Received: 10 July 2023 | Accepted: 23 October 2023

DOI: 10.1111/gcb.17033

RESEARCH ARTICLE

Global Change Biology WILEY

Effects of whole-soil warming on CH_4 and N_2O fluxes in an alpine grassland

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Funding information
National Key Research and Development Program of China, Grant/Award Number: 2022YFF0801902; National Natural Science Foundation of China, Grant/Award Number: 42141006 and 31988102; China Postdoctoral Science Foundation, Grant/Award Number: 2022M720252

Abstract

Global climate warming could affect the methane (CH_4) and nitrous oxide (N_2O) fluxes between soils and the atmosphere, but how CH_4 and N_2O fluxes respond to whole-soil warming is unclear. Here, we for the first time investigated the effects of whole-soil warming on CH_4 and N_2O fluxes in an alpine grassland ecosystem on the Tibetan Plateau, and also studied the effects of experimental warming on CH_4 and N_2O fluxes across terrestrial ecosystems through a global-scale meta-analysis. The whole-soil warming (0–100 cm, +4°C) significantly elevated soil N_2O emission by 101%, but had a minor effect on soil CH_4 uptake. However, the meta-analysis revealed that experimental warming did not significantly alter CH_4 and N_2O fluxes, and it may be that most field warming experiments could only heat the surface soils. Moreover, the warming-induced higher plant litter and available N in soils may be the main reason for the higher N_2O emission under whole-soil warming in the alpine grassland. We need to pay more attention to the long-term response of greenhouse gases (including CH_4 and N_2O fluxes) from different soil depths to whole-soil warming over year-round, which could help us more accurately assess and predict the ecosystem-climate feedback under realistic warming scenarios in the future.

KEYWORDS
CH_4 uptake, meta-analysis, N_2O emission, whole-soil warming

1 | INTRODUCTION

The global mean surface temperature has increased significantly by approximately 1°C since 1850, and it will continue to increase by up to 4°C by the end of this century (SSP5-8.5 scenario, IPCC, 2021). The rapid increase of greenhouse gas concentrations in the atmosphere due to anthropogenic activities is the most important reason for global climate warming (IPCC, 2021). There are three most important greenhouse gases (GHGs): carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) (the global warming potential [GWP] of CH_4 and N_2O is 28 and 265 times higher than that of CO_2, respectively, Voigt et al., 2017). In addition, climate warming would release more GHGs into the atmosphere from terrestrial ecosystems (the concentration of CO_2, CH_4, and N_2O increased at 0.40%, 0.75%, and 0.25% per year, respectively), and this positive feedback will exacerbate further global warming (IPCC, 2021). A wide range of field warming experiments across divergent ecosystems have been conducted globally to investigate the effects of warming on CO_2 flux (Carey et al., 2016; Luo et al., 2001; Wang et al., 2014), but with less focus on CH_4 or/and N_2O fluxes (Carter et al., 2011). Besides, according to the soil temperature predictions from IPCC models and direct observations, both surface soils (0–2 cm) and deep soils (80–140 cm) would be heated at approximately the same rate by 2100 (closely following the air warming trends, Hu & Feng, 2003; Pries et al., 2018; Soong et al., 2020), not just the surface soils as in most warming experiments (Chen et al., 2022; Lafuente et al., 2020; Ma et al., 2017; Ward et al., 2013). Therefore, studying the response of CH_4 and N_2O fluxes to whole-soil warming would help us understand the strength and direction of the response of GHGs fluxes to realistic climate warming in the future.

The strength and direction of CH_4 and N_2O fluxes from soil to the atmosphere depend on the balance between their production and consumption (Tranvik et al., 2009; Verchot et al., 2000), while these processes are regulated by the response of soil microbial activity to climate warming (Jansson & Hofmockel, 2020; Zhou et al., 2016). As elevated temperature could directly alter microbial metabolism or indirectly change soil microclimate, substrate quantity and quality, gas diffusion, the input of plant litter, and nutrient availability, thus affecting the microbial activity and associated GHGs fluxes (Domeignoz-Horta et al., 2022; Martins et al., 2017; Xu et al., 2013; Yu et al., 2022). CH_4 is taken up by methanotrophic microbes under aerobic conditions and released by methanogens under anaerobic conditions (Dunfield et al., 1993; Lai, 2009), and CH_4 is generally absorbed by soil as a potential carbon sink (Heinzle et al., 2023; Wang et al., 2021). Climate warming could change substrate and nutrient availability as well as gas diffusion, with various effects on CH_4 flux that stimulate uptake (Heinzle et al., 2023), inhibit uptake (Dijkstra et al., 2013), or show no change (Wu et al., 2020). N_2O can be released through nitrification and denitrification processes. Warming would facilitate the release of N_2O, by increasing N availability as well as microbial activity (Voigt et al., 2017). However, warming decreased soil moisture and thus inhibited the denitrification rate, which caused less N_2O release into the atmosphere (Shi et al., 2012). In addition, it was also shown that N_2O flux did not respond to warming (Hu et al., 2010). These inconsistent results make it difficult to accurately predict and assess future greenhouse gas emissions under climate warming.

The Tibetan Plateau, as the world's third pole, stores a large amount of soil organic carbon (SOC; 7.4 Pg C in the top 1 m depth, Yang et al., 2008) and has a double warming rate compared with the global average warming rate (Chen et al., 2020), therefore it is considered to be most sensitive to climate warming. Alpine grassland is the most dominant ecosystem in this plateau (nearly 60% of the total area), about 10% of the total SOC in China (Yang et al., 2008), therefore it is a key area to study the responses of greenhouse gas emissions to climate warming (Chen et al., 2022). Therefore, in order to simulate the realistic warming scenario in the future, we designed a whole-soil warming experiment in the alpine grassland to heat the entire soil profile to 1 m by +4°C to study the responses of CH_4 and N_2O fluxes to warming. Moreover, meta-analysis is a statistical analysis method that provides a comprehensive understanding of a large number of independent experiments to obtain a general response pattern (Chen et al., 2020; Gurevitch & Hedges, 2020). Consequently, in this study, we (a) first explored the response of more critical GHGs (CH_4 and N_2O) to whole-soil warming based on the first whole-soil profile field warming experiment established in an alpine grassland on the Tibetan Plateau, (b) then investigated the general pattern of CH_4 and N_2O fluxes response to warming with a global-scale meta-analysis, and (c) finally provided suggestions that need more attention in future warming experiments, which could help us better predict greenhouse gas emissions under realistic warming scenarios and develop reasonable policies to mitigate warming.

2 | MATERIALS AND METHODS

2.1 | Study site

This field warming experiment was conducted in the alpine meadow ecosystem at the Haibei National Field Research Station of Alpine Grassland Ecosystems on the northeast Tibetan Plateau, Menyuan county, Qinghai province, China (37°37′ N and 101°12′ E; 3200 m a.s.l). This area belongs to the typical plateau continental climate with mean annual precipitation (MAP) of 489 mm, of which more than 80% occurs during the growing season from May to September (Figure S1). The mean annual temperature (MAT) is −1.1°C. Alpine meadow is the main vegetation type of alpine grassland on the Tibetan Plateau. The alpine meadow is dominated by *Kobresia humilis*, *Stipa aliena*, *Elymus nutans*, and other herbaceous plants (Liu et al., 2018; Ma et al., 2017). The soil in the alpine meadow is a loam of *Mat-Cryic Cambisol* with a mean pH of 7.6 (Chen et al., 2021).

2.2 | Experimental design and soil microclimate monitoring

The whole-soil warming experiment was designed to warm the soil at 4°C to 1 m depth while maintaining the natural temperature gradient (Pries et al., 2017; Zhang et al., 2023), beginning on June 17, 2018. This warming experiment consisted of eight 3 m diameter circular plots (four paired warm and ambient plots). Twenty 1-m long resistance heating cables (HCs; BriskHeat, Ohio, USA) were installed into vertical stainless-steel conduits (gaps were filled with sand) and spaced 0.5 m outside the edge of the plots. Two concentric rings of HCs (1 and 2 m in diameter, 5 cm in depth) were buried to compensate for the heat loss from the surface. We also installed similar unheated cables in the ambient plots (disturbance control treatment).

Temperature sensors (thermistors customized by Lica United, Beijing, China) were used to monitor soil temperature at 5, 10, 20, 30, 40, 60, 80, and 100 cm depth in all plots. Moisture sensors (Delta-T, UK) were used to monitor soil volumetric water content at 10, 20, 30, 40, 60, and 100 cm depth in all plots. We used dataloggers (CR1000; Campbell Scientific, Utah, USA) to record soil temperature and moisture values continuously at 10 min intervals. The power to HCs was automatically regulated every 10 min by the computer program according to the temperature difference between paired ambient and warming plots to maintain a targeted 4°C warming in the warming plots (Figure S2b). The temperature difference of paired plots at 5, 10, and 20 cm depth was used to control surface heaters (two concentric rings of HCs), while the temperature difference at 30, 40, 60, 80, and 100 cm depth was used to control deep heaters

(1 m HCs). The details of this whole-soil warming experiment were described by Qin et al. (2023) and Yin et al. (2023).

2.3 | Measurement of CH_4 and N_2O

We monitored soil CH_4 and N_2O fluxes using a static chamber and gas chromatography technique. In July 2018, a 0.4 × 0.4 m square collar with a groove was inserted into the soil in all plots. Then we made stainless-steel opaque chambers (0.4 m long, 0.4 m wide, and 0.4 m high) and also covered the chambers with foam to reduce the rapid change of temperature inside the chambers. During the gas sampling, gas samples were taken at intervals of 0, 10, 20, and 30 min using a 100 mL plastic syringe. At the same time, the connection of chamber and base square collar was sealed with water, while a small fan inside the chamber was opened to keep the extracted gas more homogenous and not affected by the outside. The gas samples were immediately injected into a pre-evacuated 50 mL air bag (Delin, Dalian, Liaoning, China) and analyzed by gas chromatography (Agilent 7890A; Agilent Technologies, Shanghai, China). Then the separated CH_4 and N_2O from the air with a carrier gas (N_2, 99.999%) were measured by a flame ionization detector and an electron capture detector. Soil CH_4 and N_2O fluxes were only sampled and measured during the growing season (every 2 weeks from August 2018 until September 2020, with 23 sampling dates).

2.4 | Plant and soil sampling, and related analysis

Aboveground biomass (AGB, four 0.25 × 0.25 m quadrats, randomly chosen within each plot) of the 8 plots (ambient and warming treatments, four replicates) were harvested at the end of August every year (2018, 2019, and 2020), oven-dried at 65°C to constant weight and weighed. Soil samples of 0–10 cm were collected using a corer (5 cm diameter) at the end of August 2019 (after the beginning of the experiment, approximately 14 months of warming). Also, soil samples collected from two soil cores in one plot were mixed into one composite soil sample. Then fresh soil samples were stored at 4°C using a closed cooler covered with ice-bags and taken back to the laboratory within 24 h. We removed the visible stones and picked roots when all soil samples were sieved through a 2 mm sieve. Picked roots were dried at 65°C to constant weight and weighed to obtain belowground biomass (BGB).

The sieved soil samples were divided into two parts: one was air-dried for elements analysis (carbon and nitrogen concentration) and the other one was stored at 4°C for soil properties and microbial biomass within 7 days. Soil water content (SWC) was measured by drying for 48 h at 105°C. Soil pH was determined in the suspension (1:5, the ratio of soil to water) with a pH meter (S210 SevenCompact™, Mettler-Toledo, Switzerland). Soil samples were treated with 1 M hydrochloric acid (HCl) to remove carbonates and then washed to neutrality with deionized water. Then soil samples were analyzed for total SOC and total nitrogen (TN) concentration using an Elementary Analyzer (Elementar vario, Langenselbold, Germany). Soil ammonium (NH_4^+-N) and nitrate (NO_3^--N) were extracted with 2 M KCl (1:5 ratio of soil: water) and then were analyzed on a continuous flow analyzer (AA3, Bran+Luebbe, Germany). Soil microbial biomass carbon (MBC) and nitrogen (MBN) were determined using the chloroform-fumigation extraction method (the extraction efficiency coefficient is 0.45, Vance et al., 1987).

2.5 | Statistical analysis

All the statistical analyses were applied using the R (version 4.2.1) (R Core Team, 2022). To better show the temporal patterns, we averaged the daily soil temperature and water content data (continuously recorded once every 10 min, Figures S3 and S4). The repeated measures ANOVA was used to test the effects of warming and time on soil CH_4 and N_2O fluxes and it was performed using the *ezANOVA* function of the "*ez*" package. Moreover, we also calculated the net whole-soil warming effect on annual cumulative fluxes of CH_4 and N_2O combined with the GWP approach (expressed as CO_2 equivalent under ambient and warming treatments) (IPCC, 2021; Wang et al., 2021). In this study, we used sustained GWP (SGWP100, 45 for CH_4 and 270 for N_2O) over a 100-year time horizon to express the average forcing of a sustained emission rather than a pulse over time. A paired samples *t*-test was used to determine the effects of warming treatments on mean CH_4 and N_2O fluxes and their SGWP. Finally, we also explored the relationships between CH_4 and N_2O fluxes and soil temperature and moisture at surface soil (0–10 cm). In addition, a Pearson correlation analysis was conducted to determine the effects of plant and soil properties (AGB, BGB, soil pH, NH_4^+-N, NO_3^--N, SOC, TN, MBC, and MBN) on the averaged CH_4 and N_2O fluxes. Asterisks indicate statistically significant differences between warming and ambient treatment ($^{\dagger}p < .10$, $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$).

2.6 | Meta-analysis for field warming experiments

In this meta-analysis, we collected the published papers before December 20, 2022 that studied the CH_4 and/or N_2O fluxes under field warming experiments, using the Web of Science (https://www.webofscience.com), Science Direct (https://www.sciencedirect.com), China National Knowledge Infrastructure (https://www.cnki.net), and Google Scholar (https://scholar.google.com) in all terrestrial ecosystems (Figures S5 and S6) across the world. The search keywords used for the article section were: (a) field experiment or manipulated experiment, (b) warming or increased temperature or elevated temperature, (c) CH_4 or methane, and (d) N_2O or nitrous oxide. Articles selected for this meta-analysis had to meet the following criteria: (1) At least one of the two key variables (CH_4 and N_2O) were reported. (2) Control and warming treatments had to occur in the same experiment. (3) The means, standard deviations (SD) or standard errors (SE), and sample sizes of the selected variables were clearly reported or could be calculated from the data of publications. (4) The warming protocols (warming method, warming magnitude, and warming duration) were directly recorded. (5) Only the latest results from the same study were used. (6) Gas measurements for CH_4 and/or N_2O were conducted for at least one growing season. Finally, based on these criteria, 52 articles (see the reference list) and this whole-soil field warming experiment were included in this meta-analysis.

The results from different warming magnitudes in the same study were considered as independent observations. To include more data in this meta-analysis, we also used all the results from multifactor studies (e.g., fertilization vs. fertilization and warming, Chen et al., 2022). Moreover, we recorded relevant plant and soil properties, the same as in our case study. Ecosystems were divided into grassland, cropland, forest, and tundra. Warming methods were divided into open-top chamber (OTC) warming, infrared heater (IH) warming, HC warming, and other warming methods (including horizontal curtains, reflective film, and translocation). Warming magnitudes were divided into <2 and ≥2°C. Experimental durations were divided into <5 and ≥5 years. We also recorded a wide range of environmental variables related to warming experiments, including longitude, latitude, altitude, MAT, MAP, and warming-induced decreased soil water content (DSWC). In the end, 157 observations (https://github.com/yancypku/W-GHG) were included in this study.

In total, there are 53 warming experiments (including this study) around the world (meeting our selection criteria), of which 17 were distributed in cropland, 12 in forest, 23 in grassland, and 1 in tundra (Figure S5). In detail, of all 157 observations, 79 were derived from grassland, 46 from cropland, 29 from forest, and three from tundra (Figure S6). There were several ways to increase the temperature in ecosystem-scale field experiments (Zhu & Chen, 2020): OTC, IH, HCs, and other warming methods (including horizontal curtains, reflective film, and translocation). Among these warming experiments, more than 60% of them were warmed by OTC, with relatively few using other warming methods (Figure S6). Furthermore, about 60% of these experiments were warmed with the magnitude <2°C, and others were warmed by ≥2°C (Figure S6). More than 90% of the experimental warming durations were <5 years, and more than 5 years of experimental warming durations were relatively rare (Figure S6).

The effect size of warming on each variable was quantified by calculating the natural logarithm of response ratios (RR) (Hedges et al., 1999) (Equation 1):

$$\mathrm{RR} = \ln\left(\overline{X}_T / \overline{X}_C\right), \tag{1}$$

where $\overline{X}_T$ and $\overline{X}_C$ are the mean values of variables in warming and ambient treatments, respectively.

The variance (v) of each RR was calculated by Equation (2):

$$v = \frac{S_T^2}{N_T \overline{X}_T^2} + \frac{S_c^2}{N_c \overline{X}_c^2}, \tag{2}$$

with N_T and N_C as the sample sizes, S_T and S_C as the standard deviations of means in warming and ambient treatments, respectively.

As the values of CH_4 or N_2O fluxes might be negative (positive values mean gas emission and negative values mean gas uptake), we used Hedges'*d* (Hedges & Olkin, 1985) as the effect size to indicate the effects of warming on these two variables (described in detail by Chen et al., 2020). The *rma* function from the R package "*metafor*" was used to evaluate the weighted effect size and 95% confidence interval (CI) by random-effects models (Chen et al., 2022). The effects of warming were considered significant if the 95% CI did not overlap zero. The between-group heterogeneity test (Q_B) was used to compare the differences in weighted effect sizes among groups divided by ecosystem, warming method, magnitude, and duration. A significant Q_B value ($p < .05$) suggested that the weighted effect sizes differed among groups. We also estimated the relative importance of variables by calculating the sum of Akaike weights for all the models that included this predictor (based on mixed-effects meta-regression model), using the "*glmulti*" package in R (Calcagno & de Mazancourt, 2010; Chen et al., 2022). A cut-off of 0.8 was set to differentiate the nonessential and important predictors (Calcagno & de Mazancourt, 2010; Terrer et al., 2016). In addition, regression analyses showed the relationships between RR of CH_4 or N_2O fluxes and MAT. All the statistical analyses were applied using the R (version 4.2.1) (R Core Team, 2022). The statistical significance was set at $p < .05$.

3 | RESULTS

3.1 | Whole-soil warming effects on soil microclimates, plant and soil properties

Soil temperature and moisture showed clear seasonal patterns across the soil profile (5, 10, 20, 30, 40, 60, 80, and 100 cm), with high values during the growing season (especially temperatures in July or August) and low values during the non-growing season (temperatures in January or February) (Figures S3 and S4). In this whole-soil warming experiment, we wanted to heat the whole-soil-profile of 0–100 cm (below 100 cm is the parent material) by 4°C. However, although we buried two rings of HCs in the surface soil, the warming of the surface soil (0–10 cm) still did not reach the target over 3 years (from June 2018 to September 2020, only 2.55°C for 5 cm depth, Figure S2b). Meanwhile, the soils of 10–100 cm were almost heated by 4°C (Figures S2b and S3). The mean temperature was 3.89°C for ambient treatment and 7.55°C for warming treatment across the soil profile (Figure S2a). Nevertheless, whole-soil warming did not significantly alter the soil moisture (soil gravimetric water content measured by weighing during soil sampling or volumetric water content measured by sensors continuously, Figures S2c and S4). In addition, both plant and soil properties that we measured did not respond significantly to whole-soil warming (Table S1).

3.2 | Whole-soil warming effects on CH_4 and N_2O fluxes

Over the 3 years of whole-soil warming treatment, we found significant effect of warming on N_2O flux ($p < .01$), while there was no significant effect of warming on CH_4 flux (Figure 1). There were also significant temporal fluctuations in CH_4 and N_2O fluxes ($p < .001$), but there was no significant interaction between warming treatment and measurement year (Figure 1). In each year after the warming treatment commenced, either 2018, 2019, or 2020, we found that warming could enhance N_2O flux ($p = .055$, 121% increase in 2018; $p = .053$, 90% in 2019; $p = .032$, 112% in 2020, respectively, Figure S7). However, CH_4 flux did not respond significantly to warming in any of the 3 years ($p > .10$, Figure S7). According to the mean results during the 3 years, whole-soil warming significantly increased soil N_2O flux by 101%, from $3.32 \pm 0.34\,\mu g\,m^{-2}\,h^{-1}$ in ambient plots to $6.68 \pm 0.60\,\mu g\,m^{-2}\,h^{-1}$ in warming plots ($p = .011$, Figure 2b). In contrast, soil CH_4 flux was not altered significantly by 3 years of warming (-54.9 ± 4.87 and $-64.9 \pm 4.54\,\mu g\,m^{-2}\,h^{-1}$ in ambient and warming plots, respectively, Figure 2a). Based on the sustained GWP method (SGWP100) and expressed as CO_2-equivalents, the effect of whole-soil warming on SGWP was not significant (-13.8 ± 4.61 g CO_2-eq m^{-2} in ambient plots and -9.77 ± 1.79 g CO_2-eq m^{-2} in warming plots, Figure S8). Interestingly, we found a significant correlation between CH_4 and N_2O fluxes and soil temperature ($p < .001$), but not with soil moisture (Figure 3). With increasing soil temperature, the uptake of CH_4 was stronger, while the emission of N_2O was also higher (Figure 3a,c).

3.3 | Synthesis of warming effects on CH_4 and N_2O fluxes

The responses of different processes of greenhouse gas fluxes and related plant and soil properties to experimental warming were divergent (Figure 4). Experimental warming significantly enhanced AGB by 12.0% and soil available nitrogen (NH_4^+-N by 44.6% and NO_3^--N by 16.9%, Figure 4). In contrast, warming did not significantly change BGB, SOC, TN, MBC, and MBN (Figure 4). For the response of CH_4 and N_2O fluxes to warming, we found that the overall response of both gases was not significant (Figure 4; Figure S9). Ecosystem type, warming magnitude, and warming duration had no significant effect on the responses of CH_4 and N_2O fluxes to experimental warming

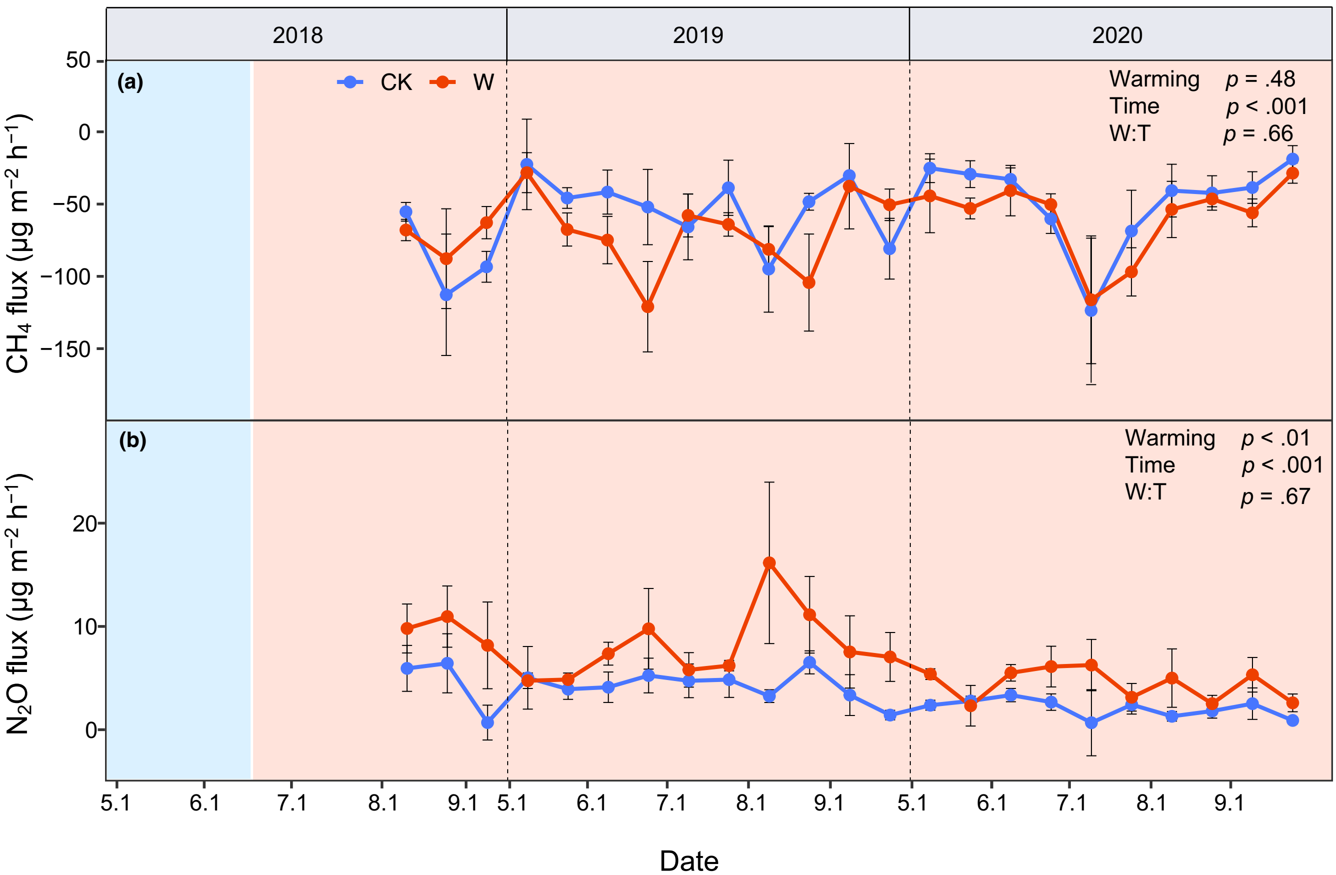

FIGURE 1 Temporal dynamics of CH_4 and N_2O fluxes under ambient (CK) and warming (W) treatments over 3 years. (a) CH_4 flux and (b) N_2O flux. In 2018–2020 growing season, measurements were made every 2 weeks. The light blue areas represent the pre-treatment period (before June 17, 2018), while the orange areas represent 3 years of whole-soil warming periods (from June 2018 to September 2020). Blue indicates ambient treatment and red indicates warming treatment. Error bars are standard errors ($n = 4$).

(Figure S9). Warming method affected the response of CH_4 flux to warming, but not the response of N_2O flux to warming. According to the results of model-averaged relative importance, the response of CH_4 flux to warming was also affected by MAT and warming method, while the response of N_2O flux was not related to these variables (Figure S10). OTC warming had a positive effect on CH_4 flux, but experimental warming by other methods had minor effects on CH_4 flux (Figure S9a).

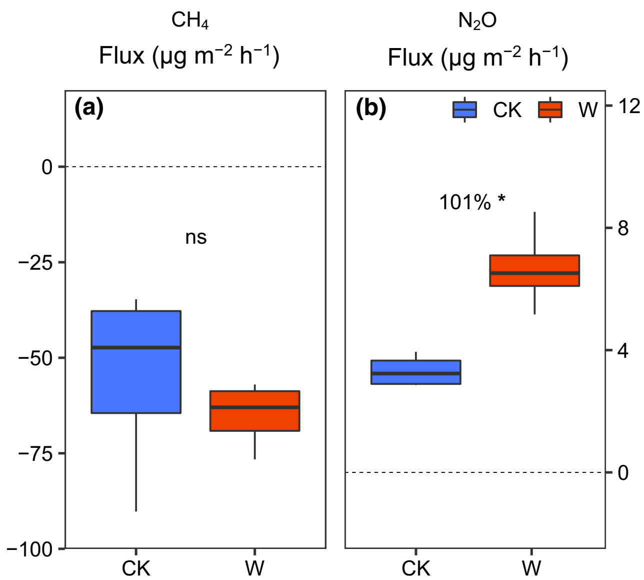

FIGURE 2 The average (a) CH_4 and (b) N_2O fluxes for growing season measurements over 3 years of whole-soil warming (from June 2018 to September 2020). Blue indicates ambient treatment (CK) and red indicates warming treatment (W). Statistical significance of differences between control and warming treatment is shown by asterisk (*$p < .05$, $n = 4$) or as non-significant (ns).

4 | DISCUSSION

4.1 | Effects of warming on CH_4 fluxes

The negative values of CH_4 fluxes in both ambient treatment and warming treatment of the whole-soil warming experiment indicated that the soil in this alpine grassland is a net sink of atmosphere CH_4 (Figures 1 and 2). The results from this experiment suggested that whole-soil warming did not significantly alter soil CH_4 uptake (Figure 2), which is consistent with the results from the global-scale meta-analysis (Figure 4). The unchanged CH_4 uptake with warming is in agreement with previous results from alpine grassland (Wu et al., 2020; Zhao et al., 2017), but differs from previous studies in alpine grassland that warming reduced or stimulated CH_4 uptake (Lin et al., 2015; Wang et al., 2021; Zhu et al., 2015). Elevated temperature could reduce soil moisture, which may be an important reason to alter CH_4 flux due to changes in soil air permeability and oxygen availability (Chen et al., 2017). At the same site, Lin et al. (2015) also found that increased CH_4 diffusion due to soil drying under warming was a potential mechanism to explain the positive effect of warming on soil CH_4 uptake. However, the whole-soil warming in this study did not significantly change soil moisture (Figures S2c

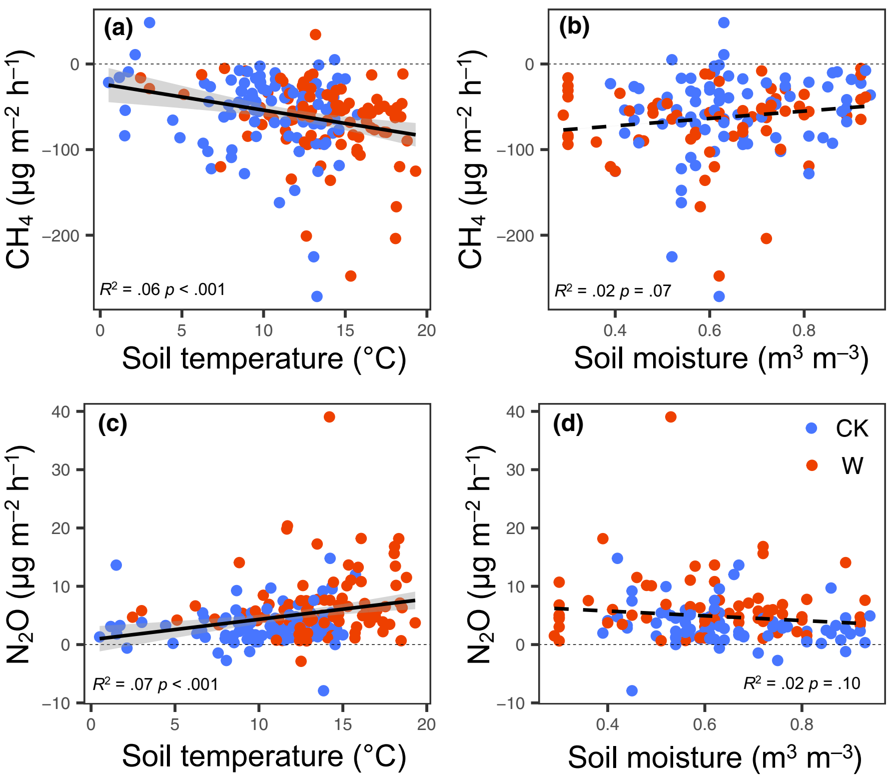

FIGURE 3 CH_4 and N_2O fluxes in relation to soil temperature (a, c) and soil moisture (b, d) at surface soil (0–10 cm). Blue points represent ambient (CK) treatment and red points represent warming (W) treatment ($n = 4$) based on the 3-year (2018–2020) whole-soil warming experiment.

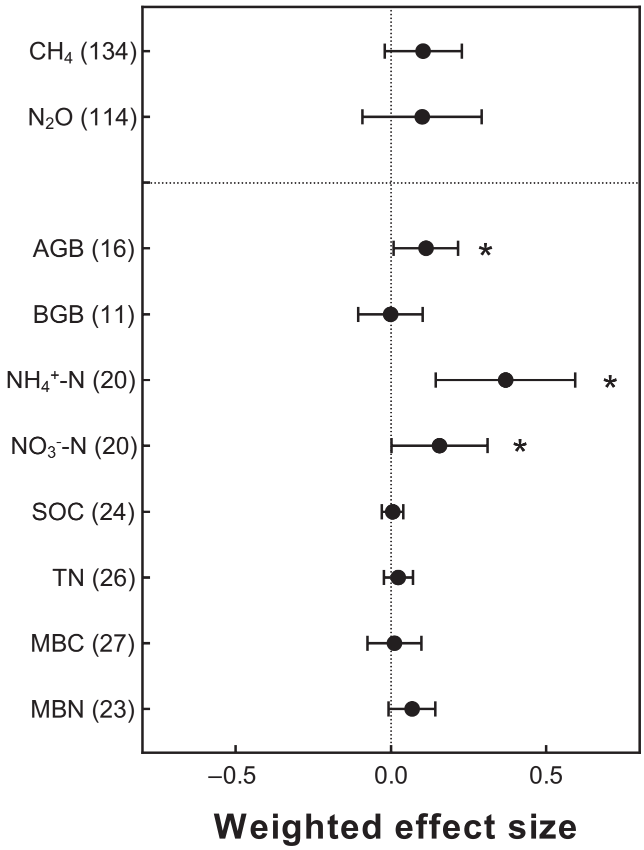

FIGURE 4 The responses of fluxes (CH_4 and N_2O) and related plant (AGB and BGB) and soil properties (NH_4^+-N, NO_3^--N, SOC, TN, MBC, and MBN) at the surface soil (0–10 cm) to warming based on the global-scale meta-analysis of field warming experiments. AGB, aboveground biomass; BGB, belowground biomass; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen; SOC, soil organic carbon; TN, total nitrogen. The sample size for each variable is in parentheses. The vertical dashed line represents weighted effect size = 0. Error bars represent 95% confidence intervals (CIs). If the 95% CI did not overlap zero, the effect of warming was statistically significant (denoted by *).

and S4). Perhaps due to the unique design of the whole-soil warming experiment (e.g., plant canopy and aboveground air were not warmed), not only our study, but also the remaining two whole-soil warming experiments (Nottingham et al., 2020, Pries et al., 2017), showed that SWC was not significantly changed by the warming. Given that the net CH_4 flux is determined by both methanogenic and methanotrophic processes, the response of methanogens and methanotrophs to increased temperature is very crucial (Galbally et al., 2008). Heinzle et al., (2023) proposed that methanotrophs were associated with soil NH_4^+-N concentrations, and higher soil NH_4^+-N due to warming would inhibit the abundance and activity of methanotrophs. However, our study found that whole-soil warming did not significantly change the measured plant and soil properties (including soil NH_4^+-N, Table S1), and no significant relationships were found between CH_4 flux and these plant and soil properties (Figure S11). This may be related to the short duration (i.e., 3 years) of this whole-soil warming experiment. We need to investigate the functional genes of two groups of soil microbes (*mcrA* and *pmoA* genes indicate methanogens and methanotrophs in the soil) that regulated the response of CH_4 flux to warming (Freitag et al., 2010) in the future. In addition, CH_4 uptake exhibited a significant positive correlation with soil temperature (Figure 3a), while the results of the meta-analysis demonstrated a significant correlation between the response of CH_4 flux to warming and MAT (Figure S12a). We only measured CH_4 flux in the alpine grassland ecosystem during the growing season, but Wang et al. (2021) revealed that warming increased the CH_4 uptake in the non-growing season by 36%. Therefore, ignoring the response of CH_4 flux in the non-growing season may be another reason why CH_4 uptake was not significantly altered by whole-soil warming in this study.

4.2 | Effects of warming on N_2O fluxes

The positive values of N_2O fluxes in both ambient and warming plots indicated that the alpine grassland soils were a net source of atmosphere N_2O (Figures 1 and 2). In our study, the whole-soil warming significantly promoted N_2O emission (Figures 1 and 2), which was consistent with previous studies (Heinzle et al., 2023; Li et al., 2020; Wang et al., 2021; Zhang et al., 2022). Nonetheless, the N_2O flux did not respond significantly to experimental warming in the meta-analysis (Figure 4), while previous studies also showed warming either reduced (Wang et al., 2021; Zhao et al., 2017) or did not change N_2O flux (Dijkstra et al., 2012; Hu et al., 2010; Zou et al., 2018). The production of N_2O is derived from soil nitrification and denitrification with NH_4^+-N and NO_3^--N as substrates respectively (Liu & Greaver, 2009). Previous studies showed that enhanced soil temperatures directly promoted the growth and activity of nitrifiers and denitrifiers, leading to greater production of N_2O (Cantarel et al., 2012). However, we did not find that whole-soil warming significantly promoted soil microbial biomass (Table S1). Additionally, increased temperatures will regulate the response of N_2O flux to warming by changing soil moisture. Warming-induced thawing could increase SWC and promote N_2O emission, while warming-induced DSWC could elevate the concentration of oxygen in the soil pores and therefore inhibit N_2O production through denitrification (Brown et al., 2012). Nevertheless, the whole-soil warming treatment in our experiment did not significantly change soil moisture (both soil gravimetric or volumetric water content).

An earlier study at the same alpine grassland showed that warming with aboveground infrared heaters caused a significant increase in soil N_2O emission in 2007 (Hu et al., 2010). Likely, the top-down warming promoted decomposition of plant litter and soil organic matter which could lead to more mineral N returning to the soil, thus leading to increased N_2O flux from the alpine grassland (Hu et al., 2010). Blagodatskaya et al. (2014) also found that increased N substrate availability due to warming could cause more N_2O flux from soil. Therefore, we inferred that there may be two reasons why the whole-soil warming caused more N_2O emissions from the alpine grassland in our experiment. The first is that elevated temperatures would increase plant biomass (especially BGB increased insignificantly by 9.4%, Table S1), leading to more plant litter (Figure S13) into soils and thus promoting N_2O emission. Another important reason is that warming could accelerate rates of N mineralization, which leads to higher concentrations of NH_4^+-N and NO_3^--N (NH_4^+-N and NO_3^--N are the main precursor substances of N_2O production), thus promoting N_2O emissions (Smith, 1997). The whole-soil warming had a tendency to increase NH_4^+-N (by 12%) and NO_3^--N (by 56%) in soils, and the meta-analysis also found that warming significantly increased them (Figure 4). Therefore, the whole-soil warming increased N_2O emission (by 101%) in this study, which was also consistent with the significant positive correlation between MAT and N_2O emission (Figure 3b).

4.3 | Uncertainties and implications for future research

According to the results of the meta-analysis, the majority of the field warming experiments were heated by OTC and IH, accounting for more than 75% of the total experiments (Figure S6). Moreover, we found that the warming method significantly affected the response of GHGs to warming, especially the CH_4 flux (Figure S10). In the current field experiments, however, most warming experiments (warmed by OTC and IH) can only increase the temperature of surface soils (<20 cm depth), while the deep soils (>20 cm) store more than 50% of global SOC stocks in the whole soil profile (Jobbágy & Jackson, 2000; Pries et al., 2017). This study is the first to show the responses of CH_4 and N_2O fluxes to the whole-soil warming, which may explain the inconsistent results between our case study and the meta-analysis (we found that whole-soil warming elevated the N_2O emission but did not change the CH_4 uptake, while the meta-analysis showed that warming had no significant effect on both GHGs). Therefore, in the future, an important frontier is to establish globally networked whole-soil warming experiments (including the same warming method and magnitude) across different ecosystems and sites to elucidate the general effects of climate warming on key ecosystem processes, especially the responses of greenhouse gas fluxes to warming.

We also need to address the responses of CH_4 and N_2O fluxes in the non-growing season to warming, as most experiments (including this study) only focused on their responses in the growing season. Non-growing season GHGs fluxes can account for a high proportion of the annual budgets. Wang et al. (2021) suggested that cumulative CH_4 uptake in the non-growing season was 40% of its annual budget in an alpine grassland, and the cumulative N_2O emission in the non-growing season was up to 59% of the annual flux. Therefore, the absence of the non-growing season data could cause large uncertainty in assessing the annual budget and ecosystem-climate feedback (Treat et al., 2018). In addition, it is important to examine the responses of GHGs emission or uptake from different soil depths or layers to warming, because climate models predicted that the effects of future warming on deep soils and surface soils will be similar (Pries et al., 2018; Soong et al., 2020). It has been shown that soil respiration at all depths (0–80 cm) respond significantly to the whole-soil warming (+4°C, Soong et al., 2021), but there have been no studies to determine the responses of CH_4 and N_2O fluxes to climate warming at different soil depths.

The results from our meta-analysis suggested that more than 90% of field warming experiments had an experimental duration <5 years (Figure S6), including the whole-soil warming experiment (only 3 years from 2018 to 2020) in our study. Nevertheless, the responses of some processes of the ecosystem carbon cycling were significantly related to warming duration (Chen et al., 2020; Luo et al., 2011), which may also result in underestimation or overestimation of the responses of CH_4 and N_2O fluxes to climate warming. Heinzle et al. (2023) determined the effects of warming duration on CH_4 and N_2O fluxes based on a soil warming experiment in a temperate mountain forest. The results showed that the response of both CH_4 and N_2O fluxes decreased in the sixteenth year of soil warming compared to the second year. Therefore, we also need to establish more field warming experiments with a long duration to better predict the future responses of GHGs fluxes to warming, which could improve the accuracy of ecosystem model predictions on the important GHGs fluxes (including CH_4 and N_2O) under climate warming.

5 | CONCLUSION

In summary, this study is the first to investigate the effects of whole-soil warming on CH_4 and N_2O fluxes. The whole-soil warming significantly increased soil N_2O emission (101%), but had a minor effect on soil CH_4 uptake in the Tibetan alpine grassland. However, the responses of CH_4 and N_2O fluxes to warming were not significant in the global-scale meta-analysis. Importantly, both CH_4 uptake and N_2O emission were positively correlated with soil temperature in the experiment. Warming-induced higher plant litter and available N in soils may be the main reason for the higher N_2O emission under whole-soil warming in the alpine grassland. We also call for establishing a coordinated distributed whole-soil warming experiment network to study the long-term responses of CH_4 and N_2O fluxes to warming from different soil depths over year-round (both the non-growing season and growing season). Therefore, the comprehensive analysis of warming effects on GHGs (including CH_4 and N_2O fluxes) will help us better understand the response mechanisms of the carbon and nitrogen cycling to climate warming, and also allow us to more accurately assess and predict the ecosystem-climate feedbacks under realistic warming scenarios in the future.

AUTHOR CONTRIBUTIONS

Ying Chen: Data curation; formal analysis; writing – original draft; writing – review and editing. **Mengguang Han:** Formal analysis; writing – original draft. **Wenkuan Qin:** Data curation; formal analysis. **Xudong Wang:** Data curation. **Yanhui Hou:** Data curation. **Zhenhua Zhang:** Project administration. **Biao Zhu:** Conceptualization; funding

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ACKNOWLEDGEMENTS

We thank the staff at the Haibei station of Chinese Academy of Sciences for providing climate data and logistical support in the field. We also sincerely thank all the scientists whose data were included in this meta-analysis. This study was financially supported by the National Key Research and Development Program of China (2022YFF0801902), the National Natural Science Foundation of China (42141006 and 31988102), and the China Postdoctoral Science Foundation (2022M720252). We are also grateful to two anonymous reviewers and the handling editor for their constructive comments and insightful suggestions which greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.24449089.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Chen, Y., Han, M., Qin, W., Hou, Y., Zhang, Z., & Zhu, B. (2023). Effects of whole-soil warming on CH_4 and N_2O fluxes in an alpine grassland. *Global Change Biology*, *30*, e17033. https://doi.org/10.1111/gcb.17033