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A global synthesis reveals more response sensitivity of soil carbon flux than pool to warming

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Abstract
Purpose Climate change continues to garner attention in the public sphere. Most recognize its potential to affect global carbon (C) dynamics in the biosphere. Many posit that global warming promotes the decomposition of soil organic C (SOC) and increases soil C release. However, it remains unclear how soil C dynamics respond to different influencing factors (e.g., warming method, magnitude/duration, mean annual temperature (MAT) and precipitation (MAP)) across ecosystems on a global scale.
Materials and methods Here, we performed a meta-analysis to identify the general global patterns of how warming impacts soil C dynamics.
Results and discussion Across all terrestrial ecosystems, warming reduced SOC by 4.96% and stimulated soil microbial biomass C (MBC), soil respiration (SR), and heterotrophic respiration (HR) by 6.30, 14.56, and 8.42%, respectively. Warming affected soil C pools in grasslands and soil C fluxes in forests. The changes in SOC did not correlate to warming magnitude/duration or climate factors (MAT and MAP). However, changes in both MBC and SR did correlate to warming magnitude/duration and MAT. The changes in HR showed a quadratic response to warming magnitude and a linear response to MAP. Open-top chamber method can effectively affect soil C pools. SR proved to be more sensitive than HR to most warming methods.
Conclusions Our results showed that soil C release exhibited more sensitivity to warming magnitude/duration or MAT/MAP than did net soil C sequestration. These results indicate that warming induces accelerated transition of soils from C sink to C source. Furthermore, they show the potential for global warming effects to exacerbate the positive feedback loop in terrestrial ecosystems. However, the declining rates-of-change in SR and HR under high magnitude warming may mitigate the positive feedback. Our analyses can improve the predictions of feedback between atmospheric and soil C pools.

Keywords Carbon cycle · Global warming · Soil carbon pools · Soil carbon fluxes · Terrestrial ecosystems

1 Introduction

Scientists expect climate change to increase global surface temperatures 1.5–2 °C by the end of the twenty-first century (IPCC 2013). Many researchers recognize increased emission of greenhouse gasses (such as carbon dioxide (CO_2)) as a primary cause of global warming (Oreskes 2005). Global warming has the potential to affect global carbon (C) cycling and climate (Darrouzet-Nardi et al. 2015). Soil remains an important C source and sink and plays a major role in the C cycle of terrestrial ecosystems. In total, Earth's soil to a 1-m depth contains 1.5×10^{12} metric tons of organic C (Scharlemann et al. 2014; Jackson et al. 2017), an amount approximately three times larger than terrestrial vegetation and twice as much as the atmosphere (Falkowski et al. 2000; House et al. 2002; Lal 2004; Singh et al. 2010). Relatively

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small changes in the soil C pool may substantially affect atmospheric CO_2 concentration and the global C cycle (Belay-Tedla et al. 2009). Thus, the changes of soil C pool under perturbations such as global warming are critical to the terrestrial C cycle (Fig. 1).

Soil C input is mainly due to photosynthesis and litter or residues input from plants or animals. The processes of soil C output mainly include root and microbial respirations, absorption, and utilization of nutrients. Soil organic C (SOC) arises from the net result of soil C input and C loss, and reflects net C sequestration in soil (Li et al. 2016; Lal 2018; Song et al. 2018). Scientists predict warming to enhance soil microbial activity and decomposition rate of organic matter; they think ultimately these outcomes reduce the SOC pool (Hopkins et al. 2012). However, existing studies reported inconsistent results for SOC when subjected to experimental warming. Previous researches demonstrated that warming increased (Welker et al. 2004), did not change (Sistla et al. 2013; Noh et al. 2017; Guan et al. 2018), or decreased (Sjogersten et al. 2012; Sorensen et al. 2018) SOC. Additionally, soil microbial biomass reflects the most active component of soil organic matter, and is the source and impetus of soil C and nitrogen (N) mineralization (Khan et al. 2016). Further, soil microbial biomass provides multiple nutrients that enable enzyme activity (Bell et al. 2010). As a part of soil C pools, soil microbial biomass C (MBC) is an important driver of ecosystem metabolism and implies the growth of soil microbes (Prommer et al. 2019). Thus, MBC plays an important role in soil C cycle.

Soil respiration (SR, including autotrophic and heterotrophic respiration (HR)) shows the second largest flux in the terrestrial C cycle (Bond-Lamberty and Thomson 2010). It correlates with a soil's ability to release C. A small change in the magnitude of SR could have a significant impact on atmospheric CO_2 concentration (Schlesinger and Andrews 2000). Additionally, HR is an important component of SR and implies soil microbial activity. SR is susceptive to temperature (Bååth and Wallander 2010) and most existing studies suggested that elevated temperatures increase the metabolic activities of soil organisms and enhance SR (Jenkinson et al. 1991; Lloyd and Taylor 1994; Kirschbaum 2000; Contosta et al. 2011; Noh et al. 2017). However, other studies investigating the impacts of global warming on SR and HR reported contrary results (Sharkhuu et al. 2013; Chen et al. 2016; Sharkhuu et al. 2016; Wang et al. 2017; Yue et al. 2018).

The different responses of SOC, MBC, SR, and HR to warming likely relate to the nature of ecosystems. Unique abiotic and biotic characteristics in each ecosystem can directly or indirectly affect soil C dynamics. SOC and SR differentially vary with hydrothermal fluctuations in diverse ecosystems (Sharkhuu et al. 2013). The intensity of soil C release feedbacks to global warming depends on spatial variability (Zhou et al. 2009). For example, SR responds more to temperature fluctuations in ecosystems with colder compared with warmer climates (Lloyd and Taylor 1994; Carey et al. 2016). Soil C shows greater losses in high compared with low-latitude areas under warming (Crowther et al. 2016; Xue et al. 2016). However, few studies have clearly investigated the responses of soil C dynamics to experimental warming in different ecosystems.

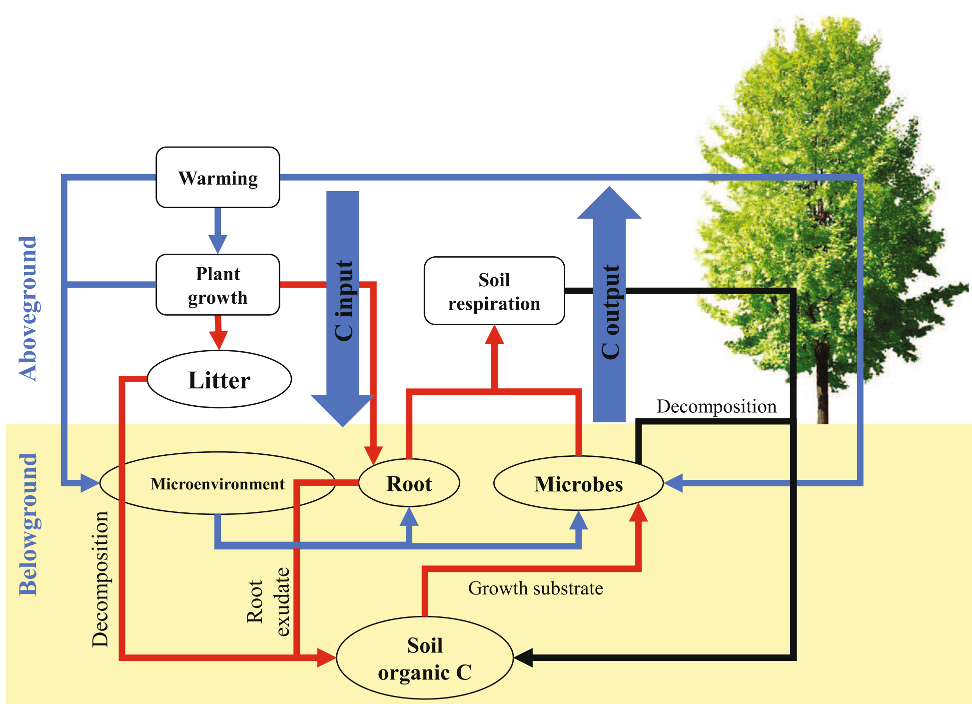

Fig. 1 A conceptual diagram of the influences of warming on soil C dynamics. Red arrows indicate positive relationships and black arrows indicate negative relationships. Thick and thin arrows represent soil C budget and soil C dynamics, respectively

Factors such as method, magnitude, and duration of warming may lead to discrepant responses in soil C dynamics. Different warming methods (such as infrared (IR) heater, IR-reflective curtain, greenhouse, heating cable, and open-top chamber (OTC)) can impact soil C dynamics in different ways because of various effects of these methods on soil temperature (ST) or soil moisture (SM) and other biotic or abiotic factors (Bai et al. 2013). Notwithstanding, disputes remain surrounding the responses of soil C pools and fluxes to different warming methods on a global scale. Different geographical regions show various magnitudes of temperature change under global warming (IPCC 2013). In addition to warming methods, we must determine how soil C dynamics respond under high-magnitude and long-term warming to better understand the global C cycle. However, previous meta-analyses indicated that warming effects on SOC or MBC showed no linear responses to warming magnitude or duration (Lu et al. 2013; Romero-Olivares et al. 2017) or the responses depended on the extents of warming magnitude and duration (Xu and Yuan 2017). For warming effects on SR or HR, no linear correlations with warming magnitude or duration were detected (Lu et al. 2013) or SR and HR declined and showed acclimation under high magnitude or long-term warming (Eliasson et al. 2005; Romero-Olivares et al. 2017; Bradford et al. 2008). However, some other meta-analyses suggested that acclimations of SR or HR did not occur under warming (Wang et al. 2014; Carey et al. 2016). These opposing results suggest soil C dynamics are needed for further evaluation across a range of experimental conditions on a global scale.

Climate factors such as mean annual temperature (MAT) and mean annual precipitation (MAP) represent underlying geographical attributes that regulate soil temperature, moisture, and ultimately many biogeochemical processes (Vitousek et al. 1997; Rustad et al. 2000). Climate change may profoundly impact these attributes that subsequently play large roles in soil C dynamics. A meta-analysis suggested that warming-induced changes in soil C pool and SR did not show significant linear correlations with MAT or MAP (Lu et al. 2013). However, research from tropical montane wet forests found that SR increased and varied more spatially as MAT increased (Litton et al. 2011). The other studies suggested that warming effects on MBC were negatively correlated with MAT on the Tibetan Plateau (Zhang et al. 2015) but positively correlated with MAP in temperate steppe (Liu et al. 2016). Thus, the relationships between climate factors and soil C dynamics under warming remain unclear.

These inconsistent results about soil C dynamics under warming could be caused by spatiotemporal variations in abiotic and biotic conditions across various ecosystems. Given the urgency of solving these problems, it is crucial to compile the latest knowledge and determine how various environmental factors interact to influence soil C dynamics under warming scenarios on a global scale. In this study, we conducted a meta-analysis to quantitate the warming effects on soil C pools and fluxes on a global scale. We aimed to map SOC, MBC, SR, and HR dynamics under warming on a broad scale. We proposed the following assumptions: (1) warming effects depend largely on ecosystem types and warming-related factors; (2) climate factors (MAT and MAP) modulate the warming effects; and (3) the responses of soil C release to global warming are more susceptive than net soil C sequestration on a global scale.

2 Materials and methods

2.1 Data collection

We searched the keywords “warming, global change, soil organic C, microbial biomass C, respiration” in the Web of Science database (1995–2019) to retrieve relevant data for our meta-analysis using the following inclusion criteria: (1) reported at least one parameter including soil organic C, soil microbial biomass C, soil respiration, soil heterotrophic respiration, and soil microclimate (soil temperature and moisture) both in experimental warming and control groups; (2) included the mean, standard deviation or error, and sample size of reported parameters; (3) reported the warming method, warming magnitude, or warming duration (of soil) and defined/described the ecosystem of the experimental site; and (4) study was conducted in natural or semi-natural ecosystems. We also collected the mean annual temperatures and precipitations of the research sites. If unreported, we used the WorldClim database (http://www.worldclim.org) (Hijmans et al. 2005) to obtain these data for 1950–2000 according to site coordinates. The data for this analysis originated from text, tables, and figures in the selected publications. We used SigmaScan Pro version 5.0.0 software (Systat Software, San Jose, CA) to extract numerical data from graphs. We collected a total of 1131 observations from 115 studies investigating experimental warming in the field across a range of different ecosystems and climates (Fig. 2) that reported data on soil microclimate, SOC, MBC, SR, and HR (a list of the data sources is found in the Electronic Supplementary Material).

2.2 Meta-analysis

To examine the effects of warming on soil C dynamics, we calculated response ratios (RRs) in each individual study as described by Hedges (Hedges et al. 1999). We calculated natural log of the response ratio (lnRR) as $\ln (X_e/X_c) = \ln X_e - \ln X_c$, where X_e and X_c are the mean values of each individual observation in the experimental warming and control, respectively. The corresponding sampling variance for each lnRR was calculated as $\ln [(1/N_e) \times (S_e/X_e)^2 + (1/N_c) \times (S_c/X_c)^2]$, where N_e, S_e, X_e, N_c, S_c, and X_c are sample size, standard

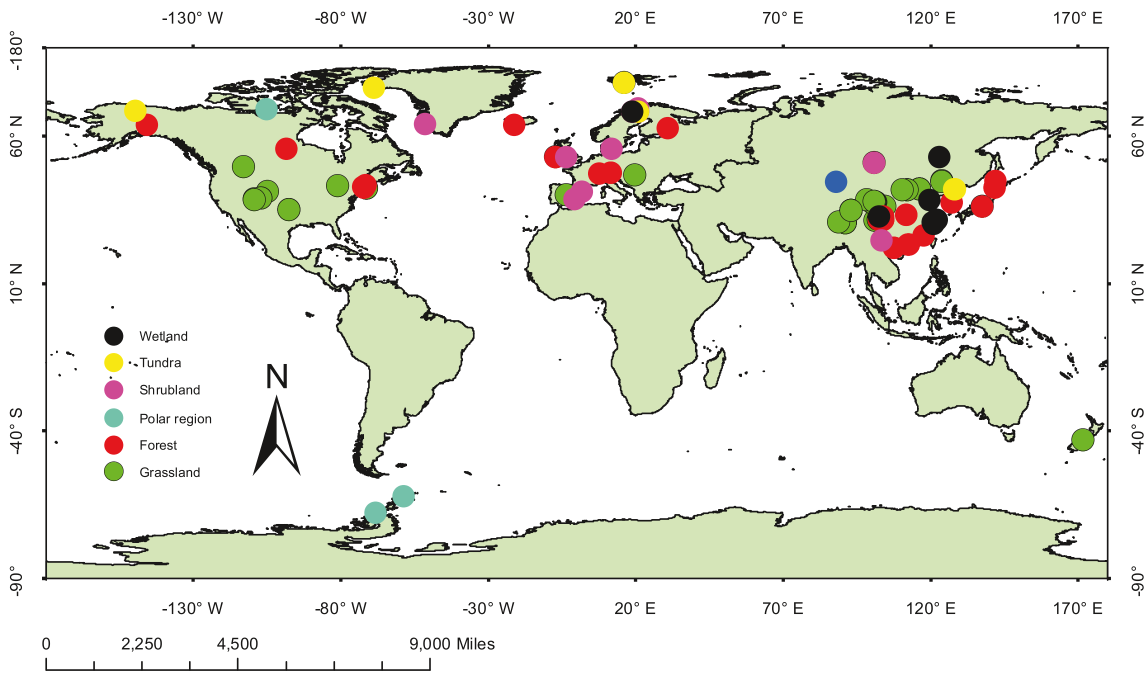

Fig. 2 Map of the experimental sites included in this meta-analysis

deviation and mean value in the experimental warming and control, respectively. The mean of response ratio (RR_{++}) and standard error [$s(RR_{++})$] of each class were calculated (Hedges et al. 1999). The $\ln RR_{++}$ was determined by specifying studies as a random factor using the *rma* model in the "metafor" package version 1.9–9 (Yuan and Chen 2015) of R version 3.6.0 (The R Project for Statistical Computing, https://www.r-project.org/). We estimated warming effects as a percentage change (%) relative to the control using the equation $[\exp(\ln RR_{++}) - 1] \times 100$. The absolute average changes in soil temperature and soil moisture were calculated by using the weighted mean difference as the effect size. We also allocated warming magnitude and duration into several classes (< 1, 1–3 and > 3 °C for magnitude; < 3, 3–6 and > 6 years for duration) with different ranges to detect subtle patterns in soil C responses to warming. The classification for warming magnitude represents low, medium, and high values compared with the expected increase by the end of the twenty-first century (IPCC 2013). The classification for warming duration represents short-term, intermediate, and long-term values. We considered warming effects significant if the 95% confidence interval (CI) did not overlap with zero. Meanwhile, the warming effects between groups or under different conditions differed if their 95% CIs did not overlap (Wan et al. 2001). Experiments that compared warming treatments to controls provided the data to compute all calculations. The meta-analysis was conducted in R with the "metafor" package version 1.9–9 (Yuan and Chen 2015). We also used multiple comparisons with examine differences in the warming effects on different groups or under different conditions (Zhou et al. 2014). We applied a continuous randomized-effects model to test the linear relationships between lnRR of variables and warming magnitude/duration or climate factors (MAT and MAP). Statistical results were reported as the difference among group cumulative effect sizes (Q_M) and the residual error (Q_E). We also conducted regression analyses to further examine if there were nonlinear relationships between lnRR of variables and warming magnitude/duration or climate factors. Statistical differences were considered as significant when $P < 0.05$. All statistical analyses were performed in R version 3.6.0.

3 Results

3.1 Overall effects of warming on soil environmental and C variables

Soil environmental and C variables displayed mixed responses to experimental warming across all ecosystems (Fig. 3). When all ecosystems were pooled together, environmental variables were significantly changed by experimental warming. Soil temperature was increased by 1.29 °C (absolute changes, 95% CI 0.91–1.67 °C) ($P < 0.001$), whereas soil moisture was decreased by 2.02% (absolute changes, 95% CI 1.20–2.83%) ($P < 0.001$). Comparisons between ecosystems showed that warming reduced SM by 2.22% (absolute changes, 95% CI 0.90–3.55%) ($P < 0.01$) in forests and 2.48% (absolute changes, 95% CI 1.36–3.59%) ($P < 0.001$) in grasslands (Fig. 4). Soil moisture decreased most when a heating cable imposed the warming (absolute changes 3.03%, 95% CI − 6.04 to 0.27%) ($P < 0.01$) or at warming magnitude of > 3

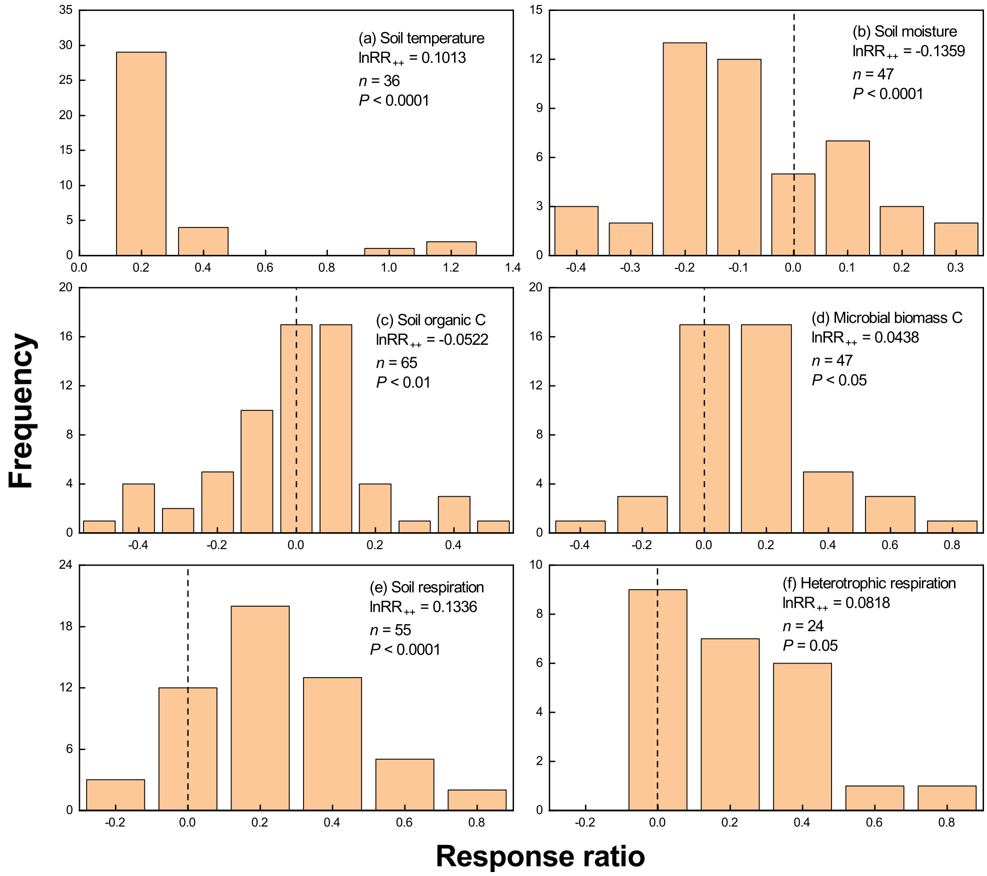

Fig. 3 The frequency distributions of response ratio (lnRR) for soil temperature (**a**), soil moisture (**b**), soil organic C (**c**), soil respiration (**d**), soil microbial biomass C (**e**), and heterotrophic respiration (**f**) to warming. The '*n*' is sample size. $lnRR_{++}$ represents the mean response ratio for each variable. Warming effects are significant when $P < 0.05$. Vertical lines are drawn at lnRR = 0

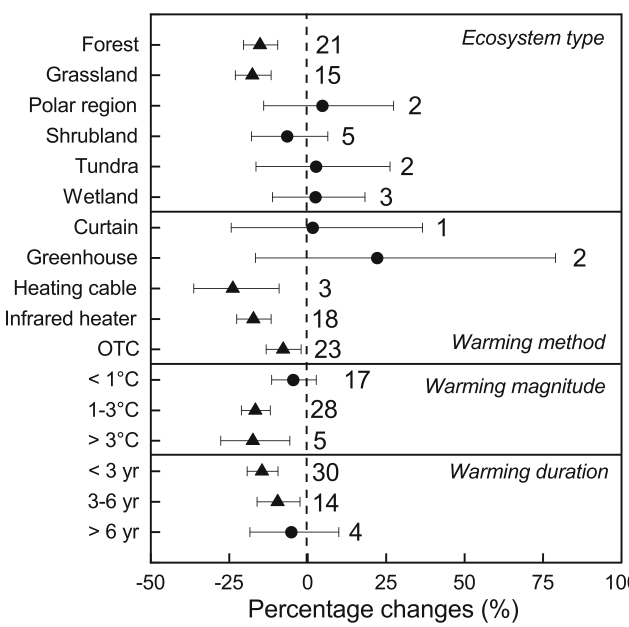

Fig. 4 Responses of soil moisture to warming as a percentage change relative to control (%). The variables are categorized into groups based on ecosystem type, warming method, magnitude and duration. Values are percentage change ± 95% CIs (confidence intervals). Numbers of observations are shown near the bar. Triangles indicate significant responses to warming (confidence intervals do not include zero); circles indicate no response to warming. Vertical lines are drawn at percentage change = 0. OTC, open-top chamber

°C (absolute changes 5.31%, 95% CI 2.14–8.48%) ($P < 0.01$). However, long-term warming mitigated the negative effect of warming on SM (Fig. 4). When all ecosystems were pooled together, experimental warming decreased soil organic C by 4.96% (95% CI 1.96–7.87%) ($P < 0.01$). In contrast, it stimulated microbial biomass C, soil respiration, and heterotrophic respiration by 6.30% (95% CI 0.31–12.66%) ($P < 0.05$), 14.56% (95% CI 8.32–21.15%) ($P < 0.001$), and 8.42% (95% CI − 0.03 to 17.56%) ($P = 0.05$) compared with control groups, respectively (Fig. 5).

3.2 Warming effects on soil C pools and fluxes in various ecosystems

Experimental warming reduced SOC in grasslands and tundra by 7.43% (95% CI 3.36–11.33%) ($P < 0.001$) and 22.49% (95% CI 5.29–33.56%) ($P < 0.05$), respectively (Fig. 6a). In contrast, warming enhanced MBC by 11.52% in grasslands (95% CI 2.72–21.06%) (Fig. 6b, $P < 0.05$). Experimental warming increased SR in forests and shrublands by 21.08% (95% CI 11.99–30.97%) ($P < 0.001$) and 23.80% (95% CI 5.90–44.79%) ($P < 0.01$), respectively (Fig. 6c). Experimental warming increased HR in forests by 18.47% (95% CI 6.83–31.38%) (Fig. 6d, $P < 0.01$). In particular, the warming-induced HR increase in grasslands differed from that in forests

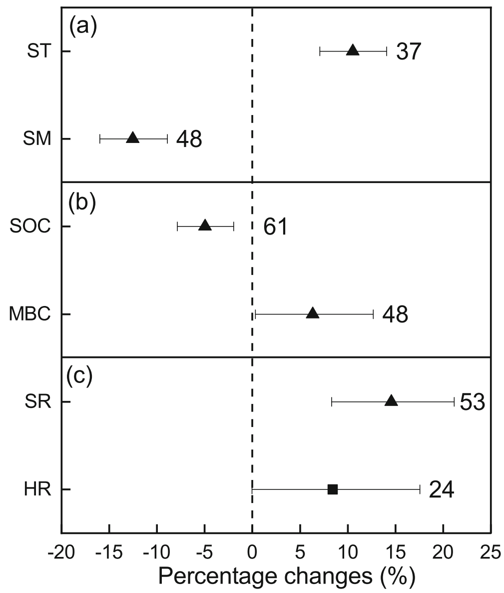

Fig. 5 Responses of soil microclimate (**a**), soil C pools (**b**), and soil C fluxes (**c**) to warming as a percentage change relative to control (%) across all ecosystems included in the meta-analysis. ST: soil temperature; SM: soil moisture; SOC: soil organic C; MBC: soil microbial biomass C; SR: soil respiration; HR: heterotrophic respiration. Values are percentage change ± 95% CIs (confidence intervals). Numbers of observations are shown near the bar. Triangles indicate significant responses to warming (confidence intervals do not include zero); squares indicate marginal responses to warming. Vertical lines are drawn at percentage change = 0

(Fig. 6d, $P < 0.05$). We omitted groups with less than three observations from the analysis.

3.3 Soil C pools and fluxes in relation to different warming-related factors

When all ecosystems were pooled together, SOC (percentage change 4.82%; 95% CI 0.39–9.05%) ($P < 0.05$) and MBC (percentage change 1.09%; 95% CI 1.01–1.18%) ($P < 0.05$) responded to the OTC method (Fig. 6a, b). The use of heating cable (percentage change 25.91%; 95% CI 9.70–44.53%) ($P < 0.01$), infrared heater (percentage change 10.62%; 95% CI 1.79–20.21%) ($P < 0.05$), and OTC (percentage change 11.81%; 95% CI 2.55–21.90%) ($P < 0.05$) each affected SR. However, no warming methods affected HR. The variations of SR (percentage change 25.91%; 95% CI 9.70–44.53%) and HR (percentage change 13.29%; 95% CI − 10.93 to 44.11%) were great under a heating cable (Fig. 6c, d). We omitted groups with less than three observations from the analysis.

Across all ecosystems, a 1–3 °C increase in temperature decreased SOC by 6.56% (95% CI 2.60–10.36%) (Fig. 6a, $P < 0.01$). We did not detect a significant relationship between changes in SOC and warming magnitude (Table 1, Fig. 7a). A 1–3 °C increase in temperature increased MBC by 10.43% (95% CI 1.84–19.75%) (Fig. 6b, $P < 0.05$). We found a quadratic correlation between changes in MBC and warming magnitude (Fig. 7b, $P < 0.001$). Across all ecosystems, temperature increases of 1–3 °C and > 3 °C increased SR by 13.60% (95% CI 4.53–23.45%) ($P < 0.01$) and 25.63% (95% CI 11.07–42.09%) ($P < 0.001$), respectively (Fig. 6c). We detected non-linear relationships between the changes in SR and warming magnitude (Fig. 7c, $P < 0.05$). Temperature increases of > 3 °C promoted HR by 28.54% (95% CI 3.28–59.98%) (Fig. 6d, $P < 0.05$). The warming-induced changes in HR were quadratically associated with warming magnitude (Fig. 7d, $P < 0.01$).

Across all ecosystems, a warming period of < 3 years decreased SOC by 7.54% (95% CI 3.74–11.19%) (Fig. 6a, $P < 0.001$). We did not detect significant relationships between changes in SOC and warming duration (Table 1, Fig. 8a). None of the warming periods showed significant effects on MBC (Fig. 6b), but we found a negatively linear relationship between changes in MBC and warming duration (Table 1, $P < 0.05$). Across all ecosystems, a warming period of < 3 years increased SR by 18.49% (95% CI 9.95–27.69%) (Fig. 6c, $P < 0.01$). We detected non-linear relationships between the changes in SR and warming duration (Fig. 8c, $P < 0.01$). However, none of the warming periods affect HR (Fig. 6d). Additionally, we did not detect a relationship between the changes in HR and warming duration (Table 1, Fig. 8d).

3.4 Climate factors affected warming-induced changes in soil C pools and fluxes

Our analysis revealed that the warming-induced changes in soil C pools and C fluxes varied in different ecosystems (Fig. 6a–d). However, across all climate ranges, the changes in SOC did not associate with MAT or MAP (Table 1, Figs. 9a and 10a). The changes in MBC showed a quadratic relationship with MAT (Fig. 9b, $P < 0.01$), whereas the relationship between the changes in MBC and MAP was not significant (Table 1, Fig. 10b). We found a quadratic relationship between warming-induced changes in SR and MAT across all climate ranges (Fig. 9c, $P < 0.001$), but no relationship existed with MAP (Table 1, Fig. 10c). The warming-induced changes in HR were not associated with MAT (Table 1, Fig. 9d), but were associated positively with MAP (Table 1, $P < 0.05$).

4 Discussion

4.1 Warming effects on soil C pools and fluxes on a global scale

Our meta-analysis revealed that experimental warming altered SOC pool and stimulated soil microbial biomass C and soil CO_2 emissions in terrestrial ecosystems on a global scale (Fig. 5). These findings suggest the stimulation of soil C loss under global warming will transform soil from a C sink to a C

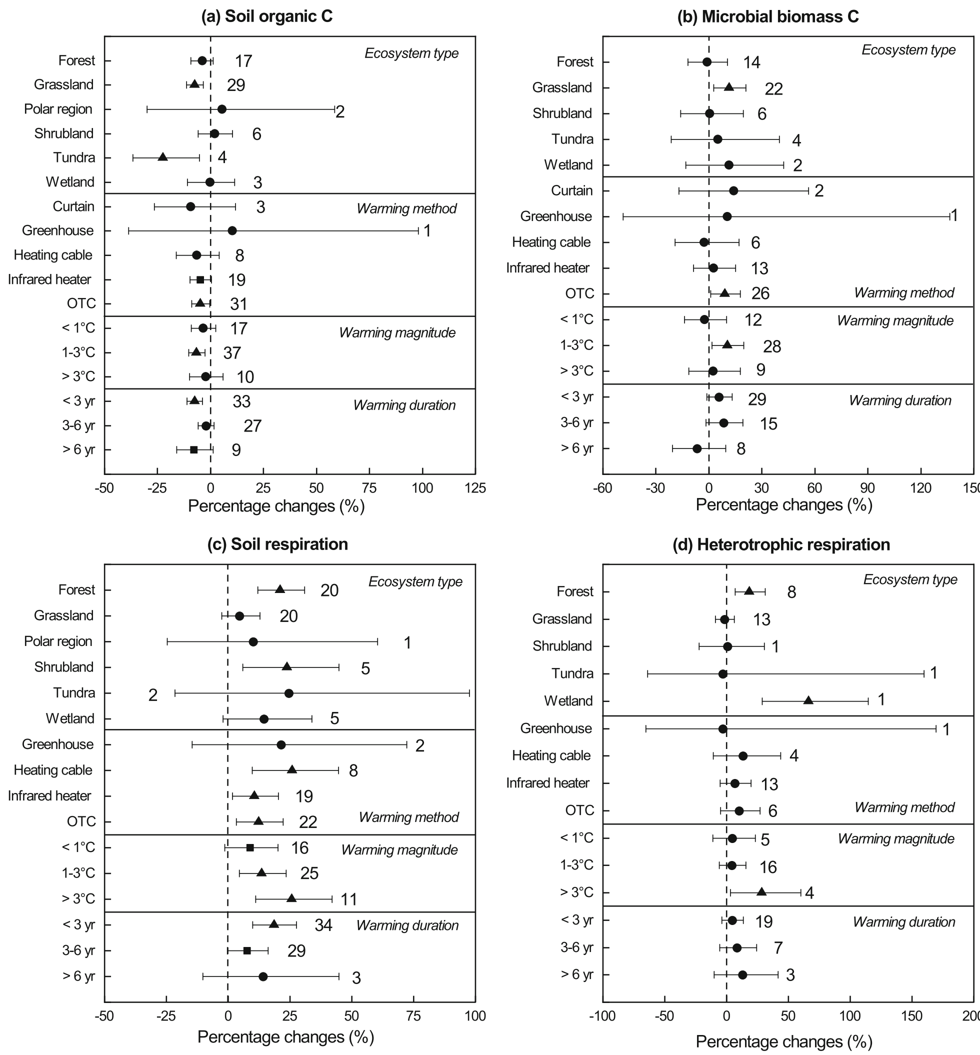

Fig. 6 Reponses of soil organic C (**a**), soil microbial biomass C (**b**), soil respiration (**c**), and heterotrophic respiration (**d**) to warming as a percentage change relative to control (%). Variables are categorized into groups based on ecosystem type, warming method, magnitude and duration. Values are percentage change ± 95% CIs (confidence intervals). Numbers of observations are shown near the bar. Triangles indicate significant responses to warming (confidence intervals do not include zero); squares indicate marginal responses to warming; circles indicate no response to warming. Vertical lines are drawn at percentage change = 0. OTC, open-top chamber

source. The warming effects on soil C pools and fluxes varied across ecosystems and differed with various factors of warming or climate. Across all ecosystems, the changes in SR (+ 14.56%) and HR (+ 8.42%) were greater than those of SOC (− 4.96%) and MBC (+ 6.30%) under warming (Fig. 5). The lack of relationships between changes in SOC and warming magnitude or duration in contrast to the significant relationships between changes in SR or HR and warming magnitude or duration indicates that changes in soil C release depend more on warming than that in soil C pool. These results indicate soil C flux are more sensitive to warming than soil C pool. Thus, the positive feedback of global warming effects on soil C cycle can be exacerbated by soil C release due to its sensitivity to warming.

Warming increases the amount of litter from aboveground and belowground parts of plants and plants provide more carbon allocation to roots, mycorrhizae, and exudates (Shaver et al. 2000; Wan and Luo 2003; Xia et al. 2009; Ziegler et al. 2013). The increased ST and plant litter might promote soil microbial growth and enhance microbial activity, thus the positive priming effect of SOC decomposition is accelerated (Hopkins et al. 2014). These processes ultimately induce an increase in MBC, and lead to increased SR or soil C release (Fig. 5). Our result was not consistent with Lu et al. (2013)'s, which found soil C pool had no response to warming (Lu et al. 2013). The sampling sizes for SOC were 33 and 61 in Lu et al. (2013)'s and our study, respectively. Thus, our sampling size was larger than that of Lu et al. (2013)'s and the larger sampling size makes our conclusions stronger. It appears climate factors such as MAT and MAP modulated the effects of warming on MBC, SR, or HR, but not on SOC (Table 1, Figs. 9 and 10). Thus, the data suggest that the SOC pool is not sensitive to environmental changes and could remain stable.

4.2 Responses of soil C dynamics to warming vary across ecosystems

Generally, soil in cold areas contains greater SOC than that of warm regions. Warming effects on SOC are contingent on the

Table 1 Linear relationships between the response ratios of soil C pools and fluxes and warming magnitude, warming duration, mean annual temperature, mean annual precipitation, and response ratio of soil moisture

	Q_M	Q_E	Slope	*P*-value
Warming magnitude				
Soil organic C	0.249	565.655	0.004	0.618
Microbial biomass C	0.007	487.948	− 0.001	0.935
Soil respiration	4.309	6572.630	0.033	0.038
Heterotrophic respiration	7.430	597.775	0.060	0.006
Warming duration				
Soil organic C	2.014	561.233	− 0.004	0.156
Microbial biomass C	4.822	475.543	− 0.011	0.028
Soil respiration	8.670	6522.511	− 0.038	0.009
Heterotrophic respiration	0.870	601.163	0.008	0.351
Mean annual temperature				
Soil organic C	0.008	564.573	0.000	0.859
Microbial biomass C	3.824	484.473	− 0.006	0.051
Soil respiration	10.852	6642.723	− 0.010	0.001
Heterotrophic respiration	1.505	628.355	0.005	0.220
Mean annual precipitation				
Soil organic C	0.000	558.548	0.000	0.990
Microbial biomass C	1.025	489.223	0.000	0.311
Soil respiration	0.000	6650.476	0.000	0.996
Heterotrophic respiration	4.519	600.984	0.000	0.034
Response ratio of soil moisture				
Soil organic C	6.397	67.979	0.246	0.011
Microbial biomass C	0.449	46.079	− 0.145	0.503
Soil respiration	0.275	377.254	− 0.086	0.600
Heterotrophic respiration	1.056	403.216	0.203	0.304

Statistical results were reported as the difference among group cumulative effect sizes (Q_M) and the residual error (Q_E) from continuous randomized-effects model meta-analyses. The relationship is significant when $P <$ 0.05

size of the initial soil C stock (Crowther et al. 2016). High-latitude ecosystems contain large reserves of partially decomposed biomass and SOC that accumulate under cold, wet conditions. Thus, warming may influence these ecosystems more than others (Davidson et al. 2000). Our data showed great decrease in SOC under warming occurred in cold or high-latitude tundra (Fig. 6a). Warming-induced decreases in soil C pools in grassland ecosystems seem more effective than in forest ecosystems. We also found a positive relationship between the warming-induced changes in SM and SOC (Table 1). Though grasslands and forests both undergone significant decreases in SM (Fig. 4), SOC pool in grasslands was more sensitive to warming-induced reduce in SM because water availability is a limiting factor in grassland ecosystems. In addition, SOC content is higher in grasslands than in forests (Schlesinger 1977) and SOC pool in grasslands is more easily affected by warming. Thus, it appears grasslands undergone a significant decrease in SOC (Fig. 6a). Warming-induced increase in MBC (Fig. 6b) may be due to enhanced plant litter input, promoted SOC decomposition (Fig. 6a), and enlarged labile C and N pools (Rui et al. 2011) which stimulates microbial growth under warming in grasslands.

The significant effects of warming on SR and HR occurred in forests (Fig. 6c, d). Warming effects on HR were mediated by water availability in forest ecosystems (Zou et al. 2018) and warming-induced reduction in SM affects microbial respiration less adversely in moist areas (Liu et al. 2016). Thus, warming promoted soil C release in forest ecosystems where soil moisture is higher than grassland ecosystems. Previous study also found that forest ecosystems have the strongest response to warming in terms of SR (Rustad et al. 2001). Our results indicate that low temperatures limit soil C release in forest ecosystems. The warming effects on HR in grasslands differed from those in forests (Fig. 6d), likely from different hydrothermal conditions between the ecosystems.

4.3 Responses of soil C pools to different warming-related factors

In our analysis, the OTC method effectively affected SOC and MBC as well as the IR-curtain method had the largest tendency to decrease SOC (Fig. 6a, b). We interpret that passive warming can effectively impact soil C pools and soil microbial growth. Warming affected SOC and MBC at the medium magnitude of 1–3 °C, and the effects declined at the high magnitude of > 3 °C (Fig. 6a, b). The results suggest that the decomposition rate of soil organic matter and soil microbial growth increase within an appropriate range of temperature, but greater temperatures likely inhibit these variables. Changes in MBC exhibited a unimodal curve to warming magnitude (Fig. 7b). The response indicates the temperature sensitivity of soil microbes may decrease and acclimatization may occur under high-temperature warming (Luo et al. 2001; Melillo et al. 2002). Perhaps the decreased soil moisture induced by high-magnitude warming (Fig. 4) restricted soil microbial growth (Liu et al. 2016). Additionally, long-term negative feedback reduces soil C mobilization under high-magnitude warming. This outcome occurs because modified substrate transformation produces more recalcitrant material at high temperatures (Dalias et al. 2001). This process ultimately attenuates the warming-induced release of CO_2 from soil.

We found that short-term warming (< 3 years) reduced SOC but long-term warming (> 3 years) did not affect it (Fig. 6a). The results may be due to the compensation by increased input of plant litter because of greater plant biomass under warming (Luo et al. 2001). However, we detected no relationships between the warming-induced changes in SOC

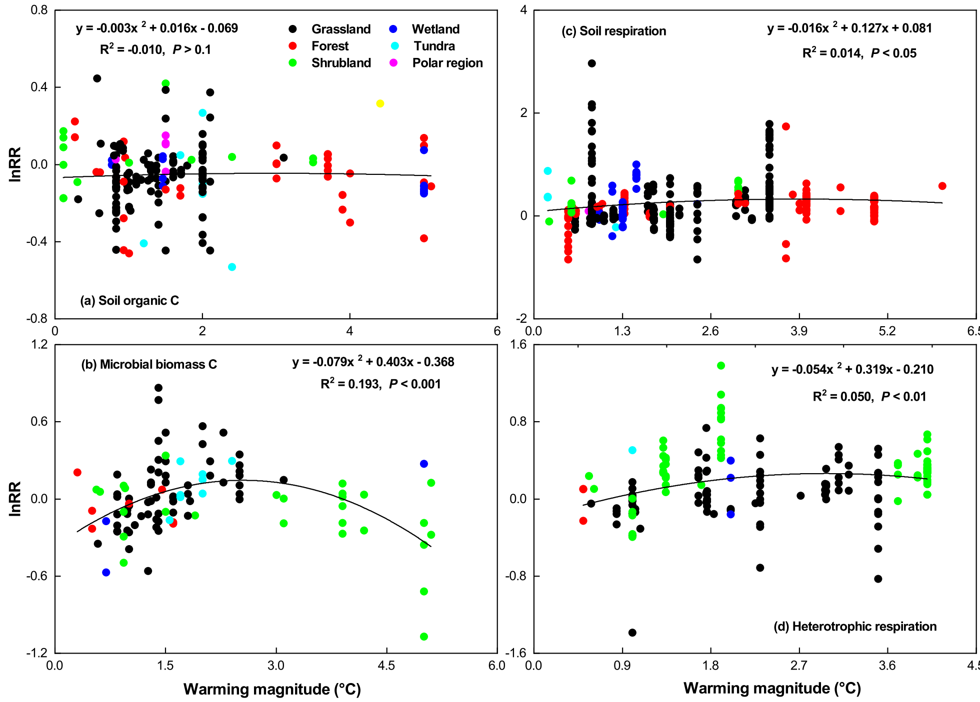

Fig. 7 Results of regression analysis for the response ratio (lnRR) of soil organic C (**a**), soil microbial biomass C (**b**), soil respiration (**c**), and heterotrophic respiration (**d**) in relation to warming magnitude. Details of the regression analysis are given in each panel

and warming magnitude or duration. Thus, changes in SOC showed no sensitivity to warming. None of the warming duration scenarios affected MBC, but changes in MBC exhibited a negative relationship with warming duration (Table 1). This result suggests long-term warming stimulates the adaptation of soil microbial growth because of the non-sensitivity of the growth under long-term warming (Bradford 2013). Potential mechanisms underlying this observation include inhibited microbial growth in response to depleted soil moisture, reduced plant production and substrate limitation after losses of labile soil C (Luo et al. 2001; Melillo et al. 2002; Oechel et al. 2000; Liu et al. 2016).

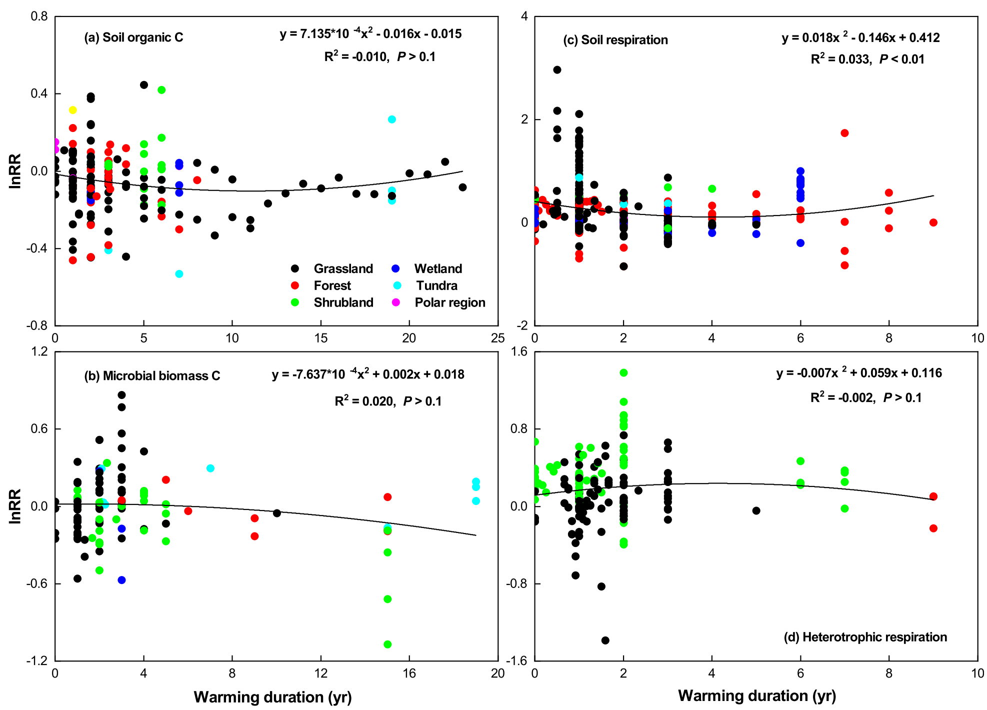

Fig. 8 Results of regression analysis for the response ratio (lnRR) of soil organic C (**a**), soil microbial biomass C (**b**), soil respiration (**c**), and heterotrophic respiration (**d**) in relation to warming duration. Details of the regression analysis are given in each panel

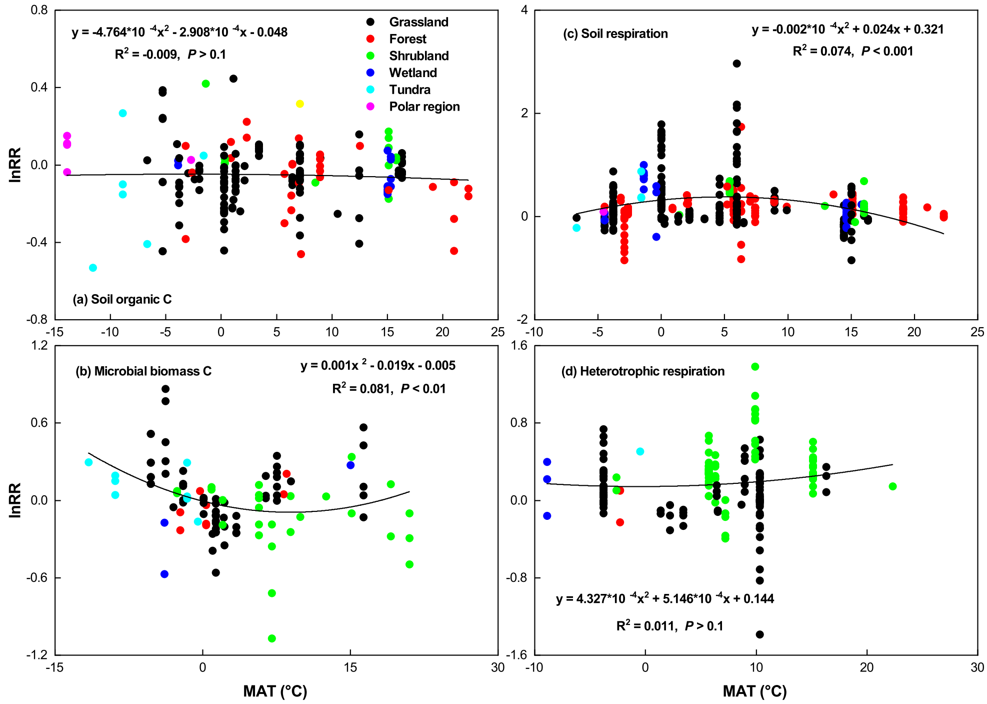

Fig. 9 Results of regression analysis for the response ratio (lnRR) of soil organic C (**a**), soil microbial biomass C (b), soil respiration (**c**), and heterotrophic respiration (**d**) in relation to mean annual temperature (MAT). Details of the regression analysis are given in each panel

4.4 Soil C fluxes response to different warming-related factors

Use of a heating cable greatly affected SR among the warming methods. This likely occurred because soil warming by heating cable can directly enhance soil temperature and then increase soil microbial activity and root respiration (Noh et al. 2017). However, we found the heating cable method reduced SM greatly among these warming methods (Fig. 4). The results suggest that positively direct effects of warming with a heating cable could be stronger than the negatively indirect effects of warming-induced decrease in SM, thus leading to enhanced microbial activity and root respiration. Additionally, we detected no significant relationship between the warming-induced changes in SR and SM (Table 1). The methods of a heating cable, infrared heater, and OTC showed significant

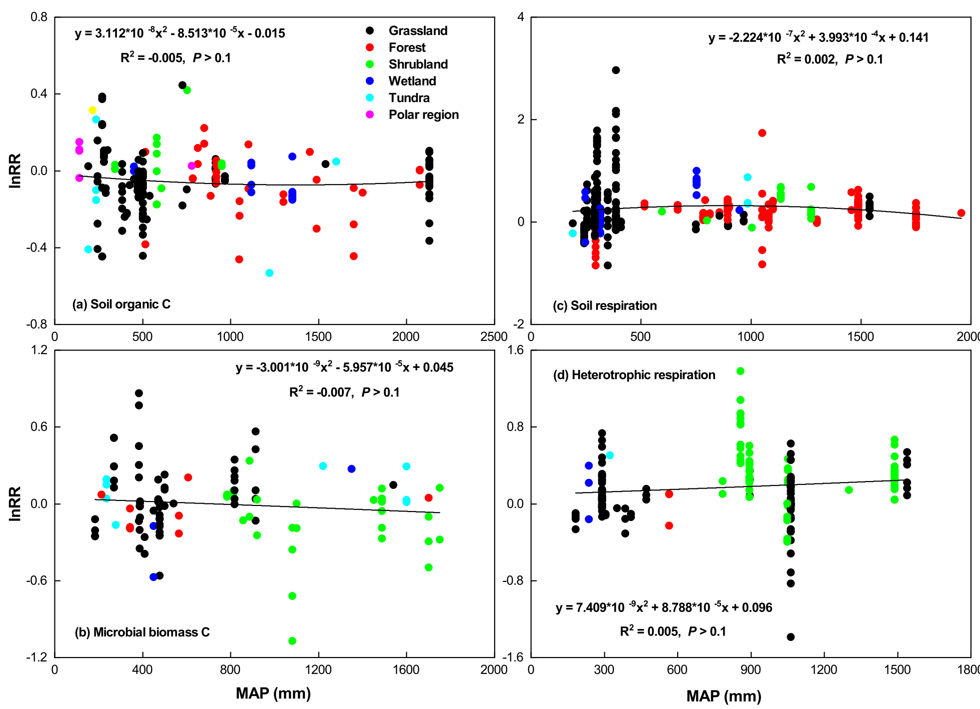

Fig. 10 Results of regression analysis for the response ratio (lnRR) of soil organic carbon (**a**), soil microbial biomass C (**b**), soil respiration (**c**), and heterotrophic respiration (**d**) in relation to mean annual precipitation (MAP). Details of the regression analysis are given in each panel

effects on SR, but none of these methods affected HR (Fig. 6c, d). The different responses between SR and HR may indicate that autotrophic respiration, rather than HR, shows more sensitivity to the three common experimental warming methods.

Warming magnitude impacted changes in SR and HR more than that in SOC (Fig. 7a–d). Response ratios of SR and HR were quadratically related to warming magnitude, and SR and HR both showed declines in the rates of change under high temperature (Fig. 7c, d). These results revealed the importance of temperature which can substantially impact soil C release. The decreasing response ratios under high-magnitude warming (Fig. 7c, d) indicates that both SR and HR may be hindered by reduced soil moisture at high temperature (Fig. 4) because reduction in SM could adversely affect microbial activity under high-magnitude warming (Oechel et al. 2000; Liu et al. 2016; Li et al. 2017). In addition, modification of substrate transformation produces more recalcitrant material at high temperatures (Dalias et al. 2001). The decreased available substrates such as MBC (Figs 6b and 7b) restrict soil C release (Bradford et al. 2008). The slowed rates of change in SR and HR under high-magnitude warming indicate soil C release may acclimatize to high temperature on a global scale. Our results align with previous studies (Giardina and Ryan 2000; Oechel et al. 2000; Luo et al. 2001) which suggested that SR acclimates to temperature under high-magnitude warming. However, warming still substantially enhanced SR and HR at high magnitude (> 3 °C) even though the rates of increase slowed (Fig. 6c, d). Thus, soil C release continued under high magnitude warming. The results also show the propensity for warming to promote soil C release rather than net soil C sequestration. Our results are inconsistent with Carey's meta-analysis (Carey et al. 2016) in which a positive relationship between the warming-induced changes in SR and warming magnitude was found. Compared with Carey et al. (2016), our analyses covered larger areas (Fig. 2) and included nearly twice the number of studies (27 studies in Carey's analyses and 53 in ours). These differences likely contributed to the inconsistent results.

The warming-induced changes in SR showed an uptrend at long-term duration in our analysis (Fig. 8c). This result conflicts with a previous study which reported negative effects on changes in SR under long-term warming (Romero-Olivares et al. 2017). We surmise the discrepant results from differences with respect to data size and variation in ecosystem types. In addition, range of warming duration in our study (0–9 years) was shorter than that of Romero-Olivares' study (0–15 years). Whereas changes in SR responded to both warming magnitude and duration, changes in HR did not show effects from duration (Table 1, Fig. 8d). This result suggests that microbial activity (implied by HR) is more sensitive to warming magnitude than duration. The fact that short-term (< 3 years) warming affected SR but not HR (Fig. 6c, d) may result from changing plant community structure and root biomass (Arndal et al. 2018), rather than changing microbial community structure in favor of thermophilic microbes (Schindlbacher et al. 2011). That is, short-term warming strongly stimulates SR due to increased plant biomass and root respiration (Oechel et al. 2000; Luo et al. 2001). Our results also suggest that stimulated soil C release under high-magnitude warming (Fig. 6c, d) can be mitigated in the long term because no relationship was detected between the warming-induced changes in HR and warming duration.

4.5 Soil C fluxes rather than SOC pool more depend on mean annual temperature or precipitation

Generally, climate factors often regulate warming effects on soil C dynamics. However, responses of SOC to warming were not associated with MAT or MAP (Table 1, Figs. 9a and 10a). This outcome suggests that SOC pool showed stability over a range of MAT and MAP. Soil microbes, as main drivers of the soil C cycle, react in different ways to warming based on original climate and ecosystem characteristics before warming. For instance, soil microbes show more sensitivity to warming in cold, dry areas compared with warm, humid regions (Blankinship et al. 2011). We showed that MAT, but not MAP, influenced responses of MBC to warming on a global scale (Figs. 9b and 10b). This result suggests MAT can regulate responses of soil microbial growth (implied by MBC) to warming. Also, MBC showed a greater response ratio to warming in cold regions but the sensitivity also slightly increased in warm areas (Fig. 9b). In contrast, MBC did not show the same responses to MAP.

SR and HR showed inconsistent responses to MAT and MAP under warming. SR showed strong warming responses to MAT, while warming-induced changes in HR did not (Fig. 9c, d). Therefore, we suggest that MAT affects autotrophic respiration more than HR under warming on a global scale because of the large contribution of autotrophic respiration to SR. MAP exhibited a positive relationship with changes in HR under warming (Table 1), but did not influence changes in SR (Table 1, Fig. 10c). These responses indicate MAP has little or negative influences on autotrophic respiration under warming on the global scale. Regions with high MAP tend to stay humid and thus SM restricts neither microbial activity (Liu et al. 2016) nor HR. Our results support previous work showing that precipitation enhances the activity of soil microbial enzymes and soil C release under warming (Li et al. 2018). As well we infer that MAP regulates the warming effects on microbial activity (implied by HR) but not microbial growth (implied by MBC) (Table 1, Fig. 10b, d), as microbial growth on a global scale might be affected by multiple factors such as temperature and ecosystem types.

5 Conclusions

Our meta-analysis revealed that warming magnitude or duration affects changes in soil C fluxes to a greater extent than that in SOC pool. More potential exists for climate factors to regulate soil C fluxes than SOC pool under warming. Soil C release shows more sensitivity to warming and climate than net soil C sequestration on a global scale. These results indicate warming-induced risk of accelerated transition from C sink to C source in soils of terrestrial ecosystems. Furthermore, they show the potential for global warming effects to exacerbate the positive feedback loop on terrestrial ecosystems. However, the declining rates-of-change in SR and HR under high magnitude warming may mitigate the positive feedback. Ecosystem effects on soil C dynamics highlight the need for adaptive management based on circumstances. SOC in tundra and SR in shrublands seem to show great sensitivity to global warming among ecosystems. Soil C pools in grasslands and soil C fluxes in forests are affected by warming. Small scale apparatus to impose warming treatments may bias outcomes based on inherent properties of experimentation. The OTC method appears to largely affect soil C pools among warming methods. However, a soil heating cable showed propensity to change soil C fluxes. These intrinsic biases are acceptable as long as they are accounted for. It appears MAP but not MAT can regulate microbial activity under warming, and MAT affects responses of microbial growth to warming more than that of soil microbial activity. The inconsistent responses for some variables in our work and that of previous researches indicate need for long-term observations. Future studies should evaluate temperature gradient increases and time spans. This meta-analysis expands the scientific community's understanding of soil C dynamics in relation to experimental warming and improves the knowledge of the underlying mechanisms of warming effects on the soil C cycle.

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