Soil responses to manipulated precipitation changes: A synthesis of meta-analyses

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Abstract. In the face of ongoing and projected precipitation changes, precipitation manipulation experiments (PMEs) have produced a wealth of data about the effects of precipitation changes on soils. In response, researchers have undertaken a number of synthetic efforts. Several meta-analyses have been conducted, each revealing new aspects of soil responses to precipitation changes. We synthesize the findings of 16 meta-analyses focused on the effects of decreased and increased precipitation on 42 soil response variables, covering a wide range of soil processes and examining responses of individual variables as well as more integrative responses of carbon and nitrogen cycles. We found a strong agreement among meta-analyses that decreased and increased precipitation inhibits and promotes belowground carbon and nitrogen cycling, respectively, while microbial communities are relatively resistant to precipitation changes. Much attention has been paid to fluxes and pools in carbon, nitrogen, and phosphorus cycles, such as gas emissions, soil carbon, soil phosphorus, extractable nitrogen ions, and biomass, but the rates of processes underlying these variables are less frequently covered in meta-analytic studies (e.g., rates of mineralization, fixation, and de/nitrification). Shifting scientific attention to these "processes" would, therefore, deepen the current understanding of the effects of precipitation changes on soil and provide new insights. By comparing meta-analyses focused on different variables, we provide here a quantitative and holistic view of soil responses to changes in precipitation.

1 Introduction

Soil is an important component of terrestrial ecosystems through which carbon, nitrogen, phosphorus, and other elements cycle. Biological processes in soils, such as those driven by plant roots, microbes, and enzymes, regulate nutrient cycling, with direct impacts on aboveground plant and animal communities (Bardgett et al., 2008). Rates of biological activity in soils are largely determined by physical parameters, one of the most influential being soil moisture (Stark and Firestone,

1995; Brockett et al., 2012; Schimel, 2018). Historical observations have shown that annual precipitation has either increased or decreased significantly in many regions, and the intensity and frequency of precipitation extremes (heavy rainfalls and droughts) have likewise increased in many regions (Frei et al., 2006; Lenderink and van Meijgaard, 2008). These changes in
35 precipitation patterns are projected to continue in the future, possibly at a faster rate (Bao et al., 2017).

The activity of plant roots, microorganisms and enzymes is maximized at optimal soil water content, which is unique to each group of organisms, soil type and ecosystem (Bouwman, 1998; Schimel, 2018). Water in soil functions as (1) a resource to promote metabolism of microbes and plants, (2) a solvent of nutrients, and (3) a transport medium to provide pathways to
40 solutes and microorganisms (Schimel, 2018; Tecon and Or, 2017). In a water-limited environment, reduced belowground activities are common (Borken et al., 2006; Sardans and Peñuelas, 2005). The negative responses of soil processes to decreased precipitation are attributed to reduced metabolism of the organisms (Salazar-Villegas et al., 2016; Schimel et al., 2007), limited substrate availability/diffusivity (Manzoni et al., 2016), restricted mobility of the organisms (Manzoni et al., 2016), or a combination of these (Schimel, 2018). Increased precipitation, on the other hand, generally promotes processes
45 by shifting the soil moisture level closer to the optimum (Zhang et al., 2013; Zhou et al., 2013). However, excess water in soil often results in lower biological activity due to the limitation of oxygen flow (Bouwman, 1998; Reinsch et al., 2017), while anaerobic processes such as methane production are greatly promoted (Le Mer and Roger, 2001).

Natural variation in precipitation provides opportunities to observe responses of belowground activities (e.g., Goldstein et
50 al., 2000; Granier et al., 2007), but targeted studies of belowground responses are difficult. Controlled precipitation manipulation experiments offer the opportunity to specifically study ecosystem responses to changes in precipitation compared to naturally occurring fluctuations and have become common in recent decades (Beier et al., 2012; Borken et al., 2006; Knapp et al., 2017). Precipitation manipulation experiments (PMEs) involve constructing an experimental structure in the field, such as rainout shelters, curtains, and/or sprinklers, to simulate alternative precipitation patterns (Beier et al., 2012).
55 These setups enable direct comparisons between a manipulated precipitation treatment and a control (ambient precipitation) in the same study system, while keeping other environmental conditions nearly identical. PMEs have been established across ecosystem types and characteristics (biome, ecosystem, soil type, and land type), and often use different methodological approaches (e.g., in terms of the magnitude and duration of the precipitation manipulation, size of the experiment, method of rain exclusion, and/or variables measured) (Vicca et al., 2014).

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A number of meta-analyses have assembled and synthesized large and diverse PME datasets (Blankinship et al., 2011; Canarini et al., 2017; Wu et al., 2011). The first to examine soil responses to precipitation changes was conducted by Wu et al. (2011), compiling 85 manipulation studies and presenting the changes in aboveground and belowground carbon dynamics. Since then, several additional meta-analyses have considered belowground responses to precipitation changes. As
65 of April 2019, according to our search criteria (details below), a total of 16 meta-analyses in this area were published. These

meta-analyses focused on different but complementary soil properties [e.g., soil C (Zhou et al., 2016) or N (Yue et al., 2019)]. A combined analysis of these meta-analyses would provide a holistic view of the potential effects of projected precipitation changes on soil processes.

70 In this paper, we synthesize 16 meta-analyses that have examined soil responses to manipulated (increased and decreased) precipitation *in-situ*, encompassing 42 response variables including greenhouse gas exchanges, carbon and nitrogen dynamics, phosphorus content, microbial community, and enzyme activities. By collating the results of the published meta-analyses, we aimed to (1) provide a more holistic view of the effects of precipitation changes on soil composition and functioning, (2) discuss the potential underlying mechanisms of each response, and (3) identify knowledge gaps and propose 75 future research directions. This study covers an unusually wide range of soil processes and examines the responses of individual variables as well as nutrient cycles.

2 Review of meta-analyses

2.1 Meta-analysis collection

We collected peer-reviewed meta-analyses focused on the effects of decreased and/or increased precipitation on soil 80 variables. We collected meta-analyses that included only field studies where the magnitude of precipitation was manipulated. We used Google Scholar and Web of Science with the search terms "meta-analysis" AND "soil" AND ("respiration" OR "CO_2" OR "carbon" OR "nutrient" OR "nitro" OR "phosph" OR "N_2O" OR "CH_4" OR "microb" OR "enzyme" OR "bacteria" OR "fungi") AND ("altered precipitation" OR "drought" OR "decreased precipitation" OR "increased precipitation" OR "water addition" OR "water reduction"). We identified 16 meta-analyses (Table 1); four of them focused 85 on decreased precipitation (DP), one of them on increased precipitation (IP), and 11 on both DP and IP. A total of 42 soil variables were covered, encompassing a wide range of soil characteristics such as soil greenhouse gas exchanges, soil carbon, nitrogen, phosphorous, microbial and bacterial communities, enzymes, and physical characteristics of soil (Table 2). Only meta-analyses written in English and published before April 2019 were included in our analysis.

2.2 Effect sizes

90 From each meta-analysis, we obtained the mean effect size of each soil variable. In this review, effect sizes are the natural log of response ratios (lnRR) defined as:

$$lnRR = \ln\left(\frac{X_t}{X_c}\right) , \tag{1}$$

where X_t and X_c are the mean values of the treatment (DP or IP) and control, respectively, for each observation. Homyak et al. (2017) used Hedge's d instead of Eq. 1 for N_2O emissions and N supply due to the negativity of RR. Hedge's d is defined 95 as $J(X_t-X_c)/S$ where S is the pooled standard deviation, and J is the correction of small sample bias (Homyak et al., 2017).

Both lnRR and Hedge's *d* are negative for inhibitory effects, and positive for stimulatory effects (Brzostek et al., 2012; Homyak et al., 2017). All meta-analyses calculated mean effect sizes and 95% confidence intervals (CI) with sample size or the inverse of the variance as the weighting function. The effect is considered significant when 95% CI does not overlap zero. Some meta-analyses applied additional weighting functions or normalized the measurements under different manipulation levels (Liu et al., 2016; Wu et al., 2011). We used these sample size- or variance-weighted effect sizes when available. We obtained the values from the main texts or supplementary materials of the articles. If necessary, we used the digitizing software Plot Digitizer (Huwaldt, 2015), to extract values from graphs. When only percent changes were reported, we converted to lnRR as in Ren et al. (2017, 2018):

$$lnRR = \ln\left(\frac{\%\ change}{100} + 1\right). \tag{2}$$

Some 95% CI were unavailable because points were not visible on graphs or because values of percent change below -100% were not convertible using Eq. 2 (e.g. He and Dijkstra, 2014). We also obtained the sample size, defined as the number of studies or observations included in the meta-analyses. The collected information is available in Abbasi et al. (2020).

3 Soil responses to precipitation changes

3.1 Responses of soil respiration and belowground biomass

Meta-analyses on autotrophic (R_a), heterotrophic (R_h), and total soil ($R_s = R_a + R_h$) respiration provide strong agreement that DP decreases, and IP increases, R_s, R_a, and R_h (Fig. 1a). Litter biomass (B) follows the same pattern (Fig. 1b). Although the response of R_a reaches significance in only one of two meta-analyses, the direction of the response is consistent. Responses of soil carbon variables [total carbon (C), soil organic C (SOC), and dissolved organic C (DOC)] to precipitation differ among meta-analyses, both in direction and significance (Fig. 1b). Interestingly, root B is strongly suppressed by both DP and IP. In contrast, IP stimulates belowground B and belowground net primary productivity (NPP), and DP increases root C (Fig. 1b).

To understand the effects of precipitation on R_s, we need to understand the responses of roots, microbes, and substrates to DP and IP. Commonly, R_a decreases under limited water supply due to (1) reduced plant growth and nutrient demand, (2) reduced root tissue activity due to limited soil water, and (3) reduced respiratory substrate production from photosynthetic activity (Hasibeder et al., 2015). In contrast, increased water supply enhances plant growth and photosynthetic rate (Heisler-White et al., 2008; Maire et al., 2015), which results in increased R_a. The responses of belowground B to IP and belowground NPP to DP and IP (Fig. 1b) are also likely to result from these changes in plant and root growth. However, not all belowground responses are consistent with this storyline. Root C and total C increase with DP, and root B decreases with IP (Fig. 1b).

This contradictory evidence could be due to variability by biome and soil type. For example, the effects of DP on total C is negative in temperate forests, and positive in tropical forests and grassland (Yuan et al., 2017; Zhou et al., 2016). Also, in our study, both significant effects (Zhou et al., 2016) and no effects (Liu et al., 2016) of DP and IP on R_a were found. This

130 difference in effects could be attributed to, for example, the IP effects on R_a depending on biome and R_a separation method. Specifically, IP effects can be significant in temperate forest and grassland, but not in boreal forest (Zhou et al., 2016), and R_a separated from R_h by clipping methods responded more positively than when trenching methods were used (Liu et al., 2016). Sample sizes remain relatively small for R_a responses to changes in precipitation, suggesting that additional research could help to identify how this process response varies with biomes and methods.

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R_h is the consequence of soil microbial activity decomposing soil organic matter (SOM) under aerobic conditions. SOM is frequently estimated by measuring its carbon component, SOC. R_h is mainly regulated by microbial access to substrate and the physiological condition of microbes (Schimel, 2018). In dry soil, substrate tends to be isolated from microbes as solute mobility is low (Manzoni et al., 2012; Schimel, 2018). Furthermore, a great number of empirical observations and synthetic

140 studies have shown that microbial activity is lower during droughts (Hueso et al., 2012; Jensen et al., 2003; Manzoni et al., 2012). This is because dry conditions force microbes into dormancy or shift their efforts from growth to survival (Salazar et al., 2018; Schimel et al., 2007). Excess water, on the other hand, not only increases substrate availability to microbes (Skopp et al., 1990), it also makes microbes dispose of osmolytes from their body cells to regulate the osmotic pressure (Schimel et al., 2007) and can activate dormant microbes (Salazar et al., 2018). These responses are particularly rapid and drastic when

145 dry soils rewet, yielding a large pulse of respiration, which could significantly affect the carbon exchanges in terrestrial ecosystems (Placella et al., 2012).

As with R_a, R_h typically decreases under DP and increases under IP, with variations among biomes and R_h separation methods. DP effects on R_h are significant in boreal forest and wetland, but not in tropical and temperate forests (Zhou et al.,

150 2016). Likewise, IP effects on R_h are significant in forest and grassland, but not in wetland (Liu et al., 2016; Zhou et al., 2016). Furthermore, DP and IP effects are significant if the clipping method was used, but not with trenching and root extraction (Liu et al., 2016).

Microbial activity in soils is strongly controlled by the actions of enzymes. Many of these enzymes, which are produced and

155 released by microbes, depolymerize complex carbon compounds (Ren et al., 2017). While enzyme activity is relatively unresponsive to IP (Fig. 2), DP increases hydrolytic enzyme activity (breakdown of labile carbon) and inhibits oxidative activity (de-polymerization of recalcitrant carbon) (Fig. 2). This indicates that under dry conditions, the relative contributions of substrates from labile carbon sources increase, while the respective relative contributions from recalcitrant sources decrease.

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The summary diagrams (Fig. 1c, 1d) illustrates how DP generally slows the belowground carbon cycle, while IP promotes it. Nearly all steps of the carbon cycle - carbon stock, substrates, microbial activity, and respiration – are altered by both types of precipitation changes. However, enzyme activity tends to be relatively unresponsive, particularly to IP, and the observations of biomass and carbon variables vary both in direction and significance among meta-analyses. These variables also tend to vary across biomes, ecosystems, and soil types.

3.2 Responses of methane uptake

We found only one meta-analysis that addressed the effects of precipitation on soil CH_4 (Yan et al., 2018). The results show a significant increase and decrease of soil CH_4 uptake in response to DP and IP, respectively (Fig. 1a). Soil CH_4 fluxes involve two groups of microbes: methanogens and methanotrophs. Methanogens produce CH_4 and are predominantly active in anaerobic conditions, while methanotrophs oxidize CH_4 and are active in aerobic environments (Conrad, 2007). CH_4 oxidation seems to peak at 10-15% volumetric water content because these conditions favor methanotroph activity as well as CH_4 and O_2 diffusion (Adamsen and King, 1993; Del Grosso et al., 2000).

The results of Yan et al. (2018) were significant across a wide range of ecosystem types, treatment durations, and magnitudes of precipitation manipulation. The effects of DP were greater in farmlands than other land types, in shorter-term (< 1 year) experiments than longer-term ones, and in more extreme experiments (> 50% rain reduction). The effects of IP were greatest in boreal forest and in longer-term experiments (1-5 years) with greater rain addition (> 50%). However, a few empirical studies have shown opposite responses to this meta-analysis (Billings et al., 2000; Christiansen et al., 2015); for instance, a precipitation removal experiment in a floodplain decreased CH_4 uptake, possibly due to the acclimation of methanotrophs to high soil moisture conditions (Billings et al., 2000), or differences in the types of methanotrophs in floodplain (low-affinity methanotrophs) versus upland soil, where most CH_4 uptake occurs (Christiansen et al., 2015).

3.3 Responses of soil nitrogen dynamics

Several soil nitrogen variables, including root nitrogen (N), N_2O emissions, total N, dissolved organic nitrogen (DON), and extractable $NH_4^+ + NO_3^-$ are significantly affected by precipitation changes (Fig. 3a). Specifically, DP decreases root N and N_2O emissions and increases total N, DON, and extractable $NH_4^+ + NO_3^-$. We also found that two meta-analyses (sample sizes < 20) suggest no change in total N, while one (sample size = 156) suggests an increase with DP. Similarly, one meta-analysis suggests an increase of extractable NH_4^+ with DP while other two meta-analyses suggest no effects. In contrast, IP increases root N, N_2O emissions, and extractable NH_4^+ (Fig. 3a). Two meta-analyses suggest that total N decreases with IP, while one meta-analysis suggests no effects.

Mineralization rate, defined as N supply by Homyak et al. (2017), does not change under DP despite the increase in substrate (i.e., DON) (Fig. 3). However, the product of mineralization is NH_4^+, and it increases according to one of three meta-

analyses even though another source of NH_4^+, N_2 fixation, could be suppressed (Hume et al., 1976; Streeter, 2003). This is reasonable considering that the consumption of NH_4^+ is likely to decrease with DP, mainly because of reduced plant nitrogen

195   uptake (He and Dijkstra, 2014; Matías et al., 2011; Yuan et al., 2017) and microbial nitrogen assimilation (Homyak et al., 2017; Månsson et al., 2014). Nitrification and denitrification are expected to slow down with DP (Bouwman, 1998; Lennon et al., 2012; Stark and Firestone, 1995), also reducing N_2O emission (Fig. 3b). This suggests that soil moisture could be a stronger regulator of nitrification and denitrification processes than the availability of NH_4^+ and NO_3^- (Weier et al., 1993). The input (nitrification) and outputs (denitrification, plant uptake and microbial assimilation) of NO_3^- both decline under DP,

200   leaving extractable NO_3^- unchanged (Fig. 3b).

Extracellular enzyme activity, here shown both as total proteolytic activity (pro-enzyme) and three particular N-acquisition enzyme activities (β-1,4-N-acetyl-glucosaminidase, leucine amino peptidase, and urease), does not change with DP or IP (Fig. 2). This indicates that the production of N-enzymes is not sensitive to water stress. Important outputs of the soil

205   nitrogen cycle (denitrification and plant uptake) decrease while inputs remain constant or decline (Fig. 3b). As a result, total soil N increases or remains unchanged.

In contrast to DP, soil nitrogen cycling is accelerated by IP (Fig. 3c). Although no mineralization indicator was included in the meta-analyses, ample evidence shows that nitrogen mineralization is likely to increase with IP (Hu et al., 2014; Sierra,

210   1997; Pilbeam et al., 1993; Mazzarino et al., 1998). Along with greater N_2 fixation (Hume et al., 1976), which contributes to increasing NH_4^+ (Fig. 3c), positive responses are also expected in nitrification and denitrification rates (Bouwman, 1998; Niboyet et al., 2011; Stark and Firestone, 1995), plant nitrogen uptake (Schaeffer et al., 2013; Liu et al., 2016; Ma et al., 2013), and microbial nitrogen assimilation (Månsson et al., 2014), which result in increased N_2O emissions, and lead to unchanged NO_3^- as well as total N.

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Soil nitrogen undergoes a wide range of chemical and biological transformations, some of which are difficult to quantify. Despite the large number of empirical studies included in meta-analyses, some nitrogen variables, such as rates of mineralization (for IP), nitrification, denitrification, and N_2 fixation, have not yet been examined in meta-analyses focused on PMEs.

220   **3.4 Responses of soil phosphorus**

We found four meta-analyses that examined how precipitation changes affect the soil phosphorus (P) cycle (He and Dijkstra, 2014; Yan et al., 2018; Yuan et al., 2017; Yue et al., 2018). The results differ among meta-analyses; for instance, according to these meta-analyses, IP can have a negative, positive, or non-significant effects on total P (Fig. 4). Yuan et al. (2017) assembled the largest dataset and found that IP decreases total P, while DP increases total P. As phosphorus is commonly a

225   limiting nutrient for vegetation, plant P uptake and concentration are frequently studied, but studies of soil phosphorus storage are rarer (He and Dijkstra, 2014; Yue et al., 2018).

Phosphorus in soil originates from weathering rocks, deposition from the atmosphere, and decomposition of organic matter (Wang et al., 2010). Outputs from soil involve plant uptake and consumption by microbes. As is the case with carbon and

230   nitrogen, microbial decomposition and consumption activities of P can be affected by precipitation changes (Van Meeteren et al., 2007). Plant P uptake tracks in the same direction as changes in precipitation (He and Dijkstra, 2014). However, challenges lie in generalizing the effects of precipitation changes on weathering and deposition, as these processes involve complex chemical and physical reactions. For example, soil water content determines the rate of chemical weathering, and humidity affects P deposition from the atmosphere (Newman, 1995). The effects on total P are strongly linked to soil type

235   (Yuan et al. 2017). Although Yuan et al. (2017) found significant effects of DP and IP on total P, the effects were small (-0.1 < effect sizes < 0.1), and other meta-analyses show that soil P, as well as P-acquisition enzyme activity, are relatively unresponsive to precipitation changes (Fig. 2, 4). Other global changes such as warming, elevated CO_2, and anthropogenic P and N deposition tend to have higher impacts on the terrestrial P cycle than precipitation changes (Yue et al., 2018).

3.5 Responses of microbial biomass and community structure

240   Microbial biomass (MB) in soil either decreases or does not respond to DP (Fig. 5a). MB responses to DP vary with the amount of precipitation that is removed (Zhou et al., 2016; Ren et al., 2017, 2018), the length of droughts (Ren et al., 2018), vegetation type (Zhou et al., 2016; Ren et al., 2017, 2018) and mean annual precipitation (MAP; Ren et al., 2017). MB is affected by DP only when reduced precipitation is larger than ~33% (Ren et al., 2017, 2018), the drought period is ≤ 2 years (Ren et al., 2018), and in wet (MAP > 600mm) regions (Ren et al., 2017). Additionally, vegetation type affects MB

245   responses to DP; DP consistently decreases MB in forests (tropical and temperate but not in boreal; Zhou et al., 2016; Ren et al., 2017, 2018) and heathlands (Blankinship et al., 2011), but not in shrublands (Ren et al., 2017, 2018). A meta-analysis conducted by Zhou et al. (2016) found that DP decreases MB in grassland soils. However, more recent meta-analyses that included more studies (Ren et al., 2017, 2018) suggest that MB in grasslands does not respond to DP.

250   In contrast, except when added precipitation is very high (> 70%; Ren et al., 2017), IP stimulates microbial growth and thus increases MB. Contrary to DP, IP affects MB in dry (MAP < 600 mm) but not in wet (MAP > 600 mm) sites (Ren et al., 2017). This is consistent with IP increasing MB in soils from ecosystems that are generally water-stressed, such as deserts, shrublands, and grasslands (Zhou et al., 2016; Ren et al., 2017). Zhou et al. (2016) found that IP increases MB in soils in temperate forests. Other meta-analyses that included more studies (also including tropical forests) suggest that MB in forest

255   soils is generally not affected by IP (Blankinship et al., 2011; Canarini et al., 2017; Ren et al., 2017).

In contrast to the responsiveness of MB to altered precipitation, the composition of bacterial and fungal communities is rather unresponsive (Fig. 5b). Although Blankinship et al. (2011) and Yan et al. (2018) estimated significant effects on the abundance of fungi and F:B ratio (n = 4), other studies with sample sizes one order of magnitude larger (e.g., Ren et al. 2018) estimated non-significant effects. The high resistance of bacteria and fungi to soil moisture changes has been frequently highlighted (Evans and Wallenstein, 2012; Schimel et al., 2007; Yuste et al., 2011). Fungi in particular, due to their filamentous structure, are capable of accessing substrates even in very dry soils (Manzoni et al., 2012). Bacteria and fungi also have a wide breadth of soil moisture niches; diverse types of bacteria and fungi tolerate water stress (Lennon et al., 2012). Differences in resistance between bacteria, fungi, and other functional types can alter microbial structure under precipitation changes; DP could promote a more fungi-dominated community (Yuste et al., 2011). Although gram-positive bacteria are more resistant to soil moisture changes than gram-negative bacteria due to their thicker and stronger cell walls (Schimel et al., 2007; Salazar et al., 2019), both gram-positive and negative bacteria have been unresponsive to DP (Fig. 5b). The sample sizes for bacteria and fungi in meta-analyses are small compared to MB meta-analyses (Fig. 5). Although an increase in the number of bacterial and fungal studies would improve our understanding of community responses to precipitation changes in terms of significance and magnitude of effects, current available data already covers a significant range of locations and conditions, and highlights the clear trend of low responsiveness of bacterial and fungal communities to DP and IP manipulations.

3.6 Responses of belowground C:N:P stoichiometry

Belowground stoichiometric relationships of carbon, nitrogen, and phosphorus can help researchers interpret and infer nutrient movements in soil organisms and their environments. Yet, few meta-analyses have synthesized belowground stoichiometric responses to precipitation treatments; greater attention has been paid to stoichiometry of aquatic systems and plants (Cleveland and Liptzin, 2007; Redfield, 1958; Yuan and Chen, 2015). He and Dijkstra (2014) and Yan et al. (2018) found no changes in soil C:N and N:P with DP (Fig. 3), but MBC:MBN responded to both precipitation changes (Fig. 5). Increased MBC:MBN with IP indicates that wetter conditions stimulated greater metabolic activity of microbes, which accumulated more carbon in their bodies. This suggests that the soil microbial biomass C:N:P ratio, which is well-constrained globally (60:7:1) (Cleveland and Liptzin, 2007), could be altered by precipitation changes. Soil N:P ratios can be heavily dependent on plant nutrient uptake; as discussed in Sect. 3.3, DP reduces plant nitrogen uptake, which could increase soil N:P. However, this effect could be mitigated by strong mycorrhizal symbioses (Mariotte et al., 2017) and depend on site aridity (Sardans et al., 2012).

4 Implications for future research

4.1 Knowledge gaps

Meta-analyses have substantially advanced our understanding of the impacts of precipitation changes on soil processes and properties. Specifically, a great number of meta-analyses have investigated soil respiration, nitrogen ions, total phosphorus, and microbial biomass. Nevertheless, there are still variables receiving less attention; for example, the sample size of autotrophic respiration is smaller than heterotrophic respiration, and substrate availability has not been analyzed while soil C, N and P content have. CH_4 fluxes have received less attention than CO_2 and N_2O, and no meta-analyses have examined the processes of nitrification, denitrification, and nitrogen fixation.

Filling these knowledge gaps could help to reveal the underlying mechanisms of soil responses to precipitation changes. For example, there is robust agreement across studies that soil respiration slows under DP and accelerates under IP, and so does heterotrophic respiration. However, the relative importance of different mechanism in the response of heterotrophic respiration is still unknown – in other words, how much of this response comes from changes in the level of microbial activity (e.g., entering and exiting dormancy) vs. substrate availability? Similarly, what are the most important mechanisms behind changes in N_2O emissions, and how quickly will total soil nitrogen respond? Interestingly, the variables receiving the greatest attention are largely the easier to measure "fluxes" (i.e., greenhouse gas emissions) and "pools" (i.e., soil carbon, biomass, and bacterial abundance). Measuring process rates (i.e., rates of nitrification, denitrification and fixation) that cannot be simply measured from gas fluxes requires more resources (time and money).

4.2 Challenges in meta-analyses

PMEs are quite diverse, adopting a variety of approaches, treatment levels, and treatment types (Beier et al., 2012; Kreyling and Beier, 2013), and so are the data derived from them. Many PMEs use long-term rainout shelters, which unavoidably modify the ambient environment in other ways (Kreyling et al., 2017). While synthesizing the results of PMEs around the globe in the context of these experimental issues could be challenging, meta-analyses provide an exhaustive statistical summary of empirical studies (Hedges et al., 1999). One of the limitations of meta-analysis, however, is that it can obscure the substantial influence of environmental characteristics and methodological differences on effect sizes. Categorization by environmental characteristics, such as climate, geography, ecosystem, soil, and soil biota, can provide a local- to regional-view of soil responses that is specific to the given environmental characteristic. Categorization by methodology, such as experimental duration, intensity of treatment, measurement method, and fertilizer use, can clarify the human-derived impacts on effect sizes. These categorization efforts can identify when and how soil responses depend on their environmental context. As more and more PMEs are implemented, sample sizes available for meta-analysis are increasing (Song et al., 2019). In this regard, the recent deployment of broad networks of PMEs with standardized methodology and sampling procedures (Halbritter et al., 2020) could ultimately contribute to more powerful meta-analyses with more easily interpreted

outcomes (Hilton et al., 2019; Knapp et al., 2012, 2017). Details of categorization by environmental characteristics and methodology can be found in the Supplement (S1).

5 Conclusions

320 This synthesis of meta-analyses provides a broad perspective on how precipitation changes affect soils and belowground processes. Belowground carbon and nitrogen cycles speed up with increased precipitation and slow down with decreased precipitation, while microbial communities are relatively resistant to precipitation changes. While response of the fluxes and pools of each cycle – gas emissions, soil carbon, nitrogen ions, and biomass – have been studied extensively, responses of the associated process rates remain less studied or unexamined by meta-analyses. We suggest that additional scientific

325 attention to these "processes" is warranted, and would strengthen the current knowledge of soil responses to precipitation changes.

Data Availability

The collected data from meta-analyses is available through Purdue University Research Repository (https://doi.org/10.4231/16NT-CW47).

330 **Author contribution**

AOA, AS, YO, MRU, IR, and JSD designed the research. AOA, AS, YO, SR, MRU, JL, and IR conducted the synthetic analysis and contributed to writing the original draft. AOA prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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580 **Table 1: List of meta-analyses used in this study.**

No.	Meta-analysis
1	Blankinship et al. 2011
2	Brzostek et al. 2012
3	Canarini et al. 2017
4	He & Dijkstra 2014
5	Homyak et al. 2017
6	Liu et al. 2016
7	Ren et al. 2018
8	Ren et al. 2017
9	Wu et al. 2011
10	Xiao et al. 2018
11	Yan et al. 2018
12	Yuan et al. 2017
13	Yue et al. 2019
14	Yue et al. 2018
15	Zhou et al. 2016
16	Zhou et al. 2018

Table 2. List of soil variables and their definitions as analyzed in the meta-analyses. The numbers indicate meta-analysis number corresponding to Table 1, examining the effects of decreased precipitation (DP) and increased precipitation (IP) on each soil variable.

Variable	Definition	DP	IP	Variable	Definition		DP		IP	
Rs	Soil respiration	3,6,8,9,11,15	6,8,9,11,15	NH_4^+	Extractable NH_4^+		5,11,13		11	
Ra	Autotrophic respiration	6,15	6,15	NO_3^-	Extractable NO_3^-		5,11,13		11	
Rh	Heterotrophic respiration	6,8,15	6,8,15	N:P	Extractable N:P		4		None	
CH_4	CH_4 uptake	11	11	Ext P	Extractable soil P		4,14		14	
Total C	Total soil C	11,12,15	11,12,15	Total P	Total soil P		11,12,14		11,12,14	
SOC	Soil organic C	8	8	MB	Microbial biomass		3,5,7,8,16		1,8,16	
DOC	Dissolved organic C	3,8,11	8,11	MBC	Microbial biomass C		11,15		10,11,15	
Litter B	Litter biomass	11	11	MBN	Microbial biomass N		11,13		11,13	
Root B	Root biomass	11	11	MBC:MBN	Microbial biomass C: Microbial biomass N		11		11	
Below B	Belowground biomass	None	9	Bacteria	Abundance of bacteria		7,11		1,11	
Below NPP	Belowground NPP	15	9,15	Fungi	Abundance of fungi		7,11		1,11	
Root C	Fine root C concentration	11	11	Gram+	Gram positive bacteria		7		None	
Root N	Fine root N concentration	11	11	Gram-	Gram negative bacteria		7		None	
Root C:N	Fine root C concentration: Fine root N concentration	11	11	F:B	Fungi:Bacteria ratio		3,7,11		11	
C:N	Total soil C:N	11	None	Hy-enzyme	C-enzyme	Hydrolytic enzyme activity[a]	C-acquisition enzyme		10		10
N_2O	N_2O emissions	5,11	11		N-enzyme		N-acquisition enzyme	8	10	8	10
Total N	Total soil N	11,12,13	11,12,13		P-enzyme		P-acquisition enzyme		10		10
Inorganic N	Inorganic N	13	13	Ox-enzyme	Oxidase activity		8,10		8,10	
N supply	N mineralization	5	None	Pro-enzyme	Potential proteolytic enzyme activity		2		2	
DON	Dissolved organic N	11	None	Soil temperature	Soil temperature		None		11	
$NH_4^+ + NO_3^-$	Extractable $NH_4^+ + NO_3^-$	4	None	pH	Soil pH		11		None	

a. C-acquisition enzymes are β-1,4-glucosidase and β-D-cellobiohydrolase, N-acquisition enzymes are β-1,4-N-acetyl-glucosaminnidase, leucine amino peptidase, and urease, and P-acquisition enzyme is acid phosphatase (Xiao et al., 2018).

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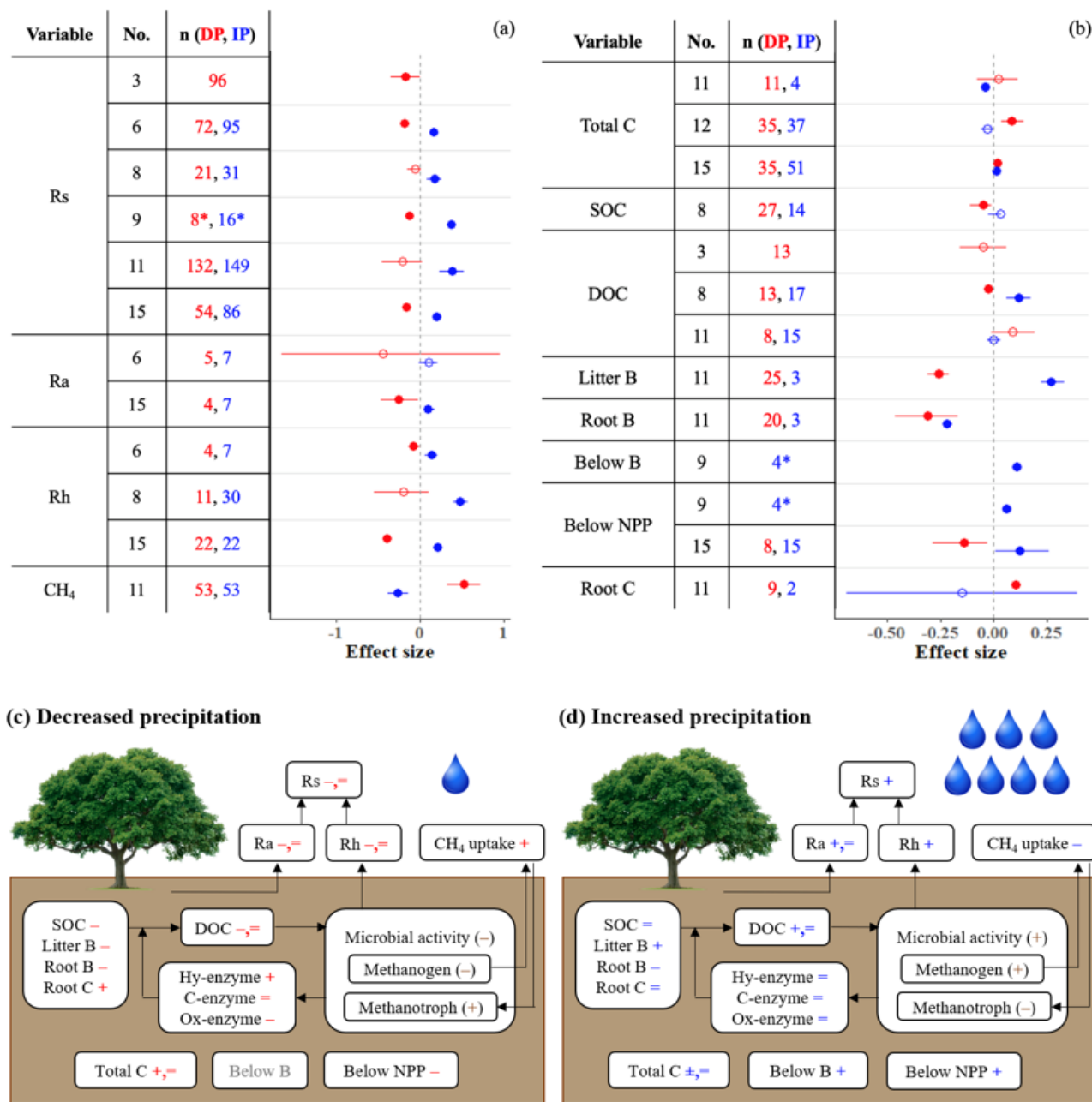
Figure 1: (a, b) The effect size of (a) soil respiration and methane uptake, and (b) carbon and belowground biomass variables with respect to decreased (red) and increased (blue) precipitation. Filled points represent a significant effect size (95% CI not overlapping 0), and open points represent a non-significant effect size. Variable names correspond to Table 2. No. is meta-analysis number and it corresponds to Table 1 and Table 2. The sample size is indicated by n. Asterisks indicate missing 95% CIs. **(c, d)** The effects of (b) decreased precipitation and (c) increased precipitation on soil carbon cycle. Negative, positive, and no effects are represented by −, +, and =, respectively. Red and blue are the variables found in one or more meta-analyses. Brown symbols in parentheses represent the variables that no meta-analyses quantified; in these cases, we estimated the effects based on our review of empirical studies in Sect. 3.1.

Variable	No.	n (DP, IP)
Hy-enzyme	8	33, 52
C-enzyme	10	16, 14
N-enzyme	10	10, 10
P-enzyme	10	9, 13
Ox-enzyme	8	12, 13
	10	5, 5
Pro-enzyme	2	4, 4
Soil temperature	11	13
pH	11	10, 43
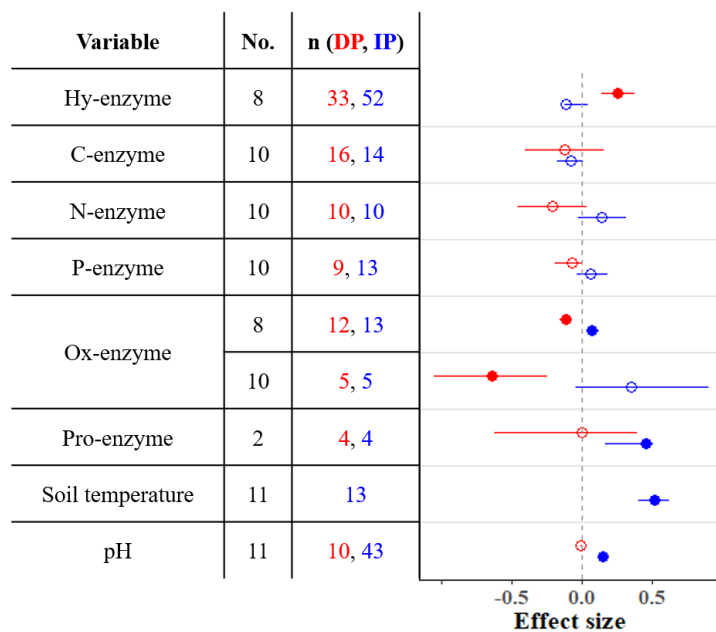
Figure 2: The effect size of soil enzyme and physical variables with respect to decreased (red) and increased (blue) precipitation. Filled points represent a significant effect size (95% CI not overlapping 0), and open points represent a non-significant effect size. Variable names correspond to Table 2. No. is meta-analysis number and it corresponds to Table 1 and Table 2. The sample size is indicated by n.

600
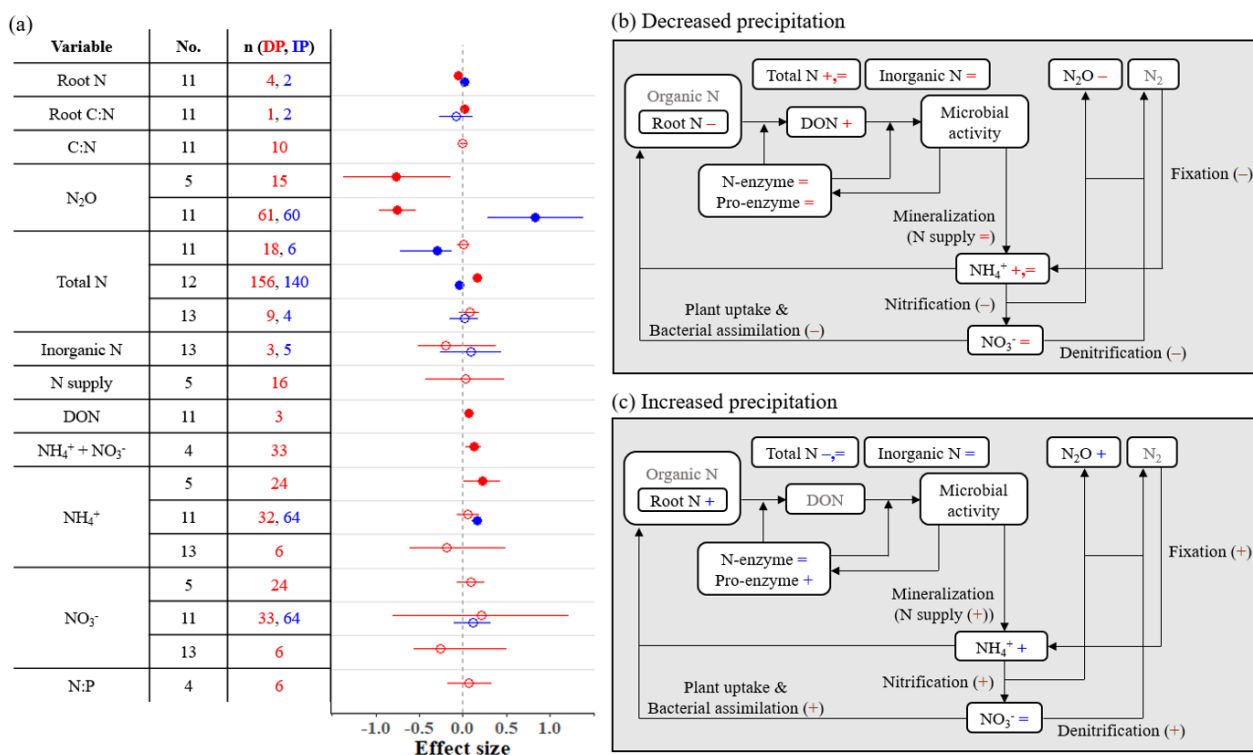
Figure 3: (a) The effect size of soil nitrogen variables with respect to decreased (red) and increased (blue) precipitation. Filled points represent a significant effect size (95% CI not overlapping 0), and open points represent a non-significant effect size. Variable names correspond to Table 2. No. is meta-analysis number and it corresponds to Table 1 and Table 2. The sample size is indicated by n. (b, c) The effects of (b) decreased precipitation and (c) increased precipitation on soil nitrogen cycle. Negative, positive, and no effects are represented by −, +, and =, respectively. Red and blue are the variables found in one or more meta-analyses. Brown symbols in parentheses represent the variables that no meta-analyses quantified; in these cases, we estimated the effects based on our review of empirical studies in Sect. 3.3.

Variable	No.	n (DP, IP)
Ext P	4	6
	14	10, 3
Total P	11	1, 2
	12	31, 36*
	14	6, 6
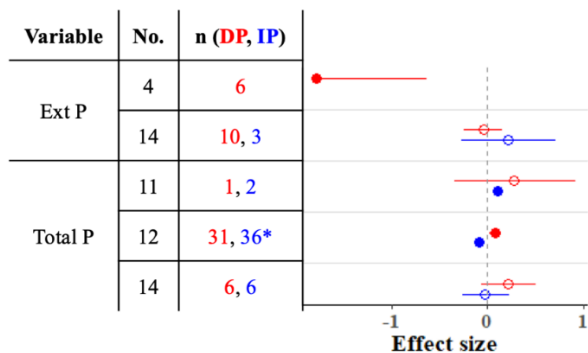
Figure 4: The effect size of soil phosphorus variables with respect to decreased (red) and increased (blue) precipitation. Filled points represent a significant effect size (95% CI not overlapping 0), and open points represent a non-significant effect size. Variable names correspond to Table 2. No. is meta-analysis number and it corresponds to Table 1 and Table 2. The sample size is indicated by n. Asterisks indicate missing 95% CIs.
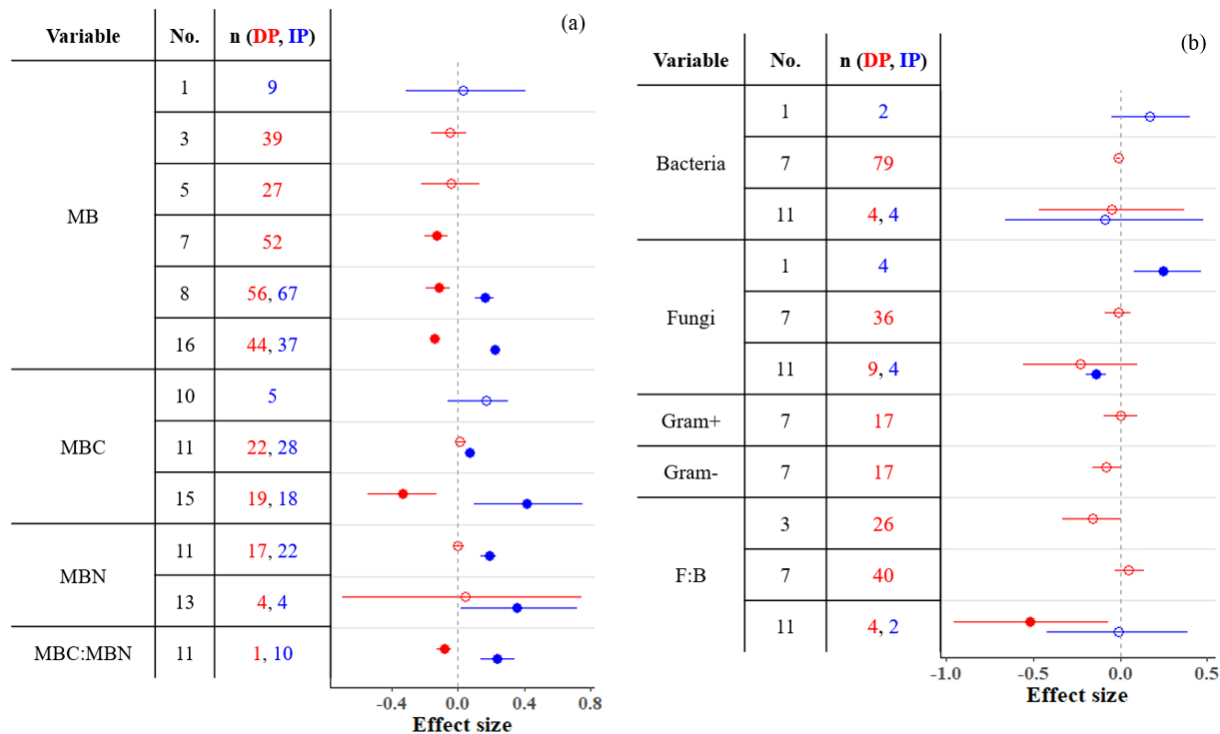
Figure 5: The effect size of (a) microbial biomass, carbon, and nitrogen, and (b) bacterial and fungal variables with respect to decreased (red) and increased (blue) precipitation. Filled points represent a significant effect size (95% CI not overlapping 0), and open points represent a non-significant effect size. Variable names correspond to Table 2. No. is meta-analysis number and it corresponds to Table 1 and Table 2. The sample size is indicated by n.