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Soil microbial respiration adapts to higher and longer warming experiments at the global scale

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Keywords: microbial carbon decomposition, microbial biomass, community composition, warming magnitude, warming duration, background conditions

Supplementary material for this article is available online

Abstract

Warming can affect soil microbial respiration by changing microbial biomass and community composition. The responses of soil microbial respiration to warming under experimental conditions are also related to background conditions and the experimental setup, such as warming magnitude, duration, and methods. However, the global pattern of soil microbial respiration in response to warming and underlying mechanisms remain unclear. Here, we conducted a global meta-analysis of the response of soil microbial respiration to warming by synthesizing data from 187 field experiments. We found that experimental warming significantly increased soil microbial respiration and microbial biomass carbon by 11.8% and 6.4%, respectively. The warming-induced increase in microbial carbon decomposition was positively correlated with increased microbial biomass carbon, but not community composition. Moreover, the positive response of soil microbial respiration marginally increased with warming magnitude, particularly in short-term experiments, but soil microbial respiration adapted to higher warming at longer timescales. Warming method did not significantly affect the response of microbial respiration, except for a significant effect with open top chamber warming. In addition, the impact of warming on soil microbial respiration was more pronounced in wetter sites and in sites with lower soil pH and higher soil organic carbon. Our findings suggest that warming stimulates microbial respiration mainly by increasing microbial biomass carbon. We also highlight the importance of the combination of warming magnitude and duration in regulating soil microbial respiration responses, and the dependence of warming effects upon background precipitation and soil conditions. These findings can advance our understanding of soil carbon losses and carbon-climate feedbacks in a warm world.

1. Introduction

Global average surface temperature is predicted to increase 3.3 °C–5.7 °C by the end of this century (Arias *et al* 2021). Climate warming not only impacts aboveground vegetation growth (Jassey *et al* 2013, Lu *et al* 2013), but also affects belowground microbial activity (Frey *et al* 2008, Melillo *et al* 2017). Soil microbial respiration, which is the release of carbon (C) from the decomposition of soil organic matter (Schlesinger and Andrews 2000), is an important pathway of soil C losses. Understanding the response of soil microbial respiration to global warming has become one of the most important challenges for ecologists, and it is important because small changes in microbial C decomposition can profoundly affect atmospheric carbon dioxide (CO_2) concentrations and thus future climate change (Bond-Lamberty *et al* 2018).

In an early meta-analysis, it showed that warming generally promoted soil microbial respiration by 21% from 17 field studies (Wang *et al* 2014). However, Zhou *et al* (2016) demonstrated that soil heterotrophic respiration did not significantly change by climate warming across 36 studies. From previous field studies we also know that experimental warming can either increase (Graham *et al* 2014, Ma *et al* 2018, Teramoto *et al* 2018, Li *et al* 2020), decrease (Zhao *et al* 2019, Shen *et al* 2020), or have a negligible effect on soil microbial respiration (Zhang *et al* 2013, Wang *et al* 2019, Yan *et al* 2021). Therefore, how warming affects soil microbial respiration and its underlying mechanisms remains largely uncertain.

Experimental warming can significantly change plant respiration by affecting biomass and community composition of aboveground plants (Chen *et al* 2016, Bai *et al* 2019). Likewise, warming can alter soil microbial respiration by affecting microbial attributes, including microbial biomass (Rousk *et al* 2013, Zhang *et al* 2013, Zhao *et al* 2019) and community composition (Schindlbacher *et al* 2015, Peng *et al* 2020). Increasing microbial biomass C under warming has enhanced microbial respiration (Xu and Yuan 2017, Ma *et al* 2018), and other studies have demonstrated that warming-induced changes in soil total phospholipid fatty acid (PLFA) biomass or arbuscular mycorrhizal biomass could alter microbial respiration (Melillo *et al* 2017, Liu *et al* 2018). Also, Shen *et al* (2020) found that soil microbial respiration acclimated to six years of warming in a temperate grassland via the modification of fatty acids C members in microbial membranes. Although the roles of microbial biomass and community composition in regulating microbial respiration have been proposed in numerous site-level studies (Schindlbacher *et al* 2015, Melillo *et al* 2017, Peng *et al* 2020), it remains unclear how the warming responses of these microbial attributes affect microbial respiration at the global scale.

Experimental warming effects on soil microbial respiration could be tightly associated with the experimental setup, including warming magnitude, duration, and method (Wang *et al* 2014, 2021a, Teramoto *et al* 2018). Different warming magnitudes can induce various changes in soil microbes and soil conditions (e.g. soil temperature, moisture, and nutrient availability) (Lu *et al* 2013, Chen *et al* 2015, Xu and Yuan 2017, Wang *et al* 2021a), which may lead to inconsistent responses of soil microbial respiration. For instance, a warming magnitude of 2.5 °C significantly decreased soil microbial respiration by an average of 15.7%, while 1.5 °C of warming showed no significant impact in an alpine meadow during three years of warming treatment (Yan *et al* 2021). The warming duration may also mediate the response of soil microbial respiration (Zhang *et al* 2013, Li *et al* 2020). Previous meta-analyses demonstrated that warming increased soil microbial respiration, and the microbial respiration response remained unchanged over the continued time of warming at the global scale (Wang *et al* 2014). Nevertheless, in a temperate forest, five years of experimental warming had a positive effect on microbial respiration, and the warming effects tended to increase with time after warming (Teramoto *et al* 2018). Furthermore, higher warming magnitudes may be associated with prolonged warming, which can aggravate drought stress and inhibit soil microbial activity.

Meanwhile, warming methods may have various impacts on microbial respiration (Liu *et al* 2020). Warming via heating cables can directly affect soil microbial processes (Noh *et al* 2016, Melillo *et al* 2017). While warming by infrared radiators, open top chambers (OTCs), or reflective curtains can directly facilitate plant C fixation and thereby indirectly impact soil microbes and their activities (Rinnan *et al* 2009, Rousk *et al* 2013). But even here, the compounding impacts of experimental warming magnitude, duration, and methods on soil microbial respiration remain elusive, which prevents accurate predictions of future soil C losses.

Warming impacts on soil microbial respiration may also vary with background environmental conditions, including ecosystem type, mean annual temperature and precipitation, and initial soil conditions. In a cool-temperate deciduous forest, microbial respiration was stimulated by 32% in the four to eight years after warming (Noh *et al* 2016). However, in a semi-arid grassland, Zhang *et al* (2013) found no response of soil microbial respiration to warming in a four-year field experiment. Similarly, the inconsistent response of microbial respiration to experimental warming has been reported across five European shrubland ecosystems (Rousk *et al* 2013). Previous field studies have also found that background precipitation drives the magnitude and direction of microbial respiration response to experimental warming (Chen *et al* 2015, Wang *et al* 2021b). In arid and semi-arid sites, warming is less likely to stimulate microbial respiration due to drought stress (Zhang *et al* 2013, Liu *et al* 2016). In a humid forest, however, Teramoto *et al* (2018) reported that warming-induced increases in litter decomposition and microbial activity enhanced microbial respiration. Furthermore, variations in the response of microbial respiration to warming may change with initial soil conditions because microbial C decomposition is more sensitive in the areas with higher initial soil C stocks (Crowther *et al* 2016, Tian *et al* 2022).

Several previous meta-analyses have been conducted to investigate the effect of climate warming on microbial respiration at the global scale (e.g. Wang *et al* 2014, Crowther *et al* 2016, Zhou *et al* 2016, Liu *et al* 2020). However, the response of microbial

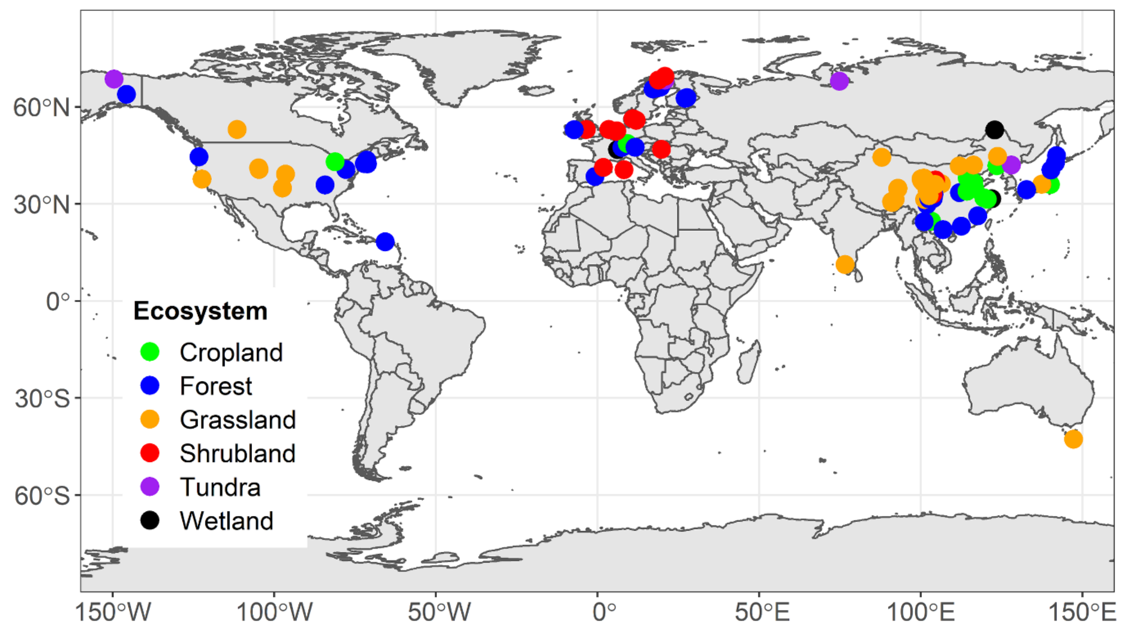

Figure 1. Global distribution of warming experiments in this meta-analysis.

respiration to warming could be jointly controlled by changes in soil microbial biomass and community composition, and have been found to vary with experimental setup and background conditions. To comprehensively understand the warming-induced responses of soil microbial respiration and their links with soil microbial biomass and community composition responses, we conducted a global meta-analysis of warming studies across a broad range of ecosystems. Specifically, the objectives of this study were to: (1) investigate the global warming responses of soil microbial respiration and their linkages with changes in soil microbial biomass and community composition; and (2) explore how microbial respiration responses varied with experimental setup and background conditions.

2. Materials and methods

2.1. Data collection

We searched journal articles published before 1st August 2022 that studied soil microbial respiration, biomass and community composition under *in-situ* experimental warming using the Web of Science, Google Scholar, and the China National Knowledge Infrastructure. The following combinations of keywords: (warming or global change or climate change or rising temperature or elevated temperature or increased temperature) and (soil microbial) and (respiration or biomass or bacteria or fungi) were used. We also used the following criteria to select the studies: (1) the control and elevated temperature treatments had the same field conditions; (2) at least one growing season of soil microbial respiration was reported; (3) at least one of the soil microbial variables (microbial respiration, biomass, or community composition) was reported; (4) the mean values and samples size can be directly extracted from the tables or indirectly extracted from the figures; and (5) warming magnitude (differences in temperature between warming and the control), warming duration, warming methods, ecosystem types, and the measurement method of microbial respiration were clearly described. A total of 187 studies met the above criteria (supporting data, figure 1). More detailed description of the data extracted can refer to the supporting information.

2.2. Data analysis

The natural logarithm of response ratio (lnRR; Hedges *et al* 1999) was used to quantitatively assess the response of each variable to experimental warming. lnRR is calculated as $\text{InRR} = \text{In}(\bar{X}_t/\bar{X}_c) = \text{In}(\bar{X}_t) - \text{In}(\bar{X}_c)$, where $(\bar{X}_t)$ and $(\bar{X}_c)$ represent the mean values of a given variable in the warming treatment and in the control group, respectively. Like the former studies (Wang *et al* 2021c), we used the replication number for weighted variance (v) of an individual observation: $v = (N_c * N_t)/(N_c + N_t)$, where N_c and N_t are the sample size for the control and the warming treatment group, respectively.

For each soil microbial variable, we used the restricted maximum likelihood estimation with the lme4 package in R to test the overall effect of warming (Bates *et al* 2014). The 'study' was treated as the random effect factor (Chen *et al* 2019, Sun *et al* 2021). If the 95% confidence interval (CI) did not bracket zero, the effect of experimental warming on soil microbial variables were significant at $\alpha = 0.05$. For ease of interpretation, lnRR was transformed back to the percentage changes as $(e^{\ln RR} - 1) * 100\%$. The residual frequency distributions of the model of lnRR of soil microbial respiration, biomass, and community composition to warming were normally distributed (figure S1).

To explore the relationships between the response ratio of soil microbial respiration and the response ratios of soil microbial biomass and community composition, we used a linear mixed model with 'study' as a random effect factor. Mixed-effect models were also conducted to investigate whether warming effect on soil microbial respiration was affected by warming magnitude (*MA*, °C), warming duration (*D*, year), warming method (*ME*), background conditions (*B*, i.e. ecosystem type, the measurement method of microbial respiration, mean annual temperate (MAT), mean annual precipitation (MAP), initial soil pH, initial soil organic carbon, and initial soil total nitrogen), and their interactions using the following model structure:

$$\begin{aligned}\ln RR = {} & \beta_0 + \beta_1 * \mathrm{MA} + \beta_2 * D + \beta_3 * \mathrm{ME} \\ & + \beta_4 * B + \beta_5 * \mathrm{MA} * D + \beta_6 * \mathrm{MA} * \mathrm{ME} \\ & + \beta_7 * \mathrm{MA} * B + \beta_8 * D * \mathrm{ME} \\ & + \beta_9 * D * B + \beta_{10} * \mathrm{ME} * B \\ & + \beta_{11} * \mathrm{MA} * D * \mathrm{ME} \\ & + \beta_{12} * \mathrm{MA} * D * B + \beta_{13} * \mathrm{MA} * \mathrm{ME} * B \\ & + \beta_{14} * D * \mathrm{ME} * B \\ & + \beta_{15} * \mathrm{MA} * D * \mathrm{ME} * B + \pi_{\mathrm{study}} + \epsilon.\end{aligned}$$

where β and ε are coefficients and sampling error and π_{study} is the random effect factor of study. Like in a previous study (Wang *et al* 2021c), we only retained warming magnitude and warming duration in the final model among all alternative models because they were important factors of the experimental warming and to prevent overfitting (Johnson and Omland 2004). Then, following the methods used in previous studies (Chen *et al* 2019, Wang *et al* 2021c), the model selection was accomplished by the 'dredge' function of the MuMIn package based on the Akaike information criterion (AIC) (Barton 2018). The models with ΔAIC $\leqslant$2 are considered equivalent, and we selected the best model with the lowest AIC. All terms associated with warming method or background conditions were excluded in the most parsimonious model. We also compared linear and log-linear responses, and ln (*MA*) and *D* were selected in all alternative models due to the model of AIC value being the smallest (table S2). Thus, we employed the following models to determine the overall effects of *MA* and *D* on soil microbial respiration:

$$\begin{aligned}\ln RR = {} & \beta_0 + \beta_1 * \ln(\mathrm{MA}) + \beta_2 * D \\ & + \beta_3 * \ln(\mathrm{MA}) * D + \pi_{\mathrm{study}} + \epsilon.\end{aligned}$$

We scaled the continuous variables (ln (*MA*) and *D*, observed values minus mean and divided by one standard deviation) (Chen *et al* 2019, Wang *et al* 2021c). To illustrate graphically whether the effect of warming magnitude on the response ratio of soil microbial respiration differed with warming duration, we calculated warming duration-dependent effects at warming durations of 1, 2, 4, 10, and 18 years, respectively (Cohen *et al* 2014). In order to quantify whether the response ratio of soil microbial respiration varied with warming methods or background conditions, we conducted an analysis with warming methods or background conditions as the only fixed factor and 'study' as the random effect factor in the linear mixed-effect model. All data analyses were performed in R.4.1.2 (R Core Team 2020).

3. Results

3.1. Effects of warming on soil microbial respiration, biomass, and community composition

Across all studies, soil microbial respiration increased significantly on average by 11.8% (95% CIs, 3.3%–20.4%, $P < 0.01$, figure 2) in experimental warming compared to the control. Experimental warming also significantly increased soil microbial biomass carbon by an average of 6.4% (1.3%–11.6%, $P < 0.05$, figure 2), while other soil microbial biomass and community composition (all $P > 0.05$, figure 2) showed no significant responses to experimental warming. We also found that the response ratio of soil microbial respiration was positively related to the response ratio of soil microbial biomass carbon ($P < 0.001$, $R^2 = 0.16$, $N = 76$, table 1, figure 3). The response ratios of other soil microbial biomass and community composition showed no significant relationships with soil microbial respiration response (all $P > 0.05$, table 1).

3.2. Soil microbial respiration response to warming varied with experimental setup

With increased warming magnitude, the effect size for soil microbial respiration marginally increased ($P = 0.07$, figure 4). The increase of soil microbial respiration with warming magnitude was more pronounced in short-term experiments, and in long-term experiments the warming effect on soil microbial respiration shifted from positive at lower warming magnitudes to negative at higher warming magnitudes ($P < 0.01$, figure 4). Moreover, warming by OTCs significantly increased soil microbial respiration by 20.7% (3.9%–37.5%, $P < 0.05$), while other warming methods did not have significant effects on soil microbial respiration (figure 5(a)). Warming significantly stimulated soil microbial respiration in trenched method by 19.8% (8.9%–30.6%, $P < 0.05$, figure 5(c)) compared to the incubation method.

3.3. Soil microbial respiration response to warming changed with background conditions

We found no significant differences in the effects of warming on soil microbial respiration among

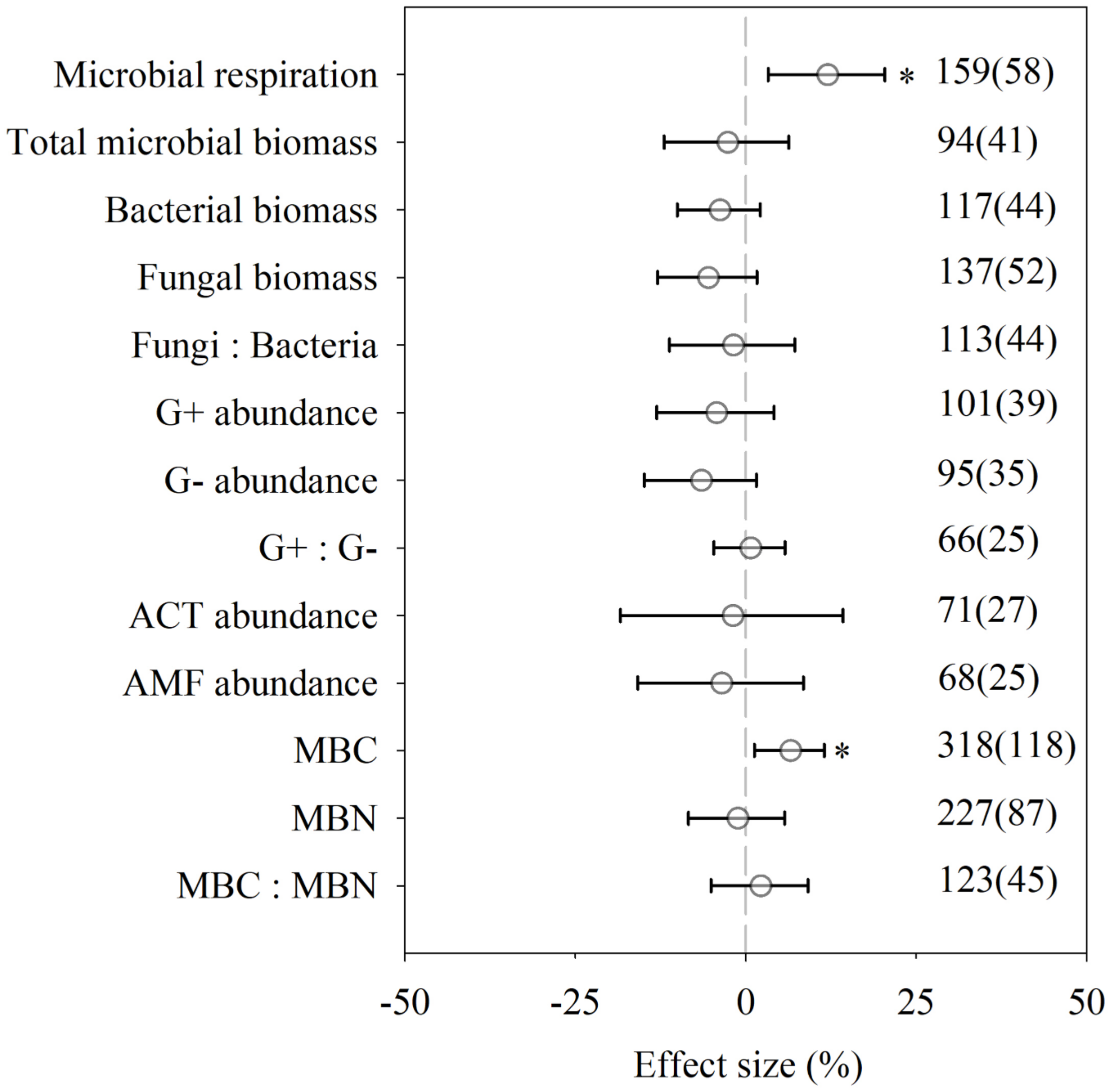

Figure 2. Effects of experimental warming on soil microbial respiration, biomass, and community composition. Circles represent mean effect size with their 95% confidence intervals (CI). The number of observations and studies are outside and within the parantheses. Abbreviations: G+ abundance: gram-positive abundance; G− abundance: gram-negative abundance; ACT abundance: actinomycetes abundance; AMF abundance: arbuscular mycorrhizal fungi abundance; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen.

Table 1. The effect (*P* values) of microbial attributes on natural log response ratios (lnRR) of microbial respiration. Abbreviations: G+ abundance: gram-positive abundance; G− abundance: gram-negative abundance; ACT abundance: actinomycetes abundance; AMF abundance: arbuscular mycorrhizal fungi abundance; MBC: microbial biomass carbon; MBN: microbial biomass nitrogen. The number in the bracket represents the studies.

	Microbial respiration		
Attribute	*P*	$R^2 adj$	*N*
Total microbial biomass	0.43	0.04	17(8)
Bacterial biomass	0.44	0.02	29(11)
Fungal biomass	0.71	0.01	30(12)
Fungi:Bacteria	0.31	0.05	23(10)
G+ abundance	0.95	0.00	18(8)
G− abundance	0.53	0.02	18(8)
G+:G−	0.61	0.02	16(7)
ACT abundance	0.08	0.34	8(5)
AMF abundance	0.72	0.01	18(8)
MBC	**0.00**	**0.16**	**76(32)**
MBN	0.09	0.03	57(24)
MBC:MBN	0.38	0.04	22(10)

Note: Bold values indicate the significance at the level of $P < 0.05$.

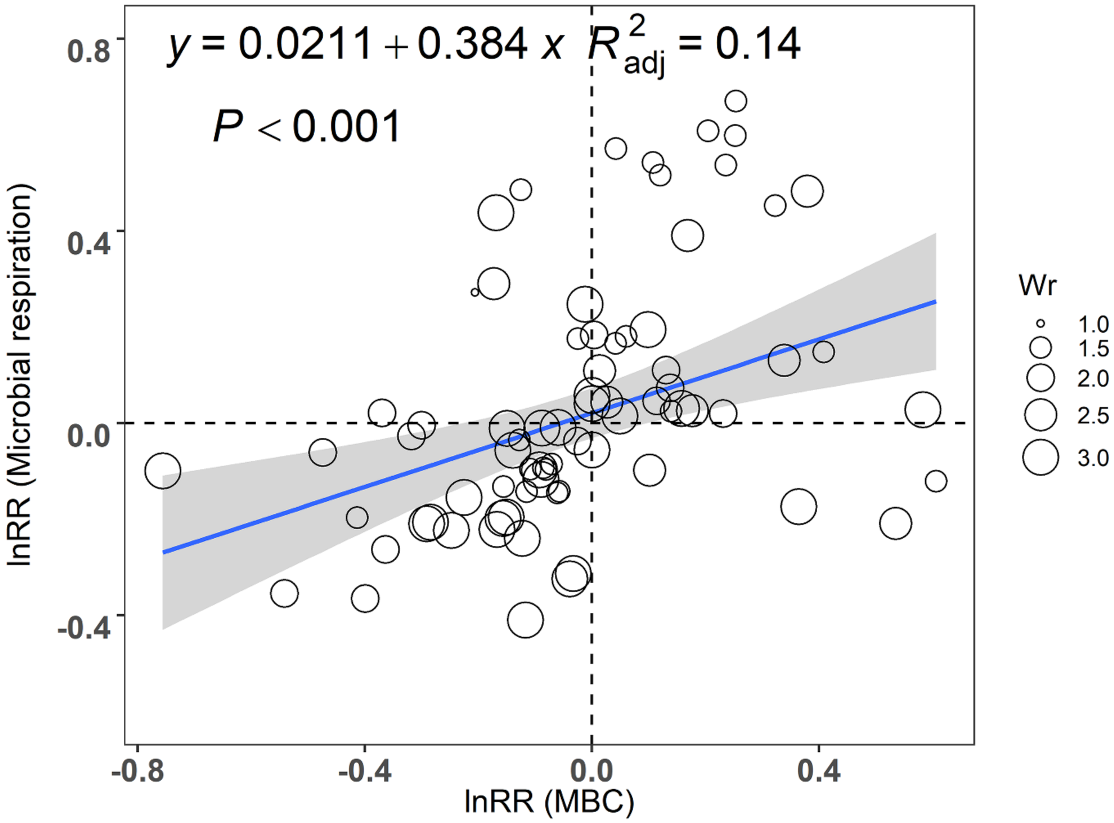

Figure 3. The relationship of log response ratios (lnRR) of soil microbial respiration with log response ratios (lnRR) of soil microbial biomass carbon. Blue lines represent the fitted regressions and shaded areas represent 95% confidence intervals. Circle sizes represent the relative weights by the numbers of replications of each observation.

ecosystem types (figure 5(b)), except for a significant and positive warming effect on soil microbial respiration in forest ecosystems. We found that the warming response of soil microbial respiration did not change with MAT ($P = 0.07$, $R^2 < 0.01$, figure 6(a)), but increased with MAP ($P = 0.01$, $R^2 = 0.06$, figure 6(b)). Moreover, the effect size for soil microbial respiration decreased with initial soil pH ($P = 0.01$, $R^2 = 0.10$, figure 7(a)), but significantly increased with initial soil organic carbon ($P = 0.04$, $R^2 = 0.12$, figure 7(b)) and marginally increased with initial soil total nitrogen ($P = 0.10$, $R^2 = 0.06$, figure 7(c)).

4. Discussion

4.1. Warming stimulates soil microbial respiration by increasing microbial biomass carbon

On average, experimental warming significantly increased soil microbial respiration and MBC, which corroborates the results of previous meta-analysis studies (Wang *et al* 2014, Xu and Yuan 2017, Liu *et al* 2020). A recent study showed that soil microbial respiration increased by 29.6% (Liu *et al* 2020) under experimental warming, which was higher than our result of 11.8% on average (figure 2). This difference may have been due to differences in data sources. The previous meta-analysis included not only the individual effect of warming, but also the interactive effects of warming and other climate change factors (e.g. warming and elevated CO_2), which dramatically stimulated soil microbial respiration (40.8%) compared to warming alone (7.1%) (Zhou *et al* 2016). Therefore, previous studies (Zhou *et al* 2016, Liu *et al* 2020) may have overestimated the effect of warming on soil microbial respiration.

We demonstrated that warming-induced increases in soil microbial respiration was closely correlated with the increase in MBC, which is consistent with previous studies (Chen *et al* 2016, Sun *et al* 2022). Warming can affect soil microbial respiration by influencing substrate supply (Kuzyakov 2006, Ye *et al* 2019). Warming-induced increases in the supply of fresh carbon from aboveground plant and belowground roots might have increased microbial activities (Rousk *et al* 2013, Liu *et al* 2020) and caused a 6.4% increase in MBC (figure 2), which could have promoted soil microbial respiration (Bell *et al* 2010, Sistla *et al* 2013, Graham *et al* 2014).

Unexpectedly, the responses of soil microbial respiration were not correlated with other microbial biomass variables (e.g. total PLFA biomass, bacterial biomass, fungal biomass, etc) and community composition (e.g. fungi: bacteria ratio and G+: G−). Previous studies showed that warming-induced increases in actinomycetal and arbuscular mycorrhizal biomass

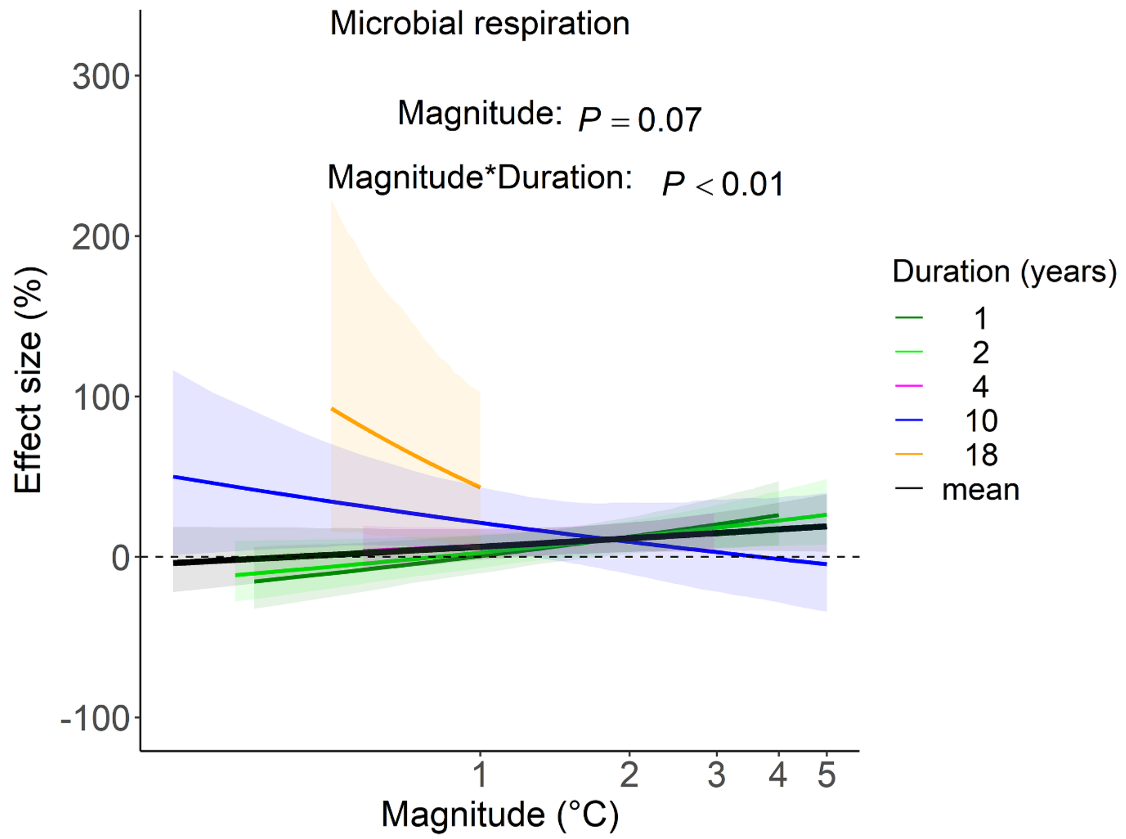

Figure 4. The interactive effects of warming magnitude and duration on soil microbial respiration. Lines are fitted warming duration-dependent regressions with 95% confidence intervals in shade. Dark green, green, magenta, blue, orange and black lines indicate warming duration on 1, 2, 4, 10, and 18 years and mean warming duration across all observations.

(Heinemeyer *et al* 2012) could produce hyphal exudates that affect the mineralization of soil organic matter (Paterson *et al* 2016), and then increase microbial respiration (Liu *et al* 2018). In contrast, Peng *et al* (2020) demonstrated that the decrease in the relative abundance of actinobacteria, increase in metabolic activity, and a lack of substrate limitation sustained the positive warming effect on microbial respiration in an alpine meadow. In addition, soil microbial respiration could acclimate to experimental warming by modifying cell membrane constitutions (Bradford *et al* 2008, Melillo *et al* 2017, Shen *et al* 2020). Some previous studies showed that *in-situ* climate warming did not affect the soil PLFAs biomass (Rousk *et al* 2013, Sun *et al* 2019, Yuan *et al* 2021). At the global scale, experimental warming did not significantly change cell membrane constitutions (figure 2), so they did not influence microbial respiration. Moreover, data that coupled microbial respiration and microbial attributes were limited in our database (e.g. most of microbial attributes <25 studies, microbial biomass carbon was 32 studies; table 1). Thus, further studies with concurrent measurements of microbial respiration and microbial attributes are warranted to verify our findings in experimental warming. It was also noticeable that the attribution of enhanced microbial respiration to MBC was somewhat weak ($R_{\mathrm{adj}}^2 = 0.14$) and causal, and future manipulative studies are necessary to explore.

4.2. Soil microbial respiration adapts to higher warming in long-term experiments

Our results suggested that responses of soil microbial respiration marginally increased with warming magnitude. Previous global syntheses showed that the response of microbes may first increase and then decrease with increasing warming magnitude (Xu and Yuan 2017), which indicates that the temperature sensitivity of microbes may decline or acclimate at high temperatures (Luo *et al* 2001, Reth *et al* 2009, Melillo *et al* 2017). The warming impact on soil microbial respiration shifted from positive to negative with longer warming duration (*ca* $\geqslant$ 10 years; figure 4). This finding provides solid evidence of adaptation of soil microbial respiration to higher temperatures (*ca* > 2 °C) in long-term experiments (*ca* $\geqslant$ 10 years, Dacal *et al* 2019) at the global scale. This threshold of warming magnitude (<2 °C) for soil microbial respiration has implications for soil C dynamics in the future global warming.

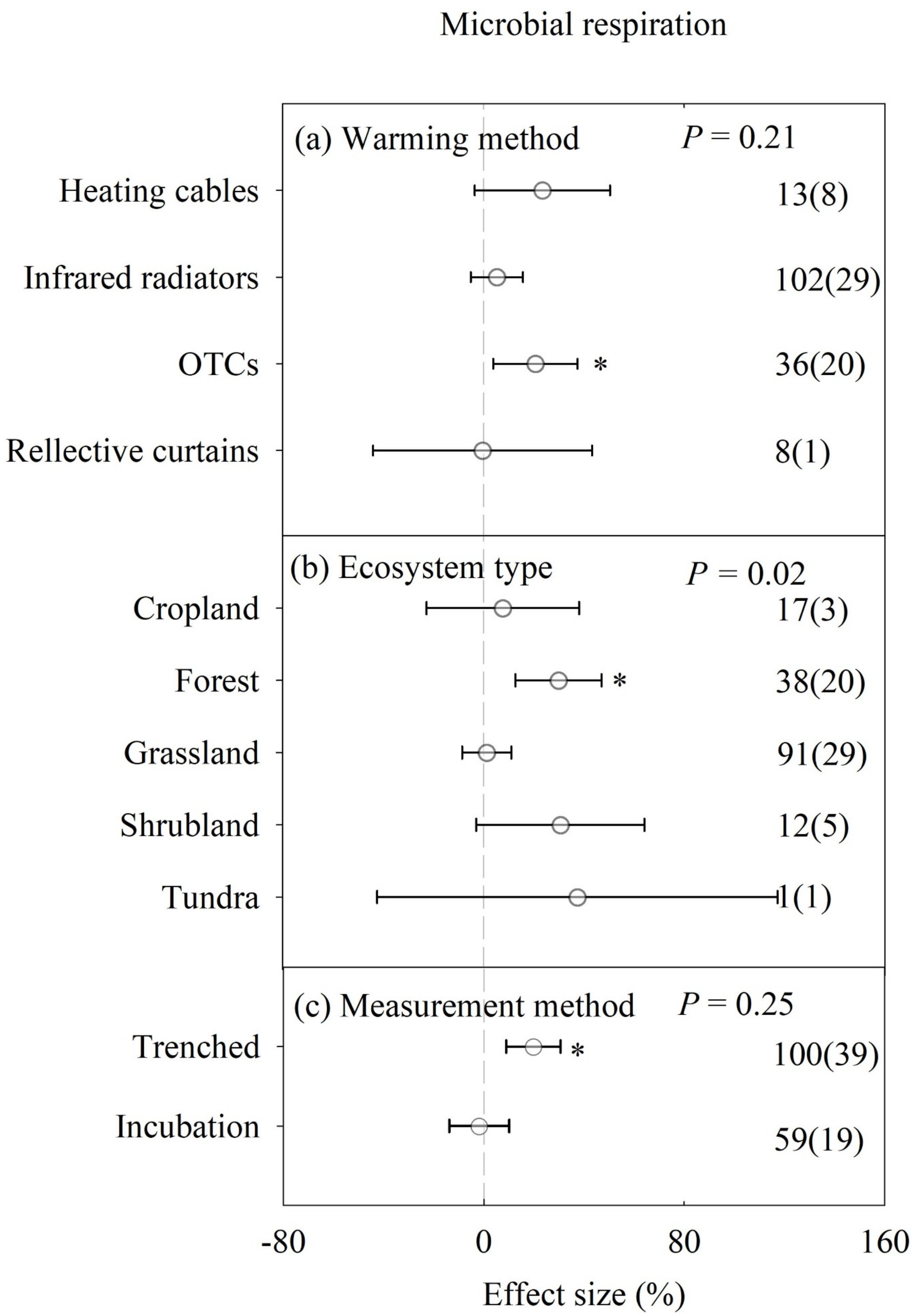

Figure 5. Relationships of relative changes in soil microbial respiration with warming method (a), ecosystem type (b), and the measurement method of microbial respiration (c). The number of observations and studies are outside and within the paratheses.

Bradford *et al* (2008) reported that soil microbial respiration adapted to soil warming (5 °C) in a mid-latitude forest across a 15 years experiment. Some results of modeling and lab incubations demonstrated that microbial respiration would adapt to warming (Rinnan *et al* 2009, Melillo *et al* 2017), mainly due to the depletion of soil C substrate (Bradford *et al* 2008, Tucker *et al* 2013), physiological adaptation of microbes (Allison *et al* 2010, Treseder *et al* 2016), and shifts in microbial community composition

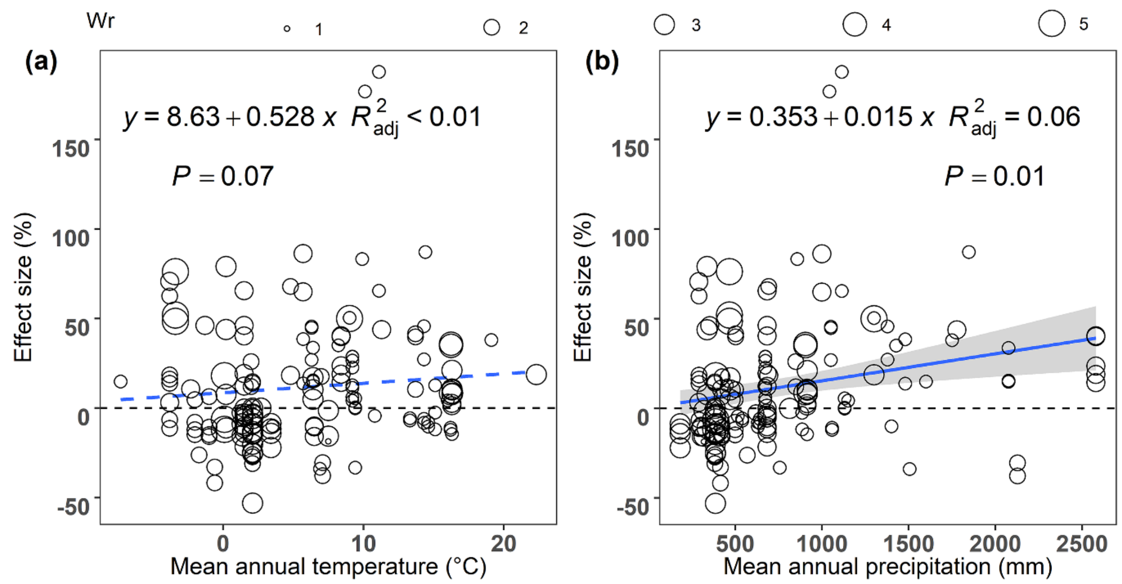

Figure 6. Relationships of relative changes in soil microbial respiration with mean annual temperature (a) and mean annual precipitation (b). Blue lines represent the fitted regressions and shaded areas represent 95% confidence intervals. Circle sizes represent the relative weights by the numbers of replications of each observation.

(Crowther and Bradford 2013, Walker *et al* 2018). Our findings provide the global evidence that microbial respiration thermally adapts to higher warming at longer timescales.

Regarding warming methods, warming only by OTCs significantly increased microbial respiration (figure 5(a)). This difference may be due to two reasons. First, the microbial biomass C was only stimulated for OTCs (figure S2(a); Xu and Yuan 2017), which implies that microbial activity was higher under OTCs warming than other warming methods. Second, OTCs were found to have a negligible effect on soil moisture (Rinnan *et al* 2009, Chen *et al* 2016), which may not constrain microbial activities and their decomposition of soil organic matter. Moreover, we found that the measurement method of trenching had a significant effect on the microbial respiration response (figure 5(c)). This result indicates that microbial respiration monitored by trenched method can truly reflect the response of soil microorganisms to climate warming. Our findings highlighted that warming methods and measurement methods of microbial respiration should be considered when evaluating warming effects on microbial respiration.

4.3. Warming responses of soil microbial respiration are modulated by background conditions

Warming effect on soil microbial respiration was regulated by mean annual precipitation across sites at the global scale (figure 6(b)), which agrees with previous syntheses (Liu *et al* 2016, Wang *et al* 2021b). In dry regions, warming reduced soil microbial activity by decreasing soil moisture (Chen *et al* 2015, Schindlbacher *et al* 2015, Fu *et al* 2019), while this inhibitory effect of warming diminished or reversed as soil moisture increased in wet sites (Quan *et al* 2019). Furthermore, the response of microbial respiration decreased with increasing initial soil pH, which indicated that microbes could be more sensitive to warming in acidic soils than in neutral or alkaline soils (figure 7(a)). Moreover, acidic soils were generally distributed in heavy precipitation areas (Liu *et al* 2018) which resulted in a stronger warming response of microbial respiration.

Our results also demonstrated that the warming impact on microbial respiration was more pronounced in nutrient-rich soils (figure 7(b)). This finding is likely due to labile C being more abundant in nutrient-rich than nutrient-limited soils (Hernández and Hobbie 2010). Soil dissolved organic matter is an important labile C source for microbes, which can respond rapidly to climate warming (Lu *et al* 2013, Liu *et al* 2020). Therefore, warming could promote the decomposition of soil organic matter when the substrate is sufficient (Xu *et al* 2010, Tian *et al* 2022). Thus, higher quantity and quality of soil C substrates could promote microbial C decomposition under warmer conditions.

The effect of experimental warming on microbial respiration differed among ecosystem types, and a significant effect was only detected in forest ecosystems (figure 5(b)). Previous studies reported that warming-induced increases in soil inorganic nitrogen and fine root nitrogen were significantly higher in forests than in other ecosystems at the global scale (Dieleman *et al* 2012, Bai *et al* 2013, Wang *et al* 2021c). This suggested that microbial respiration in forests could be increased by warming due to the increase in nitrogen available to microbes (Butler *et al* 2012).

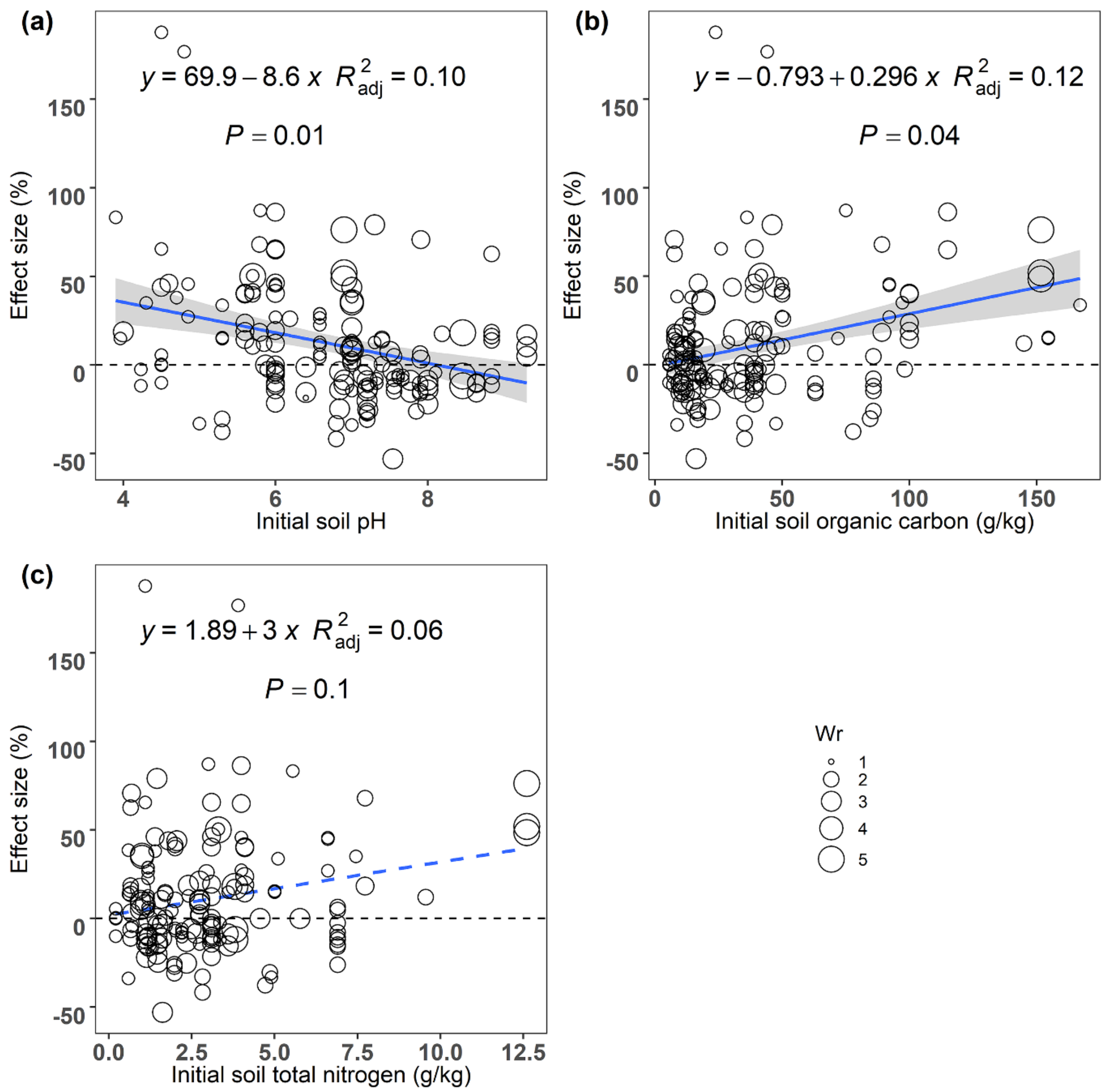

Figure 7. Relationships of relative changes in soil microbial respiration with initial soil pH (a), soil organic carbon content (b), and soil total nitrogen (c). Blue lines represent the fitted regressions and shaded areas represent 95% confidence intervals. Circle sizes represent the relative weights by the numbers of replications of each observation.

The nonsignificant responses among ecosystem types may be because most of the warming experiments were conducted in grasslands and forests, limiting our ability to detect differences in other sensitive ecosystems (figure 5(b)). This imbalance hinders our ability to broadly evaluate the significant differences among diverse ecosystems. Therefore, additional studies are further needed in these warming-sensitive regions.

4.4. Implications for future experiments

Our results from the meta-analysis of 187 field experiments may provide the following research views for future experiments. First, the response of soil microbial respiration was more associated with the response of soil microbial biomass carbon under warming. However, the microbial mechanisms underlying shifts in microbial respiration remain unclear due to the microbial community complexity (e.g. microbial activity, community profiles, and gene expression). Further study is necessary to quantify the relationship between soil microbial respiration and other microbial attributes (e.g. microbial sequencing data) under warming. Second, we detected a thermal adaptation of soil microbial respiration to higher warming at longer timescales, highlighting the importance of long-term experiments. Finally, the response of soil microbial respiration to warming varied with background conditions. Although we have thoroughly searched for *in-situ* warming experiments all over the world. Most of the experimental warming studies were located in Europe, East Asia, and North America. We encourage future experimental studies to pay more attention to the regions that are currently underrepresented in our global datasets (e.g. South America, Africa, and Southeast Asia).

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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