Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration

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Abstract

Despite decades of research, how climate warming alters the global flux of soil respiration is still poorly characterized. Here, we use meta-analysis to synthesize 202 soil respiration datasets from 50 ecosystem warming experiments across multiple terrestrial ecosystems. We found that, on average, warming by 2 °C increased soil respiration by 12% during the early warming years, but warming-induced drought partially offset this effect. More significantly, the two components of soil respiration, heterotrophic respiration and autotrophic respiration showed distinct responses. The warming effect on autotrophic respiration was not statistically detectable during the early warming years, but nonetheless decreased with treatment duration. In contrast, warming by 2 °C increased heterotrophic respiration by an average of 21%, and this stimulation remained stable over the warming duration. This result challenged the assumption that microbial activity would acclimate to the rising temperature. Together, our findings demonstrate that distinguishing heterotrophic respiration and autotrophic respiration would allow us better understand and predict the long-term response of soil respiration to warming. The dependence of soil respiration on soil moisture condition also underscores the importance of incorporating warming-induced soil hydrological changes when modeling soil respiration under climate change.

Keywords: acclimation, apparent Q10, ecosystem warming, forest, grassland, mediterranean, meta-analysis, soil moisture, tundra, warming duration

Introduction

Average global surface temperature is likely to rise 1.5-2 °C by the end of the century (IPCC, 2013). Elevated temperature could greatly alter soil respiration (R_s), the largest flux of carbon dioxide (CO_2) from terrestrial ecosystems to the atmosphere. However, despite decades of research, no consensus has been reached on how the response of R_s to climate warming will affect the global carbon balance, which brings great uncertainty in projecting the feedback between R_s and future climate changes (Bond-Lamberty & Thomson, 2010; Janssens *et al.*, 2010).

One of the main challenges to assessing the future role of R_s in the global carbon cycle is that the response of R_s to warming has a high spatial heterogeneity (Schleser, 1982; Raich & Schlesinger, 1992; Bond-Lamberty & Thomson, 2010). Over the last several decades, ecosys-

tem warming experiments have rapidly expanded across almost all terrestrial biomes. A systematic examination of extant R_s measurements from those experiments could provide important insights into global R_s patterns under a warming climate.

Besides the high spatial heterogeneity of R_s, we also do not know enough about how the complex soil processes regulate soil CO_2 fluxes. R_s is an integrated result of respiration associated with root activities (autotrophic respiration, R_a) and with soil organic matter (SOM) decomposition (heterotrophic respiration, R_h). Without separation of R_a and R_h, R_s measurements alone provide little insight in SOM cycling and are insufficient to evaluate its response to future climate warming (Kuzyakov & Larionova, 2005). Because of the high labor cost and methodological limitations for partitioning R_s, fewer warming experiments have monitored the dynamics of R_a and R_h, compared to the frequently measured R_s. However, with the importance of measuring R_a and R_h being increasingly recognized, more warming experiments have started to measure R_a and

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R_h in recent years (Zhou *et al.*, 2007; Melillo *et al.*, 2011; Li *et al.*, 2013; Suseela & Dukes, 2013). A synthesis of these studies can be expected to shed light on the mechanisms regulating the response of R_s to warming.

In addition to the need for partitioning R_s into its component fluxes, another difficulty for predicting the response of R_s to rising temperature is that we know little about whether, when and how much R_s acclimates to warming. Many studies suggested that elevated R_s caused by warming returns to prewarming values, either because of the depletion of labile carbon pools or because of thermal adaption of microbial activity, or their combined effects (Luo *et al.*, 2001; Kirschbaum, 2004; Eliasson *et al.*, 2005). We did a thorough literature search covering the last 20 years, and identified seven ecosystem warming experiments that lasted longer than 6 years (Strömgren, 2001; Melillo *et al.*, 2002, 2011; Zhou *et al.*, 2007; Reth *et al.*, 2009; Lamb *et al.*, 2011; Schindlbacher *et al.*, 2012). These long-term warming experiments have shown contradictory results on the acclimation of R_s to elevated temperature. For example, two long-term warming experiments conducted at the Harvard forest revealed different temporal patterns of R_s along treatment years. The experiment that started in 1991 found that R_s fully acclimated to temperature, with the warming effect no longer statistically significant after 6 years (Melillo *et al.*, 2002). Another warming experiment conducted in the same forest but with larger warming areas started in 2003 showed that the stimulation effect of warming on R_s was still present in 2009 (Melillo *et al.*, 2011). In a long-term grassland warming experiment, no response of R_s to warming was observed during the first 2 years (Luo *et al.*, 2001), but this was a transient effect. R_s was significantly stimulated in the following 5 years (Zhou *et al.*, 2007). Among those seven long-term warming experiments, a temperate forest site (Melillo *et al.*, 2002) and a tundra site (Lamb *et al.*, 2011) were reported no-altered R_s by warming treatment after 6 years. For the rest studies, the stimulation of R_s was sustained for the warming period although warming often decreased the temperature sensitivity of R_s (Strömgren, 2001; Zhou *et al.*, 2007; Reth *et al.*, 2009; Melillo *et al.*, 2011; Schindlbacher *et al.*, 2012). The contradictory results from long-term experiments make it difficult to determine the strength of the feedback between R_s and global temperature changes.

Here, we conducted a comprehensive integrative analysis on R_s, R_a and R_h, using data from 50 ecosystem temperature manipulation experiments across the world. We aimed to investigate the general picture of R_s under a warming climate. We were especially interested in whether the response pattern of R_s is different among biomes, how warming alters R_a and R_h and whether R_s, R_a and R_h acclimate to climate warming.

Materials and methods

Data compilation

Peer reviewed journal articles were searched using Web of Science (1994-2013). We only included studies that: (i) manipulated temperature in the field; (ii) measured R_s throughout at least one whole growing season. For each selected study, we collected a variety of information about the experiment, including control and treatment means of R_s, R_a, R_h, soil temperature, soil moisture, temperature manipulation level and experimental duration, as well as the temperature sensitivity (Q_{10}) of R_s. In our dataset, all Q_{10} values were estimated by *in situ* R_s measurements, which represents the apparent temperature sensitivity and not the intrinsic temperature sensitivity of R_s. Ancillary site information, such as ecosystem type, latitude, longitude, elevation, mean annual temperature (MAT) and precipitation (MAP) were also included.

In total, 202 data sets were collected from 50 ecosystem warming sites (Fig. S1). Those sites were located from 45.42°S to 78.93°N with mean annual temperature ranging from −18.1 to 19.6 °C and mean annual precipitation from 150 to 1741 mm, including ecosystems such as tundra, alpine, boreal forest, temperate shrubland, temperate grassland, temperate forest, Mediterranean and agricultural land (Table S1).

For those 50 sites, warming duration ranged from 1 to 19 years, with 43 sites received warming treatment less than 4 years, and the remaining seven sites were warmed between 6 to 19 years. Part of those experiments reported R_s data for multiple years (e.g. Zhou *et al.*, 2006; Schindlbacher *et al.*, 2012). To satisfy the criterion of independence of observations that is a prerequisite for statistical meta-analysis, and to include as many studies as possible, we assess the overall mean response ratio (RR) across experiments using data from the earliest reported year, which ranged from year 1 to year 4 and was referred as early warming year in later text. In parallel, we also calculated the response ratios using multi-year averages instead of single-year values. The results from this analysis basically confirm those of the single-year analysis (Table S2), but multi-year averages are less comparable across sites because of the differences in treatment duration. Data from later years were, logically, used to analyze the relation between $R_s/R_a/R_h/Q_{10}$ and treatment duration.

Meta-analysis

The responses of R_s, R_a, R_h, the apparent Q_{10} of R_s, soil temperature and soil moisture to climate warming manipulations were assessed by meta-analysis. The effect size of each response variable was calculated by the natural log of response ratio (RR): lnRR = $\ln(X_T/X_C)$, where X_T and X_C were the means of control and treatment groups, respectively (Hedges *et al.*, 1999).

We used METAWIN (Sinauer Associates, Inc. Sunderland, MA, USA) to calculate the mean response ratios and 95% bootstrap confidence intervals (CI). Treatment effect on a response variable was considered significant if the 95% bootstrap CI did not overlap 1. Total heterogeneity (Q_T) was partitioned

into within-group (Q_W) and between-group (Q_B) heterogeneities. For each investigated parameter, a subgroup analysis was conducted to assess whether the responses of different ecosystem types, manipulation methods or treatment durations are different. According to Hedges *et al.* (1999), a significant Q_B ($P < 0.05$) indicated that the response ratios are different among different groups.

In our datasets, methods used to simulate climate warming included electrical cable, field open-top chamber, close-top chamber, infrared heater and passive warming (Table S1). Warming manipulation levels, ranged from 0.3 to 7.5 °C, were different for different warming methods (Table S1, Table S3), which lead to significant between-group heterogeneity for the response of R_s among warming methods (Table S3, $Q_B = 0.83$, $P < 0.01$). To correct for the different effects associated with the different treatment levels across warming experiments, we estimated the RR of R_s at 2 °C warming by normalizing the RR of individual experiments. The calculation equation was: ln(Normalized RR) = ln{[X_C+2 × (X_T-X_C)/(T_T-T_C)]/X_C}, where X_T and X_C were defined as above, T_T and T_C were the soil temperature under warming and control plots, respectively. After normalization, the response of R_s among warming methods were no longer significant (Table S3, $Q_B = 0.26$, $P = 0.32$). The results reported in the main text were based on normalized data. The non-normalized RRs for R_s, R_a and R_h were also calculated, and the comparisons between normalized and non-normalized RRs were presented Table S4 and S5.

Different R_s partitioning methods could result in different R_a and R_h values (Phillips *et al.*, 2013). In our datasets, there were three soil respiration portioning partitioning methods: (i) stable isotopes (Lin *et al.*, 1999, 2001; Hagedorn *et al.*, 2010); (ii) trenching (Zhou *et al.*, 2007; Dorrepaal *et al.*, 2009; Luo *et al.*, 2009; Schindlbacher *et al.*, 2009; Aguilos *et al.*, 2011; Suseela & Dukes, 2013); (iii) and component integration (Melillo *et al.*, 2011). To assess whether different R_s partitioning methods affected the response of R_a or R_h to warming treatment, the data were subdivided into partitioning methods

and heterogeneity tests were conducted. The results showed that the responses of R_a or R_h did not differ between R_s partitioning methods (Table S6, $P > 0.05$). Therefore, the effect of R_s partitioning methods was not considered in later analysis.

Regression analysis was conducted to investigate the relationships between the response ratio of R_s/R_a/R_h/Q_{10} and other parameters (e.g. temperature manipulation level, experimental duration, soil temperature, soil moisture and MAT). All regression analyses were conducted with SAS software (SAS Institution Inc., Cary, NC, USA).

Results

Response of R_s

Averaged across all experiments, the warming treatments increased soil temperature by 2.43 °C, and decreased soil moisture by 10% (Table 1). When normalized, the response of R_s to a warming scenario of 2 °C, R_s was increased by 12% when averaged across all biomes during the early warming years (Table 1). Logically, the response ratio (RR) of R_s was positively correlated with the magnitude of soil temperature increase (Fig. 1a, $P < 0.01$). Biomes showed heterogeneous responses to rising temperature (Table S7). Warming by 2 °C induced nonsignificant increases in R_s in temperate forest and temperate shrubland, greatly stimulated R_s in tundra and alpine by 28% and 53% respectively, but reduced R_s in Mediterranean ecosystem by 16% (Table 1).

Furthermore, the response strength of R_s was influenced by MAT and soil moisture. The normalized RR of R_s was negatively correlated with MAT ($P = 0.03$, Fig. 2a). Meanwhile, lower RR of R_s was associated with lower RR of soil moisture ($P = 0.02$, Fig. 2b),

Table 1 Mean changes in soil temperature, and the RR of soil moisture, normalized RR of soil respiration and RR of Q_{10} in different biomes under warming treatments. The number of studies from each biome is shown in parentheses. For changes in soil temperature, bold numbers indicate that the change is significantly different from 0 ($P < 0.05$). For RR of soil moisture, normalized RR of soil respiration and RR of Q_{10}, bold numbers indicate that 95% bootstrap CI does not overlap 1

	Increased soil temperature	Soil moisture		Soil respiration		Q_{10}	
	Mean±SE (°C)	RR	95% Bootstrap CI	Normalized RR	95% Bootstrap CI	RR	95% Bootstrap CI
Total mean	**2.43 ± 0.15 (102)**	**0.90 (45)**	**0.88–0.93**	**1.12 (96)**	**1.07–1.17**	**0.86 (33)**	**0.81–0.90**
Tundra	**1.73 ± 0.20 (13)**	1.09 (2)	0.95–1.25	**1.28 (8)**	**1.18–1.40**	–	–
Alpine	**1.32 ± 0.54 (5)**	**0.89 (5)**	**0.84–0.92**	**1.53 (5)**	**1.45–1.61**	0.87 (3)	0.67–1.02
Boreal forest	**3.42 ± 0.35 (18)**	**0.85 (5)**	**0.80–0.90**	**1.10 (18)**	**1.03–1.18**	**0.81 (6)**	**0.70–0.95**
Temp. shrubland	**0.73 ± 0.12 (9)**	1.00 (3)	0.91–1.08	1.14 (9)	0.92–1.39	**0.91 (3)**	**0.82–0.98**
Temp. grassland	**2.02 ± 0.18 (25)**	**0.90 (20)**	**0.86–0.94**	1.06 (25)	1.00–1.13	**0.90 (11)**	**0.86–0.94**
Temp. forest	**3.72 ± 0.43 (20)**	**0.85 (5)**	**0.84–0.87**	1.12 (20)	0.99–1.23	**0.83 (4)**	**0.75–0.94**
Mediterranean	**0.76 ± 0.09 (3)**	–	–	**0.84 (3)**	**0.75–0.99**	–	–
Agri. land	**2.63 ± 0.15 (9)**	**0.90 (4)**	**0.87–0.94**	**1.06 (8)**	**1.01–1.12**	**0.75 (4)**	**0.65–0.86**

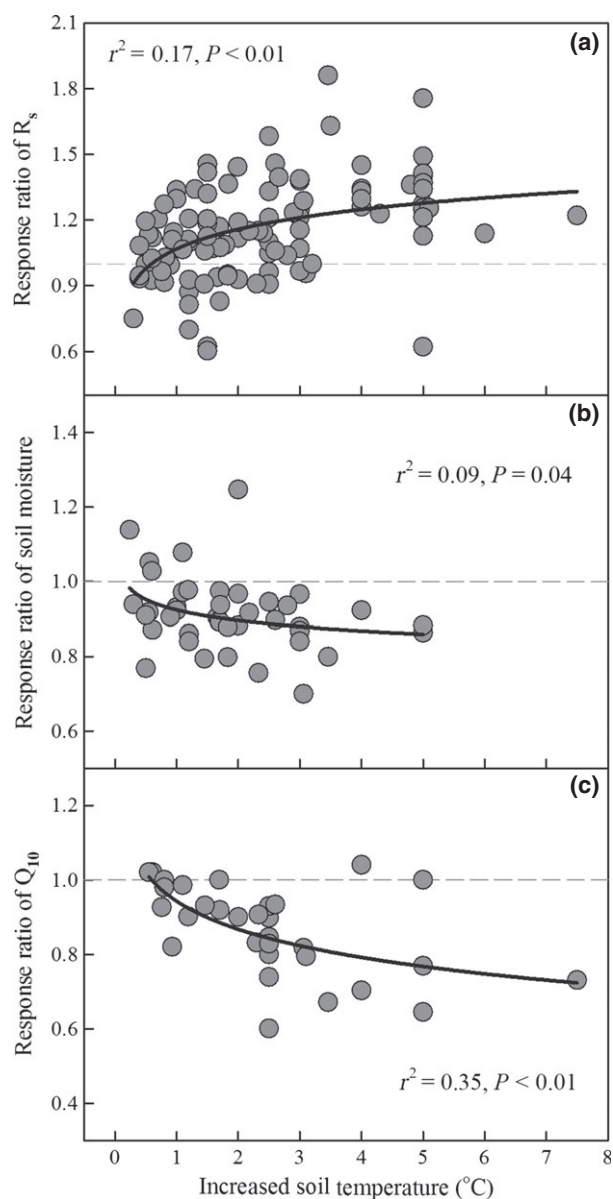Temp. means Temperate; Agri. means Agricultural.

Fig. 1 Relationships between warming manipulation level and (a) the response ratio of R_s, (b) the response ratio of soil moisture and (c) the response ratio of Q_{10}.

which was decreased with the increase in soil temperature ($P = 0.04$, Fig. 1b).

Response of the apparent Q_{10} of R_s

Averaged across all studies, the apparent Q_{10} of R_s was significantly decreased by 14% during the early warming years, and the decline was significant for all biomes except alpine ecosystems (Table 1). In addition, the RR of Q_{10} was negatively correlated with the magnitude of soil temperature increase ($P < 0.01$, Fig. 1c). When combining all Q_{10} data from both control and warming
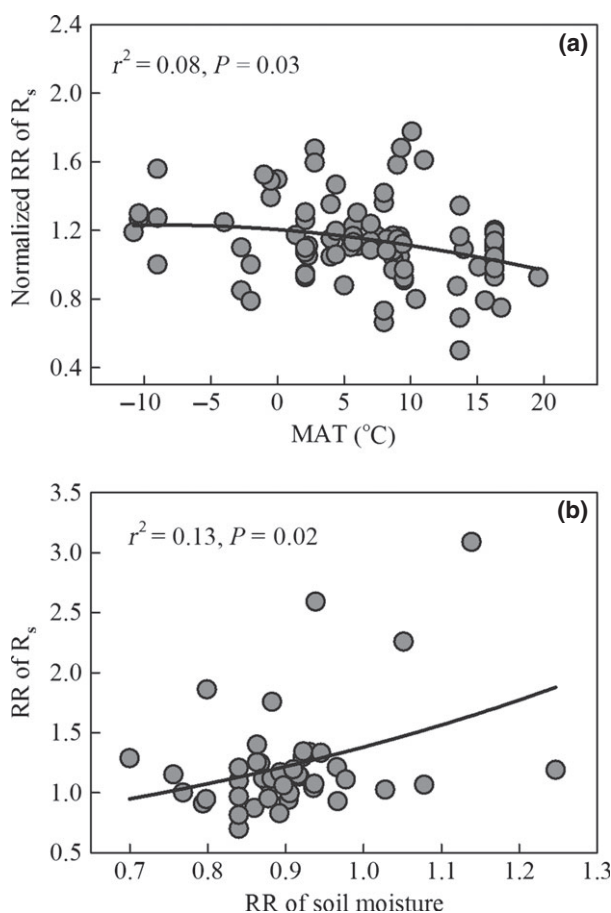

Fig. 2 Relationships between (a) MAT and the normalized response ratio of R_s, and (b) the response ratio of soil moisture and the response ratio of R_s under temperature manipulated experiments.

treatments, Q_{10} declined exponentially with soil temperature (Fig. 3a), but increased with soil volumetric moisture, although the increase leveled off at wetter sites (Fig. 3b).

Responses of R_a and R_h

Averaged across all studies, the warming effect during the early years was statistically detected in R_h, which increased by 21% under a 2 °C warming, but not in R_a (Table 2). When data were divided into different biomes, R_h in forest and grassland sites were increased by 27% and 7%, respectively (Table 2). However, warming stimulated R_a in forest sites by 19%, but had no significant impact on that in grassland sites (Table 2).

Responses of R_s, R_a, R_h and Q_{10} to warming duration

To investigate whether the responses of R_s, R_a, R_h and Q_{10} change with the increase in warming duration, we
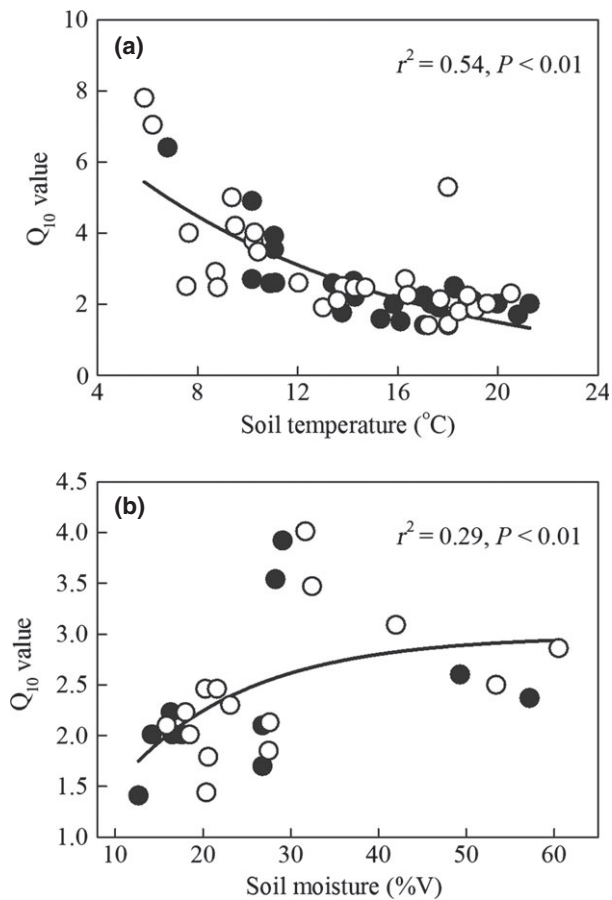
Fig. 3 Relationships between Q_{10} values and (a) mean soil temperature during the measurement period, and (b) mean soil moisture during the measurement period. Open symbols show control conditions and filled symbols show warming conditions.

built a new dataset which included both data of the earliest reported year and data of the rest years from experiments receiving warming treatment more than 2 years. The time series responses of R_s, Q_{10}, R_a and R_h were examined by computing and comparing the responses of those variables in each treatment year. The regression analysis indicated that normalized RR of R_s had no significant trend along warming treatment length (Fig. 4a). However, the reduction in response magnitude of Q_{10} diminished over warming experimental time (Fig. 4b). The response of R_a and R_h showed different responses to rising temperature over time. The normalized RR of R_a decreased along the treatment years (Fig. 4c, $P = 0.04$). Different from R_a, the normalized RR of R_h remained almost constant over the years, with values greater than 1 over the entire warming treatment period (Fig. 4d).

Discussion

It remains highly uncertain how the response of R_s to rising temperature will alter the feedback between carbon cycle and climate change. We synthesized ecosystem warming experiments across multiple terrestrial ecosystems, and investigated how warming affected the responses of R_s and its two components, R_a and R_h, over spatial and temporal scales.

Heterogeneous responses of R_s among biomes

Our analysis suggested that, averaged over all experiments, a 2 °C temperature increase elicited an increase in R_s by 12%. The RR of R_s showed heterogeneous

Table 2 Mean changes in soil temperature and RR of autotrophic respiration (R_a) and heterotrophic respiration (R_h) under warming treatments. The number of studies from each ecosystem is shown in parentheses. For changes in soil temperature, bold numbers indicate that the change is significantly different from 0 ($P < 0.05$). For RR of R_a/R_h, bold numbers indicate that the 95% bootstrap CI does not overlap 1

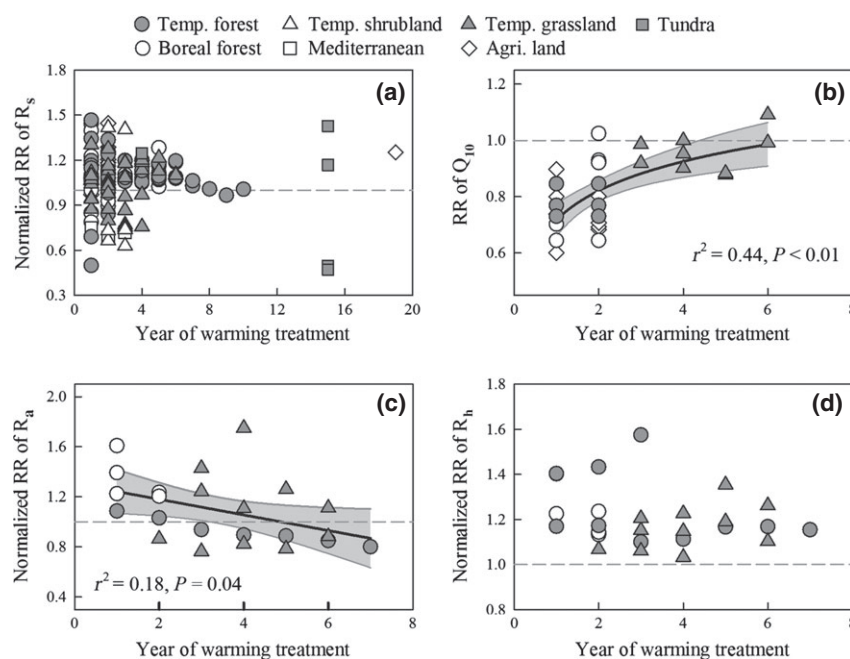|	Increased soil temperature	R_a or R_h	
	Mean±SE (°C)	Normalized RR	95% Bootstrap CI
R_a			
Mean	**2.53 ± 0.30 (15)**	1.09 (15)	0.97–1.21
Forest	**3.16 ± 0.45 (7)**	**1.19 (7)**	**1.05–1.37**
Grassland	**1.98 ± 0.29 (8)**	1.00 (8)	0.85–1.16
R_h			
Mean	**2.47 ± 0.28 (17)**	**1.21 (17)**	**1.12–1.34**
Forest	**3.14 ± 0.39 (8)**	**1.27 (8)**	**1.20–1.35**
Grassland	**1.98 ± 0.44 (8)**	**1.07 (8)**	**1.03–1.11**

Fig. 4 Effects of warming treatment duration on (a) R_s, (b) Q_{10}, (c) R_a and (d) R_h. In b and c, the black line is the regression line for all data, and the gray shade is the 95% confidence band for the regression curve.

responses to rising temperature among biomes (Table 1, Table S7). Warming resulted in greater increases in R_s in colder regions as indicated by the negative relation between the normalized RR of R_s and MAT ($P = 0.03$, Fig. 2a). The response of Q_{10}, which declined exponentially with soil temperature (Fig. 3a), also suggested that R_s is more sensitive to rising temperature in colder regions than in warmer regions (Davidson & Janssens, 2006).

Warming-induced changes in soil moisture also contributed to the heterogeneous responses of R_s among biomes. The positive relation between RR of R_s and RR of soil moisture (Fig. 2b) suggested that the constraint of soil moisture on R_s may mitigate or even eliminate the dependence of R_s on soil temperature, which has been observed in both climate manipulation experiments and also along the natural gradient of climate (Wan *et al.*, 2004; Tedeschi *et al.*, 2006; Liu *et al.*, 2009; Sheik *et al.*, 2011). The indirect effect of warming-induced drought can become a major factor for water-limited regions. Warming-induced soil moisture deficits have indeed been shown to result in reduced R_s, microbial population size, microbial activity and root biomass (Wan *et al.*, 2007; Liu *et al.*, 2009; Sheik *et al.*, 2011).

Our result also suggested that warming-induced changes in soil moisture could alter apparent Q_{10} of R_s. We found that Q_{10} of R_s increased with soil volumetric moisture, although the increase leveled off at wetter

sites (Fig. 3b). This relation suggests that the soil moisture decline caused by warming likely contributed to the observed decrease in Q_{10} at higher temperatures and to the occasional negative warming effects on R_s in arid and semiarid experiments (Table 1). These drought effects on apparent Q_{10} are commonly observed in dryer areas (Reichstein *et al.*, 2003; Suseela *et al.*, 2012), and can be related to thinner water films and the associated lower substrate diffusion rates (Davidson & Janssens, 2006), but also to reduced root activity (Wan *et al.*, 2007).

Different responses of R_a and R_h

Warming typically raises the metabolic rates of both plants and microbes, as indicated by most greenhouse and incubation experiments. Using the data from the earliest reported year, the results showed that the stimulation effect by 2 °C warming was statistically significant for R_h in both forests and grasslands (Table 2). This result contrasts a previous meta-analysis (on a 40% smaller dataset) that reported no significant changes in R_h (Dieleman *et al.*, 2012). In that analysis, grasslands exhibited a negative response of R_h to warming, whereas including more warming experiments in this analysis yielded a small yet statistically significant positive effect warming effect on R_h in grasslands (Table 2). The higher R_h under warming could be due to faster litter decomposition rate and

larger microbial biomass, as reported by Lu *et al.* (2013) in a recent meta-analysis on ecosystem responses to experimental warming. In addition, the higher R_h may also be associated with the increases in decomposition of stable organic matter (Hopkins *et al.*, 2012; Frey *et al.*, 2013).

Different from R_h, warming induced a significant increase in R_a in forests, but not in grasslands (Table 2, Table S5). Two possible reasons could be attributed to the different responses between forests and grasslands. First, most forest R_a data were came from boreal forest sites, where soil respiration is known to be highly sensitive to temperature increases (Fig. 2a, Fig. 3a). Second, the decline in soil moisture under warming treatments was likely insufficient to suppress R_a in these predominantly northern forests, while it could greatly affect the responses of R_a to warming in water-limited grasslands. Indeed, warming-induced water stress often lowered root activity in grasslands (Li *et al.*, 2013; Suseela & Dukes, 2013). However, with the increase in the duration of warming treatment, the responses of R_a of forests could start to decline (Melillo *et al.*, 2011). Warming often stimulates net nitrogen mineralization in forest (Melillo *et al.*, 2011; Dieleman *et al.*, 2012). Therefore, fine root growth could decrease due to less carbon needed to be allocated to belowground under increased N availability (Dieleman *et al.*, 2012). If the negative effects caused by decrease in soil moisture and fine root growth become more pronounced with the duration of warming treatment, warming's stimulation effect on R_a can diminish and even become negative along the treatment years (Melillo *et al.*, 2011; Fig. 4c).

The time series of the responses of R_s, R_a and R_h

Our regression analysis for warming experiments indicated that the normalized RR of R_a decreased along the treatment years (Fig. 4c). Different from R_a, the stimulation of R_h by warming remained stable over the entire warming treatment period (Fig. 4d), suggesting that R_h did not fully acclimate to warming.

Thermal acclimation of R_h has been widely discussed in recent years. Evidence from previous studies, both empirical and modeling, indicated that thermal acclimation could be due to depletion of fast cycling carbon, physiological acclimation of microbes and/or changes in microbial species composition (Kirschbaum, 2004; Eliasson *et al.*, 2005; Bradford *et al.*, 2008, 2010; Crowther & Bradford, 2013). However, most of the studies where acclimation was observed were based on lab incubations, with soil sampled from field warming experiments (Bradford *et al.*, 2008, 2010; Rinnan *et al.*, 2009; Crowther & Bradford, 2013). To our best

knowledge, no evidence from long-term warming sites actually demonstrated thermal acclimation of R_h *in situ*. Short-term, small scale lab incubations may not mimic the seasonal dynamics of soil physicochemical conditions and the interactions between plants and microbes, both of which greatly influence the *in situ* response of R_h to warming. Assessing changes in temperature sensitivity of R_h based on long-term field warming experiments would shed additional light on whether R_h's acclimate to rising temperature. Unfortunately, there were only few field warming experiments reported Q_{10} of R_h (Zhou *et al.*, 2007; Schindlbacher *et al.*, 2009). Overall, our synthesis based on field R_h data does not support the idea that R_h acclimates to rising temperature. However, the fact that acclimation has been unambiguously demonstrated in some studies highlights the need for further studies on this topic.

In agreement with R_h, our results also indicated that there was no apparent acclimation of R_s (Fig. 4a). In addition, we also found that the decline of Q_{10} observed in the initial years of the warming treatments, diminished over time, with Q_{10} values returning to prewarming level (Fig. 4b). A study based on worldwide R_s observations found that the global R_s increased by 0.1 Pg C yr^{-1} and this increase was positively correlated with the air temperature anomaly (Bond-Lamberty & Thomson, 2010), which also suggested that R_s of terrestrial ecosystems did not acclimate to climate warming.

Even though, cautious are needed when extrapolating the results of our analysis to individual biomes. Warming treatment periods ranged from 1 to 19 in our dataset, but 86% of studies sites received warming treatment less than 4 years (Table S1). Most long-term data, especially R_a and R_h data, were from boreal forests, temperate forests and temperate grasslands. Although several long-term warming experiments have been conducted in tundra (Fig. 4), surprising there were few studies reported the responses of R_a and R_h to warming. Tropical forests play critical role in regulating the feedbacks between climate and atmospheric CO_2 (Wang *et al.*, 2014). However, no study has reported how R_s and its component response to field warming in tropical forests. Because of data limitation, the responses of R_a and R_h to rising temperature in those biomes could not be assessed. With more long-term warming data becoming available, the temporal response patterns of R_s and its components may not be the same. Obviously, long-term warming studies, especially in underrepresented biomes, such as tropical forest, are necessary to test whether the acclimation of R_s is a widespread phenomenon, and separation of R_a and R_h is needed to better understand the underlying mechanisms.

Implications for predicting R_s under warming climate

Overall, our results indicated that the response of R_s to warming is highly heterogeneous. R_s of biomes in colder regions generally have higher temperature sensitivity, but this was known already three decades ago (Schleser, 1982). Alpine and tundra exhibited the most pronounced increases in R_s, +53% and +28%, respectively. Our analysis further revealed that the response of R_s to warming strongly depends on soil moisture conditions. Warming-induced soil moisture declines mitigated and even eliminated the stimulation of R_s by warming, which was especially evident in dry regions. For example, in temperate dry grassland, warming suppressed R_s significantly mostly because microbial activity and plant growth decreased with the more severe water deficit (Niu *et al.*, 2008; Liu *et al.*, 2009; Suseela *et al.*, 2012). Apparently, without considering the indirect drought effect caused by warming, we could not accurately predicate global R_s budget under changing climate conditions.

The most important finding of this study is that R_a and R_h showed different responses to rising temperature. R_h was stimulated by 21% in the earlier years (range from year 1 to year 4) of warming and subsequently did not acclimate to the elevated temperature. In contrast, R_a was not significantly altered during the earlier experimental years, and its response decreased with experimental duration. Our study did not support the common assumption that R_s or R_h acclimate to temperature. Whether and when R_s acclimates to climate change is one of the biggest challenges to predict the feedback between climate changes and carbon cycle. Because there are few long-term observations, limited progress was made to understand the occurrence of R_s acclimation. In addition, only a small part of ecosystem warming experiments reported R_a and R_h data. Long-term research on R_s, R_a, R_h and the ancillary information, especially soil moisture and plant and microbial community composition, are thus needed to better understand the mechanisms behind the responses of R_s to climate changes.

To further advance our ability in predicting how and how much R_s responds to climate warming, we need coordinated warming experiments using consortium approaches across a broad geographic range (Fraser *et al.*, 2013). Our literature search revealed that the warming magnitudes varied greatly among the five most commonly used warming methods (electrical cable, field open-top chamber, close-top chamber, infrared heater and passive warming), which resulted in a significant between-group heterogeneity of the responses of R_s among those methods (Table S3). Also, a specific warming method was often used in a specific

ecosystem. For example, electrical cables were often used in forests, and infrared heaters were commonly established in grasslands. Different experimental protocols could bring systematic bias when comparing the responses of R_s and its components within and between different biomes. Running field experiments in parallel with standardized protocols, such as same warming technique, temperature manipulation level and R_s partitioning method could greatly eliminate the variances caused by different experimental approaches. This will improve the accuracy in characterizing the general spatial/temporal patterns and also helps us better understand the heterogeneity of R_s under climate warming.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Global distribution of ecosystem warming experiments included in this meta-analysis.

Table S1. All experiments included in this meta-analysis are listed. Stars indicate which experiment provided that kind of data.

Table S2. Mean changes in soil temperature, and the response ratio (RR) of soil moisture, normalized RR of soil respiration and RR of Q_{10} in different biomes under warming treatments. The responses were estimated by using mean values of multiple years.

Table S3. Mean changes in soil temperature, and the nonnormalized and normalized response ratio (RR) of soil respiration (R_s) under different warming methods.

Table S4. The nonnormalized and normalized response ratios (RR) of soil respiration in different biomes under warming treatments.

Table S5. The nonnormalized and normalized response ratios (RR) of autotrophic respiration (R_a) and heterotrophic respiration (R_h) under warming treatments.

Table S6. The response ratios (RR) of autotrophic respiration (R_a) and heterotrophic respiration (R_h) of different soil respiration partitioning methods under warming treatments.

Table S7. Effect of warming on between-group heterogeneity (Q_B) of biome types for each response variable.