ECOLOGY LETTERS

Ecology Letters, (2018) **21**: 1108–1118 doi: 10.1111/ele.13078

REVIEW AND SYNTHESIS

Climatic role of terrestrial ecosystem under elevated CO_2: a bottom-up greenhouse gases budget

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Abstract

The net balance of greenhouse gas (GHG) exchanges between terrestrial ecosystems and the atmosphere under elevated atmospheric carbon dioxide (CO_2) remains poorly understood. Here, we synthesise 1655 measurements from 169 published studies to assess GHGs budget of terrestrial ecosystems under elevated CO_2. We show that elevated CO_2 significantly stimulates plant C pool (NPP) by 20%, soil CO_2 fluxes by 24%, and methane (CH_4) fluxes by 34% from rice paddies and by 12% from natural wetlands, while it slightly decreases CH_4 uptake of upland soils by 3.8%. Elevated CO_2 causes insignificant increases in soil nitrous oxide (N_2O) fluxes (4.6%), soil organic C (4.3%) and N (3.6%) pools. The elevated CO_2-induced increase in GHG emissions may decline with CO_2 enrichment levels. An elevated CO_2-induced rise in soil CH_4 and N_2O emissions (2.76 Pg CO_2-equivalent year^{-1}) could negate soil C enrichment (2.42 Pg CO_2 year^{-1}) or reduce mitigation potential of terrestrial net ecosystem production by as much as 69% (NEP, 3.99 Pg CO_2 year^{-1}) under elevated CO_2. Our analysis highlights that the capacity of terrestrial ecosystems to act as a sink to slow climate warming under elevated CO_2 might have been largely offset by its induced increases in soil GHGs source strength.

Keywords

Climate change, elevated CO_2, greenhouse gas, meta-analysis, plant C pool, soil C and N cycle.

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INTRODUCTION

Atmospheric carbon dioxide (CO_2) enrichment constitutes one of the primary components of human-induced global change, directly threatening the sustainability of terrestrial ecosystems (IPCC 2013). Soils contain the largest pool of terrestrial organic carbon (C) and nitrogen (N), and rising atmospheric CO_2 has altered soil C and N biogeochemical cycles. Plant photosynthesis and growth are known to increase under elevated atmospheric CO_2 (Long *et al*. 2004; van Groenigen *et al*. 2011), ultimately promoting terrestrial net primary production (NPP) and soil C storage (Yue *et al*. 2017). On the other hand, soil C input enhanced by elevated atmospheric CO_2 may also increase soil CO_2 emissions, stimulating some soil C release back to the atmosphere (van Groenigen *et al*. 2014). However, the increment of the net ecosystem production (NEP) and soil C storage as a trade-off with stimulated soil greenhouse gases (GHGs) under elevated CO_2 has not been quantitatively synthesised.

Besides CO_2, methane (CH_4) and nitrous oxide (N_2O) are two more potent long-lived atmospheric GHGs. Upland soils are the major source of atmospheric N_2O, mainly through the microbial processes of nitrification and denitrification. Soil N_2O emissions are closely associated with soil nitrifiers and denitrifiers and soil physicochemical properties, such as soil mineral N, soil carbon substrate and water content (Liu *et al*. 2017). Wetlands, including rice paddies, constitute the main source of atmospheric CH_4, while upland soils can act as a sink for atmospheric CH_4, dependent on the combined performance of methanogenic and methanotrophic bacteria. The CH_4 fluxes from wetlands are highly related to plant growth, soil C substrate and soil water status (Mosier *et al*. 2002). Elevated atmospheric CO_2 has been shown to affect soil biotic and abiotic properties that are key drivers for soil CH_4 and N_2O emissions, such as GHGs-related soil functional microbes, the root-oriented soil C input, soil mineral N availability and soil moisture (Hu *et al*. 1999, 2005; Mosier *et al*. 2002). The elevated CO_2-enhanced soil C storage may have the risk of being offset by altered soil GHGs fluxes (Pendall *et al*. 2004; van Groenigen *et al*. 2011; Dijkstra *et al*. 2012; Zhou *et al*. 2016). Thus, a full understanding of the net balance of CO_2, CH_4 and N_2O exchange between terrestrial ecosystems and the atmosphere under elevated atmospheric CO_2 would help to predict to what extent terrestrial ecosystems shape the climate.

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Despite recent concerns about the vital role of elevated CO_2 in driving global warming and climate change, our knowledge of its effects on soil C and N cycling and the subsequent feedback to climate change through GHGs emissions still remains highly elusive. The role of elevated CO_2 in influencing soil GHGs fluxes or soil C and N interactions is inconsistent across individual studies and varies with habitat-specific environmental and experimental conditions (van Groenigen *et al*. 2011; Dijkstra *et al*. 2012). The high variability in experimental results primarily results from intrinsic heterogeneity in C and N processes over time and across ecosystems, which is also likely to mask the real treatment effects of elevated CO_2 (Zhou *et al*. 2016). Recently, several meta-analyses have examined the response of major biogenic GHG fluxes or soil C sequestration to elevated CO_2, but they are limited in data volume or only focused on one or two soil greenhouse gases (e.g. CH_4 and/or N_2O) (Schlesinger & Lichter 2001; Jastrow *et al*. 2005; De Graaff *et al*. 2006; Luo *et al*. 2006; Hungate *et al*. 2009; van Groenigen *et al*. 2011, 2014; Yue *et al*. 2017). A full accounting of NEP, CH_4 and N_2O exchanges between terrestrial ecosystems and the atmosphere under elevated CO_2 is therefore urgently needed. In particular, limited studies have integrated the changes in soil C and N pools to better understand their linkages with biogenic GHGs fluxes in response to elevated CO_2. Poor understanding of how soil abiotic and biotic drivers might influence GHGs response to elevated atmospheric CO_2 will limit our ability to predict terrestrial ecosystems feedback to climate change.

Here, 1655 measurements derived from 169 peer-reviewed publications within an updated and comprehensive data set (Table S1 and Data set) were synthesised using meta-analysis to examine the effect of elevated CO_2 on GHG fluxes and soil C and N pools (Table S2). The main objective of this study was to gain an insight into the net budget of GHGs balance between terrestrial ecosystems and the atmosphere. We predicted that the capacity of terrestrial ecosystems to act as a sink under elevated CO_2 and slow climate warming might have been largely weakened by the enhancement of soil GHGs source strength under elevated CO_2. This work also attempts to build the linkages between the abiotic/biotic drivers and GHG fluxes under elevated CO_2.

MATERIALS AND METHODS

Data extraction

We launched a detailed review of the literature published in peer-reviewed journals through the year 2016 (cutoff date on September 30, 2016). We extracted original experimental results from publications that included individual measurements with soil GHG flux data. We also included data from these studies on plant C pool, soil moisture, and soil C and N fractions in the cases that they were individually or simultaneously available (Table S1 and Data set). All selected data were extracted from the Web of Science and Google Scholar, and papers published in the China Knowledge Resource Integrated Database (CNKI) with English abstracts. In addition, we gathered and re-evaluated the older literature cited in the prior reviews (Reich *et al*. 2001; van Groenigen *et al*. 2011). A combination of searching terms ['elevated CO_2' OR 'CO_2 enrichment', AND 'soil', AND 'CO_2' OR 'CH_4' OR 'N_2O'] was used for GHGs flux data extraction. Search terms for plant and soil C pools and the data select criteria were similar to those used in a recent meta-analysis (Yue *et al*. 2017). Across the studies included in our data set, the atmospheric CO_2 concentrations for the ambient and elevated treatments fell within the ranges of 320–420 ppmv and 400–780 ppmv, respectively. The concentration of CO_2 was, on average, elevated by 210–270 ppmv for different GHGs in the database. The experimental duration ranged from 0.01 to 12.00 measurement years.

Inclusion criteria

We adhered to the following criteria to avoid bias in data selection. Besides field experiments under open-top chamber and Free-air CO_2 Enrichment (FACE) conditions, pot studies in growth chamber (GC) and greenhouse (GH) facilities were also included in this analysis to better quantitatively understand the effect of elevated CO_2 on soil C and N cycling. The ambient and elevated treatments within a given study should have the same CO_2-treatment duration and history. The treatments with no replication or no reported number of replications, or grouping categories with fewer than two data pairs were excluded from the analysis to meet the criteria for rigorous meta-analysis. For data from natural habitats, the occasional field GHG flux measurements without covering the whole experimental period or where the number of consecutive measurements was less than three data-points were excluded. For data from croplands, the consecutive measurement period had to cover at least one whole cropping season and the within or multi-year data with different cropping seasons were averaged to obtain an annual mean. The daily mean of GHG measurement data from natural and cropping upland ecosystems during plant-growing seasons were assumed to be applicable to the non-growing seasons, which was thereby extrapolated to obtain annual values in this analysis. Seasonal cumulative CH_4 emissions from rice growing seasons were assumed to be representive of the annual total due to the negligible source or sink role of atmospheric CH_4 during the following seasons without waterlogging. Experiments in which the most abundant species were N_2-fixing species were excluded to guarantee the sole effect of elevated CO_2 on soil C and N pools rather than the combined effect of elevated CO_2 with plant fixation of atmospheric N_2 (Luo *et al*. 2006). For biomass data derived from natural ecosystems, where multiple measurements were taken at different times within a year, we only adopted the final measurement data. Studies on soil C and N fractions, soil moisture, plant N uptake and biomass were only included in the analysis if there was also GHG flux data available from the experiment under elevated CO_2.

When soil parameters were reported with multiple soil depths, we calculated the overall treatment effects across the entire soil profile. For multi-factor studies, we only considered the separate paired observations under elevated CO_2 alone or under both ambient and elevated CO_2 treatments combined with the same other global-change factors. One paired data

on CH_4 uptake in wetlands (Wolf *et al.* 2007) and another paired negative data on N_2O fluxes in forests (Martins *et al.* 2016) were finally discarded from our data set to minimise analysis bias. When the data were presented in figures, we extracted mean values and standard error using GraphClick. The final database consisted of 1655 measurements derived from 169 publications, including 37 simultaneous observations of CH_4 and N_2O fluxes from 12 studies (Supporting Information and Data set).

Data compilation and analyses

Data were first subjected to a standardisation process to allow for comparisons. We calculated the balanced means of all investigated paired values with the residual maximum likelihood procedure, using GENSTAT release 4.2 to minimise the heterogeneity resulting from missing values and unequal number of observations among reviewed literature (Payne 2000). In further data compiling prior to analysis, we divided the soils into four land-use types as wetland, rice paddy, cropping upland and non-cropping upland (including natural grassland and forest). To address whether the response of soil C and N cycling to elevated CO_2 might be affected by experimental method, N fertiliser and vegetation cover, we categorised these data into two groups: field or pot experiment, with or without N fertiliser input, and vegetation present or not, respectively.

The means of biogenic GHG fluxes, plant biomass and N uptake, soil moisture as well as soil C and N fractions from treatment (X_e) and control (X_a) groups were used to calculate effect size in the form of natural log-transformed response ratio ($\ln R$). For upland soils overwhelmingly acting as the sink of CH_4 for both the treatment and control in our data set, the absolute values of negative CH_4 fluxes (referring to soil uptake of CH_4) were adopted for effect size calculation to avoid making $\ln R$ problematic during meta-analysis. However, seven paired observations showed a shift from source to sink of atmospheric CH_4 following elevated CO_2 and five paired observations witnessed a shift from sink to source of CH_4 in grassland and forest soils. These twelve paired observations were finally excluded to allow for solid performance of meta-analysis procedures. We calculated the treatment effect of elevated CO_2 on soil C and N pools as the absolute changes in soil C and N contents (in g C/N kg^{-1} soil), instead of relative changes to achieve biogeochemical significance (Schlesinger & Lichter 2001). The standard deviations of both treatment and control were included as a measure of variance:

$$\mathrm{In}R = \mathrm{In}(X_e/X_a), \tag{1}$$

where X_e and X_a are means in the treatment and control groups exposed to elevated CO_2. Its pooled variance (v) is estimated as follows:

$$v = \frac{s_e^2}{n_e x_e^2} + \frac{s_a^2}{n_a x_a^2}, \tag{2}$$

where n_e and n_a are the sample sizes for the treatment and control groups, respectively; s_e and s_a are the standard deviations for the treatment and control groups, respectively.

We conducted a weighted meta-analysis using the metric of $\ln R$, where the mean response ratio ($\ln R$++) is calculated from individual $\ln R$ of each paired comparison between control and treatment groups with the weight of each $\ln R$ using a categorical random effect model. Allowing for the intrinsic relevance across all the variables under elevated CO_2, the overall mean effect size and 95% confidential interval (CI) of each grouping category generated by bootstrapping (9999 iterations) were calculated with the mixed-effect model by R (R Development Core Team, 2016). Treatment effects were considered significant if the 95% CI did not overlap with the line $\ln R = 0$.

In addition to the meta-analysis procedure, One-way ANOVA was performed to test the differences in all target variables between ambient and elevated CO_2 treatments. Linear regressions were used to examine the correlations of $\ln R$ of biogenic GHG fluxes as well as soil C and N parameters with the potential driving factors, including plant C components, soil initial C and N levels, soil C/N ratio and the intensity of CO_2 enrichment. All statistical analyses were carried out using JMP version 7.0 (SAS Institute, USA, 2007).

Scaling-up estimation

Based on the absolute mean positive or negative changes in annual GHG fluxes and the differences in soil labile C and N pools under elevated CO_2, both expressed as area-scaled metrics (U-value), we scaled up the results from this analysis by multiplying them for target variables with the corresponding total habitat areas currently summarised:

$$T = \bar{U} \times A, \tag{3}$$

where T is the net elevated CO_2-induced increase or decrease in strength of carbon sink expressed as Pg CO_2-eq. $year^{-1}$ (Shang *et al.* 2011; IPCC 2013), and A is the total habitat areas for wetlands, rice paddies and uplands, being equivalent to 5.7, 1.3 and 103.1 M km^2, respectively (Aselmann & Crutzen 1989; van Groenigen *et al.* 2011). For CO_2 fluxes, we determined the net ecosystem production (NEP) under elevated CO_2, which refers to the difference between NPP and soil heterotrophic respiration (R_H). The estimation of NEP under elevated CO_2 was only based on the NPP data in community or ecosystem levels. The significant negative effect on CH_4 uptake following CO_2 enrichment across upland soils was inversely considered as potentially intensified atmospheric CH_4 emissions in current estimation. For upland soils as hotspots of N_2O, we further scaled up N_2O fluxes by dividing into fertilised upland soils [i.e. 19.0 M km^2 of fertilised grasslands and croplands (Stehfest & Bouwman 2006), minus 1.3 M km^2 of rice paddies (Aselmann & Crutzen 1989)] and non-fertilised upland soils (103.1–19.0+1.3 = 85.4 M km^2) receiving no extra fertiliser N in addition to atmospheric N input.

For paired data, we determined the overall elevated CO_2-induced mean annual soil organic carbon (SOC) and total nitrogen (TN) change rates (MU, g C/N kg^{-1} $year^{-1}$) by plotting them versus the duration of experiments, directly linking them to changes in GHG fluxes between the controls and treatments under elevated CO_2, which was defined and calculated using the following equation (Hungate *et al.* 2009; Tian *et al.* 2015):

$$MU = (SOC_e/TN_e - SOC_a/TN_a)/t \quad (4)$$

where the subscripts e and a refer to data from the treatments under elevated CO_2 and ambient controls, respectively. Positive values indicate increased SOC and TN change rates under elevated CO_2, while negative values represent their decreases following CO_2 enrichment. Furthermore, the elevated CO_2-induced annual soil C and N sequestration potential was estimated by the following equation (Tian *et al.* 2006, 2015; Shang *et al.* 2011):

$$SOC_s/TN_s = \sum_{i=1}^{n} S_i \times MU \times BD \times H \times 0.1, \quad (5)$$

where S_i is the habitat area involved in this study corresponding to the given source area for GHG fluxes (i.e. wetland, rice paddy and upland); MU is the same as defined above, SOC_s/TN_s is the C/N sequestration potential (t C/N $year^{-1}$); BD is the soil bulk density (g cm^{-3}; an average value of 1.25 g cm^{-3} was used here); and H is the thickness of the soil layer (cm; a general investigated soil depth of 20 cm was used here to reduce uncertainties, despite the grand mean of 23.5 cm as provided in the Supporting Data set). In this estimate, we could not differentiate the response of GHGs emission to elevated CO_2 at different CO_2 enrichment years due to limited data size.

RESULTS

Plant C and N pools

Elevated atmospheric CO_2 promotes C uptake by the terrestrial biosphere, leading to an increase in plant and soil C pools. When averaged across all studies, plant C pool was significantly increased by elevated CO_2 (NPP, 20%; 95% CI: 17–28%), varying with extents for above-ground C (above-ground NPP, ANPP, 18%; 95% CI: 16–24%) and below-ground C (below-ground NPP, BNPP, 32%; 95% CI: 28–42%) components (Fig. 1a). A significant increase in the ratio of BNPP/ANPP under elevated CO_2 revealed that below-ground C response to elevated CO_2 was stronger than above-ground C (A/B-NPP ratio, Fig. 1a). Positive response of plant C components to elevated CO_2 was greater in fertilised soils, in natural wetlands and in controlled-environment studies. On the other hand, elevated CO_2 slightly increased plant N uptake (2.0%; 95% CI: -3 to 6%) although it was not statistically significant (Tables S3-S5).

Soil GHG fluxes

On average, elevated atmospheric CO_2 significantly increased soil CO_2 fluxes (R_S, soil respiration) by 24% (95% CI: 15–27%) and soil heterotrophic respiration (R_H) by 26% (95%

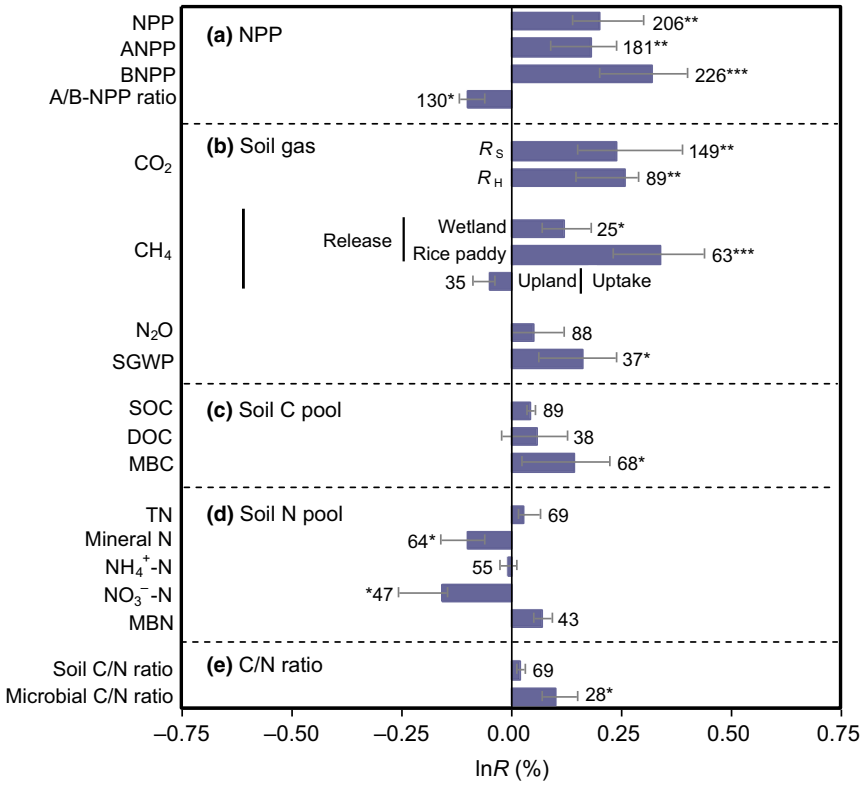

Figure 1 Plant C pools (a), soil trace gases (b), soil carbon (c) and nitrogen (d) fractions, as well as soil and microbial C/N ratios in response to elevated atmospheric CO_2. ANPP, above-ground net primary production; BNPP, below-ground net primary production; R_S, soil respiration; R_H, soil heterotrophic respiration; SGWP, sustained flux global warming potential of CH_4 and N_2O over the 100-year time horizon; SOC, soil organic carbon; DOC, soil dissolved organic carbon; MBC, soil microbial biomass carbon; TN, soil total nitrogen; Mineral N, soil (NH_4^++NO_3^-)-N; MBN, soil microbial biomass N. The numerals following the column ends indicate number of observations. Error bars represent 95% confidence intervals. Asterisks refer to statistical differences from zero representing the ambient controls (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

CI: 18–32%). Elevated CO_2 stimulated CH_4 fluxes by 34% (95% CI: 4–118%) in rice paddies and by 12% (95% CI: 7–25%) in natural wetlands (Fig. 1b). These positive responses of soil CO_2 and CH_4 fluxes were more pronounced in pot studies, and in natural wetlands and rice paddies (Tables S4 and S5). For upland soils, elevated CO_2 slightly decreased soil CH_4 uptake by 4.5% (95% CI: 1–15%) (Fig. 1b), largely contributed by a significant response in fertilised soils and under field conditions (Tables S3–S5, Fig. 1b). When averaged across all studies, elevated CO_2 induced a small and insignificant increase in soil N_2O fluxes (5.2%; 95% CI: −7 to 16%). This positive response was statistically significant only in fertilised upland soils and in natural wetlands. Elevated CO_2 significantly enhanced the combined sustained global warming potential (SGWP: IPCC, 2013) of CH_4 and N_2O emissions in studies where CH_4 and N_2O fluxes response to elevated atmospheric CO_2 were simultaneously examined (Tables S3–S5, Fig. 1b).

Soil C and N pools

Although elevated atmospheric CO_2 significantly stimulated plant growth and soil C input, it only caused a small and insignificant enhancement of soil organic C pools (SOC, 4.3%; 95% CI: 1–6%) when averaged across all studies (Fig. 1c). For soil labile organic C components, positive response of soil dissolved organic C (DOC, 6.1%; 95% CI: 2–18%) was insignificant, whereas microbial biomass C (MBC, 14%; 95% CI: 8–18%) pools were significantly enhanced by elevated CO_2, particularly in fertilised soils and in cropping uplands (Tables S3 and S4, Fig. 1c).

Similar to soil C pools, soil N pools (3.6%; 95% CI: 1–7%) were slightly stimulated by elevated CO_2 (Fig. 1d). Soil mineral N availability (−10%; 95% CI: −21% to 10%) showed a significant negative response to elevated CO_2, largely contributed by a significant decrease in nitrate (NO_3^--N, −15%; 95% CI: −27 to −1%) rather than a minor decrease in ammonium (NH_4^+-N, -1.2%; 95% CI: −4% to 14) (Fig. 1d). In contrast, soil microbial biomass N, as another essential indicator of labile N fractions in soils, was increased by 7.4% (95% CI: 1–14%) when averaged across all paired observations, more enhanced in fertilised agricultural soils (Tables S3 and S4, Fig. 1d). Elevated CO_2 did not significantly alter soil C/N ratio, while it significantly increased soil microbial C/N ratio by 10% (95% CI: −4% to 26%) (Fig. 1e), particularly in cropping upland soils with fertiliser input (Tables S3 and S4). In addition, elevated CO_2-induced changes in soil microbial C and N pools as well as microbial C/N ratios increased with the level of CO_2 enrichment (Fig. S1a and b). In contrast, the change in soil NH_4^+-N under elevated CO_2 decreased with the level of CO_2 enrichment in this analysis (Fig. S1c).

Scaling-up of results

To compare with the results obtained by the earlier meta-analysis (van Groenigen *et al*. 2011), we adopted similar scaling-up approach to integrate results of this meta-analysis into global context. We extrapolated the elevated CO_2-induced change rates in area-based GHG fluxes and soil C and N pools to global scale using Eqns (3–5) by their respective total habitat areas (Table 1, Fig. 2). Overall, plant C pool promoted by elevated CO_2 generates an additional 29.42 Pg CO_2 $year^{-1}$ of NPP in terrestrial ecosystems. The increase in soil CO_2 fluxes with rising atmospheric CO_2 corresponds to an additional source of 20.15 Pg CO_2 $year^{-1}$. By taking NPP and R_H into consideration together, elevated CO_2 stimulates NEP of terrestrial ecosystems by 3.99 Pg CO_2 $year^{-1}$. The CH_4 fluxes stimulated under CO_2 enrichment amount to an additional source of 0.30 Pg CO_2-equivalent (eq.) $year^{-1}$ from rice paddies and of 1.90 Pg CO_2-eq. $year^{-1}$ from natural wetlands. Moreover, an insignificant negative response of soil CH_4 uptake to elevated CO_2 corresponds to an additional source of 0.05 Pg CO_2-eq. $year^{-1}$ for upland soils. The elevated CO_2-stimulated soil N_2O emissions cause an additional source of 0.51 Pg CO_2-eq. $year^{-1}$, consisting of comparable strengths in fertilised (0.27 Pg CO_2-eq. $year^{-1}$) and non-fertilised upland soils (0.24 Pg CO_2-eq. $year^{-1}$). In total, the combined effect of elevated CO_2 on CH_4 and N_2O fluxes yields an additional source strength of 2.76 Pg CO_2-eq. $year^{-1}$.

The elevated CO_2-enhanced soil organic C and total N sequestration potentials were estimated to be 2.42 Pg CO_2 $year^{-1}$ and 0.02 Pg N $year^{-1}$, respectively (Table 1, Fig. 2). Results of this study suggest that the elevated CO_2-enhanced CH_4 and N_2O emissions add to the radiative forcing of terrestrial ecosystems, and these increased emissions (2.76 Pg CO_2-eq. $year^{-1}$) could negate soil C enrichment (2.42 Pg CO_2 $year^{-1}$) under elevated CO_2. The elevated CO_2-enhanced CH_4 and N_2O emissions are expected to reduce mitigation potential of terrestrial net ecosystem production by as much as 69% (NEP, 3.99 Pg CO_2 $year^{-1}$) under elevated CO_2.

DISCUSSION

To our knowledge, this synthesis is one of the first to provide a comprehensive accounting of GHG exchanges between terrestrial ecosystems and the atmosphere under elevated CO_2. Our meta-analysis builds an earlier synthesis of soil CH_4 and N_2O emissions under elevated CO_2 by van Groenigen *et al*. (2011). It encompasses a much expanded database (e.g. 63 vs. 21 for CH_4 in rice paddies; 88 vs. 73 for N_2O) that includes recent studies in China and other geographic and climatic regions not previously evaluated (Table S1 and Data set). On average, elevated CO_2-induced changes in soil CH_4 and N_2O fluxes in our meta-analysis were much larger based on more current data than the earlier meta-analysis of van Groenigen *et al*. (2011). Besides our relatively large and extensive database, the difference in budget estimates of CH_4 and N_2O under elevated CO_2 would be associated with the latest IPCC SGWP factors (IPCC 2013) for CH_4 and N_2O in our meta-analysis instead of GWP factors in van Groenigen *et al*. (2011). Nevertheless, we gained a much smaller 95% confidence interval of GHGs in response to elevated CO_2, suggesting that our meta-analysis with larger data size would be helpful to minimise the uncertainty in estimates. For instance, the 95% confidence interval of estimates was much smaller for the elevated CO_2-stimulated CH_4 emissions from rice paddies (0.23–0.40 vs. 0.11–0.48) and N_2O emissions from

Table 1 Summary of estimated results of elevated CO_2-induced GHGs source strength, total NPP C fixed, and soil C and N sequestration potentials

C or N variable	Habitat	No. of observations	Area (M km^2)	Estimate (95% CI)
Soil CO_2 flux (Pg CO_2 year^1)	Overall (all)	149	110.1	20.15 (14.64, 25.64)
Soil R_H (Pg CO_2 year^{-1})†	Overall (all)	89	110.1	25.43 (17.39, 33.47)
NPP (Pg CO_2 year^{-1})	Overall (all)	206	110.1	29.42 (32.26, 56.32)
NEP (Pg CO_2 year^{-1})	Overall (all)	—	110.1	3.99
Soil CH_4 flux (Pg CO_2-eq. year^{-1})	Overall (all)	123	110.1	2.25 (0.05, 3.95)
	Wetland	25	5.7	1.90 (0.51, 3.25)
	Rice paddy	63	1.3	0.30 (0.23, 0.40)
	Upland*	35	103.1	0.05 (−0.02, 0.10)
Soil N_2O flux (Pg CO_2-eq. year^{-1})	Overall (upland)	80	103.1	0.51 (0.12, 0.86)
	Fertilised upland soils	45	17.7	0.27 (−0.35, 1.07)
	Non-fertilised upland soils	35	85.4	0.24 (−0.01, 1.45)
SOC pool (Pg CO_2 year^{-1})	Overall (all)	89	110.1	2.42 (−1.01, 5.85)
Soil N pool (Pg N year^{-1})	Overall (all)	69	110.1	0.02 (−0.27, 0.38)

*The significant decrease in uptake of CH_4 for upland soils under elevated CO_2 was expressed as the increase in source strength of atmospheric CH_4.
†Soil heterotrophic respiration (R_H) was approximately represented by soil CO_2 fluxes measured without vegetation growth involvement in present estimation; the latest IPCC SGWP factors (mass basis) used here for CH_4 and N_2O are 45 and 270 over the time horizon of 100 years respectively (IPCC, 2013).

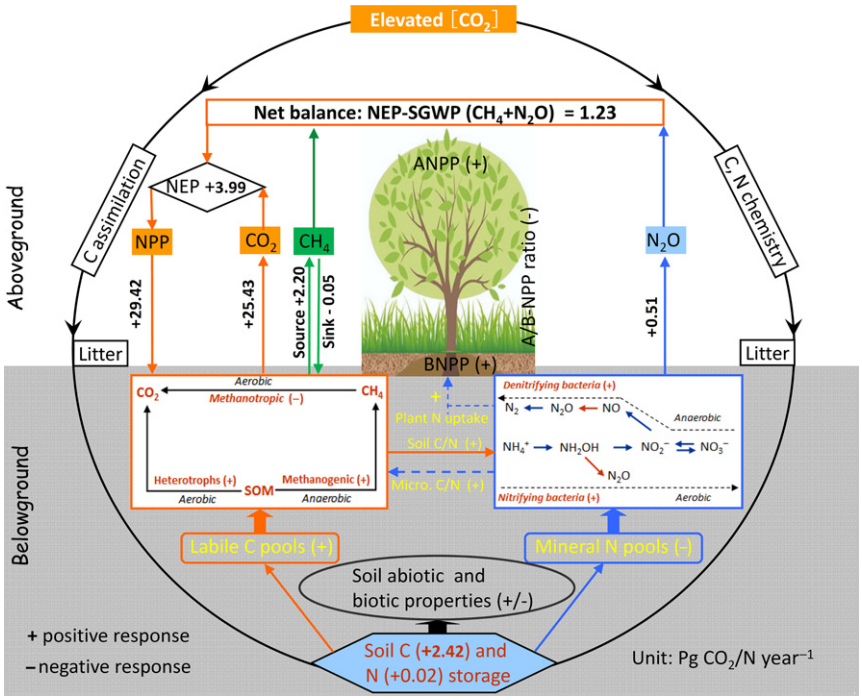

Figure 2 A complete conceptual diagram illustrating the effects of elevated CO_2 on soil C and N pools as well as greenhouse gases fluxes. ANPP, aboveground NPP; BNPP, below-ground NPP. All the figures in bold within the panel show the source or sink strengths of elevated CO_2-induced GHG fluxes expressed as Pg CO_2-eq. year^{-1}, as well as soil C sequestration potentials. Details shown in Table 1.

uplands (0.12–0.86 vs. 0.10–1.66) in this analysis than the meta-analysis of van Groenigen *et al.* (2011) (Table 1).

Terrestrial ecosystem C and soil N pools under elevated CO_2

The effect of elevated CO_2 on plant C pools has been well synthesised in previous studies (Jablonski *et al.* 2002; Luo *et al.* 2006; Yue *et al.* 2017), generally showing a positive response of plant C pools to CO_2 enrichment. The stimulation of plant C pools under elevated CO_2 has been largely attributed to its direct positive effects on photosynthesis and growth (Körner 2006) and indirect effects on reduced stomatal conductance (Volk *et al.* 2000; Morgan *et al.* 2004). Overall, our estimate of plant C pools (20%) stimulated by elevated CO_2 is generally comparable to the recent synthesis of CO_2-induced rise in plant C pools (18%) at community-level with smaller data volume (Yue *et al.* 2017). Similar to previous reported individual experimental evidence and meta-analysis syntheses (Luo *et al.* 2006; Dieleman *et al.* 2012), plant below-ground C was enhanced at elevated CO_2 to a larger extent than aboveground C, leading to a significant increase in root/shoot plant C ratios (Fig. 1a). The progressive N limitation hypothesis

proposed that plant growth under elevated CO_2 is generally limited by soil nutrients and N in particular (Luo *et al.* 2004; Hu *et al.* 2005), and thus plants expand rooting systems to take up nutrients from soils as supported by a decrease in soil mineral N under elevated CO_2 in this synthesis (Fig. 1d).

Soil organic C pools showed a weak positive response to elevated CO_2, of which soil labile C pools had a more vigorous positive response. It suggests that elevated atmospheric CO_2 induces an enhanced supply of easily metabolised substrates, such as new labile C input and mobilising C reserves assumed to be protected from microbial attack (Fontaine *et al.* 2007; Paterson *et al.* 2008; van Groenigen *et al.* 2014). Similar to soil organic C pools, soil N pools (3.6%) showed a minor stimulation under elevated CO_2, as a contrast to soil mineral N availability with a significant negative response (Fig. 1d). Elevated CO_2 is usually shown to decrease soil mineral N pools in individual manipulation studies (Reich *et al.* 2001; Mosier *et al.* 2002; Luo *et al.* 2004; Hu *et al.* 2005). Other processes, such as increased soil water content (Hungate *et al.* 2002; Schafer *et al.* 2002; van Groenigen *et al.* 2011) and N availability constrained by other nutrient elements (Hungate *et al.* 2004) under elevated CO_2, may decrease soil N availability or increase N losses. Moreover, soil microbial N pool was also increased under elevated CO_2, although its response was insignificant and smaller than soil microbial C pool response to elevated CO_2. Together with the response of soil microbial C and N pools as well as microbial C/N ratios to elevated CO_2, elevated CO_2 tended to enhance soil microbial activities and shape microbial biomass C and N allocation (Hu *et al.* 1999; Zak *et al.* 2000).

Below-ground C input driving GHG fluxes response to elevated CO_2

Enhanced soil C input under elevated CO_2 incurred an increase in soil GHG emissions. Larger soil labile C under elevated atmospheric CO_2 often causes priming effect on soil organic decomposition (Ross *et al.* 2004; van Groenigen *et al.* 2014). Methane is produced under anaerobic conditions where methanogenic archaea depends on C assimilation by plants as their ultimate source of organic substrates. Nitrous oxide is produced mainly through nitrification and denitrification. Increased soil C input under elevated CO_2 may not increase N_2O emissions from nitrification, which is largely performed by chemoautotrophs. However, given that denitrification is generally stimulated by high availability of labile C as a source of energy, and new C enters mineral soils primarily through the root system, this increase in root biomass would facilitate denitrification rates and thereby N_2O emissions (van Groenigen *et al.* 2011). This is well supported by the evidence that the negative response of soil mineral N to elevated CO_2 was substantially contributed by the decrease in NO_3^--N (Fig. 1d), suggesting an elevated CO_2-stimulated denitrification. Nevertheless, this benefit from the extra soil C supply under elevated CO_2 could be constrained both directly by N availability and indirectly by nutrients mobilised to support N_2 fixation (van Groenigen *et al.* 2006). Indeed, as shown in this analysis, elevated CO_2-induced increases in soil CH_4 and N_2O fluxes were positively and significantly correlated with the changes in below-ground C pools under elevated CO_2 (Fig. 3), indicating that elevated CO_2 stimulates soil CH_4 and N_2O production largely through its positive effect on plant growth and root-oriented soil C input (Long *et al.* 2004; van Groenigen *et al.* 2011).

Other factors associated with GHG fluxes in response to elevated CO_2

In addition to soil C input, soil properties may also play an important role in soil GHG responses to elevated CO_2. Elevated CO_2 was shown to increase soil water content (WFPS, 7.5%) (Table S4), which would enhance soil respiration, particularly in arid and semiarid ecosystems. This is mainly due to improved efficiency of soil water use by plants under CO_2-enriched environments (Wullschleger *et al.* 2002; Ross *et al.* 2004; van Groenigen *et al.* 2011). Interestingly, soil CH_4 and N_2O fluxes response to elevated CO_2 negatively depended on soil C/N ratio in this analysis (Fig. 4), suggesting that the elevated CO_2-stimulated CH_4 and N_2O fluxes will diminish with the increase in soil C/N ratio. Indeed, soil C/N ratio has been well documented to be factors important to soil GHGs emissions (Stehfest & Bouwman 2006; Chen *et al.* 2014). Besides soil physicochemical properties, soil functional microbes may play an important role in the response of GHGs to elevated CO_2, although we failed here to synthesise the general conclusion due to currently limited data available in this meta-analysis. As also observed in this analysis, soil microbial biomass components were increased under elevated CO_2 (Fig. 1c–e) and this increase would be intensified with the level of CO_2 enrichment (Fig. S1a and b). Given that the activity of GHGs-related soil microbial communities largely relies on root-oriented C input and N availability under elevated CO_2,

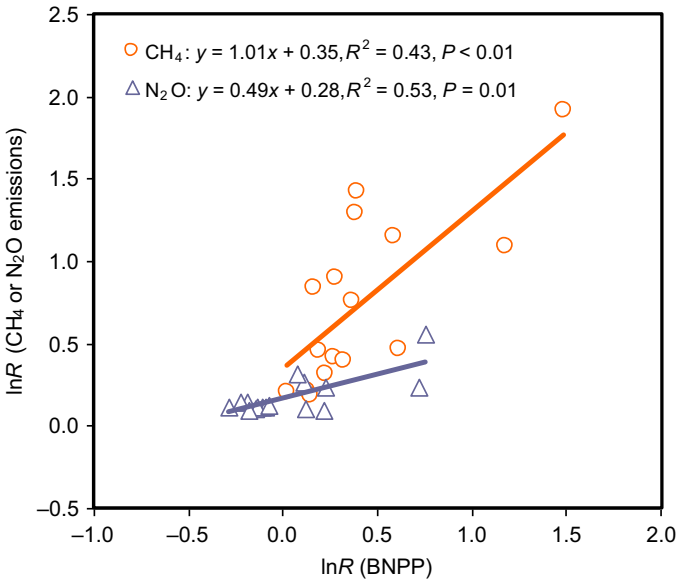

Figure 3 Elevated CO_2-induced changes in soil CH_4 fluxes from wetlands and rice paddies and soil N_2O fluxes against those of plant below-ground net primary production (BNPP). Data were gathered from studies where CH_4 or N_2O fluxes were simultaneously measured with plant below-ground C under elevated CO_2.

elevated CO_2 would improve the performance of soil microbes, including the functional microbes related to soil GHGs production (Hu *et al*. 1999; Zak *et al*. 2000).

Besides, the response of soil GHG fluxes to elevated CO_2 may depend on the level of CO_2 enrichment. Elevated CO_2-induced changes in soil CH_4 uptake were positively and significantly correlated with the level of CO_2 enrichment (Fig. S2a). Although we did not find strong relationships between elevated CO_2-induced changes in CH_4 and N_2O fluxes with the level of CO_2 enrichment, the changes in net SGWP of CH_4 and N_2O under elevated CO_2 significantly decreased with CO_2 enrichment levels in studies where soil CH_4 and N_2O fluxes were simultaneously measured (Fig. S2b). Together, these results suggest that the elevated CO_2-induced increase in GHG emissions may decline with the level of CO_2 enrichment, which is primarily ascribed to soil C/N ratio (soil microbial C/N ratio in particular) increased under elevated CO_2. Indeed, soil microbial C/N ratio significantly increased with the level of CO_2 enrichment (Fig. S1b) and elevated CO_2-induced changes in CH_4 and N_2O fluxes decreased with soil C/N ratio (Fig. 4). On the other hand, elevated CO_2-induced changes in CH_4 and N_2O fluxes highly relied on plant biomass (Fig. 3) and the stimulation of plant biomass under elevated CO_2 is well documented to diminish with the level of CO_2 enrichment (Wang *et al*. 2015). Therefore, the declined response of soil GHGs to the level of CO_2 enrichment would be associated with changes in soil properties and plant growth under elevated CO_2. In addition, responses of soil CO_2 fluxes to elevated atmospheric CO_2 were negatively dependent on the initial levels of soil C and N contents (Fig. S3).

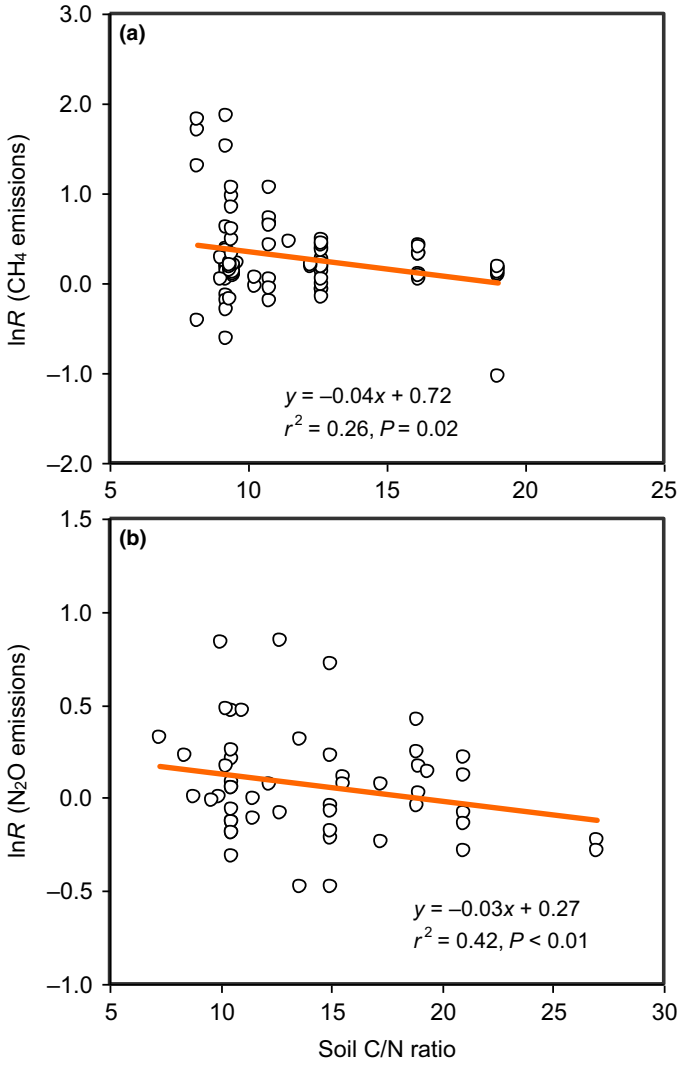

Figure 4 Dependence of soil CH_4 (a) and N_2O (b) fluxes response to elevated CO_2 on soil C/N ratio.

GHGs budget of terrestrial ecosystems under elevated CO_2

Here, we extrapolated results of this meta-analysis into global context and compared with previous syntheses. Our findings are generally comparable to the previous estimate of 0.25 Pg CO_2-eq. $year^{-1}$ for elevated CO_2-induced rise in CH_4 fluxes from rice paddies, but significantly greater than the value of 0.31 Pg CO_2-eq. $year^{-1}$ for elevated CO_2-raised CH_4 fluxes from natural wetlands (van Groenigen *et al*. 2011). The combined effect of elevated CO_2 on CH_4 and N_2O fluxes corresponds to an additional total source strength of 2.76 Pg CO_2-eq. $year^{-1}$, greater than the estimates of earlier syntheses based on individual land sources and incomplete estimation of GHGs (Ziska *et al*. 1998; van Groenigen *et al*. 2011).

Soil organic C and total N sink strengths enhanced under elevated CO_2 were estimated to be 2.42 Pg CO_2 $year^{-1}$ and 0.02 Pg N $year^{-1}$, respectively (Table 1, Fig. 2). Our estimate of soil C sequestration was lower than that of 4 Pg CO_2 $year^{-1}$ in a previous meta-analysis with limited data volume in forest soils (Schlesinger & Lichter 2001). Biogeochemical models predict that rising atmospheric CO_2 may stimulate the terrestrial C sink by 6.8 Pg CO_2 $year^{-1}$, far greater than the estimate of CO_2-induced rise in NEP (3.99 Pg CO_2 $year^{-1}$) in this synthesis (Thornton *et al*. 2007). However, the slight increment (4.3%) of SOC under elevated CO_2 in this synthesis was comparable to the difference between the increase in C input (19.8%) and the C turnover (16.5%) in soils under atmospheric CO_2 enrichment in an earlier synthesis study (van Groenigen *et al*. 2014).

Obviously, uncertainties were involved using our approach to estimate the overall actual extent at the global scale due to inherent limitations in experimental and statistical methodologies. First, we assumed that the changes in GHG fluxes and soil C and N pools induced by elevated CO_2 over 1–12 years step-change experiments can be extrapolated to gradual CO_2 effect on them expressed as area basis, which had its own problematic issues but can be adequately used for global scale climate predictions as previously addressed (Luo & Reynolds 1999). Moreover, the approach itself necessitated a saturated linear function to estimate the soil C and N sink strength, which may lead to an underestimate of the actual sequestration rate under elevated CO_2 (Gill *et al*. 2002).

CONCLUSIONS

We showed a comprehensive accounting of GHG (CO_2, CH_4, N_2O and NEP) exchanges between terrestrial ecosystems and the atmosphere, linked to soil C and N pools under elevated

CO_2. Our synthesis suggests that an elevated CO_2-induced rise in soil CH_4 and N_2O emissions could negate soil C enrichment or largely reduce mitigation potential of terrestrial NEP under elevated CO_2. Elevated CO_2-induced changes in GHG fluxes are associated with soil physicochemical properties, including soil water content, soil C/N ratio, soil C input under elevated CO_2, and the level of CO_2 enrichment. Clearly, soil biotic factors also play important roles in driving soil GHGs response to elevated CO_2, such as soil microbial C/N ratio, soil functional microbes related to GHGs production and consumption, although we failed here to synthesise the general conclusion due to limited data available in this meta-analysis. Nevertheless, our results highlight that the capacity of terrestrial ecosystems to act as a sink to slow climate warming under elevated CO_2 might have been largely offset by its induced increases in source strength of soil GHGs.

Future directions

This meta-analysis concentrated on the effects of elevated CO_2 alone on soil C and N cycling, and failed to take its interaction with other climate change factors (e.g. warming or drought) into account due to limitation of available data size. We also did not find any solid relationships between the responses of soil C and N fluxes to elevated CO_2 and experimental duration in this analysis. Despite the additive effects of multiple global change factors on soil C and N biogeochemistry may be common, the need for more long-term well-designed multifactor manipulation experiments should be highlighted in future research efforts (Dieleman *et al*. 2012; Zhou *et al*. 2016; Yue *et al*. 2017). Furthermore, the site distribution of present available data set was overwhelmingly dominated in temperate and subtropical regions, still lack of studies in the tropics, where GHG fluxes and N inputs are generally expected to be higher (Thornton *et al*. 2007). In addition, soils are nowadays generally subject to different rates of atmospheric N deposition, especially in subtropical and tropical areas, where N deposition is predicted to increase in the coming decades (Galloway *et al*. 2008). As suggested by earlier studies (van Groenigen *et al*. 2006; Galloway *et al*. 2008), elevated CO_2-induced soil C sequestration would be largely constrained by soil N availability, and hence atmospheric N deposition should also be addressed to deal with its interactive impacts with CO_2 enrichment and other climate factors on soil C and N dynamics in order to be more representative of future world. Besides, how elevated CO_2 affects other key soil essential nutrients (e.g. soil phosphorus or potassium) cycling or interacts with them to alter soil C and N cycling is the challenge of great concern in the future. Meanwhile, a better ecologically relevant metric also needs to be developed to further underpin nutrient cycling response to climate by integrating more biogeochemical factors. In particular, understanding the microbial mechanisms of GHG response to climate change is particularly important as it is widely believed that microorganisms play important roles in global C and N biogeochemical cycles, yet they are generally not included in current biogeochemical models to predict terrestrial ecosystems feedback to climate change.

ACKNOWLEDGEMENTS

This work was supported by the Natural Science Foundation of China (41771268, 41225003, 41771323), National Basic Research Program of China (2015CB150502), National Key Research and Development Program of China (2016YFD0201200), Fundamental Research Funds for the Central Universities (KYTZ201404, KYZ201621). We appreciate the anonymous reviewers and the corresponding editor for their insightful comments and Dr. David Powlson at Rothamsted Research for his work on the English edit of manuscript. We are grateful to many researchers who measured soil GHG fluxes and soil labile C and N fractions as well as other target parameters. Their work is the basis of the present data integration, which would in turn guarantee access of a full understanding of elevated CO_2 effects on soil C and N biogeochemical cycles.

CONFLICT OF INTERESTS

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

S.W.L., S.L.N. and J.W.Z. designed the investigation. S.W.L., C.J., J.C., C.W., Z.H.Z. and S.Q.L. extracted the data from literature and constructed the database. S.W.L. and Y.G.J. performed the statistical analyses. All authors contributed to writing the manuscript.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Editor, Johannes Knops
Manuscript received 18 January 2018
First decision made 19 February 2018
Second decision made 26 March 2018
Manuscript accepted 4 April 2018