LETTER

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Increased soil emissions of potent greenhouse gases under increased atmospheric CO_2

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Increasing concentrations of atmospheric carbon dioxide (CO_2) can affect biotic and abiotic conditions in soil, such as microbial activity and water content[1,2]. In turn, these changes might be expected to alter the production and consumption of the important greenhouse gases nitrous oxide (N_2O) and methane (CH_4) (refs 2, 3). However, studies on fluxes of N_2O and CH_4 from soil under increased atmospheric CO_2 have not been quantitatively synthesized. Here we show, using meta-analysis, that increased CO_2 (ranging from 463 to 780 parts per million by volume) stimulates both N_2O emissions from upland soils and CH_4 emissions from rice paddies and natural wetlands. Because enhanced greenhouse-gas emissions add to the radiative forcing of terrestrial ecosystems, these emissions are expected to negate at least 16.6 per cent of the climate change mitigation potential previously predicted from an increase in the terrestrial carbon sink under increased atmospheric CO_2 concentrations[4]. Our results therefore suggest that the capacity of land ecosystems to slow climate warming has been overestimated.

By burning fossil fuels, cutting down forests and changing land use in other ways, humans are rapidly increasing the amount of CO_2 in the atmosphere and warming the planet[5]. Plant growth is known to increase after an abrupt surge in CO_2 levels[6]. Because stimulated assimilation of carbon by plants can increase soil carbon input and soil carbon storage, terrestrial ecosystems could help to reduce the increase in atmospheric CO_2 and thereby slow climate change[7]. However, the radiative forcing of land ecosystems is not determined by their uptake and release of CO_2 alone; increased CO_2 can also alter soil emissions of N_2O and CH_4 (ref. 2). Although both of these gases occur in far lower atmospheric concentrations than does CO_2, their global warming potentials are much higher: 298 times higher for N_2O and 25 times higher for CH_4 (ref. 5). Agricultural soils are the main source of human-induced N_2O emissions[8]. Soils under natural vegetation produce roughly the same amount of N_2O as all anthropogenic sources combined[8]. Wetlands, including rice paddies, contribute 32–53% to the global emissions of CH_4 (ref. 8). Upland soils, on the other hand, act as a sink for atmospheric CH_4 through oxidation by methanotrophic bacteria[9]. Thus, changes in N_2O and CH_4 fluxes could greatly alter how terrestrial ecosystems influence climate[10].

Studies of greenhouse-gas (GHG) emissions span a variety of ecosystem types, and vary in experimental design and results, making it difficult to determine their global response to increased CO_2 from individual experiments. A quantitative synthesis of results across multiple studies can overcome this problem. Therefore, we used meta-analysis[11] to summarize the effect of atmospheric CO_2 enrichment on fluxes of CH_4 and N_2O from soil, using 152 observations from 49 published studies (see Supplementary Table 1, Supplementary Data 1 and 2, Supplementary Notes 1). We also summarized the effect of increased CO_2 on possible drivers of altered CH_4 and N_2O fluxes, using standing root biomass and soil water content from the studies in which the observations on N_2O and CH_4 fluxes were collected (Supplementary Data 3 and 4). All observations were analysed using three different weighting functions (see Methods). As CH_4 and N_2O emissions were not correlated with the concentration of CO_2 used for enrichment (Methods), we treat 'increased CO_2' as a category.

Overall, increased concentrations of atmospheric CO_2 stimulated emissions of N_2O by 18.8% (Fig. 1a). This positive response was significant for studies receiving little or no fertilizer, for non-pot studies and for studies on natural vegetation—that is, studies that most closely resembled real-world conditions (Supplementary Table 2). Increased CO_2 stimulated CH_4 emissions in wetlands by 13.2% (Fig. 1a, Supplementary Table 3). In rice paddies, increased CO_2 stimulated CH_4 emissions by 43.4% (Fig. 1a, Supplementary Table 4). In upland systems, increased CO_2 caused on average a small and insignificant net uptake of CH_4 (Supplementary Table 5).

To compare the relative importance of changed GHG fluxes in uplands, wetlands and rice paddies, we expressed the absolute effect of increased CO_2 on CH_4 and N_2O fluxes from these ecosystem types (Supplementary Tables 5–8) scaled by their respective total land area. For upland soils, we distinguished fertilized agricultural ecosystems and ecosystems receiving little or no fertilizer. Our estimates of total GHG fluxes under ambient (that is, present-day) CO_2 conditions correspond well to independent global syntheses of modern GHG fluxes (Supplementary Table 9), supporting our scaling approach.

The estimated stimulation by increased CO_2 of total soil N_2O emissions corresponds to an additional source of 0.33 Pg CO_2 equivalents (equiv.) yr^{-1} from agricultural ecosystems ($1\,Pg = 10^{15}$ g), and of 0.24 Pg CO_2 equiv. yr^{-1} for all other upland ecosystems (Fig. 2). The CO_2-stimulation of CH_4 emissions corresponds to an additional source of 0.25 Pg CO_2 equiv. yr^{-1} from rice paddies and of 0.31 Pg CO_2 equiv. yr^{-1} from natural wetlands. Our data indicate a small and non-significant effect of CO_2 on global CH_4 fluxes from upland soils for

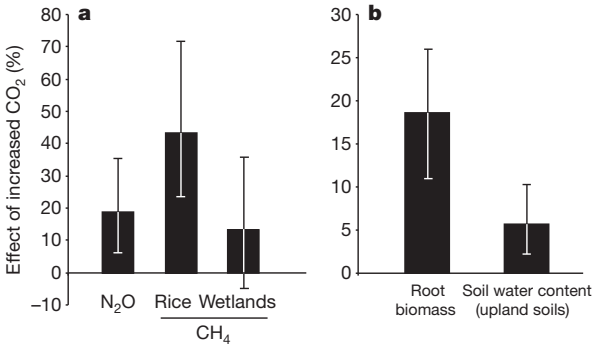

Figure 1 | Results of a meta-analysis of the response of GHG emissions and their potential drivers to rising levels of atmospheric CO_2. **a**, The effect of increased CO_2 on emissions of N_2O from upland soil and CH_4 from rice paddies and wetlands. Results are based on 73, 21 and 24 observations, respectively. **b**, The effect of increased CO_2 on root biomass and soil water content. Results are based on 83 and 55 observations, respectively. Effect sizes in all meta-analyses were weighted by replication. Error bars, 95% confidence intervals.

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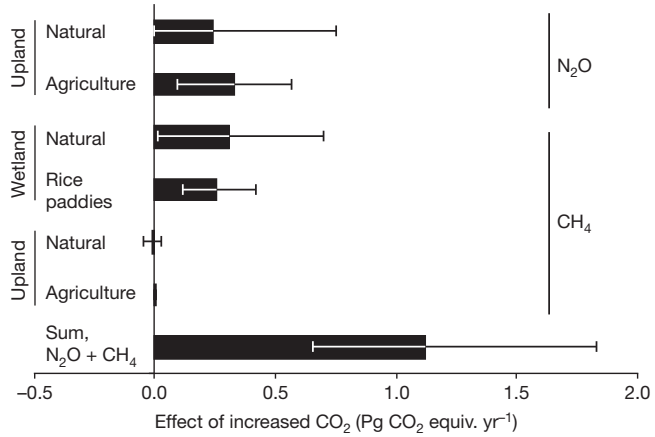

Figure 2 | The effect of rising atmospheric CO_2 on GHG emissions, expressed on the global scale. For N_2O fluxes, the results for natural and agricultural soils were based on 35 and 19 observations, respectively. For CH_4 fluxes, the results for natural wetlands, rice paddies, natural upland soils and agricultural upland soils were based on 16, 21, 10 and 8 observations, respectively. Effect sizes in all meta-analyses were weighted by replication. Error bars, 95% confidence intervals.

agricultural ecosystems (0.003 Pg CO_2 equiv. yr^{-1}) and for all other upland ecosystems (−0.011 Pg CO_2 equiv. yr^{-1}). The combined effect of increased CO_2 on emissions of these GHGs is 1.12 Pg CO_2 equiv. yr^{-1}.

Rising atmospheric CO_2 is expected to increase soil C storage in terrestrial ecosystems, which may contribute to the current residual C sink on land[7]. Meta-analysis of CO_2 enrichment experiments indicates that the sink is larger for ecosystems receiving fertilizer[12]. Scaled up by the total area of agricultural and non-fertilized ecosystems, these meta-analyses suggest that increased atmospheric CO_2 levels may increase the soil C sink by as much as 4.0 Pg CO_2 yr^{-1}. Results presented here indicate that enhanced GHG emissions under increased CO_2 reduce the C mitigation effect of soil C storage by 28% (1.12 Pg/4.0 Pg). The magnitude and significance of this result is insensitive to the choice of the weighting function used in the meta-analysis (Supplementary Fig. 1, Supplementary Table 10).

Experiments included in our database increased atmospheric CO_2 concentration to 630 p.p.m.v. on average, a level expected for the second half of this century[13]. Biogeochemical models predict that at that time, the terrestrial C sink may be as much as 6.8 Pg CO_2 yr^{-1} stronger than it is today[4] (when considering forcing by rising CO_2 alone). On the basis of our analysis, a CO_2-induced rise in GHG fluxes could negate 16.6% (1.12 Pg/6.8 Pg) of the expected increase of the entire terrestrial C sink (Supplementary Table 10).

This estimate (16.6%) is likely to be an underestimate for three reasons. First, most of the studies in our data set measured GHG fluxes during the growing season only, but we assumed these applied to the entire year. Winter emissions of CH_4 in wetlands and rice paddies are typically small[9]; however, winter emissions of N_2O during freeze-thaw cycles can contribute substantially to annual N_2O fluxes[14], and available data indicate that winter emissions of N_2O are stimulated under increased CO_2 (ref. 15). A recently published data set[16] suggests that N_2O emissions outside the growing season amount to 88% and 64% of the emissions during the growing season in agricultural systems and natural ecosystems, respectively (see Methods). Assuming that increased CO_2 affects N_2O emissions proportionately throughout the year, its effect on N_2O emissions outside the growing season would therefore amount to 0.29 Pg CO_2 equiv. yr^{-1} from agricultural systems and 0.15 Pg CO_2 equiv. yr^{-1} from natural ecosystems. Together, these fluxes negate an additional 7% of the expected increase of the terrestrial C sink.

Second, atmospheric N deposition is predicted to increase during this century[17]. Because average CO_2 responses of N_2O emissions were higher in studies receiving additional N (Supplementary Tables 2 and 6), the positive effect of CO_2 on N_2O emissions may strengthen as ecosystems become enriched in N.

Last, CO_2 effects on N_2O emissions showed a weak but significant correlation with experiment duration (Supplementary Fig. 2), suggesting that CO_2 effects on N_2O emissions may increase over time.

Why do GHG emissions respond positively to rising levels of atmospheric CO_2? Atmospheric CO_2 enrichment increased soil water contents for the studies contributing to our N_2O database (Fig. 1b, Supplementary Table 11); this result is probably due to improved efficiency of water use by plants, which reduces soil water loss through transpiration[18]. Moreover, increased CO_2 has been shown to enhance soil biological activity across a broad range of ecosystems[1,2]. Both responses promote soil anoxia, and thus stimulate denitrification[19] (anaerobic microbial respiration of nitrate), one of the major sources of N_2O from soils[3]. Increased CO_2 also enhanced root biomass in all three habitats (Fig. 1b, Supplementary Table 12). As denitrification is generally stimulated by high availability of labile C as a source of energy[20], and because new C enters mineral soil mainly through the root system, this increase in root biomass would stimulate denitrification rates—and N_2O emissions—even further.

Methane is produced only under anaerobic conditions, which are common in soils of rice paddies and natural wetlands but not uplands. Because methanogenic archaea rely on C assimilation by plants as their ultimate source of organic substrates[9], increased rates of soil C input with increased CO_2 can also stimulate CH_4 emissions. Indeed, the positive correlation between CH_4 emission rates and net ecosystem production in wetlands[21] suggests that plant productivity is a key process in the regulation of CH_4 emission from these ecosystems. The response to increased CO_2 of CH_4 emissions from rice paddies and wetlands showed significant correlation with the CO_2 response of root biomass ($r^2 = 0.17$, $P = 0.02$, Supplementary Fig. 6); this further suggests that increased CO_2 stimulates CH_4 production through its positive effect on plant growth and soil C input.

Global changes in climate and atmospheric composition have previously been suggested to affect GHG emissions from natural ecosystems. For instance, a global rise in temperature of 3.4 °C has been predicted to increase CH_4 emissions from wetlands by 78% (ref. 22). In addition to its direct effect on the global climate through radiative forcing, our results identify two indirect mechanisms through which rising atmospheric CO_2 amplifies climate change: by stimulating the release of N_2O from terrestrial ecosystems, and by enhancing CH_4 release from wetlands and rice paddies. The meta-analytic approach used here, synthesizing results across 49 studies, shows that increased N_2O and CH_4 emissions are both general and quantitatively important. Future assessments of terrestrial feedbacks to climate change should therefore consider these indirect effects of increased atmospheric CO_2 on the production by soil of trace gases like N_2O and CH_4.

METHODS SUMMARY

We extracted results for soil fluxes of CH_4 and N_2O, root biomass and soil water contents from CO_2 enrichment studies that were conducted in the field, in growth chambers or in glass houses. Soil fluxes of CH_4 from wetlands, rice paddies and upland soils were considered separately. We divided studies into two categories of N availability based on fertilization rates, that is, more or less than 30 kg N ha^{-1} yr^{-1}. This cut-off point corresponds to maximum atmospheric N deposition in the United States and most of the European Union[23]. We also made a distinction between studies in pots and field studies, and between studies with planted or natural vegetation. Agricultural ecosystems were defined as cropland and managed grasslands receiving between 30 and 300 kg N ha^{-1} yr^{-1}.

We quantified the effect of increased CO_2 on GHG fluxes by calculating the natural log of the response ratio (R), a metric commonly used in meta-analysis[24]:

$$\ln R = \ln(GHG_i/GHG_a)$$

where GHG is the flux of either CH_4 or N_2O under increased (i) or ambient (a) conditions. We also used ln$R$ to assess CO_2 responses of root biomass and soil water contents. We performed our analysis on effect sizes weighted by replication[25], on

unweighted effect sizes[12], and on effect sizes weighted by the inverse of the pooled variance[26].

Treatment effects were also expressed as the difference in annual GHG fluxes on an areal basis (U). This metric was essential for upland CH_4 flux, where values can be both positive and negative (making ln$R$ problematic).

We used METAWIN 2.1[27] to generate mean effect sizes and 95% bootstrapped confidence intervals (95% CI). Treatment effects were considered significant if the 95% CI did not overlap with 0. To scale up our results, we multiplied U by the total vegetated land area covered by each category of experiment[28,29].

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to K.J.v.G. (cjvangroenigen@nau.edu).

METHODS

Data collection. We extracted results for soil fluxes of CH_4 and N_2O, root biomass and soil water contents from atmospheric CO_2 enrichment studies, conducted in the field, in growth chambers or in glass houses. We used Google Scholar (Google Inc.) for an exhaustive search of journal articles published before January 2011, using as search terms either "elevated CO_2" or "CO_2 enrichment", and either "N_2O" and "soil", or "CH_4". Further papers were added from a comparable search using Web of Science. For a study to be included in our data set, the atmospheric CO_2 concentration for the ambient and elevated treatments had to be in the range 350–450 p.p.m.v. and 450–800 p.p.m.v., respectively. Means and sample sizes had to be reported for both ambient and elevated CO_2 treatments.

For each study, we noted experimental duration, plant species, N fertilization rates and the type of experimental facility. Estimates of standard deviation were tabulated when available, but were not required for inclusion in the analysis. We included studies involving experiments in pots (that is, any container with dimensions <1 m) or in the field, and studies on natural or planted vegetation. We only considered studies in which soil under both CO_2 treatments had the same treatment history. One study was discarded for this reason. Studies on soil water content and root biomass were only included if data on N_2O or CH_4 fluxes were available from the same site. When root biomass and soil water content were reported for multiple soil depths, we calculated the overall treatment effects across the entire soil profile. We included separate observations of increased CO_2 effects from a single ecosystem under different experimental treatments (that is, in multifactorial studies). Because wetlands are mostly anaerobic and therefore produce CH_4, whereas upland soils are mostly aerobic and oxidize CH_4, these two groups of ecosystems were considered in separate data sets. We also distinguished studies conducted in rice paddies, which like wetlands produce CH_4. Because the low number of studies on N_2O fluxes from rice paddies (1) and wetlands (3) did not warrant the construction of separate data sets, these studies were not included in our analysis.

We divided the studies into two categories of N availability based on N fertilization rates, that is, more or less than 30 kg N ha^{-1} yr^{-1}. This cut-off point was chosen because it is comparable to maximum atmospheric N depositions in the US and most of the EU[23]. We also distinguished between studies on natural or planted vegetation. Agricultural ecosystems were defined as grassland and cropland that received between 30 and 300 kg N ha^{-1} yr^{-1}. The upper cut-off point was based on reported average fertilization rates for croplands in the world's most intensively fertilized region (that is, East Asia, at 150 kg N ha^{-1} yr^{-1})[16], and the assumption that average fertilizer N use per hectare will be twofold higher in 2050[30].

Response metrics. We evaluated our data sets by using meta-analysis. As a metric for the response of GHG emissions to increased CO_2, we used the natural log of the response ratio[24]. This metric starts with an estimate of the relative change in GHG emissions between ambient and increased CO_2 treatments, and log-transforms it to improve its statistical behaviour.

$$\ln R = \ln(\mathrm{GHG_i}/\mathrm{GHG_a})$$

where GHG is the flux of either CH_4 or N_2O under increased (i) or ambient (a) conditions. We also used ln$R$ as a metric for CO_2 responses of root biomass and soil water contents. Fluxes of CH_4 from upland soils could not be analysed using this metric, because our data set included both sites with negative (that is, CH_4 uptake) and positive (CH_4 emissions) fluxes. For this reason, we also used the difference in annual emissions, expressed on an areal basis (U) as a metric:

$$U = (\mathrm{GHG_i} - \mathrm{GHG_a})$$

with GHG_i and GHG_a as before. All but one study on wetland soils found net CH_4 emissions under both ambient and increased CO_2 conditions (Supplementary Data 2). This one study, which reported that increased CO_2 turned wetland soils from a net sink of CH_4 into a net source, was therefore excluded when calculating ln$R$, but included when calculating U.

Several studies only measured N_2O and CH_4 fluxes during the growing season. In these cases, we assumed that the effect of increased CO_2 on annual fluxes occurred entirely during this period. When the length of the growing season was not explicitly indicated, we assumed a growing season of 150 days. When studies measured gas fluxes for multiple years, fluxes were averaged over time.

Weighting functions. We performed analyses using non-parametric weighting functions and generated confidence intervals (CIs) on weighted effects sizes using bootstrapping. Because effect size estimates and subsequent inferences in meta-analysis may depend on how individual studies are weighted[12], we used three different weighting functions. First, weighted by replication: $W_R = (n_a \times n_i)/(n_a + n_i)$, where n_a and n_i are the number of replicates under ambient and increased CO_2, respectively[25]. For pot studies, n equalled the number of replicate experimental facilities (that is, growth chambers, glass houses, and so on), rather than the number of pots per CO_2 treatment. Second, unweighted. Each observation was assigned an equal weight: $W_U = 1$. Third, weighted by the inverse of the pooled variance, the weighting function conventionally used in meta-analyses[26]: $W_V = 1/(\mathrm{var_a}/\mathrm{GHG_a}^2 + \mathrm{var_i}/\mathrm{GHG_i}^2)$, with GHG_a and GHG_i as before, and var_a and var_i as their respective variance.

When variance estimates were missing for a study, we calculated the average coefficient of variation (CV) within each data set, and then approximated the missing variance by multiplying the reported mean by the average CV and squaring the result.

When multiple effects were extracted from the same experimental site, we adjusted the weights defined above by the total number of observations from that site. This approach ensured that all experimental comparisons in multifactor studies could be included in the data set without dominating the overall effect size. For three experimental sites, multiple studies were done on the same GHG fluxes at different points in time. We adjusted the weights of observations from these studies by the total number of observations per site. Thus, the final weights used in the analyses were $w_{f,i} = W_{f,i}/n_c$, where n_c was the number of observations from the same site as the ith observation, and f was the index that referred to one of the three weighting functions defined above.

Mean effects sizes ($\overline{\ln R}$, $\overline{U}$) for different categories of studies were estimated as:

$$\overline{\ln R} = \sum_i \left(\ln R_i \times w_{f,i}\right) \Big/ \sum_i w_{f,i}$$

$$\overline{U} = \sum_i \left(U_i \times w_{f,i}\right) \Big/ \sum_i w_{f,i}$$

We used METAWIN 2.1[27] to generate these mean effect sizes and 95% bootstrapped CIs (4,999 iterations). Treatment effects were considered significant if the 95% CI did not overlap with 0. The results for the analyses on ln$R$ were back-transformed and reported as percentage change under increased CO_2 (that is, $100 \times (R - 1)$) to ease interpretation.

We tested whether ln$R$ for GHG emissions was correlated with ln$R$ for root biomass using the statistical package SPSS 19. Similarly, we tested whether ln$R$ for GHG emissions was correlated with experiment duration or the level of CO_2 enrichment. The effect of increased CO_2 on soil emissions of N_2O, but not CH_4, showed a weak positive correlation with experiment duration (Supplementary Figs 2 and 3). ln$R$ was not significantly correlated with the degree of CO_2 enrichment for either N_2O or CH_4 emissions (Supplementary Figs 4 and 5). This result is probably due to the large variation in treatment effects between studies, masking effects of the degree in CO_2 enrichment. Alternatively, the results may reflect that plant growth is a saturating function of CO_2 concentrations. Since experiments increased atmospheric CO_2 to a similar extent for all data sets (Supplementary Table 13), we did not normalize effect sizes for the level of CO_2 enrichment.

Results using the different weighting functions were qualitatively similar. However, the variance-based weighting function, W_v, yielded weights that varied over 1,000 times in magnitude (Supplementary Data 1 and 2). By assigning extreme importance to individual observations, average effect sizes were largely determined by a small number of studies. Because variance estimates are notoriously unreliable (especially given the small samples common in many of these studies), we favoured the use of the alternative weighting functions (which assigned less extreme weights). In this Letter, we provide results of the analyses on effect sizes that were weighted by replication; results for all weighting functions can be found in Supplementary Tables 2–8, 11 and 12.

Scaling of results. We scaled up the results from the experiments by multiplying them by the total land area covered by the particular type of habitat that was being summarized. In other words, we took the mean effects and confidence intervals for U calculated above and scaled them:

$$F = \overline{U} \times H$$

where F is expressed in Pg CO_2 equiv. yr^{-1}, and H is the amount of habitat in uplands, wetlands, or rice paddies (103.1, 5.7, and 1.3 million km^2, respectively[28,29]). Because N fertilization increases N_2O emissions[16,17] and enhances plant growth, we distinguished between upland agricultural ecosystems (that is, 19.0 million km^2 of fertilized grasslands and croplands[16], minus 1.3 million km^2 of rice paddies[28]) and ecosystems receiving little or no fertilizer (103.1 – 19.0 + 1.3 = 85.4 million km^2).

We estimated the contribution of winter N_2O emissions to total N_2O emissions from a recently published data set[16]. For agricultural soils and soils under natural vegetation, studies conducted over the growing season and lasting 100–200 days were compared to studies conducted over the entire year (that is, lasting >300 days). Because tropical and subtropical systems do not experience marked

growing seasons, we excluded studies from those regions. For agricultural soils, we only considered studies on grassland and cropland receiving 30–300 kg N ha^{-1} yr^{-1} (that is, the same restrictions that applied to our data sets 1 and 2 for the global extrapolation shown in Fig. 2). The difference in mean N_2O emissions between the two categories of study duration was assumed to be representative of N_2O emissions outside the growing season.

To estimate the CI for the combined effect of increased CO_2 on all six GHG fluxes shown in Fig. 2, we calculated the square root of the sum of the squared CIs. Because the original CIs were asymmetric, we did this separately for the upper and lower CIs. All studies on rice paddies were conducted on planted vegetation, experimental conditions resembling real-world conditions. When we combined our extrapolated data to calculate the overall CO_2 effect on CH_4 emissions, we therefore included all available data from rice paddies (Fig. 2, Supplementary Fig. 1). To compare the emissions of GHG with soil C sequestration under increased CO_2, we used results from the analyses weighted by replication and from unweighted analyses as reported in ref. 12, applying the same study selection criteria as for studies in our current data set. These results were expressed as a function of total land area, using the same approach that was used to scale up our results on GHG fluxes.

30. Tilman, D. *et al.* Forecasting agriculturally driven global environmental change. *Science* **292,** 281–284 (2001).