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Global patterns and controls of the soil microbial biomass response to elevated CO_2

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ABSTRACT

Elevated CO_2 concentrations (eCO_2) have been widely observed to stimulate microbial growth. However, the effect of eCO_2 on soil microbial biomass may depend on several factors and their interactions, such as the increase in atmospheric CO_2 levels, experimental duration and mean annual precipitation (MAP). We conducted a global *meta*-analysis from 62 studies that included the responses of soil microbial biomass to eCO_2. We found a significant positive eCO_2 effect on the bacterial biomass (+9.1 %), fungi (+11 %), arbuscular mycorrhizal fungi (AMF) (+10.2 %) and actinomycetes (ACT) (+16.4 %). The positive effects were mainly observed in studies with low eCO_2 levels (≤200 ppm) rather than high levels of eCO_2 (>200 ppm), which could be attributable to soil N limitation. It was also found that eCO_2 had a significant positive effect on soil microbial biomass in the short term (≤3 y) and under a high MAP (>800 mm). Importantly, we revealed interactive effects between the eCO_2 levels, experimental duration on soil microbial biomass. With an increase in eCO_2, the total microbial biomass (TMB), bacterial biomass and fungal biomass decreased over the long term (>3 y). These findings indicate the need to incorporate interactions between eCO_2 and environmental factors into ecosystem models, to predict future global climate change effects more accurately and their impact on ecosystem functions.

1. Introduction

The global atmospheric CO_2 concentration is likely to increase further as a consequence of fossil fuel combustion and land-use changes (IPCC, 2007). The CO_2 fertilisation of plant growth due to elevated CO_2 concentrations (eCO_2) sequesters carbon in plant biomass (Houghton et al., 2001; Carter et al., 2007; Arneth et al., 2010). Increased carbon sequestration offers more substrate for soil microorganisms (van Groenigen et al., 2014; Brienen et al., 2015; Chen et al., 2016), and will therefore increase soil microbial activity (Chung et al., 2007). Although the importance of microbial responses to eCO_2 have been recognised, there is a need to clarify the mechanisms behind the responses and to predict the likely outcomes of further increases in the atmospheric CO_2 concentration.

Studies of eCO_2 across multiple ecosystems have shown positive (Hu et al., 2001; Yang et al., 2021), small (Gorissen et al., 1995) or even negative effects (Luo et al., 2017) on soil microbial biomass. These contradictory findings could be explained by differences in experimental design, with the range of eCO_2 varying widely, in addition to various experimental durations and environmental conditions (Blagodatskaya et al., 2010; Dunbar et al., 2012; Feng et al., 2010). The actual level of eCO_2 used in experiments plays a decisive role in regulating soil microbial biomass (Luo et al., 2017; Hu et al., 2001; Yang et al., 2021). High eCO_2 may lead to low soil nutrient availability by promoting plant nutrient uptake; therefore, suppressing soil microbes and reducing their biomass (Blagodatskaya et al., 2010; Eisenhauer et al., 2012; Xiao et al.,

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2017). For example, a negative response of soil microbial biomass to eCO_2 (+400 ppm) was shown to be related to the decreasing concentration of dissolved organic nitrogen in the rhizosphere soil (Xiao et al., 2017). However, microbial biomass was increased in a grassland ecosystem where eCO_2 (+180 ppm) was assumed to fuel microbes by increasing soil labile C (Eisenhauer et al., 2012). These opposite effects observed in published studies lead to the conclusion that an eCO_2 effect always exists, but it has large variability in terms of the observed responses of soil microbial biomass because of the lack of realistic experiments comparing several different CO_2 gradients.

The response of soil microbial biomass to CO_2 fertilisation effects are likely to be restrictive over time. The N limitation feedback hypothesis suggests that negative impacts of eCO_2 on soil N availability can constrain the responses to eCO_2 (Oren et al., 2001). For example, in a one-year cross-biome study, eCO_2 increased the biomass of bacteria, fungi and actinomycetes (ACT) by increasing the soil C concentration (Song et al., 2012). However, in a long-term study (13 y), in a forest ecosystem, eCO_2 did not alter the soil fungal biomass due to the N limitation of the ecosystem (Feng et al., 2010). Through long-term monitoring of the response of the soil microbial biomass to eCO_2, new information on system function prediction may be provided. However, most published studies were not long enough to assess whether there could be any shift from positive to negative feedback over the long term.

Divergent empirical findings on the effects of eCO_2 on soil microbial biomass might also result from differences in climate (temperature and precipitation), the methods of CO_2 enrichment, ecosystem type, and the soil depth that was sampled (Yue et al., 2017; Chen et al., 2020). For example, combining eCO_2 and precipitation can increase microbial activity (Rodriguez-Caballero et al., 2018) by enhancing the soil water content (Luo et al., 2017). However, such positive effects may be offset by the negative effect of higher temperatures (Hayden et al., 2012; Delgado-Baquerizo et al., 2017). High temperatures increase soil evaporation, which will strongly influence soil microbial communities (Sheik and Beasley, 2011; Hayden et al., 2012). The methods of eCO_2 present in the soil add an additional complexity to the soil processes due to form a special microclimate (Huang et al., 2017). Unlike the situation in natural ecosystems, the soil microbial biomass response to eCO_2 may positive in controlled environment due to the absence of nutrient limitations (Hu et al., 2017). Furthermore, soil microbial biomass is generally lower in the deeper soil layers than in topsoil because of the greater plant biomass and root inputs (Chen et al., 2020). Although the effects of eCO_2 on soil microbial biomass have been studied extensively, our understanding of the regulating factors and their interactions is still limited.

To determine how eCO_2 affects soil microbial biomass, we conducted a global *meta*-analysis from 62 studies (up to April 2022). The aim of the study was to address three important questions. 1) how does eCO_2 affect soil microbial biomass? 2) what are the interactive effects between the actual level of eCO_2, experimental duration and environmental factors? 3) what are the potential factors driving the effects of eCO_2 on soil microbial biomass?

2. Materials and methods

2.1. Data collection

A *meta*-analysis method was used to analyse the published data of terrestrial ecosystems (Hedges et al., 1999; Morgan et al., 2018) (Table S1). Data were searched using CNKI (China National Knowledge Infrastructure) (https://www.cnki.net/), Google Scholar (https://scholar.google.com/), and the Web of Science (https://apps.webofknowledge.com/). The terms used were "Elevated CO_2" OR "carbon dioxide enrichment" OR "carbon dioxide" AND "microbial biomass" OR "microbial abundance" OR "microbial community" OR "fungi" OR "bacteria" OR "litter decomposition" OR "microbial respiration" OR "soil respiration" OR "microbial activity". Data extration a total of 62 publications including 61 English articles and 1 Chinese articles worldwide (Asian (10), Europe (31), Oceania (1), North America (22)) (Fig. S1, Fig. S2, Table S2 and Supplementary Data). Overall, the dataset included broad variations in ecosystem types (cropland, desert, forest, grassland, controlled environment). We used the following criteria to select relevant observations. (1) Studies had to include control and elevated CO_2 treatments (all the eCO_2 levels are above current levels). (2) The control and treatment plots were established in the field under the same abiotic and biotic conditions. (3) At least one of the selected variables was measured. (4) The means and sample sizes were reported or were possible to calculate. (5) To make sure the independence in our *meta*-analysis, the final measurement was collected if multiple repeated measurements were reported. Measurements from different ecosystems, treatment levels, species, plant organs and the final year in each study were considered as independent observations (Yuan and Chen, 2015). The Engauge software 4.1 was used to obtain data that were graphically presented. The global distribution of the experimental sites is shown in Fig. S2. The observations were categorised according to the following six factors: CO_2 concentration change (ΔCO_2) ($\leq$200, and $>$ 200 ppm), duration of the experiment ($\leq$3 y and $>$ 3 y), MAP ($\leq$400, 400–800, and $>$ 800 mm), ecosystem type (cropland, forest, grassland and controlled environment), the method of elevated CO_2 ((Free-Air CO2 Enrichment) FACE, (Opten-Top Champer) OTC and (Closed-Top Champer) CTC and the sampled soil depth ($\leq$15 and $>$ 15 cm). Due to data limitation, we were unable to perform related analysis for some categories.

2.2. meta-analysis

The effect size of the eCO_2 treatment on soil microbial biomass was evaluated by a log response ratio (ln*RR*) according to the method presented by Hedges et al. (1999):

$$\ln RR = \ln(X_e/X_c) \tag{1}$$

where X_e and X_c are the means of the concerned variable in the treatment and control, respectively. In addition, the SD and sample size of each treatment were used to calculate ln*RR*. Violin plots were used to visualize the density distributions of InRR across all the studies (Fig. 1a). For the statistical test, the variance (v), weighting factor (w_{ij}), weighted mean response ratio (RR_{++}), and the confidence interval (95 % CI) were calculated as follows:

$$v = \left(\frac{S_e^2}{n_e X_e^2}\right) + \left(\frac{S_c^2}{n_c X_c^2}\right) \tag{2}$$

where S_e and S_c are the SDs and N_e and N_c are the sample sizes of the eCO_2 treatment and control treatment, respectively:

$$W_{ij} = \frac{1}{v} \tag{3}$$

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij} RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}} \tag{4}$$

$$(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}} \tag{5}$$

$$95\%CI = RR_{++} \pm 1.96 S(RR_{++}) \tag{6}$$

The metawin software 2.1 was used to evaluate the variables. The 95 % CI value of RR_{++} for a variable including zero indicated that the eCO_2 treatment had no significant effect. The results for the data with sample size <3 are not presented. The actual percentage change transformed from ln*RR* and its corresponding CI was calculated as:

$$\left(e^{LnRR} - 1\right) \times 100\% \tag{7}$$

The paired *t*-tests and Holm-Bonferroni correction were conducted to

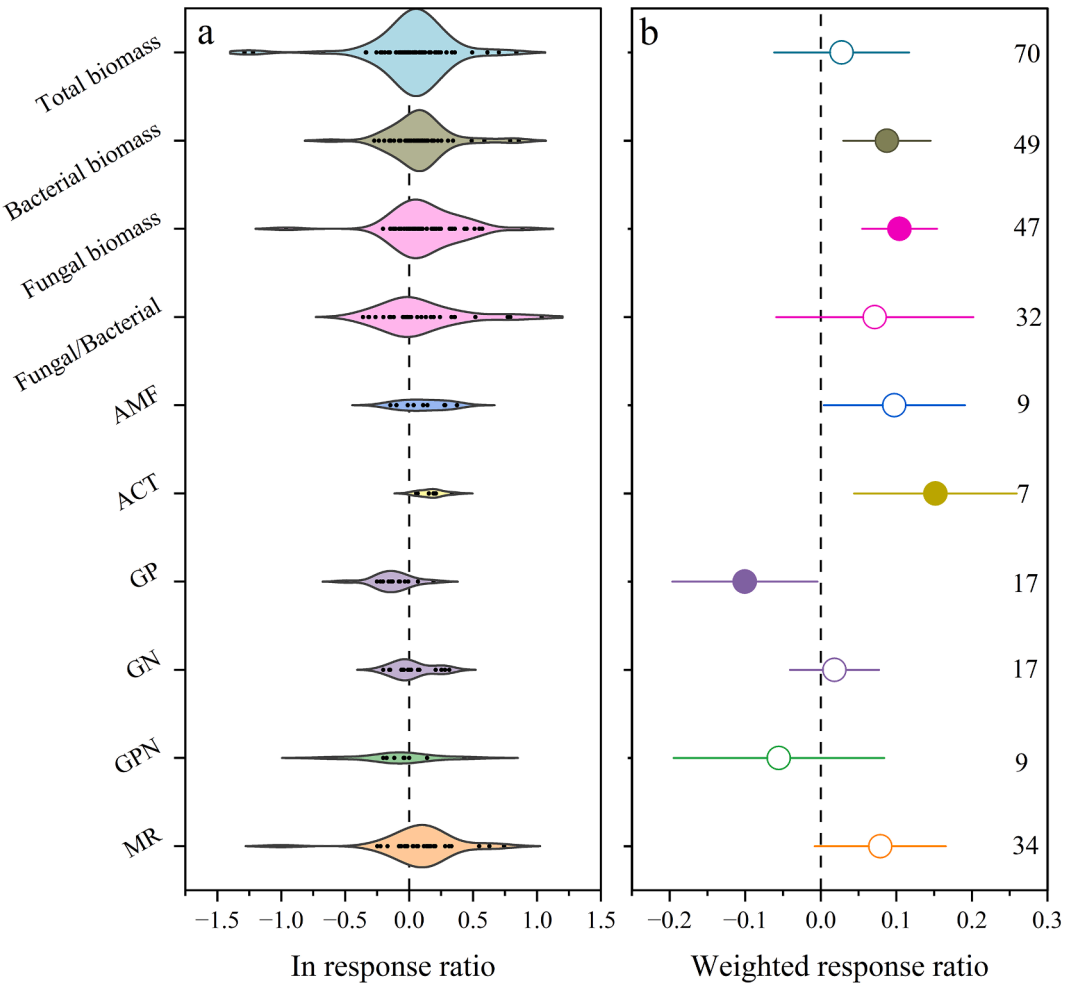

Fig. 1. Effects of eCO_2 on soil microbial biomass. In a, the ln Response ratios of eCO_2 for all studies carried out in the context. In b, Response ratios (RR) for eCO_2 on soil microbial biomass. Error bars represent ± 95 % confidence intervals of the percentage effects between the CO_2 addition and control treatments. The number of observations is in parentheses. AMF, ACT, GP, GN and MR represent the biomass of arbuscular mycorrhizal fungi, actinomycetes, gram-positive bacteria, gram-negative bacteria and microbial respiration, respectively. Solid circles indicate significant, empty circles indicate non-significant.

compare the response of soil microbial parameters to eCO_2 among different classes of various categorical moderators.

3. Results

3.1. Effects of eCO_2 on soil microbial biomass

Across all the studies, eCO_2 significantly increased bacterial biomass, fungal biomass, AMF biomass, and ACT biomass by an average of 9.1 %, 11 %, 10.2 %, and 16.4 %, and reduced the gram-positive bacteria (GP) biomass by 9.6 %, respectively (Fig. 1b). However, there was no significant effect on the total soil microbial biomass (TMB), gram-negative bacteria (GN) biomass, fungi/bacteria (F/B) ratio, and GP/GN ratio (Fig. 1b). When ΔCO_2 concentration was ≤ 200 ppm, the bacterial biomass, fungal biomass and ACT biomass increased by 14.9 %, 13.4 % and 16.4 %, respectively, but the GP biomass decreased significantly (14.8 %) at high ΔCO_2 concentration (>200 ppm) (Fig. 2a).

The duration of the experiment had various effects on the response of soil microbial biomass. The eCO_2 significantly increased bacterial biomass and fungal biomass by 14.5 %, and 15 %, respectively, during the short term. The GP biomass decreased significantly (11.1 %) over periods > 3 y. No significant effects were observed for total microbial biomass (TMB), F/B ratio, AMF biomass, ACT biomass, GN biomass and GP/GN ratio (Fig. 2b).

There were contrasting responses of the soil microbial biomass to eCO_2 under different precipitation regimes. The eCO_2 significantly increased the total microbial biomass, bacterial biomass and fungal biomass by 16.3 %, 14.4 % and 12.6 %, respectively, under > 800 mm precipitation, but the fertilisation effect did not occur under other MAP levels. The eCO_2 dereased GP biomass by 12.2 % under 400–800 mm precipitation. In contrast, eCO_2 had no significant effect on AMF, ACT, GN, F/B, and GPN in any precipitation group (Fig. 2c).

A comparison of the application CO_2 method revealed a significant increase in bacterial biomass (13.2), fungal biomass (8 %), AMF biomass (10.2 %), ACT biomass (16.4 %) with the method of OTC. There were significant decreases in GP biomass (14.9 %) by the method of FACE in response to eCO_2 (Fig. 3a). Moreover, eCO_2 significantly increased the bacterial biomass, fungal biomass and ACT biomass, in the ≤15 cm soil layers. No significant effects were observed in the soil microbial biomass response to eCO_2 at >15 cm soil depth (Fig. 3b).

In cropland ecosystems, fungal biomass, and ACT biomass increased by 16.1 %, in response to eCO_2. The stimulation of bacterial biomass by eCO_2 increased by 24.6 % and 11.7 in forests and grassland, respectively (Fig. 3c).

3.2. Correlations between soil microbial biomass and climatic factors

Averaged across eCO_2 levels and duration treatments, the effect of eCO_2 on TMB, bacterial biomass and fungal biomass also varied with experimental duration, with the highest sensitivity at >3 y (Fig. 4). We

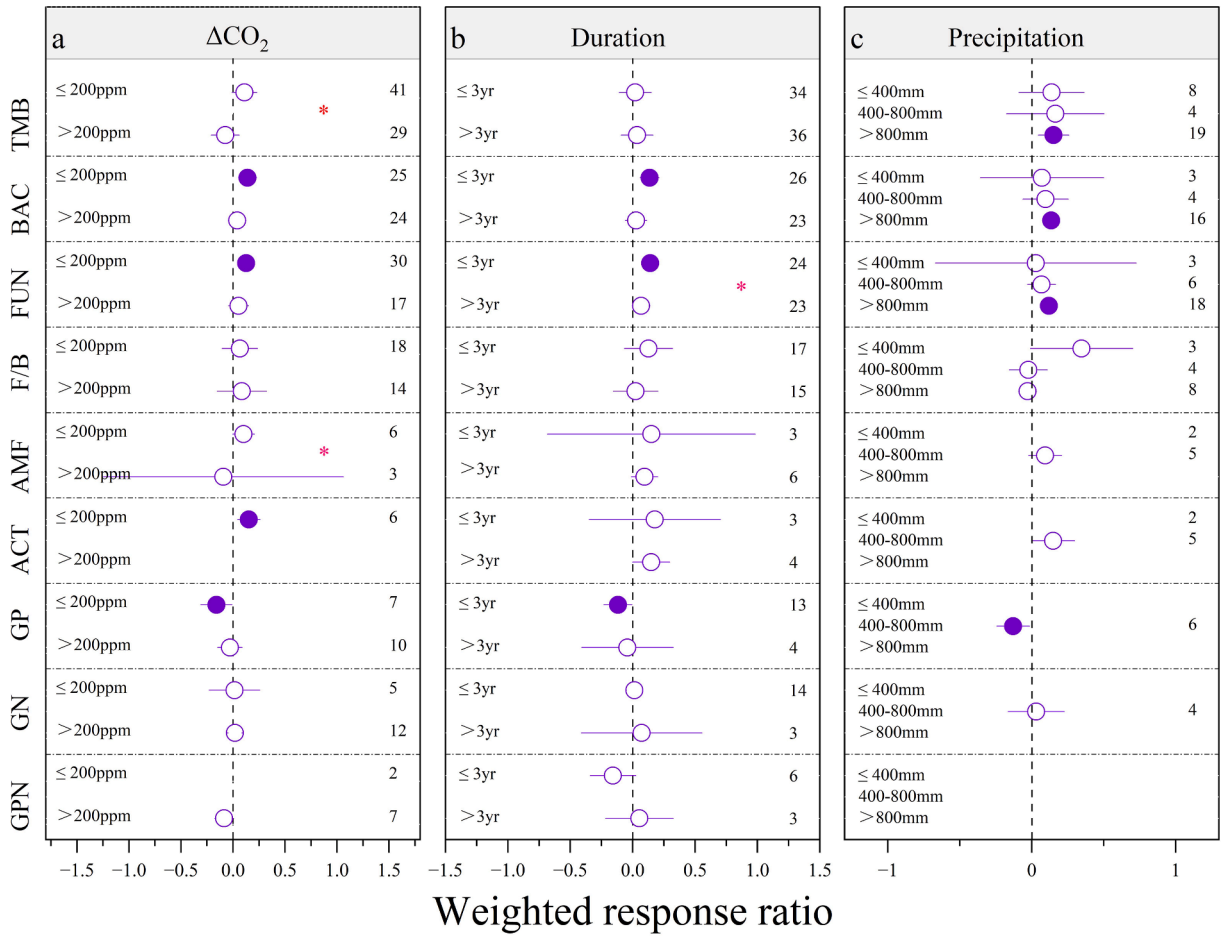

Fig. 2. Effects of eCO_2 on soil microbial biomass. The variables are categorised into different groups according to the eCO_2 level, duration of the experiment, soil depth, and mean annual precipitation (MAP). Error bars represent ± 95 % confidence intervals of the percentage effects between the CO_2 addition and control treatments. The number of observations is in parentheses. * indicate significant differences among different treatments ($P < 0.05$ after Holm-Bonferroni adjustment; paired *t*-test).

found significant negative correlations between the RRs of the C/N ratio and the RRs of TMB, and bacterial and fungal biomass (Fig. 5). Additionally, we found significant positive correlations between the RRs of the C/N ratio and eCO_2 treatment levels (Fig. 5).

4. Discussion

In total, 62 peer-reviewed publications reporting results from global terrestrial ecosystems, from tropical to boreal regions, were included in the database (Fig. S2). Most experiments included in our *meta*-analysis were conducted in the northern hemisphere. The ΔCO_2 concentration ranged between 40 and 450 ppm. Thus, the magnitudes of eCO_2 in our synthesis are consistent with projections of the end of the century (Table S1). This study presents the first global-scale empirical evidence that the effect of eCO_2 on soil microbial biomass depends on the actual level of the eCO_2. The range of eCO_2 (≤200 ppm) stimulated soil microbial biomass, while the range of eCO_2 (>200 ppm) had a neutral or even negative effect. Importantly, complex interactive effects occurred between the eCO_2, treatment levels and experimental duration, (>3yr) although they were not ubiquitous. Understanding how changes in eCO_2 interact with experimental duration to impact soil microbial biomass is therefore crucial for predicting microbiome responses to climate change. This highlights the need for future long-term field studies that apply different eCO_2 treatment levels and precipitation-associated changes that are likely to occur in a given region.

In addition to the widely presented positive effects of eCO_2 on soil microbial biomass (Eisenhauer et al., 2012), our results just found a positive effect on bacterial biomass, fungal biomass, AMF biomass and ACT biomass (Fig. 1b). Soil microorganisms can be divided into copiotrophic and oligotrophic classes, with the former having a lower biomass C to nutrient ratio, thus, needing more nutrients (Zechmeister-Boltenstern et al., 2015; Delgado-Baquerizo et al., 2017). The eCO_2 induces more C and less N into soil by stimulating plant growth, which provides a competitive advantage to oligotrophic organisms (Andrews and Harris, 1986). Therefore, some microbes can quickly gain a big competitive advantage due to their insensitivity to nutrient-limitation when the ecosystem faces eCO_2 (Zechmeister-Boltenstern et al., 2015; Delgado-Baquerizo et al., 2017). As a result, given the differing sensititivities among different microbial groups in our database when facing CO_2 enrichment (Zechmeister-Boltenstern et al., 2015; Delgado-Baquerizo et al., 2017), there was no apparent change or even a decline in TMB, F/B, GP biomass, GN biomass and GP/GN (Fig. 1b). These results suggest various CO_2 sensitivies among different microbial groups, with bacterial biomass, fungal biomass, AMF biomass and ACT biomass more sensitive to eCO_2 than others.

In our synthesis, there were more positive effects of eCO_2 on most microbes at the ranges of eCO_2 levels (≤200 ppm) than of high eCO_2 (>200 ppm) (Fig. 2a), which indicated that eCO_2 did not stimulate CO_2 fertilization of soil microbial biomass when the concentration exceeds a certain threshold level. This was a unique observation that has not been reported in previous synthesis. The likely explanation is attributable to the reduction in soil nutrition availability under high treatment level of

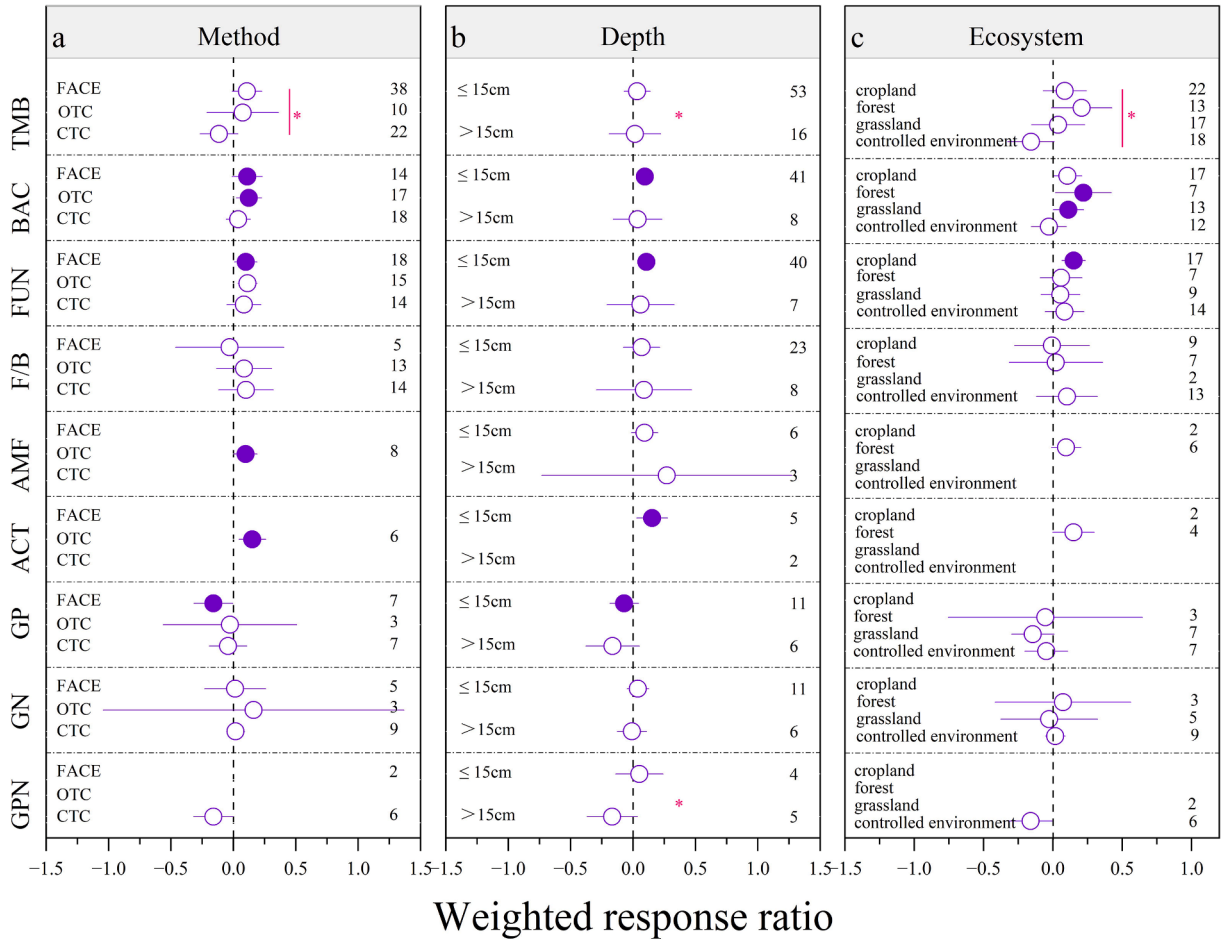

Fig. 3. Effects of eCO_2 on soil microbial biomass. The variables are categorised into different groups according to eCO_2 method, sampled depth and ecosystem. Error bars represent ± 95 % confidence intervals of the percentage effects between the CO_2 addition and control treatments. The number of observations is in parentheses. * indicate significant differences among different treatments ($P < 0.05$ after Holm-Bonferroni adjustment; paired *t*-test).

eCO_2 (Oren et al., 2001). Indeed, at the ecosystem level, individual CO_2 experiments show complex results for the magnitude of the growth and biomass response to eCO_2 with nutrient limitation, such as N, P or other element limitation in other studies (Norby, 2010). Similarly, experimental CO_2 enrichment generally enhanced the ratios of C/N by stimulating plant growth and nutrient uptake, although it was nonsignificant in some cases due to the limited observations (Hu et al., 2001; Sulman et al., 2014; Jin et al., 2019). Collectively, CO_2 enrichment probably leading to significant lower amounts of N being available in soil when CO_2 concentration exceed certain limit (Xiao et al., 2017). The consistent increase in CO_2 fertilizer efficiency when enough N is available suggests that N limtation significantly reduces the capacity of soil microbial biomass to CO_2 enrichment (Hu et al., 2001; Sulman et al., 2014; Grover et al., 2015). The pattern corresponded to a negative effect of eCO_2 levels on soil N availability in our study (Fig. 5d). Thus, extrapolating our observation of the decreased microbial biomass in *N*-limited soils to naturally fertile or fertilised soils resulted in a greater global increase in the effect of eCO_2.

As our study did for eCO_2, Dunbar et al. (2012) found a positive long-term (>3 y) effect on microbial biomass after fertiliser additions, which suggests an interaction between the CO_2 fertilisation effect and increased soil nutrient concentrations in ecosystems. However, our framework found that eCO_2 had a significant positive effect on bacterial and fungal biomass in the short term (≤3 y) rather than the long term (>3 y) (Fig. 2). In addition, based on the evidence from both treatment levels and experimental duration changes we found an interaction effect on bacterial and fungal biomass when facing long-term CO_2 enrichment (Fig. 4). The diminished CO_2 fertilisation effect may be attributed to the negative impacts of eCO_2 on N cycling, constraining the soil microbe responses to eCO_2 (Hu et al., 2001; Sulman et al., 2014). The increased inputs of CO_2 stimulated net N mineralisation and hence plant N uptake over time (Drake et al., 2011; Phillips et al., 2011), aggravating the nutrient limitation of eCO_2 on soil microbial biomass. Thus, our synthesis do support the notion that the interactive effects of eCO_2 treatment levels and long experimental duration on soil microbial biomass weaken the eCO_2 effect under long term treatments.

Our results also showed that the ranges of precipitation (>800 mm) increased the effect of eCO_2 on TMB, bacteria biomass, fungi biomass and ACT biomass (Fig. 3c). When water resources were at their highest, the effect of eCO_2 on soil biomass was even higher with an increase in the eCO_2 (Maestre et al., 2015; Dacal et al., 2019). There was evidence that water limitation could be responsible for increasing the eCO_2 fertilisation effect. Studies conducted in a grassalnd showed CO_2 fertillzation effects can be enhanced when rainfall is high, because high rainfall also leads to improved soil water availablity (Egea et al., 2012). High nutrient accumulations have been observed in soil under high precipitation levels (Han et al., 2011). These findings suggest that the CO_2 fertilisation effect on soil microbes will be enhanced in high precipitation regions, which will have a further impact on microbe-mediated ecosystem functions (Dacal et al., 2019).

Under experimental CO_2 enrichment, the positive effect on soil microbial biomass was attributed the method of OTC (Fig. 3a). The methods of OTC may be the primary modulator of soil microbial biomass responses to eCO_2 by regulating microclimate (Huang et al., 2017).

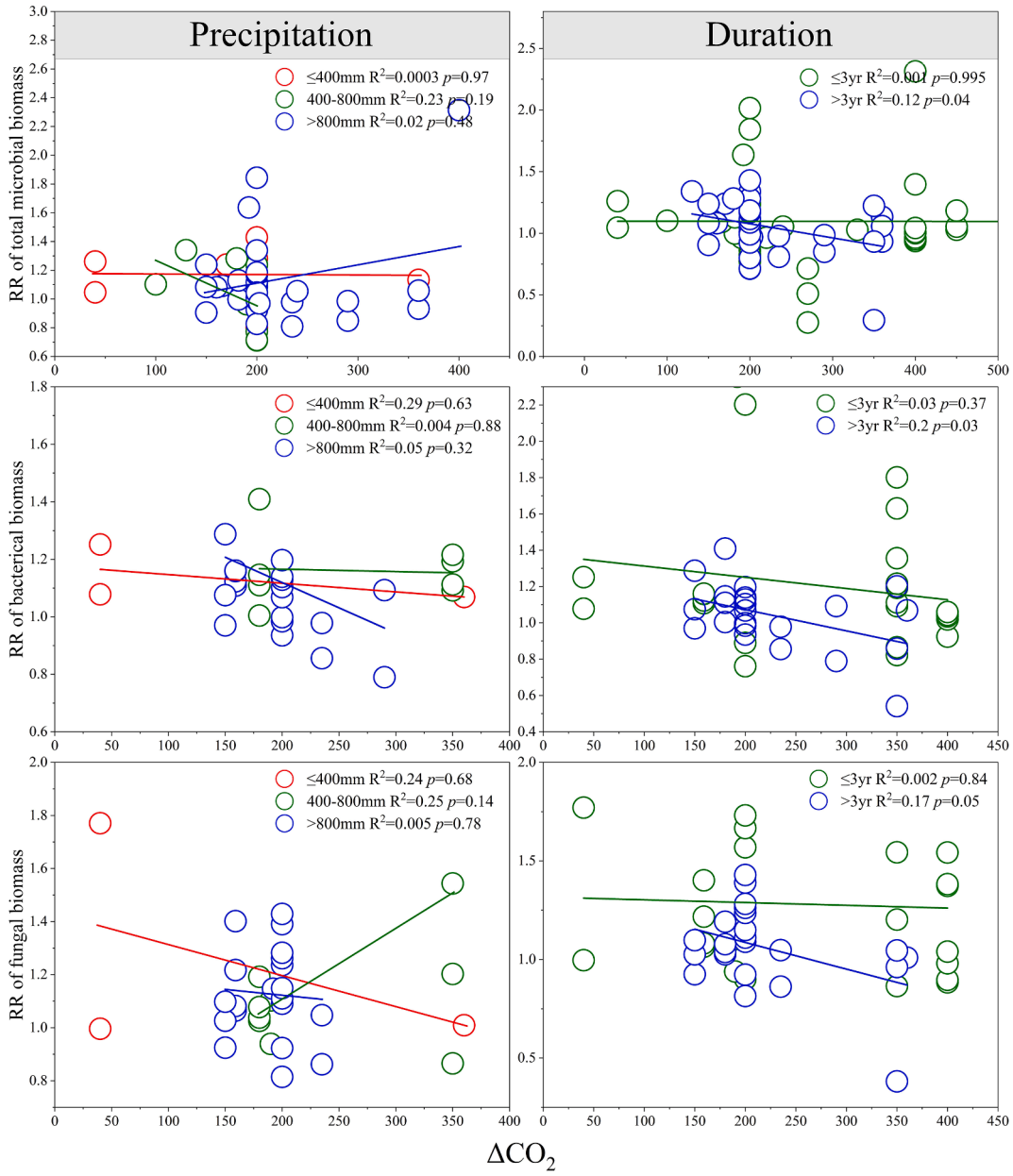

Fig. 4. Relationships between the response ratios (RRs) of total microbial biomass, bacterial biomass, fungal biomass and the eCO_2 level at different mean annual precipitation (MAP) levels and experimental durations.

Finally, the results showed that soil microbial responses were significantly increased in the topsoil (Fig. 3b), which was probably because most roots grow in topsoil, increasing the organic matter input (Chen et al., 2020). Based on a *meta*-analysis of published studies, the existing framework describes the different effects of eCO_2 on soil microbial biomass over a wide range of ecosystem types, including croplands, forests, grasslands and controlled environment (Li et al., 2004; Kandeler et al., 2008; Godbold et al., 2015). However, no significant effect of eCO_2 on the of soil microbial biomass variables only occurred in majority ecosystems (Fig. 3c). This implies that the maintenance of maximal soil microbial growth through CO_2 enrichment requires optimal nutrient concentrations, and in majortiy the abundance of CO_2 applications aggravate nutrient limitations (Soussana and Lemaire, 2014). Our findings revealed that, for a diverse range of ecosystem types, with varying soil depth and climates, the CO_2 fertilisation effects on soil microbial community composition vary depending on the exact CO_2 level.

5. Conclusions

Our results suggest that ongoing increasing atmospheric CO_2 concentrations will have profound effects on soil microbes. The positive effects of eCO_2 on soil microbial biomass and composition varied with the exact level of eCO_2. The impacts of eCO_2 levels on soil microbes were strongly linked to the experimental duration. Furthermore, these CO_2 fertilisation effects shifted across different terrestrial biomes, including forests, grasslands, croplands and controlled environment. Our *meta*-analysis reconciled conflicting evidence on the eCO_2 fertilisation effect across scales and provided an empirical estimate of soil microbial biomass sensitivity to eCO_2 that may help to predict soil microbial changes under future increasing atmospheric CO_2 concentrations.

Declaration of Competing Interest

The authors declare that they have no known competing financial

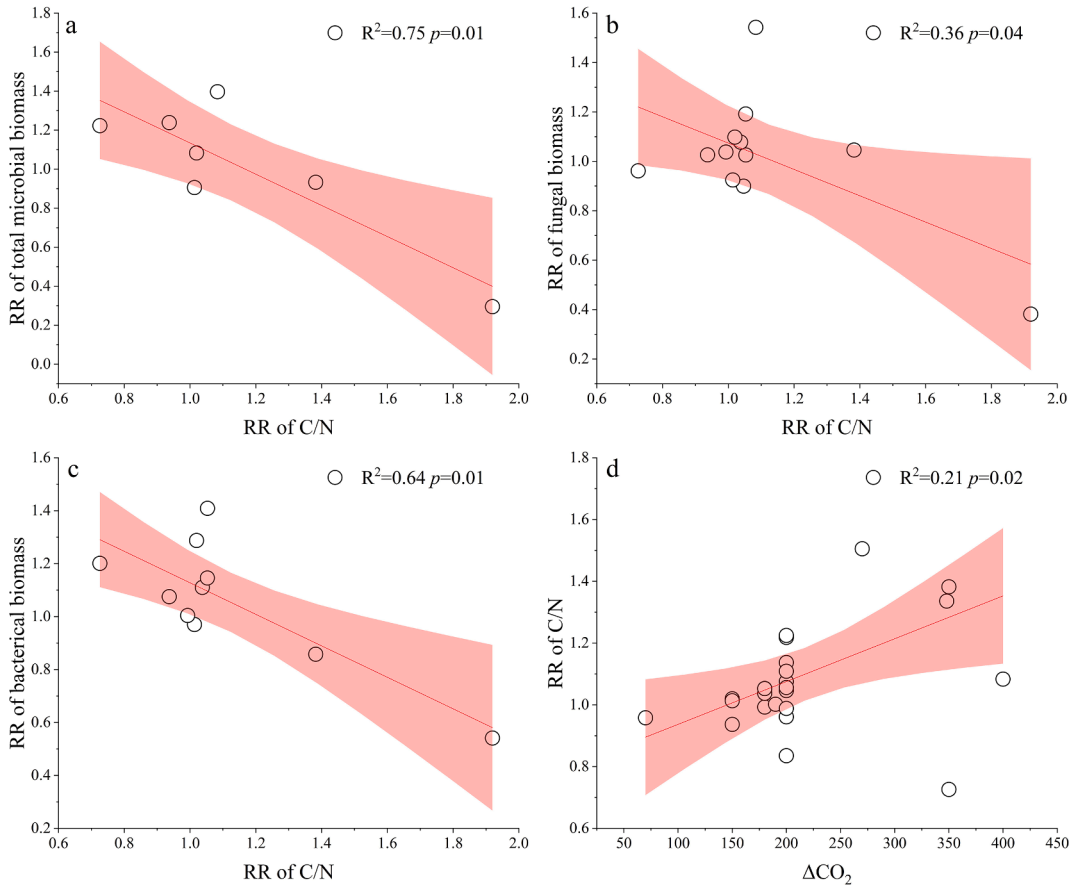

Fig. 5. Relationships between the response ratios (RRs) of total microbial biomass (a), bacterial biomass (b), fungal biomass (c), eCO_2 level (d) and the RRs of the C/N ratio with elevated CO_2.

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.116153.

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