

Response of soil microbial communities to altered precipitation: A global synthesis

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Abstract

Aim: Climate change intensifies the hydrological cycle and consequently alters precipitation regimes. Accurately assessing future carbon (C) budgets depends on understanding the influence of altered precipitation on both aboveground C cycling and belowground processes. Our goal was to explore generalities and mechanisms of responses of soil microbial communities to altered precipitation and implications for C cycling in terrestrial ecosystems.

Location: Global.

Time period: 2001–2017.

Major taxa studied: Soil microbes.

Methods: We used the meta-analytical technique to synthesize data of 41 increased (IPPT) and 53 decreased precipitation (DPPT) studies from 65 publications worldwide. The data covered broad variations in climate, percentage of precipitation change, experimental duration and soil properties.

Results: The fungi to bacteria ratio did not show a water-tolerant shift, but the community compositions within the bacteria did. Microbial biomass showed a higher response to moderate IPPT than moderate DPPT, whereas it was more sensitive to extreme DPPT than extreme IPPT, suggesting that the responses of microbial biomass to altered precipitation are double asymmetric. However, such asymmetric responses of microbial biomass varied with climate humidity and soil texture: microbial biomass was more sensitive to IPPT at xeric sites than at mesic sites, whereas it was more responsive to DPPT in humid areas; microbial biomass in coarse-textured soils was more sensitive to altered precipitation than that in fine-textured soils. In addition, microbial response was positively correlated with the responses of aboveground/belowground plant biomass, soil respiration and organic C content.

Main conclusions: Our meta-analysis provides the first evidence that the asymmetric response of microbial biomass to altered precipitation varies with climate humidity and soil texture. Given the coordinated responses in the plant–soil–microorganism C continuum, our synthesis extends the double asymmetric model and provides a framework for understanding and modelling responses of ecosystem C cycling to global precipitation change.

KEYWORDS

double asymmetric model, drought, microbial biomass, microbial community, plant–soil–microorganism, precipitation manipulation, soil texture

1 | INTRODUCTION

Global warming intensifies the water cycle on the Earth (Park, Bader, & Matei, 2016) in ways such as increasing inter-annual variability in precipitation and frequent extreme years, altering annual precipitation amount, and shifting global precipitation patterns (Singh, Tsiang, Rajaratnam, & Diffenbaugh, 2013; Wilcox et al., 2017). Such altered precipitation regimes likely have large impacts on properties, functions and services of terrestrial ecosystems (Knapp, Ciais, & Smith, 2017; Luo, Jiang, Niu, & Zhou, 2017; Wilcox et al., 2017). Accurately assessing and predicting future carbon (C) budgets require understanding of the influences of altered precipitation on both aboveground C cycling and belowground processes and their interactions (Nielsen & Ball, 2015; Schimel, 2016). Soil microbial decomposers consume a large amount of net primary production (NPP) in the biosphere and their activities drive the C cycling and mediate the atmospheric compositions (Clark et al., 2017; Don, Böhme, Dohrmann, Poeplau, & Tebbe, 2017; Xu et al., 2017). Given such importance, manipulation experiments of precipitation have been increasing rapidly during the past decade, which provides an opportunity for us to synthesize generalities of microbial responses to altered precipitation and their feedback to ecosystem processes.

Altered precipitation directly influences soil microbial communities by changing the soil water availability, but the direction and magnitude of the effect may depend on climate conditions. In xeric ecosystems, water additions can significantly increase microbial biomass (Manzoni, Schaeffer, Katul, Porporato, & Schimel, 2014; Sierra, Malghani, & Loescher, 2017); but in mesic systems, additional water input fills up the available pore spaces and reduces the oxygen levels necessary for aerobic microbial growth (Abramoff, Davidson, & Finzi, 2017; Davidson, Samanta, Caramori, & Savage, 2012; Manzoni et al., 2014; Sierra et al., 2017; Sihi et al., 2018). Changes in rainfall also regulate plant productivity and C allocation, shift both aboveground and belowground litter inputs, and consequently indirectly affect microbial communities (Luo et al., 2017; Nielsen & Ball, 2015; Yue et al., 2017). In addition, microbial responses to changes in soil moisture vary widely among species or functional types (Manzoni, Schimel, & Porporato, 2012; Zhao et al., 2017). For example, fungi may have greater capability to tolerate water stress than bacteria. This is due to their ability to accumulate osmoregulatory solutes to protect their metabolism and filamentous structure; these properties allow fungi to reach and exploit more substrates even in very dry soils (Manzoni et al., 2012, 2014; Nielsen & Ball, 2015; Schimel, Balser, & Wallenstein, 2007; Zechmeister-Boltenstern et al., 2015; Zeglin et al., 2013). Nevertheless, whether the fungi to bacteria ratio displays water-tolerant shifts under drought treatment remains controversial. For example, the Loma Ridge Global Change Experiment in southern California found that precipitation additions significantly increased the fungi to bacteria ratio, but drought treatments decreased this ratio in both grassland and shrubland ecosystems (Khalili, Ogunseitan, Goulden, & Allison, 2016). Therefore, it is necessary to explore general responses of microbial community compositions to altered precipitation and potential mechanisms at the global scale.

Recently, Knapp et al. (2017) proposed a double asymmetric model to understand the relationships between aboveground NPP (ANPP) and variations in precipitation, which exhibits a positive asymmetric response of ANPP to nominal levels of variability in precipitation and a negative asymmetric response of ANPP to extremely low precipitation. The positive asymmetry shows a higher percentage of ANPP change in response to increased (IPPT) than decreased precipitation (DPPT). The negative asymmetry describes negative impacts of extremely dry periods on ANPP as being much greater than positive effects of extremely wet periods. However, such asymmetric responses to altered precipitation are likely to be different for other ecosystem processes due to different mechanisms, such as soil respiration, microbial community and soil organic C, and their interactions (Luo et al., 2017). To date, no consistent conclusion has been reached on responses of microbial communities to DPPT and IPPT treatments. For example, Zhao et al. (2016) found that the microbial biomass at a semiarid steppe was more sensitive to IPPT than DPPT, whereas Jiang et al. (2013) showed that the microbial biomass in three subtropical forests was more sensitive to DPPT than IPPT. DPPT even increased the microbial activity in mesic systems because of improvements in aeration (Abramoff et al., 2017; Davidson et al., 2012; Manzoni et al., 2014; Sierra et al., 2017; Sihi et al., 2018). Likewise, such different responses may occur due to season-to-season variations in ambient rainfall or soil moisture.

In addition, the inverse texture effect (Epstein, Lauenroth, & Burke, 1997; Noy-Meir, 1973) suggests that the top layer of coarse-textured soils dries out quickly and forms a barrier to the conductance and evaporation of water from the deeper soil layer in dry areas. Precipitation also percolates to a greater depth in coarse- than fine-textured soils. Consequently, coarse-textured soils have higher water availability than fine-textured soils in dry regions. In humid areas where major soil water losses occur through drainage below the rooting zone of plants, fine-textured soils with high water-holding capacity reduce these losses and support greater plant production (Epstein et al., 1997; Noy-Meir, 1973). A recent decade-long experiment in a Chinese temperate grassland found that IPPT enhanced the ANPP during the first 6 years, but the effect disappeared in the following years probably due to the exacerbated nitrogen (N) limitation (Ren et al., 2017). Therefore, it is imperative to examine whether the double asymmetric model (Knapp et al., 2017) is applicable in explaining responses of soil microbes to altered precipitation and how it varies with climate conditions, soil texture and experimental duration.

To address these knowledge gaps, we used the meta-analytical technique to synthesize responses of microbial biomass and community compositions to manipulated precipitation worldwide. The questions we addressed included: (a) Do microbial community compositions display water-tolerant shifts in response to altered precipitation? (b) Do microbes respond to precipitation addition and reduction asymmetrically as do plants? (c) How do climate gradients, soil texture and experimental forcing variables (magnitude of precipitation change and experimental duration) regulate the responses of microbial communities? (d) Is there any correlation of responses to altered precipitation between microbes and other C cycling processes? Answering these questions will be important for understanding and modelling the role of

TABLE 1 Summary of the data set for the manipulation experiments of increased (IPPT) and decreased precipitation (DPPT) included in the meta-analysis

Manipulation	Sample size			ΔPPT		MD	MAP	MAT
	Treatment	Site	Observation	Mean	Range			
IPPT	41	22	125	34.5	4.7–100	1–10	167–1956	−1.4 to 21.4
DPPT	53	32	104	44.7	5.0–100	1–13	281–3500	−1.4 to 23.0

ΔPPT (%) = magnitude of precipitation manipulation in percentage of the annual precipitation; MD (year) = manipulation duration; MAP (mm) = mean annual precipitation; MAT (°C) = mean annual temperature.

microbes in terrestrial biogeochemical cycles and assessing ecosystem services across large spatial scales under global change scenarios (Luo et al., 2017; Schimel, 2016).

2 | MATERIALS AND METHODS

2.1 | Data collection and acquisition

The literature searching was conducted using Google Scholar (<https://scholar.google.com>) and China National Knowledge Infrastructure (CNKI, <http://www.cnki.net>). The keywords and terms used were (“altered precipitation” OR “drought” OR “decreased precipitation” OR “increased precipitation” OR “precipitation change” OR “rainfall change” OR “water addition” OR “water reduction” OR “water treatment”) AND (microbial biomass OR microbial communities OR fungi OR bacteria) AND (soil).

Several methods are used to assess microbial biomass and/or community compositions, among which the chloroform fumigation–extraction technique and total phospholipid fatty acid (PLFA) analysis are the most commonly used methods for microbial total biomass (Treseder, 2008). We found that all the precipitation-manipulation experiments found in the literature search used only these two methods, and thus, like a previous meta-analysis (Treseder, 2008), we adopted the microbial biomass that was measured with these two methods. Furthermore, PLFA analyses also provide information on microbial community compositions at a coarse taxonomic resolution. Therefore, we recorded the relative abundances (%) of fungi, bacteria, Gram-positive bacteria, Gram-negative bacteria, arbuscular mycorrhiza fungi and the ratios of fungi to bacteria and Gram-positive bacteria to Gram-negative bacteria. Additionally, the quantitative polymerase chain reaction analysis method (i.e., the copy numbers of bacterial 16S rRNA genes and fungal 18S rRNA genes) assesses bacterial and fungi community structures at a fine taxonomic resolution. Therefore, we documented the relative abundances of nine dominant and frequently reported bacterial phyla (i.e., *Acidobacteria*, *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Planctomycetes*, *Chloroflexi*, *Verrucomicrobia*, *Gemmatimonadetes*, *Firmicutes*; Zhao et al., 2017). We attempted to report the relative abundances of phyla within fungi, but such data were rare.

We selected published papers based on the following criteria: (a) Experiment was conducted in field; (b) the magnitude of precipitation change was clearly described; (c) no other forcing factors (e.g., nutrient addition, warming, etc.) were applied in the precipitation treatments; (d) the duration of precipitation manipulation was longer than one growing season. In order to quantify the effect of experimental

duration on microbial responses, we combined all the available papers that reported the same precipitation-manipulation experiment over multiple years as a single entry in the dataset (Supporting Information Table S1 and Appendix S1). In the cases that reported the seasonal responses of soil microbial communities to altered precipitation, we classified the data into ‘wet season’ and ‘dry season’ based on the seasonal pattern of precipitation or soil moisture regimes. Up to November 2017, a total of 41 IPPT and 53 DPPT case studies from 65 articles that reported microbial biomass and/or community compositions met the criteria above, and almost all the case studies were from the USA, China and Europe (Table 1; Appendix: Data sources; Supporting Information Table S1 and Appendix S1). There were 13 sites where the IPPT and DPPT treatments were paired.

Besides the information on microbes, the corresponding soil moisture, soil C content, soil respiration, aboveground and belowground plant biomass, soil texture properties (clay, silt and sand content) and geophysical variables [i.e., latitude, longitude, mean annual temperature (MAT) and mean annual precipitation (MAP)] were also recorded from the papers or their cited papers. The MAT for the IPPT and DPPT experiments ranged between −1.4 and 21.4 °C and −1.4 and 23 °C, respectively; the MAP for the IPPT and DPPT ranged between 167 and 1956 mm and 281 and 3500 mm, respectively.

To standardize the precipitation treatment levels across the studies, all the manipulation levels were converted into a percentage of the annual precipitation [ΔPPT (%)]. Specifically, the ΔPPTs for the DPPT and IPPT treatments were calculated as follows. For the DPPT treatments in the literature that were realized by constructing a rainout-shelter, the ΔPPT was calculated as the percentage of rainout-shelter area to the total plot area (PER_{shelter}) if the DPPT was manipulated throughout the year; or the ΔPPT was calculated using the method of Hoover, Wilcox, and Young (2018) if the DPPT was manipulated seasonally:

$$\Delta PPT = PER_{\text{shelter}} \times \frac{PPT_{\text{TP}}}{APPT} \quad (1)$$

where PPT_{TP} is the precipitation during the treatment period; APPT is the annual precipitation. For IPPT, the treatments were realized with two methods in the literature. In the first method, the rainfall was collected from the rainout shelter and then was drained into the plots of the IPPT treatments, or water was added by a fixed proportion after each rainfall event. In these cases, we calculated the ΔPPT based on Equation 1. In the second method, a constant amount of water was added in each study year. For these experiments except for the case study from Hulunbeier, Inner Mongolia, China (Zhang et al., 2017), we

recorded the annual rainfall data for each study year and calculated the Δ PPT afterwards (Supporting Information Table S1 and Appendix S1). For the study in Hulunbeier (Zhang et al., 2017), the MAP was used as a substitute following previous meta-analyses (Liu et al., 2016; Wilcox et al., 2017; Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011). Positive values of Δ PPT indicate IPPT treatments that varied from 4.7 to 100% in the dataset, whereas negative values of Δ PPT indicate DPPT treatments that ranged between -5 and -100% (Table 1 and Supporting Information Appendix S1).

2.2 | Meta-analysis

A meta-analysis was conducted to evaluate responses of soil microbes to altered precipitation by calculating the natural logarithm transformed (ln) response ratio (RR) for each observation:

$$RR = \ln\left(\frac{\bar{X}_t}{\bar{X}_c}\right) = \ln(\bar{X}_t) - \ln(\bar{X}_c) \quad (2)$$

Where \bar{X}_t and \bar{X}_c are the means of the concerned variable in the treatment and control, respectively. Its variance (v_{RR}) was calculated as:

$$v_{RR} = \frac{s_t^2}{n_t \bar{X}_t^2} + \frac{s_c^2}{n_c \bar{X}_c^2} \quad (3)$$

where n_t and n_c are sample size of the concerned variable in the treatment and control, respectively; s_t and s_c are the standard deviations of the concerned variable in the treatment and control groups, respectively. The weighted response ratio (RR_{++}) was calculated as:

$$RR_{++} = \frac{\sum_{i=1}^k w_i RR_i}{\sum_{i=1}^k w_i} \quad (4)$$

where k is the number of studies; w is the weighting factor that was calculated as:

$$w = \frac{1}{v_{RR}} \quad (5)$$

The standard error (SE) associated with RR_{++} was computed as:

$$SE(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^k w_i}} \quad (6)$$

To make the microbial responses to altered precipitation comparable across various studies, sensitivity of each study was calculated to represent the magnitude of response relative to the precipitation change. Such calculations are useful for exploring general relationships between the sensitivity and other factors such as climate and soil texture, and excluding the impact of magnitude of precipitation change to some degree, as used by previous meta-analyses (Wilcox et al., 2017; Wu et al., 2011). Specifically, the sensitivity was calculated as:

$$\text{Sensitivity} = \frac{RR}{\Delta\text{PPT}} \quad (7)$$

where the absolute value of Δ PPT is used. Consequently, the absolute value of the sensitivity reflects the magnitude of the sensitivity, and the positive/negative sign indicates the response direction. The variance of the sensitivity ($v_{\text{sensitivity}}$) was calculated as:

$$v_{\text{sensitivity}} = \frac{v_{RR}}{\Delta\text{PPT}^2} \quad (8)$$

The weighted mean of the sensitivity (Sensitivity_{++}) and its SE were calculated in the same way as the RR_{++} .

The differences in responses of microbial biomass measured by the chloroform fumigation–extraction technique versus the PLFA analysis were tested via between-group heterogeneity tests (Q_B), and no significant difference was found (Supporting Information Table S2). The Q_B test was also used to assess whether the responses differed between the wet and dry sampling periods. In the compiled data, there was only one publication that reported seasonal responses of bacterial phyla to either IPPT (Huang, Li, Su, & Li, 2018) or DPPT (Bastida et al., 2017). In this study, consequently, we analysed the seasonal responses of the microbial biomass and community compositions measured by PLFA analysis. We found that the season-to-season variations in humidity inconsistently affected the sensitivity of the microbial biomass and community compositions, and most of the effects were statistically insignificant (Supporting Information Figure S1).

For the studies that reported responses of microbial communities for more than 3 years, the temporal change in the sensitivity was assessed for each case study. No significant temporal patterns for either microbial biomass or community compositions were found except for one case study of IPPT from Duolun country, Inner Mongolia, China (Bi, Zhang, Liang, Yang, & Ma, 2011; Supporting Information Figures S2–S5). The temporal pattern for the entire dataset was also assessed, and no significant temporal trends in microbial biomass and community compositions were observed under IPPT and DPPT treatments either (Supporting Information Figures S2–S5). Therefore, we used the overall weighted mean across the entire experimental periods and sampling seasons to assess the effects of precipitation manipulation. Significance of the RR_{++} and Sensitivity_{++} was assessed using a random-effects metanalytic model.

We also tested publication bias of the sensitivity based on the rank correlation test for funnel plot asymmetry, and did not detect publication bias except for the relative abundance of Gram-positive bacteria under DPPT (Supporting Information Table S3). Augmenting the data using the trim and fill method did not change the significance of this result (Supporting Information Table S4).

2.3 | Factors analysis

To estimate whether microbial communities asymmetrically respond to altered precipitation, we grouped the Δ PPT (increased and decreased) into slight, medium and extreme IPPT/DPPT (i.e., <30 , ≥ 30 – <60 and $\geq 60\%$ of the annual precipitation, respectively). Note that one case study could be assigned to different groups for the studies that reported responses of microbial communities for more than 1 year and the Δ PPT varied inter-annually for some water addition experiments due to changes in the annual precipitation (Supporting Information Appendix S1).

To assess patterns of the sensitivity of microbial communities across climatic gradients, we first calculated the site-level sensitivity of

the microbial variables to IPPT or DPPT, and then used linear models to develop the relationship between the sensitivity and MAP; after that, we compared the sensitivity of the microbial community between 13 paired IPPT and DPPT experiments directly. The difference in the sensitivity between IPPT and DPPT (Δ sensitivity) was calculated as:

$$\Delta\text{sensitivity} = \text{Sensitivity}_{\text{IPPT}} + \text{Sensitivity}_{\text{DPPT}} \quad (9)$$

If Δ sensitivity was positive, the microbial community was regarded to be more sensitive to IPPT than DPPT; otherwise, the microbial community was considered to be more sensitive to DPPT than IPPT. The relationships between Δ sensitivity and MAP were also explored (the 13 paired experiments with the MAP range from 281 to 1956 mm; Supporting Information Table S1).

To test the inverse texture effect (Epstein et al., 1997; Noy-Meir, 1973), we first divided the dataset into 'dry region' and 'humid region' studies using a threshold value of MAP. Unfortunately, the threshold values of MAP varied remarkably in the literature (ranging between 370 and 800 mm; Bucini & Hanan, 2007; Epstein et al., 1997; Sala, Parton, Joyce, & Lauenroth, 1988). Consequently, we binned the MAP ranges into two threshold groups: 370 and 800 mm (less than threshold vs. greater than and equal to threshold). We also grouped the data into coarse-textured and fine-textured soils by the clay content of 10% (less than 10% vs. greater than and equal to 10%). The Q_B test was used to test the difference in the sensitivity between the fine-textured and the coarse-textured soils. A stepwise regression procedure was used to explore multivariate effects of MAP and soil texture and their relative importance on the sensitivity of microbial biomass to altered precipitation. Regression procedures were used to examine relationships between the sensitivity of microbial communities and soil moisture, soil texture, and ecosystem C cycling processes (including soil C content, soil respiration, aboveground and belowground plant biomass) at the case-study level. All statistical analyses were conducted in R (R Core Team, 2016) with the packages 'metafor' and 'ggplot2'.

3 | RESULTS

3.1 | Responses of soil microbial biomass and community compositions to altered precipitation

Across all studies, the effects of IPPT and DPPT on microbial biomass showed opposite trends. Specifically, IPPT increased the microbial biomass by an average of 25%, whereas DPPT reduced it by 13%. The effect size of IPPT on the microbial biomass was about 1.9 times greater than that of DPPT. The Δ PPT was significantly and positively correlated with the response ratio of microbial biomass (Supporting Information Figure S6). The sensitivities of microbial biomass to both IPPT and DPPT were significantly different from zero, and comparable (0.34 vs. -0.35 , Figure 1a).

When the data were binned by the precipitation manipulation level, the response ratios of microbial biomass to slight and medium IPPT were 279 and 144% greater than those of slight and medium DPPT, respectively (Figure 2a). In contrast, the response ratio of microbial biomass to extreme DPPT was 364% greater than that of extreme IPPT (Figure 2a).

No significant interactions were found between Δ PPT and the responses of community compositions except for a positive relationship between Δ PPT and the relative abundance of arbuscular mycorrhiza fungi (Supporting Information Figure S7). The sensitivities of microbial community compositions to altered precipitation varied with the microbial groups and methods. Both IPPT and DPPT increased the fungi to bacteria ratio, but insignificantly (Figure 1b). The IPPT and DPPT significantly and oppositely affected the Gram-positive bacteria to Gram-negative bacteria ratio and the relative abundance of arbuscular mycorrhiza fungi (Figure 1b). Altered precipitation had no effect on the relative abundance of fungi or bacteria (Figure 1b). The IPPT treatment significantly decreased and increased the relative abundance of Gram-positive bacteria and Gram-negative bacteria, respectively (Figure 1b). However, the sensitivities of relative abundance of Gram-positive bacteria and Gram-negative bacteria to DPPT were insignificant (Figure 1b).

Significantly opposite effects of IPPT versus DPPT on bacterial phyla were found only in *Planctomycetes* (Figure 1c). The DPPT significantly increased the relative abundance of *Gemmatimonadetes* and *Acidobacteria* but decreased the relative abundance of *Verrucomicrobia* and *Proteobacteria*, whereas IPPT decreased the relative abundance of *Firmicutes* significantly (Figure 1c). Both IPPT and DPPT had no significant effect on the relative abundances of *Actinobacteria*, *Bacteroidetes* or *Chloroflexi* (Figure 1c). Overall, more significant sensitivities of bacterial phyla were found under DPPT treatments than IPPT treatments.

3.2 | Factors that affect microbial responses to altered precipitation

3.2.1 | Soil moisture

Precipitation additions and reductions significantly increased and decreased the soil moisture, respectively (Supporting Information Table S5). At a case-study level, the response ratio of microbial biomass was significantly and positively correlated with the response ratio of soil moisture ($r = .77$, $p < .01$; Table 2). However, there were no significant correlations between the indices of microbial community compositions and soil moisture ($p > .05$) except for a positive relationship between *Proteobacteria* and soil moisture ($r = .50$, $p = .02$; Table 2).

3.2.2 | Climate humidity

The analysis of the data with a broad range of MAP showed that the sensitivity of microbial biomass was significantly and negatively correlated with MAP under IPPT and DPPT manipulations (Figure 2b). Similar relationships also existed if the data were binned by Δ PPT (Supporting Information Figure S8). Based on the paired IPPT and DPPT manipulations from the 13 sites, the Δ sensitivity of microbial biomass significantly decreased as the MAP increased (Figure 2c). These results suggest that the sensitivity of microbial biomass to IPPT was higher at arid sites than that at mesic sites, but the sensitivity of microbial biomass to DPPT was higher at mesic sites than that at arid sites. However, no general relationship was found between MAP and the sensitivity of microbial community compositions (Supporting Information Figure S9).

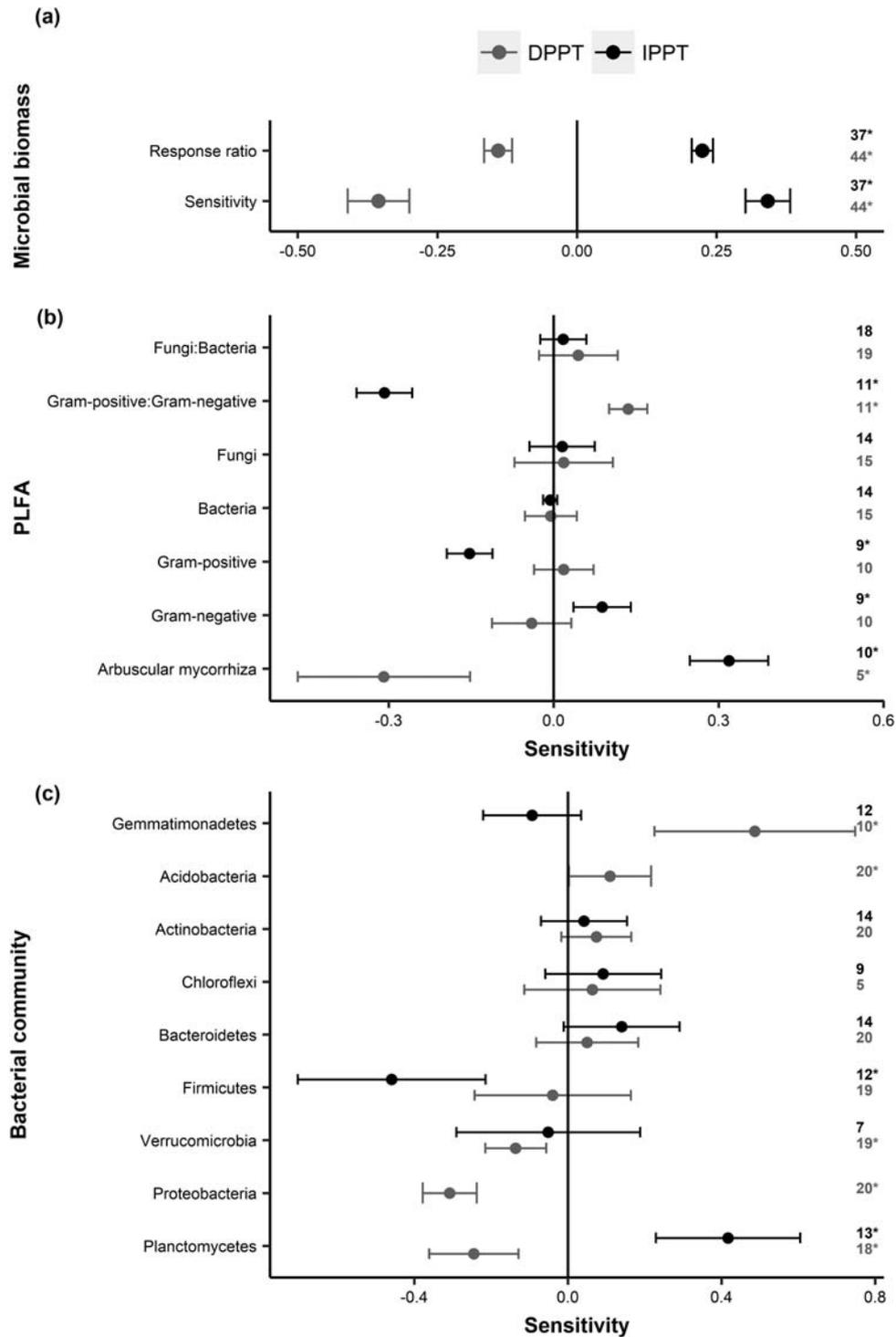


FIGURE 1 Responses of microbial biomass (a) and community compositions (b, c) to altered precipitation. Microbial community compositions were measured by total phospholipid fatty acid analysis (PLFA) and quantitative polymerase chain reaction analysis. The error bars represent 95% confidence intervals. The numbers at the right side of the figure represent the observation numbers for each estimate. The asterisks following the observation numbers indicate significant responses (the 95% confidence intervals do not overlap with zero). The vertical line is drawn at the effect size of zero. DPPT = decreased precipitation; IPPT = increased precipitation

3.2.3 | Soil texture

The sensitivities of microbial biomass to altered precipitation were affected by soil texture (Figure 3). Specifically, the sensitivity of microbial biomass to DPPT was positively correlated with the clay content

[$y = 0.26\log(x) - 1.1$, $R^2 = .44$, $p = .02$; Figure 3a] but negatively with the sand content ($y = -0.012x + 0.25$, $R^2 = .48$, $p = .01$; Figure 3b). Inversely, the sensitivity of microbial biomass to IPPT was negatively correlated with the clay content [$y = -0.92\log(x) + 2.9$, $R^2 = .47$,

$p = .01$; Figure 3c], but was not significantly correlated with the sand content (Figure 3d).

When the data were divided into dry and humid regions by the MAP threshold of 800 mm, the sensitivities of microbial biomass in the coarse-textured soils under DPPT ($Q_B = 31.82$, $p < .01$) and IPPT

treatments ($Q_B = 130.87$, $p < .01$) were 8.8 and 3.3 times higher than those in the fine-textured soils, respectively, in the arid regions (Figure 4a,b). Inversely, in the humid regions, the sensitivities of microbial biomass to both DPPT ($Q_B = 1.28$, $p = .26$) and IPPT ($Q_B = 0.15$, $p = .69$) were comparable between the fine-textured and coarse-textured soils (Figure 4a,b). Similarly, using the MAP threshold of 370 mm to analyse the data, the sensitivities of microbial biomass in the coarse-textured soil under DPPT and IPPT were significantly higher ($p < .01$) than those in the fine-textured soils in both the arid and humid regions (Figure 4c,d).

The stepwise regression analysis showed that the effect of soil texture on the sensitivity of microbial biomass was significant ($p < .05$). However, the significant contributor of the regression model was the sand content for DPPT but the clay content for IPPT. The effect of MAP on the sensitivity of microbial biomass was not significant ($p > .05$).

3.3 | Correlations of response ratios between microbial biomass and other carbon components to altered precipitation

The sensitivities of the aboveground and belowground plant biomass, soil respiration, and soil C content to both IPPT and DPPT were significantly different from zero (Figure 5a). The aboveground plant biomass showed higher sensitivity to altered precipitation than the belowground C cycling processes. Specifically, the sensitivity of aboveground plant biomass to IPPT was 4.2, 2.2, 2.3 and 4.6 times greater than that of belowground plant biomass, microbial biomass, soil respiration, and soil C content, respectively, whereas that to DPPT was 3.8, 3.0, 3.1 and 3.1 times greater, respectively (Figure 5a). In addition, the response ratios of ecosystem C cycling processes were significantly and positively correlated with Δ PPT, with the greatest slope for the aboveground plant biomass (.0072), the least slope for root biomass and soil C content (.0026 and .0021, respectively; Supporting Information Figure S6), and those for microbial biomass and soil respiration in between (Supporting Information Figure S6).

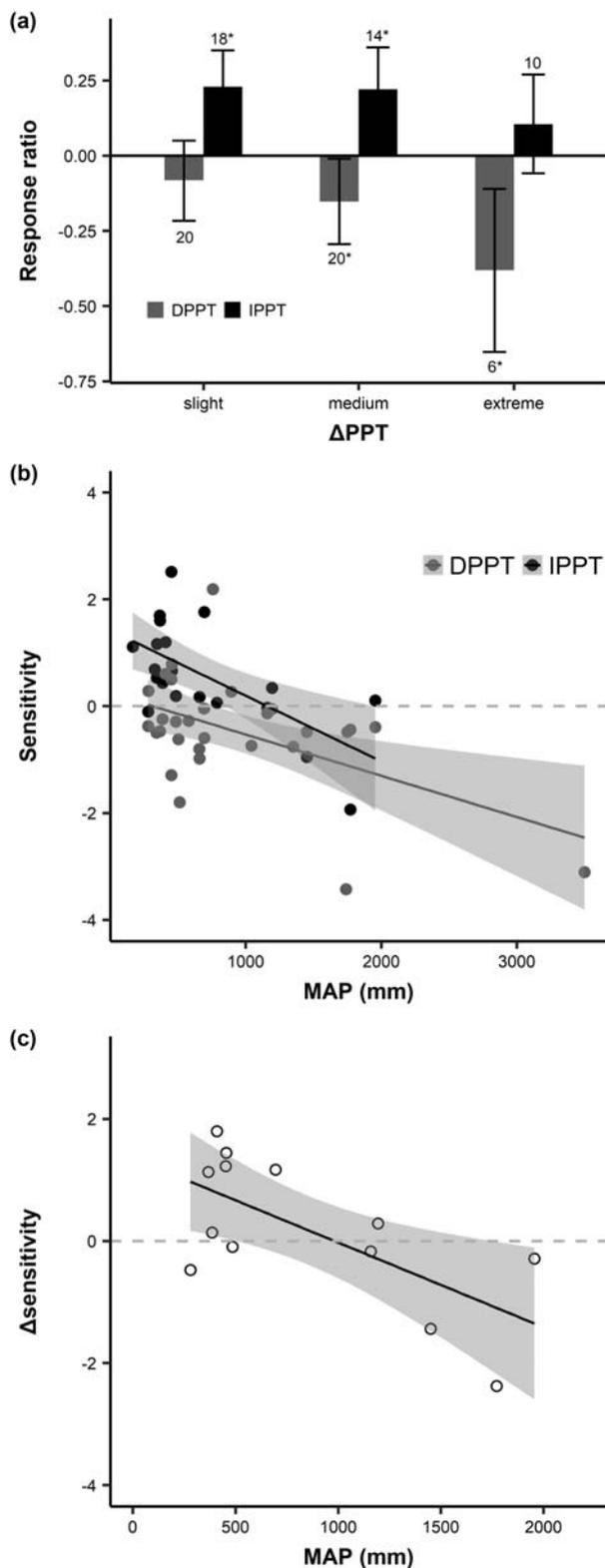


FIGURE 2.

FIGURE 2 Effects of magnitude of precipitation manipulation (Δ PPT) and mean annual precipitation (MAP) on the response of microbial biomass to altered precipitation. (a) Pooled response ratios of the microbial biomass to different Δ PPTs binned by slight ($< 30\%$), medium (≥ 30 – $<60\%$) and extreme ($\geq 60\%$) increased (IPPT) and decreased precipitation (DPPT) treatments. The error bars represent 95% confidence intervals; the numbers above the error bars represent the observation numbers for each estimate; and the following asterisks indicate significant responses (the 95% confidence intervals do not overlap with zero). (b) Relationships between sensitivity of microbial biomass to IPPT or DPPT and site-level MAP. The shaded areas represent 95% confident intervals. Sensitivity to DPPT – MAP: $y = -0.0008x + 0.24$, $R^2 = .28$, $p < .01$; sensitivity to IPPT – MAP: $y = -0.0012x + 1.3$, $R^2 = .38$, $p < .01$. (c) Relationships between the sensitivity difference between IPPT and DPPT (Δ sensitivity) and site-level MAP. Δ sensitivity – MAP: $y = -0.0014x + 1.4$, $R^2 = .46$, $p = .01$

TABLE 2 Correlations of response ratios between soil moisture and carbon cycling components or microbial community compositions

Carbon cycling component	<i>n</i>	<i>r</i>	PLFA	<i>n</i>	<i>r</i>	Bacterial phyla	<i>n</i>	<i>r</i>
Aboveground biomass	13	.85***	Fungi	22	.30	<i>Proteobacteria</i>	20	.50*
Belowground biomass	21	.71***	Bacteria	22	-.15	<i>Acidobacteria</i>	20	-.31
Soil respiration	34	.82***	Fungi: Bacteria	30	.08	<i>Actinobacteria</i>	20	-.25
Soil carbon	24	.63**	Gram-positive (GP)	18	-.36	<i>Planctomycetes</i>	16	.36
Microbial biomass	63	.77***	Gram-negative (GN)	18	.29	<i>Bacteroidetes</i>	20	.29
			GP:GN	21	-.24	<i>Chloroflexi</i>	9	-.25
			AMF	14	.38	<i>Verrucomicrobia</i>	16	.08
						<i>Gemmatimonadetes</i>	16	-.39
						<i>Firmicutes</i>	18	.05

PLFA = phospholipid fatty acid analysis; AMF = arbuscular mycorrhiza fungi; *n* = sample size; *r* = correlation coefficient; **p* < .05. ***p* < .01. ****p* < .001.

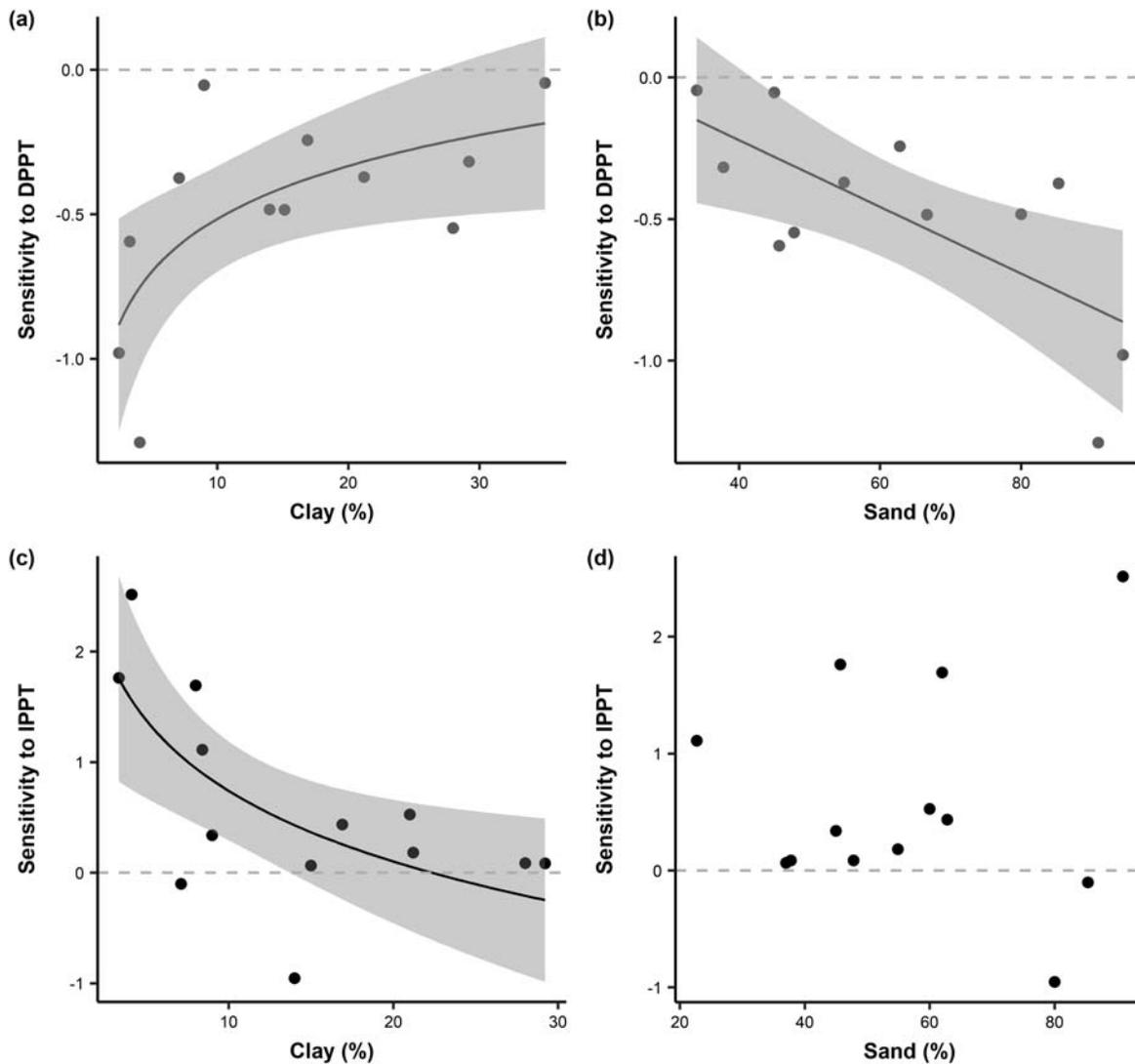


FIGURE 3 The sensitivity of microbial biomass to decreased (DPPT) (a, b) and increased precipitation (IPPT) (c, d) versus soil texture (clay or sand contents). The shaded areas represent 95% confident intervals. Sensitivity to DPPT - clay: $y = 0.26\log(x) - 1.1$, $R^2 = .44$, $p = .02$; sensitivity to DPPT - sand: $y = -0.012x + 0.25$, $R^2 = .48$, $p = .01$; sensitivity to IPPT - clay: $y = -0.92\log(x) + 2.9$, $R^2 = .47$, $p = .01$; sensitivity to IPPT - sand: no significant relationship ($p > .05$)

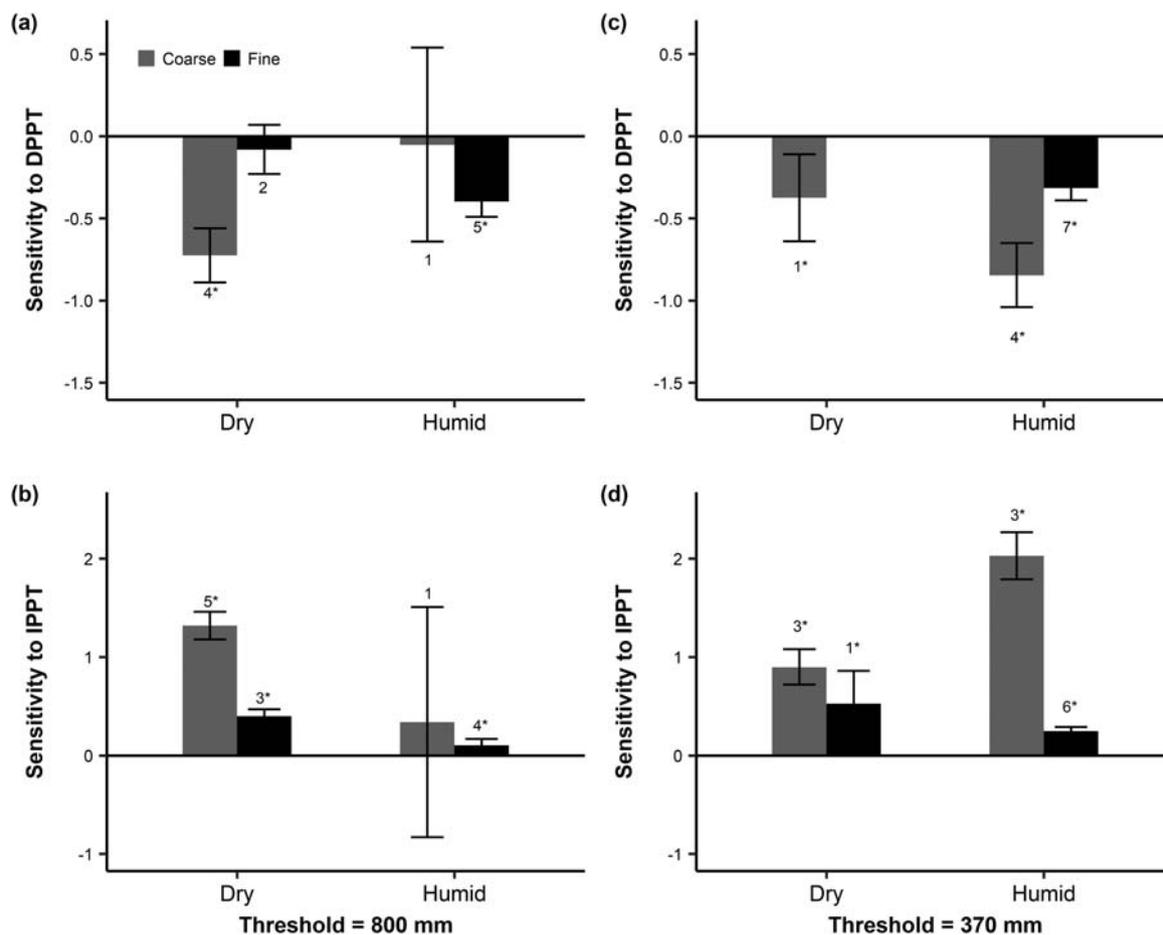


FIGURE 4 Sensitivities of microbial biomass to decreased (DPPT, a, c) and increased precipitation (IPPT, b, d) binned by soil texture and climate humidity. (a and b) A mean annual precipitation (MAP) of 800 mm is used as the threshold for dividing climate into dry (< 800 mm) and humid climate (\geq 800 mm); (c and d) a MAP of 370 mm is used as the threshold for dividing climate into dry (< 370 mm) and humid climate (\geq 370 mm). The error bars represent 95% confidence intervals; the numbers above the error bars represent the observation numbers for each estimate; and the following asterisks indicate significant responses (the 95% confidence intervals do not overlap with zero). Coarse texture, clay content < 10%; fine texture, clay content \geq 10%

At the case-study level, the sensitivity of microbial biomass to altered precipitation was positively correlated with the sensitivity of aboveground and belowground plant biomass, soil respiration, and soil C content (Figure 5b–d). The sensitivity of microbial biomass explained 53, 42, 53, and 68% of the variances of the sensitivity of plant aboveground and belowground biomass, soil C content, and soil respiration, respectively (Figure 5b–d).

4 | DISCUSSION

The current meta-analysis extended the double asymmetric model (Knapp et al., 2017) to apply to soil microbial biomass studies and improved the explanatory power of the model by considering climate and site conditions. Changes in soil moisture induced by precipitation manipulations did not result in changes in the fungi to bacteria ratio, but caused minor water-tolerant shifts in the community compositions within the bacteria group. Moreover, we found coordinated responses in the plant–soil–microorganism C continuum. These findings provide a framework for understanding and modelling responses of ecosystem C

cycling to global precipitation change. Below, we discuss potential mechanisms for the observed patterns of microbial communities in response to altered precipitation and their implications for C cycling in terrestrial ecosystems.

4.1 | Responses of microbial community compositions to altered precipitation

Fungi and bacteria are the dominant decomposers in soils, whose distinct physiologies are likely to respond differently to environmental changes (Manzoni et al., 2012; Schimel et al., 2007). Based on precipitation gradient studies, a negative relationship between the fungi to bacteria ratio and environmental humidity was evidenced for 24 arid and semi-arid grasslands on the Mongolian Plateau (Chen et al., 2015) and a 3500-km alpine transect on the Tibetan Plateau (Chen et al., 2016). However, our meta-analysis did not find any evidence for water-tolerant shifts in the fungi to bacteria ratio due to altered precipitation, that is, neither IPPT nor DPPT had an effect on the fungi to bacteria ratio (Figure 1b). In addition, the response of the fungi to

bacteria ratio to altered precipitation was inconsistent for different experimental durations, sampling seasons and magnitudes of precipitation changes (Supporting Information Figures S1, S2, S4 and S7). A long-term precipitation-control experiment also showed that rainfall reduction did not change the fungi to bacteria ratio despite the fact

that the original drier plots had higher fungi to bacteria ratios than the original wetter plots (Zeglin et al., 2013). Such inconsistent responses of the fungi to bacteria ratio in various studies may result from the variations in other ecosystem characteristics induced by altered precipitation, such as the quality and quantity of the organic substrates for microorganisms. Wet treatments stimulate plant productivity and increase plant biomass and soil organic C content (Supporting Information Table S5; Nielsen & Ball, 2015; Wilcox et al., 2017; Wu et al., 2011), leading to soil N limitation and plant competition (Ren et al., 2017). Consequently, high soil C content and low N content may shift the microbial communities from being bacteria (fast-growing copiotrophs) to fungi (slow-growing oligotrophs) dominated (Chen et al., 2016; Zechmeister-Boltenstern et al., 2015; Zhou, Wang, & Luo, 2018). In addition, the inconsistent response of the fungi to bacteria ratio to altered precipitation may also be related to the taxonomic resolutions used in different studies. Microbes have highly diverse structural and functional traits even within the fungi and bacteria groups (Ho, Lonardo, & Bodelier, 2017).

However, we did find water-tolerant shifts in the community compositions within bacteria. At a coarse taxonomic resolution, the Gram-positive to Gram-negative ratio negatively responded to IPPT but positively to DPPT (Figure 2b). The probable explanation is that Gram-positive bacteria (with strong, thick, interlinked peptidoglycan cell walls) are inherently more resistant to water stress than Gram-negative bacteria (Manzoni et al., 2012; Schimel et al., 2007). At a fine resolution, *Planctomycetes* was found to be the only one in the bacterial phylum that was significantly sensitive to both IPPT and DPPT (Table 2). *Planctomycetes*, once thought to occur primarily in aquatic environments, have been discovered in terrestrial soils worldwide (Buckley, Huangyutham, Nelson, Rumberger, & Thies, 2006), and are the only bacterial group that lack peptidoglycan in their cell walls (Fuerst & Sagulenko, 2011), which may explain why *Planctomycetes* were sensitive to changes in soil moisture induced by altered precipitation (Table 2). Drought treatments induced decreases in *Proteobacteria* and *Verrucomicrobia* and increases in *Acidobacteria*, maybe because they belong to Gram-negative and Gram-positive bacteria, respectively. However, *Gemmatimonadetes*, as Gram-negative bacteria, significantly and

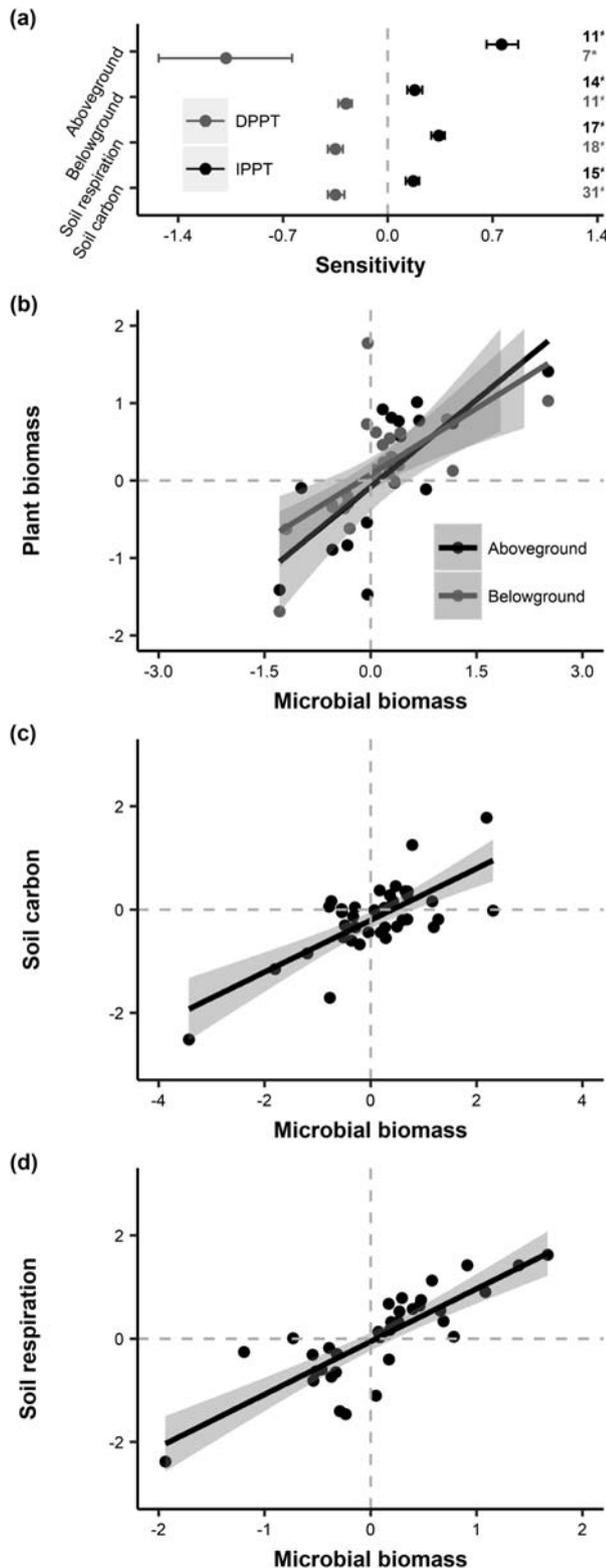


FIGURE 5.

FIGURE 5 Sensitivities of ecosystem carbon cycling components and their correlations with the microbial biomass. (a) Sensitivities of aboveground and belowground plant biomass, soil carbon content, and soil respiration. The error bars represent 95% confidence intervals. The numbers on the right side of the figure represent the observation numbers for each estimate. The asterisks following the observation numbers indicate significant responses (the 95% confidence intervals do not overlap with zero). The vertical line is drawn at the effect size of zero. (b) Relationships between microbial biomass and aboveground ($y = 0.75x - 0.082$, $R^2 = .53$, $p < .01$) and belowground plant biomass ($y = 0.57x + 0.077$, $R^2 = .42$, $p < .01$). (c) Relationship between microbial biomass and soil carbon content ($y = 0.50x - 0.21$, $R^2 = .53$, $p < .01$). (d) Relationship between microbial biomass and soil respiration ($y = 1.02x - 0.057$, $R^2 = .68$, $p < .01$). The shaded areas represent 95% confident intervals. DPPT = decreased precipitation; IPPT = increased precipitation

positively responded to DPPT. Currently, we know little about the underlying mechanisms, but the adaptation of *Gemmatimonadetes* to drier soils is supported by a global biogeographical study in which their spatial abundances were inversely correlated with soil moisture (DeBruyn, Nixon, Fawaz, Johnson, & Radosevich, 2011). We did not find significant responses of *Actinobacteria*, *Chloroflexi* or *Bacteroidetes* to altered precipitation, possibly for the taxonomic resolution reason. For example, *Chloroflexi* is similar to Gram-positive bacteria, but mostly stains Gram-negative (Sutcliffe, 2011). Even the structure and thickness of cell walls can be different among species within a phylum (Schleifer & Kandler, 1972).

4.2 | Asymmetric responses of microbial biomass to altered precipitation varied with climate humidity and soil texture

Precipitation manipulation significantly changed soil moisture (Supporting Information Table S5 and Figure S6). Consequently, IPPT stimulated microbial biomass, whereas DPPT suppressed it (Figure 1a). We also found that microbial biomass showed a higher response to moderate IPPT (< 60%) than moderate DPPT, whereas it was more sensitive to extreme DPPT ($\geq 60\%$) than extreme IPPT (Figure 2a). These results suggest that the relationship between microbial biomass and precipitation be consistent with the prediction of the double asymmetric model proposed by Knapp et al. (2017). However, this model has some limitations if the environmental humidity and soil texture (see the discussion below) are considered.

We found that the sensitivity of microbial biomass to IPPT was higher at arid sites than at mesic sites, but the sensitivity to DPPT was higher at mesic sites than at arid sites (Figure 2b and Supporting Information Figure S8). Also, the Δ sensitivity of microbial biomass significantly decreased when the MAP increased in the 13 paired experiments (Figure 2c). Several potential mechanisms may explain the climate-dependent asymmetric responses of microbial biomass to altered precipitation. First, reduction in soil moisture restricts the ability of microbes to migrate towards available substrates due to diminished pore connectivity in dry soils (Abramoff et al., 2017; Davidson et al., 2012; Manzoni et al., 2014; Sierra et al., 2017; Sihi et al., 2018). Consequently, IPPT removes the moisture-induced substrate limitation and increases the microbial biomass. In wet soils, however, IPPT may lead to oxygen limitation (Abramoff et al., 2017; Davidson et al., 2012; Manzoni et al., 2014; Sierra et al., 2017; Sihi et al., 2018), and then inhibit the microbial growth (Figure 2b,c). Second, the observed relationship between the sensitivity of microbial biomass to altered precipitation and MAP could result indirectly from the response of plant litter inputs to altered precipitation along the MAP gradients, because the sensitivity of ANPP to altered precipitation is also negatively related to MAP (Huxman et al., 2004; Wilcox et al., 2017) and soil microbes are commonly constrained by substrate availability (Zhou & Wang, 2015; Figure 5b,c). Third, as the inherent resistance of soil microbes to water stress involves evolutionary selection of growth form and life history strategies, microbial communities growing under dry conditions, like plant communities (Knapp & Smith, 2001; Wilcox et al., 2017), are

likely to have greater hydrological resilience to water stress than those in moist soils (Nielsen & Ball, 2015; Schimel et al., 2007).

Our global synthesis also showed that the microbial growth in coarse-textured soils was more sensitive to both IPPT and DPPT than that in fine-textured soils in arid regions. Inversely, the sensitivity of microbial biomass to altered precipitation was comparable between the fine- and coarse-textured soils at humid sites (Figure 4). These patterns contradict the prediction of the inverse texture effect (Epstein et al., 1997; Noy-Meir, 1973). One possible explanation is that all the data compiled in this synthesis were from the top 20 cm of topsoils (Supporting Information Appendix S1), but the inverse texture effect proposes that the top layer of coarse-textured soils dries out quickly and forms a barrier to the conductance and evaporation of water from deeper layers in dry areas (Epstein et al., 1997; Noy-Meir, 1973). As subsoils contain > 50% of the global C stock (Jobbágy & Jackson, 2000) and all depths respond to global change with similar sensitivity (Pries, Castanha, Porras, & Torn, 2017), we recommend that the microbial response of deep soils should be explored in future field experiments. Additionally, the applicability of the inverse texture effect has been questioned especially for belowground processes (Austin et al., 2004). For example, Epstein et al. (1997) revealed an MAP threshold of 800 mm for the inverse texture effect by analysing ANPP data for the Great Plains of the United States, whereas Lane, Coffin, and Lauenroth (1998) did not find any inverse texture effect in explaining the ANPP variations across the Central Grassland region of the United States. Austin et al. (2004) also suggested that the inverse texture effect should not be used to study belowground processes, including microbial community, total C and N content, particulate organic matter, and mineralizable C and N. Collectively, our results suggest that the double asymmetric model (Knapp et al., 2017) is applicable in explaining the responses of soil microbial biomass to altered precipitation, but that climate and site conditions may need to be taken into account.

4.3 | Implications for carbon cycling in terrestrial ecosystems

Responses of microbial biomass and community compositions to water stress have costs at the organismal level that can result in changes in C cycling at the ecosystem level (Nielsen & Ball, 2015; Schimel et al., 2007). Our global synthesis on the response of microbial communities to altered precipitation has important implications for studies and modelling of ecosystem C cycling and experimental designs of precipitation manipulation in the future.

First, the sensitivities of aboveground and belowground plant biomass, soil respiration and C content all displayed significantly positive correlations with the sensitivity of microbial biomass to altered precipitation (Figure 5b–d), suggesting coordinated responses in the plant–soil–microorganism C continuum to altered precipitation. We also found that the aboveground plant biomass showed higher sensitivity to altered precipitation than the belowground C cycling processes (Figure 5 and Supporting Information Figure S6), implying that microbes may be more dependent on recent photosynthate than soil organic matter or root biomass that are relatively older in age. These findings indicate

that microbial physiological adjustments are crucial to understanding the ecosystem process mediated by soil microbes under altered precipitation (Abramoff et al., 2017; Davidson et al., 2012; Sierra et al., 2017; Sihi et al., 2018). Conversely, changes in soil moisture induced by precipitation manipulations did not result in changes in the fungi to bacteria ratio, but caused minor water-tolerant shifts in bacterial community compositions (Figure 1C and Table 2), which suggests that changes in community compositions may have limited effect on ecosystem C cycling. However, caution should be taken in drawing broad conclusions on the effect of altered precipitation regime on microbial community compositions, because soil microbial species are abundant and their community compositions are complex.

Second, the double asymmetric model proposed by Knapp et al. (2017) provides a crucial step to improving our understanding of how rainfall gradients impact ecosystem productivity across the world. Recently, two other meta-analyses found that the asymmetric responses of ANPP and soil respiration to altered precipitation varied with climate humidity (Liu et al., 2016; Wilcox et al., 2017). In this study, we extended the model to apply to soil microbial biomass and improved the explanatory power of the model by considering climate and site conditions. In addition, we suggest that the double asymmetric model may be revised as: Ecosystem process shows a higher percentage change in response to nominal precipitation addition than nominal precipitation reduction in arid or semi-arid region, but shows oppositely in humid site. Furthermore, multiple levels of increased and decreased precipitation manipulated in different types of ecosystems around the world will be conducive to further improving the double asymmetric model (Figure 2c; Luo et al., 2017).

Third, soil texture, besides climate humidity, is another important driver for the sensitivity of ecosystem processes to altered precipitation. To our knowledge, we found for the first time that soil texture explained more variance in the sensitivity of microbial biomass to both IPPT and DPPT than the MAP (Figures 2b and 4; cf. Liu et al., 2016; Wilcox et al., 2017; Wu et al., 2011). Several meta-analyses have assessed how sensitivities of plant productivity and ecosystem C fluxes to precipitation manipulation vary across climate gradients (e.g., temperature, precipitation, and aridity index), and reported no or weak relationships between the sensitivity and climate gradients (Liu et al., 2016; Wilcox et al., 2017; Wu et al., 2011). However, soil properties are more critical and direct factors driving microbial growth and activity than climate. Nevertheless, many precipitation manipulation studies did not report sufficient site-level information (Figure 4 and Supporting Information Table S1; Wilcox et al., 2017). It is encouraged that future studies on responses of ecosystem processes to altered precipitation report soil texture and incorporate this factor as well as climate into the modelling of ecosystem processes under projected precipitation change regimes.

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DATA ACCESSIBILITY

All data supporting this study are extracted from published papers and provided in Supporting Information accompanying this paper.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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APPENDIX : DATA SOURCES

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