation potential of all ABS strategies), 2) The simultaneous at least 50% adoption of the most effective PB and ABS strategy, and 3) The at least 75% adoption of the most effective ABS strategy. By 2050, Europe could only meet the 1.5°C target by the simultaneous 100% adoption of the most effective PB and ABS strategies (Fig. S4C).

While technically possible, even with transformative agri-food sector actions that remove adoption barriers for the simultaneous 100% adoption of the most effective PB and ABS strategies identified in this study is unlikely. Consequently, the identified strategies to reduce enteric CH₄ emissions must be enacted together with other measures to decrease CH₄ emissions. For example, strategies to reduce CH₄ emissions from manure handling or pre- or post-farmgate measures, such as the reduction of food waste and a shift to a more plant-based diets¹¹ when per capita protein consumption is high.

Combining two or more strategies to mitigate enteric CH₄ can increase or decrease the efficacy of the strategies. However, most likely the combination of two or more strategies will give a greater reduction, than when only one is used. In this study, it was assumed that the combination of strategies would result in an additive mitigation effect, as this was observed when lipids were combined with tannins⁶⁶, 3-NOP^{67, 68}, or nitrates⁶⁹. However, more studies are needed to evaluate the effect of combining two or more strategies, as combinations of multiple mitigation strategies are likely needed to sufficiently mitigate CH₄ to limit global warming to 1.5°C.

374

375 Although one of the identified mitigation scenarios was suited to decrease global enteric CH₄
376 emissions to limit global warming to 1.5°C by 2030 but not 2050, the 1.5°C target is unlikely to be
377 achieved, because 100% of the producers would need to adopt it. While none of the mitigation
378 scenarios would allow Africa to meet the 1.5°C target, multiple scenarios that did not require a
379 100% adoption would allow Europe to reach the 1.5°C target. The reason for this is that Africa
380 had a greater projected BAU increase in enteric CH₄ emissions compared with Europe (87 vs.
381 11%) between 2012 and 2030, as a result of projected increases in human population (56 vs. 4%)
382 and per capita demand for red meat and milk protein (18 vs. 5%) resulting in a greater absolute
383 increase in demand of red meat and milk protein (84 vs. 9%). In addition, Africa compared with
384 Europe has an overall higher CH₄I_M (104 and 19 kg CO₂equivalents kg milk protein⁻¹,
385 respectively) and CH₄I_G (198 and 46 kg CO₂ equivalents kg red meat protein⁻¹), which leads to
386 proportionally greater increases in enteric CH₄ for red meat and milk protein produced in Africa
387 compared to Europe. Similar reasons led to the observed differences between 2012 and 2050.

388

389 Even though Africa may not be able to meet the 1.5°C target, the projected BAU per capita red
390 meat and milk protein demand in 2030 will still be 51% and 78% smaller than that of Europe (3.4
391 vs. 6.9 g red meat protein capita⁻¹ day⁻¹ and 4.3 vs. 19.9 g of milk protein capita⁻¹ day⁻¹,
392 respectively). Despite this large disparity in annual animal protein consumption, annual BAU per
393 capita enteric CH₄ emissions for red meat and milk consumed in Africa was 111 and 8% greater
394 than that in Europe in 2012 (245 vs. 116 kg CO₂ equivalents capita⁻¹ year⁻¹ and 144 vs. 134 kg
395 CO₂ equivalents capita⁻¹ head year⁻¹, respectively) and 161 and 25% greater than that in Europe
396 in 2050 (303 vs. 116 kg CO₂ equivalents capita⁻¹ year⁻¹ and 163 vs. 130 kg CO₂ equivalents
397 capita⁻¹ year⁻¹, respectively). This shows the need and opportunity to decrease CH₄I in Africa and
398 other LMIC where CH₄I is high. In Europe and other HIC, where CH₄I and annual per capita
399 enteric CH₄ emissions associated with red meat and milk protein consumption are low but red
400 meat and milk demand are high, emissions might be reduced by shifting demand to plant-based
401 alternatives¹¹. In addition, red meat and milk exports from HIC to LMIC could help to reduce

enteric CH₄ emissions to meet the 1.5°C target. However, these exports often do not reach food-insecure regions where the money to buy food is limited or unavailable and increases in local production are more likely to meet the demand and recommended levels of dietary protein intake.

Future research needs to 1) develop novel mitigation strategies especially for pasture-based systems (less than half of the identified strategies were relevant for pasture systems), 2) increase the understanding of the mitigation potential of combinations of enteric fermentation mitigation strategies, 3) investigate the mitigation effect of identified strategies on emissions of growing and non-lactating cattle (only half of the identified strategies had sufficient data available to evaluate CH₄I_G), 4) estimate offsets of CH₄ mitigation by increases in GHG emissions elsewhere in the supply chain including in longer supply chains characterized by international trade, and 5) identify the barriers to wide-scale adoption of effective mitigation strategies in HIC and LMIC.

Conclusion

This comprehensive meta-analysis identified in a quantitative and comparative manner three effective PB and five effective ABS strategies. The three PB strategies decreased product-based CH₄ emissions by on average 12% (ranging from 9 to 17%) and increased animal production by a median of 17% (ranging from 9 to 162%). The five ABS strategies reduced product-based CH₄ emissions by an average of 17% (ranging from 12 to 32%) and daily CH₄ emissions by an average of 21% (ranging from 12 to 35%). The 100% adoption of only one of the PB or ABS strategies at a time, cannot sufficiently decrease global enteric CH₄ emissions from agriculture by 2030 or 2050 to achieve the 1.5°C target. However, the simultaneous 100% adoption of the most effective PB and ABS strategy can sufficiently decrease global enteric CH₄ emissions to achieve the 1.5°C target by 2030 but not 2050. Adoption barriers to the identified strategies are likely to prohibit them from reaching their full technical potential. Thus, to ensure meeting the 1.5°C climate target, it will be crucial that adoption barriers are identified and removed, and the identified strategies are implemented. This also needs to be done for strategies that remove

emissions from the supply and demand site in the agricultural sector. Further, the mitigation effect of the simultaneous implementation of more than two of the identified strategies should be studied. At a regional level, projected autonomous increases in enteric CH₄ emissions may prevent meeting the 1.5°C target in studied mitigation scenarios in LMIC, such as for Africa. The projected increases in enteric CH₄ in HIC, such as Europe, are relatively small. Multiple studied scenarios may allow HIC to meet the 1.5°C target by 2030 and one scenario will also do so for the 2050 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. 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, MitiGate¹⁷, were merged with the database created in the current analysis.

The abstracts of the publications found in the search were reviewed, and based on the 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 (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, Spanish 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 CH₄-to-CO₂ ratio of exhaled breath^{70,71}).

The completed database consisted of 650 publications. From these, only the 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.

The 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 (Table S2). Only the mitigation strategies that each had at least two publications 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 kg 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, the treatment means were averaged, and their respective errors pooled, so that each experiment produced a single "Treatment" and "Control" pair of response means and SDs.

The final dataset analyzed in the present study included data from 430 peer-reviewed publications, of which 66% were of cattle, 31% of small ruminants (sheep and goats) and 3% of other ruminant species (buffalo, deer, and yak). The complete list of references used in the

current analysis is given in Table S1 and the database can be found on www.datacommons.psu.edu under the link <https://www.datacommons.psu.edu/commonswizard/MetadataDisplay.aspx?Dataset=6333> and the DOI 10.26208/6em7-k817. The majority of the publications reported daily CH₄ emissions (92%), feed intake (84%), and CH₄Y (71%), but 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%) (Fig. S5). 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 the publications 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^{72,73}. 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 comparisons⁷³. 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 error⁷⁴ (SAS, V. 9.4; SAS Inst. Inc, Cary, NC). The effect of a mitigation strategy was considered significant for adjusted $P < 0.05$ and $0.05 \leq \text{adjusted } P \leq 0.10$ was considered as a trend.

Estimation of the potential for identified strategies to decrease methane emissions

The potential of the identified strategies to decrease global, LMIC (e.g. countries in the African Region), and HIC (e.g. countries in the European Region) enteric CH₄ emissions between 2012 and 2030 and between 2012 and 2050 was estimated using three mitigation scenarios. In the mitigation scenarios, identified measures to mitigate enteric CH₄ from the current analysis (Fig. 2) were applied to demand projections under a BAU scenario. Further, a sensitivity analysis for 100%, 75%, 50%, and 25% adoption rate of mitigation measures was performed.

The BAU scenario was defined by the FAO⁷⁵ as a continuation of historical trends of food preferences and inclusion of current initiatives to address SDG targets. Annual demands for protein from red meat (bovine meat, mutton, and goat meat) and milk for 2012, 2030, and 2050 were projected by using published per capita demand projections by Henchion et al. (2021)⁶⁴ and human population projections by FAO⁶⁵. Consistent with the demand projections by Henchion et al. (2021)⁶⁴ projections were classified into the six regions defined by the World Health Organization (WHO; African Region, Region of the Americas, South-East Asia Region, European Region, Eastern Mediterranean Region, and Western Pacific Region)⁷⁶. The regional production of red meat and dairy protein by production system (feedlot, grassland, and mixed) reported by GLEAM⁵ for 2010 was applied to demand projections. As some of the regional classifications in GLEAM differed from the WHO regions, best judgment was used to match GLEAM regions to WHO regions. The countries/regions included in each WHO region in our analysis for demand projections, population projection, and GLEAM are listed in Table S4. Further, intensities for enteric CH₄ emissions (enteric CH₄ per kg of red meat or milk protein) by animal production system (feedlot, grassland, and mixed) reported by GLEAM for 2010 were multiplied by projected animal protein demand by animal production system to estimate enteric CH₄ emissions for each system. For this, the underlying assumption was that demand will be met by increased production in each region.

The three mitigation scenarios were: 1) Adoption of one PB strategy (increasing feeding level, decreasing grass maturity, or decreasing dietary forage-to-concentrate ratio), 2) Adoption of one

ABS strategy (the inclusion of CH₄ inhibitors, tanniferous forages, electron sinks, oils or fats, or oilseeds), and 3) Simultaneous adoption of one PB and one ABS.

For a 100% adoption rate of one PB strategy, the identified average (average of all mitigation potentials of strategies applicable to a production system), minimum and maximum (strategies with lowest and highest mitigation potential applicable to a production system, respectively) reductions of CH₄I for a production system were used to adjust the emission intensities reported by GLEAM⁴ for red meat and dairy protein for each of the projected years. When there were no data for the CH₄I_G reduction potential of a strategy, it was assumed that the minimum reduction potential was 0%, the maximum reduction potential was the one identified for CH₄I_M, and the average reduction potential was the average of the minimum and maximum reduction potential.

For a 100% adoption rate of one ABS strategy, the identified average, minimum, and maximum reductions of daily CH₄ emission for a production system were used to adjust the projected annual CH₄ emissions for all red meat and dairy protein of a given productions system of the projected years. For a 100% adoption rate of one PB strategy and one ABS strategy, the reduction for the adoption of one PB strategy was first projected, and afterward, the adoption of one ABS strategy was projected. Similar calculations were done for the other three assumed adoption rates (75%, 50%, and 25%).

Acknowledgments

The authors want to thank the GLOBAL NETWORK project for generating part of the database. The GLOBAL NETWORK project (<https://globalresearchalliance.org/research/livestock/collaborative-activities/global-research-project/>; accessed 20 June, 2020) was a multi-national initiative funded by the Joint Programming Initiative on Agriculture, Food Security and Climate Change and was coordinated by the Feed and Nutrition Network (<https://globalresearchalliance.org/research/livestock/networks/feed-nutrition-network/>; accessed 20 June, 2020) within the Livestock Research Group of the Global

566 Research Alliance on Agricultural GHG (<https://globalresearchalliance.org>; accessed 20 June,
567 2020).

568 The authors want to thank MitiGate, which was part of the AnimalChange project funded by the
569 EU under Grant Agreement FP7-266018 for sharing their database with us
570 (<http://mitigate.ifers.aber.ac.uk/>, accessed July 1, 2017). Part of C. Arndt's, A. N. Hristov's, and
571 S. C. McClelland's time in the early stages of this project was funded by the Kravis Scientific
572 Research Fund (New York, NY) and a gift from Sue and Steve Mandel to Environmental Defense
573 Fund. Another part of C. Arndt's work on this project was supported by the FONDECYT contract
574 (N° 016-2019-FONDECYT-BM-INC.INV) and by German Federal Ministry for Economic
575 Cooperation and Development (BMZ issued through GIZ) through the research "Programme of
576 Climate Smart Livestock" (PCSL, Programme No. 2017.0119.2) and of A. Hristov's work by the
577 USDA (Washington, DC) National Institute of Food and Agriculture Federal Appropriations under
578 Project PEN 04539 and Accession Number 1000803. E. Kebreab was supported by the Sesnon
579 Endowed Chair Fund of the University of California, Davis.

580

581 **References**

5821. M. A. Clark, et al., Global food system emissions could preclude achieving the 1.5° and 2°C
583 climate change targets. *Science* **370**, 705-708 (2020).
5842. R. Jackson, et al., Increasing anthropogenic methane emissions arise equally from agricultural
585 and fossil fuel sources. *Environ. Res. Lett.* **15**, 071002 (2020).
5863. M. Crippa et al., Food systems are responsible for a third of global anthropogenic GHG
587 emissions. *Nature Food* **2**, 198-209 (2021).
5884. FAO. (2017). GLEAM 2.0 - Assessment of greenhouse gas emissions and mitigation potential.
589 *Food and Agriculture Organization of the United Nations (FAO)*. Available at:
590 <http://www.fao.org/gleam/results/en/>.
5915. IPCC. (2014). Climate Change 2014: Mitigation of Climate Change. Contribution of Working
592 Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change

593 [Edenhofer, O., R. Pichs-Madruga, Y. Sokona, E. Farahani, S. Kadner, K. Seyboth, A. Adler, I.
594 Baum, S. Brunner, P. Eickemeier, B. Kriemann, J. Savolainen, S. Schlömer, C. von Stechow, T.
595 Zwickel and J.C. Minx (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New
596 York, NY, USA.

5976. United Nations Environment Programme and Climate and Clean Air Coalition, Global Methane
598 Assessment: Benefits and Costs of Mitigating Methane Emissions (United Nations Environment
599 Programme, Nairobi, 2021).

6007. IPCC. In *Global Warming of 1.5°C* (eds. V. Masson-Delmotte et al.) (IPCC, Geneva, 2018).

6018. United Nations (2015) World Population Prospects: The 2015 Revision. United Nations
602 Department of Economic and Social Affairs, Population Division.

6039. L. Iannotti et al. Livestock-derived foods and sustainable healthy diets. UN Nutrition Secretariat
604 Rome, Italy, 2021.

60510. W. J. Ripple et al. Ruminants, climate change and climate policy. *Nat. Clim. Change* **4**, 2-5
606 (2014).

60711. W. Willet et al., Food in the Anthropocene: the EAT-Lancet Commission on healthy diets from
608 sustainable food systems. *The Lancet*, **393**, 447-492.

60912. A. N. Hristov et al., Special topics - Mitigation of methane and nitrous oxide emissions from
610 animal operations: I. A review of enteric methane mitigation options. *J. Anim. Sci.* **91**, 5045-5069
611 (2013).

61213. M. Balehgn et al., Improving adoption of technologies and interventions for increasing supply of
613 quality livestock feed in low- and middle-income countries. *Glob. Food Sec.* **26**, 100372 (2020).

61414. P. J. Gerber, T. V. Vellinga, C. Opio, H. Steinfeld, Productivity gains and greenhouse gas
615 emissions intensity in dairy systems. *Livest. Sci.* **139**, 100-108 (2011).

61615. J. Chang, et al. The Key Role of Production Efficiency Changes in Livestock Methane Emission
617 Mitigation. *AGU Advances* **2**, e2021AV000391 (2021).

61816. M. Herrero et al., Greenhouse gas mitigation potentials in the livestock sector. *Nat. Clim. Change*
619 **6**, 452-461 (2016).

62017. J. B. Veneman, E. R. Saetnan, A. J. Clare, C. J. Newbold, MitiGate; an online meta-analysis
621 database for quantification of mitigation strategies for enteric methane emissions. *Sci. Total*
622 *Environ.* **572**, 1166-1174 (2016).

62318. J. Dijkstra, A. Bannink, J. France, E. Kebreab, S. van Gastelen, Short communication:
624 Antimethanogenic effects of 3-nitrooxypropanol depend on supplementation dose, dietary fiber
625 content, and cattle type. *J. Dairy Sci.* **101**, 9041-9047 (2018).

62619. M. Eugène, D. Massé, J. Chiquette, C. Benchaar, Meta-analysis on the effects of lipid
627 supplementation on methane production in lactating dairy cows. *Can. J. Anim. Sci.* **88**, 331-337
628 (2008).

62920. X. Y. Feng, et al., Antimethanogenic effects of nitrate supplementation in cattle: A meta-analysis.
630 *J. Dairy. Sci.* **103**, 11375-11385 (2020).

63121. G. Congio et al. Enteric methane mitigation strategies for ruminant livestock systems in the Latin
632 America and Caribbean region: A meta-analysis. *J. Clean. Prod.* **127693** (2021).

63322. IPCC, *2006 IPCC Guidelines for National Greenhouse Gas Inventories, Volume 4: Agriculture,*
634 *Forestry and Other Land Use* (eds H. S. Eggleston, L. Buendia, K. Miwa, T. Ngara, K. Tanabe)
635 Ch.10, 1-89 (IGES, Hayama 2006).

63623. E. H. Bennetzen, , P. Smith, J. R. Porter. Decoupling of greenhouse gas emissions from global
637 agricultural production: 1970–2050. *Glob. Change Biol.*, **22**, 763-781 (2016).

63824. D. von Soosten, U. Meyer, G. Flachowsky, S. Dänicke, Dairy Cow Health and Greenhouse Gas
639 Emission Intensity. *Dairy* **1**, 20-29. (2020).

64025. P. Huhtanen, M. Rinne, J. Nousiainen, A meta-analysis of feed digestion in dairy cows. 2. The
641 effects of feeding level and diet composition on digestibility. *J. Dairy Sci.* **92**, 5031-5042 (2009).

64226. J. P. Goopy et al., Severe below-maintenance feed intake increases methane yield from enteric
643 fermentation in cattle. *Br. J. Nutr.* **123**, 1239-1246 (2020).

64427. A. N. Hristov et al., Special topics - Mitigation of methane and nitrous oxide emissions from
645 animal operations: III. A review of animal management mitigation options. *J. Anim. Sci.* **91**, 5095-
646 5113 (2013).

64728. FAO & New Zealand Agricultural Greenhouse Gas Research Centre. *Low Emissions*
648 *Development of the Beef Cattle Sector in Uruguay – Reducing Enteric Methane for Food Security*
649 *and Livelihoods*. (FAO/NZAGGRC, Rome, 2017).

65029. R. Demanet, M. L. Mora, M. Á. Herrera, H. Miranda, J. M. Barea, Seasonal variation of the
651 productivity and quality of permanent pastures in Andisols of temperate regions. *J. Soil Sci. Plant*
652 *Nutr.* **15**, 111-128 (2015).

65330. F. Montes et al., Special topics – Mitigation of methane and nitrous oxide emissions from animal
654 operations: II. A review of manure management mitigation options. *J. Anim. Sci.* **91**, 5070-5094
655 (2013).

65631. C. E. van Middelaar, J. Dijkstra, P. B. M. Berentsen, I. J. M. De Boer, Cost-effectiveness of
657 feeding strategies to reduce greenhouse gas emissions from dairy farming. *J. Dairy Sci.* **97**,
658 2427-2439 (2014).

65932. E. M. Ungerfeld, Metabolic hydrogen flows in rumen fermentation: principles and possibilities of
660 interventions. *Front. Microbiol.* **11**, 595 (2020).

66133. N. Abdela, Sub-acute Ruminal Acidosis (SARA) and its Consequence in Dairy Cattle: A Review of
662 Past and Recent Research at Global Prospective. *Achievements in the Life Sciences*, **10**, 187-
663 196 (2016).

66434. U. Ermler, W. Grabarse, S. Shima, M. Goubeaud, R. Thauer, Crystal structure of methyl-
665 coenzyme M reductase: The Key Enzyme of Biological Methane Formation. *Science* **278**, 1457-
666 1462 (1997).

66735. S. H. Kim et al., Effects of 3-nitrooxypropanol on enteric methane production, rumen
668 fermentation, and feeding behavior in beef cattle fed a high-forage or high-grain diet. *J. Anim. Sci.*
669 **97**, 2687-2699 (2019).

67036. S. van Gastelen et al., 3-Nitrooxypropanol decreases methane emissions and increases
671 hydrogen emissions of early lactation dairy cows, with associated changes in nutrient digestibility
672 and energy metabolism. *J. Dairy Sci.* **103**, 8074-8093 (2020).

67337. A. N. Hristov, A. Melgar, Short communication: Relationship of dry matter intake with enteric
674 methane emission measured with the GreenFeed system in dairy cows receiving a diet without or
675 with 3-nitrooxypropanol. *Animal* **14**, s484-s490 (2020).

67638. C. K. Reynolds et al., Effects of 3-nitrooxypropanol on methane emission, digestion, and energy
677 and nitrogen balance of lactating dairy cows. *J. Dairy Sci.* **97**, 3777-3789 (2014).

67839. S. Muetzel et al., Conference abstract in *Proceedings of the 7th International Greenhouse Gas
679 and Animal Agriculture Conference. Iguassu Falls, Brazil* (eds A. Berndt, L. G. Pereira Ribeiro, A.
680 L. Abdala), 81 (Embrapa Southeast Livestock, São Carlos, SP, 2019).

68140. D. Vyas et al., The combined effects of supplementing monensin and 3-nitrooxypropanol on
682 methane emissions, growth rate, and feed conversion efficiency in beef cattle fed high-forage and
683 high-grain diets. *J. Anim. Sci.* **96**, 2923-2938 (2018).

68441. B. Roque et al., Red seaweed (*Asparagopsis taxiformis*) supplementation reduces enteric
685 methane by over 80 percent in beef steers. bioRxiv; 2020. DOI: 10.1101/2020.07.15.204958

68642. H. Stefanoni et al., Effects of the macroalga *Asparagopsis taxiformis* and oregano leaves on
687 methane emission, rumen fermentation, and lactational performance of dairy cows. *J. Dairy Sci.*
688 **104**, 4157-4173 (2021).

68943. Bromoform Fact Sheet, US Environmental Protection Agency (2000). Available at
690 <https://www.epa.gov/sites/production/files/2016-09/documents/bromoform.pdf>

69144. L. Machado et al., Identification of bioactives from the red seaweed *Asparagopsis taxiformis* that
692 promote antimethanogenic activity in vitro. *J. Appl. Phycol.* **28**, 3117-3126 (2016).

69345. M. A. Navarro et al., Airborne measurements of organic bromine compounds in the Pacific
694 tropical tropopause layer. *Proc. Natl. Acad. Sci. U.S.A* **112**, 13789-13793 (2015).

69546. H. Liu et al., Effects of lespedeza condensed tannins alone or with monensin, soybean oil, and
696 coconut oil on feed intake, growth, digestion, ruminal methane emission, and heat energy by
697 yearling alpine doelings. *J. Anim. Sci.* **97**, 885-899 (2019).

69847. D. A. Häring et al., Tanniferous forage plants: Agronomic performance, palatability and efficacy
699 against parasitic nematodes in sheep. *Renew. Agric. Food Syst.* **23**, 19-29 (2008).

70048. J. Zhang et al., Effect of different tannin sources on nutrient intake, digestibility, performance,
701 nitrogen utilization, and blood parameters in dairy cows. *Animals* **9**, 507 (2019).

70249. S. van Zijderveld et al., Persistency of methane mitigation by dietary nitrate supplementation in
703 dairy cows. *J. Dairy Sci.* **94**, 4028-4038 (2011).

70450. P. A. Farra, L. D. Satter, Manipulation of ruminal fermentation. III. Effect of nitrate on ruminal
705 volatile fatty acid production and milk composition. *J. Dairy Sci.* **54**, 1018-1024 (1971).

70651. A. R. Alaboudi, G. A. Jones, Effect of acclimation to high nitrate intakes on some rumen
707 fermentation parameters in sheep. *Can. J. Anim. Sci.* **65**, 841-849 (1985).

70852. L. Li et al., Effect of added dietary nitrate and elemental sulfur on wool growth and methane
709 emission of Merino lambs. *Anim. Prod. Sci.* **53**, 1195-1201 (2013).

71053. S. O. Petersen et al., Dietary nitrate for methane mitigation leads to nitrous oxide emissions from
711 dairy cows. *J. Environ. Qual.* **44**, 1063-1070 (2015).

71254. M. Doreau, L. Bamière, S. Pellerin, M. Lherm, M. Benoit, Mitigation of enteric methane for French
713 cattle: Potential extent and cost of selected actions. *Anim. Prod. Sci.* **54**, 1417-1422 (2014).

71455. H. Liu, V. Vaddella, D. Zhou, Effects of chestnut tannins and coconut oil on growth performance,
715 methane emission, ruminal fermentation, and microbial populations in sheep. *J. Dairy Sci.* **94**,
716 6069-6077 (2011).

71756. E. Jordan et al., Effect of refined coconut oil or copra meal on methane output and on intake and
718 performance of beef heifers. *J. Anim. Sci.* **84**, 162-170 (2006).

71957. D. J., Schauff, J. H. Clark, Effects of feeding diets containing calcium salts of long-chain fatty
720 acids to lactating dairy cows. *J. Dairy Sci.* **75**, 2990-3002 (1992).

72158. D. L. Palmquist, T. C. Jenkins, A 100-Year Review: Fat feeding of dairy cows. *J. Dairy Sci.* **100**,
722 10061-10077 (2017).

72359. H. Bonesmo et al., Greenhouse gas emission intensities and economic efficiency in crop
724 production: A systems analysis of 95 farms. *Agric. Syst.* **110**, 142-151 (2012).

72560. A. Horrillo, P. Gaspar, M. Escribano, Organic Farming as a Strategy to Reduce Carbon Footprint
726 in Dehesa Agroecosystems: A Case Study Comparing Different Livestock Products *Animals* **10**,
727 162 (2020).

72861. G. Thoma, et al., Greenhouse gas emissions from milk production and consumption in the United
 729 States: A cradle-to-grave life cycle assessment circa 2008. *Int. Dairy J.* **31**, S3-S14 (2013).

73062. W. Wang et al., Greenhouse gas mitigation in Chinese agriculture: Distinguishing technical and
 731 economic potentials. *Glob. Environ. Change* **26**, 53-62 (2014).

73263. M. Doreau, A. Meynadier, V. Fievez, A. Ferlay, *Ruminal metabolism of fatty acids: modulation of*
 733 *polyunsaturated, conjugated, and trans fatty acids in meat and milk*. (eds R. R. Watson, F. De
 734 Meester) Handbook of Lipids in Human Function Ch 19 - 521-542 (AOCS Press, 2016).

73564. M. Henchion, A. P. Moloney, J. Hyland, J. Zimmermann, and S. McCarthy, Review: Trends for
 736 meat, milk and egg consumption for the next decades and the role played by livestock systems in
 737 the global production of proteins. *Animal*, 100287 (2021).

73865. FAO, Global Perspectives Studies dataset. Population projections were retrieved on 26 January
 739 2021.

74066. S. R. O. Williams et al. Supplementing the diet of dairy cows with fat or tannin reduces methane
 741 yield, and additively when fed in combination. *Animal*, **14**, s464-s472 (2020).

74267. R. Gruninger et al. Application of 3-nitrooxypropanol and canola oil to mitigate enteric methane
 743 emissions of beef cattle results in distinctly different effects on the rumen microbial community.
 744 Preprint under consideration at Animal Microbiome. Preprint published in Research Square,
 745 doi:10.21203/rs.3.rs-391068/v1.

74668. X. M. Zhang et al., Combined effects of 3-nitrooxypropanol and canola oil supplementation on
 747 methane emissions, rumen fermentation and biohydrogenation, and total tract digestibility in beef
 748 cattle. *J. Anim. Sci.* **99**, 1-10 (2021).

74969. J. Guyader et al., Additive methane-mitigating effect between linseed oil and nitrate fed to cattle.
 750 *J. Anim. Sci.* **93**, 3564-3577 (2015).

75170. P. Huhtanen, A. R. Bayat, P. Lund, A. Hellwing, M. Weisbjerg, Short communication: Variation in
 752 feed efficiency hampers use of carbon dioxide as a tracer gas in measuring methane emissions in
 753 on-farm conditions. *J. Dairy Sci.* **103**, 9090-9095 (2020).

75471. K. J. Hammond et al., Review of current in vivo measurement techniques for quantifying enteric
 755 methane emission from ruminants. *Anim. Feed Sci. Technol.* **219**, 13-30 (2016).

75672. M. Borenstein, L. V. Hedges, J. P. T. Higgins, H. R. Othstein, *Introduction to Meta-analysis*.
 757 (Chichester, John Wiley & Sons, 2009).
75873. J. O. Friedrich, N. K. Adhikari, J. Beyene, The ratio of means method as an alternative to mean
 759 differences for analyzing continuous outcome variables in meta-analysis: A simulation study.
 760 *BMC Med. Res. Methodol.* **8**, 32 (2008).
76174. S. Holm, A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65-70 (1979).
76275. FAO. (2018). The future of food and agriculture—Alternative pathways to 2050. Food and
 763 Agriculture Organization of the United Nations, Rome, Italy.
76476. WHO. (2020). World health statistics 2020: monitoring health for the SDGs, sustainable
 765 development goals. World Health Organization, Geneva, Switzerland.

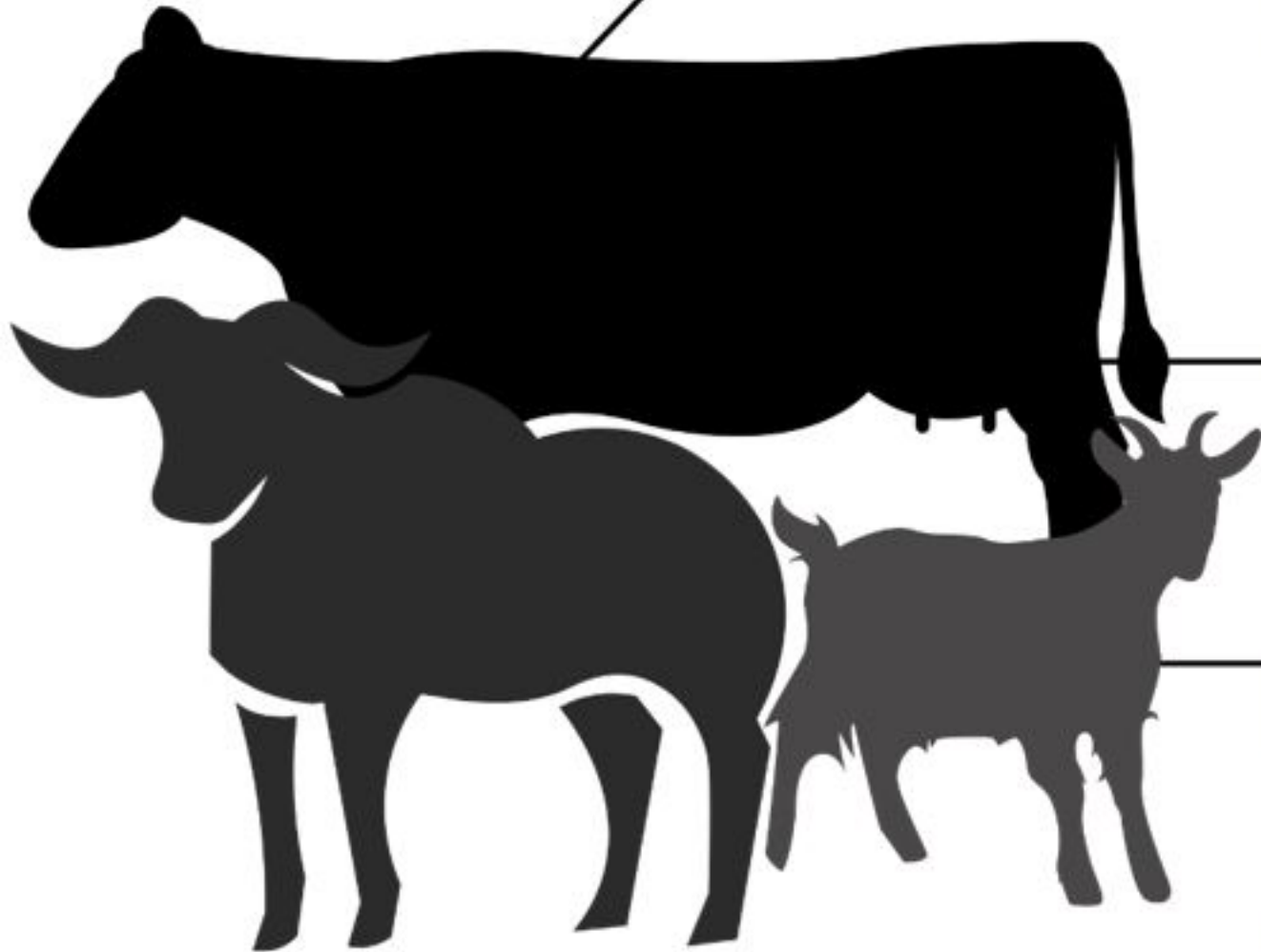
Figures

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

Figure 2. Effective mitigation strategies and their effect on methane (CH₄) emissions (A) and animal performance metrics (B). CH₄I_M = CH₄ emission intensity for milk (CH₄ g per kg of milk); CH₄I_G = CH₄ emission intensity for weight gain (g CH₄ per kg of weight gain for growing animals); Daily CH₄ = daily CH₄ emissions (g animal⁻¹ day⁻¹); Intake = dry matter intake (kg d⁻¹); Digestibility = apparent digestibility of neutral detergent fiber (%); Milk = milk yield (kg d⁻¹); Gain = average daily gain (kg d⁻¹); when numeric values are shown a significant effect was observed (adjusted *P* < 0.05) and no effect when adjusted *P* ≥ 0.05.

Figure 3. Projected change in enteric methane (CH₄) emissions between 2012 and 2030 without mitigation strategy under business as usual (BAU) and modeled mitigation scenarios for enteric CH₄ emission changes globally (A), in the African region (B), and in the European region (C). Error bars represent the average mitigation effect of the least and most effective mitigation strategy. Numbers in squares indicate the percentage of change from BAU.

ENTERIC METHANE MITIGATION STRATEGIES



ANIMAL & FEED MANAGEMENT

- Feed processing
- Genetic selection
- Improving animal health
- Improving pasture management
- Increasing feeding level
- Increasing forage quality
- Optimizing temperature
- TMR feeding

DIET FORMULATION

- By-products
- Decreasing forage-to-concentrate ratios
- Minerals and salts
- Oils and fats
- Oilseeds
- Protein feeds
- Tanniferous forages
- Urea

RUMEN MANIPULATION

- Additive
- Defaunation
- Electron sink

Product-Based Reductions

MITIGATION STRATEGY		POTENTIAL EMISSIONS REDUCTION		RELEVANT PRODUCTION SYSTEM
1	INCREASING FEEDING LEVEL	CH ₄ I _M CH ₄ I _G	-17% No Data	 
2	DECREASING GRASS MATURITY	CH ₄ I _M CH ₄ I _G	-13% No Data	 
3	DECREASING DIETARY FORAGE-TO-CONCENTRATE RATIO	CH ₄ I _M CH ₄ I _G	-9% -9%	

Absolute Reductions

1	CH ₄ INHIBITORS	CH ₄ I _M CH ₄ I _G	-32% No Data	Daily CH ₄ CH ₄ Y	-35% -34%	
2	TANNIFEROUS FORAGES	CH ₄ I _M CH ₄ I _G	-18% No Data	Daily CH ₄ CH ₄ Y	-12% -10%	 
3	ELECTRON SINKS	CH ₄ I _M CH ₄ I _G	-13% -12%	Daily CH ₄ CH ₄ Y	-17% -15%	
4	OILS & FATS	CH ₄ I _M CH ₄ I _G	-12% -22%	Daily CH ₄ CH ₄ Y	-19% -15%	
5	OILSEEDS Lactating animals only	CH ₄ I _M CH ₄ I _G	-12% No Effect	Daily CH ₄ CH ₄ Y	-20% -14%	

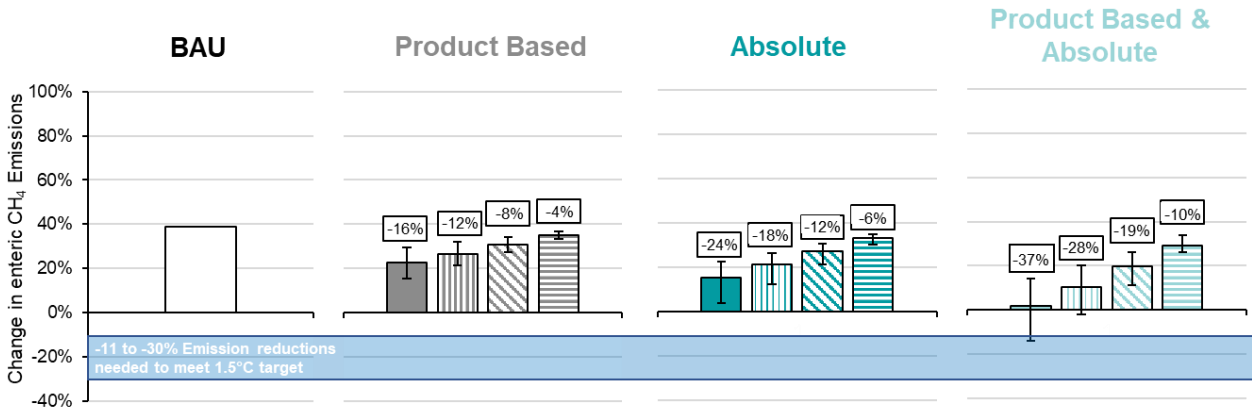
Production system

FEEDLOT & MIXED SYSTEMS

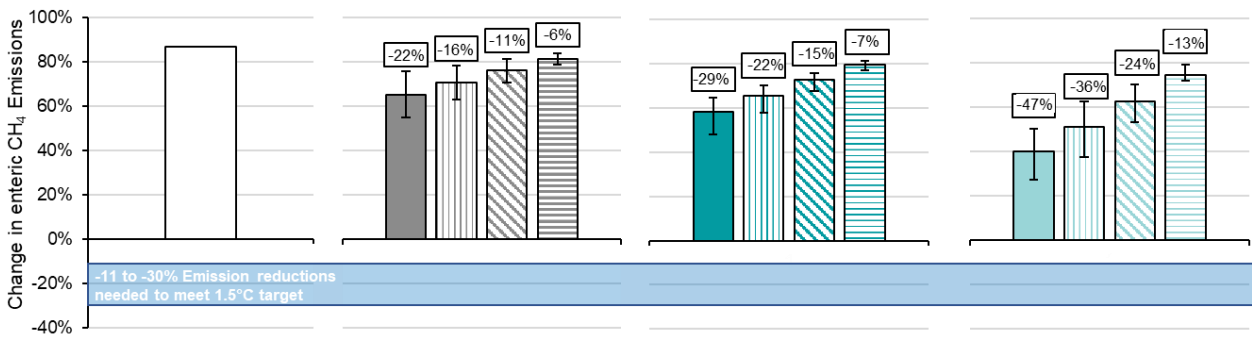
GRASSLAND SYSTEMS

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

A Projected change in global emissions between 2012 and 2030 under different scenarios



B Projected change in African emissions between 2012 and 2030 under different scenarios



C Projected change in European emissions between 2012 and 2030 under different scenarios

