



META-ANALYSIS

The effects of nitrogen enrichment on soil CO₂ fluxes depending on temperature and soil properties

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ABSTRACT

Aim The continuous increase in anthropogenic nitrogen (N) may have a substantial impact on soil carbon (C) fluxes; thus, understanding the dynamics of soil C fluxes under N enrichment is important. Our main goal was to resolve the conflicting results presented to date and to expand our knowledge about the response of soil respiration (Rs) to N enrichment, which may be affected by the physico-chemical properties of soil and environmental factors.

Methods We assembled a large dataset for meta-analysis, including 563 datasets on annual and seasonal Rs with N enrichment from 154 published papers at 163 sites, covering seven types of biomes world-wide.

Results (1) N enrichment was not significantly related to global Rs but we found a negative relationship in forests and a positive one in other biomes. (2) Rs showed a negative correlation with the N levels in forests and croplands and a positive correlation with the N levels in deserts; heterotrophic respiration exhibited negative correlations with N levels globally, and its response was correlated with the incubation environment. (3) The response of Rs to N enrichment was also correlated with mean annual temperature and soil properties, with 15 °C being the threshold for switching between increasing and decreasing Rs. (4) The estimated total C flux for global terrestrial lands was 97.01 Pg C year⁻¹, and 1 kg of N enrichment at ha⁻¹ year⁻¹ induced an average efflux of 1.33 kg C ha⁻¹ year⁻¹.

Main conclusions The response of Rs to future N enrichment should be predicted separately for each biome. The association between changes in Rs and temperature and soil properties under N enrichment makes soil C flux a more complex challenge in the context of future increases in temperature and N deposition.

Keywords

C flux, heterotrophic respiration, nitrogen, Q10, soil respiration, temperature.

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INTRODUCTION

The continuous increase in the carbon dioxide (CO₂) concentration in the atmosphere is predicted to lead to significant changes in global temperature (Betts, 2000). Soil carbon (C) emission, also termed soil respiration (Rs), is the flux of microbial and plant-respired CO₂ from the soil surface to the atmosphere; it is the second-largest terrestrial carbon flux (Schlesinger, 1977; Raich & Potter, 1995) and plays a vital role in regulating Earth's atmospheric CO₂ concentration and climate

dynamics (Luo & Zhou, 2006). The annual input of anthropogenic reactive nitrogen (N), mainly through intensive application of N fertilizers and fossil fuel combustion, has increased more than 10-fold in the last 150 years, and atmospheric deposition rates of N are predicted to increase another two- or threefold in the coming years (Galloway & Cowling, 2002). The widespread N enrichment in the atmosphere and soil has considerably altered regional and global environments and affected the terrestrial C cycle (Luo & Zhou, 2006), which is projected to affect future climate change (Luo, 2007; Luo *et al.*,

2009). Thus, knowledge of the dynamics of Rs under N enrichment is important for understanding the global C flux (Bond-Lamberty & Thomson, 2010).

Numerous studies have investigated the responses of Rs to experimental N enrichment. However, the effects of N enrichment on Rs remain controversial, not only in terms of magnitude but also regarding direction. The disagreement among studies may be due to the heterogeneity of biome types, N application rates, soil conditions, environmental conditions and even experimental methods (Schlesinger, 1977; Craine *et al.*, 2001; Xu & Wan, 2008). Rs includes microbial/heterotrophic respiration (Rh) during the decomposition of organic matter and litter and root/autotrophic respiration (Ra) in live roots and their symbionts (Luo & Zhou, 2006; Schindlbacher *et al.*, 2009). These two components respond differently to N enrichment, and differences in the methods used to distinguish Rh and Ra, as well as the lack of studies, increase the difficulty of assessing Ra and Rh in response to N enrichment (Zhou *et al.*, 2014). Many previous studies have estimated Rh in the laboratory under controlled conditions; however, the responses range from a reduction of 57% to an increase of 63%, as reported by Janssens *et al.* (2010). Such discrepancies may be caused by different incubation conditions, including soil weight, incubation temperature, moisture and time. Nevertheless, how these factors influence Rh remains unclear. Due to complex interactions and the high spatial variability of various competing processes, the controversy regarding Rs and the uncertainty in Rh are unlikely to be effectively resolved by studies performed at individual sites. Therefore, to reveal a central tendency and to identify large-scale patterns of N-induced changes in soil C emission, it is necessary to integrate results across studies.

Four meta-analyses related to the effects of N enrichment on Rs have been conducted (Janssens *et al.*, 2010; Liu & Greaver, 2010; Lu *et al.*, 2011; Zhou *et al.*, 2014). However, the results of these meta-analyses varied widely because of differences in the compiled data sets. Two of them mainly emphasized the central tendency of the soil C pool and associated C processes (Liu & Greaver, 2010; Lu *et al.*, 2011), whereas Janssens *et al.* (2010) only examined the responses of Rs to N enrichment in temperate forests. Although Zhou *et al.* (2014) analysed 273 Rs results produced by N enrichment on a global scale, with more detailed information than previous analyses, they also mentioned the presence of uncertainties due to the inherent limitations of the methodology and to some extent even literature bias.

N enrichment rates vary among biomes, and it remains unclear whether the effects of N on Rs are related to the N enrichment rate. Indeed, many confounding factors among study sites, such as climate conditions, soil physical conditions (e.g. pH and soil bulk density) and even plant species composition, can cause different responses of Rs to N enrichment (Bobbink *et al.*, 2010; Zhou *et al.*, 2014). Moreover, as reported by Bond-Lamberty & Thomson (2010) and Rustad *et al.* (2001), global Rs has exhibited temperature-associated increases, and understanding how the temperature sensitivity of Rs (the Q10 index – the factor by which Rs increases with a 10 °C increase in temperature) responds to N enrichment could help us better

understand the C fluxes in response to N enrichment and global warming.

To clarify these controversial and uncertain issues, we conducted a meta-analysis of studies based on Rs data from studies world-wide using N enrichment. Our main goal was to resolve the conflicting results presented to date and to expand our knowledge regarding the response of Rs to N enrichment, which may be affected by the physico-chemical properties of soil and environmental factors. We address the following: (1) how Rs and Rh respond to N enrichment in different biomes; (2) which factors are correlated to Rs and Rh with N enrichment; and (3) how the temperature sensitivity of Rs changes in response to N enrichment. Our results will help further our understanding of the C flux under future climate change.

MATERIALS AND METHODS

Data preparation

Peer-reviewed journal articles were identified using Web of Science (1900–2015) with the following search term combinations: (nitrogen/N/fertilizer) AND (soil respiration/CO₂/carbon emission). To avoid bias in the selection of publications, the studies were selected based on the following considerations: (1) experiments were conducted using at least one pair of data sets (control and treatment), including N application rate and soil C flux (Rs); (2) only field-based experiments conducted in terrestrial ecosystems were included, and pot studies were excluded; (3) Rs was only included for *in situ* measurement data, and measurements of soil under laboratory conditions, including microbial heterotrophic respiration (Rh) and microbial substrate-induced respiration studies that added C or other sources, were excluded; (4) Rs values measured annually or as the mean of growing seasons (or wet seasons) were denoted differently; and (5) the means, standard deviations/errors and samples sizes of variables in the control and treatment groups should be able to be extracted directly from the context, tables or digitized graphs.

In addition, environmental variables, such as the latitude, mean annual temperature and mean annual precipitation, were recorded directly from papers or cited papers. Basic soil physico-chemical properties, such as the pH, soil bulk density, soil organic carbon (SOC) content and total N content, were also collected. The reported root biomass, microbial biomass content (MBC), Q10, soil temperature and moisture in the control and treatment groups were also collected. For Rh, the soil incubation conditions were collected, including the incubation soil weight, time, temperature, moisture, SOC and MBC. Studies that involved more than one rate of N enrichment or more than one vegetation type were treated as multiple data points.

In total, 154 published papers, at 163 sites (Fig. 1), concerning N fertilization and/or simulated deposition studies that satisfied our selection criteria for the meta-analysis were selected from more than 3000 published papers. (A list of the literature sources is given in Appendix 1 and data are shown in Tables S1 & S2 in Supporting Information.) All original data were extracted from

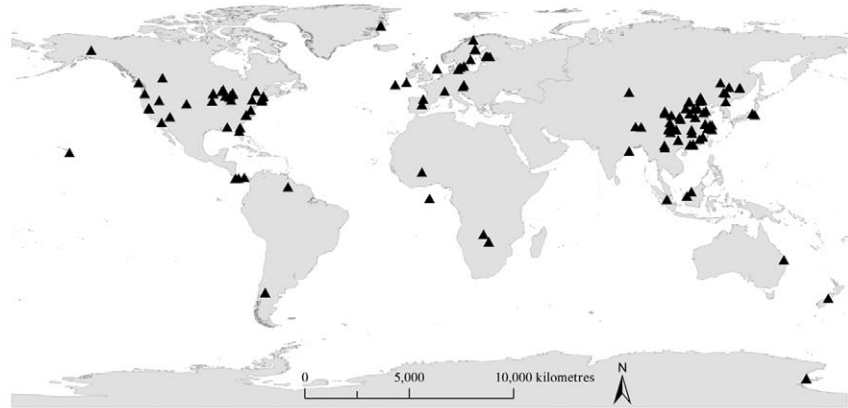


Figure 1 Global distribution of N enrichment experiments selected for this meta-analysis.

the text, tables, figures and appendices of these publications. When data were presented graphically, numerical data were obtained using the GetData Graph Digitizer v. 2.20 (<http://www.getdata-graph-digitizer.com/>). To test differences in the responses of Rs to N enrichment, seven types of biomes were included: tropical forests, temperate forests, boreal forests, croplands, grasslands, deserts and wetlands. The mean annual or mean growing season C fluxes of forests were also differentiated in this analysis.

Analysis

We followed the methods used by Hedges *et al.* (1999) to evaluate the responses of Rs and Rh to N enrichment. A response ratio (RR, the natural log of the ratio of the mean value of a variable of interest in N treatment plots to that in the control) was used to represent the magnitude of the effects of simulated N deposition as follows:

$$RR = \ln(X_e/X_c) = \ln X_e - \ln X_c, \quad (1)$$

where X_e and X_c are the response values of each individual observation in the treatment and control, respectively. The corresponding sampling variance for each $\ln RR$ was calculated according to equation 2 as follows:

$$v_i = \ln\left[\frac{1}{n_e} \times (S_e/X_e)^2 + \frac{1}{n_c} \times (S_c/X_c)^2\right], \quad (2)$$

where n_e , n_c , S_e , S_c , X_e and X_c are the sample sizes, standard deviations and mean response values in the experimental and control groups, respectively. The meta-analyses were performed using the R software package (v.3.1.1) (R Development Core Team, 2014). 'regtest()' was used to test the bias of our data, with $P > 0.05$ indicating no bias in data collection (Fig. S1). When we compared the distributions and means of our dataset with a global soil respiration dataset (Bond-Lamberty & Thomson, 2010) (Fig. S2), we found that our dataset showed relatively little bias compared with the global dataset. The RRs for individual and combined treatments were determined by specifying studies as a random factor using the 'rma model' in R with the package 'metafor' (Viechtbauer, 2010).

The effects of N enrichment on soil C emission were considered significant if the 95% confidence intervals (CIs) of RR did not overlap with zero. To address whether the responses of C emission to N enrichment differ between different types of biomes or climate conditions, we tested whether the interactions between multiple treatments were significant by using the rma.uni models in the 'metafor' package, with treatments as the categorical variables. Regression analysis was conducted to detect relationships between biotic and/or abiotic factors and the Rs and N enrichment rate. Because the standard error/deviation of Q10 is not reported in many studies, the quoted RR used is the mean value of each RR in the study.

Based on the Intergovernmental Panel on Climate Change guidelines for national greenhouse gas inventories (Mosier *et al.*, 1998; Liu & Greaver, 2009), the N enrichment-induced emission/uptake factor (F) was estimated for those response variables that were significantly influenced by N enrichment:

$$F = (G_N - G_C)/N, \quad (3)$$

where G_N is the annual flux of C from N fertilized treatment ($\text{kg C ha}^{-1} \text{ year}^{-1}$), G_C is the annual flux of C from the control ($\text{kg C ha}^{-1} \text{ year}^{-1}$) and N is the annual N input ($\text{kg N ha}^{-1} \text{ year}^{-1}$).

RESULTS

Responses of Rs to N enrichment

The RRs of Rs to N enrichment were not significant in all terrestrial systems ($RR = 0.002$, $P > 0.05$) but did differ among different biome types (Fig. 2a). Overall, forests exhibited a significantly negative response in our meta-analysis. When separated into different types of forest depending on the temperature zone, boreal forests ($RR = -0.19$, $P < 0.001$) and temperate forests ($RR = -0.07$, $P < 0.001$) exhibited significantly negative responses to N enrichment; in contrast, the RR of tropical forests ($RR = -0.04$, $P > 0.05$) was not significant. Interestingly, other ecosystems, such as croplands, grasslands, deserts and wetlands, exhibited significantly positive responses to N enrichment, with RRs of 0.14, 0.08, 0.12 and 0.43, respectively. The response of Rh to N enrichment was significantly negative in all

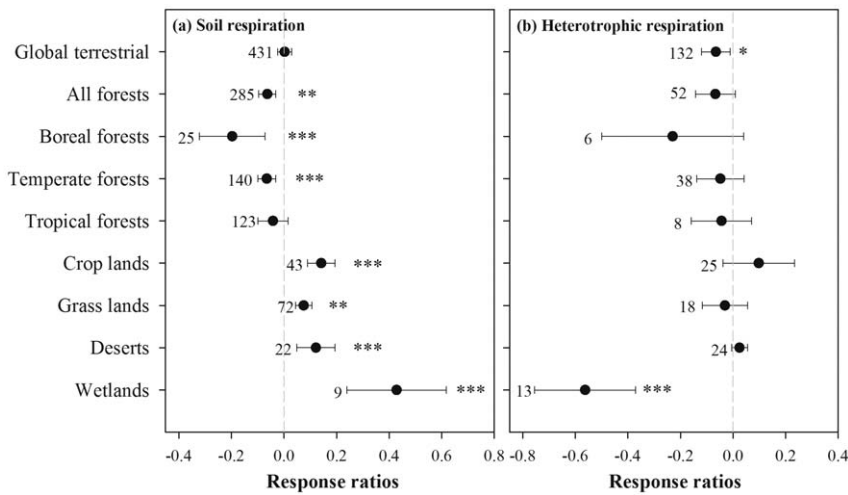


Figure 2 Response ratios of soil respiration (a) and heterotrophic respiration (b) in all biomes. The numbers by the symbols specify the numbers of data points. The proportion of variation is shown by the 95% confidence intervals (CIs); if there was no overlap with zero, the N-induced response was considered significant. Symbols (* $P < 0.05$, ** $P < 0.01$; *** $P < 0.001$) after the number indicate statistical significance.

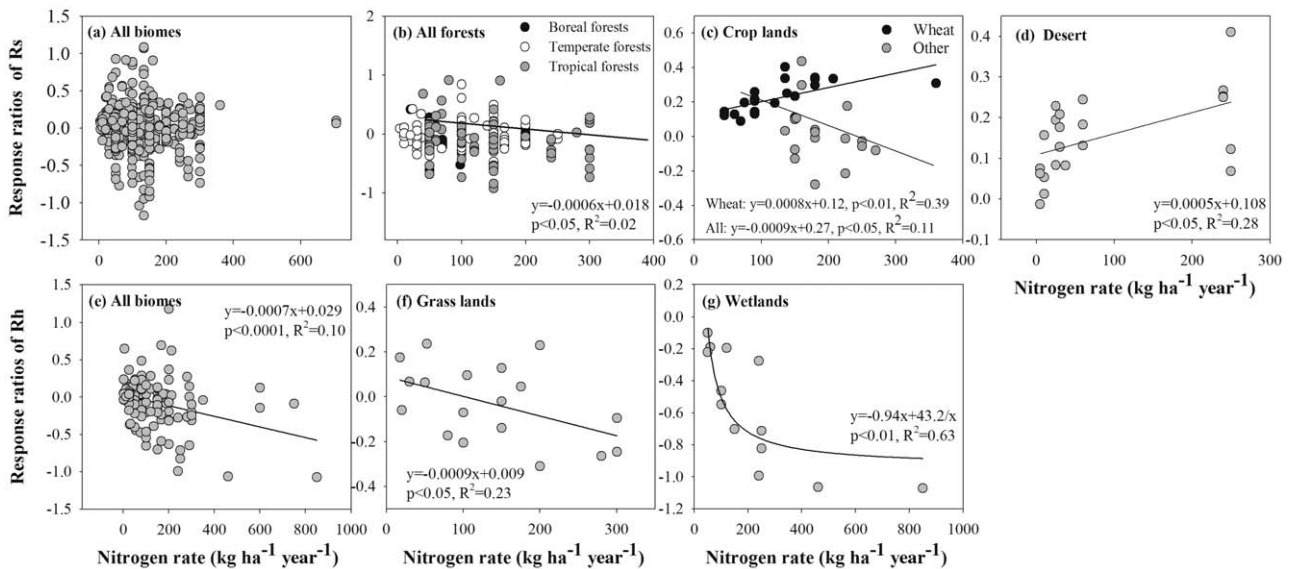


Figure 3 The relationships between the N enrichment rates and response ratios of soil respiration (Rs; a–d) and heterotrophic respiration (Rh; e–g).

terrestrial biomes ($RR = -0.07$, $P < 0.05$); however, the RR value was not significant when calculated separately for each biome, except for wetlands (Fig. 2b).

Relationships between RRs of Rs and N enrichment rates

Because the amount of N enrichment differed among biomes, the relationships between the RRs and N enrichment rates were analysed for each type of biome (Fig. 3). Combining all biomes, the response of Rs showed no significant relationship with the N enrichment rate (Fig. 3a), and different types of biomes exhibited different relationships (Fig. 3b–d). In forests, the RRs of Rs showed a significant negative correlation with the N enrichment rate. In croplands, the RRs exhibited a significant negative cor-

relation with the N enrichment rate. However, the RRs of wheat lands exhibited the opposite trend, showing a significant positive relationship with the N enrichment rate. In deserts, the RRs also exhibited a significantly positive relationship with the N enrichment rate. In contrast, no significant relationships between RRs and N enrichment rates were detected for the other biomes (Fig. S3a, b).

When combining the data for all biomes, the response of Rh to N enrichment showed a significantly negative relationship with N enrichment rate. Separately, the RRs of grassland exhibited a significantly negative linear relationship with the N enrichment rate, and that of wetlands exhibited a negative exponential relationship with the N enrichment rate. No significant relationship between the N enrichment rate and the RR of Rh was detected in the other biomes (Fig. S3).

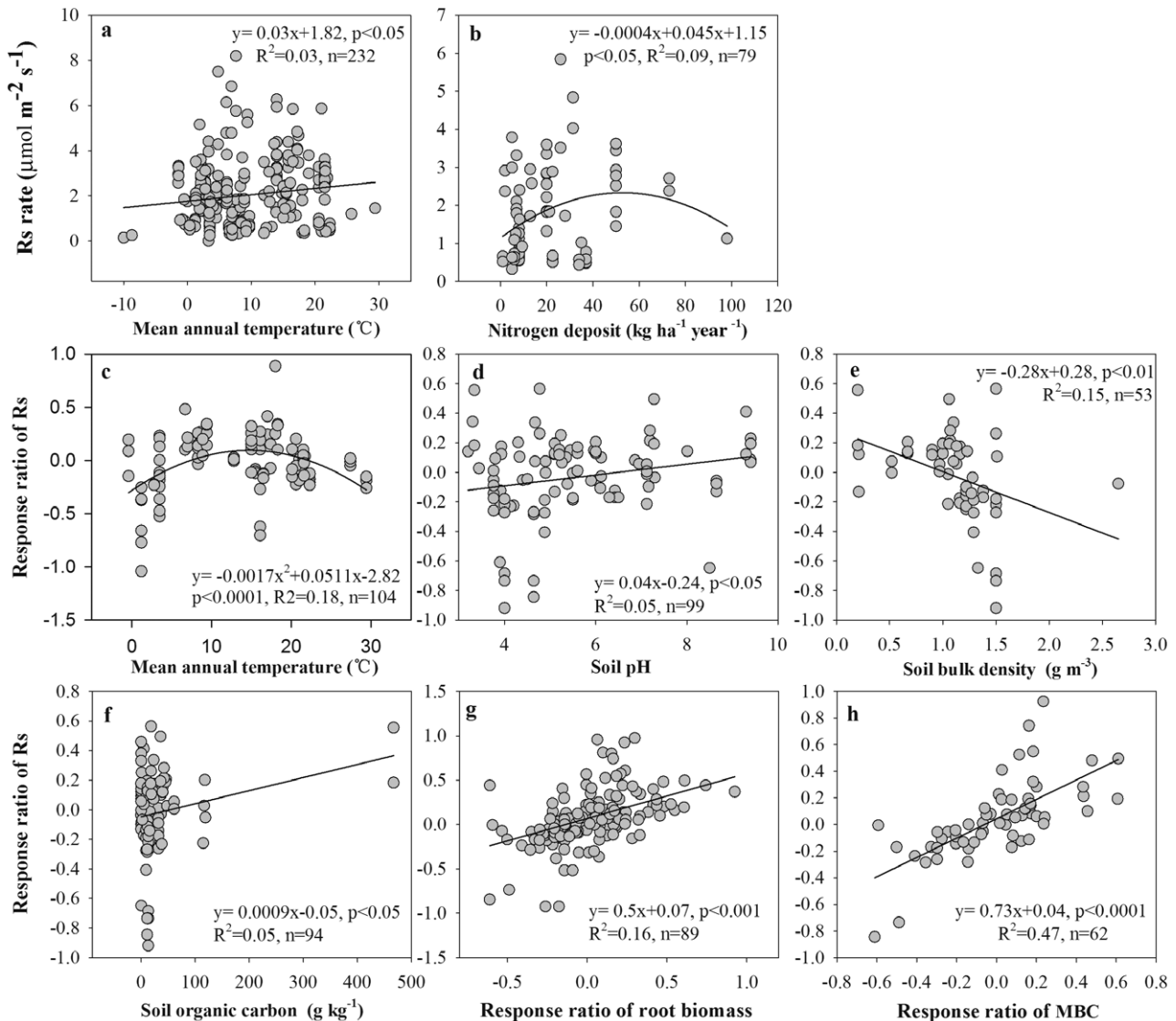


Figure 4 The relationships of soil respiration (R_s) and the response ratio of R_s with climate and soil properties. MBC, microbial biomass carbon.

Relationships between R_s and its RRs with abiotic factors

Under natural conditions R_s exhibited strong relationships with climatic factors (Fig. 4), including a positive linear relationship with mean annual temperature and a parabolic relationship with the amount of local N enrichment. These results indicated that R_s increased as the amount of N enrichment increased and then decreased as the N enrichment rate exceeded $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ (vertex of the parabola). However, no significant relationship was observed between R_s and the other soil factors (Fig. S4).

The RRs of the annual mean R_s exhibited a significant parabolic relationship with mean annual temperature. The RR of R_s increased as the mean annual temperature increased when it was less than 15°C (the vertex of the parabola); when it was more

than 15°C , the RR decreased as the mean annual temperature increased. The RR of R_s showed no significant relationship with elevation or mean annual precipitation (Fig. S5) but did show positive relationships with soil pH and SOC content and a significantly negative relationship with soil bulk density. The RR of R_s exhibited significantly positive relationships with the RRs of MBC and root biomass.

The dependences of R_h and the RRs of R_h on climate factors and incubation conditions are listed in Table 1. The magnitude of R_h was significantly negatively correlated with the incubation soil weight but significantly positively correlated with the incubation temperature, MBC and SOC. The response of R_h to N enrichment showed significant positive relationships with the incubation soil weight, temperature and soil MBC and negative relationships with the incubation days and SOC content.

Table 1 Relationships of heterotrophic respiration (Rh) and the response ratio (RR) of Rh with climate and incubation factors.

| | Rh | <i>n</i> | RR of Rh | <i>n</i> |
|---------------------------------------|---------------|----------|----------------|----------|
| Mean annual temperature (°C) | -0.18 | 27 | 0.41** | 75 |
| Mean annual precipitation (mm) | -0.02 | 47 | -0.05 | 79 |
| Soil weight (g) | -0.39* | 40 | 0.25* | 87 |
| Temperature (°C) | 0.56** | 33 | 0.32* | 56 |
| Incubation days | -0.19 | 57 | -0.34** | 96 |
| Soil moisture (%) | -0.43 | 18 | -0.25 | 29 |
| MBC (CK) (mg kg ⁻¹) | 0.55** | 23 | -0.38* | 34 |
| MBC (T) (mg kg ⁻¹) | -0.22 | 19 | 0.67** | 27 |
| pH | -0.29 | 42 | 0.15 | 77 |
| SOC (g kg ⁻¹) | 0.31* | 47 | -0.39** | 94 |
| Total N content (g kg ⁻¹) | 0.29 | 25 | -0.25 | 54 |
| Soil C:N | 0.11 | 17 | 0.26 | 33 |

The values are the Pearson correlation coefficient: * (*P* < 0.05) and ** (*P* < 0.001) indicate significant relationships.

MBC (CK), microbial biomass carbon in no nitrogen enrichment treatment; MBC (T), microbial biomass carbon in nitrogen treatment; SOC, soil organic carbon concentration; Soil C:N, mass ratio of soil carbon to nitrogen.

Because Rs and the RRs of Rs showed significant relationships with mean annual temperature, we determined Q10 and its response to N enrichment (Fig. 5). Our results revealed that the average Q10 value for all biomes was 2.37. Q10 was 2.56, 2.00, 2.09 and 1.78 for forest, croplands, grasslands and wetlands, respectively (Fig. 5a). The mean RR of Q10 to N enrichment was negative in all biomes (RR = -0.07) (Fig. 5b), and it exhibited significant negative linear relationships with mean annual temperature and mean annual precipitation and a parabolic relationship with soil temperature and moisture, in which the vertices of the parabola were 17.1 °C and 2.24%, respectively. No significant relationships were observed between Q10 and the RR of Q10 and other factors (Fig. S6).

Average C flux on a global scale and net changes of C flux caused by N enrichment

Based on our data, the estimated average Rs rate was 9.05 Mg C ha⁻¹ year⁻¹ in terrestrial biomes; tropical forest had the highest average C emission (11.93 Mg C ha⁻¹ year⁻¹) and desert had the lowest (1.38 Mg C ha⁻¹ year⁻¹) (Table 2). N enrichment induced an average of 1.33 kg C ha⁻¹ year⁻¹ when added at 1 kg N ha⁻¹

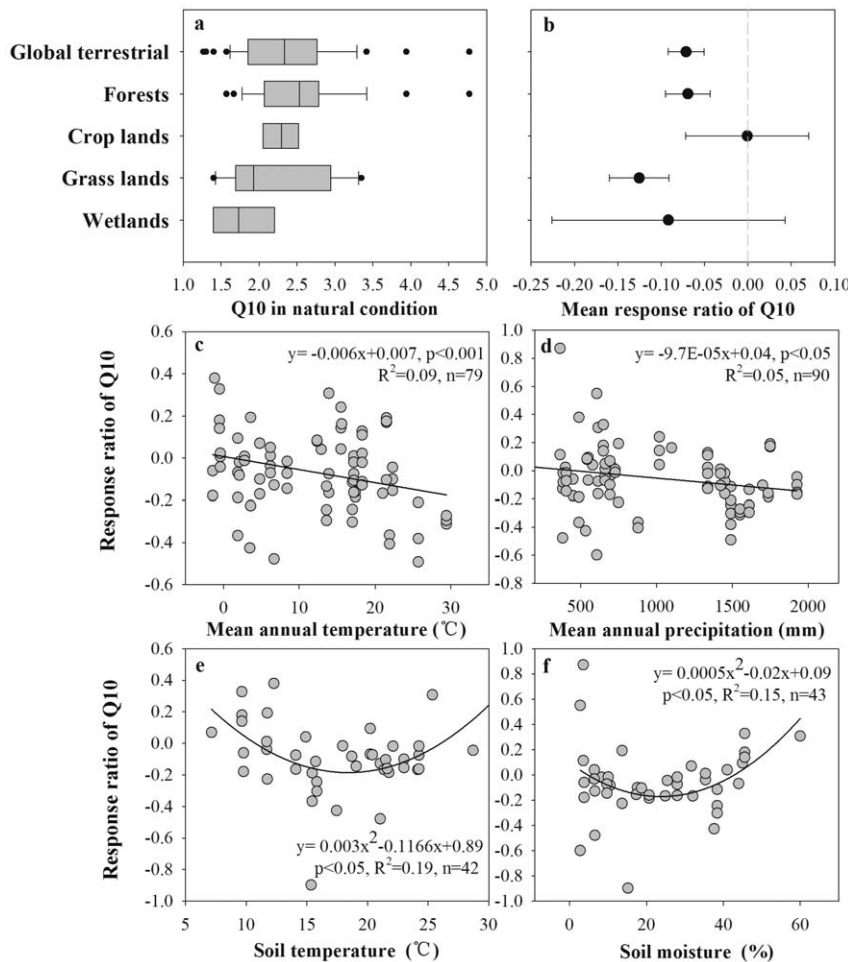


Figure 5 The Q10 index (a) and the mean response ratio of Q10 (b) under natural conditions and the relationships of the response ratio of Q10 with the mean annual temperature (c), mean annual precipitation (d), soil temperature (e), and soil moisture (f).

Table 2 Estimates of carbon flux in global and net changes of carbon flux caused by nitrogen enrichment.

| Biomes | Area (10 ⁸ ha) | Average soil carbon efflux (Mg C ha ⁻¹ year ⁻¹) | | Total efflux Pg C year ⁻¹ | N-induced C efflux (kg C ha ⁻¹ year ⁻¹ per 1 kg N ha ⁻¹ year ⁻¹) | | Total efflux Pg C year ⁻¹ |
|--------------------|------------------------------|---|---------|---|---|---------|---|
| | | Means | SE | | Means | SE | |
| Boreal forests | | 6.70 | 1.25 ab | | -8.30 | 4.77 c | |
| Temperate forests | | 9.26 | 0.65 a | | -5.44 | 3.32 bc | |
| Tropical forests | | 11.93 | 1.60 a | | -5.90 | 2.64 bc | |
| All forests | 41.6 | 9.93 | 0.56 a | 41.31 | -5.88 | 2.01 bc | -0.024 |
| Croplands | 13.5 | 5.80 | 1.26 ab | 7.83 | 12.30 | 3.61 b | 0.017 |
| Grasslands | 42.6 | 8.73 | 0.94 a | 37.17 | 11.53 | 3.12 b | 0.049 |
| Wetlands | 12.8 | 5.35 | 0.51 ab | 6.84 | 84.99 | 17.17 a | 0.109 |
| Deserts | 27.9 | 1.38 | 0.23 b | 3.85 | 6.78 | 1.69 bc | 0.019 |
| Global terrestrial | | 9.05 | 0.53 | 97.01 | 1.33 | 1.67 | 0.169 |

The values are the means of the collected data. Different letters within the same column indicate significant differences ($P < 0.05$) among the different biomes.

year⁻¹ in the entire terrestrial ecosystem, with a decrease in forests of 5.88 kg C ha⁻¹ year⁻¹ and a marked increase in wetlands of 84.9 kg C ha⁻¹ year⁻¹. When integrated with data on the area of each biome, the estimated global terrestrial C efflux was 97.01 Pg C year⁻¹, with forests showing the highest C efflux. For all terrestrial biomes, enrichment by 1 kg N ha⁻¹ year⁻¹ induced 0.169 Pg C year⁻¹ efflux.

DISCUSSION

Rs responds differently to N enrichment across biomes

The effects of N enrichment on Rs were very different in different biomes, with both positive (Xu & Wan, 2008; Shao *et al.*, 2014; Zhang *et al.*, 2014) and negative or unchanged effects being reported (Deng *et al.*, 2010; Sun *et al.*, 2014). In our study, no significant effects on C fluxes due to N enrichment were observed across all the biomes examined, a result that differed from the previous two meta-analyses conducted with all-biome data (Lu *et al.*, 2011; Zhou *et al.*, 2014), which reported a significantly positive response of Rs to N enrichment. This difference may, to some extent, be due to bias in their data. For example, some Rh data, which were measured in indoor incubation studies, were confounded into the Rs dataset in the study of Zhou *et al.* (2014), and pot studies were also included.

The lack of a significant response of Rs to N enrichment was caused by heterogeneity, one type of which was biome heterogeneity. The RRs of Rs in different biomes differed not only in magnitude but also in direction. In forests, as well as the boreal forest lands, a significantly negative response to N enrichment was observed, consistent with the previous analysis by Zhou *et al.* (2014). Temperate forest also exhibited a negative response in our study, consistent with Janssens *et al.* (2010) but different from Zhou *et al.* (2014); the reduction of Rs in temperate forests may be due to N impeding the decomposition of organic matter because N was not a limiting factor in temperate forest soils

(Janssens *et al.*, 2010). No significant effect of N enrichment on Rs was observed in tropical forests. This result also differed from that of Zhou *et al.* (2014), perhaps because we collected 92 more datasets than their work (31 in their study), which should more accurately reflect the response of Rs to N enrichment in tropical forests. Interestingly, croplands, grasslands, deserts and wetlands all exhibited significant positive responses to N enrichment, consistent with Zhou *et al.* (2014), who reported that the addition of N significantly increased Ra in croplands and grasslands but had no effect in forests. Forests are less influenced by anthropogenic activity, being stable ecosystems with a balanced soil N cycle; thus, the growth of forests is less affected by the addition of exogenous N (Aber *et al.*, 1998). N enrichment can inhibit the activity of soil microbes and impede soil C decomposition, which would lead to a reduction in Rs. However, other ecosystems, especially croplands and grasslands, are usually affected by anthropogenic activity (e.g. tillage, grazing). We calculated the RR of Rs to N enrichment separately in natural ecosystem and anthropogenic ecosystems: the anthropogenic ecosystems showed positive responses to N enrichment, but the RRs decreased significantly with increasing N enrichment (Fig. S7). In anthropogenic ecosystems, plant growth largely relies on the addition of N because of the absorption of N by plants usually removed through harvest or grazing; thus, N enrichment promotes plant growth and increases Rs (Zhou *et al.*, 2014). However, the RRs decreased with high levels of N enrichment; thus, further studies must address the threshold N rate leading to the reduction in Rs in these biomes. Wetlands showed a positive response of Rs to N enrichment, which is consistent with the results of Wang *et al.* (2014b) and Zhu *et al.* (2013), who reported that the root biomass of plants was significantly enhanced by N enrichment, thus increasing Ra and Rs in wetlands.

Our results show that Rh exhibited a significantly negative response to N enrichment across all biomes, which is consistent with Zhou *et al.* (2014). However, when separated into different biomes, N enrichment was not significantly related to Rh, except

in wetlands, consistent with Tao *et al.* (2013) and Song *et al.* (2013), who reported that N enrichment decreased MBC content and decreased soil organic C mineralization, leading to decreased Rh in wetlands. Wetlands are different from other ecosystems because their soil is water-logged, anaerobic and acidic; thus, the enrichment of wetlands with N led to decreases in soil pH and MBC, resulting in significant suppression of Rh (Tao *et al.*, 2013). Wetlands are considered to have a large C pool, representing up to about a third of the global soil C pool (Smith *et al.*, 2004); thus, more studies on Rs and its components in response to N enrichment in wetlands should also be conducted to predict the C fluxes in future climate change. The lack of a significant response to N enrichment in biomes indicates the possible existence of other factors that cause the different effects of N enrichment on Rh; we will address these below.

Relationships between the RRs of Rs and N enrichment rates

Previous studies reported that the N enrichment rate had no relationship to the RRs of Rs (Liu & Greaver, 2010; Zhou *et al.*, 2014); however, the results of our meta-analysis indicated a relationship between the RRs of Rs and N enrichment rates in certain biomes. Across all biomes, no significant relationships were observed because of the large heterogeneity among the different biomes. However, in forest biomes, the RR of Rs exhibited a negative relationship with N enrichment rate, thereby indicating that the RR of Rs decreased as the N enrichment rate increased in forests. In croplands, the RR exhibited a significantly negative overall correlation with the N fertilization rate. However, interestingly, the RR of Rs showed a positive correlation with N enrichment in wheatfields (a subset of croplands data), possibly because N fertilization promoted the growth of wheat and caused an increase in Rs. Indeed, Reich *et al.* (2008) reported that maintenance respiration is positively correlated with the tissue N content, which increases with N fertilization.

The overall data indicated negative relationships of the RR of Rs with N fertilization in croplands, mostly caused by the maize Rs. The maize data exhibited negative trends, which were largely caused by the N demands of maize being roughly met through decomposing organic matter; hence, the higher root or microbial respiration resulted in slightly greater soil CO₂ emissions in unfertilized soil compared with N-fertilized but N-unlimited soils, as reported by Ding *et al.* (2007). Ni *et al.* (2012) suggested that the response of maize Rs to N fertilization may also depend on the concentration of labile organic C in the soil. It could also be due to higher temperature during the maize-growing season, because higher temperatures may lead to decreasing effects of N on Rs, as shown in our results (Fig. 4c); however, this requires further study. Meanwhile, in deserts, the RR of Rs exhibited significantly positive correlations with N enrichment, even under conditions of high temperature, mainly because N enrichment can promote the growth of herbaceous plants in these areas, which suffer from nutrient deficiency (Zhou & Zhang, 2014). Moreover, in hot desert environments the optimal

temperature before the decline in Rs was 41 °C (Parker *et al.*, 1983; O'connell, 1990), and this temperature threshold may explain the lack of decrease in the RR of Rs in deserts.

The RR of Rh exhibited a significantly negative relationship with N enrichment rates, thus indicating that Rh would be inhibited as the N enrichment rate increased, mainly because of the decreasing MBC content and imbalance of nutrients caused by N enrichment (Ramirez *et al.*, 2010; Lu *et al.*, 2011; Zhou *et al.*, 2014). Chronic N inputs can cause soil acidification, inducing the accumulation of toxic compounds (Guo *et al.*, 2010), thus decreasing soil microbial activity (Pregitzer *et al.*, 2008) and biomass (Treseder, 2008) and eventually inhibiting soil microbial respiration (Ramirez *et al.*, 2010).

Rs and its response to N enrichment have significant relationships with abiotic factors

Under natural conditions Rs exhibited a significant linear relationship with mean annual temperature; however, the RR of Rs exhibited a parabolic relationship with mean annual temperature (Fig. 4). The RR of Rs increased as the mean annual temperature increased and then decreased above 15 °C, which is consistent with the results of Bond-Lamberty & Thomson (2010) and Zhou *et al.* (2014). However, Zhou *et al.* (2014) reported no relationship when the mean annual temperature was higher than 15 °C, possibly due to the inclusion of the growing season Rs in that study because the temperature in the growing season (or wet season) is usually higher. We did not observe a significant correlation between the mean annual temperature and the RR of Rs during growing seasons (Fig. S4).

Under natural conditions Rs exhibited a parabolic relationship with the amount of N deposited, indicating that N enrichment promoted Rs when the amount of N was low and inhibited Rs when the amount exceeded a threshold value (50 kg ha⁻¹ year⁻¹). Not surprisingly, both Rs and Rh were significantly correlated to the soil MBC, consistent with numerous studies (Ramirez *et al.*, 2010; Zhou *et al.*, 2014). The RR of Rs was not only related to the mean annual temperature but also significantly related to the pH, soil bulk density and SOC. Under conditions of lower soil pH, N enrichment inhibited Rs, mainly because N enrichment in these low-pH areas increased the soil acidity, reduced the microbial biomass and altered the microbial composition (Lu *et al.*, 2011; Wei *et al.*, 2013). As the soil bulk density increased, the RR of Rs decreased because plant root growth and microbial respiration were inhibited with increasing soil bulk density. The RR of Rs showed a positive correlation with SOC, thereby indicating that the effects of N enrichment on Rs were enhanced as SOC increased because N enrichment with high SOC would promote microbial activity, which would augment Rs (Mooshammer *et al.*, 2014). The RR of Rs was positively correlated to the RR of root biomass and the RR of MBC, thus indicating that increases in both roots and microorganisms would directly promote Rs, consistent with many previous studies (Ramirez *et al.*, 2010).

Our results also demonstrated that Rh and the response of Rh to N enrichment were significantly related to the experimental

conditions, including incubation conditions and soil basal nutrition (Table 1). The mean annual temperature exhibited a positive relationship with Rh because temperature can increase microbial activity and accelerate C decomposition (Rustad *et al.*, 2001; Bond-Lamberty & Thomson, 2010). Although Rh showed a negative relationship with soil weight, a positive relationship between the RR of Rh and soil weight was observed because light soil is more easily affected by environmental changes, with a higher Rh. It was easy to understand the relationship between the RR of Rh and incubation time because of the short-term instability of soil, with Rh decreasing with increasing incubation time (Rodriguez *et al.*, 2014; Wang *et al.*, 2014a). Thus, our results suggest that the incubation conditions cause different responses of Rh to N enrichment. Consequently, appropriate incubation conditions should be considered when researching Rh in future studies.

Both Rs and the RR of Rs showed significant relationships with the mean annual temperature, indicating that temperature may be an important factor regulating Rs and the effects of N on Rs. Therefore, we analysed the Q10 under conditions of no N enrichment and the response to N enrichment. The mean Q10 in our study was higher than that reported by Bond-Lamberty & Thomson (2010), perhaps because the Q10 value in their study was based on air temperature instead of soil temperature, and studies using soil temperatures typically report higher Q10 values. Zhang *et al.* (2014) reported that the addition of N may affect the Q10 by changing the metabolism of plant roots and soil microbes; thus, the mechanisms underlying the different Q10 values in different ecosystems require further study. The Q10 under the condition without N enrichment did not reveal a significant relationship with climate factors in our study (Fig. S5), but the RR of Q10 significantly decreased as the mean annual temperature and mean annual precipitation increased, thus suggesting that N enrichment could decrease the temperature sensitivity of Rs in areas of high temperature and precipitation. In general, soil temperature and moisture are significantly correlated with each other (Davidson *et al.*, 2006); in our study, the RR of Q10 exhibited a parabolic relationship with both of these factors. This is because a lower or higher soil water content could affect root growth and the diffusion of oxygen, which could limit soil microbial respiration (Linn & Doran, 1984; Skopp *et al.*, 1990), and because temperature is related to enzyme activity, which would affect Q10 and change soil microbial respiration. These results also indicated that under suitable soil temperature and moisture conditions N enrichment is more likely to decrease Q10, whereas N enrichment is more likely to increase Q10 in colder or warmer seasons.

Estimates of global C flux and net changes of C flux caused by N enrichment

Based on our results, the average Rs rate was highest in tropical forests, at 11.93 Mg C ha⁻¹ year⁻¹, and lowest in deserts, at 1.38 Mg C ha⁻¹ year⁻¹. The Rs induced by enrichment with 1 kg of N averaged 1.33 kg C ha⁻¹ year⁻¹, increasing the most in wetlands and decreasing the most in forests. When integrating

the area data for each biome, the total Rs of global terrestrial regions was 97.01 Pg C year⁻¹, which is quite comparable with the results of Bond-Lamberty & Thomson (2010) who reported 98 ± 12 Pg C in 2008 based on global Rs flux, and is slightly higher than the mean annual global Rs of 91 Pg C year⁻¹ reported by Hashimoto *et al.* (2015). The C efflux caused by N enrichment was quite comparable with the 0.179 Pg C year⁻¹ reported by Liu & Greaver (2009) in forests and croplands. Forests showed a negative C flux induced by N enrichment; however, due to the smaller area of forest compared with the total area of the other biomes (Saugier *et al.*, 2001; Liu & Greaver, 2009), the decreased C flux in forests cannot offset the increase in other biomes, and further increases in N enrichment still promote soil C efflux.

Our meta-analysis based on the global terrestrial ecosystem focused on the response of the soil C flux to N enrichment and its relationship with environmental and soil factors. Based on our results, we conclude that N enrichment is not significantly related to global Rs but we found negative relationships in forests and positive ones in other biomes. In certain biomes, the effects of N enrichment on Rs and Rh showed significant relationships with the N enrichment rate. The response of Rh to N enrichment was significantly correlated with the incubation soil weight, temperature, MBC and SOC. Rs in terrestrial ecosystems showed a linear positive relationship with the mean annual temperature, thus indicating an increasing trend of soil C fluxes in the future, whereas a potential decrease in soil C efflux was observed when N enrichment exceeded 50 kg ha⁻¹ year⁻¹. This situation makes the prediction of soil C flux a more complex challenge when faced with increases in both temperature and N enrichment. Moreover, the effects of N enrichment on Rs also depend on soil conditions (such as the pH, soil bulk density, SOC and MBC) and mean annual temperature, for which a threshold of 15 °C was observed for the effects of N enrichment to increase or decrease the Rs, and Q10 showed a negative response to N enrichment. The estimate of C flux induced by N enrichment was an average of 1.33 kg C ha⁻¹ year⁻¹, as the decrease C flux induced by N enrichment in forests cannot offset the increasing C flux in other biomes due to N enrichment. The response patterns of Rs to N enrichment as revealed in this study can be used as benchmarks for future modelling and experimental studies.

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SUPPORTING INFORMATION

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

Figure S1 Funnel plots of soil respiration (Rs) and heterotrophic respiration (Rh) dataset.

Figure S2 The violin plots and box plots of the global soil respiration dataset (Bond-Lamberty & Thomson, 2010) and our dataset.

Figure S3 The relationships between the response ratios of soil respiration (Rs) and heterotrophic respiration (Rh) with the rate of nitrogen enrichment were not significant in these biomes.

Figure S4 There are no significant relationships between the soil respiration (Rs) rates and these biotic and abiotic factors.

Figure S5 There are no significant between the response ratios of soil respiration (Rs) and these climate and soil properties.

Figure S6 There are no significant relationships between Q10 and the response ratio of Q10 and abiotic factors.

Figure S7 Response ratio of soil respiration (Rs) to nitrogen enrichment in natural and anthropogenic ecosystems and the relationships with the nitrogen enrichment rate.

Table S1 Response ratio (RR) and weighting factor of soil respiration (Rs) extracted from each of the papers.

Table S2 Response ratio (RR) and weighting factor of heterotrophic respiration (Rh) extracted from each of the papers.

BIOSKETCHES

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APPENDIX 1 DATA SOURCES

A list of 154 papers from which the data were extracted for this meta-analysis.

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