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Interactive effects of global change factors on soil respiration and its components: a meta-analysis

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Abstract

As the second largest carbon (C) flux between the atmosphere and terrestrial ecosystems, soil respiration (Rs) plays vital roles in regulating atmospheric CO_2 concentration ([CO_2]) and climatic dynamics in the earth system. Although numerous manipulative studies and a few meta-analyses have been conducted to determine the responses of Rs and its two components [i.e., autotrophic (Ra) and heterotrophic (Rh) respiration] to single global change factors, the interactive effects of the multiple factors are still unclear. In this study, we performed a meta-analysis of 150 multiple-factor (≥2) studies to examine the main and interactive effects of global change factors on Rs and its two components. Our results showed that elevated [CO_2] (E), nitrogen addition (N), irrigation (I), and warming (W) induced significant increases in Rs by 28.6%, 8.8%, 9.7%, and 7.1%, respectively. The combined effects of the multiple factors, EN, EW, DE, IE, IN, IW, IEW, and DEW, were also significantly positive on Rs to a greater extent than those of the single-factor ones. For all the individual studies, the additive interactions were predominant on Rs (90.6%) and its components (≈70.0%) relative to synergistic and antagonistic ones. However, the different combinations of global change factors (e.g., EN, NW, EW, IW) indicated that the three types of interactions were all important, with two combinations for synergistic effects, two for antagonistic, and five for additive when at least eight independent experiments were considered. In addition, the interactions of elevated [CO_2] and warming had opposite effects on Ra and Rh, suggesting that different processes may influence their responses to the multifactor interactions. Our study highlights the crucial importance of the interactive effects among the multiple factors on Rs and its components, which could inform regional and global models to assess the climate–biosphere feedbacks and improve predictions of the future states of the ecological and climate systems.

Keywords: drought, elevated CO_2, irrigation, nitrogen addition, soil respiration, warming

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Introduction

Soil respiration (Rs) represents carbon dioxide (CO_2) efflux from the soil surface, including two source components: heterotrophic or microbial respiration (Rh) and autotrophic or root respiration (Ra). The Rh includes the decomposition of litter and soil organic matter (SOM), while the Ra is carbon efflux from live roots and their symbionts (Schlesinger & Andrews, 2000; Luo & Zhou, 2006). As the second largest carbon (C) flux between the atmosphere and terrestrial ecosystems, the Rs is approximately 10 times higher than the current rate of fossil fuel combustion (Raich & Schlesinger, 1992; Bond-Lamberty & Thomson, 2010). Therefore, even small changes in Rs have the potential to significantly exacerbate or mitigate rising CO_2 levels, and then impact the consequent C cycle feedbacks to climate change (Rustad *et al.*, 2000).

As the combined metabolism of roots and soil microbes (Raich & Schlesinger, 1992), Rs is affected by a complex array of biotic and abiotic factors (e.g., temperature, moisture, soil nitrogen, and organic matter availability, Orchard & Cook, 1983; Lloyd & Taylor, 1994; Robertson *et al.*, 1999). Rapid ongoing climate change, including elevated [CO_2], warming, altered

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precipitation, and nitrogen deposition, may also significantly affect Rs and its components and then the global C cycle, which could potentially impact the climate–C cycle feedback. Numerous ecosystem-level manipulative experiments have been conducted to examine the responses of Rs and its components (Ra and Rh) to global change factors, especially to the single ones. Furthermore, to obtain a central tendency from the diverse results at a global scale, many meta-analyses have been carried out to probe effects of single global change factors. For example, Rustad *et al.* (2001), Wu *et al.* (2011), and Lu *et al.* (2013) synthesized extensive data sets and indicated significant increases in Rs by 9–20% under experimental warming. Zak *et al.* (2000) and Dieleman *et al.* (2012) found that elevated [CO_2] increased Rs in almost all the field studies compared with the control. The Ra was also found to increase significantly by 58.9% in response to elevated [CO_2] (Nie *et al.*, 2013). Simulated nitrogen deposition resulted in a significant increase (+2.0%) in Rs across all biomes, although the response directions of Ra and Rh were opposite in some biomes (Lu *et al.*, 2011; Zhou *et al.*, 2014). Increased precipitation (i.e., irrigation) also caused a positive effect on Rs with an increase of 45%, whereas drought induced a negative one with a decrease of 12% (Wu *et al.*, 2011).

Global climate change usually involves simultaneous changes in multiple environmental factors (e.g., atmospheric [CO_2], temperature, and precipitation, IPCC, 2013), which may interactively affect Rs and its components (Luo *et al.*, 2008; Suseela *et al.*, 2012). Although many single-factor manipulative experiments have been conducted to examine the responses of the C cycle (Luo *et al.*, 2001; Körner *et al.*, 2005; Hyvönen *et al.*, 2008), multifactor studies are limited due to the challenges in cost, technological difficulties, and ecosystem complexities in the past decades (Zhou *et al.*, 2008, 2013). The combined effects of multiple global change factors were generally assumed to be the additive accumulation of single-factor effects (Crain *et al.*, 2008). However, a modeling analysis showed that two-way interactive effects between warming and elevated [CO_2], or between warming and doubled precipitation on Rh were positive (i.e., amplification of one factor's effect by the other factor, Luo *et al.*, 2008). Synergistic and antagonistic interactions (Folt *et al.*, 1999) may also occur among multiple global change factors in influencing Rs and its components (Wildung *et al.*, 1975; Selsted *et al.*, 2012). Therefore, the single-factor experiments may be inadequate to fully comprehend the tendency of Rs and its components under the changing climate (Dermody, 2006).

Over the last decades, an increasing number of multifactor experiments have been conducted to investigate the effects of global change factors on the terrestrial C cycle (Bannayan *et al.*, 2009; Bloor *et al.*, 2010; Albert *et al.*, 2011). Substantial empirical data from manipulative field experiments are available now on Rs and its components for two or more global change factors (Billings & Ziegler, 2008; Yan *et al.*, 2009; Deng *et al.*, 2010). The combined effects of two or more global change factors on Rs, its components, or both have been examined in these experiments with a full-factorial design as well as the main effects of each single factor. Owing to lack of operational definitions of interactions among multiple factors and the complexity of disentangling multifactor effects (Wan *et al.*, 2007), the combined effects were defined as 'worse than' or 'better than' (Folt *et al.*, 1999). Distinguishing the interactions of multiple global change factors on Rs and its components could largely improve our understanding of global change effects on the terrestrial C cycle in the future (Hyvönen *et al.*, 2007; Luo *et al.*, 2008).

To examine general patterns of multifactor interactions (including additive, synergistic, or antagonistic) on Rs and its components (Rh and Ra) as well as the individual and main effects of global change factors, a meta-analysis of 150 multiple-factor (≥2) experiments was conducted in this study. Our objectives were to (i) examine the average interactive effects of multiple global change factors (including additive, synergistic, and antagonistic effects) on Rs and its components across all available studies and (ii) evaluate the potential impacts of biome types, the number of factors, and experimental duration on the responses of Rs and its components to global change factors.

Materials and methods

Data sources

More than 1500 published papers searched from Web of Science (1900–2015), which were related to changes in Rs and its components under experimental manipulations of multiple factors, were reviewed. To avoid publication bias, papers meeting the following criteria were selected: (i) At least a 2 × 2 full-factorial design was used to examine the effects of global change factors including elevated [CO_2], nitrogen addition, warming, irrigation, and/or drought; (ii) at least one of the selected variables [i.e., Rs, soil autotrophic (Ra), and soil heterotrophic respiration (Rh)] was examined in all treatments and the control at the same temporal and spatial scales; (iii) the plots for all treatments had the same ecosystem type, dominant vegetation composition, and environmental conditions as the control at the beginning of the experiments; (iv) the methods for treatments of elevated [CO_2] [e.g., free-air CO_2 enrichment or open top chamber (OTC)], warming (e.g., infrared heater, soil heating cable, or OTC), nitrogen addition, drought (e.g., rain exclusion shelter), or irrigation were clearly indicated; (v) the experimental duration should be longer than one growing season; and (vi) the means, standard deviations/errors, and samples sizes of the variables could be extracted from the context, tables, or digitized graphs. In total, 65 published papers with 150 multiple-factor (≥2) studies were selected in this study (Data S2, Table S1).

The compiled database contained three variables: Rs, Ra, and Rh, under multiple global change factors, including the single and combined treatments with elevated [CO_2], nitrogen addition, warming, irrigation, and/or drought (Table S1). Meanwhile, the environmental variables including latitude (40°20′ S–74°30′N, Fig. 1), mean annual temperature (MAT, −10 to 21.5 °C), and mean annual precipitation (MAP, 200–1750 mm) were recorded directly from papers or cited papers, or extracted from the database at http://www.worldclim.org/ using the location information. Furthermore, the experimental duration (1–9 years) at each study was also recorded from the detailed description in Materials and Methods section of the selected papers.

Data analysis

Individual effects. The individual effect of a factor or combined factors was defined as the response of a variable in the treatment compared with the control (Crain *et al.*, 2008), which was indicated by the response ratio (RR) in this study (Hedges *et al.*, 1999; Luo *et al.*, 2006). The detailed calculation of the individual RR, the variance (v_1) and weight (w_1) of each RR, and the mean RR (RR_{++}) were described in the Supporting Information (Data S1).

Main and interactive effects. Main effect of a global change factor represents the difference by comparing its net effect in the presence and absence of a second factor, similar to main effect tests in ANOVA (Crain *et al.*, 2008). We employed Hedge's d to evaluate the main effect sizes of two factors on the variables according to the methods of Gurevitch *et al.* (1992) and Crain *et al.* (2008) as well as their interaction. The individual Hedge's d of a factor was calculated using Eqn (1).

$$d = \frac{\overline{X}_t - \overline{X}_c}{s} J(m) \tag{1}$$

where $\overline{X}_t$ and $\overline{X}_c$ are means of a variable in the treatment and control groups, respectively, and s and $J(m)$ are the pooled standard deviation and correction term for small sample bias, respectively (Hedges & Olkin, 1985), which were estimated by Eqns (2) and (3), respectively.

$$s = \sqrt{\frac{(n_t - 1)(s_t)^2 + (n_c - 1)(s_c)^2}{n_t + n_c - 2}} \tag{2}$$

$$J(m) = 1 - \frac{3}{4m - 1} \tag{3}$$

where n_t, n_c, s_t, and s_c are the sample sizes (n_t, n_c), and standard deviations (s_t, s_c) in the treatment (n_t, s_t) and control (n_c, s_c) groups; m is the degree of freedom ($m = n_t + n_c - 2$). The variance (v_2) of the individual d was estimated by Eqn (4).

$$v_2 = \frac{n_t + n_c}{n_t n_c} + \frac{d^2}{2(n_t + n_c)} \tag{4}$$

The weight (w_2) was the reciprocal of the variance (i.e., $1/v_2$), which was used to calculate the weighted d [d_{++}, in Eqn (5)], and standard error [$s(d_{++})$, Eqn (6)].

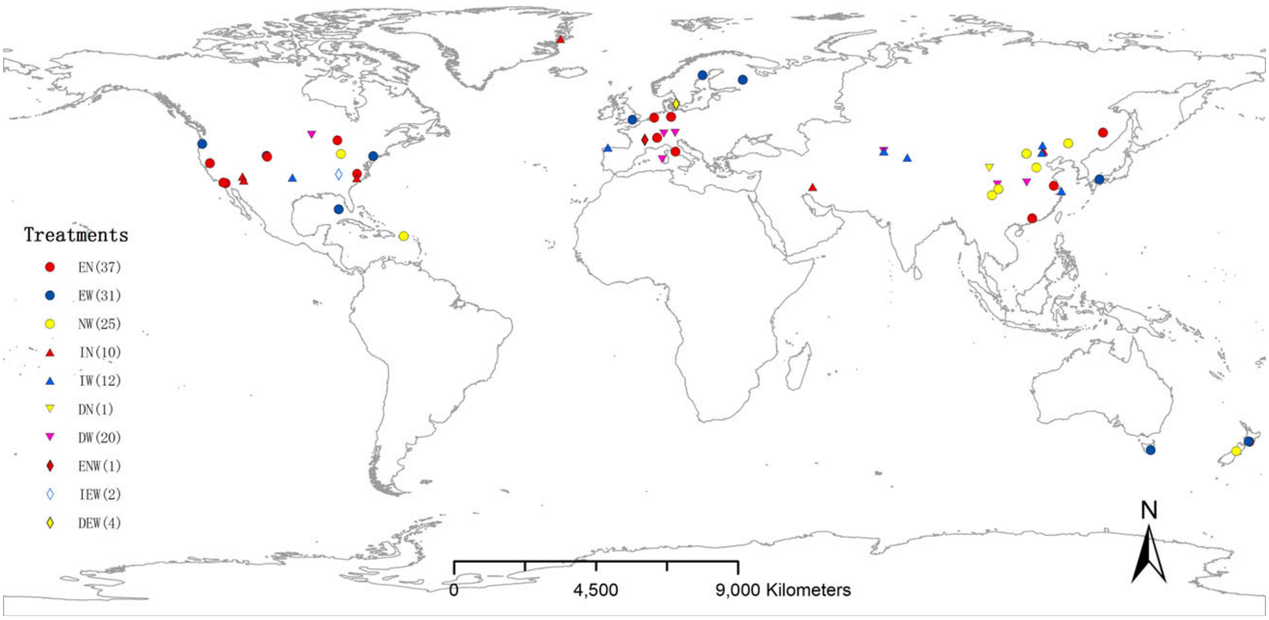

Fig. 1 Global distribution of 150 multifactor studies selected in this meta-analysis. Numbers in parentheses is the actual number of sites with different factorial designs. E, N, W, I and D represent elevated [CO_2], nitrogen addition, warming, irrigation and drought, respectively.

$$d_{++} = \frac{\sum_{i=1}^{l}\sum_{j=1}^{k} w_{ij} d_{ij}}{\sum_{i=1}^{l}\sum_{j=1}^{k} w_{ij}} \quad (5)$$

$$s(d_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{l}\sum_{j=1}^{k} w_{ij}}} \quad (6)$$

where l is the number of groups (e.g., the different combinations in the treatments), and k is the number of comparisons in the ith group.

The main effects of factors A and B (d_A and d_B) and their interaction (d_I) were calculated by Eqns (7)–(9), respectively.

$$d_A = \frac{(\overline{X}_A + \overline{X}_{AB}) - (\overline{X}_B + \overline{X}_c)}{2s} J(m) \quad (7)$$

$$d_B = \frac{(\overline{X}_B + \overline{X}_{AB}) - (\overline{X}_A + \overline{X}_c)}{2s} J(m) \quad (8)$$

$$d_I = \frac{(\overline{X}_{AB} - \overline{X}_A) - (\overline{X}_B - \overline{X}_c)}{2s} J(m) \quad (9)$$

where $\bar{X}_c, \overline{X}_A, \overline{X}_B$, and $\overline{X}_{AB}$, are means of a variable in the control and treatment groups of A, B, and their combination (A + B), respectively. The standard deviation (s) and degree of freedom (m) were estimated by Eqns (10) and (11), respectively, for the main and interactive effects.

$$s = \sqrt{\frac{(n_c-1)(s_c)^2 + (n_A-1)(s_A)^2 + (n_B-1)(s_B)^2 + (n_{AB}-1)(s_{AB})^2}{n_c + n_A + n_B + n_{AB} - 4}} \quad (10)$$

$$m = n_c + n_A + n_B + n_{AB} - 4 \quad (11)$$

According to the methods in Folt *et al.* (1999) and Crain *et al.* (2008), we classified the interactions between two factors into three types, that is, additive, antagonistic, and synergistic (see Fig. S1). The variance (v_3) of the d of the main effects and interactions was estimated by Eqn (12).

$$v_{3i} = \left[\frac{1}{n_c} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_i^2}{2(n_c + n_A + n_B + n_{AB})}\right] \Big/ 4 \quad (12)$$

where i was treatments of A, B, or their combination (A + B); the weight (w_3) was also the reciprocal of the variance as before. Weighted d_i (d_{i++}) and standard error were calculated according to Eqns (5) and (6), respectively.

When the number of data points (i.e., the number of individual RR or d values) in a group was larger than 20, the 95% confidence interval (CI) of RR_{++} and d_{++} was calculated as $RR_{++} \pm C_{\alpha/2} \times s(RR_{++})$ and $d_{++} \pm C_{\alpha/2} \times s(d_{++})$, respectively, where $C_{\alpha/2}$ is the two-tailed critical value of the standard normal distribution. If the number was lower than 20, we used bootstrapping method (Adams *et al.*, 1997; Janssens *et al.*, 2010) for resampling to obtain the lowest and highest 2.5% values as CI based on 5000 iterations. If the 95% CI did not overlap with zero, the individual and main effects of elevated [CO_2], nitrogen addition, warming, irrigation, drought, or their combinations were insignificant and the interactive effect was considered to be additive. For factor pairs whose individual effects were either both negative or one negative and one positive, interaction effect sizes less than zero were synergistic and greater than zero antagonistic. In cases where the individual effects were both positive, the interactions were interpreted in the opposite manner (>0 is synergistic and <0 antagonistic). Due to the large uncertainty from the limited studies, we mainly described and discussed the results with at least eight independent studies for the multiple global change factors.

Results

A total of 150 studies related to Rs and/or its components from 65 papers (Data S2) met our criteria for experimental manipulations of multiple global change factors, including elevated [CO_2] (E), nitrogen addition (N), warming (W), drought (D), irrigation (I), and their combinations (e.g., EN, EW, NW, IE, IN, IW, DE, DW, ENW, IEW, DEW, Fig. 1). The majority of the selected studies were distributed in North America and Europe (Fig. 1). The number of the studies with two-factor pairs was 190, 66% of which were on Rs, 21% were on heterotrophic respiration (Rh), and 13% were on autotrophic respiration (Ra, Table 1).

Individual effects of single and combined factors on Rs and its components. Across all the multifactor studies, elevated [CO_2], nitrogen addition, warming, and irrigation increased Rs by 28.6%, 8.8%, 7.1% and 9.7%, respectively ($P < 0.05$), while drought did not significantly affected Rs ($P > 0.05$, Fig. 2a). The responses of Rs to the single factors in the multifactor studies were similar to those in the single-factor experiments (Fig. 2a). Nitrogen addition did not significantly affect Rh in the multifactor studies, whereas it significantly decreased Rh in the single-factor experiments (Fig. 2b). Elevated CO_2 significantly increased Rh by 35.8% (Fig. 2b), while drought decreased Rh by 10.1% with a small sample size (only 2) in the multifactor studies but with larger magnitude in the single-factor studies. However, N

Table 1 Number of two-factor pairs meeting the criteria listed in the text

	W			N			D			I		
	Rs	Rh	Ra	Rs	Rh	Ra	Rs	Rh	Ra	Rs	Rh	Ra
E	29	13	6	32	9	8	3	0	0	2	0	2
W				25	1	1	20	4	4	8	9	1
N							1	0	0	6	3	3
Total pairs: 190												

E, elevated [CO_2]; N, nitrogen addition; W, warming; D, drought; I, irrigation; Rh, heterotrophic respiration; Ra, autotrophic respiration; Rs, soil respiration.

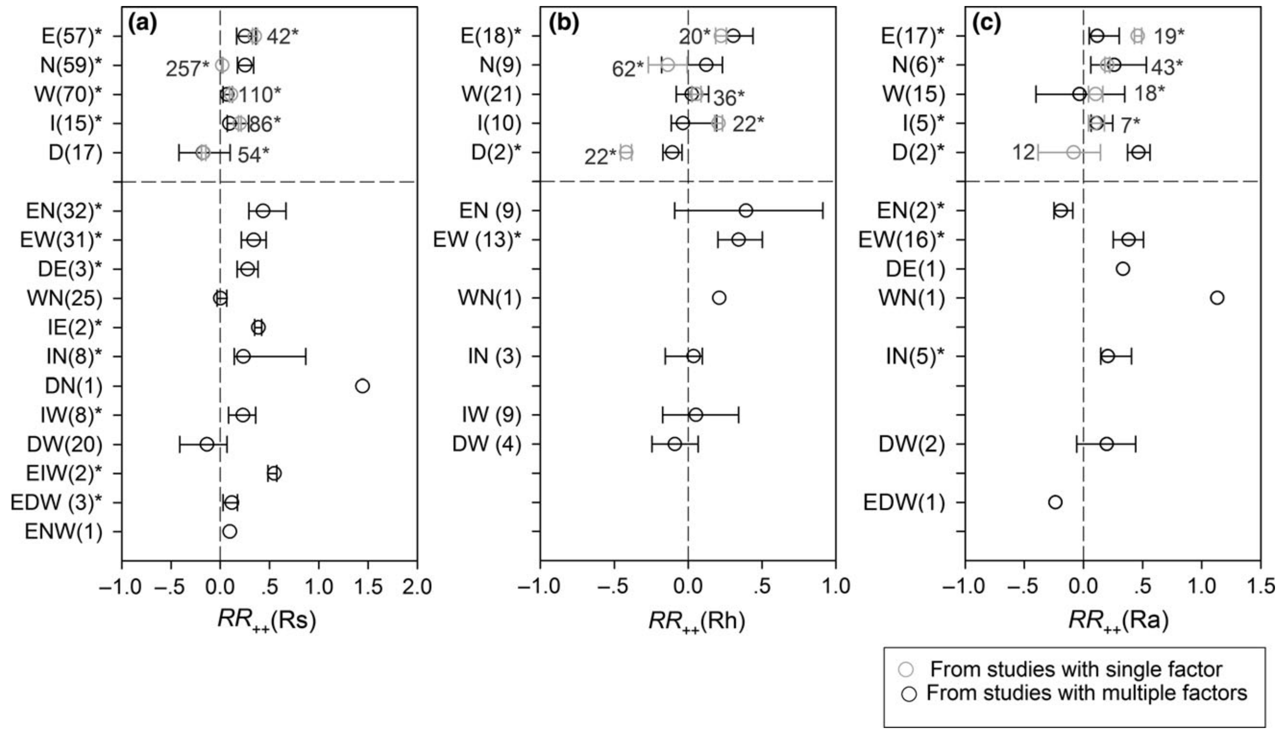

Fig. 2 Weighted response ratio (RR_{++}) of soil respiration (Rs, a), soil heterotrophic respiration (Rh, b), and soil autotrophic respiration (Ra, c) to the effects of single factors, two and three combined factors. E, N, W, I and D represent elevated [CO_2], nitrogen addition, warming, irrigation and drought, respectively. The error bars indicated the 95% confidence interval (CI). If the CI did not overlap with zero, a response was considered to be significant.

addition and irrigation had nonsignificant effects due to the large variation (Fig 2b). For Ra, the results were highly uncertain because the significant effects of nitrogen addition, irrigation, and drought were all based on small sample sizes (<8). With the relatively large sample size, elevated [CO_2] significantly increased Ra while warming did not significantly affect Ra (Fig. 2c).

The combined effects of the multiple factors were significant on Rs for EN (+51.6%) and EW (+40.4%), while the NW and DW had little effect on Rs (Fig. 2). The EW also increased Rh (+40.8%) and Ra (+46.6%), whereas the EN and IW did not affect Rh (Fig. 2). However, it is difficult to evaluate the effects of other combined factors due to the insufficient data (i.e., the sample size ≤8). The treatment type, biomes, and their interaction (Treatment × biomes) all regulated the responses of Rs to global change factors to some degree, while only the Treatment × Biome interaction and the biomes significantly affected the response of Rh and Ra to these factors, respectively (Table 2, Fig. 5b).

Table 2 ANOVA results of the effects of treatment types [treatments: elevated (CO_2), nitrogen addition, warming, drought, irrigation, and all the types of multiple-factor combinations] and biome types (biomes: tropical, temperate, and boreal forests, shrublands, croplands, grasslands, tundras, deserts, and wetlands) on the response ratios (RR) of soil respiration (Rs), heterotrophic respiration (Rh), and autotrophic respiration (Ra)

	RR(Rs)			RR(Rh)			RR(Ra)		
	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.
Treatments	16	8.452	0.000**	10	0.553	0.847	11	1.751	0.089
Biomes	5	5.315	0.000**	3	1.802	0.153	2	3.676	0.032*
Treatments × biomes	33	7.059	0.000**	12	2.187	0.020*	8	1.449	0.199
Residual	299			81			51		

*indicates Sig.< 0.05.
**indicates Sig. < 0.001.

Main and interactive effects of global change factors on Rs and its components. The main effects of elevated [CO_2] were significantly positive on Rs in EN and EW and on Rh and Ra in EW (Fig. 3d–f), while the main effects of drought were negative on Rs in DW (Fig. 3d). Warming significantly induced positive main effects on Rs and Ra in EW (Fig. 3d, f). Nitrogen addition also had the positive main effects on Rs in EN but a neutral one in NW (Fig. 3d). Other significant results were not described here due to the large uncertainty from the limited studies (<8).

In all the two-factor pairs (190 pairs), additive interaction exhibited a substantial predominance (90.6%) on Rs compared with synergistic and antagonistic ones (Fig. 3a). The synergistic interactions on Rs (6.3%) were more frequent than antagonistic ones (3.1%). The dominance of additive interaction was also observed for both Rh (69.2%) and Ra (68%). However, the antagonistic interaction on Rh (28.2%) was more dominant than synergistic one (2.6%), while the synergistic and antagonistic interactions on Ra were comparable (i.e., 12.0% vs. 20.0%, respectively, Fig. 3a–c). This general pattern did not significantly change for each of those two-factor combinations with relatively high sample sizes (>8, Fig. 3).

When considering only those interactions which were tested for at least eight independent studies (Fig. 3), the number of additive, synergistic, and antagonistic interactions did not significantly differ (Fig. 3d and f). Specifically, the interactions in EN on Rs and EW on Ra were synergistic with significantly positive effects (Fig. 3d and f), while the interactions in NW, EW, DW, and IW on Rs and IW on Rh were additive. Antagonistic interactions of elevated [CO_2] with warming and nitrogen addition displayed negative effects on Rh (Fig. 3e).

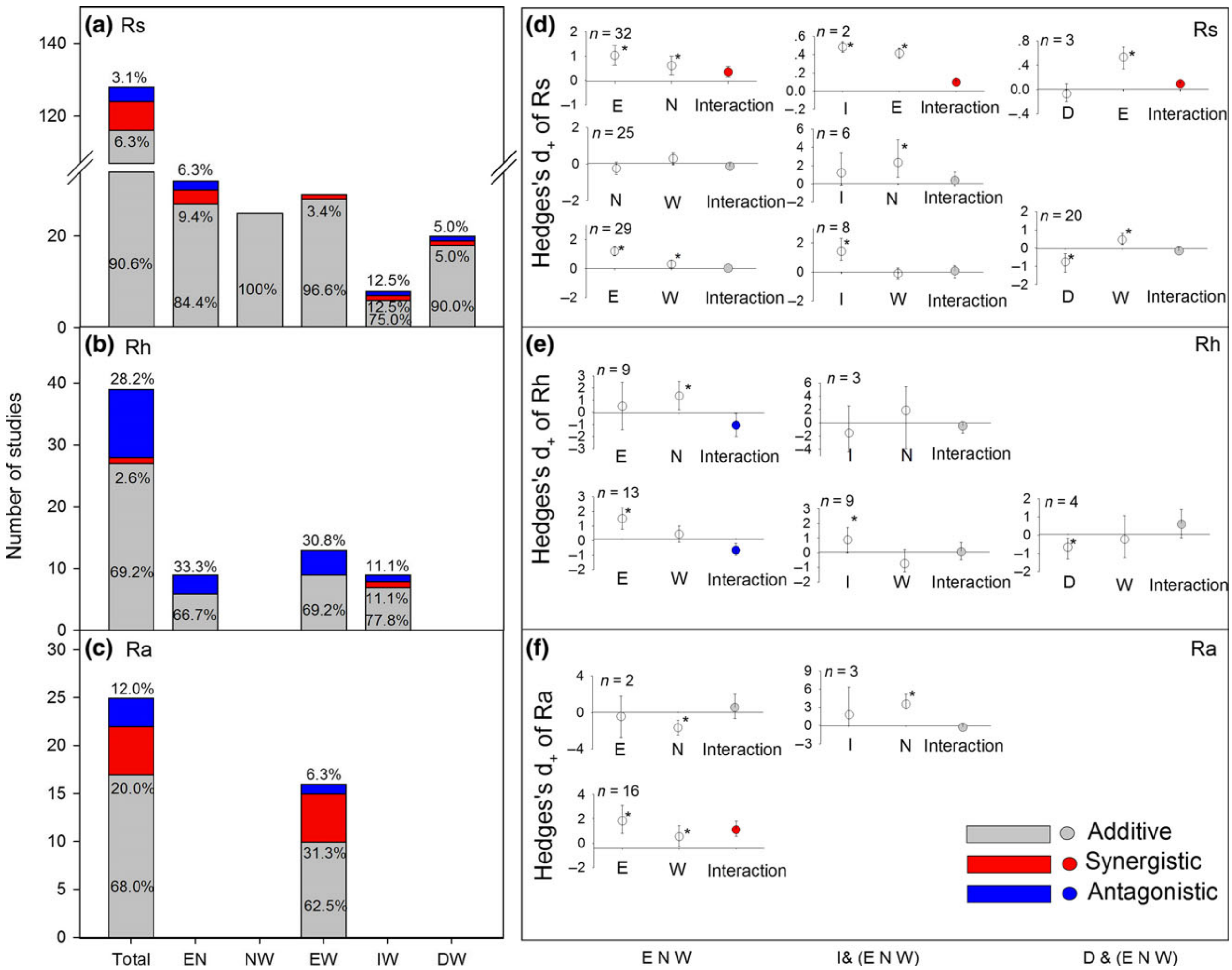

Fig. 3 Frequency distribution of interaction types in individual studies with two-factorial designs for soil respiration (Rs, a), soil heterotrophic respiration (Rh, b), and soil autotrophic respiration (Ra, c). E, N, W, I and D represent elevated [CO_2], nitrogen addition, warming, irrigation and drought, respectively. Asterisk in panel d, e and f indicated statistical significance ($P < 0.05$).

Regulation of biomes, the number of factor, and duration. Both response ratios (RR) of Rh and Ra [i.e., RR(Rh) and RR(Ra)] to global change factors exhibited significant positive linear correlations with the RR(Rs) in single- and two-factor treatments in all the multifactor studies (Fig. 4). The slope between RR(Rh) vs. RR(Rs) was not significantly different from that between RR (Ra) vs. RR(Rs) as well as those between single- and two-factor treatments (Fig. 4). Although most treatments (including single- and multifactor treatments, Fig. 5a) in different biomes (including forest, cropland, grassland, wetland, and desert, Fig. 5b) induced positive effects on Rs, the estimated mean RR(Rs) under the single-factor treatments was lower than that under two-factor treatments (Fig. 5a). The RR(Rs) induced by nitrogen addition and its combination with elevated [CO_2] displayed significant negative correlations with duration, while the RR(Rs) under drought and DW increased with experimental duration (Fig. 6b–c, e–f). The EW-induced RR(Rh) was negatively correlated to the duration, despite of the nonsignificant correlations between RR(Rh) and duration under either elevated [CO_2] or warming (Fig. 6g–i). In addition, MAT, MAP, and ecosystem type did not significantly affect the responses of Rs and its components (Table S2).

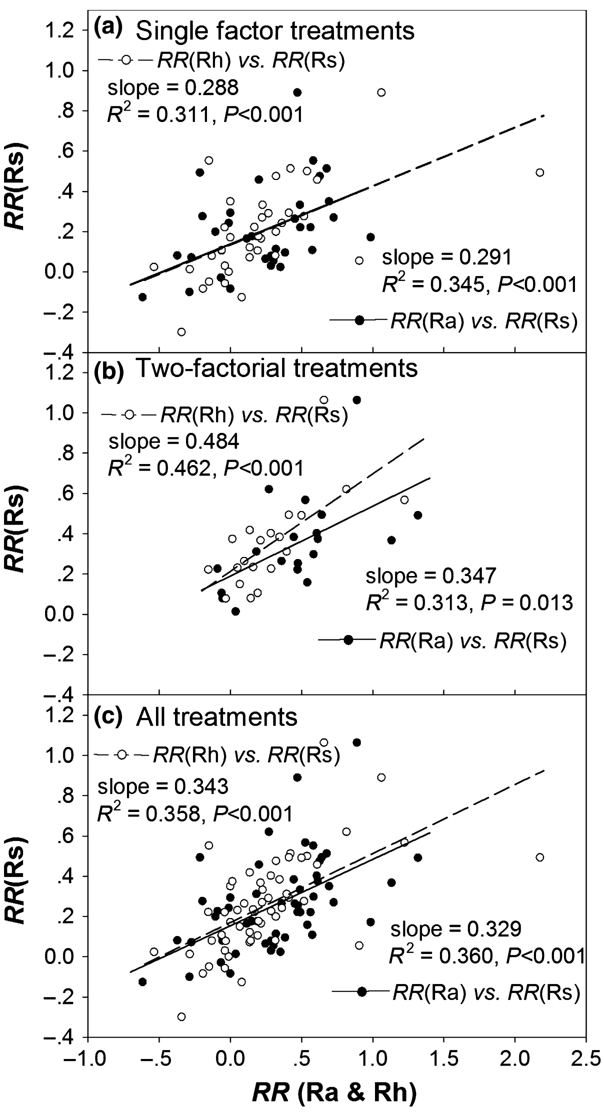

Fig. 4 Correlations of the response ratios (RR) of soil respiration (Rs) with RRs of its two components, autotrophic respiration (Ra) and heterotrophic respiration (Rh) in single factor (a), two-factorial (b) and all treatments (c).

Discussion

Individual effects of single global change factors on Rs and its components

Across all the studies with multiple global change factors, Rs increased significantly in response to elevated [CO_2] (E), nitrogen addition (N), warming (W), and irrigation (I, Fig. 2a). Among these factors, elevated [CO_2] caused the largest stimulation in Rs compared to other factors (Fig. 2a). In general, elevated [CO_2] enhanced plant photosynthesis and growth through increased water-use efficiency (WUE), nitrogen-use efficiency, and efficiency of Rubisco (Davey *et al.*, 1999; Qiao *et al.*, 2010). Meanwhile, elevated [CO_2] may also increase the allocation of newly fixed C to belowground with increased root biomass and root/ shoot ratio (Van Veen *et al.*, 1991; Canadell *et al.*, 1995; Luo *et al.*, 1996, 2004). Hence, elevated [CO_2] might increase C availability in plant-derived substrate inputs into the soil (e.g., root exudates and biomass) for both root metabolism and microbial decomposition (Zak *et al.*, 2000; Adair *et al.*, 2011; Dieleman *et al.*, 2012) and then largely enhanced Rs. In addition, some studies found that the priming effect induced by increased substrates could cause the greater decomposition of native SOM under elevated [CO_2] (Cheng *et al.*, 2012; Groenigen *et al.*, 2014), resulting in the largest stimulation in Rs compared with other single factors.

The responses of Rs to nitrogen addition depended on positive and/or negative effects of nitrogen-induced changes in the soil on Rs. Nitrogen addition generally increased plant biomass and then organic C inputs to the soil by promoting N availability, resulting in the positive effects on Rs (Zhou *et al.*, 2014), while nitrogen-induced decrease in soil pH might depress root and microbial activity and then decreased Rs (Lu *et al.*, 2011; Tian & Niu, 2015). The different contributions of the two effects in diverse biomes resulted in the decreased Rs in forests (Janssens *et al.*, 2010) but increased Rs in grasslands and croplands (Zhou *et al.*,

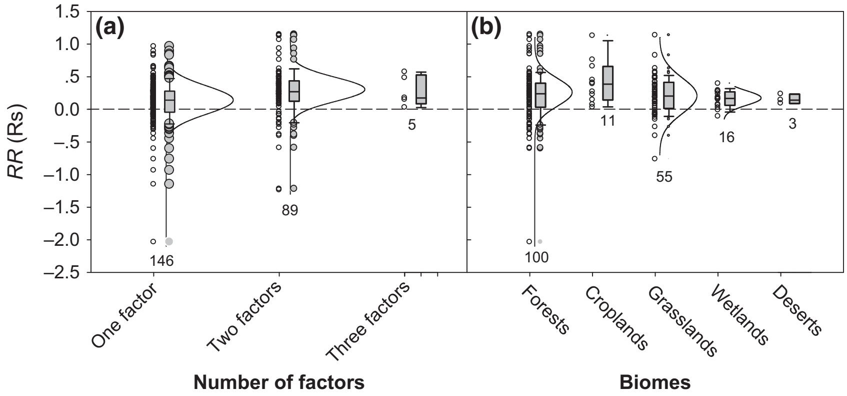

Fig. 5 Effects of the number of factors (a) and biome types (b) on the response ratios of soil respiration [RR(Rs)]. The curves displayed the frequency distribution of the response ratio (RR) of soil respiration (Rs) in studies with one factor and two factors in panel (a), and in biomes of forest, grassland and wetland in panel (b).

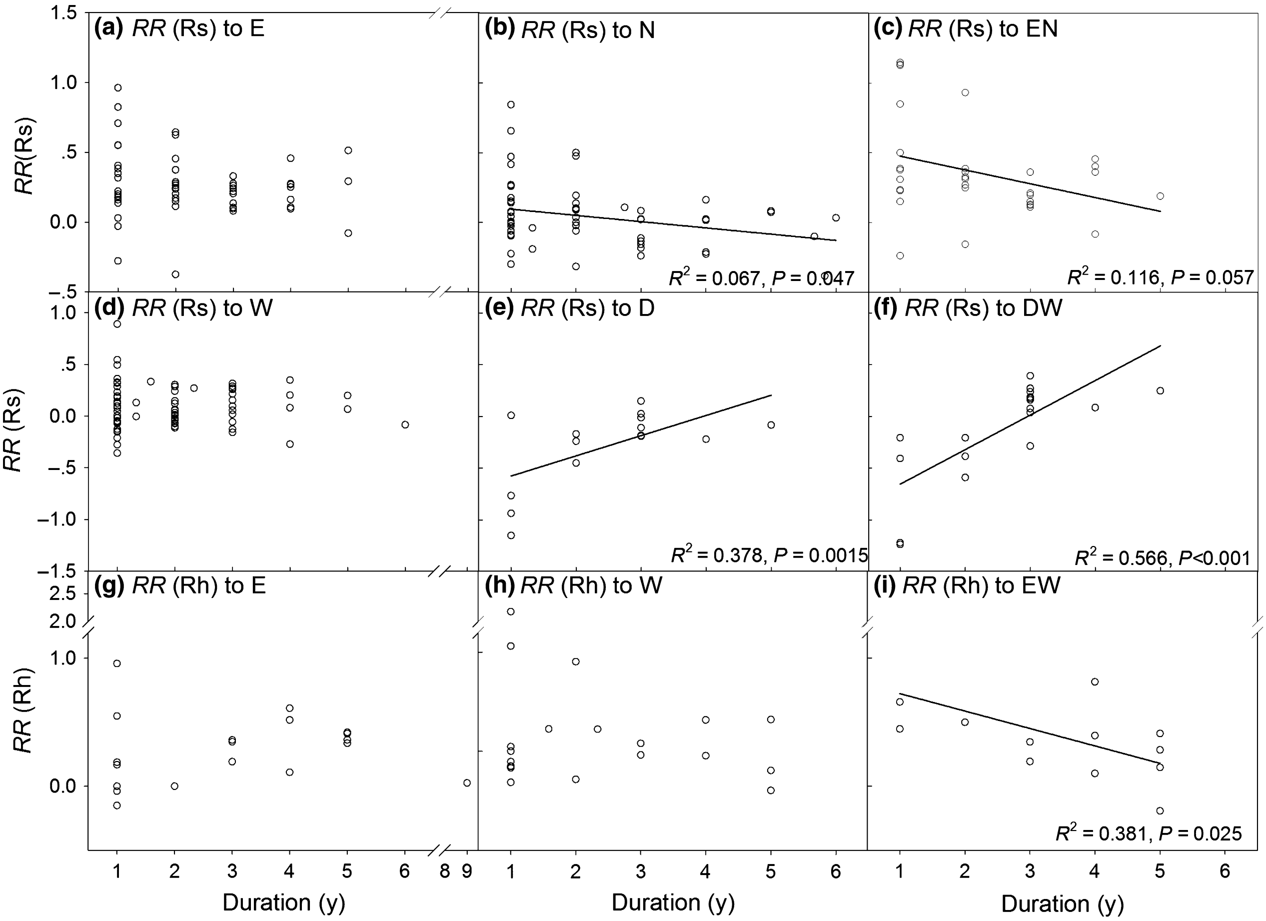

Fig. 6 Effects of duration on the response ratios of soil respiration [RR(Rs)] to elevated [CO_2] (E, a), nitrogen addition (N, b), the combined treatments of E and N (EN, c), warming (W, d), drought (D, e), and the combined treatments of W and D (DW, f), and the effects of duration on the *RR* of heterotrophic respiration (Rh) to E (g), to W (h) and to the combined treatments of E and W (EW, i).

2014), although the general tendency was positive on the responses of Rs to nitrogen addition (Lu *et al.*, 2011; Zhou *et al.*, 2014).

Warming and irrigation-induced stimulation in Rs largely resulted from the positive effects of increased soil temperature and water availability, respectively

(Fig. 2a; Davidson *et al*., 1998; Wan *et al*., 2007). However, previous studies found that the increase in Rs declined over time due to plant and microbial acclimation under the long-term warming or irrigation treatments (Luo *et al*., 2001; Melillo *et al*., 2002; Ryan *et al*., 2015). Our results showed that the significant positive effects of warming or irrigation on Rs did not decline over time, indicating the little impacts of acclimation (Fig. 6d, Table S2). Due to decreases in the mobility of substrates and microbes, ectoenzyme and microbial activity, and C input into belowground, drought (D) could significantly reduce Rs (Farooq *et al*., 2009; Wang *et al*., 2014). The drought-induced decrease in Rs was not significant in the multifactor studies but was strongly supported by the single-factor experiments, probably resulting from the large variation of Rs in the multifactor studies (Fig. 2a).

The responses of Rs to global change factors are the combined responses of Rh and Ra. However, the results for these two components were much more uncertain due to the small sample sizes and the great heterogeneity in the multifactor studies compared to those in the single-factor experiments (Fig. 2b and c). Although the responses of Rh and Ra to global change factor in the multifactor studies were similar to those in the single-factor experiments (Fig. 2b and c), the distribution of the data may significantly affect the response directions of Rh or Ra. For example, the experiments with nitrogen addition were mostly conducted in croplands and grasslands in the multifactor studies, resulting in different effects on Rh in the single- and multifactor studies. The significant stimulation in Ra under drought in only two samples was largely due to a large increase in a wetland ecosystem.

Individual effects of multifactor combinations on Rs and its components

Elevated [CO_2], nitrogen addition, warming, and irrigation induced positive effects on Rs (Fig. 2a, Rustad *et al*., 2001; Lu *et al*., 2013; Zhou *et al*., 2014), and most of their combinations between or among them also positively increased Rs (Fig. 2a), although some combinations had small sample sizes. The negative effects of drought on Rs seemed to be offset by elevated [CO_2], resulting in the positive effects of DE and DEW on Rs (Fig. 2a). This is because elevated [CO_2] would induce an improved WUE to a greater extent under drought compared with those in the control (Lawlor & Mitchell, 1991; Mooney *et al*., 1991; Qiao *et al*., 2010). In addition, drought-induced reduction in stomatal conductance and plant transpiration (Morison & Gifford, 1984) might decrease the water loss and stimulated mycorrhizal infection on roots could increase the water uptake (Mohan *et al*., 2014), which would relieve the effects of water and nutrient limitations on ecosystem processes and then Rs (Van Veen *et al*., 1991; Nadeem *et al*., 2014).

Although the relative contributions of Ra and Rh to total Rs are difficult to determine across all the studies as there is substantial variability between vegetation types and seasons (Hanson *et al*., 2000; Rey *et al*., 2002), Rh and Ra were strongly correlated with annual Rs across a wide range of ecosystems (Bond-Lamberty *et al*., 2004). In this study, we found no significant differences between the relationships of RR(Rs) with RR (Rh) and RR(Ra) in both single- and two-factor experiments, suggesting that contributions of Rh and Ra to Rs were relatively constant across all the studies.

Interactive effects of multiple global change factors on Rs and its components

Interaction between two factors is considered as synergism or antagonism when their combined effect is significantly stronger or weaker than the sum of the two individual effects, while additive interaction indicates that the combined effect is equal to or has no significant difference from the sum (Hay *et al*., 1994; Folt *et al*., 1999; Coors & De Meester, 2008). For the individual studies, the additive interactions exhibited a predominance on Rs and its components (Fig. 3a–c). However, the three types of interactions seemed to all be important when considering the different combinations of global change factors (e.g., two for synergistic, two for antagonistic, and five for additive effects with at least eight independent experiments, Fig. 3d–f). The difference might be caused by the overestimated amount of additive interactions associated with the large variance of some studies (Crain *et al*., 2008). Nevertheless, the statistical analysis showed that the average weights of the interaction (d_I) were 3.88, 3.75, and 3.05 in Rs, Rh, and Ra, respectively, for the significant results, which were similar to those for the nonsignificant ones with 4.80, 3.72, and 4.03, respectively. Therefore, the overestimation of additive interactions might not be the problem in this study. Actually, the nonadditive interactions were caused by relatively high d_I in several individual studies. For example, although the additive interactions accounted for 84.4% of the total individual interactions under elevated [CO_2] and nitrogen addition (Fig. 3a), the interactive type was synergistic when we pooled all the data from EN (Fig. 3d). This was because the d_I of the individual synergistic interactions (1.15–4.55) was much larger than those of the antagonistic and additive ones (1.23–1.44 and −0.77 to 0.95, respectively).

Previous studies suggested that the interactions between or among multiple global change factors might be antagonistic (Leuzinger *et al*., 2011; Wu *et al*., 2011; Dieleman *et al*., 2012), which contradicted our results. The difference might arise from the differences in the analytical methods and the concerned variables. For example, Dieleman *et al.* (2012) compared the relationships between the combined effects and the sum of single effects with the 1 : 1 line to determine the type of interactions between two factors, which was based on all the available data rather than the individual studies. To eliminate any discrepancy caused by methodological difference, we applied our approach to the data from Dieleman *et al.* (2012) as well as the Dieleman *et al.*'s approach to our data. The intercomparison indicated additive interaction, which was similar between Dieleman *et al.* (2012) and our results (Fig. S2). In addition, in Wu *et al.* (2011) and Dieleman *et al.* (2012), the antagonistic interactions were mainly found on the aboveground biomass and net primary productivity, while neither synergistic nor antagonistic ones were found on Rs or ecosystem respiration. Leuzinger *et al.* (2011) pooled all variables together to examine the interaction, which might be different only for Rs. Therefore, the interactions of global change factors may show differential effects on diverse variables.

Specifically, the synergistic interaction on Rs mainly occurred in combination of elevated [CO_2] and nitrogen addition, especially in subtropical and temperate forests (Fig. 3d, e.g., Vose *et al*., 1995; Deng *et al*., 2010), which could be ascribed to the positive main effect of nitrogen addition on elevated [CO_2]-induced increase in Rs (Fig. 3d). Therefore, the combined effects of elevated [CO_2] and nitrogen addition in subtropical and temperate forests may profoundly contribute to stimulation of Rs (Bala *et al*., 2013). The synergistic interactions on Rs were also observed in IE, IN, and IW in some croplands (e.g., winter wheat crops, in Raiesi, 2004) and grasslands (e.g., Garten *et al*., 2009), respectively, although no certain conclusions could be drawn based on the small sample size (Fig. 3d).

For the interactions on Rh, antagonism was more dominant compared with synergism, while the interactions on Ra showed the opposite pattern (Fig. 3b). This result mainly came from the experiments combining elevated [CO_2] and warming. Dieleman *et al.* (2012) has suggested that these two factors might exhibit synergistic interactions on biomass production in water- and nutrient-limited ecosystems, because the CO_2-induced increase in WUE and the warming-induced increase in nutrient mineralization will allow the full effects of another factor. In addition, warming stimulated more consumption of newly fixed C by roots, which increased the proportion of Ra to Rs (Saxe *et al*., 2001). Therefore, the synergistic interactions on production might largely result in the synergistic interactions on Ra (e.g., Carter *et al*., 1999; Wang *et al*., 2012). On the other hand, the interactions between elevated [CO_2] and warming on Rh were antagonistic, which was mainly found in forest plantation with evergreen trees (e.g., *Pseudotsuga menziesii* seedlings and *Quercus glauca*, in Lin *et al*., 2001 and Wang *et al*., 2012; respectively). This might be because the elevated [CO_2] and warming both increased the leaf area and thus the evapotranspiration. Therefore, the soil water under the combined treatment might deplete more rapidly than that under the single-factor treatment (Dieleman *et al*., 2012), likely causing an antagonistic interaction on Rh. As a result, the differentially interactive mechanisms on Rh and Ra induced an additive interaction on Rs (Fig. 3d).

Temporal variation in effects of global change factors on Rs

The study duration might be crucial in evaluating the responses of Rs and its components to global change factors, because biotic responses to environmental change are likely to vary over time (Hopkins & Hüner, 1995; Isbell *et al*., 2013). A previous study indicated that the responses of Rs to nitrogen addition decreased with experimental duration (Zhou *et al*., 2014), which was consistent with our results (Fig. 6b). Under the long-term experiments, nitrogen-induced increase in Rs may be depressed gradually as a result of changes in the composition of microbial community and soil properties (e.g., pH, exchangeable base cation, and aluminum ion, Högberg *et al*., 2001; Treseder, 2008; Phoenix *et al*., 2012). The combined effects of nitrogen addition with elevated [CO_2] on Rs also followed the negative correlation with duration, with the higher mean responses of Rs to EN compared with that under only nitrogen addition due to their synergistic interaction on Rs (Figs. 3d, 6c). Interestingly, the combined effect of DW on Rs was positively correlated with experimental duration (Fig. 6f), which was also seen under drought (Fig. 6e). Under drought condition, the Rs initially displayed a great negative response (Fig. 6e). However, with an increase in plant WUE and a shift in vegetation composition toward a drought-tolerant plant community under the long-term drought stress (Hsiao, 1993; Sanaullah *et al*., 2011), the negative responses of Rs to drought became less significant (close to zero, Fig. 6e). Due to the additive interaction between drought and warming on Rs (Fig. 3d), the combined effect of DW displayed a similar correlation with duration as the individual effect of drought (Fig. 6f).

Nevertheless, a significant negative correlation was found between RR(Rh) to EW and experimental duration (Fig. 6i), which may be attributed to the antagonistic interaction between elevated [CO_2] and warming on

Rh (Fig. 3e). The initial positive responses of Rh to elevated [CO_2] may mainly result from an increase in root-derived carbon (Zak *et al.*, 1993). The increased substrate availability may significantly stimulate soil microbial growth, probably causing the priming effect in the short term (Allard *et al.*, 2006). Over time, the antagonistic interaction between elevated [CO_2] and warming on Rh increased due to changing the soil water condition (Dieleman *et al.*, 2012). In addition, the decline in litter quality with a greater C/N and lignin/N (Cotrufo *et al.*, 1994; Luo *et al.*, 2004, 2006) would also inhibit the positive effect of elevated [CO_2] and warming on Rh.

Implications for land surface models and future experiments

Understanding the main and interactive effects of multiple stressors on Rs and its components and revealing their key mechanisms will help to improve our prediction of ecosystem responses to future environmental changes. Our results from the meta-analysis of 150 multifactor studies may provide some insights to what extent Rs and its components respond to single and combined global change factors. Thus, our study will offer suggestions for developing and improving of land surface models as well as the design of manipulative experiments in the future. First, our results show that, across all the multifactor studies, although the additive interaction on Rs and its two components (Ra and Rh) was predominant compared with synergistic and antagonistic interactions, different combinations of global change factors might have different interactive effects (Figs. 3, S2), indicating the needs to treat the responses of Rs and its components differently to multiple global change factors in land surface modeling (e.g., in the Lund-Potsdam-Jena model, Smith *et al.*, 2005).

Second, the responses of Rs to global change factors increased slightly with the number from one to three factors (Fig. 5a). On the contrary, Leuzinger *et al.* (2011) suggested that the pooled responses of the nine response variables (including Rs) generally declined with the increasing number of factors. For both studies, indeed, there were few manipulative experiments with at least three global change factors compared with those with single- and two-factor ones, which made it difficult to detect significant differences. Therefore, more well-designed experiments with multiple global change factors ($\geq$3) are necessary to better capture the tendency of soil C processes under global change. Third, experimental duration may be crucial in evaluating the responses of C processes to environmental changes, as the effects of global change drivers on ecosystem processes will largely change over time (Gifford, 1995; Zhou *et al.*, 2014). Our results showed the significant relationships between duration and the responses of Rs to EN and DW (Fig. 6). Temporal changes in the responses of Rs to global change factors should thus be considered in modeling predictions in the future. More research under field manipulative experiments is therefore required to develop our understanding about the feedbacks of terrestrial C cycle to global change.

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Supporting Information

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

Data S1. Calculation of individual effects.
Data S2. A list of 65 papers from which the data were extracted for this meta-analysis.
Figure S1. Conceptual approach to interpreting interactive effects of two factors in each factorial studies.
Figure S2. Intercomparison of the results between Dieleman *et al*. (2012) and our analysis.
Table S1. Response ratio (RR), Hedges'd (*d*) and weights (*w*) of three variables extracted from studies used in the meat-analysis.
Table S2. The ANOVA results of Rs and its components vs. Duration (Dur), Ecosystem type (Eco), mean annual temperature (MAT) and mean annual precipitation (MAP).