Received: 22 October 2022 | Accepted: 10 January 2023

DOI: 10.1111/gcb.16627

RESEARCH ARTICLE

Global Change Biology WILEY

Nitrogen availability mediates soil carbon cycling response to climate warming: A meta-analysis

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Funding information
National Natural Science Foundation of China, Grant/Award Number: 32001140, 32171553 and 32171646

Abstract

Global climate warming may induce a positive feedback through increasing soil carbon (C) release to the atmosphere. Although warming can affect both C input to and output from soil, direct and convincing evidence illustrating that warming induces a net change in soil C is still lacking. We synthesized the results from field warming experiments at 165 sites across the globe and found that climate warming had no significant effect on soil C stock. On average, warming significantly increased root biomass and soil respiration, but warming effects on root biomass and soil respiration strongly depended on soil nitrogen (N) availability. Under high N availability (soil C:N ratio < 15), warming had no significant effect on root biomass, but promoted the coupling between effect sizes of root biomass and soil C stock. Under relative N limitation (soil C:N ratio > 15), warming significantly enhanced root biomass. However, the enhancement of root biomass did not induce a corresponding C accumulation in soil, possibly because warming promoted microbial CO_2 release that offset the increased root C input. Also, reactive N input alleviated warming-induced C loss from soil, but elevated atmospheric CO_2 or precipitation increase/reduction did not. Together, our findings indicate that the relative availability of soil C to N (i.e., soil C:N ratio) critically mediates warming effects on soil C dynamics, suggesting that its incorporation into C-climate models may improve the prediction of soil C cycling under future global warming scenarios.

KEYWORDS
climate warming, meta-analysis, root biomass, soil C stock, soil C:N ratio, soil respiration

1 | INTRODUCTION

Soil organic carbon (C) is the largest biologically active C pool in terrestrial ecosystems, with 2200–2500 Pg organic C in the top 2 m soil (Jobbagy & Jackson, 2000; Kochy et al., 2015). Prior to the Industrial Revolution, soil C stock was annually balanced because C gains from plant inputs offset C losses to the atmosphere through respiration of soil organisms and plant roots (Jackson et al., 2017). However, the observed global temperature has increased by >1.2°C since the 1850 to 1900 baseline period (Matthews et al., 2022), and this increase may perturb this balance through altering plant-derived C input and/or soil microbial C mineralization (i.e., C output from soil) (Bradford et al., 2016). Despite the wealth of research into warming effects on soil C dynamics (Melillo et al., 2017; Nottingham et al., 2020; Shaver et al., 2000; Walker et al., 2018), there is still a high uncertainty about the direction and magnitude of warming-induced changes in soil C stocks (Conant et al., 2011; Crowther et al., 2016).

Tongshuo Bai and Peng Wang contributed equally to the manuscript.

The size of soil C pool is simultaneously controlled by both C formation and decomposition processes, which are influenced by complex interactions among plant, microbes and soil minerals (Bradford et al., 2016; Davidson & Janssens, 2006). Recent studies have shown that plant rhizodeposition, rather than aboveground litter input, plays a dominant role in soil C formation (Sokol & Bradford, 2019; Villarino et al., 2021). Because soil organic matter (SOM) has a relatively narrow range of C:N ratio, the capacity of soil to sequestrate root-derived C is highly related to its N availability (Tipping et al., 2016). Over the last several decades, many field studies have examined how simulated warming may affect plant growth, microbial activities and C fluxes in order to generate information to predict the potential effects of warming on soil C balance (Day et al., 2008; Hopkins et al., 2012; Luo et al., 2001; Zhou et al., 2012). Diverse effects of warming on soil C dynamics have been reported, as warming induces changes in an array of parameters that mediate soil C dynamics (Dorrepaal et al., 2009; Giardina et al., 2014; Xue et al., 2016). Climate warming often enhances plant biomass allocation belowground via increasing fine root growth and turnover (Briones et al., 2009; Malhotra et al., 2020; Wang et al., 2021). Whether this increase in C input belowground under warming can be transformed into soil C may depend on N availability (Bradford et al., 2016; Liang et al., 2017). When soil N is abundant, microorganisms can quickly break down plant litter and tend to invest more C in biomass synthesis rather than in respiration, which results in high microbial carbon use efficiency (CUE; Spohn et al., 2016), leading to microbial necromass accumulation in soil C (Cotrufo et al., 2013; Kallenbach et al., 2016). In contrast, soil N limitation often leads to low plant litter quality, litter decomposition rate and microbial CUE (Chen, Liu, Mao, et al., 2018; Hobbie, 2000; Manzoni et al., 2008). Then warming-increased belowground C input may be mainly converted into CO_2 through respiration, rather than into soil C pool.

On the other hand, warming often stimulates soil C loss through increasing microbial respiration and/or microbial decomposition of SOM (Bond-Lamberty & Thomson, 2010; Lu et al., 2013). When soil N is abundant, fast-growing r-strategy microorganisms dominate the soil microbial community (Blagodatskaya et al., 2007) and mainly decompose labile C such as root exudates (Chen et al., 2014). Warming-induced increase in soil CO_2 efflux may simply be a product of increased C input rates to the soil and/or labile C pool sizes (Bradford et al., 2008), thereby only reflecting altered turnover of recently C input without inducing significant changes in the total SOC stock (Conant et al., 2011). Under N-limiting conditions, in contrast, warming may stimulate microbial secretion of N-acquiring enzyme (Cui et al., 2020) for N acquisition from SOM (Kopittke et al., 2018), which may promote decomposition of old soil C and reduce the SOC stock.

Although N availability is critical in predicting soil C transformation processes, it is difficult to characterize the relative availability of N in soils on the global scale. Cleveland and Liptzin (2007) reviewed global soil data and found the average soil C:N ratio of 14.3 (±0.5). Also, in the global map of soil C:N ratio from ISRIC-WISE (Figure S2; Batjes, 2016), boreal forests, which in general are considered N-limited, have C:N ratios between 16 and 29; and tropical forests, which are considered P limited with relatively high N, have C:N ratios between 10 and 15. Together, these findings suggest that soil C:N ratio can be taken as a proxy of relative soil N availability (Terrer et al., 2019), and that the C:N ratio of 15 can be used as a tipping point to distinguish relatively N abundant/limited across the globe.

Besides the relative N availability in soils, the method and duration of manipulated warming experiments may affect the magnitude and direction of warming effects on soil C stock. For example, direct soil warming may have stronger effects on soil microbial activities and C loss than canopy air warming (Liu et al., 2020). Also, short-term warming often enhances microbial metabolism, turnover and/or enzymatic activities (Chen, Luo, García-Palacios, et al., 2018; Hagerty et al., 2014), likely promoting decomposition of microbially accessible C (Melillo et al., 2002). However, the majority of soil C is protected from microbial attack by chemical complexity or by physico-chemical interactions within the soil matrix (von Lutzow et al., 2006). The effects of long-term warming on soil C stock may largely depend on depolymerization of chemically complex C pool (Chen et al., 2020; Feng et al., 2017).

Climate warming is primarily due to the increasing atmospheric CO_2 concentration, and, to a less degree, emissions of other greenhouse gases, mainly CH_4 and N_2O (IPCC, 2013). In parallel with the increasing CO_2 concentration in the atmosphere, reactive N input has also increased due to N deposition or fertilizer application (Galloway et al., 2008), which not only increases N availability for plants and microbes, but also induces more N_2O emissions. Further, climate warming is projected to induce changes in precipitation temporally and spatially. All these global change factors can significantly affect plants and microbes that mediate the response of soil C stock to climate warming. For example, Carrillo et al. (2018) found that elevated atmospheric CO_2 amplified warming-induced soil C loss in a semi-arid grassland. Also, precipitation increase can alleviate warming-induced water limitation (Quan et al., 2019), which may strengthen warming enhancement of soil CO_2 efflux and induced soil C loss. In contrast, reactive N input often increases litter input and suppresses microbial growth and metabolism because of N-induced soil acidification (Chen et al., 2015; Treseder, 2008), which might alleviate warming-induced soil C loss and increase soil C stock (Janssens et al., 2010). Yet, it remains unclear whether these global change factors (elevated CO_2 concentration, altered precipitation, and N input) mediate warming effect on soil C stock across the globe.

We synthesized the diverse, even contrasting impacts of warming on soil C stock, root biomass and soil respiration through meta-analyzing field experimental results across global terrestrial ecosystems. We hypothesized that warming affects soil C stock mainly through influencing root input when soil N is abundant (Hypothesis 1). In contrast, warming influences soil C largely by altering soil respiration when soil N is limited (Hypothesis 2). Given that long-term warming may stimulate chemically complex C degradation by shifting the composition of the microbial community (Pold et al., 2015), we also predict that warming-induced soil C loss would increase with experimental duration (Hypothesis 3).

2 | MATERIALS AND METHODS

2.1 | Data compilation

To gather data for analysis, we collected publications from two sources: (1) we cited publications from previous meta-analyses, specifically Crowther et al. (2016) and Van Gestel et al. (2018); and (2) conducted an exhaustive literature survey of peer-reviewed publications using the "Web of Science" (apps.webofknowledge.com) and the "China National Knowledge Infrastructure" (http://www.cnki.net/) to search for peer-reviewed literatures that investigated soil C storage, root biomass and soil respiration response to field warming before December 2021. We searched on Web of Science using the "TS = (warming OR eleva* temperature) AND TS = (soil carbon OR root OR belowground biomass OR soil CO_2 OR soil respiration) AND TS = (field)". Then, we screened the papers for analysis based on the criteria as follows: (i) field experiments were conducted with both control and warming treatments, (ii) the variable of soil C storage, root biomass and soil respiration were shown by its mean and sample size, (iii) warming treatments by transplanting soils along climate gradients were excluded, and (iv) duration of warming lasted for more than 1 year. If the results were reported for different soil layers, we included only the data for the uppermost soil layer because the simulated climate warming mainly affected C cycling of surface soils and very few studies sampled deeper soil layers in the collected studies. Some studies reported measurements at multiple timepoints, and we used the last measurement of soil C to provide a single estimate for the net change in soil C stock after an experiment, and averaged the measurements for root biomass and soil respiration in each study to represent their mean responses during the experiment. Standard deviation of each measurement was pooled using the formula:

$$\mathrm{SD}_{\text{across measurements}} = \sqrt{\sum \left[s_i^2 \times (n_i - 1) \right] / \sum (n_i - 1)}$$

in which s_i and n_i is the standard deviation and replicate number of each measurement.

Data from the control and warming treatment in each study were extracted to examine warming effects on soil C, root biomass and soil respiration. A total of 253 studies (see Note S1 for Data sources; Supporting Information), 165 sites (Figure S1) and 503 observations were finally selected. Data presented in tables were directly extracted, and data presented in figures were obtained using the software GetData Graph Digitizer (version 2.22).

For each experiment in our dataset, other relevant information was also gathered, including on warming duration, warming magnitude (warming effect on soil temperature), warming method, ecosystem type, mean annual temperature (MAT), mean annual precipitation (MAP) and soil C:N ratio (an indicator for soil N availability) (Terrer et al., 2019). Data of MAT, MAP and soil C:N ratio were obtained from the reference or from other studies conducted at the same experimental site. Finally, in order to examine whether other global change factors (i.e., N input, elevated CO_2 concentration, and precipitation increase/reduction) mediated warming effect on soil C storage, we further analyzed the data based on two- or multi-factor field global change experiments at 50 sites.

2.2 | Meta-analysis

In this meta-analysis, we quantified the effect of warming on soil C storage, root biomass and soil respiration by calculating effect size using the natural log of the response ratio (RR) (Hedges et al., 1999). The lnRR and its corresponding pooled variance (v) were calculated as follow (using the "*escalc*" function from the R package "*metafor*")

$$\ln(\mathrm{RR}) = \ln\left(X_t / X_c\right) = \ln\left(X_t\right) - \ln\left(X_c\right).$$

$$v = \frac{S_t^2}{N_t X_t^2} + \frac{S_c^2}{N_c X_c^2}$$

where X_t and X_c are the mean values of the variables in the warming treatment and control group, respectively. S_t, N_t, S_c, and N_c, are the standard deviation and replicate number in the treatment and control group, respectively. When the standard deviations or standard errors of the means were not provided in studies, we imputed missing standard deviations using the coefficient of variation from all complete cases with the "*impute_SD*" function of the R package "*metagear*".

We used the "*rma.mv*" function in "*metafor*" package to calculate the weighted effect size (lnRR_{++}) and 95% confidence intervals (CIs) with the method of restricted maximum likelihood (REML). Because several studies in one site contributed more than one observation, we included the variable "site" as a random factor to account for non-independence of observations derived from the same site (Chen, Luo, van Groenigen, et al., 2018; Terrer et al., 2021). The effects of warming were considered significant if the 95% CI did not overlap with zero. The results of lnRR_{++} were back-transformed and reported as the percentage change under warming based on following equations (Wang et al., 2022):

$$\text{Percentage change}\,(\%) = \left(e^{\mathrm{lnRR}_{++}} - 1\right) \times 100$$

The heterogeneity in effect sizes captured by categorical moderators (i.e., ecosystem type, warming method, soil N level) were analyzed using mixed-effects models with omnibus tests (Q_M), whereby significant Q_M ($p < .05$) indicates significant differences between groups. Also, we ran univariate mixed-effects meta-regression models to examine the relationships between the effect sizes and continuous moderators (i.e., warming magnitude, warming duration, MAT and MAP). We also evaluated the publication bias with funnel plot and the funnel plot was approximately symmetrical (Figure S3), suggesting that results are robust without potential publication bias.

3 | RESULTS

Across 196 observations focusing on warming effect on soil C storage, experimental warming did not have a significant effect on soil C pool: The weighted mean of effect size ($\ln RR_{++}$) (and 95% CIs) across all studies were 0.0042 (−0.0205–0.0290) (Figure 1a) as only 53.1% of the effect sizes were higher than zero (Figure S4). Also, there was a significantly negative relationship between warming duration and $\ln RR_{++}$ of soil C ($Q_M = 12.19$; $p = .0005$; Table 1; Figure 2a). However, warming effect on soil C was little influenced by warming methods, ecosystem type (Table 1; Figure 1a), or soil N level (Figure 3), and was not correlated with the magnitude of warming, MAT or MAP (Table 1).

Globally, warming significantly increased root biomass by 6.84% (1.50%–12.47%, 95% CIs) across 157 observations (Table 1; Figure 1b), and warming-enhancement of root biomass mainly occurred in forest and tundra ecosystems heated with the infrared radiation (IR) heater method. Also, warming significantly stimulated soil respiration (150 observations) by an average of 8.45% (4.39%–12.67%, 95% CIs). Warming stimulation of soil respiration occurred mainly with warming by IR heaters and heating cables, while passive warming by reflective curtain, open top chamber or greenhouse (Figure 1c) had no significant effects. Warming effect on soil respiration exhibited distinct trends in different ecosystems: warming significantly enhanced soil respiration in grasslands, forests and croplands, but significantly suppressed it in deserts (Figure 1c). Also, lnRR of soil respiration positively correlated with MAP ($p = .0007$; Table 1; Figure 2b).

Soil N level affected warming effects on root biomass and soil respiration ($p = .0387$ and .0564, respectively; Table 1; Figure 3). Warming had no significant effect on root biomass (+2.44%) under high soil N availability (soil C:N ratio < 15), but significantly increased it (+13.15%) under low N conditions (soil C:N ratio > 15). Similarly, warming effects on soil respiration was higher under low soil N (+12.74%) than high soil N (+4.78%). Moreover, lnRR of soil C positively correlated with that of root biomass ($p = .0032$; Table 2; Figure 4a) under high soil N availability (soil C:N ratio < 15), but not under low N availability (soil C:N ratio > 15) ($p = .3656$; Figure 4b). Yet, lnRR of soil C did not show any significant correlations with lnRR of soil respiration under either high or low N levels (Table 2). Across all the two- or multi-factorial experiments, reactive N input marginally offset the warming-induced soil C loss ($p = .0544$; Table 3; Figure 5), but elevated atmospheric CO_2 and precipitation increase/reduction did not significantly affect warming effect on soil C stock (Table 3; Figure 5).

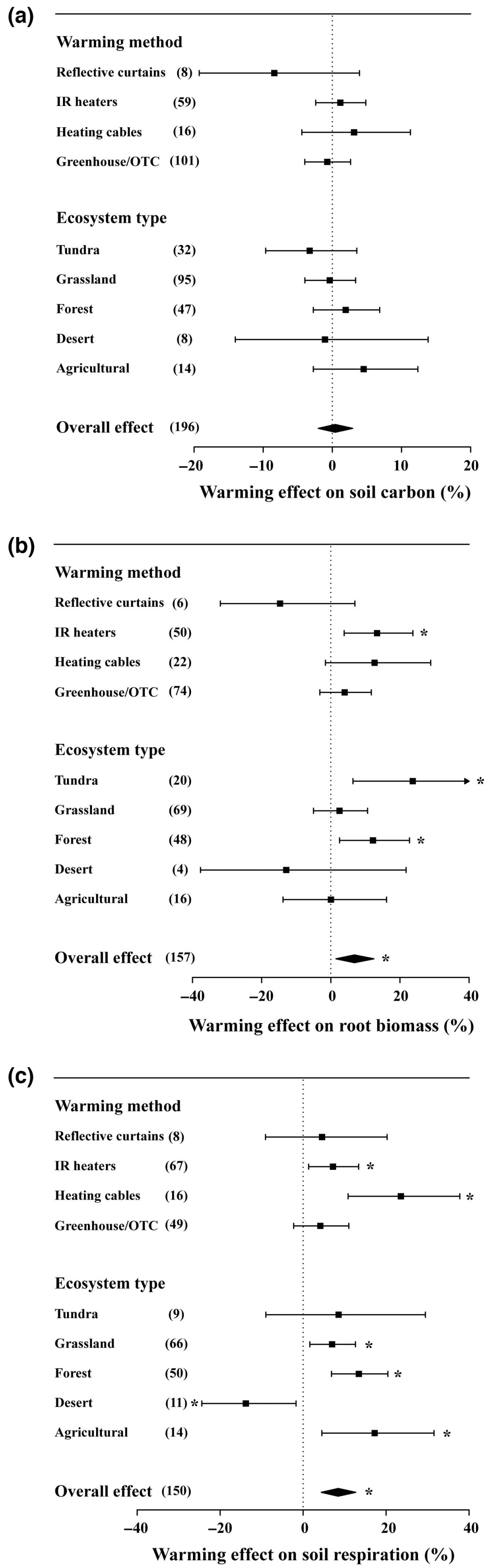

FIGURE 1 Warming effects (percentage change) on soil C (a), root biomass (b), and soil respiration (c) in different warming methods and ecosystem types. Means and 95% confidence intervals are given. Asterisks denote significant warming effects whose confidential intervals do not overlap with the zero line. Arrows represent 95% confidence intervals that extend beyond the limits of the plot. Values in parentheses are sample sizes. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Results from our meta-analysis showed that, on the global scale, warming significantly increased root biomass and soil respiration,

TABLE 1 Factors controlling effect of warming on soil carbon, root biomass and soil respiration in this meta-analysis.

	Soil C		Root biomass		Soil respiration	
	Q_M	*p* value	Q_M	*p* value	Q_M	*p* value
Warming method	3.3413	0.3419	6.9070	0.0749	7.3780	0.0608
Ecosystem	3.0205	0.5544	8.0716	0.0890	16.0148	**0.0030**
Warming magnitude	0.0830	0.7732	5.0200	**0.0251**	2.1211	0.1453
Warming duration	12.1933	**0.0005**	1.0789	0.2990	4.1428	**0.0418**
MAT	1.1664	0.2801	4.5098	**0.0337**	1.1656	0.2803
MAP	0.2222	0.6374	3.7933	0.0515	11.4057	**0.0007**
Soil N level	1.5359	0.2152	4.2736	**0.0387**	3.6402	0.0564

Note: Q_M represents the heterogeneity in effect sizes associated with moderator variable. Significant *p* values ($p < .05$) are shown in bold.
Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

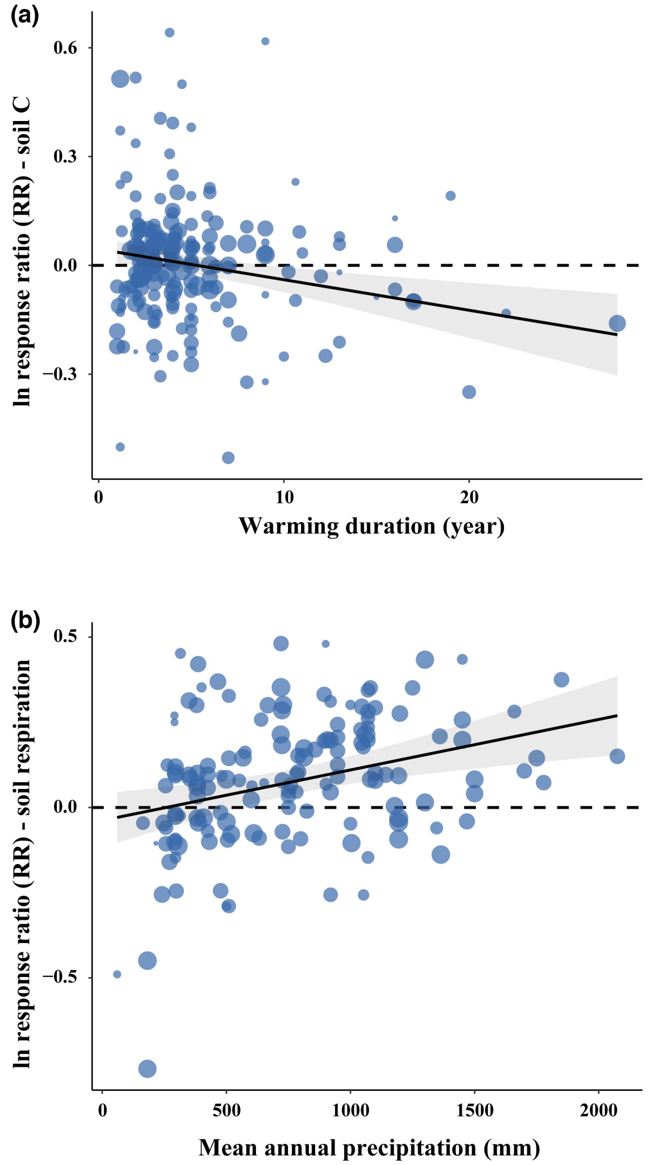

FIGURE 2 The relationship between ln response ratio (RR) of soil C and warming duration (a), and the relationship between lnRR of soil respiration and mean annual precipitation (b). Regression lines with 95% confidence intervals represent significant relationships found in the meta-analyses based on mixed-effects meta-regression models. Dots represent individual experiments, with dot size proportional to model weights. [Colour figure can be viewed at wileyonlinelibrary.com]

but did not significantly impact soil C stock (Figure 1). Facilitative effects of warming on root biomass (C input) and soil respiration (C output) depended on relative soil N availability (Figures 3 and 4), suggesting that different N availability may affect soil C formation and decomposition through distinct mechanisms and/or processes under climate warming (Figure 6).

4.1 | Soil N availability mediated warming effect on soil C input, output and transformations

Our results showed that warming significantly promoted root growth (Figure 1b) and likely increased soil C input as rhizodeposition and dead fine roots are important sources of soil C (Keller et al., 2021; Sokol & Bradford, 2019; Villarino et al., 2021). Warming can enhance root biomass through multiple mechanisms. First, warming can increase microbial N mineralization and thus soil available N for plant growth, which may enhance plant photosynthate allocation to roots (Liu et al., 2022; Melillo et al., 2011; Wu et al., 2012). Second, warming often reduces soil moisture by enhancing evapotranspiration (Ettinger et al., 2019), and plants consequently increase C allocation belowground to roots and their associated microbes for H_2O uptake (Zhou et al., 2022). Third, warming may shift plant community composition in the long-term, resulting in denser and deeper root systems, particularly in cold regions (Liu et al., 2018). Our results also showed that warming enhancement of root biomass was more profound under low (soil C:N ratio > 15) than high soil N availability (soil C:N ratio < 15) (p = .0387; Table 2; Figure 3). Most terrestrial plants are limited by soil N (LeBauer & Treseder, 2008), particularly those growing in tundra or boreal forests with high soil C:N ratios (Lu et al., 2021; Schulte-Uebbing & de Vries, 2018). As most plants cannot directly utilize organic N, warming stimulates microbial N mineralization and alleviates N limitation of plant growth (Liu et al., 2022), which likely dominates the high warming-enhancement of root biomass (+13.15%) in N-deficient regions observed in our study.

Consistent with our first hypothesis, we found that the relative C:N availability of soil critically affected transformation of root-derived C into soil matrix (Figure 4) as the relationship between lnRR of root biomass and lnRR of soil C was different in low and high N soils (Figure 4). In soils with low N availability, enhanced root biomass under warming did not induce a corresponding C accumulation (−1.52%) (Figures 3 and 4b), likely because of two major reasons. First, in face of N limitation, plants allocate more photosynthates belowground to fine roots, root-associated microbes such as mycorrhizal fungi, and root exudates in search of soil available N. Fresh roots or associated microbes can enhance microbial activities and thus increase the mineralization of "old" OM in soils

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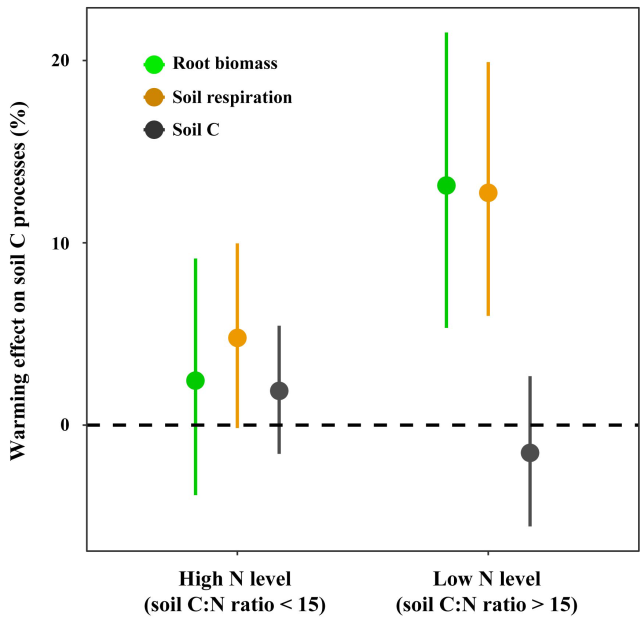

FIGURE 3 Percentage changes in soil C, root biomass and soil respiration to simulated warming under high N level (soil C:N ratio < 15) and low N level (soil C:N ratio > 15). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of meta-regression between ln response ratio (RR) of soil carbon with ln RR of root biomass and ln RR of soil respiration under high (soil C:N ratio < 15) and low N level (soil C:N ratio > 15).

	High N level		Low N level	
	Q_M	*p* value	Q_M	*p* value
lnRR of root biomass	8.7102	**0.0032**	0.8187	0.3656
lnRR of soil respiration	2.7940	0.0946	0.5655	0.4521

Note: Significant *p* values ($p < .05$) are shown in bold.

(i.e., the rhizosphere priming effect) (Cheng et al., 2012; Dijkstra et al., 2021; Fontaine et al., 2007). This effect can be strong so that decomposition of SOM offsets the positive effect of increased root-derived C (Chen et al., 2014; Terrer et al., 2021). Second, N limitation often leads to recalcitrant root litter (Parton et al., 2007), which decreases microbial CUE (Chen, Liu, Mao, et al., 2018; Cotrufo et al., 2013). Low litter decomposition rate and microbial CUE likely limit transformation of root C into microbial necromass and soil C pool (Kirkby et al., 2014; Zhou et al., 2019). Thus, under low N availability, warming led to higher enhancement of root biomass and soil respiration (Figure 3), likely accelerating SOM turnover to alleviate plant and microbial nutrient limitation (Figure 6).

When soil N is relatively abundant, in contrast, warming-induced changes in root biomass were correlated with soil C stock (Figure 4a). High N availability can increase microbial CUE and result in high microbial residues and dissolved organic C content (Huang et al., 2011), both of which play important roles in soil C formation (Kallenbach et al., 2016; Liang et al., 2019). Therefore, warming-increased root C inputs under high N availability can be transformed, and

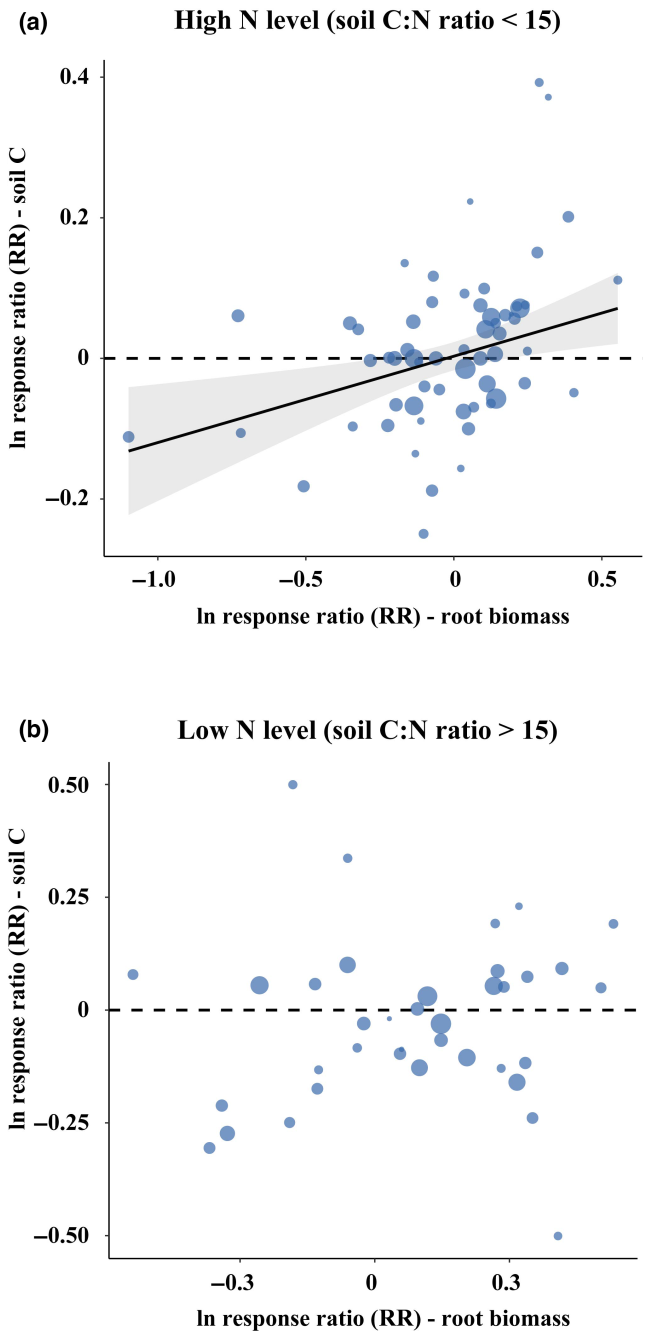

FIGURE 4 Different relationships between ln response ratio (RR) of soil C and lnRR of root biomass under high [soil C:N ratio < 15; (a)] and low N [soil C:N ratio > 15; (b)] availability. The solid line with 95% confidence interval denotes significant relationships ($p < .05$). [Colour figure can be viewed at wileyonlinelibrary.com]

subsequently incorporated effectively into the soil matrix (Cotrufo et al., 2015), forming more stabilized C. Also, when soil bioavailable N is high, microbes does not necessarily induce high SOM depolymerization and organic N solubilization (Daly et al., 2021), suppressing warming-induced soil CO_2 efflux and SOM turnover (Figure 6).

Contrary to our second hypothesis, we did not find significant relationships between lnRR of soil respiration and lnRR of soil C stock

TABLE 3 Effects of other global change factors (i.e., N fertilization, elevated CO_2 and precipitation increase/reduction) on soil C storage response to climate warming.

	Q_M	*p* value
N Fertilization	3.7008	*0.0544*
Elevated CO_2	1.1812	0.2771
Precipitation increase	0	0.9984
Precipitation reduction	0.2080	0.6483

Note: Marginally significant *p* values (.05 < *p* < .1) are shown in italic.

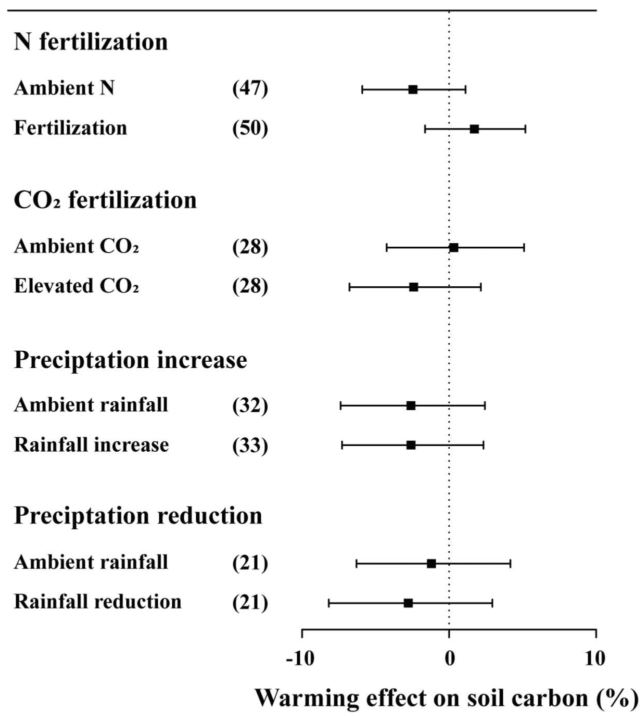

FIGURE 5 Effects of N fertilization, elevated CO_2 concentration, precipitation increase and reduction on soil C response to warming in two- or multi- global-change-factor experiments. Values in parentheses denote the number of observations. Error bars indicate 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

under either low or high soil N (Table 2), suggesting that higher CO_2 release from soil under warming is not necessarily translated into higher net soil C losses (Giardina et al., 2014). Warming-enhancement of soil CO_2 release may occur due to increased root respiration and the loss of newly added, non-protected C derived from plant residues and root exudates, rather than the decomposition of "old soil C" (Smith & Fang, 2010). Thus, caution is needed while scaling up of soil CO_2 efflux to predict soil C balance under warming.

Our synthesis of full-factorial warming × N addition experiments further confirmed the key role of soil N availability in mediating soil C response to warming. We found that reactive N input marginally offset the negative warming effect on soil C ($p = .0544$, Figure 5). Reactive N input affects both C input to soil and C output from soil. It often enhances plant photosynthesis and net primary production, enhancing litter production and photosynthate allocation belowground (LeBauer & Treseder, 2008; Liu & Greaver, 2010; Lu et al., 2011). Although reactive N addition stimulates cellulase activity, it generally suppresses production and activities of lignin-degrading enzymes in soil (Carreiro et al., 2000; Fog, 1988). The challenge remains to identify the magnitude of N input needed to sustain/promote C accumulation in soils in a warming climate (Fornara & Tilman, 2012; Lu et al., 2021; Riggs et al., 2015). Taken together, these results underline the key role of soil N availability in driving soil C cycling under climate warming. Incorporating the soil N availability (soil C:N ratio) of ecosystems into future Earth system models will improve projections for soil C responses and feedbacks to climate change.

4.2 | Responses of soil C pool to short-term versus long-term warming

Consistent with our third hypothesis, our synthesis identified a negative relationship between warming duration and lnRR of soil C stock (Figure 2a), suggesting that long-term warming induce more profound C losses. Multiple processes, including depletion of labile C pools, reductions in microbial biomass, shifts in microbial CUE, and changes in the soil microbial community composition, can influence the magnitude of soil C loss during different stages of warming (Melillo et al., 2017). Over the short term, warming often stimulates microbial metabolism and utilization of labile soil C. Labile soil C is of limited size and its depletion may not significantly change soil total C stock (Dorrepaal et al., 2009; Melillo et al., 2002). However, depletion of readily accessible C pool likely induces microbial starvation and death, reducing microbial biomass C pool and shifting microbial communities to be more oligotrophic (DeAngelis et al., 2015; Zhang et al., 2005). For example, DeAngelis et al. (2015) examined the responses of soil microbes to 5, 8 and 20 years of warming, and found that only the 20-year warming significantly altered bacterial community structure and increased bacterial diversity. This change of microbial community caused by long-term warming may alter C-degradation genes and accelerate microbial degradation of lignin-derived (chemically stabilized) compounds (Pold et al., 2015). A recent meta-analysis also indicated that long-term (>5 years) warming increased the ratio of ligninase to cellulase activity (Chen et al., 2020), suggesting that soil microbes acclimate to C starvation through utilization of chemically stabilized C substrates (Feng et al., 2017; Tao et al., 2020). These changes may depolymerize macromolecules and increase microbial accessibility to previously protected C, aggravating soil C loss as warming continues.

4.3 | MAP mediated soil respiration response to climate warming

The positive relationship between MAP and lnRR of soil respiration (Figure 2b) and negative warming effect on soil respiration in deserts

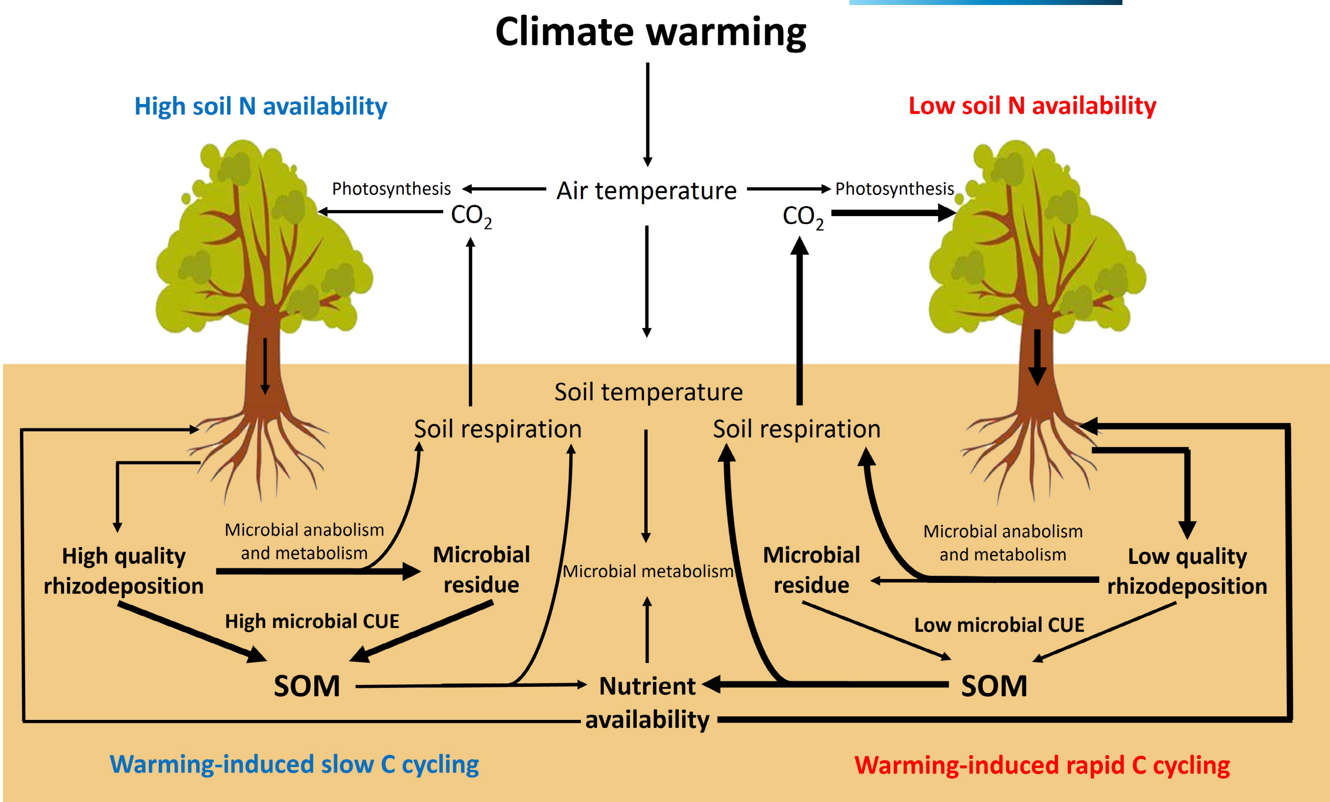

FIGURE 6 Schematic diagram summarizing the effect of climate warming on soil C cycling under high and low soil N availability. The thickness of the line indicates the strength of the effect. [Colour figure can be viewed at wileyonlinelibrary.com]

suggest that low soil moisture suppress warming enhancement of soil CO_2 efflux (Figure 1c). In arid systems, water, rather than temperature, is the primary limiting factor for microbial decomposition (Allison & Treseder, 2008; Liu et al., 2009). Warming often reduces soil moisture by enhancing evapotranspiration (Ettinger et al., 2019), which could further exacerbate water stress to microbes and reduce the interaction of a substrate with an enzyme (Sheik et al., 2011). This indirect negative effect can surpass the direct positive effect of warming on soil respiration in water-limited ecosystems (Guan et al., 2019; Wertin et al., 2017). Under wet conditions, oxygen (O_2) limitation often leads to the inhibition of oxidative enzymes involved in depolymerization of macromolecules (Sinsabaugh, 2010), and warming-induced drought can promote O_2 diffusion in soil pores and promote soil CO_2 release (Fenner & Freeman, 2011). Thus, soil respiration is more sensitive to climate warming in areas with higher moisture content.

4.4 | Conclusions and implications for predicting soil C cycling under warming

Understanding effects of climate warming on soil C cycling is essential to accurately predict C-climate feedback under future global change scenarios. Our synthesis of simulative warming experiments at 165 sites across the globe indicated that relative C to N availability in soil critically mediated warming effect on soil C input, output and transformations. This finding helps reconcile varying magnitudes and directions of observed C-climate feedbacks across different biomes. Under low N availability, warming induced higher soil CO_2 emission but lower C transformations into soil matrix, suggesting that soil C in the high latitude regions with limited N (e.g., boreal forest and tundra) are more vulnerable to climate warming. In regions with relatively high N, in contrast, warming-enhancement of organic C (e.g., root) belowground tended to promote soil C accumulation via microbial necromass. These results suggest that relative N availability in soils may function as a primary driver regulating soil C cycling responses to climate warming. Also, our result showed that N input offset warming-induced soil C loss, suggesting that in managed and semi-managed ecosystems, effective N management may provide a practical tool to enhance soil C sequestration under future global warming scenarios. Major challenges remain to identify the optimal rates, types, and timing of N input that enhance root and microbial growth, and subsequent C input to soil, while constraining root and microbial respiration responses to warming.

AUTHOR CONTRIBUTIONS

Tongshuo Bai and Shuijin Hu conceived the study; Tongshuo Bai, Yunpeng Qiu, and Yi Zhang collected and analyzed the data; and Tongshuo Bai, Peng Wang and Shuijin Hu wrote the manuscript.

ACKNOWLEDGMENTS

This research was supported by the National Natural Science Foundation of China (32171646, 32171553, 32001140).

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo digital repository (https://doi.org/10.5281/zenodo.7581090).

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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: Bai, T., Wang, P., Qiu, Y., Zhang, Y., & Hu, S. (2023). Nitrogen availability mediates soil carbon cycling response to climate warming: A meta-analysis. *Global Change Biology*, *29*, 2608–2626. https://doi.org/10.1111/gcb.16627