



Effects of warming and precipitation changes on soil GHG fluxes: A meta-analysis

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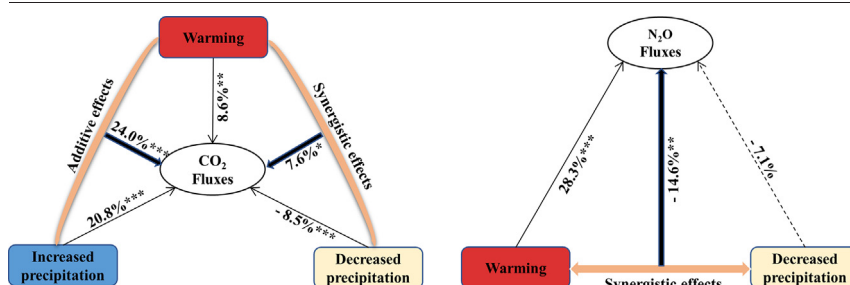
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HIGHLIGHTS

- A meta-analysis of warming and precipitation changes effects on GHG fluxes were conducted.
- The effects of warming and decreased precipitation on CO₂ and N₂O emissions were synergistic.
- Responses of soil GHG fluxes depended on climate and manipulation treatment.
- Threshold effects of soil moisture and temperature on CO₂ and N₂O emissions were observed.

GRAPHICAL ABSTRACT



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ABSTRACT

Increased atmospheric greenhouse gas (GHG) concentrations resulting from human activities lead to climate change, including global warming and changes of precipitation patterns worldwide, which in turn would have profound effects on soil GHG emissions. Nonetheless, the impact of the combination of warming and precipitation changes on all three major biogenic GHGs (CO₂, CH₄ and N₂O) has not been synthesized, to build a global synthesis. In this study, we conducted a global meta-analysis concerning the effects of warming and precipitation changes and their interactions on soil GHG fluxes and explored the potential factors by synthesizing 39 published studies worldwide. Across all studies, combination of warming and increased precipitation showed more significant effect on CO₂ emissions (24.0%) than the individual effect of warming (8.6%) and increased precipitation (20.8%). Additionally, warming increased N₂O emissions (28.3%), and decreased precipitation reduced CO₂ (−8.5%) and N₂O (−7.1%) emissions, while the combination of warming and decreased precipitation also showed negative effects on CO₂ (−7.6%) and N₂O (−14.6%) emissions. The interactive effects of warming and precipitation changes on CO₂ emissions were usually additive, whereas CO₂ and N₂O emissions were dominated by synergistic effects under warming and decreased precipitation. Moreover, climate, biome, duration, and season of manipulations also affected soil GHG fluxes as well. Furthermore, we also found the threshold effects of changes in soil temperature and moisture on CO₂ and N₂O emissions under warming and precipitation changes. The findings indicate that both warming and precipitation changes substantially affect GHG emissions and highlight the urgent need to study the effect of the combination of warming and precipitation changes on C and N cycling under ongoing climate change.

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1. Introduction

Climate change caused by increased atmospheric concentrations of greenhouse gases (GHG) has led to global warming and precipitation pattern changes worldwide, which in turn profoundly affects GHG emissions (Armarego-Marriott, 2020). Among the three major biogenic GHGs (CO_2 , CH_4 and N_2O), CO_2 contributes approximately 76.0% of the greenhouse effect (Fagodiya et al., 2017). However, the global warming potential of CH_4 and N_2O are 25 and 298 times greater than that of CO_2 on the centennial scale, and both contribute 22.2% to the total emissions (Greenhouse Gas Bulletin, 2020; IPCC, 2013). Temperature and precipitation are key drivers of terrestrial ecosystem processes (Wu et al., 2011), both can alter soil microclimate (Harte et al., 1995), carbon (C) allocation from aboveground to belowground (Zhang et al., 2015), soil substrate availability and microbial activity (Zhou et al., 2018; Zhang et al., 2019), thereby impacting GHG emissions. Therefore, understanding the feedback between terrestrial GHG emissions and ongoing climate change is essential for predicting C and N cycling changes in terrestrial ecosystems.

A growing number of studies focus the response of soil GHG emissions to warming and precipitation changes. However, these individual studies have produced inconsistent results, including positive effects (Peng et al., 2014; Cui et al., 2018; Liu et al., 2020), negative effects (Niu et al., 2008; Pendall et al., 2013), or no effect (Phillips et al., 2011; Wu et al., 2012) under experimental warming, as well as under precipitation change (Liu et al., 2002; Fierer and Schimel, 2003; Wang and Fang, 2009; Yan et al., 2018). In general, warming and increased precipitation positively affect plant growth and microbial activity, which promote GHG emissions (Niu et al., 2008; Shi et al., 2012). In contrast, a decline in soil moisture caused by warming and decreased precipitation inhibits plant growth and microbial activity, resulting in reduced soil GHG emissions (Hartmann and Niklaus, 2012; Shi et al., 2012). In addition, soil GHG fluxes in different biomes respond differently to global changes (Ward et al., 2013; Du et al., 2020) due to vegetation composition, soil microorganisms, and root activity differences (de Vries et al., 2012; Wang et al., 2020). The duration of the experiment will also affect the soil GHG flux results (Dacal et al., 2020). For example, the stimulating effect of warming on CO_2 emissions will disappear in the long-term experiments (Wang et al., 2019). Therefore, to gain a comprehensive understanding of the effect of warming and precipitation changes on global GHG emissions, we should consider climate, biomes, and duration of manipulations.

Warming and precipitation changes can simultaneously change soil temperature and moisture. A higher soil temperature will lead to a lower soil moisture, and increased soil moisture will also reduce soil temperature (Liu et al., 2009). Thus, climate mediates the effects of soil temperature and soil moisture on soil GHG emissions. In colder regions, the soil organic C and microbial decomposition are more sensitive to experimental warming, which leads to a higher sensitivity to GHG emissions (Li et al., 2012; Crowther et al., 2016). In contrast, in semi-arid and arid regions, where soil moisture becomes a major limiting factor of ecosystems, the stimulation of plant growth and microbial activity by warming may be offset by decreased soil moisture (Verburg et al., 2009). Therefore, considering the comprehensive effect of warming and precipitation changes on soil GHG fluxes, it is necessary to improve our ability to predict soil C and N cycling in terrestrial ecosystems under climate changes.

Recently, several meta-analyses have examined the effects of warming and precipitation changes on GHG fluxes, but such studies have focused mainly on one type of GHG fluxes under one type of climate change. For example, Bai et al. (2013) and Li et al. (2019b) and Homyak et al. (2017) studied the effect of individual warming or precipitation changes on N_2O emissions; Wang et al. (2014) studied the effect of warming on soil respiration, and Liu et al. (2020) studied the impact of warming on all three GHG fluxes. Individual studies focusing on GHG emissions under the combination of warming and precipitation change have increased (Selsted et al., 2012; Wu et al., 2020), but the interaction of warming and precipitation changes on soil GHG fluxes has not been exhaustively synthesized. A global analysis of warming and precipitation changes on soil GHG fluxes would

provide a more accurate assessment of the global soil GHG budget under ongoing climate change.

To address these knowledge gaps in how soil GHG fluxes from terrestrial ecosystems response to combination of warming and precipitation change, we compiled 385 paired observational data from 39 published papers to quantitatively synthesize GHG fluxes under warming and precipitation changes. The objectives of this study were to investigate (1) the global patterns and sensitivities of soil GHG fluxes in response to warming and precipitation changes; (2) the impacts of biomes, climates, manipulation treatment, and other factors on soil GHG fluxes; and (3) threshold effects of changes in soil temperature and soil moisture on soil GHG fluxes caused by warming and precipitation changes. These results will help make thorough inquiries and predict terrestrial GHG emissions under ongoing climate change.

2. Materials and methods

2.1. Data preparation

We searched for peer-reviewed journal articles using the Web of Science, Google Scholar and China National Knowledge Infrastructure from 2005 to October 2020 using the following search terms: (warming and precipitation/warming and rainfall/warming and drought/increased temperature and precipitation/increased temperature and rainfall/increased temperature and drought/climate change) and (GHG/ CO_2 fluxes/ N_2O fluxes/ CH_4 fluxes/ CO_2 emissions/ N_2O emissions/ CH_4 uptakes/soil respiration). We avoided bias by selecting, articles based on the following criteria: (1) only field experiments were included, and included at least four treatments simultaneously (control (CK), warming (W), precipitation change (P+ or P-), and a combination of warming and precipitation change (WP+ or WP-)) at the same site were selected; (2) the means, standard deviations (SDs) or standard errors (SEs) and sample sizes could be directly extracted from the content, tables or digitized graphs of the publication. In total, our meta-analysis included 385 paired observations from 39 published papers in 37 sites worldwide (Fig. S1).

Environmental variables including latitude and longitude, mean annual temperature (MAT), mean annual precipitation (MAP), biome, treatment season, duration, and warming method were recorded directly from published materials or cited papers. In addition, soil temperature, soil moisture, total aboveground biomass, and total belowground biomass were also collected. When the data were presented graphically, numerical data were obtained using the GET-DATA GRAPH DIGITIZER (ver. 2.20, Russian Federation).

2.2. Data analysis

2.2.1. Individual and combined effects of warming and precipitation changes

The individual effect of a global change driver or the combined effect of a two-driver pair was defined as the response of a specific variable in the treatment compared to the control (Crain et al., 2008). This was described by the natural logarithm of response ratio (lnRR) in this study (Hedges and Curtis, 1999). The individual lnRR for each observation was calculated using Eq. (1):

$$\text{RR} = \ln \left(\frac{\bar{X}_t}{\bar{X}_c} \right) = \ln (\bar{X}_t) - \ln (\bar{X}_c) \quad (1)$$

where \bar{X}_t and \bar{X}_c are refer to variables in the treatment and control groups, respectively. The variance (v_1) of each RR was calculated by Eq. (2) using the sample size (n_t and n_c) and standard deviations (s_t and s_c) of the specific variable in the treatment (t) and control (c) groups.

$$v_1 = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (2)$$

The reciprocal of the variance ($1/v_1$) was considered the weight (w_1) of each RR and used in the calculation of the mean RR (RR_{++}) in Eq. (3), in

which m was the number of groups (e.g., different combinations in treatments), and k was the number of comparisons in the i the group.

$$RR_{++} = \frac{\sum_{i=1}^m \sum_{j=1}^k w_{ij} RR_{ij}}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}} \quad (3)$$

The standard error of the RR_{++} was estimated by Eq. (4).

$$s(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^m \sum_{j=1}^k w_{ij}}} \quad (4)$$

The R software package (v.3.6.3) (R Core Team, 2014) was used to conduct the meta-analysis. Natural logs of the RRs for individual and combined treatments were determined by specifying studies as random factors in the model with the “metafor” package. The weight mean response ratio (RR_{++}) was transformed back to the percentage change using the equation $(e^{\ln RR_{++}} - 1) \times 100\%$. If the 95% confidence intervals (CIs) of the RR did not overlap with zero, the RR was considered indicative of a significant response. Then, the relationship between continuous moderator variables (MAT, MAP, soil temperature, soil moisture, and duration) and $\ln RR$ was assessed by conducting meta-regression. Subgroup analysis was used to assess whether CO_2 emissions, N_2O emissions, and CH_4 uptakes showed different responses to warming and precipitation changes among different biomes, treatment seasons, and warming methods. Besides, the between-group heterogeneity test (Q_b) was performed in OpenMEE (Wallace et al., 2017), which could indicate a significant difference among different groups.

2.2.2. Main and interactive effects

The main effect of a global change factor represents the difference by comparing its net effect in the presence and absence of a second factor, like main effect tests in ANOVA (Crain et al., 2008). We employed Hedge's d to evaluate the main effect sizes of the two factors on the variables and their interaction according to the methods of Gurevitch et al. (1992) and Crain et al. (2008). The main effects of factors A and B (d_A and d_B , A and B indicate warming and precipitation changes, respectively) and their interaction (d_I) were calculated using Eqs. (5)–(7), respectively.

$$d_A = \frac{(\bar{X}_A + \bar{X}_{AB}) - (\bar{X}_B + \bar{X}_C)}{2s} J(m) \quad (5)$$

$$d_B = \frac{(\bar{X}_B + \bar{X}_{AB}) - (\bar{X}_A + \bar{X}_C)}{2s} J(m) \quad (6)$$

$$d_I = \frac{(\bar{X}_{AB} - \bar{X}_A) - (\bar{X}_B - \bar{X}_C)}{2s} J(m) \quad (7)$$

where \bar{X}_C , \bar{X}_A , \bar{X}_B , and \bar{X}_{AB} were means of a variable in the control and treatment groups of A, B and their combination (A + B), respectively. The standard deviation (s), correction term for small sample bias ($J(m)$), and degree of freedom (m) for the main and interactive effects were estimated using Eqs. (8)–(10), respectively.

$$s = \sqrt{\frac{(n_C - 1)s_C^2 + (n_A - 1)s_A^2 + (n_B - 1)s_B^2 + (n_{AB} - 1)s_{AB}^2}{n_C + n_A + n_B + n_{AB} - 4}} \quad (8)$$

$$J(m) = 1 - \frac{3}{4m - 1} \quad (9)$$

$$m = n_C + n_A + n_B + n_{AB} - 4 \quad (10)$$

The variance of d_I (v_2) was estimated by Eq. (11),

$$v_2 = \frac{1}{4} \left[\frac{1}{n_C} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_I^2}{2(n_C + n_A + n_B + n_{AB})} \right] \quad (11)$$

The weighted mean d_I (d_{++}) and standard error [$s(d_{++})$] were calculated according to Eqs. (12) and (13), respectively:

$$d_{++} = \frac{\sum_{i=1}^i \sum_{j=1}^k w_{ij} d_{ij}}{\sum_{i=1}^i \sum_{j=1}^k w_{ij}} \quad (12)$$

$$s(d_{++}) = \sqrt{\frac{1}{\sum_{i=1}^i \sum_{j=1}^k w_{ij}}} \quad (13)$$

where i was the number of groups, k was the number of comparisons in the group, and w was weight, which was also the reciprocal of the variances ($1/v_2$). The 95% CI of d_{++} was calculated as $d_{++} \pm C_{\alpha/2} \times s(d_{++})$, where $C_{\alpha/2}$ was the two-tailed critical value of the standard normal distribution.

The interactions between two drivers were classified into three types: additive, synergistic and antagonistic (Crain et al., 2008). If the 95% CI overlap was zero, the interactive effect was additive. For two-driver pairs whose individual effects were either negative or in opposite directions, the interactions < 0 were synergistic and > 0 antagonistic. In cases where the individual effects were both positive, the interaction effect sizes > 0 were synergistic and < 0 antagonistic. Three-dimensional (3-D) analysis was used to evaluate the interaction effects of soil temperature and moisture on the GHG fluxes.

3. Results

3.1. Effects of warming and precipitation change on soil GHG fluxes

Our results showed that soil CO_2 emissions significantly increased by 8.6%, 20.8%, and 24.0% under W, P+, and WP+ treatments, respectively, whereas CO_2 emissions decreased by 8.5% and 7.6% under P- and WP- treatments, respectively (Fig. 1a). Warming, precipitation changes, and their combinations did not affect CH_4 uptakes (Fig. 1b). In addition, the W treatment significantly increased N_2O emissions (+28.3%). However, WP- treatment significantly reduced N_2O emissions (−14.6%, Fig. 1c).

WP+ and WP- did not significantly affect CO_2 emissions compared to that in precipitation change treatments, but WP+ and WP- altered CO_2 emissions compared to that in warming treatment (Fig. S2a). In addition, WP+ significantly promoted CH_4 uptakes compared to that in increased precipitation treatment, WP+ treatment suppressed CH_4 uptakes compared to that in warming treatment (Fig. S2b). WP- significantly suppressed N_2O emissions compared to that in warming treatment (Fig. S2c).

3.2. Main and interactive effects of global change factors on soil GHG fluxes

The main effects of warming had a significantly negative effect on CO_2 emissions in the WP+ treatment, but warming positively affected on CO_2 and N_2O emissions in WP- treatment. Increased precipitation significantly induced positive effects on CO_2 emissions in WP+ treatment. In turn, decreased precipitation showed negative effects on CO_2 and N_2O emissions in WP- (Fig. 2).

In the two-factor interaction, additive interaction exhibited a substantial predominance (66.0%) in CO_2 emissions compared with synergistic and antagonistic effects in WP+ treatment. The synergistic interactions on CO_2 emissions (18.9%) were more frequent than antagonistic interactions (15.1%) in the WP+ treatment (Fig. 2). The antagonistic effects of CO_2 emissions in the WP- treatment were minimal (16.7%), and the

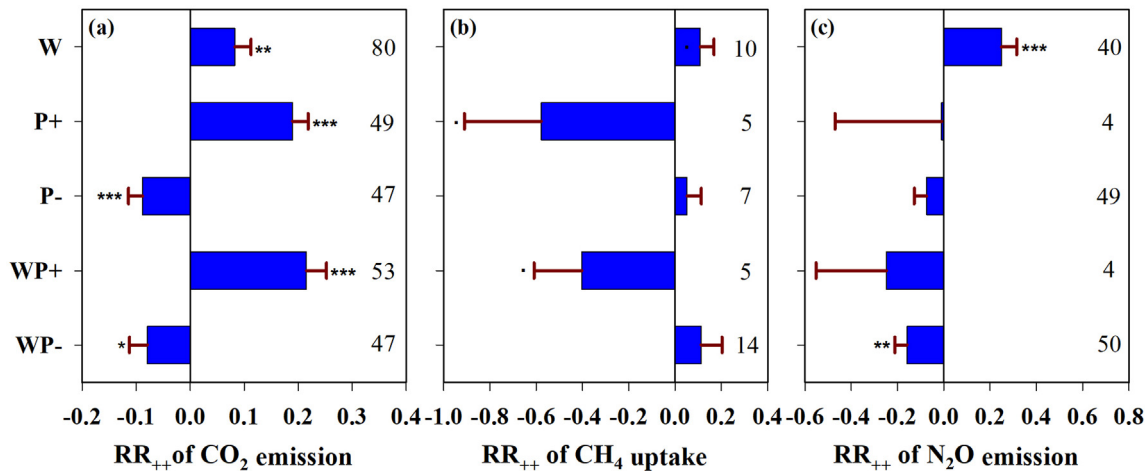


Fig. 1. The weighted mean response ratio (RR₊₊) of warming, precipitation changes, and combination of warming and precipitation changes on CO₂ emissions (a), CH₄ uptakes (b), N₂O emissions (c). The numbers are sampling size. W, P+, and P- represent warming, increased precipitation, and decreased precipitation. Indicated by *** when $P < 0.001$, ** when $P < 0.01$, * when $P < 0.05$ and ns (not statistically significant) when $P > 0.10$.

additive effects (43.8%) were slightly greater than the synergistic effects (39.6%). The synergistic interaction of N₂O emissions in the WP- treatment were dominant (62.0%), and the additive effects (28.0%) were higher than the antagonistic effects (10.0%, Fig. 2).

3.3. Factors affecting the responses of soil GHG fluxes

3.3.1. Effect of biomes, treatment season, climate factors, and durations of manipulation on soil GHG fluxes

The biome affected the CO₂ emissions under the P- and WP- treatments but did not affect CH₄ uptakes and N₂O emissions under warming and precipitation changes (Table 1). Warming significantly increased CO₂ emissions in croplands and forests, whereas P+ and WP+ treatments promoted CO₂ emissions in grasslands, and P- treatment decreased CO₂

emissions in croplands and grasslands (Fig. 3a). In addition, warming promoted CH₄ uptakes in grasslands and N₂O emissions in croplands, and WP- treatments significantly suppressed N₂O emissions in forests and croplands (Fig. 3b and c). CO₂ emissions of P-, P+, and WP+ treatments also changed significantly with treatment season ($P < 0.05$; Table 1), with P+ and WP+ treatments having a significant positive effect during the growing season, while P- treatment showed a significant negative effect on CO₂ emissions (Fig. 3a). Warming also promoted N₂O emissions during the growing season (Fig. 3c). The studies of CH₄ uptakes were all whole year treatments, where W, P-, and P+ treatment had significant effects on CH₄ uptakes (Fig. 3b).

The response of CO₂ emissions to warming and precipitation changes also depends on individual climate factors. The results showed that CO₂ emissions positively correlated with MAT under W, P-, and WP+

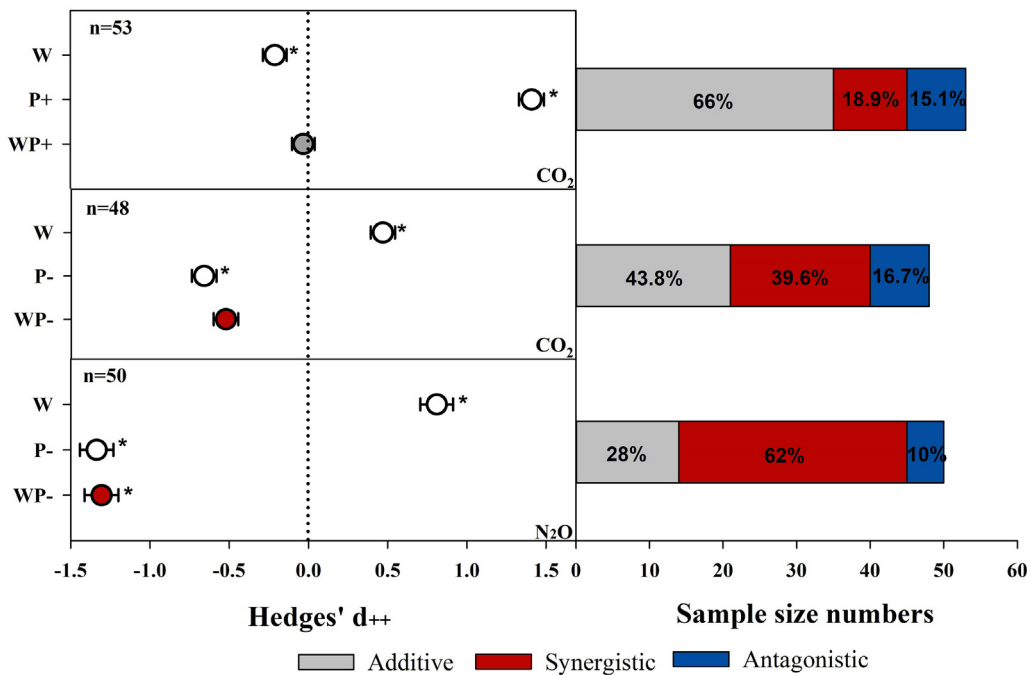


Fig. 2. Frequency distribution of interaction types in individual studies with two-factorial designs for CO₂ and N₂O emissions. W, P+ and P- represent warming, increased precipitation, and decreased precipitation. Asterisk indicated statistical significance ($P < 0.05$).

Table 1

The between-group heterogeneity (Q_b) of soil CO_2 emissions, CH_4 uptakes and N_2O emissions effects on various response variables. W, P+, and P- represent warming, increased precipitation, and decreased precipitation. MAP, mean annual precipitation; MAT, mean annual temperature. The bold font indicates statistical significant.

Manipulative type	Categorical variables	CO_2 emissions			CH_4 uptakes			N_2O emissions		
		df	Q_b	P	df	Q_b	P	df	Q_b	P
W	Biome	2	0.90	0.64	1	0.16	0.69	2	0.46	0.79
	MAT	1	2.53	0.11	1	0.25	0.62	1	0.24	0.62
	MAP	1	2.74	0.10	1	0.01	0.97	1	0.15	0.70
	Treatment seasons	1	0.24	0.63	1			1	0.84	0.36
	Duration	1	2.64	0.11	1	1.92	0.17	1	2.34	0.13
P+	MAT	1	1.00	0.32	1	0.71	0.40	1	10.67	<0.01
	MAP	1	7.05	<0.01	1	0.71	0.40	1	0.10	0.75
	Treatment seasons	1	3.79	<0.05						
	Duration	1	0.14	0.71	1	0.85	0.36	1	0.85	0.36
	Biome	2	9.65	<0.01				2	2.85	0.24
P-	MAT	1	4.88	<0.05	1	0.84	0.36	1	0.02	0.88
	MAP	1	0.15	0.70	1	2.20	0.14	1	0.36	0.55
	Treatment seasons	1	9.82	<0.01				1	3.15	0.08
	Duration	1	7.12	<0.01	1	6.39	<0.05	1	1.81	0.18
	MAT	1	11.18	<0.01	1	0.40	0.53	1	1.03	0.31
WP+	MAP	1	0.39	0.53	1	0.40	0.53	1	1.90	0.17
	Treatment seasons	1	16.00	<0.01						
	Duration	1	4.39	<0.05	1	0.20	0.66	1	0.01	0.93
	Biome	2	9.53	<0.01	1	2.06	0.15	2	2.27	0.32
	MAT	1	0.58	0.45	1	0.10	0.92	1	0.21	0.65
WP-	MAP	1	0.79	0.37	1	4.15	<0.05	1	0.01	0.91
	Treatment seasons	1	0.01	0.94				1	0.41	0.52
	Duration	1	0.07	0.79	1	<0.01	0.99	1	0.44	0.51

treatments (Fig. 4a). In addition, CO_2 emissions showed a positive linear relationship with MAP under W treatment, whereas negative linear relationships between CO_2 emissions and WAP were observed under P+ and WP- treatments. Under P- treatment, CO_2 emissions increased with increasing MAP when MAP < 735 mm and then decreased when MAP > 735 mm (Fig. 4b). However, N_2O emissions showed a significant correlation with MAP only under warming (Fig. 4d). The experimental duration also affected the response of CO_2 emissions to warming and precipitation changes (Table 1). For example, CO_2 emissions decreased with increasing

experimental durations under P+ and WP+ treatments and increased under P- treatment. (Fig. 4c).

3.3.2. Relationships between change in soil temperature and moisture and soil GHG fluxes

Warming and precipitation changes also changed soil temperature and soil moisture, which are related to the RR of GHG fluxes. Across all climate change studies, different relationships between CO_2 and N_2O emissions and changes in soil temperature or soil moisture were observed (Fig. 5). For

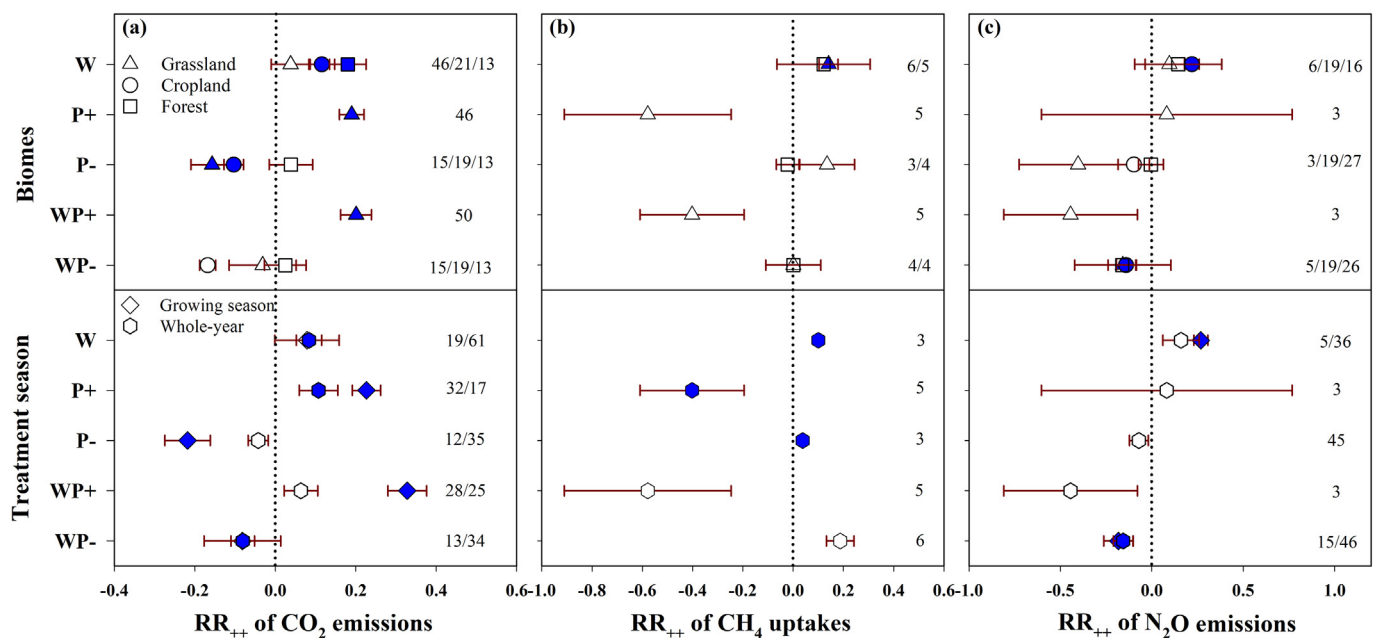


Fig. 3. The weighted mean response ratio (RR_{++}) of biomes and treatment seasons on soil CO_2 emission (a), CH_4 uptakes (b), and N_2O emissions (c) under warming and precipitation changes. W, P+, and P- represent warming, increased precipitation, and decreased precipitation. The error bars represent 95% confidence intervals. The solid blue symbols represent significant differences ($P < 0.05$) between the weighted mean response ratios and zero. The vertical dotted line represents a mean effect size of 0.

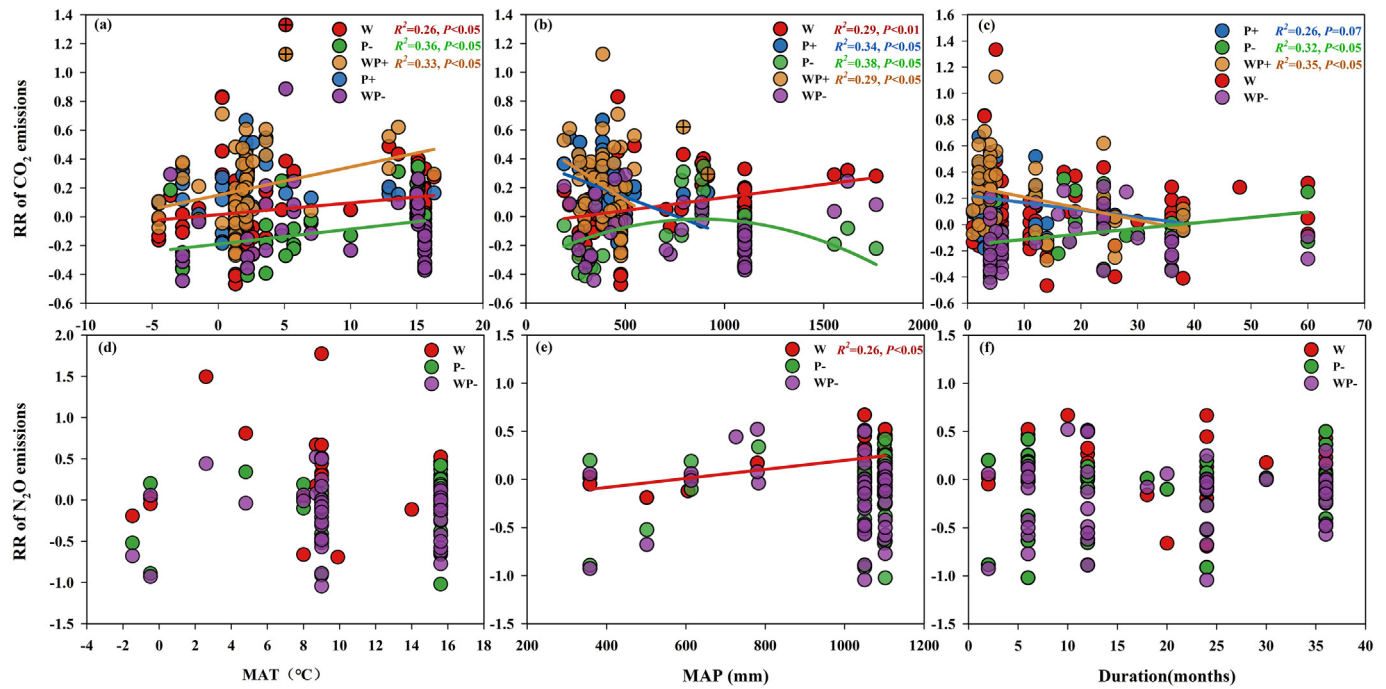


Fig. 4. Relationships between the response ratios (RRs) of MAT, MAP, and duration on soil CO₂ (a, b, c) and N₂O emissions (d, e, f) and under warming and precipitation changes. W, P+, and P- represent warming, increased precipitation, and decreased precipitation. MAP, mean annual precipitation; MAT, mean annual temperature.

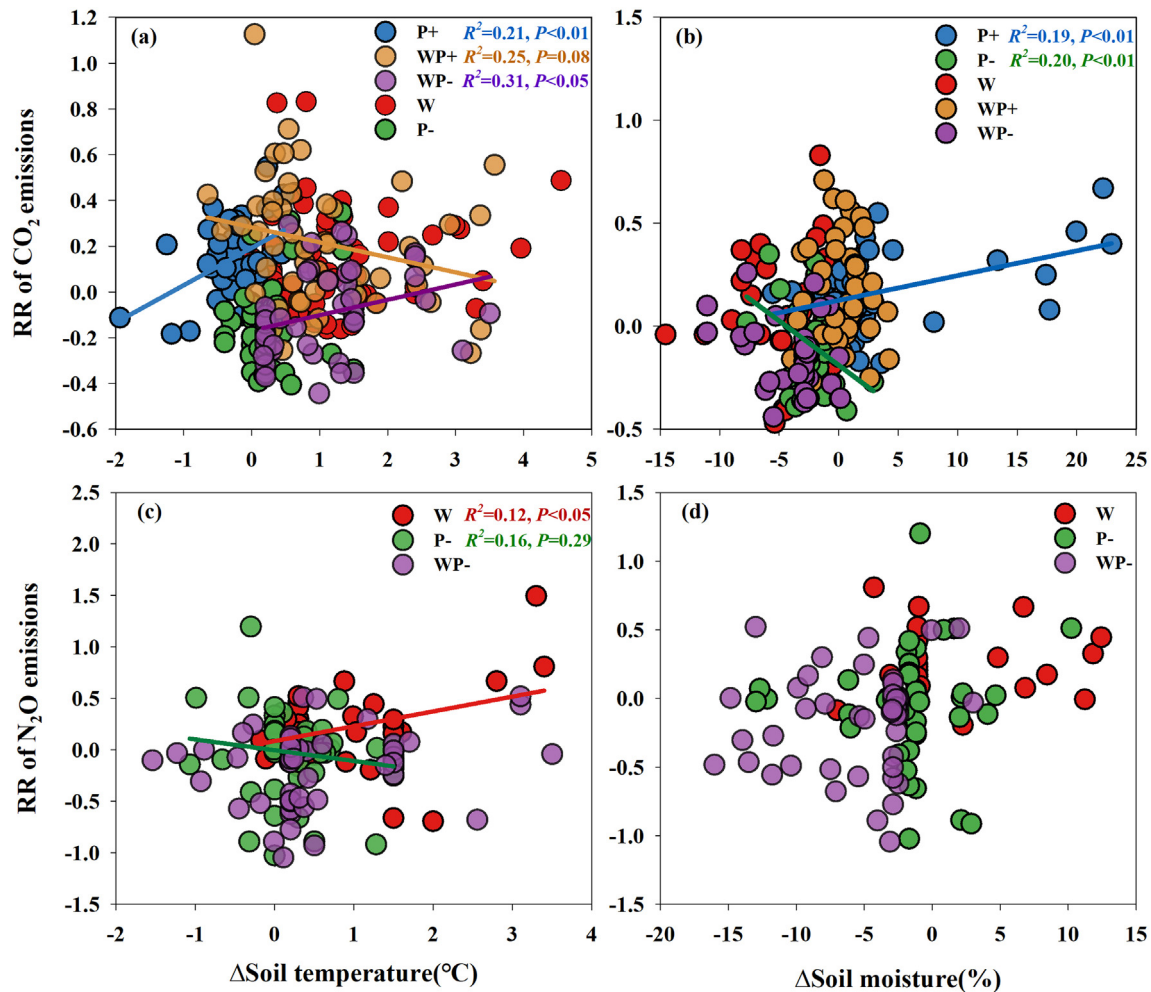


Fig. 5. Relationship between the response ratios (RRs) of soil CO₂ (a, b) and N₂O (c, d) emissions and experimental intensity under warming and precipitation changes. W, P+, and P- represent warming, increased precipitation, and decreased precipitation.

example, CO₂ emissions showed a positive relationship with changes in soil temperature and moisture in the P+ treatment, whereas CO₂ emissions showed a negative relationship with changes in soil moisture in the P- treatment. In addition, an increase in the soil temperature promoted CO₂ and N₂O emissions under warming. 3-D functions integrating satisfied simultaneous both soil temperature and soil moisture changes in all treatments explained 10% and 15% of the variation in CO₂ and N₂O emissions under warming and precipitation changes treatments, respectively (Fig. 6). The results showed that CO₂ emissions increased with increasing soil temperature, and the threshold of Δ soil moisture for CO₂ emissions was -6.27% (Fig. 6a). Moreover, N₂O emissions increased with increasing soil moisture, and the threshold of Δ soil temperature on N₂O emissions was 0.27°C (Fig. 6b).

4. Discussion

4.1. Individual effects of single and combined factors on soil GHG fluxes

GHG fluxes are often affected by plant growth and microorganisms (Singh et al., 2010; Fender et al., 2013), whereas soil temperature and soil moisture play important roles in this process by altering the structure and function of plant roots (Chen et al., 2009) and soil microbes (Sponseller, 2007). This study found that warming and increased precipitation significantly increased CO₂ emissions, consistent with previous studies (Yan et al., 2018; Tan et al., 2021). The combination of increased precipitation and warming showed more considerable stimulation of CO₂ emissions than the warming or increased precipitation treatment individually. In contrast, a larger decrease in CO₂ emissions was observed under decreased precipitation than the combination of warming and decreased precipitation. This indicates that studies focusing only on the effect of warming or precipitation changes on CO₂ fluxes would increase the uncertainty of CO₂ emissions under ongoing climate change, which may be due to shifting of soil temperature and soil moisture under climate change (Bell et al., 2010). For example, warming generally increased soil temperature but decreased soil moisture, and P+ treatment could increase soil moisture and decrease soil temperature. A combination of increased precipitation and warming increased both soil temperature and soil moisture (Fig. S3a and b). Therefore, a higher CO₂ emission was observed under the combination of warming and increased precipitation. In addition, the positive effect of increasing soil temperature can offset part of the negative effect of decreased soil moisture on CO₂ emissions (Schindlbacher et al., 2012). Thus, decreased precipitation showed a larger negative effect impact than the combination of decreased precipitation and warming.

We also investigated the responses of CH₄ uptakes and N₂O emissions to warming and precipitation changes. We found that warming and precipitation changes did not affect CH₄ uptakes (Fig. 1b), and N₂O emissions were significantly stimulated by warming, but the combination of warming and decreased precipitation suppressed N₂O emissions (Fig. 1c), which is likely owing to shifting of soil temperature and soil moisture under climate change (Bell et al., 2010). The larger decrease of soil moisture under WP- treatment (Fig. S3b). Previous studies reported inconsistent effects of warming on N₂O emissions (Bai et al., 2013; Li et al., 2019b). Rising soil temperature caused by warming would increase soil N₂O emissions by affecting soil microbial abundance and N mineralization rates (Qiu et al., 2018). In turn, decreased soil moisture resulting from warming could also suppress N₂O emissions (Davidson et al., 2000). In this study, soil temperature was the most important factor affecting N₂O emissions under warming (Fig. S4f), which could also explain the increased N₂O emissions under warming treatment. Additionally, the limited field experiments focusing on CH₄ uptake under warming and precipitation changes limit our knowledge of the effects of a combination of warming and precipitation changes on CH₄ uptakes (Blankinship et al., 2010; Liu et al., 2019).

The WP+ and WP- treatments significantly increased and decreased CO₂ emissions compared with the W treatment (Fig. S2a). This may be due to changes in soil moisture (Fig. S3d) and total aboveground (Fig. S5c), because WP+ and WP- treatments significantly increased and decreased soil moisture and aboveground biomass compared with the W treatment, respectively (Song et al., 2016; Li et al., 2019a; Su et al., 2019). Additional warming significantly increased CH₄ uptakes compared to the P+ treatment, and additional increased precipitation significantly decreased CH₄ uptakes than under the W treatment (Fig. S2b). This may result from changes in soil moisture, which are usually lower with more potent methane-oxidizing bacterial activity and enhanced CH₄ uptakes, and conversely, reduced CH₄ uptakes (Adamsen and King, 1993; Sjögersten and Wookey, 2002). Meanwhile, WP- treatment significantly suppressed N₂O emissions compared with the W treatment (Fig. S2c). The model selection analysis showed that soil moisture was vital for N₂O under WP- treatment (Fig. S4h), and decreased precipitation can reduce soil moisture, microbial activity, and denitrification to reduce N₂O emissions (Zhang et al., 2010).

4.2. Interactive effects of warming and precipitation changes on soil GHG fluxes

Understanding the interactive effects of warming and precipitation changes on soil GHG fluxes is essential for assessing and predicting global soil GHG changes under ongoing climate change. We found that the

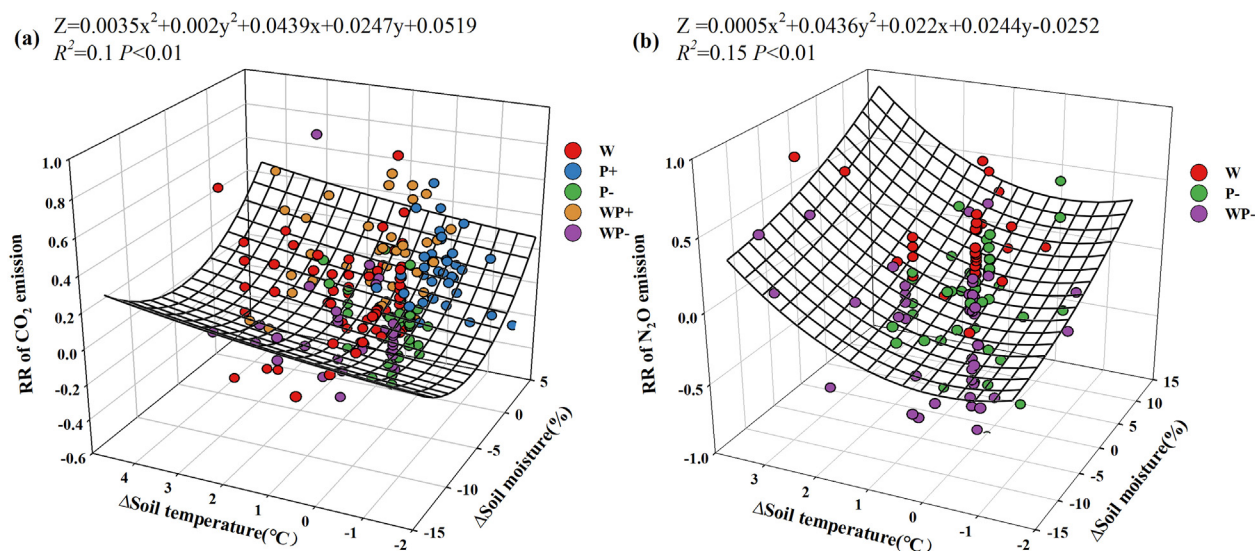


Fig. 6. The response ratios (RRs) of soil CO₂ (a) and N₂O (b) emissions as a function of soil moisture temperature change under warming and precipitation changes. The grid is fitted by a parabolic equation. W, P+, and P- represent warming, increased precipitation, and decreased precipitation treatment, respectively.

additive interaction of warming and precipitation change showed dominance on CO₂ emissions in terms of total individual interactions, but when we pooled all data, the interaction type of warming and decreased precipitation was synergistic (Fig. 2). This discrepancy may result from the large variance in some studies, leading to the overestimation of additive interactions (Crain et al., 2008). We also found that warming and precipitation changes have antagonistic interactions (Fig. 2), which is inconsistent with the results of Zhou et al. (2019), who reported that there were no antagonistic interactions between warming and precipitation changes when studying the interaction of global change factors on soil respiration in grassland ecosystems. This may be attributable to their small sample size (WP-, $n = 10$; WP+, $n = 12$), which would mask potential antagonistic interactions (He et al., 2021).

The interaction of warming and decreased precipitation showed a synergistic interaction with N₂O emissions (Fig. 2), which may be due to the decline in soil microbial biomass and activities, and exacerbating the inhibitory effect on N₂O emissions (Shi et al., 2012). Therefore, the interaction effects of warming and decreased precipitation may profoundly affect N₂O emissions (Hu et al., 2019).

4.3. Responses of soil GHG fluxes to warming and precipitation changes depend on the biome, experimental conditions, and climates

Previous studies have mainly focused on the effect of single factors such as warming or precipitation changes on soil GHG fluxes and have reported inconsistent results (Bijoor et al., 2008; Bork et al., 2019; Wang et al., 2021b), which perhaps due to the different biomes, treatment season, and durations (Bai et al., 2013; Liu et al., 2016). Our results showed that the biome, experimental conditions, and climate have different effects on soil GHG fluxes (Table 1). Warming significantly promoted CO₂ emissions in forests and farmlands but did not affect CO₂ emissions in grasslands (Fig. 3a) forasmuch as decreased soil moisture in grasslands, which could reduce plant and microbial growth and offset the positive effects of warming on CO₂ emissions (Li et al., 2013). We also found that precipitation change significantly affected CO₂ emissions in grasslands (Fig. 3a), indicating that CO₂ emissions are more sensitive to moisture changes in grasslands (Du et al., 2020). In addition, there were significant positive feedbacks of CH₄ uptakes in grasslands and N₂O emissions in cropland, while N₂O emissions in cropland were suppressed under the WP- treatment (Fig. 3b and c), indicating that N₂O emissions in cropland may be more vulnerable to climate change. The above results suggest that biomes should be considered when predicting changes in soil GHG dynamics in the context of future climate change.

The treatment seasons and duration of the P-, P+, and WP+ treatments also significantly affected CO₂ emissions (Figs. 3a and 5c), consistent with previous studies (Zhou et al., 2016; Tan et al., 2021), suggesting that soil moisture changes may have a profound effect on CO₂ emissions at the time scale. Interestingly, the duration did not significantly affect the CO₂ emissions under WP- treatment (Fig. 4c), probably due to because of the dominant effect of warming under WP- treatment (Fig. 3), but the effect of warming diminishes with duration (Wang et al., 2019; Dacal et al., 2020). Furthermore, we did not observe relationships between N₂O emissions and experimental duration in this study (Fig. 4f), which is consistent with the results of Li et al., 2019b. In summary, the high variability of soil GHG fluxes in response to warming and precipitation changes can pose a significant challenge in predicting C and N cycling under ongoing climate change.

A significant positive correlation between MAT and RR of CO₂ emissions was observed in this study, which is consistent with previous studies (Bond-Lamberty and Thomson, 2010). However, it has also been suggested that MAT is negatively correlated with the RR of CO₂ emissions (Wang et al., 2014), and this difference is influenced by the warming method. OTC is the most common warming method in colder regions (Aronson and McNulty, 2009), where CO₂ emissions are more sensitive to warming (Davidson and Janssens, 2006). We also found that CO₂ emissions under warming and precipitation changes were significantly positively correlated

with MAT (Table 1; Fig. 4a), which implies that the sensitivity of CO₂ emissions to warming and precipitation changes maybe higher in warmer regions. Nonetheless, MAT had no significant effect on N₂O emissions (Fig. 4d), which possibly on account of the nitrification and denitrification are directly influenced by soil microorganisms, substrate effectiveness and soil temperature (Shi et al., 2012), making N₂O seasonal fluxes highly variable (Dijkstra et al., 2012). A significant positive correlation between CO₂ emissions and MAP was also observed in warming, but the effects of P+ and WP+ treatments on CO₂ emissions declined with increasing MAP (Table 1; Fig. 4b), consistent with previous studies (Wu et al., 2011). This means that increased precipitation positively impacts CO₂ emissions in arid regions (Thomey et al., 2011). It is worth mentioning that the relationship between N₂O emissions and MAP was significant and positive in the W treatment, which could be attributed to the fact that N₂O emissions were strongly regulated by soil temperature in the W treatment (Fig. S4f). Overall, environmental factors profoundly impact GHG emissions under warming and precipitation changes, and environmental factors should be incorporated into future model predictions.

4.4. Threshold effects of soil temperature and moisture on soil GHG fluxes

Soil temperature and moisture are the two main direct factors affecting soil GHG fluxes. Soil temperature was the best predictor of CO₂ and N₂O emissions under W and P+ treatments, respectively, and soil moisture was a significant predictor of CO₂ and N₂O emissions under WP- treatment (Fig. S4). In general, elevated soil temperature and soil moisture could promote CO₂ emissions (Mizoguchi et al., 2005). Interestingly, there was a negative correlation between soil temperature and CO₂ emissions for the WP+ treatment in this study (Fig. 5a), probably because the impact of soil temperature on CO₂ emissions could be offset or masked by the change in soil moisture (Tu and Li, 2017), and we also found a significant negative correlation between CO₂ emissions and soil moisture under the P- treatment (Fig. 5b). In addition, N₂O emissions were positively correlated with soil temperature under the warming treatment which is consistent with previous findings (Li et al., 2019b), but N₂O emissions were negatively correlated with soil temperature under the P- treatment (Fig. 5c). These results indirectly suggest that there is a threshold effect of soil temperature or soil moisture on soil CO₂ or N₂O emissions under warming and precipitation changes.

Previous studies have only modeled the relationships between soil temperature or soil moisture and CO₂ or N₂O emissions independently (Xu et al., 2013; Liu et al., 2016; Wang et al., 2021a). However, warming and precipitation changes can cause changes in both soil temperature and soil moisture, so we attempted to investigate the relationship between changes in soil temperature and soil moisture on CO₂ or N₂O emissions under warming and precipitation changes simultaneously by constructing 3-D functions of Δ soil temperature and Δ soil moisture with RR of CO₂ or N₂O emissions under all treatments. We found that changes in Δ soil moisture under warming and precipitation changes had a threshold effect on CO₂ emissions. When the reduction of soil moisture was greater than 6.27%, the CO₂ emissions have increased (Fig. 6a), probably due to the positive effect of warming on CO₂ emissions offset the negative effect of decreased soil moisture on CO₂ emissions under warming and precipitation changes (Fig. S4; Martins et al., 2017). We also found a threshold effect of Δ soil temperature for N₂O emissions under warming and precipitation changes (Fig. 6b). The data on N₂O emissions in this study were mainly from areas with high precipitation, elevated soil temperature enhances root respiration and consumes O₂ from the soil to promote N₂O production through anaerobic denitrification and stimulation of microbial activity and abundance (Shi et al., 2012; Saggar et al., 2013). High soil moisture reduces soil aeration, providing an anaerobic environment to promote denitrification for N₂O production (Mathieu et al., 2006). Our study indirectly indicates that optimum soil moisture and temperature may exist for soil CO₂ and N₂O emissions under climate change. However, owing to the lack of data on N₂O emissions under all treatments in this study, the

optimum soil temperature for N₂O emissions needs to be further demonstrated.

4.5. Uncertainty analysis and improvement

This study aimed to understand the impact of warming and precipitation changes on soil GHGs and its potential mechanisms, which would have profound implications for future projections of carbon and nitrogen cycling in terrestrial ecosystems under climate change. Although our findings provide some insights, uncertainties to be considered in future studies remain. For example, the data in this study are mainly from the Northern Hemisphere (Fig. S1), and whether they reflect the overall global situation requires further research. In addition, we found that warming methods also affect the soil GHG fluxes under warming and precipitation change (Fig. S6). Furthermore, there are few long-term in-situ experiments on the combination of warming and precipitation on soil GHG fluxes, thus long-term in-situ experiments considering the warming methods on soil GHGs under climate change should be conducted in the future.

5. Conclusions

In summary, this study analyzed the effects of warming and precipitation changes and their interactions on soil GHG fluxes using a global dataset from different biomes and experimental conditions. The results show that warming and increased precipitation have positive individual and combined effects on CO₂ emissions, and the combined effect is greater than the individual effect. In addition, warming promotes N₂O emissions, and decreased precipitation suppresses CO₂ and N₂O emissions, but the combination of warming and decreased precipitation suppresses CO₂ and N₂O emissions. Warming and precipitation changes had no significant effect on CH₄ emissions. Additionally, the interactive effects of warming and precipitation changes on CO₂ emissions are usually additive, but a synergistic effect is also essential. The synergistic effect of warming and decreased precipitation on N₂O emissions is dominate. Furthermore, the response of soil GHG fluxes to warming and precipitation changes can be affected by climate, biomes, treatment seasons, and durations. Moreover, we found a soil moisture threshold for CO₂ emissions and a soil temperature threshold for N₂O emissions under warming and precipitation changes. These findings indicate that warming and precipitation changes significantly impacts soil GHG emissions. To accurately predict the C and N cycling of terrestrial ecosystems under climate change, more field experiments are needed to explore GHG emissions under ongoing climate change.

CRedit authorship contribution statement

Jingyi Yang: Conceptualization, Methodology, Data curation, Writing-original draft, Formal analysis. **Xiaoyu Jia:** Data curation, Formal analysis. **Hongze Ma:** Software, Formal analysis. **Xi Chen:** Writing-review, **Jin Liu:** Formal analysis. **Zhouping Shangguan:** Writing-review & editing, Supervision. **Weiming Yan:** Methodology, Validation, Writing-review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.154351>.

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