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META-ANALYSIS

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Elevated CO_2 shifts soil microbial communities from *K*- to *r*-strategists

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Abstract

Aims: Soil microbes are key to myriad processes in terrestrial ecosystems. Elevated CO_2 represents a dominant driver of global climate change; however, it remains unclear to what extent elevated CO_2 impacts soil microbial communities at ecosystem and global scales. Here, we sought to address the following questions: (a) Do the compositions of microbial communities shift from *K*- to *r*-strategists under elevated CO_2? (b) What is the extent of the compositional shifts of microbial communities affected by elevated CO_2 concentrations, experimental duration, ecosystem types and/or background climates? (c) Are the responses of microbial communities to elevated CO_2 associated with changes in soil pH and carbon and nitrogen availabilities?

Location: Global.

Time period: 1998–2020.

Major taxa studied: Soil microbes.

Methods: We performed a global meta-analysis of 965 observations from 122 studies, which tested the effects of elevated CO_2 on microbial communities. The data covered broad variations in ecosystems, climate, CO_2 concentrations, experimental duration, and soil factors.

Results: We revealed that elevated CO_2 decreased the *K*- to *r*-strategist ratios with decreasing fungi : bacteria, Gram+ : Gram− bacteria, and Acidobacteria : Proteobacteria ratios, and increased bacterial biomass, microbial biomass carbon, Gram− bacteria, and Acidobacteria abundance. Moreover, the shifts from *K*- to *r*-strategists were more pronounced under higher CO_2 concentrations and longer experimental durations. The responses of microbial attributes to elevated CO_2 did not differ significantly among croplands, forests and grasslands. Furthermore, the response of microbial biomass to elevated CO_2 was negatively correlated with the response of soil pH, while those of bacterial biomass and fungi : bacteria ratios were positively correlated with those of soil organic carbon and soil carbon : nitrogen ratios, respectively.

Main conclusions: Our results suggest that elevated CO_2 shifts soil microbial communities from *K*- to *r*-strategists, and provide supportive evidence for understanding responses of soil microbial processes to elevated CO_2.

KEYWORDS

elevated CO_2, global climate change, *r*/*K*-selection theory, soil C : N ratio, soil microbial biomass, soil microbial community

1 | INTRODUCTION

Global scale anthropogenic activities have led to significant increases in ambient atmospheric CO_2 concentrations, which are anticipated to further increase from the current 400 to 700 ppm by the end of this century (Cotton et al., 2015; Kumar et al., 2019; Panneerselvam et al., 2020). Soil microbes play key roles in myriad ecosystem processes (Bardgett & van der Putten, 2014; Crowther et al., 2019; Delgado-Baquerizo et al., 2018), as they are critical for mediating the release of CO_2 into the ambient atmosphere from soils, which store approximately 60% of global terrestrial carbon (C) (Blagodatskaya et al., 2010). Elevated CO_2 concentrations increase photosynthesis and thus plant biomass (Ainsworth & Long, 2005; Hill et al., 2007), while simultaneously altering the above- and belowground allocation of C (Drigo et al., 2009) and soil C cycles (Castañeda-Gómez et al., 2020). Although soil microbes play a critical role in maintaining plant productivity and terrestrial C cycles (Bennett et al., 2017; Chen et al., 2019; Teste et al., 2017), our understanding of the effects of elevated CO_2 on the composition of microbial communities remains elusive. Therefore, an improved elucidation of the responses of soil microbes to elevated CO_2 is critical for predicting the consequences of increasing anthropogenically elevated CO_2 for terrestrial ecosystems.

In macroecology, Pianka (1970) proposed the theory of *r*/*K*-selection, which states that disturbed ecosystems have *r*-strategist dominated structures with features of fast growth, whereas undisturbed and mature ecosystems possess *K*-strategist dominated communities characterized by lower maximal-specific growth rates. Changes in the relative abundances of *r*- and *K*-strategists in microbial communities are useful indicators of the responses of soil microbes to stressors (Simonin et al., 2017). Given such importance, the *r*/*K*-selection theory has recently been broadly applied in microbial ecology (Chen et al., 2014; Fierer et al., 2012; Kaiser et al., 2014). A previous meta-analysis verified that Pianka's theory could be applied to soil microbial ecology related to forest degradation (Zhou et al., 2018b). However, whether this theory might be employed to interpret the responses of soil microbes to climate change remains debatable (Ho et al., 2017). Soil microbes are commonly C-limited (Soong et al., 2020), and so the enhanced availability of C due to increased plant production inputs in conjunction with higher soil C concentrations under elevated CO_2, may contribute to greater microbial biomass (Singh et al., 2010). This can lead to *r*-strategists that quickly metabolize available substrates, which outcompete slow-growing *K*-strategists (Blagodatskaya et al., 2010; Fierer et al., 2007). The ratios of fungi : bacteria, Gram-positive (G+) : Gram-negative (G−) bacteria, and Acidobacteria : Proteobacteria have been suggested as proxies of *K*-strategists in soil microbial communities (de Vries & Shade, 2013; Zhou et al., 2018b), which are expected to decrease with high C availability under elevated CO_2. Therefore, we hypothesized that elevated CO_2 could shift microbial communities from being dominated by *K*- to *r*-strategists.

Numerous experiments have been conducted to investigate the responses of soil microbial communities to elevated CO_2; however, the responses are divergent. For example, elevated CO_2 was reported to have either negligible effects on soil microbial communities (Gutknecht et al., 2012) or lead to significant increases in fungal biomass and fungi : bacteria ratios (Zhong et al., 2018). Furthermore, elevated CO_2 decreased bacterial biomass in a eucalyptus forest (Castañeda-Gómez et al., 2020), but had no significant influences on bacterial biomass in grassland ecosystems (Simonin et al., 2017). Moreover, a study by Janus et al. (2005) observed positive G− bacteria responses and negative G+ : G− bacteria responses in a poplar forest; however, elevated CO_2 had no significant effects on G+ : G− bacteria in a semi-natural wet grassland (Guenet et al., 2012). Divergent empirical findings regarding the effects of elevated CO_2 on soil microbial communities may result from the differences in CO_2 concentrations, experimental duration, and background environments. A quantitative synthesis of results across various studies could assist in determining the overall effects of elevated CO_2 on microbial communities and identify sources of variations (Gurevitch et al., 2018).

Elevated CO_2 effects on soil microbial communities may change with CO_2 concentrations and experimental duration. For example, previous research has shown that soil microbial biomass increases with the magnitude of elevated CO_2 concentrations (Blagodatskaya et al., 2010). Additionally, the effect of elevated CO_2 on the relative abundance of G− bacteria becomes significant only after several months of CO_2 fertilization, probably due to increased C availability for soil microbes under prolonged CO_2 enrichment (Castañeda-Gómez et al., 2020). Therefore, we hypothesized that the effects of elevated CO_2 on soil microbial communities would increase with higher CO_2 concentrations and longer experimental duration.

The effects of elevated CO_2 on soil microbial communities may vary contingent on biogeographical factors. The responses of soil microbes to CO_2 enrichment may differ among ecosystem types due to differences in vegetation types, soil properties and environmental conditions (Zhou et al., 2020). For example, under *c*. 500 ppm CO_2, fungal biomass did not change in forests (Lesaulnier et al., 2008), while it increased significantly in croplands (Liu et al., 2014). Moreover, a regional study revealed that under elevated CO_2 treatments, the abundances of Proteobacteria were greater in humid climates, whereas the abundances of Acidobacteria were increased in drier environments (Castro et al., 2010). Therefore, we anticipated that the effects of elevated CO_2 on soil microbial communities would differ with ecosystem types and associated background climates.

The responses of soil microbial communities to elevated CO_2 may be altered through soil factors. Soil pH was the main driver for total microbial biomass across biomes, while fungi : bacteria ratios

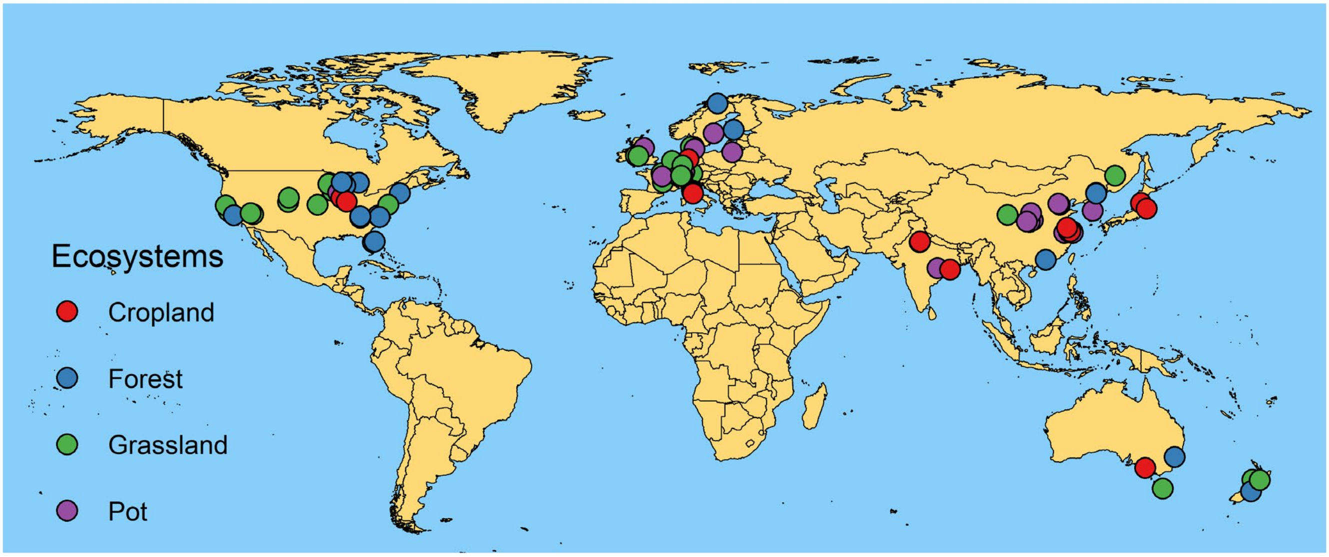

FIGURE 1 Global distributions of the 122 studies included in this meta-analysis [Colour figure can be viewed at wileyonlinelibrary.com]

increased with soil C : N ratios (Fierer et al., 2009). Also, CO_2 effects on microbial communities are mediated via changes in soil organic C (SOC) and total nitrogen (TN) contents (Jansson & Hofmockel, 2020), or reduced soil pH due to greater base nutrient uptake from the soil to support higher biomass production (Yu et al., 2019). Therefore, elevated CO_2 may impact soil microbial communities by affecting soil pH, SOC, TN, and soil C : N.

Recent meta-analyses have addressed the responses of soil microbes to N addition (Zhang et al., 2018; Zhou et al., 2017), altered precipitation (Ren et al., 2018; Zhou et al., 2018a), or warming (Xu & Yuan, 2017). Further data regarding the impacts of another major global climate change driver (elevated CO_2) on soil microbial communities are required. For this study, we endeavoured to address three questions. (a) Do microbial community compositions exhibit *K*- and *r*-selective characteristics? (b) Are the effects of the investigated microbial attributes in these original studies the result of variations in CO_2 concentrations, experimental duration, ecosystems, and background climates? (c) Are the responses of microbial communities to elevated CO_2 associated with changes in soil pH, SOC, TN, and soil C : N? To answer these questions, we performed a global meta-analysis of 965 paired observations from 122 papers to analyse the impacts of elevated CO_2 on soil microbial communities and tested whether these effects were influenced by CO_2 concentrations, experimental duration, ecosystem types, and associated background climates. Moreover, we examined whether these responses were associated with changes in soil pH, SOC, TN, and soil C : N.

2 | METHODS

2.1 | Data collection

The literature search for this study was conducted using Web of Science, and Science Direct prior to June 2020. The keywords and terms employed were (elevated CO_2 OR increased CO_2 OR rising CO_2 OR CO_2 enrichment) AND (microbial communities OR microbial biomass OR fungi OR bacteria). The following criteria were applied: (a) the experimental and control plots under study were subject to the same abiotic and biotic conditions; (b) if experiments included other influencing factors (e.g. N addition, precipitation reduction, etc.), data were selected only from the elevated CO_2 treatments; (c) the elevated CO_2 concentrations and experimental duration were clearly reported; (d) the values and sample sizes for the treatment and control groups were directly reported or could be extracted by WebPlotDigitizer (Burda et al., 2017).

Additionally, matched CO_2 concentrations, experimental duration, soil pH, SOC, TN, and soil C : N ratios were also collected. For studies conducted in the field, the relevant geophysical variables [mean annual temperature (MAT), mean annual precipitation (MAP), and ecosystem types (croplands, forests, and grasslands)] were also obtained from the original papers or cited papers. Croplands, forests, grasslands and pot contributed 20, 23, 33 and 24% observations of the dataset, respectively. Measurements of different microbial attributes, CO_2 concentrations, experimental duration, and ecosystems within single study were distinctly recorded as observations. Experiments with sample sizes lower than 5 were not included. Finally, a total of 965 CO_2 enrichment observations from 122 papers satisfied the above criteria; thus, they were included in the meta-analysis (Figure 1).

We also included pot experiments (greenhouse and/or growth chamber experiments) as they accounted for 216 of 965 observations in our dataset. Field experiments were commonly conducted under ambient precipitation and temperatures, but pot experiments were usually performed in artificial environments. However, across all studies, the responses of soil microbial communities to elevated CO_2 did not differ significantly between field and pot experiments (Supporting Information Table S1). We, therefore, pooled field and pot data for further analysis.

In the original studies, soil microbial biomass was quantified by chloroform fumigation, phospholipid fatty acid (PLFA), or substrate-induced respiration approaches. The biomass of fungi, bacteria, G+ bacteria, G− bacteria, fungi : bacteria ratios, and G+ : G− bacteria ratios were determined by quantitative polymerase chain reaction or PLFA methods. The methods for relative abundances of arbuscular mycorrhizal fungi (AMF), Proteobacteria, Acidobacteria and Actinobacteria included PLFA, quantitative polymerase chain reaction and high-throughput sequencing methods (Supporting Information Table S2).

2.2 | Data analysis

We examined the effects of elevated CO_2 on microbial attributes and soil factors between the control and treated groups by calculating log response ratios (lnRRs) as effect sizes (Hedges et al., 1999) from each study. The lnRR was calculated as $\ln (X_t/X_c) = \ln X_t - \ln X_c$, where X_t and X_c are the values of each observation in the treated and control groups, respectively. The lnRR was weighted by the replication number (Chen & Chen, 2018), which was calculated by $(n_t \times n_c)/(n_t + n_c)$, where n_t and n_c represent the numbers of treatment and control group replicates, respectively.

For each microbial attribute, soil pH, SOC, TN, and soil C : N, we tested whether its lnRR differed from zero and whether the lnRR was impacted by CO_2 concentrations (CC, ppm) and experimental duration (ED, days) using the following model:

$$\text{lnRR} = \beta_0 + \beta_1 \ln(\text{CC}) + \beta_2(\text{ED}) + \pi_{\text{study}} + \varepsilon. \tag{1}$$

where β_n, π_{study} and ε are coefficients, the random effect factor of 'study', and sampling error, respectively. The continuous predictors in Equation 1, ln (CC) and ED, were scaled; thus, β_0 is the mean lnRR at the mean ln (CC) and ED (Chen et al., 2019). We employed linear mixed-effect models using restricted maximum likelihood estimation with the *lme4 1.1–21* package (Bates et al., 2015). We also compared the logarithmic and linear terms of CC and ED, and the interaction terms for both. The identified logarithmic terms for CC and linear terms for ED yielded similar or lower Akaike information criterion (AIC) values (Supporting Information Table S3). For consistency, our final analysis was based on Equation 1. We also assessed whether the responses of soil microbial communities to elevated CO_2 differed with technical methods. We did not find a significant effect of these methods on lnRRs of microbial attributes (Supporting Information Table S4).

To graphically show whether elevated CO_2 effects on lnRR of microbes changed with CO_2 concentrations and experimental duration, we employed partial regressions using residuals from Equation 1 plus the intercept coefficients (β_0), and the concentration (β_1) and duration coefficients (β_2), respectively. Similar to previous meta-analyses (Chen & Chen, 2019; Sun et al., 2020), for studies conducted in the field, we compared the AIC values of models regarding soil microbes with and without interactions of CC × geographical factors (MAT, MAP, and ecosystems including croplands, forests and grasslands) and ED × geographical factors and found that the models without interactive terms had the lowest AICs (Supporting Information Table S5). Therefore, we added the MAT, MAP, or ecosystem terms to Equation 1 to test whether the microbial lnRR changed geographically.

Finally, we performed Pearson correlation analyses using the *PerformanceAnalytics* package (Peterson et al., 2018) to test associations between the lnRRs of soil pH, SOC, TN, and C : N and microbial biomass [pooled microbial biomass C (MBC) and total microbial biomass (Zhou et al., 2017)], bacterial biomass, and fungi : bacteria ratio, respectively. To facilitate interpretation, the lnRR and its 95% confidence intervals were transformed to percentages using [exp (lnRR) − 1] × 100%. If the 95% confidence interval did not cover zero, the effect of elevated CO_2 was significant at $\alpha = 0.05$. All statistical analyses were conducted in R 4.0.3 (R Development Core Team, 2020).

3 | RESULTS

3.1 | Microbial communities and soil factors under elevated CO_2

Across all ecosystem types, elevated CO_2 did not significantly affect the total microbial biomass or fungal biomass, but did increase the bacterial biomass by 30.1% (95% confidence interval, 13.1 to 47.1%; $p < .01$), which resulted in a significant decrease in the fungi : bacteria biomass ratio ($p = .04$). Elevated CO_2 significantly increased the MBC by 13.4% (9.0 to 17.8%; $p < .01$); however, it had no significant effects on microbial biomass N (MBN) and the MBC : MBN ratio (all $p > .05$). Concomitantly, G+ bacteria did not change with elevated CO_2 ($p = .41$), while G− bacteria increased by 8.0% (3.7 to 12.2%; $p < .01$), which resulted in a significant decrease of the G+ : G− bacteria ratio by 9.3% (−14.2 to −4.5%; $p = .02$). Additionally, elevated CO_2 significantly increased relative abundances of Acidobacteria by 23.5% (7.9 to 39.2%; $p = .02$) and decreased the Acidobacteria : Proteobacteria ratios by 20.3% (−30.6 to −9.9%; $p = .01$); however, it had no significant effects on abundances of AMF, Proteobacteria and Actinobacteria (Figure 2a). Elevated CO_2 significantly decreased the soil pH by 1.4% (−2.4 to −0.5%; $p < .01$; Figure 2b) and increased the SOC by 4.7% (1.3 to 8.1%; $p < .01$), whereas it had no significant effects on the TN or soil C : N ratio.

3.2 | Effects of CO_2 concentrations, experimental duration, ecosystems, and climates

The effect sizes for the G+ : G− bacteria and Acidobacteria : Proteobacteria ratios both decreased with CO_2 concentrations and experimental duration (all $p < .05$; Figure 3a, b, d, and e, Supporting Information Table S6), the effect size for AMF increased with higher CO_2 concentrations ($p = .02$; Figure 3c, Supporting Information Table S6), and the effect size for MBN decreased with experimental duration ($p = .01$; Figure 3f, Supporting Information Table S6). Other

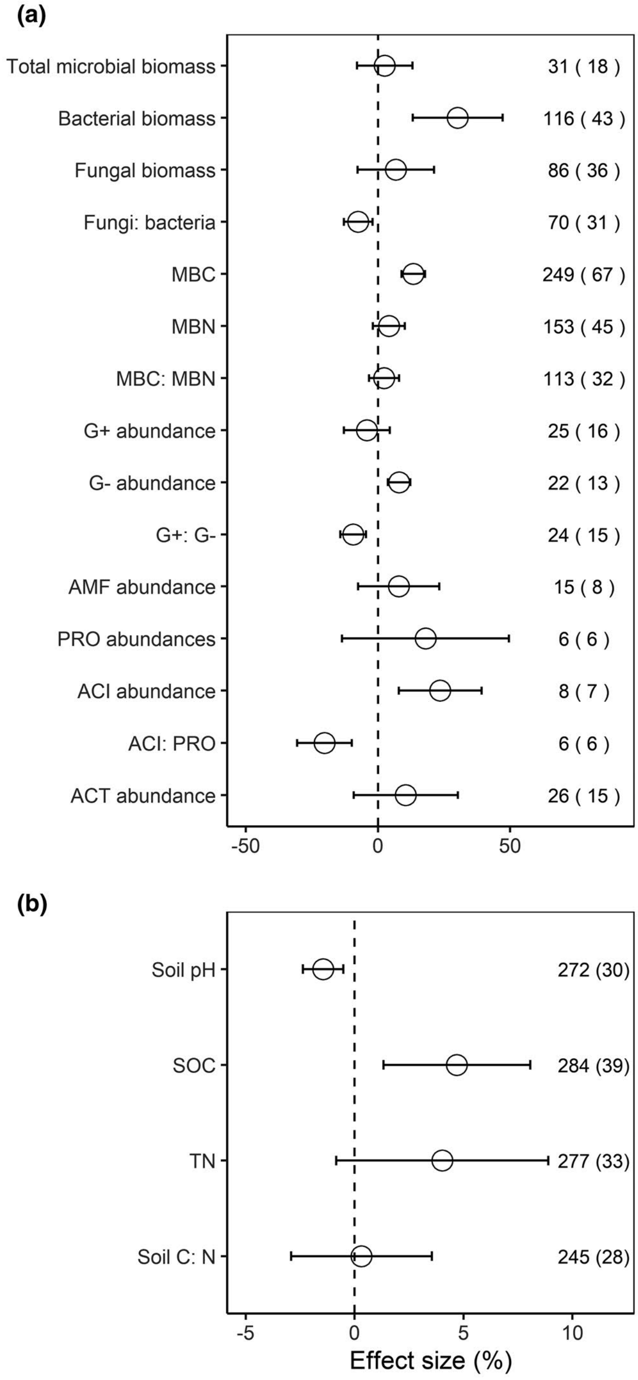

FIGURE 2 Effects of elevated CO_2 on microbial attributes (a) and soil factors (b). Values (estimated β_0 in Equation (1)) are means ± 95% confidence intervals of the percentage effects between elevated CO_2 and control groups. Dashed lines represent lnRR = 0 and numbers within and outside the parentheses represent the number of studies and observations, respectively. MBC = microbial biomass C; MBN = microbial biomass N; G+ = Gram-positive bacteria; G− = Gram-negative bacteria; AMF = arbuscular mycorrhizal fungi; PRO = proteobacteria; ACI = acidobacteria; ACT = actinobacteria; SOC = soil organic C; TN = total N

microbial attributes did not show any significant changes with CO_2 concentrations or experimental duration (all $p > .05$; Supporting Information Table S6). For field studies, the responses of microbial attributes (except for MBC) to elevated CO_2 did not change significantly with the MAT, MAP, or ecosystems including croplands, forests and grasslands (Table 1). However, the lnRR of MBC increased with MAT and MAP (Figure 4), indicating the effects of elevated CO_2 on MBC were more positive under warmer and wetter climates.

3.3 | The correlation between the responses of soil microbial attributes and soil pH, SOC, TN and C : N

The responses of soil microbes and at least one soil factor (e.g. pH, SOC, TN, C : N ratio) were simultaneously measured across all studies. It was found that the lnRR of the microbial biomass was negatively correlated with the lnRR of the soil pH (Figure 5a), whereas the lnRR of the bacterial biomass was positively correlated with the lnRR of the SOC (Figure 5b). The lnRR of the fungi : bacteria ratio showed a positive correlation with the lnRR of the soil C : N ratio (Figure 5c). Furthermore, the lnRRs of the microbial biomass, bacterial biomass, and fungi : bacteria ratio had no significant relationships with the lnRRs of other soil factors (Supporting Information Table S7).

4 | DISCUSSION

The present meta-analysis investigated, for the first time, the responses of soil microbial communities to elevated CO_2 at two taxonomic resolutions based on 965 observations, which were tested with field and pot experiments from 122 independent studies encompassing a wide range of MAT, MAP, and ecosystems worldwide. Overall, our results supported Pianka's *r*/*K*-selection theory, with decreasing ratios of fungi : bacteria, G+ : G− bacteria and Acidobacteria : Proteobacteria, and increasing bacterial biomass and abundances of G− bacteria under CO_2 enrichment. We also found that elevated CO_2 significantly increased MBC and Acidobacteria abundances. Moreover, the shift from *K*- to *r*-strategists was more pronounced with higher CO_2 concentrations and longer experimental duration, and these responses were consistent across ecosystems. Below, we discuss the observed patterns of elevated CO_2 effects on microbial communities and suggest their implications for soil C cycling.

4.1 | Effects of elevated CO_2 on microbial communities

The adoption of Pianka's *r*/*K*-selection theory, which is commonly used in macroecology, to explain the microbial responses to elevated CO_2 is controversial. This is likely because soil microbial communities are complex owing to environmental selection pressures (Sun, Chen, et al., 2020), where finer taxonomic resolutions for microbial communities are still lacking (Ho et al., 2017). Despite this limitation, we found that, on average, elevated CO_2 decreased the fungi : bacteria,

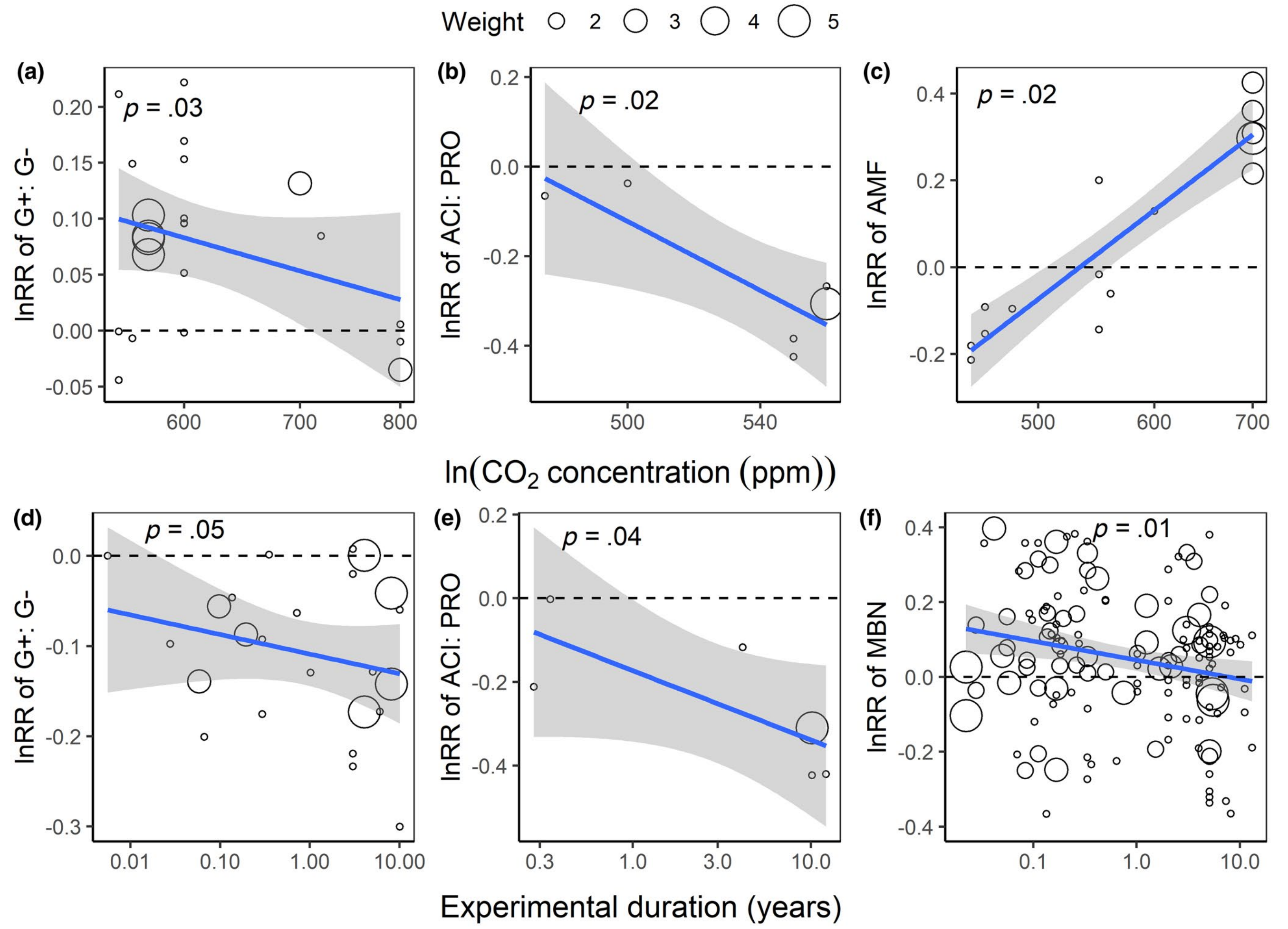

FIGURE 3 Effects of CO_2 concentrations on lnRRs of G+ : G– (a), ACI : PRO (b) and AMF (c), and experimental duration on lnRRs of G+ : G– (d), ACI : PRO (e), and MBN (f). Horizontal dashed lines represent lnRR = 0 and blue lines are fitted by partial-linear regressions with 95% confidence intervals (CIs) in grey shading. Circle sizes are proportional to weights of each observation and significance (*p* values) is shown for each microbial attribute tested. lnRR = log response ratio; G+ = Gram-positive bacteria; G– = Gram-negative bacteria; ACI = acidobacteria; PRO = proteobacteria; AMF = arbuscular mycorrhizal fungi; MBN = microbial biomass N [Colour figure can be viewed at wileyonlinelibrary.com]

G+ : G– bacteria, and Acidobacteria : Proteobacteria ratios (Figure 2a), which supports Pianka's *r*/*K*-selection theory (Fierer et al., 2007). This is likely because of higher plant-derived C inputs into soils and increased root exudates (Phillips et al., 2009, 2011) under elevated CO_2. Two previous field studies also found that elevated CO_2 resulted in an increasing trend in the *r*-strategist to *K*-strategist ratio (Blagodatskaya et al., 2010; Simonin et al., 2017). Given the fact that it has been effectively applied in recent microbial studies (Chen et al., 2016; Kaiser et al., 2014; Zechmeister-Boltenstern et al., 2015; Zhou et al., 2018b), application of Pianka's *r*/*K*-selection theory to microbial ecology can improve our understanding of the responses of microbial communities to global climate change. Moreover, the observed increases in G– bacteria might be related to greater root biomass (Johnson, 2006), as the growth of G– bacteria is favoured in the rhizosphere (Janus et al., 2005).

Our study also revealed that at a fine taxonomic resolution, Acidobacteria was found to be the only one of the bacterial phyla that was significantly sensitive to elevated CO_2 (Figure 2a). Acidobacteria are found extensively in terrestrial soils on a global scale (Delgado-Baquerizo et al., 2018), and are the only bacterial group that are characterized as acidophiles (Jones et al., 2009). This is in conjunction with lower pH induced by elevated CO_2 (Figure 2b), which may explain why Acidobacteria was increased under elevated CO_2. However, we did not find significant responses of Proteobacteria and Actinobacteria to elevated CO_2. Currently, we know little about the potential mechanisms involved; however, we speculated on these for taxonomic resolution reasons due to methodological limitations (Ho et al., 2017; Zhou et al., 2018b), and their smaller sample sizes (Yue et al., 2017).

4.2 | Effects of CO_2 concentration, experimental duration, ecosystems, and climates

Our analysis demonstrated that the ratios of G+ : G– bacteria and Acidobacteria : Proteobacteria both decreased with higher CO_2

TABLE 1 Responses of studied microbial attributes to mean annual temperature (MAT), mean annual precipitation (MAP), and ecosystems (croplands, forests and grasslands) in the field. The degrees of freedom (*df*), *p* values and sample sizes (*n*) are given

	MAT		MAP		Ecosystem		*n*
Attribute	*df*	*p*	*df*	*p*	*df*	*p*	720 (98)
Total microbial biomass	1, 22	.84	1, 22	.52	2, 21	.85	26 (14)
Bacterial biomass	1, 26	.48	1, 41	.14	2, 38	.88	82 (31)
Fungal biomass	1, 23	.78	1, 32	.21	2, 45	.23	50 (23)
Fungi : bacteria	1, 20	.57	1, 22	.53	2, 12	.41	39 (19)
MBC	1, 43	**.03**	1, 48	**< .01**	2, 36	.11	202 (55)
MBN	1, 27	.15	1, 48	.50	2, 25	.48	124 (37)
MBC : MBN	1, 13	.16	1, 20	.94	2, 15	.77	87 (25)
G+ abundance	1, 6	.93	1, 4	.25	1, 6	.59	21 (12)
G− abundance	1, 14	.44	1, 14	.11	1, 14	.58	18 (9)
G+ : G−	1, 7	.43	1, 5	.19	1, 4	.56	19 (10)
AMF abundances	1, 3	.77	1, 4	.62	1, 3	.51	14 (7)
PRO abundances	1, 2	.81	1, 2	.61	1, 2	.11	6 (6)
ACI abundance	1, 3	.52	1, 3	.87	2, 2	.52	8 (7)
ACI : PRO	1, 3	.75	1, 3	.33	1, 3	.68	6 (6)
ACT abundance	1, 6	.64	1, 10	.67	2, 5	.07	18 (11)

Abbreviations: MBC = microbial biomass C; MBN = microbial biomass N; G+ = Gram-positive bacteria; G− = Gram-negative bacteria; AMF = arbuscular mycorrhizal fungi; PRO = Proteobacteria; ACI = Acidobacteria; ACT = Actinobacteria. The *df* was calculated by Satterthwaite's method in linear mixed-effect models. Bold values indicate $p < .05$.

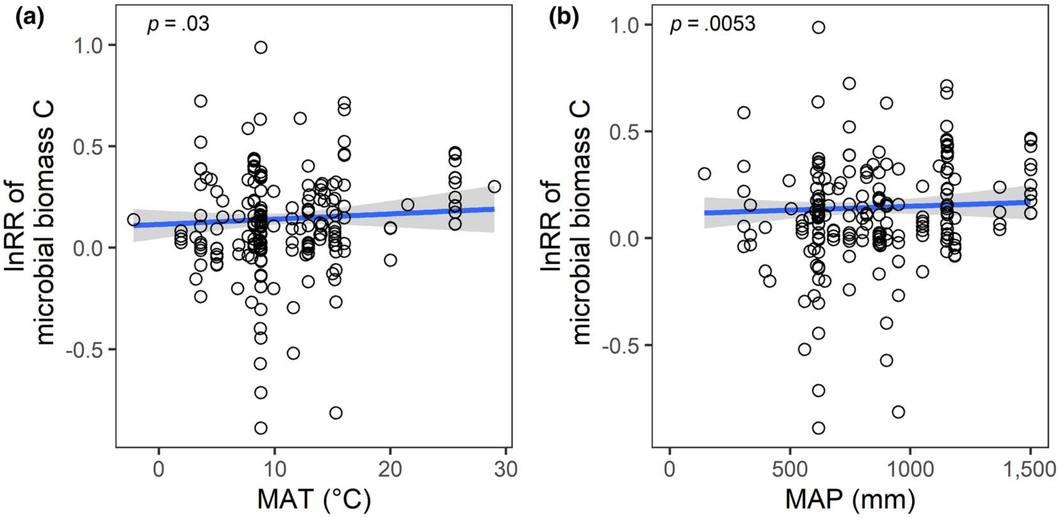

FIGURE 4 Relationships between log response ratio (lnRR) of microbial biomass C and mean annual temperature (MAT; a) and mean annual precipitation (MAP; b). Blue lines and shaded areas represent fitted regressions and 95% confidence intervals, respectively. The significance (*p* values) is shown for the tested relationship [Colour figure can be viewed at wileyonlinelibrary.com]

concentrations and longer experimental duration (Figure 3 and Supporting Information Table S6). This suggested that the shift from *K*- to *r*-strategists was more pronounced with elevated CO_2 concentrations and longer experimental durations. The increases in this shift from *K*- to *r*-strategists were expected because plant-derived C available for soil microbes increases with CO_2 concentrations and experimental durations (Blagodatskaya et al., 2010; de Graaff et al., 2006). Therefore, our analysis indicates that the lack of elevated CO_2 effects on soil microbial communities in certain studies may be due to low CO_2 concentrations and short experimental duration (Chen et al., 2019). Collectively, our results indicate lasting and deepening effects of elevated CO_2 on soil microbial communities with increasing concentrations and duration of elevated CO_2.

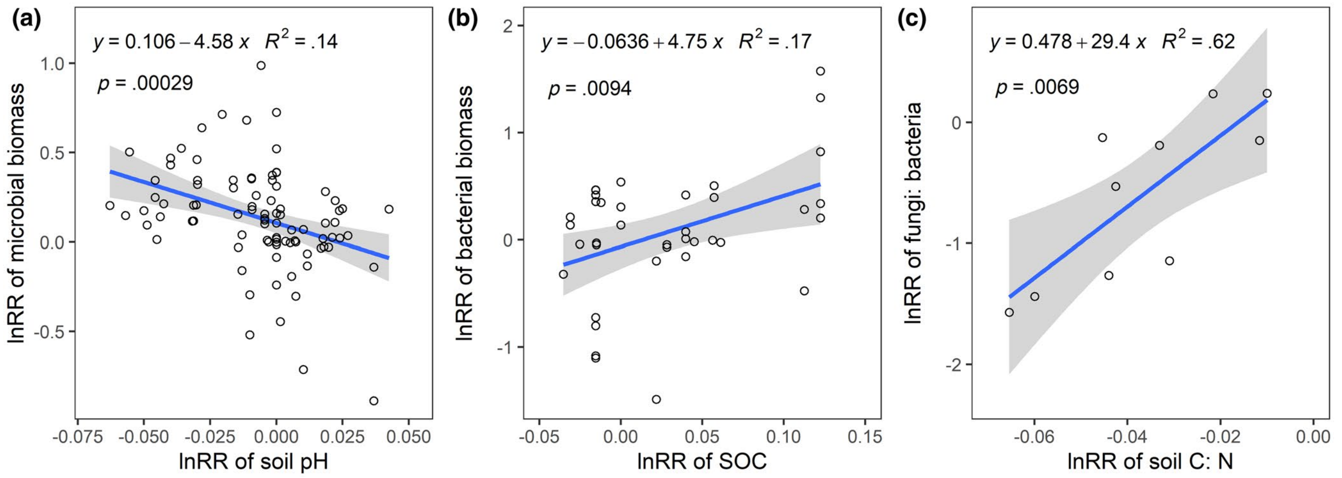

FIGURE 5 Correlations of log response ratios (lnRRs) between soil microbial biomass and soil pH (a), bacterial biomass and soil organic C (SOC; b), and fungi : bacteria and soil C : N (c). Blue lines and shaded areas represent fitted regressions and 95% confidence intervals, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

We observed a significant increase in the AMF with increasing CO_2 concentrations (Figure 3c and Supporting Information Table S6), which was consistent with a previous meta-analysis (Treseder, 2004) and a recent review (Mohan et al., 2014). This was likely because plants allocated additional C to roots and the AMF associated with satisfying the increased demand for nutrients; thus, enhancing their activities and biomass (Johnson et al., 2013). Changes in the allocation of plant C in response to elevated CO_2, including its allotment to the AMF, can profoundly influence terrestrial ecosystem C cycles (Mohan et al., 2014; Treseder & Holden, 2013).

Moreover, our analysis revealed that the MBN declined with longer experimental duration (Figure 3f and Supporting Information Table S6). The probable explanation is that N limitation in microbes will be more pronounced over time under elevated CO_2 treatments (Terrer et al., 2016; Zhu et al., 2016). Unsurprisingly, we found that, on average, elevated CO_2 increased the MBC (Figure 2a), which was consistent with a previous meta-analysis by de Graaff et al. (2006) based on a total of 30 studies, in which the MBC was increased by 7.1% under elevated CO_2 treatments. This was likely because increases in the availability of C to microbes under elevated CO_2 treatments benefitted microbial growth via increasing MBC (Singh et al., 2010).

Despite the wide range of ecosystem types (Figure 1) and technical methods (Supporting Information Table S2) covered in this study, we found no significant differences in the responses of soil microbial community attributes to elevated CO_2 (Table 1 and Supporting Information Table S4), indicating the effects of elevated CO_2 on compositions of microbial communities are globally consistent. Alternatively, although we complied a large dataset for this meta-analysis, the number of observations becomes too small to allow for a meaningful analysis of potentially divergent responses associated with each individual ecosystem (Sun, Wang, et al., 2020; Zhang et al., 2018). The exceptions were the MAT- and MAP-dependent responses of MBC on ecosystem soil resident microbial attributes under ambient climates (Figure 4, Table 1). These results suggested that increases in ecosystem functions and services (e.g. nutrient cycles, bioenergy production, and pollutant retention) with higher MBC (Chen et al., 2020) were more pronounced in warmer and wetter environments.

4.3 | Effects of soil factors

Consistent with previous research (Bahram et al., 2018; Fierer et al., 2009), we found the response of soil pH was negatively correlated with that of soil microbial biomass (Figure 5a, Supporting Information Table S7), indicating the effects of CO_2 on soil microbial biomass are mediated via the changes in soil pH because high productivity associated with elevated CO_2 may increase base nutrient uptake, and thus reduce soil pH (Yu et al., 2019). The response of SOC was significantly related to that of bacterial biomass (Figure 5b). This was likely because higher SOC contents may provide additional C sources and energy to soil bacteria (Demoling et al., 2007). The positive relationships between fungi : bacteria and soil C : N ratios (Figure 5c) were aligned with previous evidence (Fierer et al., 2007, 2009). This may be attributed to the fact that bacteria require more N per unit biomass C accumulation than fungi (De Deyn et al., 2008).

4.4 | Implications for soil C cycling

Our study has significant implications for the elucidation of ecosystem biogeochemical dynamics. A growing body of evidence over the past decade has revealed that microbial community compositions play vital roles in soil C cycling (Crowther et al., 2019; Fierer et al., 2007; Malik et al., 2016; Sun, Chen, et al., 2020; Waring et al., 2013; Xu et al., 2020). When elevated CO_2 shifts soil microbial communities from *K*- to *r*-strategists, this can accelerate soil C cycling, which may be attributed to the higher resource use efficiency of *r*-strategists (Blagodatskaya et al., 2010; Zhou et al., 2018b). Current soil C models are primarily developed using the soil C decomposition process (Todd-Brown et al., 2013), and rarely integrate microbial mechanisms to predict soil C dynamics (Buchkowski et al., 2015). Soil microbial attributes, such as microbial community compositions and biomass, are very sensitive to climate changes (Li et al., 2020; Sun, Liao, et al., 2020). With mounting data on microbial biomass (Xu et al., 2013), it is urgent to incorporate soil microbial mechanisms into the global C cycling model (Wieder et al., 2015).

In theory, changes in MBC in the context of climate change will affect the availability of soil N by altering N mineralization (Li et al., 2019). In this study, elevated CO_2 increased the MBC by 13.4%, which might, in turn, enhance the mineralization of N (Li et al., 2020). Changes in soil N availability could have cascading effects on ecosystem processes (Keuper et al., 2017). For example, the stimulation of N mineralization due to increased MBC may contribute to the augmentation of net primary production (Liu et al., 2009) or gross ecosystem photosynthesis (Lu et al., 2013).

We are aware that soil extracellular enzymes are important participants in terrestrial C cycling (Peng & Wang, 2016), which have garnered increased attention in soil biogeochemical processes (Chen et al., 2018). Furthermore, the stoichiometry of soil extracellular enzyme activity, as the proximate agent of microbial physiology, can be employed to parameterize biogeochemical models that correlate microbial C use efficiency with enzyme stoichiometry (Sinsabaugh et al., 2009). However, soil extracellular enzymes were not included in this study due to data paucity. Therefore, future research that accounts for soil extracellular enzyme activities holds promise for improving confidence in the prediction of soil C cycling in response to the effects of global scale climate change.

5 | CONCLUSIONS

In conclusion, we have demonstrated that elevated CO_2 prompts soil microbial communities dominated by *r*-strategists, with decreasing ratios of fungi : bacteria, G+ : G− bacteria and Acidobacteria : Proteobacteria, which supports Pianka's *r*/*K*-selection theory to some degree. Moreover, elevated CO_2 increased bacterial biomass, MBC, G− bacteria and Acidobacteria abundances. The shift from *K*- to *r*-strategists was more pronounced with higher CO_2 concentrations and longer experimental duration. The impacts of elevated CO_2 on microbial communities are closely linked with those on soil pH, SOC, and C : N. Furthermore, the effects of elevated CO_2 on soil microbes were consistent across ecosystems. Our results raise concerns that global increases in CO_2 concentrations might have ubiquitously negative global impacts on microbial communities through decreases in soil MBC in colder and drier environments.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTIONS

Y.S. and H.R. designed the study, Y.S and H.Y.H.C. performed the meta-analysis, Y.S. and C.W. collected data and wrote the first draft of the manuscript, and all authors wrote interactively through multiple rounds of revisions.

DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available in Figshare (https://doi.org/10.6084/m9.figshare.12979124).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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