# 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

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## 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): $\ln RR = \ln(X_T/X_C)$, 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** |

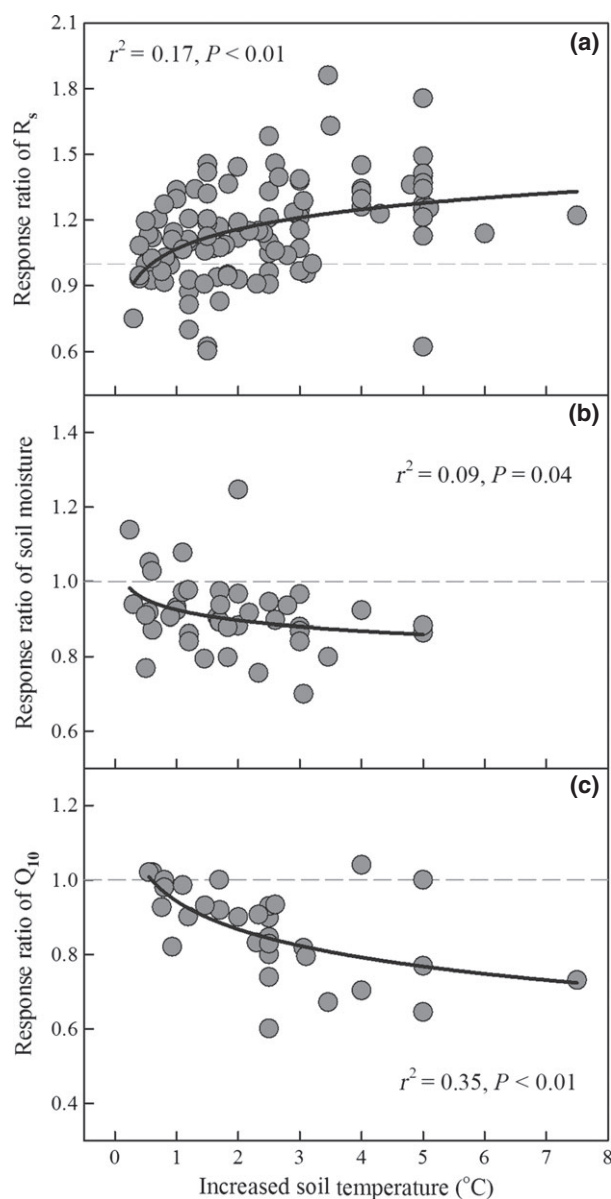Temp. means Temperate; Agri. means Agricultural.

**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
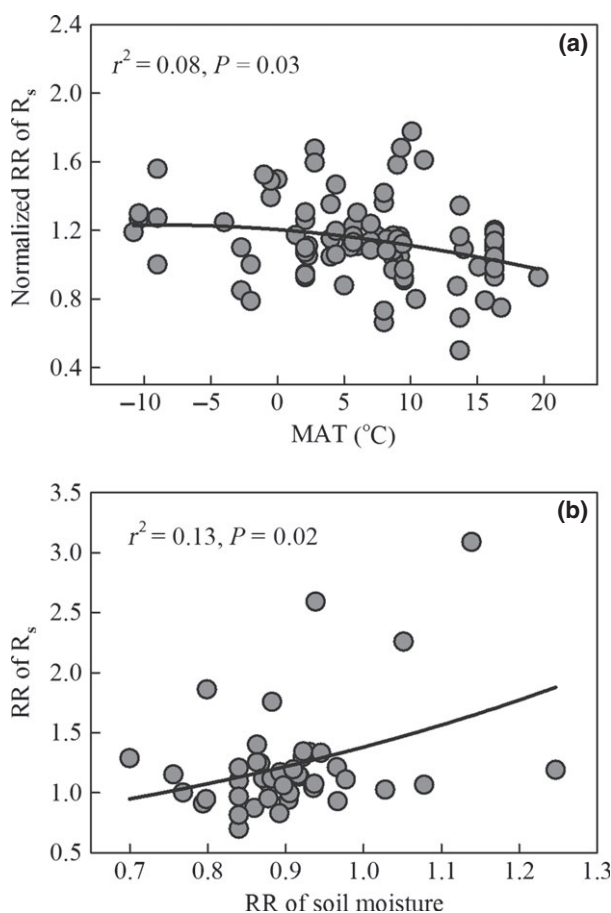


**Fig. 2** Relationships between (a) MAT and the normalized response ratio of $R_s$, and (b) the response ratio of soil moisture and the response ratio of $R_s$ under temperature manipulated experiments.

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
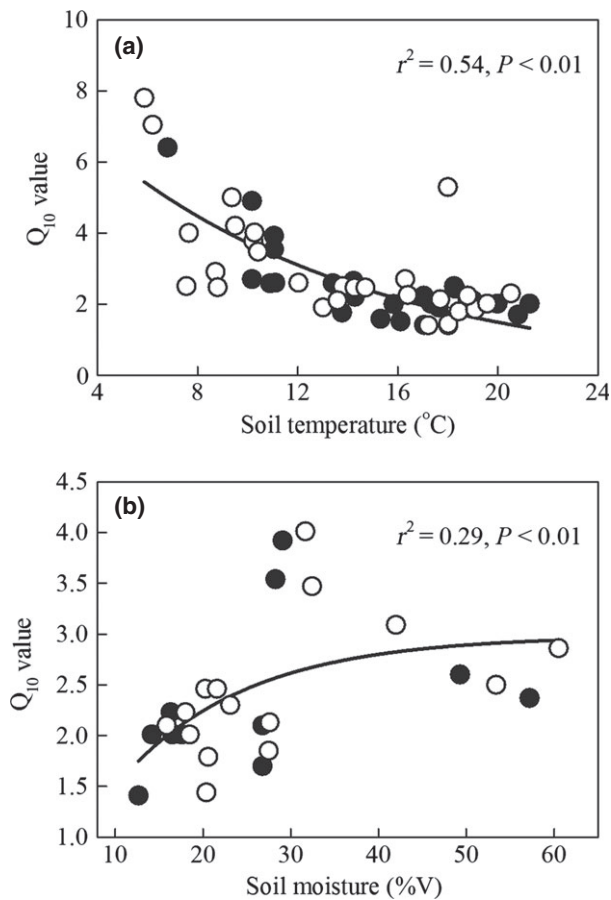
**Fig. 3** Relationships between $Q_{10}$ values and (a) mean soil temperature during the measurement period, and (b) mean soil moisture during the measurement period. Open symbols show control conditions and filled symbols show warming conditions.

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

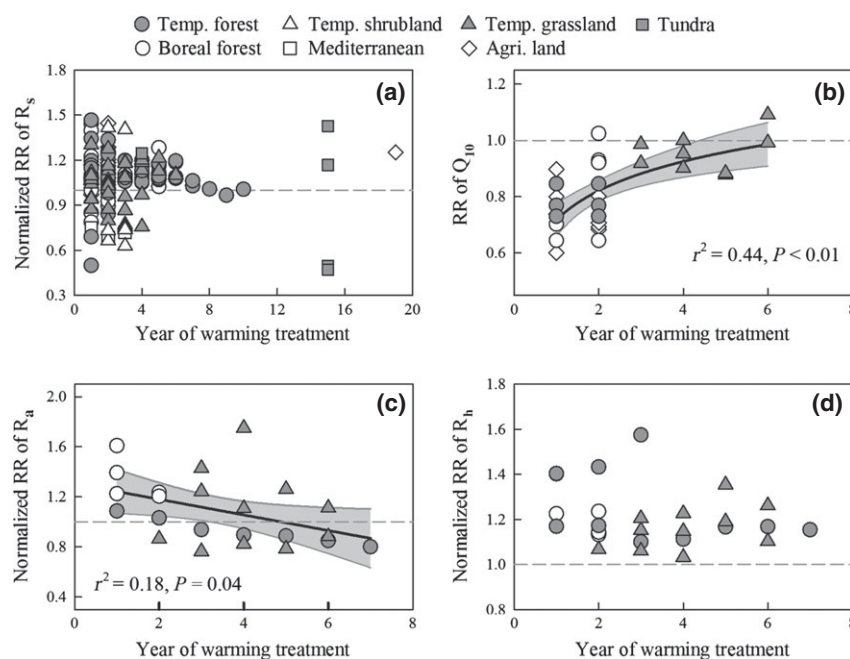| | Increased soil temperature | $R_a$ or $R_h$ | |
| | Mean±SE (°C) | Normalized RR | 95% Bootstrap CI |
|---|---|---|---|
| $R_a$ | | | |
| Mean | **2.53 ± 0.30 (15)** | 1.09 (15) | 0.97–1.21 |
| Forest | **3.16 ± 0.45 (7)** | **1.19 (7)** | **1.05–1.37** |
| Grassland | **1.98 ± 0.29 (8)** | 1.00 (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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## References

Aguilos M, Takagi K, Liang N *et al.* (2011) Soil warming in a cool-temperate mixed forest with peat soil enhanced heterotrophic and basal respiration rates but $Q_{10}$ remained unchanged. *Biogeosciences Discuss*, **8**, 6415–6445.

Bond-Lamberty B, Thomson A (2010) Temperature-associated increases in the global soil respiration record. *Nature*, **464**, 579–582.

Bradford MA, Davies CA, Frey SD *et al.* (2008) Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters*, **11**, 1316–1327.

Bradford MA, Watts BW, Davies CA (2010) Thermal adaptation of heterotrophic soil respiration in laboratory microcosms. *Global Change Biology*, **16**, 1576–1588.

Crowther TW, Bradford MA (2013) Thermal acclimation in widespread heterotrophic soil microbes. *Ecology Letters*, **16**, 469–477.

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.

Dieleman WIJ, Vicca S, Dijkstra FA *et al.* (2012) Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of $CO_2$ and temperature. *Global Change Biology*, **18**, 2681–2693.

Dorrepaal E, Toet S, van Logtestijn RSP, Swart E, van de Weg MJ, Callaghan TV, Aerts R (2009) Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, **460**, 616–619.

Eliasson PE, Mcmurtrie RE, Pepper DA, Strömgren M, Linder S, Gren GI (2005) The response of heterotrophic $CO_2$ flux to soil warming. *Global Change Biology*, **11**, 167–181.

Fraser LH, Al Henry H, Carlyle CN *et al.* (2013) Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, **11**, 147–155.

Frey SD, Lee J, Melillo JM, Six J (2013) The temperature response of soil microbial efficiency and its feedback to climate. *Nature Climate Change*, **3**, 395–398.

Hagedorn F, Martin M, Rixen C *et al.* (2010) Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. *Biogeochemistry*, **97**, 7–19.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.

Hopkins FM, Torn MS, Trumbore SE (2012) Warming accelerates decomposition of decades-old carbon in forest soils. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, E1753–E1761.

IPCC (2013) Summary for Policymakers. In: *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 4–20. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Janssens IA, Dieleman W, Luyssaert S *et al.* (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, **3**, 315–322.

Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology*, **10**, 1870–1877.

Kuzyakov Y, Larionova AA (2005) Root and rhizomicrobial respiration: a review of approaches to estimate respiration by autotrophic and heterotrophic organisms in soil. *Journal of Plant Nutrition and Soil Science*, **168**, 503–520.

Lamb EG, Han S, Lanoil BD, Henry GHR, Brummell ME, Banerjee S, Siciliano SD (2011) A High Arctic soil ecosystem resists long-term environmental manipulations. *Global Change Biology*, **17**, 3187–3194.

Li D, Zhou X, Wu L, Zhou J, Luo Y (2013) Contrasting responses of heterotrophic and autotrophic respiration to experimental warming in a winter annual-dominated prairie. *Global Change Biology*, **19**, 3553–3564.

Lin G, Ehleringer JR, Rygiewicz PT, Mark Johnson G, Tingey David T (1999) Elevated $CO_2$ and temperature impacts on different components of soil $CO_2$ efflux in Douglas-fir terracosms. *Global Change Biology*, **5**, 157–168.

Lin G, Rygiewicz PT, Ehleringer JR, Johnson MG, Tingey DT (2001) Time-dependent responses of soil $CO_2$ efflux components to elevated atmospheric $CO_2$ and temperature in experimental forest mesocosms. *Plant and Soil*, **229**, 259–270.

Liu W, Zhang Z, Wan S (2009) Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Global Change Biology*, **15**, 184–195.

Lu M, Zhou X, Yang Q *et al.* (2013) Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology*, **94**, 726–738.

Luo YQ, Wan SQ, Hui DF, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature*, **413**, 622–625.

Luo YQ, Sherry R, Zhou XH, Wan SQ (2009) Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy*, **1**, 62–74.

Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.

Melillo JM, Butler S, Johnson J *et al.* (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9508–9512.

Niu SL, Wu MY, Han Y, Xia JY, Li LH, Wan SQ (2008) Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist*, **177**, 209–219.

Phillips CL, Mcfarlane KJ, Risk D, Desai AR (2013) Biological and physical influences on soil 14CO2 seasonal dynamics in a temperate hardwood forest. *Biogeosciences*, **10**, 7999–8012.

Raich JW, Schlesinger WH (1992) The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B-Chemical and Physical Meteorology*, **44**, 81–99.

Reichstein M, Rey A, Freibauer A *et al.* (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochemical Cycles*, **17**, 1104.

Reth S, Graf W, Reichstein M, Munch JC (2009) Sustained stimulation of soil respiration after 10 years of experimental warming. *Environmental Research Letters*, **4**, 024005.

Rinnan R, Rousk J, Yergeau E, Kowalchuk GA, Baath E (2009) Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. *Global Change Biology*, **15**, 2615–2625.

Schindlbacher A, Zechmeister-Boltenstern S, Jandl R (2009) Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? *Global Change Biology*, **15**, 901–913.

Schindlbacher A, Wunderlich S, Borken W, Kitzler B, Zechmeister-Boltenstern S, Jandl R (2012) Soil respiration under climate change: prolonged summer drought offsets soil warming effects. *Global Change Biology*, **18**, 2270–2279.

Schleser GH (1982) The response of $CO_2$ evolution from soils to global temperature changes. *Zeitschrift für Naturforschung*, **37a**, 287–291.

Sheik CS, Beasley WH, Elshahed MS, Zhou X, Luo Y, Krumholz LR (2011) Effect of warming and drought on grassland microbial communities. *Isme Journal*, **5**, 1692–1700.

Strömgren M (2001)Soil-surface $CO_2$ flux and growth in a boreal Norway Spruce stand effects of soil warming and nutrition. Doctoral thesis.

Suseela V, Dukes JS (2013) The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. *Ecology*, **94**, 403–413.

Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology*, **18**, 336–348.

Tedeschi V, Rey A, Manca G, Valentini R, Jarvis PG, Borghetti M (2006) Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing. *Global Change Biology*, **12**, 110–121.

Wan SQ, Norby RJ, Pregitzer KS, Ledford J, O'neill EG (2004) $CO_2$ enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. *New Phytologist*, **162**, 437–446.

Wan S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to elevated $CO_2$, air warming, and changing soil water availability in a model old-field grassland. *Global Change Biology*, **13**, 2411–2424.

Wang X, Piao S, Ciais P *et al.* (2014) A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature*, **506**, 212–215.

Zhou XH, Sherry RA, An Y, Wallace LL, Luo YQ (2006) Main and interactive effects of warming, clipping, and doubled precipitation on soil $CO_2$ efflux in a grassland ecosystem. *Global Biogeochemical Cycles*, **20**, GB1003.

Zhou X, Wan S, Luo Y (2007) Source components and interannual variability of soil $CO_2$ efflux under experimental warming and clipping in a grassland ecosystem. *Global Change Biology*, **13**, 761–775.

## 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.