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Changes in plant inputs alter soil carbon and microbial communities in forest ecosystems

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Abstract

Global changes can alter plant inputs from both above- and belowground, which, thus, may differently affect soil carbon and microbial communities. However, the general patterns of how plant input changes affect them in forests remain unclear. By conducting a meta-analysis of 3193 observations from 166 experiments worldwide, we found that alterations in aboveground litter and/or root inputs had profound effects on soil carbon and microbial communities in forest ecosystems. Litter addition stimulated soil organic carbon (SOC) pools and microbial biomass, whereas removal of litter, roots or both (no inputs) decreased them. The increased SOC under litter addition suggested that aboveground litter inputs benefit SOC sequestration despite accelerated decomposition. Unlike root removal, litter alterations and no inputs altered particulate organic carbon, whereas all detrital treatments did not significantly change mineral-associated organic carbon. In addition, detrital treatments contrastingly altered soil microbial community, with litter addition or removal shifting it toward fungi, whereas root removal shifting it toward bacteria. Furthermore, the responses of soil carbon and microbial biomass to litter alterations positively correlated with litter input rate and total litter input, suggesting that litter input quantity is a critical controller of belowground processes. Taken together, these findings provide critical insights into understanding how altered plant productivity and allocation affects soil carbon cycling, microbial communities and functioning of forest ecosystems under global changes. Future studies can take full advantage of the existing plant detritus experiments and should focus on the relative roles of litter and roots in forming SOC and its fractions.

KEYWORDS
carbon cycling, meta-analysis, microbial community, mineral-associated organic carbon, nutrient pools, particulate organic carbon, plant detritus, DIRT, soil organic carbon

1 | INTRODUCTION

Plant inputs from litter (refers to aboveground litter hereafter) and roots are the dominant source of carbon (C) pools in soils and regulate soil biogeochemical processes and microbial communities in terrestrial ecosystems (Dove et al., 2019). The altered plant productivity and C allocation between above- and belowground

components under global changes (e.g., elevated CO_2, warming and nutrient deposition) can change the quantity and quality of plant inputs introduced into the soil (Janssens et al., 2010; Sayer et al., 2011; Terrer et al., 2016). Such changes can have profound effects on soil C dynamics, and microbial communities and their functions (Brant et al., 2006; Chen & Chen, 2018; Xu, Liu, et al., 2013). Among various ecosystems, forests are fundamental in driving global C cycles

because of its large area, high productivity, litterfall, and C stocks (Pan et al., 2011). Therefore, it is very necessary to reveal large-scale patterns and underling mechanisms of how altered plant inputs regulate soil C and microbial communities in forest ecosystems, which can help to better predict the dynamics of soil C storage and release under global changes.

Soil organic carbon (SOC) is very complex in composition and consists of various functional pools that differ in stability and turnover rates, and these pools often show contrasting responses to plant inputs (Lavallee et al., 2020; Six et al., 2002; von Lützow et al., 2007). Separating SOC into fractions of particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) is suggested to be an efficient method that can help us better understand the formation and stabilization of SOC (Cotrufo et al., 2019; Lavallee et al., 2020). POC is mainly formed through the fragmentation of plant detritus (litter and dead roots) and is mainly composed of light-weight fragments and less protected from decomposition (Figure 1; Lavallee et al., 2020; von Lützow et al., 2007). MAOC is predominantly formed through mineral adsorption of dissolved organic C (DOC) and microbial necromass C derived from microbial decomposition and transformation of plant detritus and root exudates (Figure 1; Lavallee et al., 2020; Liang et al., 2017; Sokol, Sanderman, et al., 2019). In contrast to POC, MAOC is protected by mineral association, not easily decomposed by soil microbes, and has much longer residence times in soil (Lavallee et al., 2020; von Lützow et al., 2007). In addition to contributing to SOC formation, plant inputs can also promote SOC loss through litter- and living root-induced priming effect, a phenomenon that fresh C inputs can strongly increase microbial activity and its decomposition of native SOC.

Given the role of plant inputs in SOC formation, the relative importance of plant inputs from litter and roots is different. Previous studies suggest that roots have greater contributions to SOC formation than litter (Jackson et al., 2017; Sokol & Bradford, 2019; Sokol, Kuebbing, et al., 2019), and several mechanisms can account for this difference. First, belowground roots can supply more C than aboveground litter (Jackson et al., 2017; Rasse et al., 2005). Second, the rhizosphere is a microbial hotspot, and roots can supply labile root exudates for soil microbes and stimulate their growth and transformation of plant C into SOC (Figure 1; Huang et al., 2000; Sokol & Bradford, 2019; Villarino et al., 2021). Meanwhile, roots and root-associated symbiotic fungi can increase SOC physical protection by improving soil aggregate formation (Leifheit et al., 2014). Third, after death, roots can immediately interact with soil minerals, microbes and aggregates, whereas litter has to be transferred from the soil surface to mineral soil through bioturbation and leaching (Jackson et al., 2017; Sokol, Kuebbing, et al., 2019). Thus, root-derived C can be more efficient to form stable SOC than litter-derived C (Sokol & Bradford, 2019; Sokol, Kuebbing, et al., 2019).

The dynamics of SOC are determined by the processes of C gains derived by plant inputs and C outputs mainly via microbial decomposition (Figure 1; Jackson et al., 2017; Janssens et al., 2010). It is generally assumed that there is a strong causal link between plant productivity, plant inputs and SOC sequestration (Gottschalk et al., 2012). However, the response of SOC to elevated plant inputs is complex and temporally dynamic, which can be affected by plant input quantity, priming effects, and C saturation capacity of soils (Carney et al., 2007; Jackson et al., 2017; Lajtha et al., 2018). The accelerated soil C loss via priming effects caused by plant inputs can offset plant input–derived C introduced into soil (van Groenigen et al., 2014; Sayer et al., 2011). In addition, constrained by climate and soil minerals, the capacity of soils to sequester C is finite and can be saturated; thus, soil C saturation capacity can also limit SOC increase with increased plant inputs (Jackson et al., 2017; Mayzelle et al., 2014; Six et al., 2002). By contrast, decreased plant inputs can reduce SOC pool, as the supply of exogenous C is reduced but microbial decomposition of soil organic matter (SOM) continues. In some cases, SOC pools may not respond immediately to plant input changes if the initial soil C pool is large and the quantity of plant inputs is low (Lajtha, Townsend, et al., 2014; Wu et al., 2018). This implies that the effects of plant input changes on SOC may be very weak in the short term, and may manifest gradually over time and plant input quantity. In addition, recent studies have suggested that

FIGURE 1 Conceptual illustration of how changes in plant inputs would affect soil organic carbon (SOC) and microbial communities in forest ecosystems. "Litter" indicates aboveground litter, DOC indicates dissolved organic carbon, and "no inputs" refers to removal of both aboveground litter and roots. The thickness of red arrows indicates the decomposability of SOC fractions. The gray arrow of CO_2 indicates carbon outputs from microbial decomposition and/or transformation of plant detritus, DOC, root exudates, and particulate and mineral-associated organic carbon. [Colour figure can be viewed at wileyonlinelibrary.com]

microbial transformation of plant C is a dominant pathway of SOC formation and stabilization (Liang et al., 2017, 2019), highlighting the critical role of soil microbes as contributors of SOC accumulation. Therefore, considering the changes of soil microbial communities would be very helpful to understand how altered plant inputs affect SOC dynamics.

Microbial growth and activity in soils are controlled by substrate (carbon and nutrients) availability, and microbes in different functional groups have specific preferences and strategies for substrate utilization (Dove et al., 2019; Soong et al., 2020). Hence, the changes in quantity and quality of soil carbon and nutrients can radically change microbial biomass, community composition and function (Brant et al., 2006; Dove et al., 2019; Huang et al., 2000; Rousk & Frey, 2015). It is considered that roots have larger controls on soil microbial communities than litter (Brant et al., 2006; Whalen et al., 2021). This is because root-derived C is the major source of C for microbes in the mineral soil layer, and roots are the hosts for symbiotic fungi and the hotspots for rhizosphere-associated microbes, and can stimulate microbial growth through the inputs of root exudates (Huang et al., 2000; Kramer et al., 2010). Therefore, the reduction in belowground C inputs from roots may have larger negative effects on soil microbial communities (particularly symbiotic fungi and rhizosphere-associated microbes) than that in aboveground C inputs from litter (Brant et al., 2006; Whalen et al., 2021). Changes in microbial communities under altered plant inputs could affect the overall microbial metabolism, and the dynamics of SOC, as soil microbes can act as not only the decomposer of SOC but also the contributor of SOC formation (Liang et al., 2017, 2019; Sokol & Bradford, 2019).

Under global changes, many efforts have been made to study the effects of plant input changes on soil C and/or microbial communities using manipulation experiments, namely the Detritus Input and Removal Treatment (DIRT, Lajtha et al., 2018). Based on such manipulation experiments, two previous meta-analyses demonstrated that litter addition increased, whereas litter removal decreased soil C pools (Xu, Liu, et al., 2013, 2021). However, these two studies only included aboveground litter alterations (addition and removal) and mainly focused on bulk SOC, and half of the observations were from grasslands and croplands (Xu, Liu, et al., 2013, 2021). Global changes can alter both above- and belowground plant inputs via regulating plant productivity and C allocation, which, thus, can affect soil C and microbial communities via changing plant inputs into the soil (Figure 1; Lajtha, Townsend, et al., 2014; Whalen et al., 2021). However, neither of these two meta-analyses considers belowground root alterations (Xu, Liu, et al., 2013, 2021). As such, the general patterns of how alterations in above- and/or belowground plant inputs affect soil C and its fractions, and microbes, the possible linkages among such effects and underling mechanisms remain unclear in widely distributed forest ecosystems.

In this study, we synthesized the detritus manipulation experiments in global forests, and focused on four manipulation treatments (Figure 1), including litter addition, litter removal, root removal, and no inputs (removal of both litter and roots). Our objectives were to determine (i) how changes in above- and belowground plant inputs

affect soil C pools and microbial communities (biomass and composition), (ii) whether litter and roots have different effects on SOC pools and microbial communities, and (iii) how experimental variables affect the responses of SOC pools to plant detritus manipulations. By conducting a meta-analysis of 3193 observations from 166 experiments worldwide, we tested the following hypotheses:

(H1) Litter addition stimulates soil C pools and microbial biomass due to extra substrate supply, whereas detritus removal treatments inhibit them due to reduced substrate supply.

(H2) The effects of roots on SOC pools and microbial communities (mainly biomass) are greater than those of litter, because roots have greater efficiency of SOC formation than litter and are the hosts for symbiotic fungi, and root-derived C is the major source of C for soil microbes.

(H3) The magnitude of SOC responses to detrital treatments will increase with experimental duration and rate of plant input changes because these factors control the quantity of C input to soils.

2 | METHODS

2.1 | Data source and selection criteria

We searched studies that investigated the effects of plant detritus manipulations on soil belowground processes using the Web of Science and China National Knowledge Infrastructure (CNKI, http://www.cnki.net). The cut-off date for our search is May 15, 2021. The keywords we used were related to: (carbon OR nitrogen OR phosphorus OR "microbial biomass" OR "microbial composition") AND ("litter manipulation" OR "detritus manipulation" OR "litter alteration" OR "litter addition" OR "litter removal" OR "root input" OR "root exclusion") AND (forest OR plantation OR stand OR "forested land" OR woodland). The detailed search term is listed in Table S1. Additional studies that were not covered by these search terms were revealed by literature citations, and two previous meta-analyses (Xu, Liu, et al., 2013, 2021) were also screened to search for case studies.

To increase the comparability of data, the following criteria were applied to select appropriate studies. (i) The study reported in situ detritus manipulation experiments in forest ecosystems. (ii) The study must contain at least one of the four detrital treatments, including litter addition, litter removal (aboveground litter excluded from plots), root removal (roots excluded from plots by trenching), and no inputs (removal of both litter and roots; Lajtha et al., 2018). (iii) The study must include at least one of the variables relevant to soil biogeochemical processes and measured in the mineral soil. The detailed variables are listed in Table S2. Briefly, these variables included soil physicochemical properties, carbon pools (expressed as concentration with g kg^{-1} or stocks with kg m^{-2}) and SOC fractions (directly separated as, or could be grouped into, POC and MAOC), nutrient pools (mainly expressed as concentration), microbial biomass (measured by widely used chloroform-fumigation extraction or

phospholipid fatty acid, PLFA) and community composition (ratios of fungi to bacteria and Gram-positive to Gram-negative bacteria (GP-to-GN) that were measured by PLFA), soil respiration, and SOM decomposition (measured by collecting soils in the field followed by laboratory incubation). (iv) Means, standard deviations or errors, and the number of replicates for a given variable in the control and treatment groups could be obtained from text, tables or digitized graphs.

2.2 | Data extraction

Following the criteria mentioned above, 175 publications were obtained. In case studies, SOC fractions are separated by density or particle size. Following previous studies, we grouped soil fraction with density lighter than 1.6–1.85 g cm^{-3} or particle-size larger than 53 μm into POC, and grouped soil fraction with density heavier than 1.6–1.85 g cm^{-3} or particle-size smaller than 53 μm into MAOC (Lavallee et al., 2020; Rocci et al., 2021). Despite the differences in manipulations, the same fractions (POC or MAOC) separated by density and particle size have similar characteristics, for example, C contents and turnover rates (Lavallee et al., 2020; von Lützow et al., 2007; Poeplau et al., 2018). In some studies, multiple litter input rates or different litter types under the same treatments were used. As such, a same experiment can contribute more than one paired observation within detrital treatments, and all the observations were extracted and treated as independent (Lu, Hua, et al., 2021; Lu, Vitousek, et al., 2021). For each study, we extracted the means, standard deviations or errors, and the number of replications of the target variables. When data from different years were available in the same study, we adopted the latest data according to the commonly used approach in meta-analysis studies (e.g., Lu, Huo, et al., 2021; Lu, Vitousek, et al., 2021). Similarly, when data of the same variable from multiple soil layers were given, we only used data from the uppermost mineral soil layer (e.g., Lajtha, Townsend, et al., 2014). In total, we collected 3193 observations from 166 independent experiments worldwide (Figure S1), and the dataset was reposed in figshare (Feng et al., 2022). Here, the "experiment" refers to an independent experiment with detrital treatments conducted in a specific forest at a site. As an experiment may generate more than one publication but with different variables, the number of experiments (166) was less than that of publications (175).

In addition to response variables, we also recorded site and treatment information of these experiments, including location, climatic factors (mean annual temperature, MAT; and mean annual precipitation, MAP), soil types, litter input rates (g C m^{-2} year^{-1}) and total litter input (g C m^{-2}), experimental durations (year), litter types, and litter treatment modes. Soil types were extracted from the original case studies, and then were unified into the soil orders according to the USDA Soil Taxonomy (Soil Survey Staff, 2014). Litter types were divided into three groups, that is, broadleaf litter, conifer litter and mixed litter from broadleaf and conifer trees. In DIRT experiments, two treatment modes for aboveground litter were used, including addition or removal of only fresh litterfall (fresh) or both fresh

litterfall and forest floor material at the beginning (floor+fresh), and both of them are evenly distributed along the latitude (Figure S1). In the former treatment (floor+fresh), litter input rate (g C m^{-2} year^{-1}) was calculated as the sum of C stock (g C m^{-2}) in forest floor material divided by the duration (year) plus the fresh litterfall (g C m^{-2} year^{-1}). Across all studies, most observations (69%) were from 0–10 cm mineral soils (with a range of 0–5 to 0–30 cm), litter input rates ranged from −988 to 997 g C m^{-2} year^{-1}, and experimental duration ranged from 0.17 to 50 years, with 72% of these experiments lasting for less than 5 years (Figure S2).

2.3 | Statistical analysis

We quantified the effects of detrital treatments on the studied variables using the meta-analysis approach (Hedges et al., 1999). The response ratio (RR) for each observation and its within-study variance (v) were calculated as follows:

$$RR = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = \ln(\overline{X}_t) - \ln(\overline{X}_c), \quad (1)$$

$$v = \frac{s_t^2}{n_t \overline{X}_t^2} + \frac{s_c^2}{n_c \overline{X}_c^2}, \quad (2)$$

where $\overline{X}_t$, S_t, and n_t are the mean, standard deviation and sample size of a given variable observed in the treatment group, respectively; and $\overline{X}_c$, S_c, and n_c are the mean, standard deviation and sample size of a given variable in the control group, respectively.

To determine whether detrital treatments had significant effects on the target variables, we applied the mixed-effects model with "experiment" as a random factor to calculate the weighted RR and its 95% confidence intervals (CIs; Borenstein et al., 2010; Chen et al., 2020). The included random factor "experiment" was to account for the dependence among multiple RRs within an experiment (e.g., an experiment may include several addition rates for litter addition treatment). In the mixed-effects model, two sources of variance are considered, including within-study variance (v) and between-study variance (τ^2), both of which were used to calculate the weighting factor (w) of each RR (Borenstein et al., 2010).

$$w = \frac{1}{v + \tau^2}. \quad (3)$$

In addition, we conducted subgroup meta-analysis to examine the effects of categorical moderator variables (e.g., litter treatment modes) on the RRs of the target variables. Statistical results reported include total heterogeneity among all observations, the heterogeneity in RRs associated with each moderator variable (Q_M), and the residual error. A significant Q_M indicates significant effect of moderator variable on the RR (Hedges et al., 1999). In these meta-analyses, the calculations were performed using the rma.mv function in the metafor package (Viechtbauer, 2010). The

weighed *RR* larger than zero indicates positive effect of detrital treatments, while that lower than zero indicates negative effect. To facilitate interpretation, weighed response ratio (RR_{++}) and 95% CIs were converted into the percentage change (relative to controls) as follows:

$$\text{Percentage change} = (e^{RR_{++}} - 1) \times 100\%. \quad (4)$$

In this study, we used the responses of SOC pools and microbial variables to litter removal and root removal to compare the relative effects of litter versus roots on SOC and microbial community. Given the sufficient SOC data (concentration in particular) in three detritus removal treatments, we also explored the relative effects of litter versus roots on SOC by comparing SOC pools in litter removal and root removal with those in no inputs. By comparing litter removal versus no inputs and root removal versus no inputs, we can get the effects of "roots" and "litter" on SOC, respectively. These analyses were conducted based on the data from all experiments and the experiments with paired treatments. Based on experiments simultaneously measuring soil respiration (in the field) responses to litter addition and litter removal, we estimated the priming effect induced by litter using the method described by Crow, Lajtha, Bowden, et al. (2009) and Chen and Chen (2018). Detailed calculations are as following:

$$SR_{litter} = SR_{control} - SR_{NL}, \quad (5)$$

$$SR_{expected} = SR_{control} + SR_{litter}, \quad (6)$$

$$\text{Priming effect} = \frac{(SR_{DL} - SR_{expected})}{SR_{DL}} \times 100\%, \quad (7)$$

where $SR_{control}$, SR_{NL}, SR_{DL} are measured soil respiration in the control, litter removal and litter addition treatments, respectively; $SR_{expected}$ is the expected soil respiration in litter addition treatment (assuming that litter respiration remained constant).

Publication bias within each variable and detrital treatment was examined using Begg's test and Egger's test (Koricheva et al., 2013). Results showed that most variables were without publication bias, and the potential publication bias within some variables would not affect the results because the Rosenthal's fail-safe number was much larger than $5n + 10$ (*n*, number of observations; Table S3). A linear mixed-effects model with "experiment" as a random factor was used to evaluate the relationships of the *RR*s of belowground variables with litter input rate and total litter input (only for litter alteration treatments). We conducted this analysis using the restricted maximum likelihood estimation with the *lme4* package (Bates et al., 2015).

Given the relatively sufficient data for SOC (refer to concentration) and its importance in biogeochemical cycles and ecological functions, we examined the relative effects of multiple controlling factors on their responses to detrital treatments using model-selection analysis (Feng & Zhu, 2021; van Groenigen et al.,

2017; Terrer et al., 2016). These analyses were conducted using the *glmulti* package (Calcagno & de Mazancourt, 2010). The relative importance for each controlling variable was calculated as the sum of Akaike weights for all the models in which the variable was included, and such values can be considered as the overall support for each controlling variable across all models (Terrer et al., 2016). In the model-selection analysis for SOC responses, MAT, MAP, forest type, litter input rate, litter type, litter treatment mode, and duration were included. As for forest type, tropical (0–23.5°S/N) and subtropical (23.5°–30°S/N) forests were grouped into "sub/tropical forest," and forests (for SOC responses, most are temperate forests with only one boreal forest) within other latitude ranges were grouped into "boreal/temperate forest" (Lu, Vitousek, et al., 2021; Xu et al., 2021). In addition, two additional factors of initial SOC concentration and soil type (mainly includes Alfisols, Andisols, Entisols, Inceptisols, Oxisols, Spodosols, Ultisols) were also included in such analysis of SOC responses under litter addition, as they can potentially affect the C saturation capacity of soils and SOC responses (Dove et al., 2019; Jackson et al., 2017). However, in these analyses of SOC, litter input rate and litter treatment mode were excluded under root removal because they were not applicable, and litter input rate was excluded under no inputs because this factor cannot be obtained from most observations in this treatment. Within each treatment, two types of model-selection analysis were conducted, by treating duration as a numeric or categorical variable, and the latter was used as a complementary analysis. The reason for treating duration as a categorical variable was that the duration across studies was uneven, with more short-term and fewer long-term experiments. According to the distribution of duration in our dataset (Figure S2b) and the cutoff of duration used in previous large-scale meta-analyses (e.g., Chen et al., 2020), experiments were divided into short-term (<5 years) and long-term (≥5 years) groups. All statistical analyses in this study were performed on the R platform (version 3.6.1, R Core Team, 2019).

3 | RESULTS

3.1 | Responses of soil physicochemical properties and nutrients

Results from meta-analysis showed that detrital treatments had contrasting effects on soil bulk density and nutrient pools (Figure 2). Across studies, litter addition decreased, whereas removal of litter, roots, or both increased soil bulk density (all $p < .05$). By contrast, detrital treatments generally did not change soil pH. As for soil nutrients, litter addition significantly increased the pools of total and available nitrogen (N) and phosphorus (7.5%–23.3%), and litter removal decreased them (5.8%–18.6%). However, root removal and no inputs generally did not change soil nutrient pools except the significant increase in nitrate N under root removal and the decreases in total and ammonium N under no inputs.
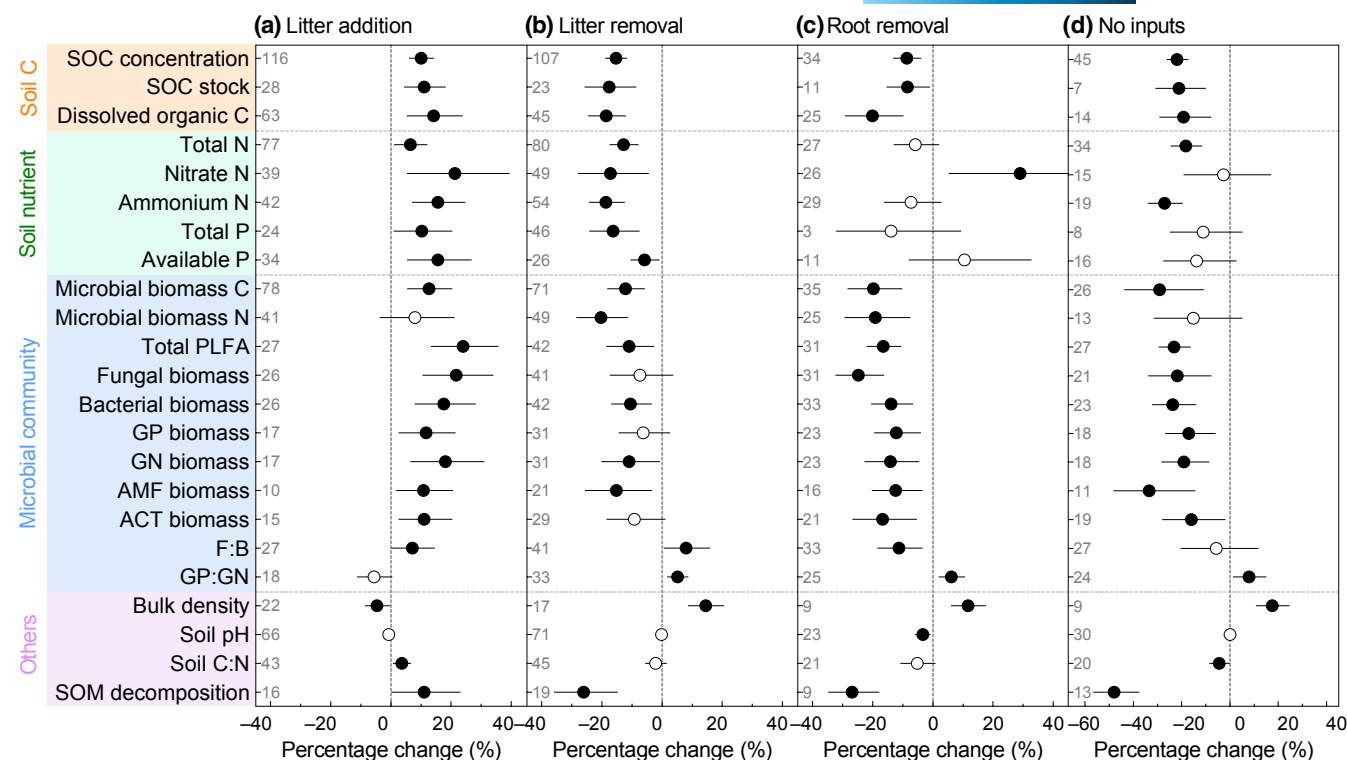
FIGURE 2 Meta-analysis of average effects (%) of plant detritus manipulation on belowground processes. No inputs, removal of both litter and roots; DOC, dissolved organic C; GP, Gram-positive bacteria; GN, Gram-negative bacteria; AMF, arbuscular mycorrhizal fungi; ACT, actinomycetes; F:B, fungal-to-bacterial biomass ratio; GP:GN, the biomass ratio of Gram-positive to Gram-negative bacteria; SOC, soil organic C; SOM, soil organic matter. SOM decomposition is measured by collecting soils in the field followed by laboratory incubation. The error bars represent 95% confidence intervals, and they are not shown when error bars are smaller than the symbol. The solid black dot (●) indicates significant effect of plant detritus manipulation at $p < .05$, whereas the hollow circle (○) indicates $p > .05$. The vertical dashed lines are zero lines, and the gray numbers on the left indicate sample sizes of observations [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Responses of soil carbon and its fractions

Detrital treatments induced significant changes in total SOC and DOC pools ($p < .05$; Figure 2). Regardless of the altered soil bulk density by detrital treatments, the responses of SOC concentration and stock to detrital treatments were consistent in direction and closely correlated with each other (Figure 2; Figure S3). Across studies, litter addition on average increased SOC pools by 10.3%–11.1%, whereas removal of litter, roots or both decreased them by 8.5%–21.9%. Results from all experiments and experiments with paired litter alteration treatments both showed that the declines in SOC (14.2%–17.6%) under litter removal were slightly larger than the increases in SOC (10.3%–11.4%) under litter addition (Figure 3a). Similarly, the declines in SOC (12.2%–15.3%) under litter removal were larger than or equivalent to the declines (8.5%–8.7%) under root removal (Figure 3b). Results from comparing litter removal versus no inputs and root removal versus no inputs showed that the effects of litter and roots on SOC were similar (Figure 3c).

Across studies, detrital treatments had distinct effects on the pools of SOC fractions (Figure 4). Results from combined data of POC and MAOC separated by density or particle size showed that litter addition increased POC, litter removal and no inputs decreased

it, whereas root removal did not significantly change it. In contrast to POC, detrital treatments did not significantly change MAOC.

Linear mixed-effects model showed that litter input rate and total litter input showed positive effects on the responses of SOC concentration and stock, and accounted for 30.8%–46.2% of their variations across litter alteration treatments (Figure S4; Table S4). Model-selection analysis suggested that the responses of SOC to litter addition, litter removal and no inputs were best predicted by duration and/or litter treatment mode (only for litter addition). This was true regardless of whether duration was treated as numeric variable (Figure 5) or categorical variable (Figure S5). By contrast, the response of SOC to root removal was not predicted well by any included factors. The response of SOC to litter addition, litter removal and no inputs were amplified over time (Figure 6; Figure S6).

3.3 | Responses of microbial biomass and community composition

Results from meta-analysis showed that detrital treatments induced contrasting effects on soil microbial communities (Figure 2). Litter addition stimulated microbial biomass C and N, total PLFA and the biomass in different microbial groups (fungi, bacteria, Gram-positive
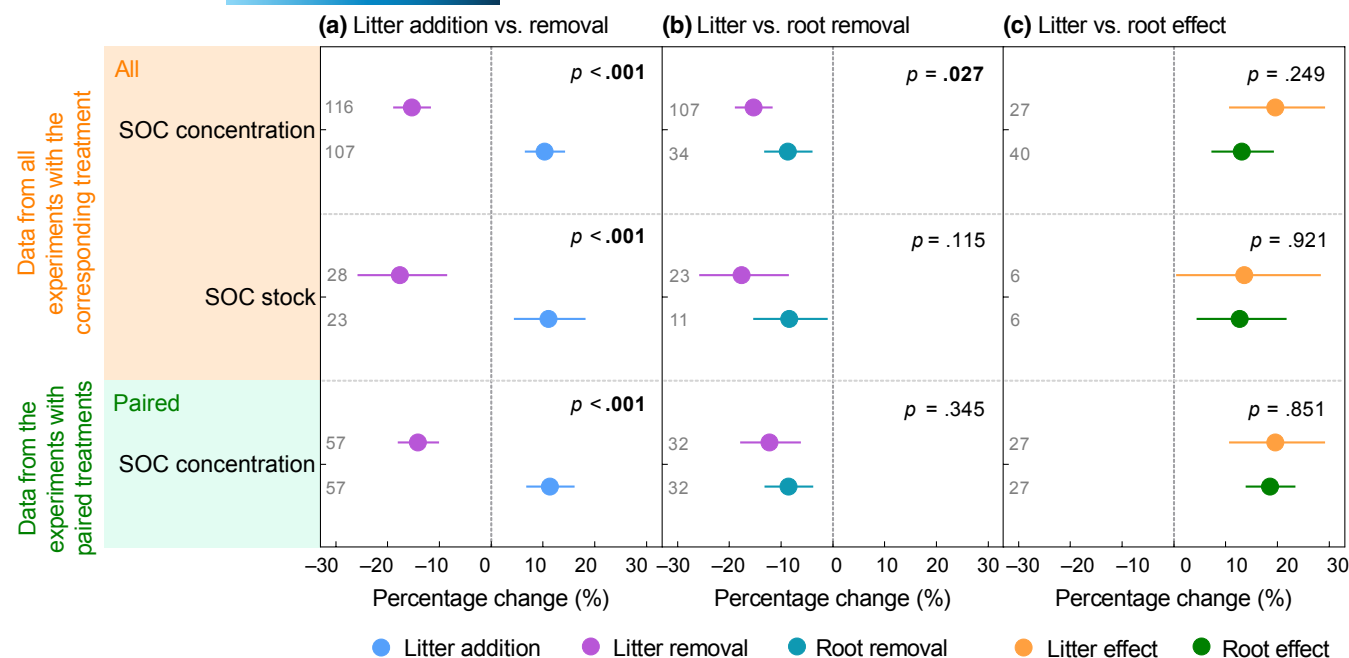
FIGURE 3 Meta-analysis of average effect (%) of litter addition versus litter removal and litter removal versus root removal, and litter versus root effect on soil organic carbon. In panel (a) and (b), the percentage change is calculated by comparing SOC pools in litter addition, litter removal, and root removal to those in untreated control. In panel (c), the percentage change is calculated by comparing SOC pools in litter removal and root removal to those in no inputs (removal of both aboveground litter and roots), and "litter effect" and "root effect" indicate the comparisons of root removal versus no inputs and litter removal versus no inputs, respectively. "All" indicates observations from all experiments with the corresponding treatment, and "paired" indicates observations from experiments simultaneously having the treatments of: (a) litter addition and litter removal, (b) litter removal and root removal, and (c) litter removal, root removal and no inputs. The error bars represent 95% confidence intervals, and the p values on the right indicate the significance for the differences between groups (litter addition vs. litter removal; litter removal vs. root removal; litter effect vs. root effect). The vertical dashed line is zero line, and the numbers on the left indicate sample size [Colour figure can be viewed at wileyonlinelibrary.com]

bacteria, Gram-negative bacteria, arbuscular mycorrhizal fungi and actinomycetes) by 8.0%–24.0%, while detrital removal treatments generally decreased them by 6.2%–33.4%. The fungal-to-bacterial ratio was increased by litter addition (7.2%) and litter removal (8.0%), was decreased by root removal (11.3%, all $p < .05$) but was not significantly altered by no inputs. As for GP-to-GN ratio, it was significantly increased by detrital removal treatments (5.2%–8.0%) but was not altered by litter addition ($p > .05$). Results from all experiments and the experiments with paired litter removal and root removal both showed that the magnitudes for their effects on soil microbial communities were similar (Figure S7). Across litter alteration treatments, the responses of microbial biomass in different functional groups increased significantly with litter input rate and total litter input (Table S4).

4 | DISCUSSION

By integrating DIRT experiments in global forests, we systematically investigated the effects of plant input changes on forest soil C and microbial communities (Figure 7) and explored the regulations of litter input quantity, experimental and climatic factors on the responses of SOC to detritus manipulations. To our knowledge,

this meta-analysis is among the first large-scale synthesis in forest ecosystems that not only included alterations in above- and belowground plant inputs but also covered multiple soil processes.

4.1 | Soil organic carbon responses and controlling factors

The net change in SOC pools depends on the balance between C inputs from litter and roots and C outputs mainly via SOM decomposition (Kuzyakov, 2011; Lajtha et al., 2018). Despite the reductions in SOM decomposition, removal of litter, roots or both significantly decreased SOC pools (Figures 2 and 7). These results suggest that maintaining soil C requires the inputs of exogenous C from fresh litter and/or roots (Bowden et al., 2014; Leff et al., 2012). However, inputs of fresh litter and root exudates may accelerate the decomposition of older SOM via priming and induce a neutral or even negative C balance (Sayer et al., 2011; Zhu et al., 2014). This was partly supported by previous findings from the DIRT network (Lajtha et al., 2018) and our results at many sites that SOC pools responded slightly or negatively to litter addition (Figure 6). However, our results of SOC responses from all experiments with litter addition (Figure 2a) were not consistent with those from the DIRT network
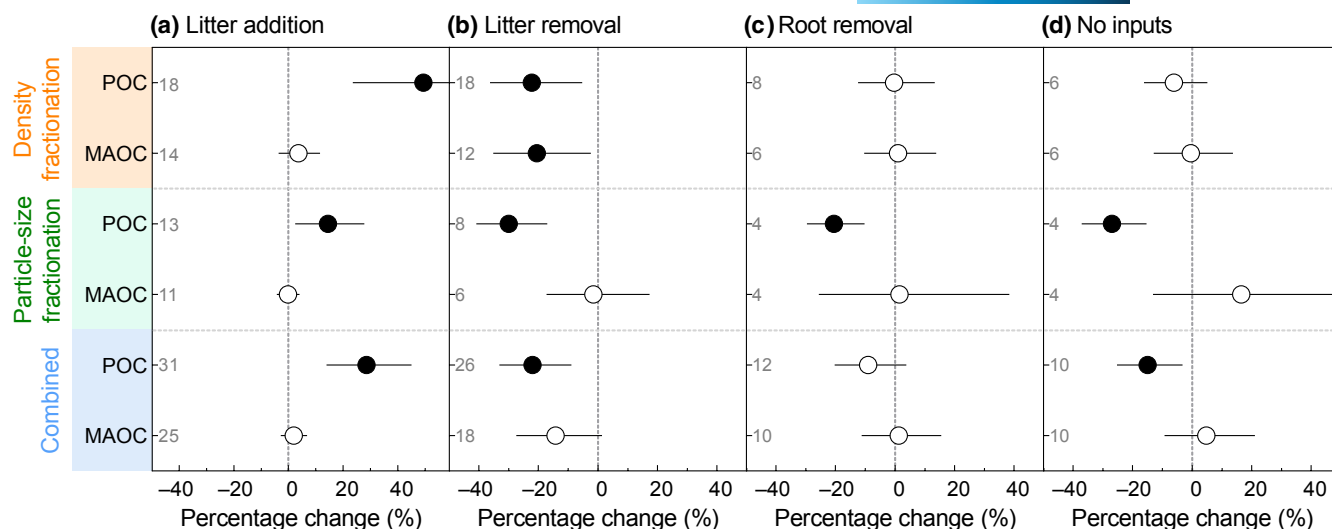
FIGURE 4 Meta-analysis of average effects (%) of plant detritus manipulation on the pools of soil organic carbon fractions. No inputs, removal of both aboveground litter and roots; POC, particulate organic carbon; and MAOC, mineral-associated organic carbon. In the "combined" group, the analyses are based on the observations of POC and MAOC separated by density or particle-size fractionation. The error bars represent 95% confidence intervals. The solid black dot (●) indicates that the plant detritus manipulation effect was significant at $p < .05$, whereas the hollow circle (○) indicates $p > .05$. The vertical dashed line is zero line, and the numbers on the left of each panel indicate sample size [Colour figure can be viewed at wileyonlinelibrary.com]
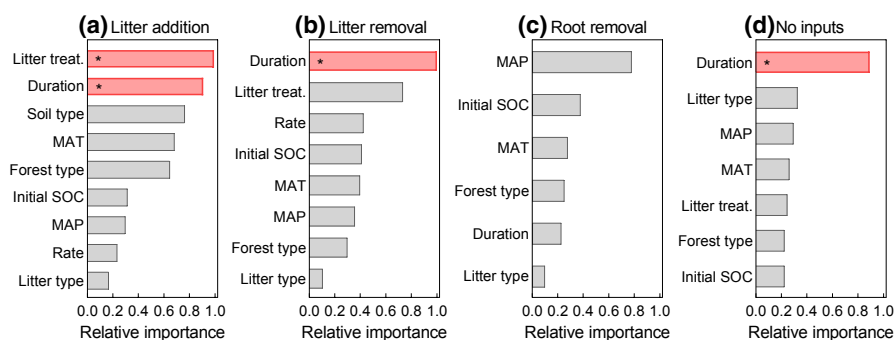
FIGURE 5 Model-averaged importance of the predictors of plant detritus manipulation effects on soil organic carbon (SOC). In this analysis, duration (year) was treated as a numeric variable. No inputs, removal of both litter and roots; MAT, mean annual temperature; MAP, mean annual precipitation; Forest type: boreal/temperate and sub/tropical forest; Rate, aboveground litter input rate; Litter type: broadleaf litter, conifer litter, and mixed litter from broadleaf and conifer trees; Litter treat.: aboveground litter treatment modes, including addition or removal of only fresh litterfall or both fresh litterfall and forest floor. The relative importance is based on the sum of Akaike weights derived from model-selection analysis using corrected Akaike's information criteria, and different colors are used to differentiate important and significant (red, $p < .05$, denoted by *) from nonessential (gray) predictors [Colour figure can be viewed at wileyonlinelibrary.com]

including eight experiments in temperate forests (Lajtha et al., 2018). Such inconsistency might be associated with the litter input rate and initial SOC. The averaged litter input rate in the DIRT network experiments is much lower than that in experiments included in our meta-analysis (168 g C m^{-2} year^{-1} vs. 313 g C m^{-2} year^{-1}; Table S5). In this case, litter-derived C inputs into soil cannot well compensate for litter-induced increased decomposition of new inputs and priming of old SOM (Bowden et al., 2014; Crow, Lajtha, Filley, et al., 2009; Lajtha, Bowden, et al., 2014, 2018). In contrast to litter input rate, the initial SOC in the DIRT network experiments is much higher (58 g kg^{-1} vs. 41 g kg^{-1}; Table S5), which, thus, may lead to a relatively small response of SOC to litter addition. Alternatively, soils with high initial SOC may have a limited capacity to sequester additional C (Xu et al., 2021). The overall significant positive response of SOC pool to

litter addition in our present study suggested that aboveground litter inputs can cause a net increase in SOC storage despite the litter-induced priming (5.3%) of native SOM decomposition (Figure S8). This finding based on in situ field experiments worldwide also supports a previous result from meta-analysis of laboratory incubation experiments with glucose or plant material additions that increasing C input to soils benefits SOC accumulation despite C-induced priming (Liang et al., 2018).

Although litter addition increased and litter removal decreased SOC pools, the increases in SOC under litter addition was slightly lower than the declines in SOC under litter removal (Figure 3). This phenomenon might be caused by three reasons. First, the formation of new SOM is offset by the accelerated decomposition of older SOM via priming effects (5.3%, Figure S8; Chen & Chen, 2018;
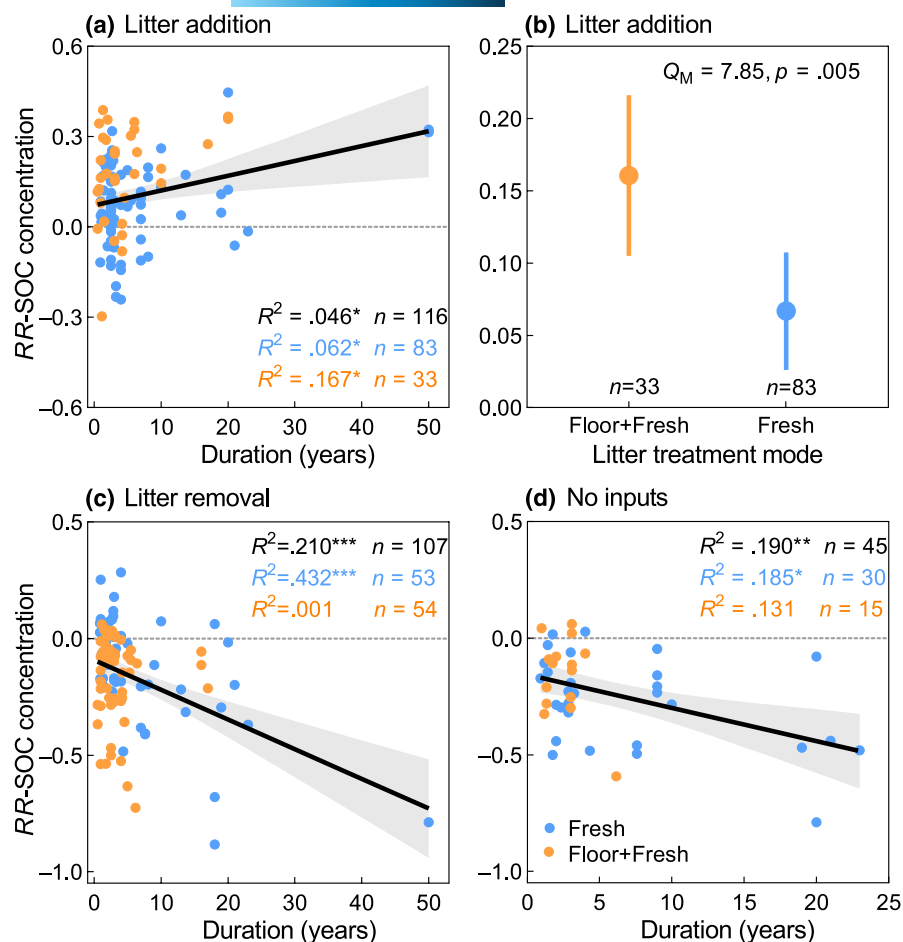
FIGURE 6 Factors affecting the responses of soil organic carbon (SOC) to plant detritus manipulation. Litter treatment mode includes addition or removal of only fresh litterfall (fresh) or both fresh litterfall and forest floor (floor+fresh). In panel (a), (c), (d), the analysis is conducted by linear mixed-effects model, the R^2 values are generated by different data (black: all data, blue: fresh, brown: floor+fresh; $^*p < .05$, $^{**}p < .01$, $^{***}p < .001$), and the black lines and gray shaded areas are the mean and 95% CIs of the slope across all data. In panel (b), the Q_M represents the heterogeneity in response ratios (RRs) associated with moderator variable, and a significance of Q_M indicates significant differences among groups ($p < .05$). The n indicates sample size of observations [Colour figure can be viewed at wileyonlinelibrary.com]

Lajtha et al., 2018). Second, litter addition could enhance microbial turnover and decrease microbial C use efficiency via increasing soil C:N ratio and microbial N limitation (relative to C), consequently leading to more microbial respiration (Figure 2a) and slower SOC formation and accumulation (Guo et al., 2021; Sinsabaugh et al., 2016). Third, soils in some forests likely have a finite capacity to sequester additional SOC (particularly mineral-associated fraction) and might be saturated (Lajtha, Townsend, et al., 2014; Mayzelle et al., 2014; Sayer et al., 2019).

In addition to bulk SOC, detritus treatments induced distinct effects on the pools of POC and MAOC (Figures 4 and 7). Given that POC is mainly made up of newly inputted and relatively-undecomposed plant residues, it tends to have the fastest turnover rate and is more vulnerable to loss (Cusack et al., 2011; Lavallee et al., 2020). Therefore, the addition or removal of litter and/or roots can directly affect the accumulation of POC in both short and long term (Guo et al., 2021; Pierson et al., 2021). This was confirmed by our results that POC increased after addition of litter and declined after removal of litter or both litter and roots (Figure 4). By contrast, POC was not changed by root removal. The possible reason might be that root trenching increased dead root residues and their incorporation into POC in a short period, and the absence of living roots decreased microbial biomass and its decomposition of this C pool (Figure 2c; Bowden et al., 2014; Pierson et al., 2021). In contrast to

POC, mineral adsorption of DOC and microbial necromass C derived from microbial turnover is an important pathway for MAOC formation (Lavallee et al., 2020; Liang et al., 2017; Sokol, Sanderman, et al., 2019). Litter addition and removal of litter, roots or both significantly changed DOC pool and microbial biomass, but they did not alter MAOC. DOC and microbial biomass account for only a small proportion (often <2%) of SOC pool (Guo et al., 2020; Xu, Thornton, et al., 2013), whereas MAOC is a dominant portion (often >50%) of SOC pool and cannot be easily used by soil microbes because of physical and chemical protection (Cotrufo et al., 2019; Lavallee et al., 2020). Therefore, the increased or decreased DOC and microbial biomass and its newly-formed necromass C under altered plant inputs will not have a significant effect on MAOC in the short term (Wu et al., 2018), and it may take a long time to observe the considerable detritus-treatment effects on MAOC (Lajtha, Townsend, et al., 2014; Sayer et al., 2021).

Consistent with the third hypothesis, our results suggested that the responses of SOC pools to detrital treatments were regulated by litter input quantity and duration. Specifically, SOC responses to litter alterations (addition and removal) increased significantly with litter input rate and total litter input, and the magnitude of such responses to litter alterations and no inputs became stronger over time (Figure 6; Figure S6). These results suggest that, without exogenous C inputs from plants, microbial decomposition of SOM will cause continuous
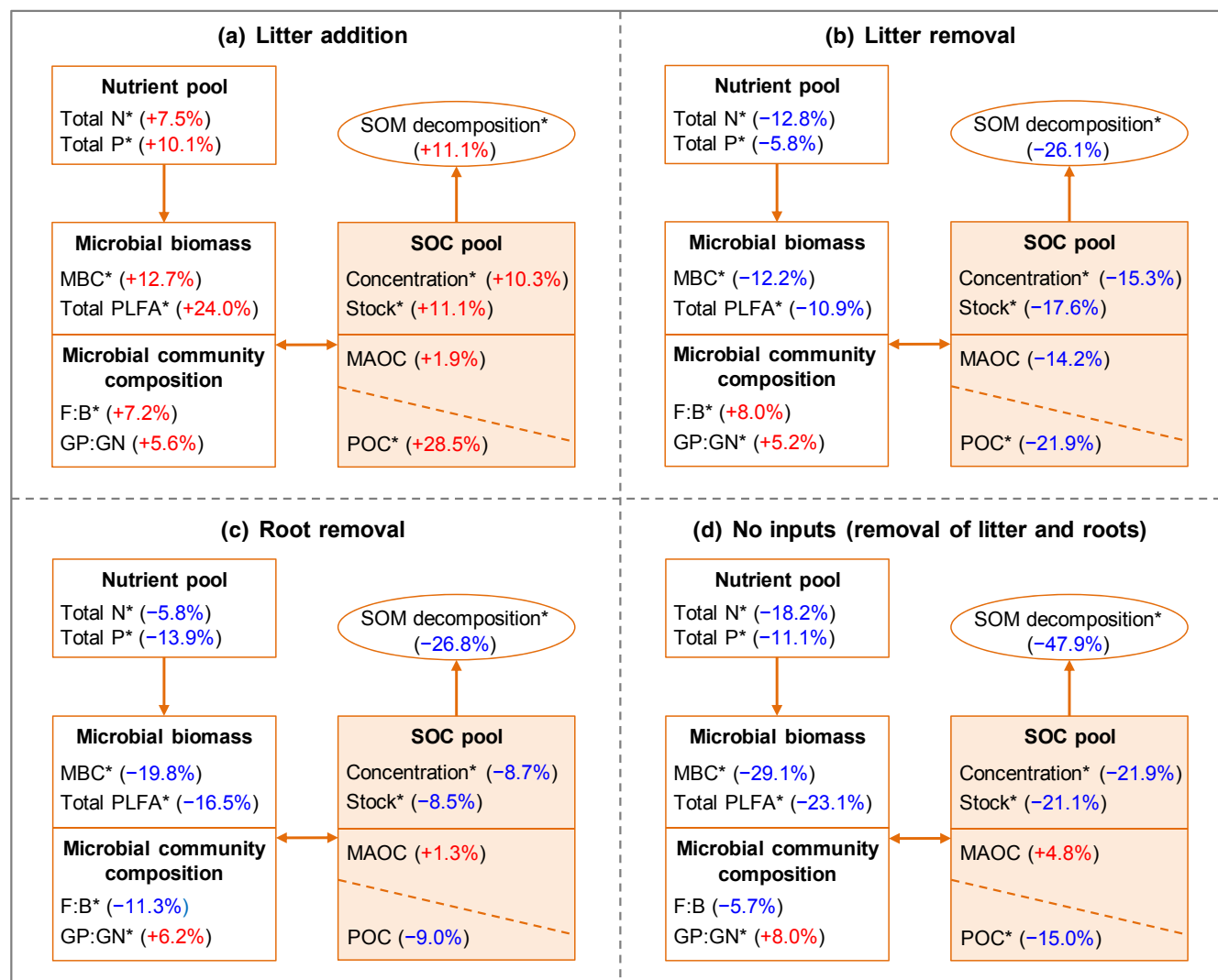
FIGURE 7 Schematic summary of the effects of plant input changes on main belowground processes in forest ecosystems. MBC, microbial biomass carbon; PLFA, phospholipid fatty acid; F:B, fungi-to-bacteria ratio; GP:GN, Gram-positive to Gram-negative bacteria ratio; SOC, soil organic carbon; and SOM, soil organic matter. SOM decomposition (per gram soil mass) is measured by collecting soils in the field followed by laboratory incubation. The analyses for particulate (POC) and mineral-associated organic carbon (MAOC) are based on combined observations from density or particle-size fractionation. The numbers in parentheses indicate average effects (%) on variables, and the symbol "+" indicate positive effects (indicated by red font), and the symbol "−" indicate negative effects (indicated by blue font). Asterisks (*) indicate significant effects of detrital treatments on variables at $p < .05$ [Colour figure can be viewed at wileyonlinelibrary.com]

loss of soil C, especially in the long term (Figure 6; Figure S9; Dove et al., 2019). Under litter addition, the response of SOC showed a significant increasing trend with duration ($p = .029$), in accordance with a previous meta-analysis (Xu et al., 2021). However, duration had a limited explanation for the variations in SOC responses ($R^2 = .046$), particularly when the data with the longest duration were excluded from the regression analysis ($R^2 = .011$; Figure S9). This might be caused by three reasons. First, in addition to duration, the responses of SOC to litter addition were also affected by litter treatment mode (fresh+floor vs. fresh), and the former treatment (fresh+floor) can induce large positive effects on SOC in the short term, comparable with the effects of the latter treatment in the long term (e.g., the points with 50-year treatment in Figure 6a). Second, litter-induced priming effects may lower SOC in early-stage treatments, and it may take many

years before enhanced litter inputs are able to replenish the C released by priming effects and increase SOC (Bowden et al., 2014; Lajtha, Bowden, et al., 2014). This phenomenon was partly supported by the responses of SOC to litter addition shown in Figure 6a, with many negative responses before 5-year treatment and only two unchanged or negative responses after 20-year treatment. Third, the responses of SOC to litter addition may also be regulated by litter quality and C saturation capacity of soils, which vary with tree species, climatic and soil mineralogical conditions (Castellano et al., 2015; Jackson et al., 2017; Pierson et al., 2021). Taken together, all these factors can potentially regulate the responses of SOC to litter addition and affect the relationship between duration and SOC responses. However, the priming effects, litter quality, and soil mineralogy are rarely reported in case studies, limiting our further analysis. Future studies can measure these

factors and explore their regulations on the responses of SOC to litter addition, which can advance our understanding on how SOC responds to elevated litter inputs.

4.2 | Relative importance of litter and roots in forming SOC

Previous studies showed that roots had greater contribution to soil C pools than litter (Rasse et al., 2005; Sokol & Bradford, 2019; Whalen et al., 2021; Wu et al., 2018). This is mainly due to greater C supply from roots, more stable root-derived C that is chemically or physically protected from microbial activity, and more efficient retention of root-derived C (Crow, Lajtha, Filley, et al., 2009; Rasse et al., 2005; Schmidt et al., 2011; Sokol & Bradford, 2019). However, inconsistent with these previous studies and our Hypothesis 2 that roots have greater effects on SOC than litter, our results indicated that the effects on SOC pools induced by roots were lower or equivalent to those by litter (Figure 3b,c). This inconsistency in the relative importance of litter and roots on SOC pools between the present study and previous studies might mainly depend on the study method used (Keller et al., 2021; Sokol, Kuebbing, et al., 2019, Sokol, Sanderman, et al., 2019).

Unlike direct measurements of litter- and root-derived C incorporated into SOC (often with isotopic tracing), our results were based on indirect measurements of SOC change by excluding litter and roots. Such study method can lead to the observed result that litter had relatively greater contributions to SOC than roots in two ways. First, in root removal and no inputs treatments, trenching can result in a large amount of dead root residues in a short time, which can take many years to decompose (e.g., Pierson et al., 2021). As such, the extra inputs of C from decomposing roots to soil (Mayzelle et al., 2014; Pierson et al., 2021) can partly offset the expected decrease in SOC caused by root removal (particularly in a short duration), thereby leading to an underestimate of root contribution to SOC (by comparing paired root removal vs. control treatments or by comparing paired litter removal vs. no inputs treatments). Second, litter removal can indirectly inhibit root growth via decreasing soil nutrients. As indicated by our results, litter removal significantly decreased soil nutrient pools (Figure 2b), which, thus, can reduce root biomass and production, and reduce root-derived C incorporated into soil (Pierson et al., 2021; Rodtassana & Tanner, 2018). That is, in addition to directly reducing litter-derived C input to soil, litter removal can also reduce root-derived C input to soil by reducing soil nutrients. By contrast, root removal is unlikely to affect aboveground litter-derived C input to soil because this treatment did not significantly alter soil nutrient pools and the plots for root removal in DIRT experiments are often too small to affect forest productivity and litterfall production.

4.3 | Soil microbial community responses

Soil microbes are generally constrained by the availability and quality of carbon and nutrients (Rousk & Frey, 2015; Soong et al., 2020);

thus, alterations in plant inputs from above- and belowground can directly affect the size of microbial biomass (Huang et al., 2000; Rousk & Frey, 2015). Across all studies, litter addition significantly increased microbial biomasses, whereas detrital removal treatments tended to decrease them (Figure 2). In addition, the responses of microbial biomass in different functional groups generally increased with those of carbon and nutrient pools (SOC, DOC and total N; $p < .05$; Figure S10). Collectively, these findings suggest that detritus input-induced changes in C and N availability can have profound controls on the dynamics of microbial biomass.

As root-derived C rather than litter-derived C is the major source of C for microbes, particularly rhizosphere-associated microbes (Dove et al., 2019; Huang et al., 2000; Kramer et al., 2010), roots should induce a larger effect on soil microbial communities. However, inconsistent with the Hypothesis 2 that roots have greater effects on microbial biomass than litter, our results from comparing microbial responses to litter removal versus root removal demonstrated that their effects on microbial biomass were similar (Figure S7). This phenomenon might be associated with two reasons. One is that when fresh C sources (e.g., exudates) from living roots are reduced, soil microbes (particularly fungi and Gram-positive bacteria) can use the substrate from old SOM to alleviate the C limitation on their growth and activity (Feng et al., 2011). Another one is that root removal did not reduce, whereas litter removal reduced soil total and available nutrient pools (Figure 2b,c). As such, soil microbes are less limited by soil nutrient availability under root removal compared with litter removal. That is, under root removal, the sufficient N supply can partly offset the negative effects of reduced C availability on soil microbes, whereas it is not the case under litter removal.

In addition to microbial biomass, detrital treatments also shifted the microbial community composition (Figures 2 and 7). Across all studies, litter addition increased fungal-to-bacterial ratio, suggesting that aboveground litter input has greater promotion on the biomass of fungi than that of bacteria and shifts soil microbial community toward fungi. This can be explained by two reasons. First, fresh litter contains recalcitrant components (e.g., lignin and cellulose), which can be preferentially used by fungi (relative to bacteria) in the early stage of litter decomposition (Zhang et al., 2021). Second, as plant aboveground litter often has high C:N ratio (about 61.2 globally, Zechmeister-Boltenstern et al., 2015), the addition of litter increased soil C:N ratio (Figure 2a) and can induce a lower N availability (relative to C), which generally favors fungal growth (Fierer et al., 2009; Hicks et al., 2021; Strickland & Rousk, 2010). Similar to litter addition, litter removal also increased fungal-to-bacterial ratio, likely because litter removal caused continuous losses of soil labile C (Figures 2 and 6b; Lajtha, Townsend, et al., 2014), and fungi can produce oxidative enzymes more efficiently than bacteria to decompose recalcitrant C to maintain their growth (Cusack et al., 2011). This mechanism can also explain the increased GP-to-GN ratio under litter removal, as most Gram-positive bacteria are oligotrophic communities and can use more recalcitrant C sources from SOM like fungi (Kramer & Gleixner, 2008; Zechmeister-Boltenstern et al., 2015). Beyond

reducing belowground C inputs by root exclusion, root removal can also directly decrease the biomass of symbiotic fungi (e.g., arbuscular mycorrhizal and ectomycorrhizal fungi) associated with plant roots (Dove et al., 2019; Whalen et al., 2021). Therefore, root removal induced larger negative effects on fungi than bacteria (24.8%, 95% CI: 16.2%–32.4% vs. 13.9%, 95% CI: 6.6%–20.6%; $p = .049$), and consequently decreased fungal-to-bacterial ratio (Figure 2c). Collectively, the opposite effects of litter removal and root removal on fungal-to-bacterial ratio resulted in its nonsignificant change under no inputs (Figure 2d).

4.4 | Limitations, implications, and future study

Using the meta-analysis approach, this study revealed the global-scale patterns and regulations of how above- and belowground plant input changes affect soil C and microbial communities in forest ecosystems (Figure 7). However, results from this meta-analysis may still have some limitations. First, field detritus manipulation experiments were unequally distributed geographically (Figure S1), and some variables had limited sample sizes (e.g., SOC fractions in root removal and no inputs treatments). Currently, most of experiments have been carried out in temperate forests, with relatively fewer experiments in tropical forests with the highest litterfall production and SOM turnover among forest types (Vogt et al., 1986). Given the positive correlation between the responses of multiple variables and litter input quantity (Table S3), the relative lack of observations from tropical forests might underestimate the overall effects of plant inputs on soil C and microbes globally. Second, durations of most experiments (72%) were shorter than 5 years (Figure S2b). Such short time may not be long enough to induce a threshold response of some processes, particularly when the mean-residence time of litter is longer than experimental duration (Keller & Phillips, 2019; Matthews, 1997) and may lead to an underestimate of plant detritus effects.

Regardless of these limitations, our meta-analysis can greatly expand our knowledge on how plant input changes affect forest soil C and microbes compared with previous meta-analyses only having aboveground litter alteration treatments (Xu, Liu, et al., 2013, 2021) and has some important implications. DIRT experiments provide excellent opportunities to assess the effects of changing plant productivity and C allocation under global changes on soil C cycling and microbial communities in forest ecosystems (Brant et al., 2006; Pierson et al., 2021; Sayer et al., 2021). The positive correlations of soil C and microbial biomass with litter input rate and total litter input suggest that altered plant productivity and C allocation under global changes may have larger effects on belowground processes in forests with high productivity. Global changes, such as elevated CO_2, warming and nutrient deposition, are considered to increase forest productivity and the quantity of C inputs to soils (Lu, Vitousek, et al., 2021; Terrer et al., 2016). Hence, we can predict that enhanced plant inputs by these global changes may benefit SOC sequestration in forests, especially in high-productivity topical forests. However, the lack of monitoring the C saturation capacity of soils makes it difficult to determine how much litter- and root-derived C can be sequestered by soils and should be explored by future studies.

Microbes act as not only the consumer of SOC but also the contributor of SOC formation because necromass C from microbial biomass and turnover can be highly protected against decomposition and are important determinants for MAOC (Lavallee et al., 2020; Liang et al., 2017). Our current results showed that detrital treatments had minimal effects on MAOC but significantly changed microbial biomass. This implies that elevated litter inputs may increase, and removal of litter, roots or both may reduce MAOC via altering microbial biomass and its necromass in the long term. In addition, measuring methods (indirect vs. direct) can greatly affect the estimation of the contributions of litter- and root-derived C to SOC, and living root inputs can be more efficient than litter (root plus shoot) inputs in forming SOC (Sokol, Kuebbing, et al., 2019). In the field condition, adding roots without destroying soil structure remains a challenge, but the dual ingrowth-core isotopic technique (see Keller et al., 2021; Panzacchi et al., 2016) provides an opportunity to quantify and compare the relative contributions of litter and living roots to SOC formation and stabilization. Litter and roots may have distinct effects on different SOC fractions, and their effects on total SOC pool may also depend on the time of manipulation (Lajtha, Townsend, et al., 2014; Sokol, Sanderman, et al., 2019). As such, it is important to extend ongoing experiments in time to conduct further investigation.

In summary, by conducting a large-scale meta-analysis of DIRT experiments in forests, this study quantified the effects of altered litter and root inputs on soil C and microbial communities in forest ecosystems and identified the critical roles of litter input quantity in regulating their responses to litter alterations. Specifically, litter addition stimulated soil C pools and microbial biomass, whereas removal of litter, roots, or both decreased them. By contrast, litter removal and root removal differently affected soil microbial community, with litter removal shifting it toward fungi and root removal shifting it toward bacteria. In addition, we determined experimental duration as an important controller for the responses of SOC to detritus treatments and found that litter alterations and no inputs altered particulate (but not mineral-associated) organic carbon. Collectively, these findings suggest that changes in plant inputs are fundamental in mediating soil C and microbial communities and imply that changes in plant productivity and inputs under global changes will have substantial effects on soil biogeochemical processes.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.18910619.v5

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