

# Increased soil release of greenhouse gases shrinks terrestrial carbon uptake enhancement under warming

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## Abstract

Warming can accelerate the decomposition of soil organic matter and stimulate the release of soil greenhouse gases (GHGs), but to what extent soil release of methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) may contribute to soil C loss for driving climate change under warming remains unresolved. By synthesizing 1,845 measurements from 164 peer-reviewed publications, we show that around 1.5°C (1.16–2.01°C) of experimental warming significantly stimulates soil respiration by 12.9%, N<sub>2</sub>O emissions by 35.2%, CH<sub>4</sub> emissions by 23.4% from rice paddies, and by 37.5% from natural wetlands. Rising temperature increases CH<sub>4</sub> uptake of upland soils by 13.8%. Warming-enhanced emission of soil CH<sub>4</sub> and N<sub>2</sub>O corresponds to an overall source strength of 1.19, 1.84, and 3.12 Pg CO<sub>2</sub>-equivalent/year under 1°C, 1.5°C, and 2°C warming scenarios, respectively, interacting with soil C loss of 1.60 Pg CO<sub>2</sub>/year in terms of contribution to climate change. The warming-induced rise in soil CH<sub>4</sub> and N<sub>2</sub>O emissions (1.84 Pg CO<sub>2</sub>-equivalent/year) could reduce mitigation potential of terrestrial net ecosystem production by 8.3% (NEP, 22.25 Pg CO<sub>2</sub>/year) under warming. Soil respiration and CH<sub>4</sub> release are intensified following the mean warming threshold of 1.5°C scenario, as compared to soil CH<sub>4</sub> uptake and N<sub>2</sub>O release with a reduced and less positive response, respectively. Soil C loss increases to a larger extent under soil warming than under canopy air warming. Warming-raised emission of soil GHG increases with the intensity of temperature rise but decreases with the extension of experimental duration. This synthesis takes the lead to quantify the ecosystem C and N cycling in response to warming and advances our capacity to predict terrestrial feedback to climate change under projected warming scenarios.

## KEYWORDS

climate change, greenhouse gas, meta-analysis, soil C and N pool, warming

## 1 | INTRODUCTION

Temperature is a key factor regulating carbon (C) and nitrogen (N) biogeochemical processes in terrestrial ecosystems (Van Gestel

et al., 2018; Viogt et al., 2017). It has been suggested that, the projected warming intensity between 1.1°C and 6.4°C over the next 100 years would shape the C balance of terrestrial ecosystems by altering biogeochemical processes such as soil organic C decomposition and microbial activities driving soil C and N cycling (Crowther et al., 2016; IPCC, 2013). Indeed, warming has been individually

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documented to either accelerate the decomposition of soil organic matter or stimulate the release of soil greenhouse gases (GHGs). However, a full budget of soil GHG fluxes relative to the changes in terrestrial carbon pools under warming remains poorly understood (Carter et al., 2011; Melillo et al., 2017; Yue et al., 2017). In recent decades, a growing number of individual studies spanning a variety of environment-specific biomes have examined the response of soil C storage or biogenic GHG fluxes to warming, which would allow us to use the meta-analysis to assess warming-induced changes in soil C storage and GHG fluxes (Arora et al., 2013; Crowther et al., 2015; Viogt et al., 2017; Yvon-Durocher et al., 2014). In particular, an insight into how rising temperature might influence the budget of GHG exchange between terrestrial ecosystems and the atmosphere would help to incorporate these potential effects into predictive biogeochemical models (Van Gestel et al., 2018).

Recently, several studies have concentrated on the effects of experimental warming on soil C pools by either meta-analysis or modeling approaches, showing a general net loss of soil C under warming scenarios (Crowther et al., 2016, 2018; Van Gestel et al., 2018; Yue et al., 2017). However, these synthesis studies are limited in scope and have not attempted to quantify the changes in soil C pools with a linkage to GHG fluxes. Besides CO<sub>2</sub>, methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) are another two potent long-lived atmospheric GHGs. One of the major sources of atmospheric N<sub>2</sub>O is ascribed to upland soils, where N<sub>2</sub>O is produced mainly through the microbial processes of nitrification and denitrification (Liu et al., 2017). Wetlands, including rice paddies, constitute the main source of atmospheric CH<sub>4</sub>, while upland soils can act as a sink for atmospheric CH<sub>4</sub>, depending on the combined performance of methanogens and methanotrophs (Van Groenigen, Osenberg, & Hungate, 2011). Given that rising temperature has been shown to enhance soil C losses and affect soil biotic and abiotic factors regulating soil CH<sub>4</sub> and N<sub>2</sub>O fluxes (Crowther et al., 2016; Frey, Lee, Melillo, & Six, 2013; Viogt et al., 2017; Yvon-Durocher et al., 2014), to what extent soil release of CH<sub>4</sub> and N<sub>2</sub>O may contribute to soil C loss to shrink terrestrial C uptake under projected warming thresholds needs to be quantitatively synthesized globally.

To date, the knowledge gap still exists on warming as a vital role in driving climate change, especially on how terrestrial C and N cycling responds to warming and the subsequent feedback to climate change (Yin, Chen, & Liu, 2012; Yvon-Durocher et al., 2014). Quantifying soil C losses in response to experimental warming has been of great concern worldwide (Crowther et al., 2016; Davidson & Janssens, 2006), but there is still a lack of robust accounting of soil CH<sub>4</sub> and N<sub>2</sub>O fluxes in response to warming, which would highly limit our ability to predict terrestrial feedback to climate (Yue et al., 2017). Furthermore, limited studies have integrated the changes in terrestrial C and N pools to better associate them with biogenic GHG flux response to warming (Liu et al., 2018). Although experimental studies can directly warm the soil or canopy air within an ecosystem, the practical difference in soil GHG flux responses to increased temperature between soil and canopy air warming experiments remains to be examined (Crowther et al., 2016). It is well documented that soil CH<sub>4</sub> and N<sub>2</sub>O fluxes are greatly affected by

agricultural practices, such as irrigation regime and fertilizer application (Liu et al., 2017; Wang et al., 2018), while no synthesis studies have examined the difference in their responses to warming between croplands and non-agricultural ecosystems (e.g., rice paddy vs. natural wetlands, fertilized cropping uplands vs. unfertilized uplands). Poor understanding of how agricultural practices might influence GHG response to warming will limit our access to predict terrestrial feedback to climate change.

To this end, we compiled global available literature-derived experimental measurements (Tables S1–S3) using mixed-effect meta-analysis response metrics. The objectives of this study were to generalize the experimental warming-induced changes in biogenic GHG fluxes and examine the difference in their responses to soil and canopy air warming. We also aimed to explore how the potential soil biotic and abiotic drivers regulate the response of soil GHG fluxes to warming. We hypothesized that experimental warming would stimulate soil release of GHGs to the atmosphere, reduce soil C and N storage, thereby shrinking soil C sequestration due to plant-derived soil C input under warming. We also predicted that this positive response of soil GHGs would depend on warming intensity, experimental duration, and habitat-specific environmental conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Data extraction

We launched a detailed review of the literature published in peer-reviewed journals through the year 2018–2019 (cutoff date on August 30, 2019). We extracted original experimental results from publications enclosing individual measurements with soil GHG flux data and also the data on soil C and N fractions in cases that they were simultaneously available (Tables S1 and S2). All selected data were extracted from the Web of Science and Google Scholar, papers published in the China Knowledge Resource Integrated Database with English abstract, and also the publication sources by gathering and reevaluating the older literature cited in the prior review (Yue et al., 2017). A combination of searching terms ["warming" OR "elevated temperature" OR "rising temperature" OR "increased temperature", AND "soil", AND "CO<sub>2</sub>" OR "soil respiration" OR "CH<sub>4</sub>" OR "N<sub>2</sub>O"] was used for GHG data extraction. Search terms for plant and soil C pools and the data select criteria were similar to those used in a recent meta-analysis (Yue et al., 2017).

### 2.2 | Inclusion criteria

We adhered to the following criteria to avoid publication bias in GHG data selection. The ambient and warmed treatment within a given study should have the same warming duration and treatment history. Different treatment durations within the same study were considered as individual observations in data collection to allow for duration sensitivity analysis. Besides field or outdoor pot

experiments conducted using Open Top Chamber, infrared heater, heating cable, and inflective curtain, the controlled-environment studies at community level in large-scale Growth Chamber, and Greenhouse with vegetation growth were also included in this analysis to fully quantitatively understand the effect of warming on terrestrial C and N cycling. Aside from continuous warming, long-term intermittent warming studies were also included in this analysis. The warming studies through shift in geographical latitude or location to achieve increased temperature were removed from this analysis to avoid noise caused by site bias. In order to be more representative of the real world, laboratory incubation studies were excluded from this analysis. Studies with no replication or no reported number of replications and grouping categories with fewer than two data pairs were excluded from the analysis. Experiments in which  $N_2$ -fixing species dominate were excluded from the main analysis to guarantee the sole influence of warming on soil C and N pools. For data from natural habitats, the occasional field GHG flux measurements without covering the whole experimental period were excluded. For data from croplands, the consecutive measurement period covers at least one whole cropping season and the within or multiyear data with different cropping seasons were extrapolated or averaged to obtain annual mean. Seasonal GHG measurement data from natural and cropping upland ecosystems were assumed to be applicable and extrapolated to obtain annual-based rates in current analysis. For data extrapolation from rice paddies, the seasonal cumulative  $CH_4$  emissions from rice growing seasons were assumed to be representative of the annual total due to the general negligible source or even sink role of atmospheric  $CH_4$  for rice-based upland cropping rotation systems.

When soil parameters were reported with multiple soil depths, we chose to include the data measured in 0–20 cm topsoil. For multi-factor studies, we only considered the separate paired observations under warming alone or both ambient and increased treatments combined with the other similar climate change factors to minimize data bias. For upland soils usually acting as a sink of atmospheric  $CH_4$ , several positive data on  $CH_4$  fluxes (referring to  $CH_4$  source) in forest soils were finally discarded from the dataset to strengthen our analysis. When the data were presented in figures, we extracted

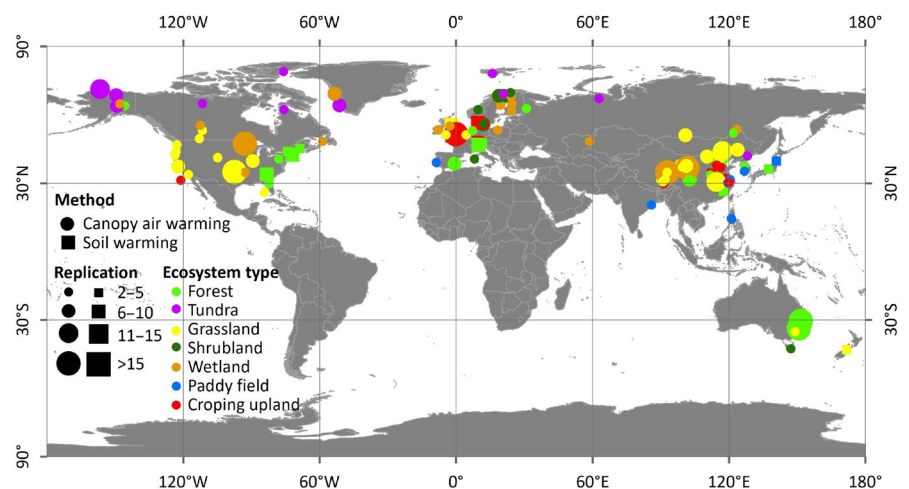
means and standard errors using GraphClick. The final database consisted of 1,845 paired measurements derived from 164 publications, of which 48 simultaneous observations of  $CH_4$  and  $N_2O$  fluxes from 17 studies were available in the database (Table S1). The experimental locations were mostly clustered in Asia, Europe, and North America, with only several studies scattered in South Hemisphere, and in Northern Hemisphere at high latitudes and tropics (Figure 1).

### 2.3 | Data compilation and analyses

Data were first subjected to a standardization process to allow for comparisons. We calculated the balanced means of all investigated paired values with the residual maximum likelihood procedure using GENSTAT release 4.2 to minimize the heterogeneity resulting from missing values and unequal number of observations among reviewed literature (Payne, 2000). In further data compiling prior to analysis, we divided the soils into four land-use types as wetland, rice paddy, cropping upland, and non-cropping upland (including natural grassland, tundra, shrubland, and forest) based on current dataset. We also distinguished the upland data by two levels of N availability with or without N fertilizer input. In addition, we examined the response of terrestrial C and N cycling to rising temperature partitioned by ecosystem warming manipulative options (soil or canopy air warming) for their different effects on soil processes.

The means of biogenic GHG fluxes, soil moisture, and plant and soil C and N fractions from treatment ( $X_e$ ) and control ( $X_c$ ) groups were used to calculate effect size in the form of natural log-transformed response ratio ( $\ln R$ ). For upland soils overwhelmingly acting as the sink of  $CH_4$  for both the treatment and control in our dataset, the absolute values of negative  $CH_4$  fluxes (indicating soil uptake of  $CH_4$ ) were adopted for effect size calculation to avoid making  $\ln R$  problematic during meta-analysis. While three paired observations showed a shift from source to sink of atmospheric  $CH_4$  following warming treatment, which finally led to their exclusion from this analysis to allow for solid performance of meta-analysis procedures. Here we calculated the treatment effect of warming on soil C and N pools as the absolute changes in soil C and N contents (in g C/kg soil

**FIGURE 1** Location of 189 data measurements used in our analysis. Square and circular points indicate studies under soil and canopy air warming, respectively. The point sizes represent the number of replications, and different colors denote ecosystem types [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



or g N/kg soil), instead of relative changes to achieve biogeochemical significance (Hungate et al., 2009). The standard deviations of both treatment and control were included as a measure of variance:

$$\ln R = \ln(X_e/X_a), \quad (1)$$

where  $X_e$  and  $X_a$  are means in the warmed treatment and control groups. Its pooled variance ( $v$ ) is estimated as:

$$v = \frac{s_e^2}{n_e X_e^2} + \frac{s_a^2}{n_a X_a^2}, \quad (2)$$

where  $n_e$  and  $n_a$  are the sample sizes for the treatment and control groups, respectively;  $s_e$  and  $s_a$  are the standard deviations for the treatment and control groups, respectively.

In this study, we conducted a weighted meta-analysis using the metric of  $\ln R$ , where the mean response ratio ( $RR_{++}$ ) is calculated from individual  $\ln R$  of each paired comparison between control and treatment groups with the weight of each  $\ln R$  using a categorical random effect model. Groups with less than two paired measurements were excluded from the study to meet the criteria for rigorous meta-analysis. Allowing for the intrinsic relevance across all the variables under warming, the overall mean effect size and 95% confidence interval (CI) of each grouping category generated by bootstrapping (9,999 iterations) were calculated with the mixed-effect model, where treatment effects were considered significant if the 95% CI did not overlap with the line  $\ln R = 0$ .

In addition to the meta-analysis procedure, one-way ANOVA was performed to test the differences in all target variables between ambient and warmed treatments. The ANCOVA was used to test the differences in sensitivity of GHG response to warming between different terrestrial C and N pools. Linear regressions were also used to examine the dependence of warming-induced changes in biogenic GHG fluxes on potential driving factors. All statistical analyses were carried out using JMP version 7.0 (SAS Institute, USA, 2007) and R (R Development Core Team, 2016).

## 2.4 | Estimation of warming-enhanced climatic impacts of GHGs

Global warming potential (GWP) has been developed to evaluate the contribution of GHG emissions from a given ecosystem to climate change. Recently, Neubauer and Megonigal (2015) have moved on to improve the metrics of GWP evaluation based on sustained-flux global warming potential (SGWP) for gas emission and sustained-flux global cooling potential (SGCP) for gas uptake. In this synthesis, we quantified the combined radiative forcing of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  across all habitats by integrating SGWP and SGCP over a 100 year time horizon using the following equations (Neubauer & Megonigal, 2015):

$$\begin{aligned} \text{Non-upland: climatic impact } (\text{CH}_4 + \text{N}_2\text{O}) \\ = \text{SGWP} \times \text{N}_2\text{O} + \text{SGWP} \times \text{CH}_4 \text{ (source),} \end{aligned} \quad (3)$$

$$\begin{aligned} \text{Upland: climatic impact } (\text{CH}_4 + \text{N}_2\text{O}) \\ = \text{SGWP} \times \text{N}_2\text{O} - \text{SGCP} \times \text{CH}_4 \text{ (sink),} \end{aligned} \quad (4)$$

where climatic impact here refers to the combined radiative forcing of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  expressed as  $\text{CO}_2$ -equivalent (kg  $\text{CO}_2$ -eq/ha); SGWP and SGCP are the sustained-flux global warming and sustained-flux global cooling potentials of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  on the 100 year time horizon (respective potential values are 45 for  $\text{CH}_4$  emission or uptake and 270 for  $\text{N}_2\text{O}$  emission; Neubauer & Megonigal, 2019).

## 2.5 | Scaling-up estimation

Based on the ecosystem-level absolute mean positive or negative changes in annual GHG fluxes and the differences in soil organic C and N pools under warming, both expressed as area-scaled metrics ( $U$ -value), we scaled up the results from this analysis by multiplying them for target variables with the corresponding total habitat areas currently summarized (Crowther et al., 2016; Liu et al., 2018; Van Groenigen et al., 2011):

$$T = \bar{U} \times A, \quad (5)$$

where  $T$  is the net warming-induced increase or decrease in strength of carbon sink expressed as Pg  $\text{CO}_2$ -eq/year, and  $A$  is the total habitat areas for wetlands, rice paddies, and uplands (equivalent to 5.7, 1.3, and 103.1 M  $\text{km}^2$ , respectively; Aselmann & Crutzen, 1989; World Resources Institute, 2003). For  $\text{CO}_2$  fluxes, we determined the net ecosystem production (NEP) under warming, referring to the difference between NPP and soil heterotrophic respiration ( $R_H$ ). The data used for estimation of the changes in GHGs and NEP under warming were only based on those at ecosystem levels. The significant positive effect on  $\text{CH}_4$  uptake following warming across upland soils was considered as potential removal of atmospheric  $\text{CH}_4$  in current estimation. For upland soils as hotspots of  $\text{N}_2\text{O}$ , we further scaled up  $\text{N}_2\text{O}$  fluxes by dividing into fertilized upland soils (i.e. 19.0 M  $\text{km}^2$  of fertilized grasslands and croplands, Stehfest & Bouwman, 2006; minus 1.3 M  $\text{km}^2$  of rice paddies, Aselmann & Crutzen, 1989) and non-fertilized upland soils (10 3.1 – 19.0 + 1.3 = 85.4 M  $\text{km}^2$ ) receiving no extra fertilizer N in addition to atmospheric N input from deposition. Meanwhile, given the mean warming threshold of 1.5°C in this analysis, we used linear regression models to predict the changes in soil GHG fluxes under projected warming scenarios for a given individual GHG component.

For paired observation data, we determined the overall warming-induced mean annual soil organic carbon (SOC) and total nitrogen (TN) change rates (MU, g C/N  $\text{kg}^{-1} \text{year}^{-1}$ ) by plotting them versus the duration of experiments, directly linking them to changes in GHG fluxes between the controls and treatments under warming, which were defined and calculated using the following equation (Hungate et al., 2009; Tian et al., 2015):

$$\text{MU} = \frac{\text{SOC}_e/\text{TN}_e - \text{SOC}_a/\text{TN}_a}{t}, \quad (6)$$

where the subscripts  $e$  and  $a$  refer to data from the treatments under warming and ambient controls, respectively. Positive values indicate increased SOC and TN change rates under warming; Negative values indicate declines of those following warming treatment. Then, the warming-induced net annual soil C and N loss potential was further estimated by the following equation (Hungate et al., 2009; Shang et al., 2011; Tian et al., 2006):

$$\text{SOC}_s/\text{TN}_s = \sum_{i=1}^n S_i \times \text{MU} \times \text{BD} \times H \times 0.1, \quad (7)$$

where  $S_i$  is the habitat area involved in this study corresponding to the given source area for GHG fluxes (i.e., wetland, rice paddy, and upland); MU is the same as defined above,  $\text{SOC}_s/\text{TN}_s$  is the C/N loss potential (t C/N/year); BD is the soil bulk density ( $\text{g}/\text{cm}^3$ ; an average value of  $1.25 \text{ g}/\text{cm}^3$  was used here); and  $H$  is the thickness of the soil layer (cm; a general investigated soil depth of 20 cm was used here to reduce uncertainties).

## 2.6 | Sensitivity analyses

We performed sensitivity analyses to test the robustness of our meta-analysis on the response of terrestrial C and N cycling to warming to reduce uncertainties (Liu et al., 2017). We removed the outlier studies to perform the same meta-analysis procedure

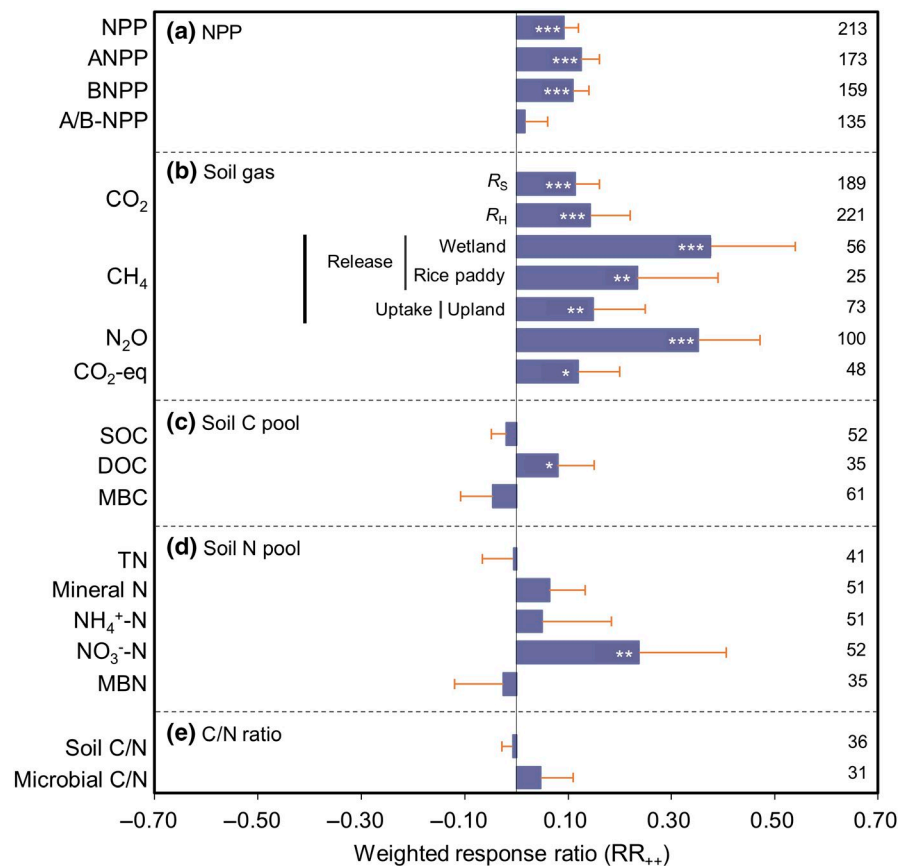
and compared the results with those of the original meta-analysis. Besides, we conducted the same meta-analysis procedure by excluding datasets without variances reported, and then repeated the comparisons with the results of the original meta-analysis. For both bias examinations, we obtained similar mean effect sizes with overlapped corresponding bias-corrected 95% bootstrap confidences (CI) between the complete and reduced database, leading to all data confidently included in the analysis. The publication bias was assessed using Egger's regression model combined with the trim and fill method that calculates the number of missing studies related to publication bias and estimates the effect size and standard error. The results were adjusted by adding the missing studies to the analysis (Table S6).

## 3 | RESULTS

### 3.1 | Plant C pools

When pooled the data across all studies, warming enhanced removal of atmospheric  $\text{CO}_2$  by terrestrial biosphere, leading to a significant increase in plant C pool [NPP, 9%; 95% CI: 6%–12%], with comparable extents between aboveground C (aboveground NPP [ANPP], 12%; CI: 10%–16%) and belowground C (belowground NPP [BNPP], 11%; CI: 8%–14%) components (Figure 2a). A small increase in the ratio of ANPP/BNPP (A/B-NPP ratio) under warming revealed that

**FIGURE 2** Plant C pools (a), soil greenhouse gases (b), soil C (c) and N (d) pools, and their C/N ratios (e) in response to experimental warming by pooling available data under soil warming and canopy air warming conditions.  $R_S$  and  $R_H$  represent soil respiration with vegetation growth and soil heterotrophic respiration, respectively.  $\text{CO}_2$ -eq, the climatic impact of  $\text{CH}_4$  and  $\text{N}_2\text{O}$  referring to their combined radiative forcing over the 100 year time horizon; DOC, soil dissolved organic C content; MBC, soil microbial biomass C content; MBN, soil microbial biomass N content; Mineral N, soil  $(\text{NH}_4^+ + \text{NO}_3^-)$ -N content; SOC, soil organic C content; TN, soil total N content. The numbers inserted aside the vertical axis indicate number of observations. Error bars represent 95% confidence intervals. Asterisks refer to significant differences from zero representing the ambient controls (\* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



the positive temperature response of aboveground C was slightly stronger than that of belowground C (Figure 2a). This positive effect of warming on plant C components was enhanced in non-fertilized soils, in natural wetlands, and under canopy air-warmed conditions (Tables S3–S5).

### 3.2 | Soil GHG fluxes

Across the studies warmed through soil and canopy air, the experimental temperature for the ambient and warmed treatments averaged 8.75°C and 10.25°C, respectively, referring to an overall average of 1.5°C of warming scenario. In warmed treatments relative to the ambient control, on average, soil CO<sub>2</sub> fluxes were significantly greater (13%, CI: 10%–15%) across all habitats, and soil CH<sub>4</sub> fluxes were 23% (CI: 5%–39%) greater in rice paddies and 37% (CI: 21%–54%) greater in natural wetlands (Figure 2b). These positive responses of soil CO<sub>2</sub> and CH<sub>4</sub> fluxes were more pronounced under soil-warmed conditions and in natural wetlands (Tables S4 and S5; Figure 3a). By pooling all data from soil and canopy air warming experiments, 1.5°C of warming significantly increased upland soil uptake of CH<sub>4</sub> by 15% (CI: 3%–26%, Figure 2b). This positive response of upland soil CH<sub>4</sub> uptake was enhanced under soil warming conditions as compared to the use of canopy air warming methods (Figure 3a).

Similarly, soil N<sub>2</sub>O fluxes were significantly higher (35%, CI: 18%–53%) in warmed soils, and this positive effect was amplified under canopy air-warmed conditions and in non-fertilized soils (Tables S4 and S5). Overall, a significant enhancement was found for the combined climatic impact of CH<sub>4</sub> and N<sub>2</sub>O in studies where CH<sub>4</sub> and N<sub>2</sub>O fluxes' response to warming was simultaneously examined (Figure 2b).

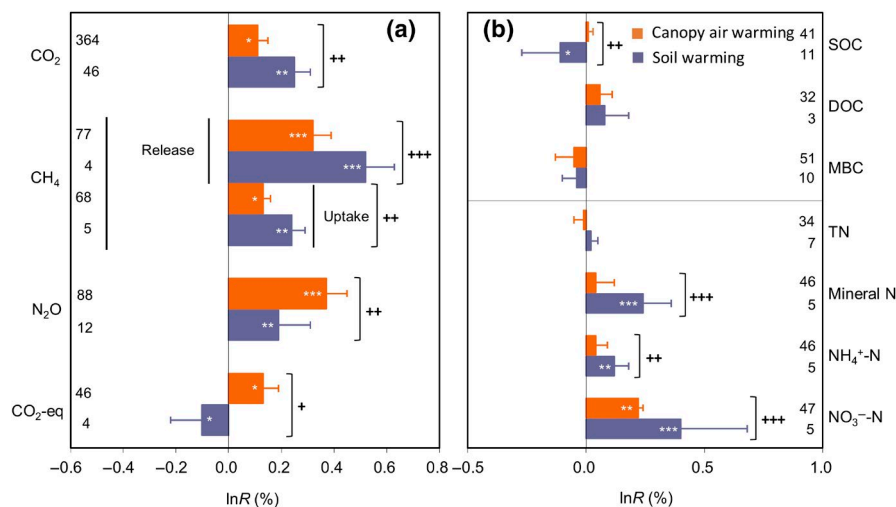
### 3.3 | Soil C and N pools

Relative to the ambient control, soil organic C pool was slightly lower (2%, CI: –5% to 3%) under warming when averaged across all studies, and this minor negative response was dominated by soil-warming experiments (Table S5; Figure 2c). For soil labile C components, in contrast, soil dissolved organic C (DOC, 8%; CI: 1%–16%) was higher while microbial biomass C (MBC, –5%; CI: –11% to 1%) was lower in warmed soils, particularly in fertilized soils (Table S3; Figure 2c).

Similar to soil organic C pool, soil total N loss (TN, –1%; CI: –7% to 4%) only showed a small rise under warming (Figure 2d). Soil mineral N (6%, CI: –6% to 21%) showed a positive response to warming, largely contributed by a significant increase in nitrate (NO<sub>3</sub><sup>–</sup>-N, 24%; CI: 10%–41%) relative to a minor increase in ammonium (NH<sub>4</sub><sup>+</sup>-N, 5%; CI: –7% to 18%). Microbial biomass N, as another essential indicator of labile N fractions in soils, had a decrease by 3% (CI: –12% to 7%) under warming, occurring only in soils with low N availability (Table S3; Figure 2d). Soil C/N ratio showed a slight decrease by 1% (CI: –3% to 1%), while an increase by 5% occurred for microbial C/N ratio under warming (CI: –3% to 11%, Figure 2e), particularly in fertilized agricultural soils with a more sensitive response (Table S3).

### 3.4 | Scaling-up of results

The linear temperature response of GHG fluxes allowed us to adopt similar scaling-up approach to integrate results of this meta-analysis into global context. We extrapolated the warming-induced change rates in area-based GHG fluxes and soil C and N pools under around 1.5°C (1.16°C–2.01°C across different C and N components at ecosystem levels) of warming in this meta-analysis to global scale using Equations (5–7) by their respective total habitat areas (Table 1;



**FIGURE 3** Changes in soil greenhouse gases (a) and soil C and N pools (b) under soil warming and canopy air warming. Related abbreviations of target variables are defined as in Figure 1. The numbers inserted aside the vertical axis indicate the number of observations. Error bars represent 95% confidence intervals for a given sub-group mean. Asterisks within each column refer to significant differences from zero representing the ambient controls (\**p* < .05; \*\**p* < .01; \*\*\**p* < .001), and plus signs between every two columns indicate significant differences between two heating ways (\**p* < .05; \*\**p* < .01; \*\*\**p* < .001) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 1** Summary of estimated results of greenhouse gas source strengths and soil C and N losses in response to experimental warming

C or N variable	Habitat	No. of observations	Area (M km <sup>2</sup> )	Estimate (95% CI)
Soil $R_s$ (Pg CO <sub>2</sub> /year)	All	182	110.1	61.54 (42.28, 80.92)
Soil $R_H$ (Pg CO <sub>2</sub> /year)	All	217	110.1	29.62 (20.59, 38.75)
NPP (Pg CO <sub>2</sub> /year)	All	167	110.1	51.87 (28.01, 75.82)
NEP (Pg CO <sub>2</sub> /year)	All	—	110.1	22.25
Soil CH <sub>4</sub> flux (Pg CO <sub>2</sub> -eq/year)	All	147	110.1	1.12 (0.82, 1.36)
	Wetland	56	5.7	1.86 (1.05, 2.67)
	Rice paddy	16	1.3	0.15 (0.06, 0.18)
	Upland <sup>a</sup>	75	103.1	0.89 (0.43, 1.36)
Soil N <sub>2</sub> O flux (Pg CO <sub>2</sub> -eq/year)	All	89	110.1	0.72 (0.31, 1.52)
	Wetland	18	5.7	0.18 (0.12, 0.79)
	Rice paddy	6	1.3	0.01 (-0.02, 0.06)
	Fertilized upland soils	31	17.7	0.28 (0.12, 0.45)
	Non-fertilized upland soils	34	85.4	0.25 (0.11, 0.59)
SOC pool (Pg CO <sub>2</sub> /year)	All	46	110.1	1.60 (-0.18, 4.23)
Soil N pool (Pg N/year)	All	35	110.1	0.06 (-0.01, 0.11)

Note: The CO<sub>2</sub>-eq conversion factors (mass basis) used here are 45 for CH<sub>4</sub> emission or uptake and 270 for N<sub>2</sub>O over the time horizon of 100 years (Neubauer & Magonigal, 2015).

<sup>a</sup>The increase in uptake of CH<sub>4</sub> for upland soils under warming was expressed as the decrease in the source of CH<sub>4</sub> emissions in this estimation.

**FIGURE 4** A complete conceptual diagram illustrating the response and feedback of terrestrial carbon and nitrogen cycling to warming. ANPP, above-ground NPP; BNPP, below-ground NPP; DOC, soil dissolved organic C; MBC, microbial biomass C; MBN, microbial biomass N; NEP, net ecosystem production; SOC, soil organic C; TN, soil total N content; WUE, water use efficiency. The narrow straight and broad curved arrows indicate determined (statistically significant or not) and potential effects (not directly tested, but believed to be important), respectively. The figures in bold within the panel show the source or sink strengths of warming-induced greenhouse gases fluxes expressed as Pg CO<sub>2</sub>-eq/year and soil C sequestration potentials. The figures not in bold show the changes in plant and soil C and N pools under warming. Details are shown in Table 1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

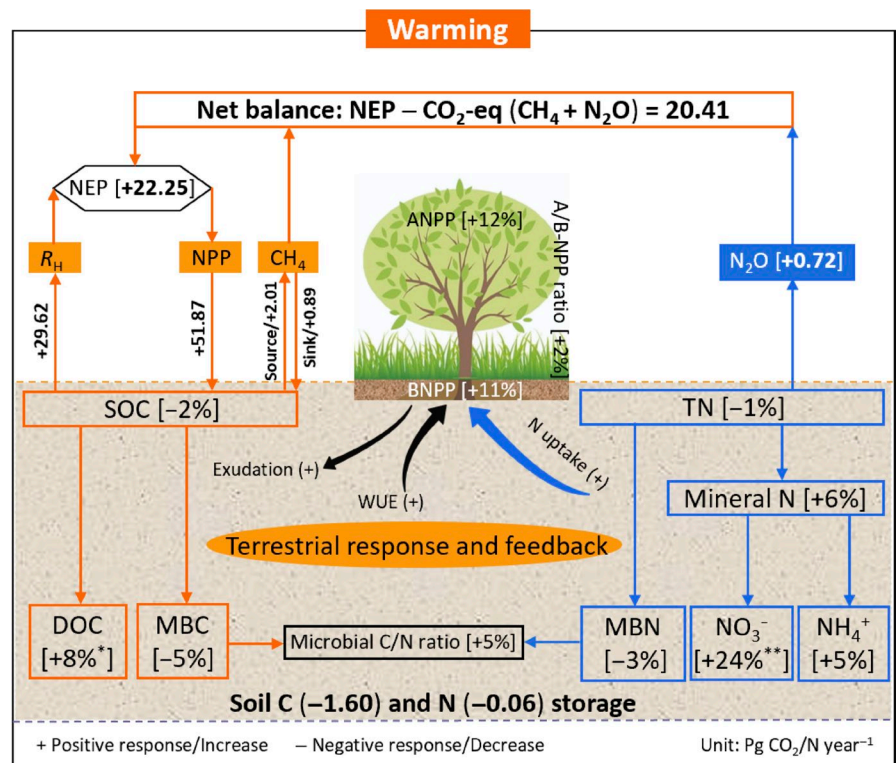
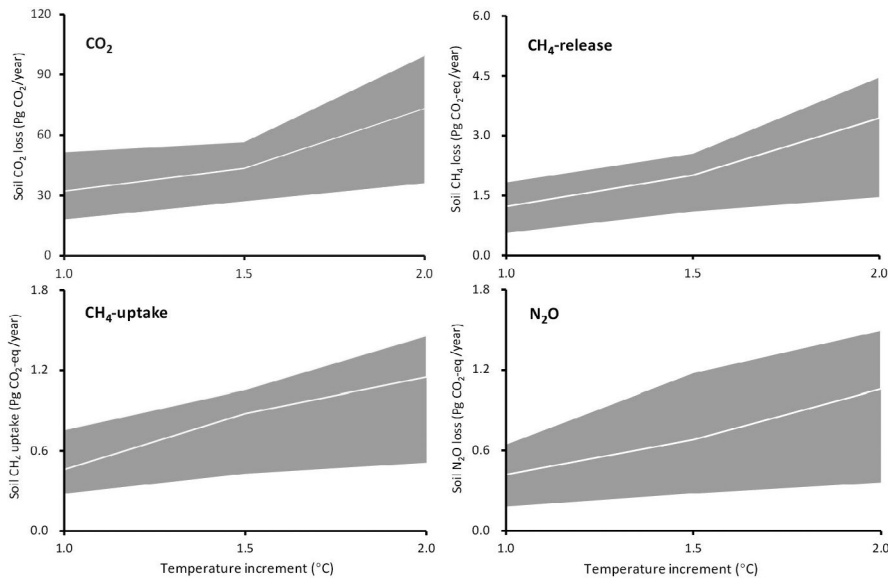


Figure 4). In general, warming-promoted removal of atmospheric CO<sub>2</sub> by terrestrial ecosystems contributes an additional increase of 51.87 Pg CO<sub>2</sub>/year in plant C pool. The enhancement of soil CO<sub>2</sub> fluxes under warming generates an additional source of 43.71 Pg CO<sub>2</sub>/year. By linking the changes in NPP and  $R_H$ , NEP was enhanced by 22.25 Pg CO<sub>2</sub>/year under warming (Table 1; Figure 4). The CH<sub>4</sub>

fluxes stimulated under warming amount to an additional source of 0.15 Pg CO<sub>2</sub>-equivalent (eq.)/year (CI: 0.06–0.18) from rice paddies and of 1.86 Pg CO<sub>2</sub>-eq./year (CI: 1.05–2.67) from natural wetlands (Table 1). The positive response of soil uptake of CH<sub>4</sub> to warming corresponds to a potential reduced source of 0.89 Pg CO<sub>2</sub>-eq./year (CI: 0.43–1.36) for upland soils (Table 1; Figure 4).



**FIGURE 5** Predicted changes in soil greenhouse gas release or uptake rates under projected warming scenarios. Soil  $\text{CO}_2$  loss is represented across all habitats. Soil  $\text{CH}_4$  loss is estimated by combining results from both natural wetlands and rice paddies. Soil  $\text{CH}_4$  uptake and  $\text{N}_2\text{O}$  loss are predicted based on results from uplands and all habitats, respectively. Shaded areas indicate the range of uncertainty expressed as 95% CI. Soil  $\text{CO}_2$  and  $\text{CH}_4$  losses were intensified following 1.5°C warming threshold, as compared to soil  $\text{CH}_4$  uptake and  $\text{N}_2\text{O}$  loss with a reduced and less positive response, respectively

The increase in soil  $\text{N}_2\text{O}$  emissions under warming contributes to an additional source of 0.72 Pg  $\text{CO}_2$ -eq./year (CI: 0.31–1.52), consisting of a source role of 0.18 Pg  $\text{CO}_2$ -eq./year (CI: 0.12–0.79) for natural wetland, a source role of 0.01 Pg  $\text{CO}_2$ -eq./year (CI: –0.02 to 0.06) for rice paddies, and a source role of 0.28 Pg  $\text{CO}_2$ -eq./year (CI: 0.12–0.45) and 0.25 Pg  $\text{CO}_2$ -eq./year (CI: 0.11–0.59) for fertilized and non-fertilized upland soils, respectively (Table 1). Together, the combined positive effect of warming on  $\text{CH}_4$  and  $\text{N}_2\text{O}$  fluxes corresponds to an additional total source strength of 1.84 Pg  $\text{CO}_2$ -eq./year.

To quantify soil GHG fluxes under different projected warming thresholds, we further estimated the warming-induced changes in soil GHGs under 1°C, 1.5°C, and 2°C warming scenarios based on the fitted linear regressions (Figure 5). The warming-enhanced soil  $\text{CO}_2$  emissions are projected to be 32.45 Pg  $\text{CO}_2$ -eq./year (CI: 18.02–52.78), 43.71 Pg  $\text{CO}_2$ -eq./year (CI: 26.90–57.83), and 59.67 Pg  $\text{CO}_2$ -eq./year (CI: 22.34–86.45) when exposed to 1°C, 1.5°C, and 2°C increments, respectively. The enhanced soil  $\text{N}_2\text{O}$  emissions amount to 0.42 Pg  $\text{CO}_2$ -eq./year (CI: 0.18–0.65), 0.72 Pg  $\text{CO}_2$ -eq./year (CI: 0.32–1.32), and 1.12 Pg  $\text{CO}_2$ -eq./year (CI: 0.35–1.56), while soil  $\text{CH}_4$  emissions by combining both natural wetlands and rice paddies come up to 1.23 Pg  $\text{CO}_2$ -eq./year (CI: 0.56–1.85), 2.01 Pg  $\text{CO}_2$ -eq./year (CI: 1.10–2.57), and 3.21 Pg  $\text{CO}_2$ -eq./year (CI: 1.23–4.25) under 1°C, 1.5°C, and 2°C warming scenarios, respectively. The increased upland soil uptake of  $\text{CH}_4$  due to the raised 1°C, 1.5°C, and 2°C temperature gradients would reduce a projected source of 0.46 Pg  $\text{CO}_2$ -eq./year (CI: 0.28–0.76), 0.89 Pg  $\text{CO}_2$ -eq./year (CI: 0.34–1.07), and 1.21 Pg  $\text{CO}_2$ -eq./year (CI: 0.57–1.52), respectively.

Overall, the increases in annual soil  $\text{CH}_4$  and  $\text{N}_2\text{O}$  emissions on the global scale under the projected 1°C, 1.5°C, and 2°C warming scenarios could contribute 1.19 Pg  $\text{CO}_2$ -eq./year, 1.84 Pg  $\text{CO}_2$ -eq./year, and 3.12 Pg  $\text{CO}_2$ -eq./year to shaping the climate change, respectively. In contrast, soil  $\text{CO}_2$  and  $\text{CH}_4$  losses were intensified following the mean warming threshold of 1.5°C, as a contrary to soil  $\text{CH}_4$  uptake and  $\text{N}_2\text{O}$  loss with a reduced and less positive response, respectively (Figure 5). The annual incremental losses of soil organic C and total N storage

under warming were estimated to be 1.60 Pg  $\text{CO}_2$ /year (CI: –0.18 to 4.23) and 0.06 Pg N/year (CI: –0.01 to 0.11), respectively (Table 1). These estimates could be projected to drive net soil C and N losses of 14.03 Pg C and 1.89 Pg N under around 1.5°C of business-as-usual warming conditions by 2050, respectively.

## 4 | DISCUSSION

This synthesis takes the lead to provide a full accounting of GHG exchanges between terrestrial ecosystems and the atmosphere under experimental warming. Our meta-analysis builds a link of GHG fluxes to terrestrial C and N pools with synchronous observational dataset under warming and advances our current understanding on the global patterns of terrestrial C and N cycling in a warming climate, relative to previous synthesized efforts by focusing only on soil respiration or other soil C components (Carey et al., 2016; Crowther et al., 2016; Van Gestel et al., 2018; Yue et al., 2017). Our results highlight that the warming-stimulated  $\text{CH}_4$  and  $\text{N}_2\text{O}$  emissions will not drive a significant loss of soil organic C storage due to enhanced terrestrial plant-derived soil C input under warming. However, this mitigation effect can be realized only under canopy air warming, rather than under soil warming conditions that will intensify climate change. The findings also suggest that the changes in soil C and N substrates under warming would result in profound influences on soil microbial processes driving GHG release or uptake.

### 4.1 | Terrestrial ecosystem C and N pools under experimental warming

Recent meta-analysis studies have shown that warming can stimulate C storage in plant pools (Lu et al., 2013; Yue et al., 2017). This positive response of plant C pools to increased temperature can be achieved by altering plant phenology (Arft et al., 1999), prolonging plant growing



season (Sherry et al., 2007), or promoting plant growth through shifting species composition (Peñuelas et al., 2007). In this study, plant C pools were greater by 9% under warming, which is close to a recent synthesized estimate of 6% enhancement at community levels based on limited data volume (Yue et al., 2017). Plant aboveground C pool tended to be more enhanced than belowground C pool, leading to a minor increase in shoot/root C ratios under warming (Figure 2a). As highlighted in previous studies, primary productivity is often N limited in human-impacted terrestrial ecosystems (Elser et al., 2007), while the increase in soil mineral N under warming may buffer this limitation to maintain plant growth as we had determined in this analysis. Soil organic C pool showed a weak negative response to warming, while soil labile C components had a significant positive response, particularly in fertilized soils and under soil-warmed conditions. This suggests that warming incurs an enhanced supply of microbially accessible C substrates, such as new labile C input by plant and mobilizing C reserves for potential risks (Fontaine et al., 2007). As shown in a previous meta-analysis (Lu et al., 2013), soil organic C pool did not significantly respond to warming in this study, demonstrating that the enhanced plant-derived soil C gain (influx) might compensate soil C loss (efflux) under warming. Recently, several meta-analyses have examined the response of plant or soil C pools to warming (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011; Yue et al., 2017), generally suggesting that compared with plant C pools, soil C pools showed a much weaker temperature response. Our synthesized findings with robust expanded data volume further confirmed the previous results on responses of soil C and MBC pools to warming. Therefore, compared with soil C pools, the relatively stronger positive temperature response of plant C pools may largely offset C loss from soils.

Similarly, warming led to a minor decrease in soil organic N pool when averaged across studies, contrary to soil mineral N substrates showing a positive warming response where the nitrate N had the largest extent. This pronounced increase in nitrate N accumulation is associated with enhanced soil nitrification in response to warming (Rustad et al., 2001). Consistent with previous experimental evidence, warming is usually shown to accelerate N cycling rate, leading to an increase in soil N availability to the vegetation (Abdalla, Jones, & Williams, 2010; Yin et al., 2012). Other processes including warming-induced decrease in soil water content and stimulation of soil organic N mineralization may increase soil N availability or decrease N loss (Manzoni & Porporato, 2009). Likewise, soil microbial C and N pools had consistently negative responses to warming, although varying with extents. Together with the warming responses of soil microbial biomass as well as microbial C/N ratio, we proposed that warming would shape MBC and N allocation but need further long-term experimental confirmation.

## 4.2 | Warming-stimulated release or uptake of soil GHGs

The increase in soil CO<sub>2</sub> and CH<sub>4</sub> fluxes under warming in this analysis was consistent with previous individual experimental findings, suggesting that soil microbial CO<sub>2</sub> production and methanogenesis

as both temperature-sensitive processes tend to accelerate under warming conditions due to enhanced soil organic C decomposition (Schädel et al., 2016; Yvon-Durocher et al., 2014), although the temperature sensitivity of aerobic CO<sub>2</sub> production and anaerobic CH<sub>4</sub> production may differ (Carey et al., 2016; Roy Chowdhury et al., 2015). Indeed, as supported by results in this analysis, warming increased soil labile C components and thereby enriched soil C substrate for both respiration and methanogenesis (Figure 2c).

Interestingly, soil uptake of CH<sub>4</sub> was also significantly enhanced under warming, with a dominated positive response when subject to soil warming and in non-cropping upland soils with no fertilizer input. Upland soil CH<sub>4</sub> uptake occurs first through CH<sub>4</sub> diffusion into soils and then through its consumption by soil methanotrophs (Galbally, Kirstine, Meyer, & Wang, 2008). These two processes were facilitated by experimental warming due to its lowered soil water content and then increased soil aeration (Table S5). Moreover, warming stimulated plant-derived soil labile C input in this analysis (Figure 2a), causing microbial CH<sub>4</sub> oxidation less substrate-limited in upland soils. However, once soil water reaches to its extreme low limit in dry seasons, soil methanotrophs would cease metabolizing and in turn reduce CH<sub>4</sub> consumption (Galbally et al., 2008). Therefore, soil water interacts with C substrate to shape the upland sink role of atmospheric CH<sub>4</sub>.

Similar to soil C release, soil N<sub>2</sub>O fluxes showed a significant increase in warmed soils, to a larger extent under canopy air-warmed conditions and in non-fertilized soils. This general finding vigorously confirmed the previous individual field evidence in upland soils (Cantarel et al., 2012; Carter et al., 2011), primarily attributed to warming-improved N availability. Cantarel et al. (2012) also found that in situ N<sub>2</sub>O fluxes had strong correlations with microbial population size of N<sub>2</sub>O reducers and NH<sub>4</sub> oxidizers under warming conditions. Denitrification is generally stimulated by high availability of labile C as a source of energy (Weier, Doran, Power, & Walters, 1993). Therefore, the observed enhanced microbially accessible soil labile C and N pools in this analysis may largely account for the massive release of soil N<sub>2</sub>O under warming conditions (Figure 2c,d).

## 4.3 | Soil GHG budget under warming scenarios

Here we extrapolated results of this meta-analysis into global context and compared with previous syntheses. In this study, soil organic C losses were estimated to be 1.60 Pg CO<sub>2</sub>/year or 14.03 Pg C under around 1.5°C of warming by 2050. A recent modeling result suggests that warming could drive the net loss of approximately 5.76 Pg CO<sub>2</sub>/year or 55 Pg C from the upper soil horizon under 2° of warming by 2050 (Crowther et al., 2016). The lower soil C loss in this study might have been largely attributed to the canopy air warming studies dominated the source of dataset in this analysis (sample size: 41 paired measurements from canopy air warming vs. 11 from soil warming experiments, Figure 3b). Indeed, the significant soil C pool loss was found only under soil warming, in contrast to its insignificant response to canopy air

warming in this study (Figure 3b), suggesting that previous syntheses or modeling estimates based on soil warming experiments could have been overestimated due to inherent differences in soil environment and C turnover between soil and canopy air heating methods (Crowther et al., 2016; Wang et al., 2018). Nevertheless, our estimates showed that the combined radiative forcing of CH<sub>4</sub> and N<sub>2</sub>O emissions enhanced by warming corresponded to a total soil C release of 1.84 Pg CO<sub>2</sub>/year to the atmosphere, interacting with soil C loss of 1.60 Pg CO<sub>2</sub>/year in terms of contribution to climate change.

When compared with recent synthesized findings on terrestrial C and N cycling in response to other climate change drivers such as N deposition and elevated CO<sub>2</sub> (Deng et al., 2020; Liu et al., 2018), we found that warming-induced increases in GHG emissions are quite lower than those stimulated by N deposition and elevated CO<sub>2</sub> (warming in this study: 1.84 Pg CO<sub>2</sub>/year; N deposition: 10.20 Pg CO<sub>2</sub>/year; elevated CO<sub>2</sub>: 2.76 Pg CO<sub>2</sub>/year). Soil C sink, however, tends to shrink under warming, but is enhanced by N deposition and elevated CO<sub>2</sub> (warming in this study: 1.60 Pg CO<sub>2</sub>/year; N deposition: 6.34 Pg CO<sub>2</sub>/year; elevated CO<sub>2</sub>: 2.42 Pg CO<sub>2</sub>/year). At ecosystem levels, warming-induced rise in NEP (22.25 Pg CO<sub>2</sub>/year) is significantly greater than the terrestrial C sink (3.99 Pg CO<sub>2</sub>/year) enhanced by elevated CO<sub>2</sub> (Liu et al., 2018), suggesting that the warming relative to elevated CO<sub>2</sub> benefits more of terrestrial C uptake. However, this overall warming-induced impact on terrestrial C feedback to climate change should be evaluated by integrating the response of GHG fluxes with a close link to soil C pools based on synchronous observational datasets.

Uncertainties, however, still existed in estimating the overall actual extent on the global scale. Limitations were first rooted from the simple extrapolation approach using a single number for the global coverage of the ecosystem types (Liu et al., 2018; Van Groenigen et al., 2011). Ideally, the sample size of warming experiment measurements should be large enough to be widely and evenly distributed in Earth's terrestrial habitats. Unfortunately, the warming experiments available have mostly been clustered in Asia, Europe, and North America, while only several warming experiments have been taken in South Hemisphere, and in Northern Hemisphere at high latitudes and tropics (Figure 1). Future warming experiments are certainly anticipated to focus on regions that are currently underrepresented in our global database although the synthesis based on data from a greater number of sites may not change the patterns of soil C stock response to warming as suggested by Crowther et al. (2016). While this study has stressed on the difference in soil GHG flux responses to warming between croplands and non-agricultural ecosystems (e.g., rice paddies vs. natural wetlands, fertilized cropping uplands vs. unfertilized uplands), limited available data would not allow us to better capture more diverse terrestrial habitat categories in the world. Besides, there was a small difference (with a variation of 3.5%) in the averages of rising temperature for different GHGs in this synthesis. Furthermore, we assumed that the changes in GHG fluxes and soil C and N pools under warming over

multiple duration step-change experiments can be extrapolated to gradual warming effect on them, which had its own problematic issues but can be adequately used for global scale climate predictions as previously addressed (Luo & Reynolds, 1999). In addition, the approach itself necessitated a saturated linear function to estimate the magnitude of soil C and N losses, which likely to some extent underestimate the actual source or sink potential under warming (Gill et al., 2002). However, despite these uncertainties in our estimates, the direction of soil GHG response to warming is consistent across projected scenarios. This suggests that warming raised emission of GHGs to the atmosphere will intensify with the increasing temperature gradients in the warmer future.

#### 4.4 | Other factors associating GHG fluxes in response to warming

In addition to soil C input, soil properties also play an important role in driving soil GHG responses to warming. Soil GHG emission response to warming was positively related to soil C/N ratio (Figure S1a–c), while upland soil uptake of CH<sub>4</sub> showed a negative correlation with soil C/N ratio (Figure S1d), indicating an overall increasing trend of atmospheric GHG source strength with the rise of soil C/N ratio under warming. Indeed, soil C/N ratio has been reported to drive soil GHG emissions in response to climate change in particular (Chen, Zou, Hu, Chen, & Lu, 2014; Stehfest & Bouwman, 2006). Warming was shown to decrease soil water content by 17% (WFPS; Tables S3–S5). This is mainly due to lowered efficiency of soil water use by plants under warming, ultimately leading to an increase in soil water loss through plants or other pathways. Soil CO<sub>2</sub> emissions and CH<sub>4</sub> uptake response to warming have been found to positively depend on soil moisture (Figure S2a,c), which might have been associated with relatively higher moisture sensitivity of soil organic C decomposition under warming (Liu et al., 2016). In particular, soil water content decreased by warming may facilitate upland soil uptake of CH<sub>4</sub>, and this stimulation is amplified by soil warming as we found in this analysis (Figure 3a). Besides, soil the response of CO<sub>2</sub> emissions to warming were consistently positively related to plant biomass C and MBC and N pools (Figure S3), with more sensitive response to plant belowground C and MBC components, indicating that warming tends to strengthen the dependence of soil CO<sub>2</sub> emissions on microbially accessible C substrate such as plant-derived soil C input (Davidson & Janssens, 2006). In contrast, warming response of soil N<sub>2</sub>O release was shown to be positively dependent on soil initial C and N levels (Figure S2b), but there was no significant difference in their responses to warming (Figure S2d). It suggests that soil microbial processes responsible for N<sub>2</sub>O production such as nitrification and denitrification might rely to a larger extent on soil initial C and N availability relative to their balance in a warming climate (Cantarel et al., 2012).

The intensity of temperature increase was shown to influence the response of soil GHG fluxes to experimental warming. Soil release of three major GHGs and the combined radiative forcing of

CH<sub>4</sub> and N<sub>2</sub>O were observed to have a consistently positive dependence on warming intensity (Figure S4a–d), suggesting an enhanced source strength of atmospheric GHGs as warming intensified. To our knowledge, however, currently no robust synthesized evidence has been found to address the gap of soil GHG fluxes as affected by warming intensity. Plant C pool and microbial biomass to warming were also shown to be positively dependent on warming intensity, in contrast to the ratio of ANPP/BNPP with a negative response (Figure S4e–f). This finding confirms the previous evidence that plant biomass C accumulation tends to be enhanced with intensifying temperature increase, but this increase can be limited by concurrently reduced microbial activity (Arft et al., 1999; Lu et al., 2013). Particularly, warming-induced changes in microbial C/N ratio and the combined climatic impact of CH<sub>4</sub> and N<sub>2</sub>O were negatively correlated with the duration of warming (Figure S5), which suggests that the impacts of climate warming on soil GHG fluxes will diminish with the extension of warming duration, associated with the changes in microbial C and N allocation (Allison & Treseder, 2008; Peterjohn et al., 1994). Additionally, long-term warming will facilitate labile C and N substrate depletion and ultimately constrain substrate available to microbes involved in soil GHG production and uptake (Bradford et al., 2008; Frey et al., 2013; Yuste, Ma, & Baldocchi, 2010).

#### 4.5 | Soil warming versus canopy air warming

Understanding the response of terrestrial C and N cycling to warming partitioned by different heating ways remains poorly constrained in previous studies (Crowther et al., 2016; Lu et al., 2013; Melillo et al., 2017). Based on similar mean warming thresholds in this analysis, soil warming had a significant positive effect on soil CO<sub>2</sub> and CH<sub>4</sub> fluxes (Figure 3a), a negative effect on soil C storage, in contrast to canopy air warming without significantly altering soil C pools, either its total or labile components (Figure 3b). Soil warming is believed to directly impose on soil microbial processes and rhizosphere activities within a given ecosystem, leading to the depletion of total soil C storage (Carey et al., 2016; Crowther et al., 2016; van Gestel et al., 2018). In contrast, canopy air warming can facilitate plant C fixation and thereby enhance soil C inputs, which may largely or completely offset warming-induced C loss from soils (Figure 3b). Due to plant vegetation cover and agricultural practices (e.g., soil waterlogging, crop residue cover), in addition, soil temperature may hardly track the controlled air temperature closely in canopy air warming experiments (Thornton, Lamarque, Rosenbloom, & Mahowald, 2007), where the C and N turnover rates under canopy air warming could be largely weakened at the ecosystem scale. However, compared to canopy air warming, the enhanced mineral N pools under soil warming did not guarantee the increase in N<sub>2</sub>O emissions (Figure 3), which are largely attributed to the decreased activity of microbes under direct soil warming with greater intensity (Cantarel et al., 2012). Meanwhile, the enhanced positive response of mineral N availability under soil warming might have been also

associated with the easier loss of soil water relative to under canopy air warming that constrains plant N uptake (Table S5).

#### 4.6 | Implications for future directions

This study concentrated on the temperature response of soil GHG fluxes with a close link to terrestrial C and N pools using the meta-analysis method. However, this meta-analysis mainly focused on effects of warming alone on terrestrial C and N cycling and did not address its interaction with other climate change factors (e.g., N deposition, elevated CO<sub>2</sub>, drought). Furthermore, the site distribution of present available dataset was overwhelmingly dominated in temperate and subtropical regions but limited in the tropics, where higher GHG fluxes and higher N load are generally expected to occur (Thornton et al., 2007). In particular, how warming affects the key soil essential nutrient cycling or interacts with them to alter terrestrial C and N cycling is the challenge of great concern in the future (Galloway et al., 2008), especially in subtropical and tropical areas, where soil C storage shows greater vulnerability to rising temperature. Overall, our global compilation of experimental data allows us to generalize the past conflicting results from single-site studies and in turn provides quantitative support for the development of terrestrial C and N cycle-climate feedback models to rigorously capture the complex response of terrestrial ecosystems to climate change.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### AUTHOR CONTRIBUTION

S.L. and J.Z. designed the investigation. Y.Z., R.M., and Z.H. extracted the data from literature and constructed the database. S.L., Y.Z., and R.M. performed the statistical analyses. Z.L. mapped the distribution of experimental locations enclosed in this study. All authors contributed to writing and finalizing the manuscript.

#### DATA AVAILABILITY STATEMENT

All data used for this study are freely available from the corresponding author upon reasonable request.

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## REFERENCES

- Abdalla, M., Jones, M., & Williams, M. (2010). Simulation of N<sub>2</sub>O fluxes from Irish arable soils: Effect of climate change and management. *Biology and Fertility of Soils*, 46(3), 247–260. <https://doi.org/10.1007/s00374-009-0424-5>
- Allison, S. D., & Treseder, K. K. (2008). Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology*, 14(12), 2898–2909. <https://doi.org/10.1111/j.1365-2486.2008.01716.x>
- Arft, A., Walker, M., Gurevitch, J., Alatalo, J., Bret-Harte, M., Dale, M., ... Wookey, P. A. (1999). Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, 69(4), 491–511. <https://doi.org/10.2307/2657227>
- Arora, V. K., Boer, G. J., Friedlingstein, P., Eby, M., Jones, C. D., Christian, J. R., ... Wu, T. (2013). Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models. *Journal of Climate*, 26(15), 5289–5314. <https://doi.org/10.1175/JCLI-D-12-00494.1>
- Aselmann, I., & Crutzen, P. J. (1989). Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *Journal of Atmospheric Chemistry*, 8(4), 307–358. <https://doi.org/10.1007/BF00052709>
- Bradford, M. A., Davies, C. A., Frey, S. D., Maddox, T. R., Melillo, J. M., Mohan, J. E., ... Wallenstein, M. D. (2008). Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters*, 11(12), 1316–1327. <https://doi.org/10.1111/j.1461-0248.2008.01251.x>
- Cantarel, A. A., Bloor, J. M., Pommier, T., Guillaumaud, N., Moirou, C., Soussana, J. F., ... Poly, F. (2012). Four years of experimental climate change modifies the microbial drivers of N<sub>2</sub>O fluxes in an upland grassland ecosystem. *Global Change Biology*, 18(8), 2520–2531. <https://doi.org/10.1111/j.1365-2486.2012.02692.x>
- Carey, J. C., Tang, J., Templer, P. H., Kroeger, K. D., Crowther, T. W., Burton, A. J., ... Tietema, A. (2016). Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences of the United States of America*, 113(48), 13797–13802. <https://doi.org/10.1073/pnas.1605365113>
- Carter, M. S., Ambus, P., Albert, K. R., Larsen, K. S., Andersson, M., Priemé, A., ... Beier, C. (2011). Effects of elevated atmospheric CO<sub>2</sub>, prolonged summer drought and temperature increase on N<sub>2</sub>O and CH<sub>4</sub> fluxes in a temperate heathland. *Soil Biology and Biochemistry*, 43(8), 1660–1670. <https://doi.org/10.1016/j.soilbio.2011.04.003>
- Chen, S. T., Zou, J. W., Hu, Z. H., Chen, H. S., & Lu, Y. Y. (2014). Global annual soil respiration in relation to climate, soil properties and vegetation characteristics: Summary of available data. *Agricultural and Forest Meteorology*, 198, 335–346. <https://doi.org/10.1016/j.agrfo.2014.08.020>
- Crowther, T. W., Machmuller, M. B., Carey, J. C., Allison, S. D., Blair, J. M., Bridgman, S. D., ... Bradford, M. A. (2018). Crowther et al reply. *Nature*, 554(7693), E7–E8. <https://doi.org/10.1038/nature25746>
- Crowther, T. W., Thomas, S. M., Maynard, D. S., Baldrian, P., Covey, K., Frey, S. D., ... Bradford, M. A. (2015). Biotic interactions mediate soil microbial feedbacks to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 112(22), 7033–7038. <https://doi.org/10.1073/pnas.1502956112>
- Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B., ... Bradford, M. A. (2016). Quantifying global soil carbon losses in response to warming. *Nature*, 540(7631), 104–108. <https://doi.org/10.1038/nature20150>
- Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165–173. <https://doi.org/10.1038/nature04514>
- Deng, L., Huang, C. B., Kim, D. G., Shangguan, Z. P., Wang, K. B., Song, X. Z., & Peng, C. (2020). Soil GHG fluxes are altered by N deposition: New data indicate lower N stimulation of the N<sub>2</sub>O flux and greater stimulation of the calculated C pools. *Global Change Biology*, 26(4), 2613–2629. <https://doi.org/10.1111/GCB.14970>
- Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., ... Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10(12), 1135–1142. <https://doi.org/10.1111/j.1461-0248.2007.01113.x>
- Fontaine, S., Sébastien, B., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 450(7167), 277–280. <https://doi.org/10.1038/nature06275>
- Frey, S. D., Lee, J., Melillo, J. M., & Six, J. (2013). The temperature response of soil microbial efficiency and its feedback to climate. *Nature Climate Change*, 3(4), 395–398. <https://doi.org/10.1038/nclimate1796>
- Galbally, I. E., Kirstine, W. V., Meyer, C. P., & Wang, Y. P. (2008). Soil-atmosphere trace gas exchange in semiarid and arid zones. *Journal of Environmental Quality*, 37(2), 599–607. <https://doi.org/10.2134/jeq2006.0445>
- Galloway, J. N., Townsend, A. R., Erismann, J. W., Bekunda, M., Cai, Z., Freney, J. R., ... Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, 320(5878), 889–892. <https://doi.org/10.1126/science.1136674>
- Gill, R. A., Polley, W., Johnson, H. B., Anderson, L. J., Maherali, H., & Jackson, R. B. (2002). Nonlinear grassland responses to past and future atmospheric CO<sub>2</sub>. *Nature*, 417, 279–282. <https://doi.org/10.1038/417279a>
- Hungate, B. A., Van Groenigen, K.-J., Six, J., Jastrow, J. D., Luo, Y., De Graaff, M.-A., ... Osenberg, C. W. (2009). Assessing the effect of elevated carbon dioxide on soil carbon: A comparison of four meta-analyses. *Global Change Biology*, 15(8), 2020–2034. <https://doi.org/10.1111/j.1365-2486.2009.01866.x>
- IPCC. (2013). Summary for policymakers. In T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, ... P. M. Midgley (Eds.), *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 1–27). Cambridge, UK and New York, NY: Cambridge University Press.
- Liu, L., Wang, X., Lajeunesse, M. J., Miao, G., Piao, S., Wan, S., ... Deng, M. (2016). A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. *Global Change Biology*, 22(4), 1394–1405. <https://doi.org/10.1111/gcb.13156>
- Liu, S. W., Ji, C., Wang, C., Chen, J., Jin, Y. G., & Zou, Z. H. (2018). Climatic role of terrestrial ecosystem under elevated CO<sub>2</sub>: A bottom-up greenhouse gases budget. *Ecology Letters*, 21(7), 1108–1118. <https://doi.org/10.1111/ele.13078>
- Liu, S. W., Lin, F., Wu, S., Ji, C., Sun, Y. I., Jin, Y., ... Zou, J. (2017). A meta-analysis of fertilizer-induced soil NO and combined NO+N<sub>2</sub>O emissions. *Global Change Biology*, 23(6), 2520–2532. <https://doi.org/10.1111/gcb.13485>
- Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., ... Li, B. O. (2013). Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology*, 94(3), 726–738. <https://doi.org/10.1890/12-0279.1>
- Luo, Y., & Reynolds, J. F. (1999). Validity of extrapolating field CO<sub>2</sub> experiments to predict carbon sequestration in natural ecosystems. *Ecology*, 80(5), 1568–1583. [https://doi.org/10.1890/0012-9658\(1999\)080\[1568:VOEFCE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1568:VOEFCE]2.0.CO;2)
- Manzoni, S., & Porporato, A. (2009). Soil carbon and nitrogen mineralization: Theory and models across scales. *Soil Biology and Biochemistry*, 41(7), 1355–1379. <https://doi.org/10.1016/j.soilbio.2009.02.031>
- Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., ... Grandy, A. S. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science*, 358(6359), 101–105. <https://doi.org/10.1126/science.aan2874>

- Neubauer, S. C., & Megonigal, J. P. (2015). Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, 18(6), 1000–1013. <https://doi.org/10.1007/s10021-015-9879-4>
- Neubauer, S. C., & Megonigal, J. P. (2019). Correction to: Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, 22(8), 1931–1932. <https://doi.org/10.1007/s10021-019-00422-5>
- Payne, R. W. (2000). *Genstat release 4.2. Reference manual*. Harpenden, UK: Lawes Agricultural Trust (Rothamsted Experimental Station).
- Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., De Angelis, P., de Dato, G., ... Tietema, A. (2007). Response of 59 plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: Reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology*, 13(12), 2563–2581. <https://doi.org/10.1111/j.1365-2486.2007.01464.x>
- Peterjohn, W. T., Melillo, J. M., Steudler, P. A., Newkirk, K. M., Bowles, F. P., & Aber, J. D. (1994). Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications*, 4(3), 617–625. <https://doi.org/10.2307/1941962>
- R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Roy Chowdury, T., Herndon, E. M., Phelps, T. J., Elias, D. A., Gu, B., Liang, L. Y., ... Graham, D. E. (2015). Stoichiometry and temperature sensitivity of methanogenesis and CO<sub>2</sub> production from saturated polygonal tundra in Barrow, Alaska. *Global Change Biology*, 21(2), 722–737. <https://doi.org/10.1111/gcb.12762>
- Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., ... Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126(4), 543–562. <https://doi.org/10.1007/s004420000544>
- Schädel, C., Bader, M.-F., Schuur, E. A. G., Biasi, C., Bracho, R., Čapek, P., ... Wickland, K. P. (2016). Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils. *Nature Climate Change*, 6(10), 950–953. <https://doi.org/10.1038/nclimate3054>
- Shang, Q. Y., Yang, X. X., Gao, C. M., Wu, P. P., Liu, J. J., Xu, Y. C., ... Guo, S. (2011). Net annual global warming potential and greenhouse gas intensity in Chinese double rice-cropping systems: A 3-year field measurement in long-term fertilizer experiments. *Global Change Biology*, 17(6), 2196–2210. <https://doi.org/10.1111/j.1365-2468.2010.02374.x>
- Sherry, R. A., Zhou, X., Gu, S., Arnone, J. A., Schimel, D. S., Verburg, P. S., ... Luo, Y. (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 104(1), 198–202. <https://doi.org/10.1073/pnas.0605642104>
- Stehfest, E., & Bouwman, L. (2006). N<sub>2</sub>O and NO emission from agricultural fields and soils under natural vegetation: Summarizing available measurement data and modelling of global annual emissions. *Nutrient Cycling in Agroecosystems*, 74, 207–228. <https://doi.org/10.1007/s10705-006-9000-7>
- Thornton, P. E., Lamarque, J. F., Rosenbloom, N. A., & Mahowald, N. M. (2007). Influence of carbon-nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Global Biogeochemical Cycles*, 21(4), GB4018. <https://doi.org/10.1029/2006GB002868>
- Tian, H., Wang, S., Liu, J., Pan, S., Chen, H., Zhang, C., & Shi, X. (2006). Patterns of soil nitrogen storage in China. *Global Biogeochemical Cycles*, 20(1), GB1001. <https://doi.org/10.1029/2005GB002464>
- Tian, K., Zhao, Y. C., Xu, X. H., Hai, N., Huang, B., & Deng, W. J. (2015). Effects of long-term fertilization and residue management on soil organic carbon changes in paddy soils of China: A meta-analysis. *Agriculture, Ecosystems and Environment*, 204, 40–50. <https://doi.org/10.1016/j.agee.2015.02.008>
- Van Gestel, N., Shi, Z., Van Groenigen, K. J., Osenberg, C. W., Andresen, L. C., Dukes, J. S., ... Hungate, B. A. (2018). Predicting soil carbon loss with warming. *Nature*, 554(7693), E4–E5. <https://doi.org/10.1038/nature25745>
- Van Groenigen, K. J., Osenberg, C. W., & Hungate, B. A. (2011). Increased soil emissions of potent greenhouse gases under increased atmospheric CO<sub>2</sub>. *Nature*, 475(7355), 214–216. <https://doi.org/10.1038/nature10176>
- Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., ... Biasi, C. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases-carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, 23(8), 3121–3138. <https://doi.org/10.1111/gcb.13563>
- Wang, C., Jin, Y., Ji, C., Zhang, N. A., Song, M., Kong, D., ... Pan, G. (2018). An additive effect of elevated atmospheric CO<sub>2</sub> and rising temperature on methane emissions related to methanogenic community in rice paddies. *Agriculture, Ecosystems and Environment*, 257, 165–174. <https://doi.org/10.1016/j.agee.2018.02.003>
- Weier, K. L., Doran, J. W., Power, J. F., & Walters, D. T. (1993). Denitrification and the dinitrogen/nitrous oxide ratio as affected by soil water, available carbon, and nitrate. *Soil Science Society of America Journal*, 57(1), 66–72. <https://doi.org/10.2136/sssaj1993.03615995005700010013x>
- World Resources Institute. (2003). Land area classification by ecosystem type.
- Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, 17(2), 927–942. <https://doi.org/10.1111/j.1365-2486.2010.02302.x>
- Yin, H., Chen, Z., & Liu, Q. (2012). Effects of experimental warming on soil N transformations of two coniferous species, Eastern Tibetan Plateau, China. *Soil Biology and Biochemistry*, 50, 77–84. <https://doi.org/10.1016/j.soilbio.2012.03.004>
- Yue, K., Fornara, D. A., Yang, W., Peng, Y., Peng, C., Liu, Z., & Wu, F. (2017). Influence of multiple global change drivers on terrestrial carbon storage: Additive effects are common. *Ecology Letters*, 20(5), 663–672. <https://doi.org/10.1111/ele.12767>
- Yuste, J. C., Ma, S., & Baldocchi, D. D. (2010). Plant-soil interactions and acclimation to temperature of microbial-mediated soil respiration may affect predictions of soil CO<sub>2</sub> efflux. *Biogeochemistry*, 98(1), 127–138. <https://doi.org/10.1007/s10533-009-9381-1>
- Yvon-Durocher, G., Allen, A. P., Bastviken, D., Conrad, R., Gudas, C., St-Pierre, A., ... del Giorgio, P. A. (2014). Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. *Nature*, 507(7493), 488–491. <https://doi.org/10.1038/nature13164>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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