Ecological Processes

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Warming and altered precipitation rarely alter N addition effects on soil greenhouse gas fluxes: a meta-analysis

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Abstract

Background Changes in soil greenhouse gas (GHG) fluxes caused by nitrogen (N) addition are considered as the key factors contributing to global climate change (global warming and altered precipitation regimes), which in turn alters the feedback between N addition and soil GHG fluxes. However, the effects of N addition on soil GHG emissions under climate change are highly variable and context-dependent, so that further syntheses are required. Here, a meta-analysis of the interactive effects of N addition and climate change (warming and altered precipitation) on the fluxes of three main soil GHGs [carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O)] was conducted by synthesizing 2103 observations retrieved from 57 peer-reviewed articles on multiple terrestrial ecosystems globally.

Results The interactive effects of N addition and climate change on GHG fluxes were generally additive. The combination of N addition and warming or altered precipitation increased N_2O emissions significantly while it had minimal effects on CO_2 emissions and CH_4 uptake, and the effects on CH_4 emissions could not be evaluated. Moreover, the magnitude of the combined effects did not differ significantly from the effects of N addition alone. Apparently, the combined effects on CO_2 and CH_4 varied among ecosystem types due to differences in soil moisture, which was in contrast to the soil N_2O emission responses. The soil GHG flux responses to combined N addition and climate change also varied among different climatic conditions and experimental methods.

Conclusion Overall, our findings indicate that the effects of N addition and climate change on soil GHG fluxes were relatively independent, i.e. combined effects of N addition and climate change were equal to or not significantly different from the sum of their respective individual effects. The effects of N addition on soil GHG fluxes influence the feedbacks between climate change and soil GHG fluxes.

Keywords N addition, Warming, Altered precipitation, Global change, CO_2 emission, CH_4 uptake, N_2O emission

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Background

Carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), as the three major greenhouse gases (GHGs) (World Meteorological Organization 2020), have been observed to increase over the past several decades, mainly originating from anthropogenic activities, including fossil fuel combustion, land use change, and chemical fertilizer application (IPCC 2013). Another consequence of the anthropogenic activities is increased nitrogen (N) loads in terrestrial ecosystems (Du et al. 2021; He et al. 2021). N addition can alter the biogeochemical processes of ecosystems and alter soil GHG fluxes (Li et al. 2020; Liu and Greaver 2009), further contributing to changes in both temperature and the hydrological cycle (IPCC 2022). As two key factors regulating terrestrial ecosystem processes, temperature and precipitation influence soil microclimate, microbial activity, and soil substrate availability (Harte et al. 1995; Zhang et al. 2019; Zhou et al. 2018), thus potentially influencing the effects of N addition on soil GHG fluxes (Chen et al. 2021). Therefore, understanding how climate change regulates the feedback between soil GHGs and N addition would improve our capacity to predict future soil GHG fluxes and such potential effects could be incorporated into predictive biogeochemical models.

Globally, researchers have experimentally examined the effects of N addition on soil CO_2, CH_4, and N_2O fluxes. The main underlying mechanisms by which N addition increases soil GHG fluxes are the regulation of plant growth and microbial activities directly associated with soil GHG production and consumption processes (Chen et al. 2021; Niu et al. 2010; Quinn Thomas et al. 2010). In addition, projected shifts in temperature have been documented to enhance microbial activity thereby accelerating soil organic matter decomposition and stimulating soil GHG release (Liu et al. 2020; Zhang et al. 2020). Therefore, warming and N addition can interact to synergistically increase soil GHG fluxes (Chen et al. 2017a; Yang et al. 2022). However, warming can also negate the positive effects of N addition on soil GHGs as warming-induced soil water deficits can suppress microbial activity and plant physiological activity (Zong et al. 2018; Cheng et al. 2022). In addition, the effects of N addition on soil GHG fluxes may be suppressed under decreased precipitation due to reduced plant carbon (C) inputs and limited soluble C substrate availability (Fuchslueger et al. 2014; Aronson et al. 2019). Conversely, higher soil water availability caused by increased precipitation can increase soil labile C availability and microbial activity (Zhou et al. 2016). The findings suggested that stimulated GHG emissions by N addition may particularly occur under high precipitation regimes (Brown et al. 2012).

The effects of N addition in combination with warming or altered precipitation remain ambiguous due to differences in outcomes across ecosystem types, climatic conditions, and experimental methods (Deng et al. 2020; Gong and Wu 2021). Among individual studies, the soil CH_4 fluxes' responses to N addition in combination with warming vary from potential increase to potential decrease (Chen et al. 2017a, b; Wu et al. 2020; Liu et al. 2015). The directions of soil CH_4 fluxes are highly dependent on ecosystem type and soil condition, as soil CH_4 is produced by methanogens in wet anaerobic soils and consumed by methanotrophs in drier aerobic soils (Le Mer and Roger 2001; Ni and Groffman 2018). In addition, the responses of CO_2 to N addition in combination with climate change are dependent on ecosystem type (Lu et al. 2011). The potential mechanisms that alter CO_2 emissions are (a) transfer of nutrients that stimulate microbial growth and respiration and (b) priming effects on SOM decomposition by microorganisms (Fontaine et al. 2007; Janssens et al. 2010; Oertel et al. 2016). For example, N addition in combination with climate change can have a greater impact on soil CO_2 flux in grasslands than in forests due to higher stimulation of autotrophic respiration in grasslands (Zhou et al. 2014). Climate condition is the another key determinant of differences in reported effects in empirical studies. Previous studies have reported that N addition plus increased precipitation at a dry or mesic site could stimulate GHG emissions, as opposed to a wet site, where responses are neutral or even negative (Shi et al. 2021; Wu et al. 2020). The results may be because dry regions are more sensitive to increased precipitation than moist regions. In addition, experimental methods such as the duration and magnitude of N addition, warming, and altered precipitation can drive differences in responses (Sánchez-Martín et al. 2017; Zhang et al. 2008). No overall conclusions have been reached regarding the combined effects of N addition and warming or altered precipitation, limiting our mechanistic understanding of the responses of soil GHG fluxes to global changes. A meta-analysis across multiple ecosystem types with heterogeneous climatic conditions could facilitate adequate assessment of the effects of global change on GHG emissions at the global scale.

The aims of the present study were to (1) determine how warming and altered precipitation contribute to the effects of N addition on soil GHG emissions; (2) evaluate the interactions between N addition and warming or altered precipitation; and (3) explore the major drivers of the context-dependency observed in empirical studies. Accordingly, a meta-analysis of 2103 observations from published articles that reported both single-driver (N addition, warming, increased precipitation, and decreased precipitation) and corresponding two-driver effects on soil GHG fluxes was conducted. The observations were mainly collected from grassland and forest ecosystems in the Northern Hemisphere, particularly China. We hypothesized that (1) warming and increased precipitation will enhance the positive effect of N addition on soil GHG fluxes, while decreased precipitation will inhibit it and (2) these effects vary across different ecosystems and climatic conditions.

Materials and methods

Data compilation

Peer-reviewed articles published before September 2022 were searched in Web of Science (http://apps.webofknowledge.com/) and China National Knowledge Infrastructure (https://www.cnki.net/) using the following search string: ("nitrogen addition" OR "nitrogen deposition" OR "nitrogen fertilization") AND (warming OR precipitation OR rainfall OR drought) AND ("greenhouse gas" OR CO_2 OR "carbon dioxide" OR CH_4 OR methane OR N_2O OR "nitrous oxide"). The inclusion criteria were as follows: (1) experiments were conducted in the field and the impacts of N addition and at least one of the climate change factors (warming, increased, or decreased precipitation) were recorded, including both their single-driver and corresponding two-driver effects; (2) at least one variable among CO_2 emissions, CH_4 emissions, CH_4 uptake, and N_2O emissions was measured; (3) except for climate change factors and N addition, the conditions of the control and treatment groups were the same; and (4) the means, standard deviations (or standard errors), and sample sizes of the variables were directly provided or could be calculated.

The experiments manipulating two or more treatments, including different climate change factors or magnitudes with the same control, were divided into different control–treatment pairs. If the individual and combined effects on GHGs in a particular study were observed several times at different experimental stages, we used all observations to facilitate the evaluation of experimental duration effects. Data were directly extracted from the main text, table, or appendices, or from figures using Engauge Digitizer version 11.2 (Free Software Foundation, Boston, MA, USA). The ecosystem types (desert, cropland, wetland, forest, and grassland), experimental methods (experimental magnitude and experimental duration), climate conditions [mean annual temperature (MAT) and mean annual precipitation (MAP)], and edaphic characteristics (pH, water content, C content, and N content) were extracted from the studies to assess the impacts of moderator variables. If the MAT or MAP of the experimental sites was not provided in the studies, we extracted them from the WorldClim database (https://www.worldclim.org/).

We calculated the De Martonne (1926) aridity index for each experimental site using the MAT and MAP data as follows:

$$\text{Aridity index} = \frac{\text{MAP}}{\text{MAT} + 10} \tag{1}$$

A total of 2103 paired observations were collected from 57 articles. CH_4 emissions were not included owing to the small number of studies. In these articles, 2, 3, 6, 9, and 37 studies were conducted in deserts, croplands, wetlands, forests, and grasslands, respectively, accounting for 4%, 5%, 10%, 16%, and 65% of the studies, respectively (Additional file 1: Table S1). The form of N addition in 92% of the experiments was NH_4NO_3 and 8% were urea, $CaNO_3$, and $Ca(NO_3)_2$. The latitude ranged from 26.32°N to 48.25°N, the altitude from 20 to 4763 m, the MAT from −5.3 °C to 19.1 °C, and the MAP from 200 to 1850 mm (Fig. 1).

Statistical analysis

Individual and combined effects

To quantify the individual and combined effects of N addition, warming, and altered precipitation on soil GHG fluxes, we calculated the response ratio (ln*RR*) as a proxy for effect size as follows:

$$\ln RR = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) \tag{2}$$

where $\overline{X}_t$ and $\overline{X}_c$ are the mean values of the treatment and control groups, respectively. The variance (v) of each ln*RR* was calculated as follows:

$$v = \frac{S_t^2}{n_t\overline{X}_t^2} + \frac{S_c^2}{n_c\overline{X}_c^2} \tag{3}$$

where $\overline{X}_t$, S_t, and n_t represent the mean, standard deviation, and sample size of the treatment group (t), respectively; and $\overline{X}_c$, S_c, and n_c are the mean, standard deviation, and sample size of the control group (c), respectively.

To estimate the overall effect size ($\ln RR_{++}$), we performed linear mixed-effects models using the "lme4" package (Bates et al. 2015) in R version 4.2.0 (R Core Team 2022) with the individual ln*RR* fitted as the response variable and the identity of the study and plots (nested inside study identity) as the random effect factors (Additional file 2). This approach explicitly accounts for the potential dependence of observations collected from a single study. To investigate whether the ecosystem type, climate (MAT and MAP), edaphic characteristics (moisture, pH, C content, and N content), and experimental

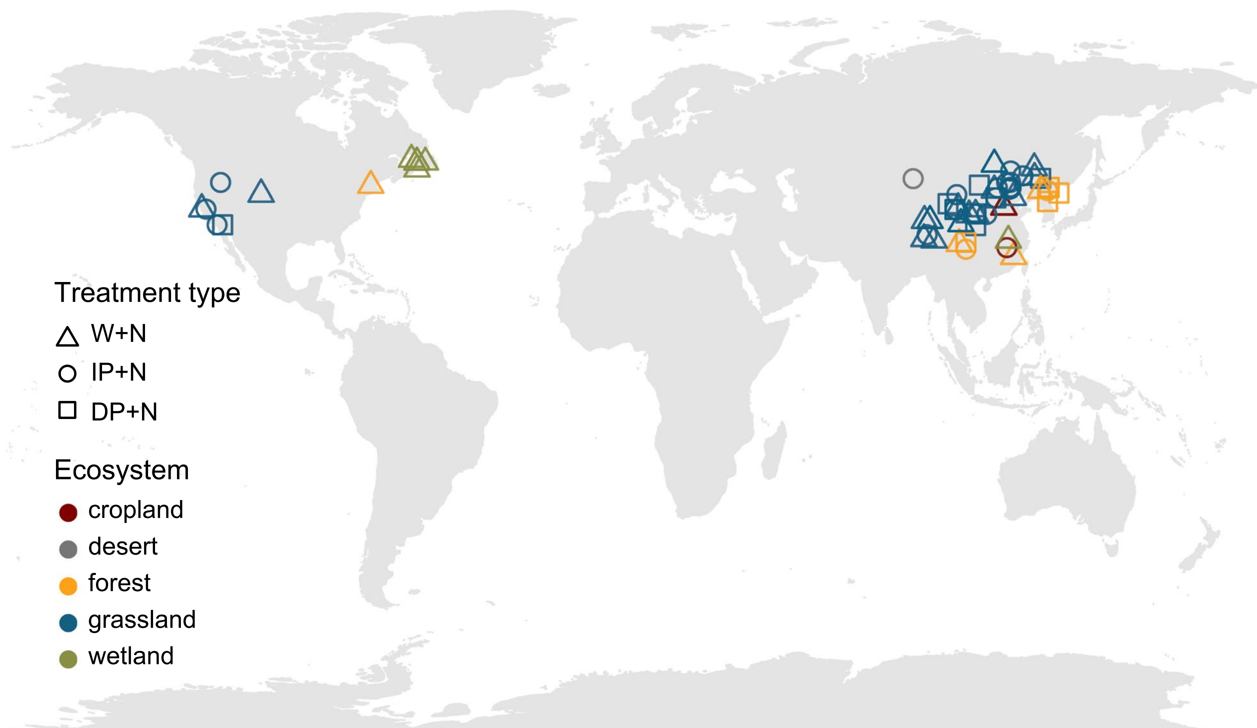

Fig. 1 Global distribution of observations derived from 57 articles used in the meta-analysis. The different treatment types are indicated by symbol shape, and the ecosystem types are represented by color

methods (N addition rate, warming magnitude, and duration) influence the response of GHGs to N addition and the interaction with climate change, these factors were fitted as continuous or categorical fixed-effect factors. Data were subjected to *z*-score standardization prior to analysis to allow for comparisons (Ali and Faraj 2014). *z*-scores were determined by standardization by subtracting the mean value from the raw data and dividing the resulting number by the standard deviation of the mean. The corresponding 95% confidence interval (CI) and percentage change (%) were calculated as follows:

$$95\%\mathrm{CI}_S = \ln RR_{++} \pm 1.96 S_{\ln RR_{++}} \tag{4}$$

$$\text{Percentage change} = \left(e^{\ln RR_{++}} - 1\right) \times 100 \tag{5}$$

The treatment effects were considered non-significant if the 95% CI of $\ln RR_{++}$ overlapped with zero. When the 95% CI of $\ln RR_{++}$ did not overlap with zero, the effect was identified as positive if $\ln RR_{++}$ was greater than zero; otherwise, the effect was identified as negative if $\ln RR_{++}$ was less than zero.

Furthermore, publication bias was assessed to analyze whether the studies used in the present meta-analysis were representative or not using Egger's regression tests (Egger et al. 1997). Funnel plots were generated using the response ratios ($\ln RR$) and their standard errors. All results indicated that studies used in this meta-analysis were robust against publication bias (Additional file 1: Fig. S1).

Interactive effects

To further understand the interactive effects of two drivers occurring simultaneously (combined effects), Hedges' *d* was used to calculate interactive effect size (d_I) as previously described (Gurevitch et al. 2000):

$$d_I = \frac{\left(\overline{X}_{AB} - \overline{X}_A\right) - \left(\overline{X}_B - \overline{X}_c\right)}{s} J(m) \tag{6}$$

where $\overline{X}_c$, $\overline{X}_A$, $\overline{X}_B$, and $\overline{X}_{AB}$, are the means of the variables in the control group, treatment groups A and B, and their combination (A + B), respectively.

The standard deviation (s), degrees of freedom (m), and correction term ($J(m)$) were estimated using Eqs. (7–9).

$$\mathrm{s} = \sqrt{\frac{(n_c - 1)(s_c)^2 + (n_A - 1)(s_A)^2 + (n_B - 1)(s_B)^2 + (n_{AB} - 1)(s_{AB})^2}{n_c + n_A + n_B + n_{AB} - 4}} \tag{7}$$

$$m = n_c + n_A + n_B + n_{AB} - 4 \tag{8}$$

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

where n_c, n_A, n_B, and n_{AB} are the sample sizes and s_c, s_A, s_B, and s_{AB} are the standard deviations in the control and treatment groups of A, B, and their combination (A + B), respectively.

The variance (v_2) of d_I was estimated as follows:

$$v_2 = \frac{1}{4}\left[\frac{1}{n_C} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_I^2}{2(n_C + n_A + n_B + n_{AB})}\right] \tag{10}$$

We performed linear mixed-effects models to calculate the weighted mean of d_I (d_{++}) with d_I as the response variable and study identity and plots (nested inside study identity) as the random effect factors. All the analyses were conducted in R version 4.2.0 (R Core Team 2022) using the 'lme4' package (Bates et al. 2015).

The interactions between treatments were classified into three types: additive, synergistic, and antagonistic (Folt et al. 1999; Crain et al. 2008). Additive effects occurred when their combined effects were not significantly different from the sum of their individual effects; synergistic interactions were observed when the combined effect was significantly greater than the sum of their individual effects and antagonistic interactions when the combined effect was less than the sum of their individual effects. In terms of Hedges' d, interactions were considered additive if the 95% CI of the weighted mean d_I overlapped with zero. If the 95% CI did not overlap with zero, we determined the interaction effect through their individual effects. If the individual effects of the two drivers were both negative or one negative and one positive, interaction effect sizes less than zero were considered synergistic, and those greater than zero were antagonistic. In cases where the individual effects were both positive, interaction effect sizes greater than zero were synergistic, and those less than zero were antagonistic.

Results

Overall responses of soil GHG fluxes

Overall, soil CO_2 emissions did not respond significantly to N addition alone, but it increased by an average of 17.2% and 21.7% under warming alone and warming plus N addition, respectively (Fig. 2a). N addition alone or in combination with warming or altered precipitation minimally affected soil CH_4 uptake, while warming alone significantly increased CH_4 uptake by an average of 28.2% (Fig. 2b). In contrast, N_2O emissions increased significantly by 106.2%, 112.2%, 108.2%, and 105.2% under N addition alone, warming plus N addition, increased precipitation plus N addition, and decreased precipitation plus N addition, respectively. However, individual climate change treatments did not affect soil N_2O emissions, except for decreased

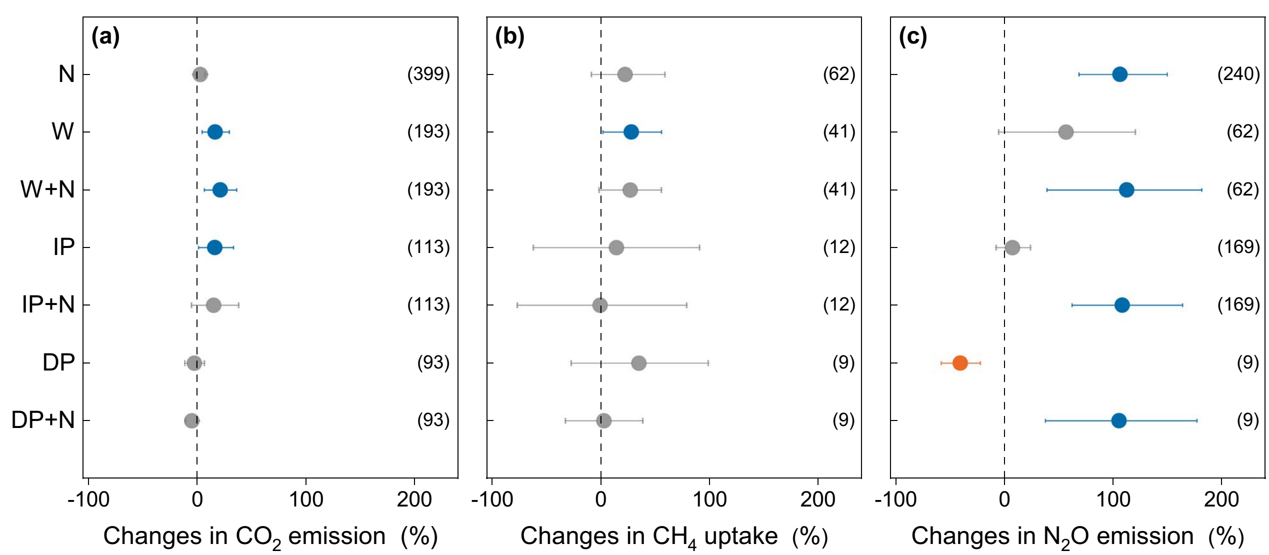

Fig. 2 Effects of N addition (N), warming (W), increased precipitation (IP), and decreased precipitation (DP) alone or N addition combined with warming (W + N), increased precipitation (IP + N), and decreased precipitation (DP + N), on soil CO_2 emissions (**a**), CH_4 uptake (**b**), and N_2O emissions (**c**). Data are means with 95% confidence intervals (CI). The number of observations is shown along the right axis. Blue, orange, and gray solid dots indicate significantly positive, significantly negative, and non-significant effects, respectively. The vertical dashed lines are zero lines

precipitation, which significantly decreased N_2O emissions by 40.6% (Fig. 2c).

Variation among ecosystem types

The effects of N addition alone on CO_2 emissions were independent of ecosystem type, whereas the effects of N addition plus warming or altered precipitation were different among ecosystem types, significantly affecting grasslands but not forests (Fig. 3a). The individual and combined effects of N addition and warming positively impacted soil CH_4 uptake in grasslands, but their effects were negative in croplands (Fig. 3b). The responses of soil

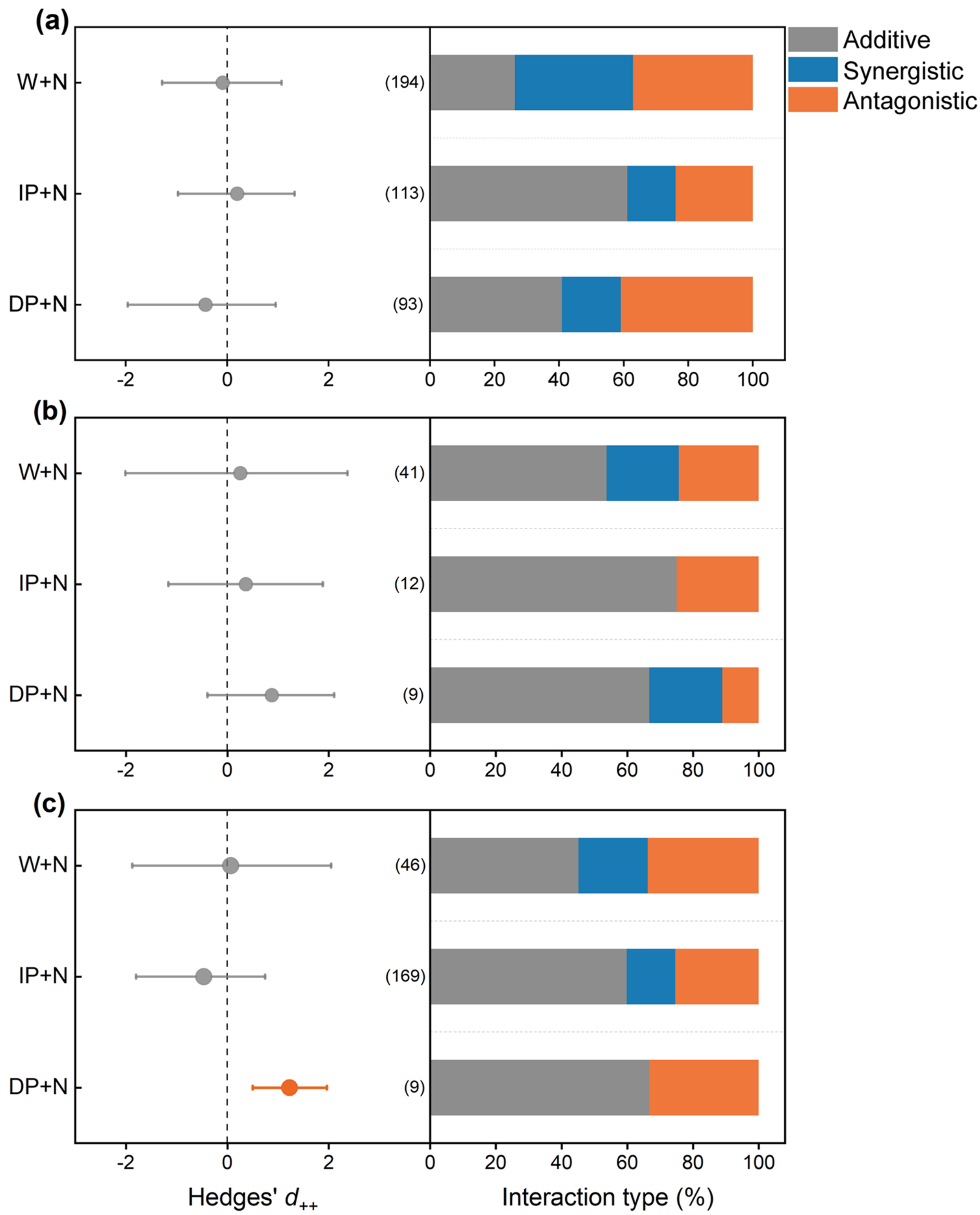

Fig. 3 Influence of ecosystem type on the individual and combined effects of N addition (N), warming (W), increased precipitation (IP), and decreased precipitation (DP) on soil CO_2 emission (**a**), CH_4 uptake (**b**), and N_2O emission (**c**). The *p* values ($p < 0.05$) indicate the significance of the differences in the changes in GHG fluxes among ecosystems. Data are means with 95% confident intervals (CI). The numbers of observations are shown on the right. Blue, orange, and gray solid dots indicate significantly positive, significantly negative, and non-significant effects, respectively. The vertical dashed lines are zero lines

N_2O emissions to various treatments were independent of ecosystem type (Fig. 3c). Based on the results of linear mixed-effects models, the most important regulator of the differences among ecosystem types was soil moisture rather than soil pH, and initial soil C and N content (Table 1). Soil moisture had significantly negative effects on the ln*RR* of CO_2 emissions to N addition plus warming, increased precipitation alone, and N addition plus increased precipitation, and the ln*RR* of CH_4 uptake to warming alone and N addition plus warming.

Effects of climate and experimental methods

The ln*RR* of GHG fluxes to N addition plus warming or altered precipitation was significantly influenced by climate and experimental methods (Table 1). Aridity index was the most important driver of the combined effects of N addition and increased precipitation on soil CH_4 uptake, showing significant negative effects. The ln*RR* of CO_2 and N_2O under warming plus N addition was positively affected by the magnitude of warming. Altered precipitation magnitude, N addition rate (Additional file 1: Fig. S2), and experimental duration had non-significant effects on the ln*RR* of GHG fluxes.

Interactions between N addition and climate change

Across all two-driver pairs, the overall interactive effects of N addition and warming or altered precipitation on GHG fluxes were generally additive, except for the antagonistic interaction between decreased precipitation and N addition on N_2O emissions (Fig. 4). Additive interactions accounted for a higher proportion than synergistic or antagonistic effects among individual pairwise observations, representing 26–54%, 60–75%, and 41–67% of the combined effects of warming plus N addition, increased precipitation plus N addition, and decreased precipitation plus N addition, respectively.

Discussion

Responses of soil CO_2 emissions

The combined effects of N addition and warming or increased precipitation raised CO_2 emissions more than N addition alone, partially supporting our first hypothesis. Soil CO_2 emissions did not respond significantly to N addition alone, but it increased significantly under warming alone and increased precipitation alone. Therefore, the increases in CO_2 emissions were mainly attributed to the effect of warming and increased precipitation, rather than N addition. These results suggested that temperature and precipitation are key drivers regulating soil CO_2 emissions, which is consistent with the previous studies (Deng et al. 2020; Yang et al. 2022). Moreover, the overall interactions between N addition and warming or increased precipitation were additive, indicating that combined N addition and warming or increased precipitation on CO_2 emissions were not substantially different from the sum of their respective individual effects. Therefore, the effects of N addition and climate change factors on CO_2 emissions were relatively independent. The non-significant effects of N addition on CO_2 emissions revealed in our meta-analysis may be attributed to the possibility that the level of N addition reached or exceeded the N critical load due to continuous N enrichment (Zong et al. 2016; Bai et al. 2019). Various studies have suggested that N addition initially stimulated soil respiration but gradually suppressed CO_2 emissions (Xia et al. 2009; Yan et al. 2010). Moreover, Hui et al. (2020) have demonstrated that the absence of other nutrients, such as phosphorus, may suppress the effect of N addition. Therefore, the potential mechanisms by which N addition influenced ecosystem CO_2 emission and the long-term effects of continuous N enrichment should be further explored.

Consistent with our second hypothesis, the effects of N addition in combination with warming or increased precipitation were influenced by climatic condition. Aridity index primarily regulated CO_2 emissions under altered precipitation plus N addition (Table 1). Increased precipitation alleviated water shortages in arid areas and promoted soil respiration (Sierra et al. 2017), while decreased precipitation exacerbated the dry conditions, strongly affecting soil biotic processes by limiting water availability, leading to a decrease in CO_2 emissions (de Dato et al. 2010). Differences in the soil moisture may explain the various responses of CO_2 emissions to N addition plus increased precipitation between forests and grasslands, as forests have higher soil moisture than grasslands (Additional file 1: Fig. S3). Moreover, the combined effect of N addition plus warming on soil CO_2 emissions was positively correlated with warming magnitude, indicating that these combined effects were stimulated by warming (Carey et al. 2016). Although climatic condition has been observed to be a major factor influencing differences in the soil CO_2 emissions of forests and grasslands, the lack of observations from other ecosystems still contributes to our poor understanding of soil CO_2 emissions among different ecosystems globally. Therefore, we propose more multifactorial experiments in various ecosystems in future work.

Responses of soil CH_4 uptake

In contrast to CO_2 emissions, the effects of N addition on soil CH_4 uptake remained unaltered when combined with warming or altered precipitation. Additive interactions between N addition and warming or altered precipitation on soil CH_4 uptake appeared to be much more common compared with synergistic and

Table 1 Linear mixed-effects model analysis of the relationship between local climate, experimental, or edaphic conditions and the effects of N addition (N), warming (W), increased precipitation (IP), decreased precipitation (DP), N addition plus warming (W + N), N addition plus increased precipitation (IP + N), and N addition plus decreased precipitation (DP + N) on soil GHG fluxes

ln*RR*	Treatment	Aridity index		W/IP/DP magnitude		N addition rate		Duration		Soil pH		Soil moisture		Soil C		Soil N	
		Estimate	*n*	Estimate	*n*	Estimate	*n*	Estimate	*n*	Estimate	*n*	Estimate	*n*	Estimate	*n*	Estimate	*n*
	N	0.009	399			0.025	399	0.005	399	0.014	399	0.044	178	0.018	126	0.033	60
	W	0.081	194	**0.136***	194			− 0.010	194	0.043	194	− 0.076	75	0.016	33	0.023	31
	W + N	0.032	194	**0.143***	194	− 0.049	194	− 0.044	194	0.096	194	− **0.061***	75	− 0.051	33	− 0.040	31
CO_2	IP	− **0.102***	111	0.082	111			0.039	111	− 0.071	111	− **0.234*****	55	− 0.128	29	− **0.032*****	13
	IP + N	− 0.072	113	0.169	113	− **0.125***	113	− 0.002	113	− 0.114	113	− **0.127***	55	− 0.023	29	− **0.049***	13
	DP	− 0.016	93	− **0.041****	93			− 0.027	93	0.000	93	**0.073*****	48	− 0.005	65	− 0.074	17
	DP + N	**0.044***	93	− 0.032	93	0.024	93	− 0.024	93	− 0.023	93	0.043	48	**0.063***	65	**0.090***	17
	N	0.019	62			-0.159	62	0.026	62	− 0.072	62	− 0.325	32	− 0.052	27	0.230	28
	W	0.106	41	0.094	41			− 0.020	41	− 0.070	41	− **0.397*****	15	0.122	23	− 0.102	23
	W + N	0.039	41	0.048	41	− **0.227***	41	− 0.049	41	-0.103	41	− **0.383***	12	**0.205***	22	− **0.221***	22
CH_4	IP	− **0.668*****	12	0.241	12			0.622	12	2.086	12	− 2.766	10				
	IP + N	− **0.813***	12	0.472	12	0.191	12	0.023	12	1.444	12	− 3.474	10				
	DP	− 0.307	9	-0.089	9			0.178	9	− 0.230	9	− 0.429	7				
	DP + N	− 0.017	9	-0.166	9	0.110	9	0.058	9	− 0.183	9	− 0.162	7				
	N	**0.185***	240			0.017	240	0.048	240	− **0.165***	240	**0.340****	53	− 0.173	176	− 0.040	176
	W	0.438	62	**0.562*****	62			0.049	62	0.021	62	0.237	37	0.009	53	− 0.064	53
	W + N	0.011	62	**0.403***	62	− 0.230	62	0.011	62	− 0.037	62	0.022	37	− 0.006	53	− 0.002	53
N_2O	IP	0.098	169	0.113	169			− 0.053	169	− **0.124***	169	**0.598***	7	0.008	122	− 0.088	119
	IP + N	0.106	169	0.102	169	0.098	169	0.137	169	− 0.138	169	− 0.141	7	− 0.096	122	0.051	119
	DP	− 0.102	9	− 0.753	9			0.313	9	− 0.764	9	− 0.318	9				
	DP + N	− 0.103	9	− 0.074	9	− 0.146	9	0.015	9	− 0.017	9	− 0.363	9				

Data are standardized prior to analysis. Bold estimate values indicate significant effects. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

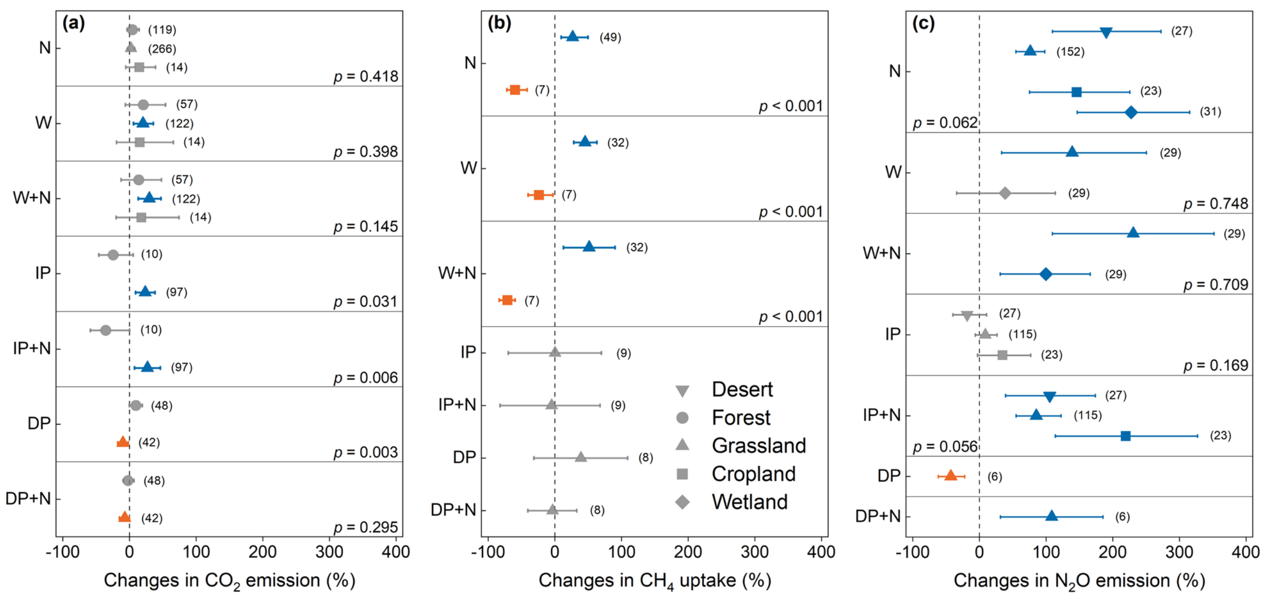

Fig. 4 Interactions of N addition (N), warming (W), increased precipitation (IP), and decreased precipitation (DP) on soil CO_2 emission (**a**), CH_4 uptake (**b**), and N_2O emission (**c**) (left), and corresponding frequency distribution of interaction types across individual pairwise observations (right). Solid circles indicate means with ± 95% confidence intervals (CI). The number of observations is shown along the right axis. Interactive effects were additive (gray, where 95% CIs overlap zero); otherwise, effects were synergistic (blue) or antagonistic (orange)

antagonistic interactions. Warming increased soil CH_4 uptake significantly by increasing the biomass of methane-oxidizing and decreasing the biomass of methanogenic microorganisms (Qi et al. 2022). However, warming in combination with N addition suppressed this significantly positive effect, which may be related to the increase in soil acidity (Bowman et al. 2008; Jamil et al. 2022). Therefore, the response of soil CH_4 uptake to warming plus N addition was negatively related to the N addition rate.

We found that the response of soil CH_4 uptake to N addition combined with warming was negatively correlated with higher soil moisture content. Furthermore, the effect of N addition plus increased precipitation was negatively correlated with aridity index. These findings may be related to the CH_4 production and consumption processes of soil microorganisms. Soil CH_4 is produced by methanogens in wet anaerobic soils and consumed by methanotrophs in drier aerobic soils (Fest et al. 2017; Liu et al. 2019); therefore, warming and increased precipitation could enhance the emissions of soil CH_4 by increasing the activities of methanogenic archaea and methanotrophic bacteria in humid areas (Aronson et al. 2013; Kammann et al. 2001; Zhao et al. 2017). This could also explain the significant differences in soil CH_4 uptake between grasslands and croplands. Due to observational limitations, we could not analyze the effects of altered precipitation plus N addition on CH_4 uptake among different ecosystem types; more experiments conducted in various ecosystems are required to predict CH_4 emissions under future climate change scenarios.

Responses of soil N_2O emissions

The increases in N_2O emissions caused by N addition plus warming or altered precipitation did not differ from that of N addition alone, while warming and increased precipitation alone had non-significant effects. This implies that temperature and precipitation are not major factors affecting soil N_2O emissions (Yang et al. 2021), which was inconsistent with the results of Zhang et al. (2021) and Huang et al. (2014). N addition was an important factor influencing soil N_2O emissions because soil N_2O released as an intermediate product when ammonium (NH_4^+) is oxidized to nitrate (NO_3^-) by nitrification, or during the reduction of NO_3^- or nitrite (NO_2^-) by denitrification (Snyder et al. 2009; Hube et al. 2017). Therefore, soil N_2O emissions are mainly limited by soil N availability (Gao et al. 2015). Increased N supply can stimulate soil N_2O emissions directly by promoting the proliferation of microbial communities involved in nitrification and denitrification (Pajares and Bohannan 2016). Similar findings were reported by Deng et al. (2020) and Du et al. (2021), they found that N addition increased soil N_2O emissions by 164% and 91%, respectively, which were consistent with our result (+ 106%). In the present study, an overall antagonistic interaction between N addition and decreased precipitation on N_2O emissions was observed. In this case, the negative effects of decreased precipitation on N_2O emissions would be counteracted by N addition in the combined effects (Geng et al. 2017). However, overall interactions of N addition and warming or increased precipitation on N_2O emissions were generally additive, indicating that the effect of N addition, warming, and increased precipitation on N_2O emissions would not be changed in the combined effects. Although synergistic and antagonistic interactions were observed among the individual observations, additive interactions remained predominant. This finding may be attributed to the interactions between multiple region-dependent global change factors, where different climatic conditions and ecosystem types generate various effects (Baah-Acheamfour et al. 2016; Liu and Greaver 2009).

The responses of soil N_2O emissions to individual and combined effects of N addition, warming, and altered precipitation did not vary significantly among ecosystem types. These results indicated that ecosystem type had only a minor impact on soil N_2O emissions (Deng et al. 2020; Li et al. 2020). In addition, the positive effects of N addition combined with warming or altered precipitation on soil N_2O emissions were hardly affected by climatic and experimental conditions. Soil N_2O is consistently released rapidly at the beginning of N addition, irrespective of the experimental duration (Li et al. 2022; Xu et al. 2017; Song and Niu 2022). These observations suggested that N addition is the major driver of increased soil N_2O emissions and the feedbacks between them are not altered by climate change.

Main limitations and future perspectives

We found that soil GHG fluxes could be stimulated to some extent by multiple global change factors, including N addition, warming, and altered precipitation. The responses of soil GHG fluxes to N addition were not significantly affected by warming or altered precipitation, as illustrated by the additive interaction effects. Our study provides a comprehensive analysis of soil GHG fluxes by considering the effects of N addition under joint warming or altered precipitation in multiple terrestrial ecosystems. Nevertheless, we acknowledge some limitations of our study. First, the compiled data were mainly from studies in grassland of Northern Hemisphere, particularly China (Fig. 1), with other regions of the world being poorly represented, which possibly led to a misrepresentation of global change effects on soil GHG fluxes. In addition, multiple subtypes existed in these broad categories of ecosystem types that could not be categorized due to the limited observations, which hampered our ability to draw robust and general conclusions on the effects of global change on soil GHG fluxes among different ecosystems. Second, our results showed that decreased precipitation plus N addition did not affect soil CH_4 uptake, but increased N_2O emissions significantly. However, the sample size of the combined effects was insufficient and only represented grassland ecosystems, which may contribute to the uncertainty of our estimations. Third, in most experiments N addition was applied in the form of NH_4NO_3, yet research has shown that the response of soil GHG fluxes to N addition is influenced significantly by N form (Du et al. 2021). To improve our understanding of how GHG fluxes will respond to global climate change scenarios, future multi-factor experimental studies should focus on underrepresented regions, especially the effects of altered precipitation and N addition on soil CH_4 and N_2O.

Conclusion

This study examined the effects of N addition combined with warming and altered precipitation on GHG fluxes at a multi-continental scale. Warming and altered precipitation rarely influenced the effects of N addition on soil GHG fluxes, both in magnitude and direction. Their overall interactions on GHG fluxes were generally additive (i.e., not differing from the sum of their individual effects) rather than synergistic or antagonistic, suggesting the relative independence of these factors. Soil CO_2 emissions were mainly regulated by temperature and precipitation rather than by N addition, whereas N_2O emissions were overall limited by N addition. The effects of N addition plus increased precipitation on soil CO_2 emissions and the effects of N addition plus warming on soil CH_4 uptake showed contrasting results among different ecosystems, which were mainly related to soil moisture. In contrast, the soil N_2O emissions did not significantly differ among ecosystems. The individual and combined effects of these treatments on soil GHG fluxes were regulated by climate and experimental methods. Overall, our results not only quantitatively synthesized the patterns of N addition and climate change on soil GHG fluxes, but also showed that the effects of N addition, warming, and altered precipitation were relatively independent. These findings advance current understanding of the response of soil GHG fluxes to N addition in combination with warming and altered precipitation and provide insights into C and N cycling under global climate change.

Abbreviations

GHG	Greenhouse gas
N	Nitrogen
CO_2	Carbon dioxide
CH_4	Methane
N_2O	Nitrous oxide
SOM	Soil organic matter

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-023-00470-9.

Additional file 1: Fig. S1. Assessments of publication bias. Funnel plots displaying the response ratio ($\ln RR$) of CO_2 emission, CH_4 uptake, and N_2O emission and standard error for each data under N addition (N), warming (W), increased precipitation (IP), decreased precipitation (DP), and N addition in combined with warming (W+N), increased precipitation (IP+N), and decreased precipitation (DP+N). Results of publication bias tests using Egger's regression are given at the top of each panel (*z* and *P* values). *P* values > 0.05 indicate the absence of publication bias. **Fig. S2.** Effects of N addition rate on the response of soil CO_2 emission (a), CH_4 uptake (b), and N_2O emission (c) to N addition (N), warming plus N addition (W+N), increased precipitation plus N addition (IP+N), and decreased precipitation plus N addition (DP+N). Data are presented as means with 95% confident intervals (CIs). Blue solid dots indicate significant positive effects, orange solid dots indicate significant negative effects, and gray solid dots indicate non-significant effects. The vertical dashed lines are zero lines. **Fig. S3.** Initial soil moisture in different ecosystems under combined effects of N addition and warming or altered precipitation on CO_2 emission (**a**) and CH_4 uptake (**b**). Mean (solid circles), median (horizontal line), interquartile range (box) and nonoutlier range (vertical line) are shown. Lowercase letters indicate differences among different ecosystems. **Table S1.** Overview of the experiments involving N addition, warming, and altered precipitation included in this meta-analysis as well as their interactions.

Additional file 2. Data used in this meta-analysis.

Acknowledgements
We are grateful to the editor and two anonymous referees for their insightful comments and kind suggestions that significantly improved our manuscript. We also thank Yaoyi Zhang, Zihao Chen, and Hongrong Guo for their assistance with writing.

Author contributions
XW, XN, and FW conceived the study. XW and XN collected the raw data. XW, KVM, and KY performed data analyses and all authors contributed to subsequent revisions.

Funding
This work was supported by the National Natural Science Foundation of China (No. 32171641, 32101509, and 32271633) and the Ph.D. programme grant from China Scholarship Council (202109107009).

Availability of data and materials
The data that support the findings of this study are available at https://doi.org/10.1186/s13717-023-00470-9.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
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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Received: 24 April 2023 Accepted: 17 November 2023
Published online: 30 November 2023

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