

# Increased soil emissions of potent greenhouse gases under increased atmospheric CO<sub>2</sub>

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Nature 475, 214–216 (14 July 2011) doi:10.1038/nature10176

## Abstract

Increasing concentrations of atmospheric carbon dioxide (CO<sub>2</sub>) can affect biotic and abiotic conditions in soil, such as microbial activity and water content<sup>1, 2</sup>. In turn, these changes might be expected to alter the production and consumption of the important greenhouse gases nitrous oxide (N<sub>2</sub>O) and methane (CH<sub>4</sub>) (refs 2, 3). However, studies on fluxes of N<sub>2</sub>O and CH<sub>4</sub> from soil under increased atmospheric CO<sub>2</sub> have not been quantitatively synthesized. Here we show, using meta-analysis, that increased CO<sub>2</sub> (ranging from 463 to 780 parts per million by volume) stimulates both N<sub>2</sub>O emissions from upland soils and CH<sub>4</sub> 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<sub>2</sub> concentrations<sup>4</sup>. Our results therefore suggest that the capacity of land ecosystems to slow climate warming has been overestimated.

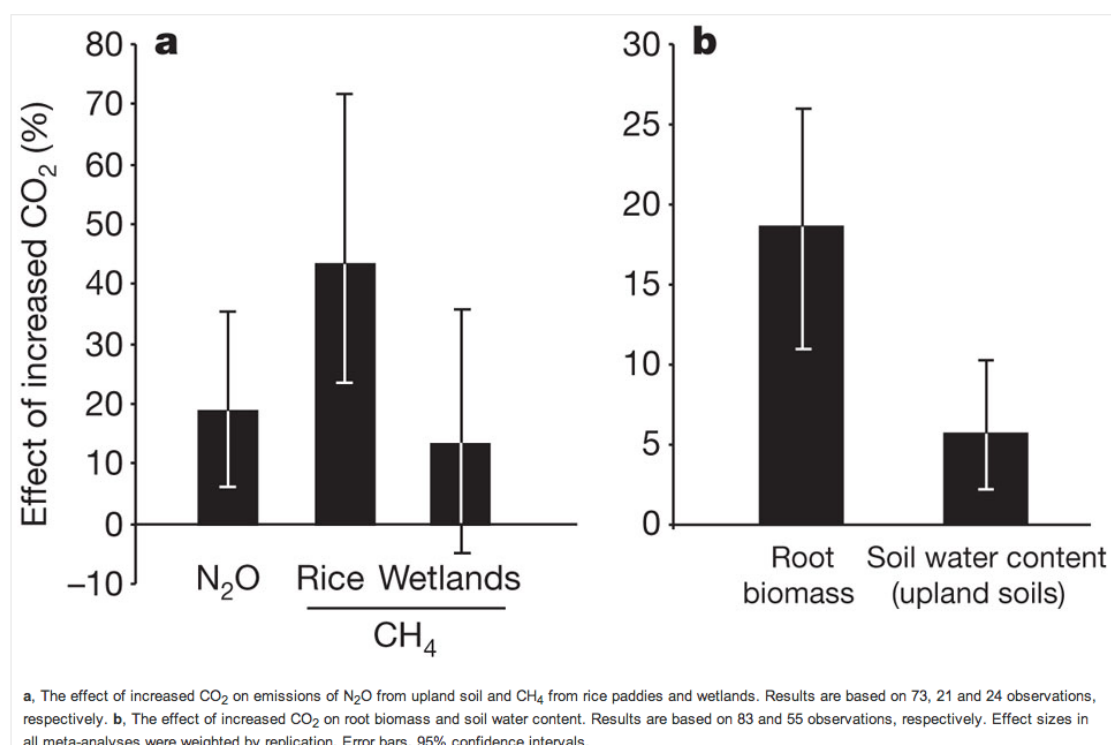
## Introduction

By burning fossil fuels, cutting down forests and changing land use in other ways, humans are rapidly increasing the amount of CO<sub>2</sub> in the atmosphere and warming the planet<sup>5</sup>. Plant growth is known to increase after an abrupt surge in CO<sub>2</sub> levels<sup>6</sup>. 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<sub>2</sub> and thereby slow climate change<sup>7</sup>. However, the radiative forcing of land ecosystems is not determined by their uptake and release of CO<sub>2</sub> alone; increased CO<sub>2</sub> can also alter soil emissions of N<sub>2</sub>O and CH<sub>4</sub> (ref. 2). Although both of these gases occur in far lower atmospheric concentrations than does CO<sub>2</sub>, their global warming potentials are much higher: 298 times higher for N<sub>2</sub>O and 25 times higher for CH<sub>4</sub> (ref. 5). Agricultural soils are the main source of human-induced N<sub>2</sub>O emissions<sup>8</sup>. Soils under natural vegetation produce roughly the same amount of N<sub>2</sub>O as all anthropogenic sources combined<sup>8</sup>. Wetlands, including rice paddies, contribute 32–53% to the global emissions of CH<sub>4</sub> (ref. 8). Upland soils, on the other hand, act as a sink for atmospheric CH<sub>4</sub> through oxidation by methanotrophic bacteria<sup>9</sup>. Thus, changes in N<sub>2</sub>O and CH<sub>4</sub> fluxes could greatly alter how terrestrial ecosystems influence climate<sup>10</sup>.

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<sub>2</sub> from individual experiments. A quantitative synthesis of results across multiple studies can overcome this problem. Therefore, we used meta-analysis<sup>11</sup> to summarize the effect of atmospheric CO<sub>2</sub> enrichment on fluxes of CH<sub>4</sub> and N<sub>2</sub>O 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<sub>2</sub> on possible drivers of altered CH<sub>4</sub> and N<sub>2</sub>O fluxes, using standing root biomass and soil water content from the studies in which the observations on N<sub>2</sub>O and CH<sub>4</sub> fluxes were collected (Supplementary Data 3 and 4). All observations were analysed using three different weighting functions (see Methods). As CH<sub>4</sub> and N<sub>2</sub>O emissions were not correlated with the concentration of CO<sub>2</sub> used for enrichment (Methods), we treat ‘increased CO<sub>2</sub>’ as a category.

Overall, increased concentrations of atmospheric CO<sub>2</sub> stimulated emissions of N<sub>2</sub>O 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<sub>2</sub> stimulated CH<sub>4</sub> emissions in wetlands by 13.2% (Fig. 1a, Supplementary Table 3). In rice paddies, increased CO<sub>2</sub> stimulated CH<sub>4</sub> emissions by 43.4% (Fig. 1a, Supplementary Table 4). In upland systems, increased CO<sub>2</sub> caused on average a small and insignificant net uptake of CH<sub>4</sub> (Supplementary Table 5).

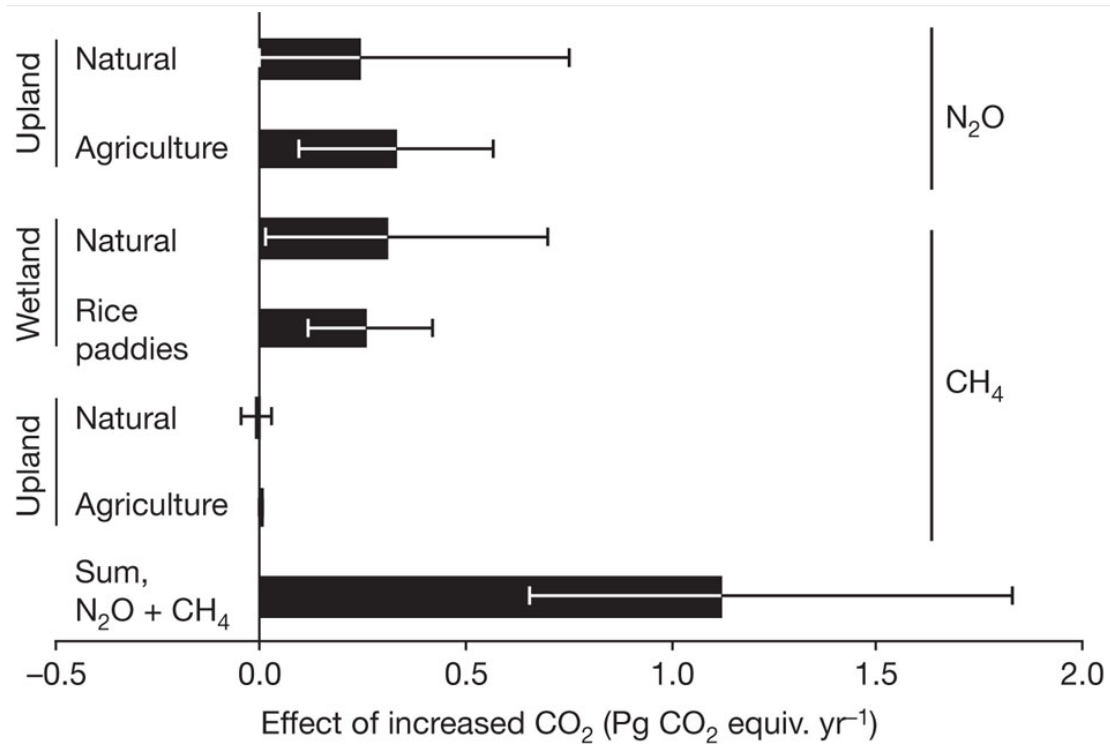
Figure 1: Results of a meta-analysis of the response of GHG emissions and their potential drivers to rising levels of atmospheric CO<sub>2</sub>.



To compare the relative importance of changed GHG fluxes in uplands, wetlands and rice paddies, we expressed the absolute effect of increased CO<sub>2</sub> on CH<sub>4</sub> and N<sub>2</sub>O 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<sub>2</sub> conditions correspond well to independent global syntheses of modern GHG fluxes (Supplementary Table 9), supporting our scaling approach.

The estimated stimulation by increased CO<sub>2</sub> of total soil N<sub>2</sub>O emissions corresponds to an additional source of 0.33 Pg CO<sub>2</sub> equivalents (equiv.) yr<sup>-1</sup> from agricultural ecosystems (1 Pg = 10<sup>15</sup> g), and of 0.24 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup> for all other upland ecosystems (Fig. 2). The CO<sub>2</sub>-stimulation of CH<sub>4</sub> emissions corresponds to an additional source of 0.25 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup> from rice paddies and of 0.31 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup> from natural wetlands. Our data indicate a small and non-significant effect of CO<sub>2</sub> on global CH<sub>4</sub> fluxes from upland soils for agricultural ecosystems (0.003 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup>) and for all other upland ecosystems (-0.011 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup>). The combined effect of increased CO<sub>2</sub> on emissions of these GHGs is 1.12 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup>.

Figure 2: The effect of rising atmospheric CO<sub>2</sub> on GHG emissions, expressed on the global scale.



For N<sub>2</sub>O fluxes, the results for natural and agricultural soils were based on 35 and 19 observations, respectively. For CH<sub>4</sub> 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.

Rising atmospheric CO<sub>2</sub> is expected to increase soil C storage in terrestrial ecosystems, which may contribute to the current residual C sink on land<sup>7</sup>. Meta-analysis of CO<sub>2</sub> enrichment experiments indicates that the sink is larger for ecosystems receiving fertilizer<sup>12</sup>. Scaled up by the total area of agricultural and non-fertilized ecosystems, these meta-analyses suggest that increased atmospheric CO<sub>2</sub> levels may increase the soil C sink by as much as 4.0 Pg CO<sub>2</sub> yr<sup>-1</sup>. Results presented here indicate that enhanced GHG emissions under increased CO<sub>2</sub> 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<sub>2</sub> concentration to 630 p.p.m.v. on average, a level expected for the second half of this century<sup>13</sup>. Biogeochemical models predict that at that time, the terrestrial C sink may be as much as 6.8 Pg CO<sub>2</sub> yr<sup>-1</sup> stronger than it is today<sup>4</sup> (when considering forcing by rising CO<sub>2</sub> alone). On the basis of our analysis, a CO<sub>2</sub>-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<sub>4</sub> in wetlands and rice paddies are typically small<sup>9</sup>; however, winter emissions of N<sub>2</sub>O during freeze-thaw cycles can contribute substantially to annual N<sub>2</sub>O fluxes<sup>14</sup>, and available data indicate that winter emissions of N<sub>2</sub>O are stimulated under increased CO<sub>2</sub> (ref. 15). A recently published data set<sup>16</sup> suggests that N<sub>2</sub>O 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<sub>2</sub> affects N<sub>2</sub>O emissions proportionately throughout the year, its effect on N<sub>2</sub>O emissions outside the growing season would therefore amount to 0.29 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup> from agricultural systems and 0.15 Pg CO<sub>2</sub> equiv. yr<sup>-1</sup> 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<sup>17</sup>. Because average CO<sub>2</sub> responses of N<sub>2</sub>O emissions were higher in studies receiving additional N (Supplementary Tables 2 and 6), the positive effect of CO<sub>2</sub> on N<sub>2</sub>O emissions may strengthen as ecosystems become enriched in N.

Last, CO<sub>2</sub> effects on N<sub>2</sub>O emissions showed a weak but significant correlation with experiment duration (Supplementary Fig. 2), suggesting that CO<sub>2</sub> effects on N<sub>2</sub>O emissions may increase over time.

Why do GHG emissions respond positively to rising levels of atmospheric CO<sub>2</sub>? Atmospheric CO<sub>2</sub> enrichment increased soil water contents for the studies contributing to our N<sub>2</sub>O 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<sup>18</sup>. Moreover, increased CO<sub>2</sub> has been shown to enhance soil biological activity across a broad range of ecosystems<sup>1, 2</sup>. Both responses promote soil anoxia, and thus stimulate denitrification<sup>19</sup> (anaerobic microbial respiration of nitrate), one of the major sources of N<sub>2</sub>O from soils<sup>3</sup>. Increased CO<sub>2</sub> 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<sup>20</sup>, and because new C enters mineral soil mainly through the root system, this increase in root biomass would stimulate denitrification rates—and N<sub>2</sub>O 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<sup>9</sup>, increased rates of soil C input with increased CO<sub>2</sub> can also stimulate CH<sub>4</sub> emissions. Indeed, the positive correlation between CH<sub>4</sub> emission rates and net ecosystem production in wetlands<sup>21</sup> suggests that plant productivity is a key process in the regulation of CH<sub>4</sub> emission from these

ecosystems. The response to increased CO<sub>2</sub> of CH<sub>4</sub> emissions from rice paddies and wetlands showed significant correlation with the CO<sub>2</sub> response of root biomass ( $r^2 = 0.17$ ,  $P = 0.02$ , Supplementary Fig. 6); this further suggests that increased CO<sub>2</sub> stimulates CH<sub>4</sub> 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<sub>4</sub> 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<sub>2</sub> amplifies climate change: by stimulating the release of N<sub>2</sub>O from terrestrial ecosystems, and by enhancing CH<sub>4</sub> release from wetlands and rice paddies. The meta-analytic approach used here, synthesizing results across 49 studies, shows that increased N<sub>2</sub>O and CH<sub>4</sub> 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<sub>2</sub> on the production by soil of trace gases like N<sub>2</sub>O and CH<sub>4</sub>.

## Methods

Main Methods References Acknowledgements Author information  
Supplementary information

### Data collection

We extracted results for soil fluxes of CH<sub>4</sub> and N<sub>2</sub>O, root biomass and soil water contents from atmospheric CO<sub>2</sub> 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<sub>2</sub>” or “CO<sub>2</sub> enrichment”, and either “N<sub>2</sub>O” and “soil”, or “CH<sub>4</sub>”. 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>O or CH<sub>4</sub> 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<sub>2</sub> effects from a single ecosystem under different experimental treatments (that is, in multifactorial studies). Because wetlands are mostly anaerobic and therefore produce CH<sub>4</sub>, whereas upland soils are mostly aerobic and oxidize CH<sub>4</sub>, these two groups of ecosystems were considered in separate data sets. We also distinguished studies conducted in rice paddies, which like wetlands produce CH<sub>4</sub>. Because the low number of studies on N<sub>2</sub>O 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<sup>-1</sup> yr<sup>-1</sup>. This cut-off point was chosen because it is comparable to maximum atmospheric N depositions in the US and most of the EU23. 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<sup>-1</sup> yr<sup>-1</sup>. 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<sup>-1</sup> yr<sup>-1</sup>)<sup>16</sup>, and the assumption that average fertilizer N use per hectare will be twofold higher in 2050<sup>30</sup>.

### **Response metrics**

We evaluated our data sets by using meta-analysis. As a metric for the response of GHG emissions to increased CO<sub>2</sub>, we used the natural log of the response ratio<sup>24</sup>. This metric starts with an estimate of the relative change in GHG emissions between ambient and increased CO<sub>2</sub> treatments, and log-transforms it to improve its statistical behaviour.

$$\ln R = \ln(\text{GHG}_i - \text{GHG}_a)$$

where GHG is the flux of either CH<sub>4</sub> or N<sub>2</sub>O under increased (i) or ambient (a) conditions. We also used lnR as a metric for CO<sub>2</sub> responses of root biomass and soil water contents. Fluxes of CH<sub>4</sub> from upland soils could not be analysed using this metric, because our data set included both sites with negative (that is, CH<sub>4</sub> uptake) and positive (CH<sub>4</sub> emissions) fluxes. For this reason, we also used the difference in annual emissions, expressed on an areal basis (U) as a metric:

$$U = (\text{GHG}_i - \text{GHG}_a)$$

with GHG<sub>i</sub> and GHG<sub>a</sub> as before. All but one study on wetland soils found net CH<sub>4</sub> emissions under both ambient and increased CO<sub>2</sub> conditions (Supplementary

Data 2). This one study, which reported that increased CO<sub>2</sub> turned wetland soils from a net sink of CH<sub>4</sub> into a net source, was therefore excluded when calculating lnR, but included when calculating U.

Several studies only measured N<sub>2</sub>O and CH<sub>4</sub> fluxes during the growing season. In these cases, we assumed that the effect of increased CO<sub>2</sub> 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<sup>12</sup>, we used three different weighting functions. First, weighted by replication:  $WR = (n_a \times n_i) / (n_a + n_i)$ , where  $n_a$  and  $n_i$  are the number of replicates under ambient and increased CO<sub>2</sub>, respectively<sup>25</sup>. 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<sub>2</sub> treatment. Second, unweighted. Each observation was assigned an equal weight:  $WU = 1$ . Third, weighted by the inverse of the pooled variance, the weighting function conventionally used in meta-analyses<sup>26</sup>:  $WV = 1 / (var_a / GHG_a^2 + var_i / GHG_i^2)$ , 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  $i$ th observation, and  $f$  was the index that referred to one of the three weighting functions defined above.



Mean effects sizes ( , ) for different categories of studies were estimated as:

We used METAWIN 2.127 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 lnR were back-transformed and reported as percentage change under increased CO<sub>2</sub> (that is,  $100 \times (R - 1)$ ) to ease interpretation.

We tested whether lnR for GHG emissions was correlated with lnR for root biomass using the statistical package SPSS 19. Similarly, we tested whether lnR for GHG emissions was correlated with experiment duration or the level of CO<sub>2</sub> enrichment. The effect of increased CO<sub>2</sub> on soil emissions of N<sub>2</sub>O, but not CH<sub>4</sub>, showed a weak positive correlation with experiment duration (Supplementary Figs 2 and 3). lnR was not significantly correlated with the degree of CO<sub>2</sub> enrichment for either N<sub>2</sub>O or CH<sub>4</sub> 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<sub>2</sub> enrichment. Alternatively, the results may reflect that plant growth is a saturating function of CO<sub>2</sub> concentrations. Since experiments increased atmospheric CO<sub>2</sub> to a similar extent for all data sets (Supplementary Table 13), we did not normalize effect sizes for the level of CO<sub>2</sub> 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:

where  $F$  is expressed in  $\text{Pg CO}_2 \text{ equiv. yr}^{-1}$ , and  $H$  is the amount of habitat in uplands, wetlands, or rice paddies (103.1, 5.7, and 1.3 million  $\text{km}^2$ , respectively<sup>28, 29</sup>). Because N fertilization increases  $\text{N}_2\text{O}$  emissions<sup>16, 17</sup> and enhances plant growth, we distinguished between upland agricultural ecosystems (that is, 19.0 million  $\text{km}^2$  of fertilized grasslands and croplands<sup>16</sup>, minus 1.3 million  $\text{km}^2$  of rice paddies<sup>28</sup>) and ecosystems receiving little or no fertilizer ( $103.1 - 19.0 + 1.3 = 85.4$  million  $\text{km}^2$ ).

We estimated the contribution of winter  $\text{N}_2\text{O}$  emissions to total  $\text{N}_2\text{O}$  emissions from a recently published data set<sup>16</sup>. 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  $\text{kg N ha}^{-1} \text{ yr}^{-1}$  (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  $\text{N}_2\text{O}$  emissions between the two categories of study duration was assumed to be representative of  $\text{N}_2\text{O}$  emissions outside the growing season.

To estimate the CI for the combined effect of increased  $\text{CO}_2$  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  $\text{CO}_2$  effect on  $\text{CH}_4$  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  $\text{CO}_2$ , 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.

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## Acknowledgements

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We thank S. A. Prior, G. B. Runion, F. Hagedorn, A. Niboyet, J. C. Blankinship, W. Cheng, T. Kanerva, R. S. Nowak, S. F. Zitzer, F. A. Dijkstra and J. P. Megonigal for sharing their data. Financial support for this study was provided by DOE-NICCR, NSF (DEB-0949460) and the Irish Research Council for Science, Engineering and Technology, co-funded by Marie Curie Actions under FP7.

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## **Contributions**

K.J.v.G. and B.A.H. designed the investigation. K.J.v.G. extracted the data from the literature and constructed the database. K.J.v.G. and C.W.O. performed the statistical analyses. All authors contributed to writing the paper.

## **Competing financial interests**

The authors declare no competing financial interests.

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