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Effects of root dominate over aboveground litter on soil microbial biomass in global forest ecosystems

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Abstract

Background: Inputs of above- and belowground litter into forest soils are changing at an unprecedented rate due to continuing human disturbances and climate change. Microorganisms drive the soil carbon (C) cycle, but the roles of above- and belowground litter in regulating the soil microbial community have not been evaluated at a global scale.

Methods: Here, we conducted a meta-analysis based on 68 aboveground litter removal and root exclusion studies across forest ecosystems to quantify the roles of above- and belowground litter on soil microbial community and compare their relative importance.

Results: Aboveground litter removal significantly declined soil microbial biomass by 4.9% but root exclusion inhibited it stronger, up to 11.7%. Moreover, the aboveground litter removal significantly raised fungi by 10.1% without altering bacteria, leading to a 46.7% increase in the fungi-to-bacteria (F/B) ratio. Differently, root exclusion significantly decreased the fungi by 26.2% but increased the bacteria by 5.7%, causing a 13.3% decrease in the F/B ratio. Specifically, root exclusion significantly inhibited arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and actinomycetes by 22.9%, 43.8%, and 7.9%, respectively. The negative effects of aboveground litter removal on microbial biomass increased with mean annual temperature and precipitation, whereas that of root exclusion on microbial biomass did not change with climatic factors but amplified with treatment duration. More importantly, greater effects of root exclusion on microbial biomass than aboveground litter removal were consistent across diverse forest biomes (expect boreal forests) and durations.

Conclusions: These data provide a global evidence that root litter inputs exert a larger control on microbial biomass than aboveground litter inputs in forest ecosystems. Our study also highlights that changes in above- and belowground litter inputs could alter soil C stability differently by shifting the microbial community structure in the opposite direction. These findings are useful for predicting microbe-mediated C processes in response to changes in forest management or climate.

Keywords: Forest ecosystems, soil microorganisms, Fungi, Litter, Root, Carbon input, Meta-analysis

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Introduction

Intensified human disturbances and climate change have greatly influenced above- and belowground litter (root) inputs to forest soils. For example, harvesting forest products significantly decreases the aboveground litter input (Achat et al. 2015), but nutrient deposition may increase litter inputs more from aboveground than belowground parts via enhanced plant growth and decreased root-to-shoot ratios (Song et al. 2019; Li et al. 2020). These changes in litter inputs can profoundly alter soil carbon (C) stocks, because plant litters are the main source of C into the soil (Lajtha et al. 2018; Reynolds et al. 2018). However, we currently have insufficient capability to predict the litter-induced changes in soil C dynamics. This is mainly due to a critical knowledge gap on the general patterns of soil microorganism response to litter changes in forest ecosystems, where approximately one-third of the terrestrial C is stored in soil (Dixon 1994).

Soil microorganisms play a key role in soil C formation and stabilization (Schimel and Schaeffer 2012; Jing et al. 2019) and respond rapidly to changes in above- and belowground litter (Brant et al. 2006; Wang et al. 2017a; Jing et al. 2019). Numerous studies have quantified the roles of above- and belowground litter in driving the soil microbial community via litter removal experiments (Hogberg et al. 2007; Weintraub et al. 2013; Xu et al. 2013; Wang et al. 2017a; vanden Enden et al., 2018; Jing et al. 2019). Despite these efforts, to what extent above- and belowground litter influence soil microorganisms remains largely unknown due to diverse microbial responses. For instance, the microbial biomass has been reported to increase (Feng et al. 2002; Pisani et al. 2016), decrease (Högberg and Högberg 2002; Li et al. 2004; Weintraub et al. 2013), or to change insignificantly under litter exclusion treatments (Blazier et al. 2008; Prevost-Boure et al. 2011). Besides, the microbial community structure indicated by the fungi-to-bacteria ratio (F/B) also decreases (Brant et al. 2006) or increases (Pisani et al. 2016; Wang et al. 2017b) in response to removing litters. Moreover, above- and belowground litters differ in chemical properties, turnover rates, and pathways entering into the soil (Hatton et al. 2015; Fulton-Smith and Cotrufo 2019; Sokol et al. 2019), meaning that they may exert different controls on soil microorganisms. Aboveground litters are traditionally believed to be equal to or more important than roots in affecting the microbial community (Li et al. 2004; Wang et al. 2017a). This notion clashes with the emerging evidence that root exclusion inhibits the microbial biomass greater than aboveground litter removal (vanden Enden et al., 2018; Liu et al. 2019). Unfortunately, to date, few studies have compared the importance of above- and belowground litters to the soil microbial community, and thus are unlikely to identify the global relative importance due to soil ecological complexity and spatial heterogeneity (Culina et al. 2018). A quantitative synthesis that reveals the global-scale patterns of above- and belowground litter effects on soil microorganisms and compares their relative importance is urgently needed.

The effects of above- and belowground litter on soil microorganisms may vary depending on climate or forest biomes because forest productivity (Huston and Wolverton 2009), biomass allocation (Luo et al. 2012), and litter decomposition rate (Luo et al. 2012; See et al. 2019) are dependent on climate. A previous meta-analysis has revealed that the microbial biomass in subtropical forests is more sensitive to aboveground litter removal than that in temperate forests (Xu et al. 2013). Nevertheless, evidence is lacking on whether the effect of belowground litter on soil microorganisms is also climatic- or biome-dependent. Moreover, litter inputs and associated priming effect (defined as litter input triggers decomposition of pre-existing SOC) are dependent on time (Huo et al. 2017; Wu et al. 2018), indicating that litter effects on soil microorganisms may vary over time. However, this speculation remains untested.

To address the above-mentioned issues, we performed a meta-analysis of the soil microbial community in response to aboveground litter removal and root exclusion by collecting 68 published litter experiments conducted in forest ecosystems. Our study seeks to (1) quantify the effects of above- and belowground litter on microbial community, (2) compare their relative importance, and (3) explore the environmental factors that can explain the various effects of litter exclusion on the microbial biomass across studies.

Methods

Data collection

Peer-reviewed journal articles published before December 2020 were searched using the Web of Science (http://apps.webofknowledge.com/) and the China National Knowledge Infrastructure (http://www.cnki.net/). The searched terms were "(carbon input OR litter inputs OR litter manipulation OR litter removal OR detrital input and removal treatment OR root exclusion OR trenching OR girdling) AND (microbe OR microbial OR phospholipid fatty acid OR PLFA) AND (forest)". To minimize publication bias, only studies that satisfied the following criteria were included in this meta-analysis. (1) Only field experiments were selected; (2) The control and treatment plots were established in the same climatic types, dominant plant groups, and soil conditions; (3) The means, standard deviations (or standard errors) and numbers of replicates were reported; (4) Only the latest results were used if multiple observations were made at different times in the same study site; (5) Only the topmost soil layer was included if multiple soil depths were reported; (6)

Different litter-removal treatments, soil or vegetation types in the same study were regarded as an independent study. Ultimately, a total of 60 aboveground litter removal and 71 root exclusion experiments obtained from 68 papers met the criteria above and were utilized for this meta-analysis (Supporting Information).

For each of the selected studies (Fig. 1), we extracted data of total microbial biomass, the biomass of fungi, bacteria, Gram-positive bacteria (GP), Gram-negative bacteria (GN), actinomycetes (ACT), arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EMF), fungi-to-bacteria ratio (F/B) and the ratio of Gram-positive to Gram-negative bacteria (GP/GN). If the case study used both chloroform fumigation (CF) and phospholipid fatty acid (PLFA) methods to measure microbial biomass, we chose the former as Ren et al. (2017) did. Methods for determining the fungal and bacterial biomass included PLFA (Jing et al. 2019) and microscope (Subke et al. 2004). Root exclusion included trenching and girdling experiments, because these two methods yield quantitatively similar outcomes for microbial biomass ($P > 0.05$, Fig. S1).

Besides the information on microbes, we also recorded forest biomes (boreal, temperate, and sub/tropical forests), mean annual temperature (MAT), mean annual precipitation (MAP), experimental duration [grouped into short (< 3 years) and long duration (≥3 years)], dissolved organic C (DOC), and other soil properties (e.g. soil temperature, and soil moisture). If studies did not report climate variables, the WorldClim data (http://www.worldclim.com/) were used to reconstruct climate values based on latitude and longitude. These data covered a wide gradient of climatic conditions, with MAT and MAP ranging from − 4.9 °C to 35 °C, and from 420 to 5000 mm, respectively. We collected data directly from either tables or indirectly from figures by using GetData Graph Digitizer 2.24 software.

Meta analysis

We used the natural log of the response ratio (lnRR), defined as the 'effect size' to determine the significance of microbial responses to above- or belowground input removal (Hedges et al. 1999). For a given variable, the response ratio (RR) was calculated as below:

$$\ln RR = \ln\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \ln\left(\overline{X_t}\right) - \ln\left(\overline{X_c}\right) \tag{1}$$

where $\overline{X_t}$ and $\overline{X_c}$ are the means of litter removal treatments and the control, respectively. The variance within each study was calculated by:

$$v = \frac{{s_t}^2}{n_t\overline{X_t}^2} + \frac{{s_c}^2}{n_c\overline{X_c}^2} \tag{2}$$

where s_t, n_t versus s_c, n_c are the standard deviation and sample size under litter removal and control treatments, respectively.

We calculated the weight (w) of each lnRR by the inverse of variance as below:

$$w = \frac{1}{v} \tag{3}$$

Finally, the mean variance-weighted effect size lnRR for all observations was calculated as Eq. 4 using a fixed

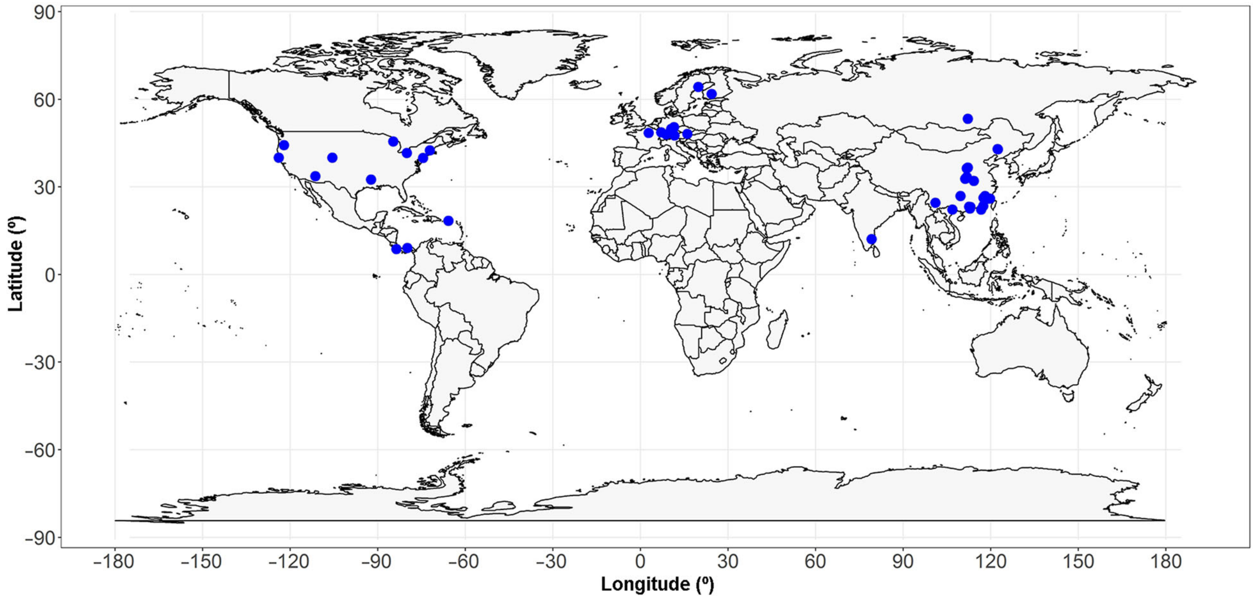

Fig. 1 Global distribution of locations of studies included in this meta-analysis

effects model in MetaWin software (2.1) (Hedges et al. 1999; Ren et al. 2017).

$$\ln\mathrm{RR}_{++} = \frac{\sum_i (w_i) \times \ln\mathrm{RR}_i}{\sum_i (w_i)} \quad (4)$$

If 95% confidence intervals (CIs) of $\ln\mathrm{RR}_{++}$ did not overlap with 0, then effects were significant at $P < 0.05$. The changes caused by input treatments for a certain response variable were calculated as:

$$\text{Percentage } (\%) = \exp(\ln\mathrm{RR}_{++} - 1) \times 100\% \quad (5)$$

The statistic differences between the effect sizes of aboveground litter removal (ALR) and that of root exclusion (RE) were analyzed by between-group heterogeneity (Ren et al. 2017; Chen and Chen 2018). Regression and correlation analyses were adopted to examine the relationships of lnRRs of microbial biomass and F/B ratio to duration, climatic variables and soil properties using SPSS 22.0 software (SPSS Inc.).

Results

Effects of above- and belowground litter on the soil microbial community

At the global scale, aboveground litter removal significantly decreased the total microbial biomass by 4.9% (Fig. 2a, $P < 0.05$). In comparison to the above-ground litter removal, root exclusion caused a stronger decline in the microbial biomass, reaching11.7% (Fig. 2b, $P < 0.05$). The aboveground litter removal significantly enhanced fungi by 10.1% ($P < 0.05$) but showed no effect on other specific microbial groups, leading to a 46.7% enrichment in the F/B ratio (Fig. 2a, $P < 0.01$). However, root exclusion significantly increased bacteria by 5.7% and decreased fungi by 26.2%, resulting in a 13.3% decrease in the F/B ratio (Fig. 2b, all $P < 0.05$). In detail, root exclusion significantly increased GP bacteria by 4.2%, but significantly inhibited AMF, EMF, and ACT by 22.9%, 43.8%, and 7.9%, respectively (Fig. 2b, all $P < 0.05$). Moreover, aboveground litter removal and root exclusion increased the GP/GN bacteria ratio to a similar extent (Fig. 2, both $P < 0.05$).

Factors controlling the microbial responses

Regression analysis revealed that across all forest ecosystems, the lnRR of soil microbial biomass to aboveground litter removal increased with MAT (Fig. 3a, $R^2 = 0.129$, $P < 0.01$) and MAP (Fig. 3b, $R^2 = 0.111$, $P < 0.01$), but did not change with experimental duration or other soil variables (Figs. 3c–d and Table S1). Regarding forest biomes, above-ground litter removal significantly inhibited the microbial biomass in sub/tropical forests ($P < 0.05$) but not in temperate forests or boreal forests (Fig. 4). Conversely, the microbial biomass response to root exclusion did not show any significant correlation with MAT or MAP (Figs. 3a–b, both $P > 0.05$) but decreased linearly with experimental duration (Fig. 3c, $R^2 = 0.135$, $P = 0.003$), with a 90.8% greater response in long- compared to short-term studies (Fig. 4, $P = 0.001$). Moreover, the stronger effect of root exclusion than aboveground litter removal on microbial biomass was consistent across diverse forest biomes (except boreal forests) and durations (all $P \le 0.005$).

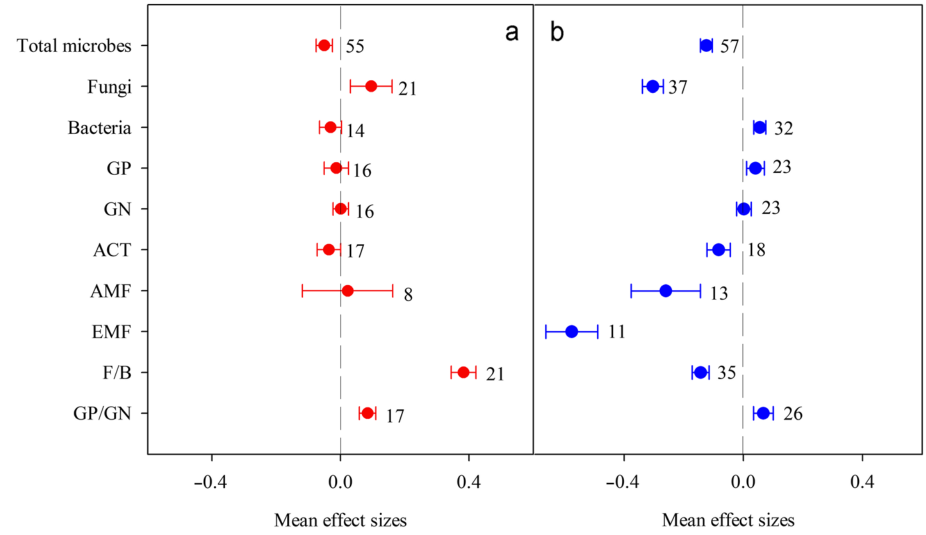

Fig. 2 Effects of ALR (**a**) and RE (**b**) on soil microbial community. The number of observations for each variable is shown next to the point. Error bars represent 95% CIs. AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi; GP, Gram-positive bacteria; GN, Gram-negative bacteria; ACT, actinomycetes; F/B, fungi to bacteria ratio; ALR, aboveground litter removal; RE, root exclusion

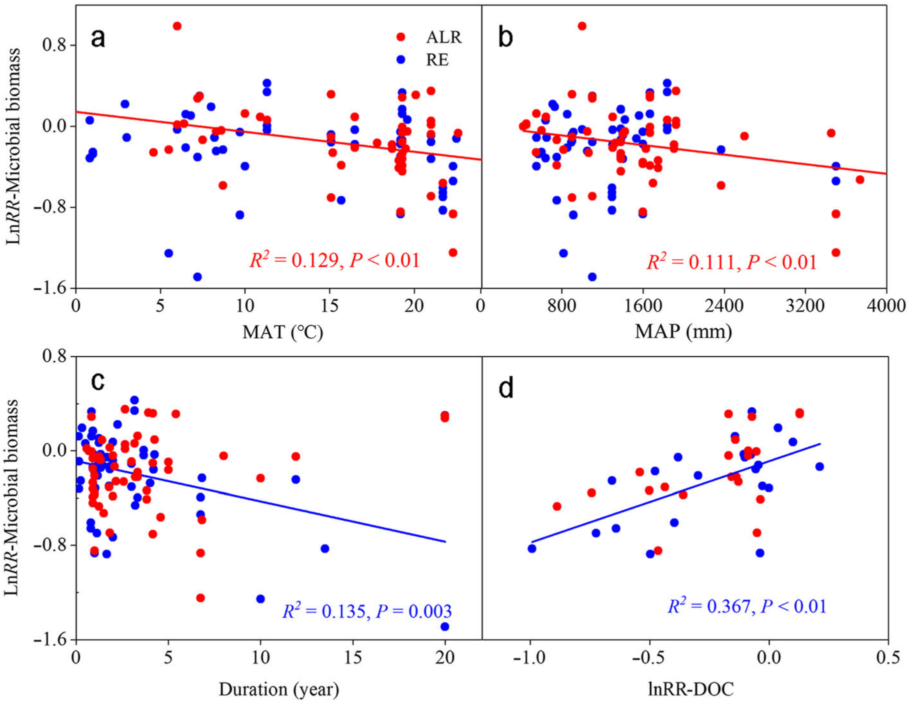

Fig. 3 Relationships of lnRR of microbial biomass with MAT, MAP, duration, and lnRR of DOC. Red and blue lines represent ALR and RE effects, respectively. ALR, aboveground litter removal; RE, root exclusion

Based on the current limited number of observations, the aboveground litter-induced changes in the F/B ratio exhibited significantly positive correlations with treatment duration ($P < 0.01$, Table S1) but did not show any significant correlation with climatic variables or soil properties. By contrast, the effects of root exclusion on the F/B ratio significantly increased with the lnRR of soil nitrate nitrogen but decreased with the lnRR of soil ammonium nitrogen (both $P < 0.05$, Table S1).

Discussion

Distinct roles of above- and belowground litter on the microbial community

Our results showed that globally, aboveground litter removal decreased microbial biomass by an average of 4.9% (Fig. 2a), suggesting that aboveground litter is an important C source for microbial growth. This finding confirms the aboveground litter effects on microbial biomass reported earlier (Xu et al. 2013), but the magnitudes of effects differ, which may be partly due to the different numbers of observations (55 studies vs. 14 studies for our analysis vs. previous analysis, respectively) and data source (more temperate and boreal studies in our analysis than previous one). DOC, which is a labile soil C that depends strongly on plant C inputs (Sokol et al. 2019), significantly decreased with aboveground litter removal (Fig. S2). This may contribute to decreases in microbial biomass with aboveground litter

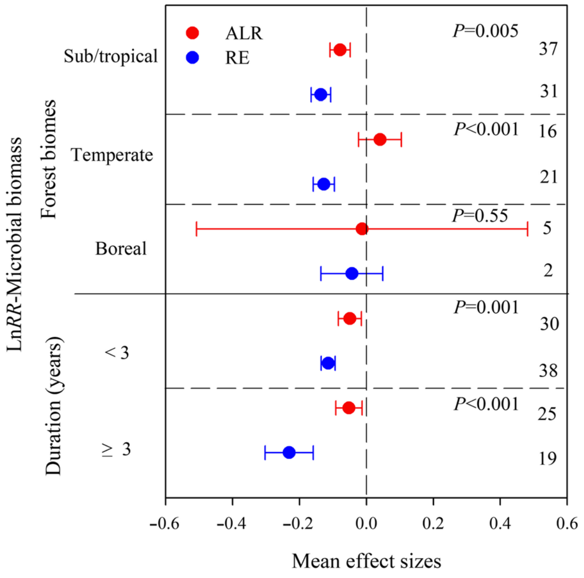

Fig. 4 The lnRR of microbial biomass to ALR and RE. The variables are categorized into different forest biomes and durations. The number of observations for each variable is shown next to the point. Error bars represent 95% CIs. ALR, aboveground litter removal; RE, root exclusion

removal, because soil microbes are highly dependent on DOC (Fig. 3d; Ren et al. 2017; Li et al. 2019). Importantly, this study, as the first, revealed that root exclusion reduced microbial biomass to a larger extent than aboveground litter removal (Fig. 2), thus supporting the newly-developing view that root litter inputs exert a stronger control on microbial biomass than aboveground litter does (vanden Enden et al., 2018; Liu et al. 2019). Root-derived DOC are nearly three times more than aboveground litter-derived DOC (Sokol et al. 2019). Thus, the greater decline in DOC under root exclusion than aboveground litter removal (Fig. S2) likely contributes to the lower microbial biomass under root exclusion.

We also found that litter exclusion showed diverse effects on microbial groups. Aboveground litter removal significantly increased fungi but had no effects on bacteria (Fig. 2a), suggesting that fungi are more sensitive to aboveground litter alterations than bacteria. Continuous aboveground litter removal decreases soil labile C (Fig. S2; vanden Enden et al., 2018) and increases recalcitrant C compounds (Pisani et al. 2016). In this case, relative to bacteria, fungi have higher capability of acquiring recalcitrant C via producing C-degrading enzymes and relocating nutrients by fungal hyphal (Strickland and Rousk 2010). Furthermore, fungi have higher C use efficiency, and thus higher biomass yield efficiency (Strickland and Rousk 2010; Kallenbach et al. 2016). These may increase fungal biomass under aboveground litter removal.

Different from aboveground litter removal, root exclusion significantly inhibited fungi, especially AMF and EMF (Fig. 2b). These results are consistent with those of ^{13}C-labelling studies, which shows that fungi utilize most of rhizodeposition-derived C (Denef et al. 2009; Bai et al. 2016) but offer global evidence that fungi especially mycorrhizal fungi rely much on root-derived C input. This finding is not surprising, because mycorrhiza fungi, as a large fungal biomass pool, form symbiosis with the roots of over 90% plants (Brundrett and Tedersoo 2018) and receive up to 22% of net photosynthetic products (Hobbie 2006). However, it is surprising that root exclusion stimulated bacterial biomass (Fig. 2b), as bacteria also have high ability of utilizing root-derived C (Huang et al. 2020). This may be due to that the loss of fungi with root exclusion alleviates the antagonistic effects towards bacterial growth (Schneider et al. 2010) and provides their residues for utilization by bacteria (Ryckeboer et al. 2003; Apostel et al., 2018).

Given these diverse responses of microbial groups, our study offers new insights into the variations of the F/B ratio associated with removing litter inputs, which was stimulated by aboveground litter removal but decreased by root exclusion (Fig. 2). This result suggests that the removing aboveground litter and root shift the microbial community structure in the opposite direction. It is commonly accepted that a high F/B ratio has greater potential to benefit soil C-sequestration because fungi invest more C to growth, produce more recalcitrant residues, and stimulate aggregate formation which sequester C from microbial decomposition than bacteria do (Strickland and Rousk 2010; Jing et al. 2019). Thus, the present findings imply that reducing root inputs or relative allocation tend to induce greater soil C vulnerability than the loss of aboveground litter. Therefore, further studies on soil C storage and stability in response to above- and belowground litter exclusion are necessary.

Different factors controlling the responses of microbial biomass

We focused our discussion on the microbial biomass because the F/B ratio was relatively insufficient to draw firm conclusions. We found that climate-related variables are key factors regulating the effect of aboveground litter on microbial biomass, with more pronounced aboveground litter effect in higher MAT and MAP regions (i.e., sub/tropical forests; Figs. 3a, b and 4). This finding suggests that the microbial biomass in warmer and wetter forests would be more vulnerable to future aboveground litter loss than that in colder and drier forests. Similar results have been reported in a previous meta-analysis (Xu et al. 2013). Aboveground litters indirectly enter into the soil by leaching and bioturbation (Vidal et al. 2017). Higher MAT and MAP are not only accompanied with more production of aboveground litter (Luo et al. 2012), fast litter decomposition (Campo and Merino 2016; See et al. 2019) but also with stronger leaching and more soil fauna (Xu et al. 2020). These can explain why soil microbes are more reliant on aboveground inputs in warmer and wetter forests. The lack of correlation between microbial biomass under aboveground litter removal and experimental duration may be because soil microorganisms adjust their community structure (Fig. 2a) or their C utilization strategies (Wang et al. 2019) to maintain their biomass over time after removing aboveground litter.

Surprisingly, the effect of root exclusion on the microbial biomass did not change with MAT or MAP (Fig. 3a and b). However, it should be noted that the existing two observations on microbial biomass in boreal forests remained unchanged under root exclusion (Fig. 4), which limits our ability to confirm whether root effects on microbial biomass is consistent across the globe. Therefore, further studies should be carried out in these forests to provide a quantitative estimation of the response of microbial biomass to root exclusion. While we observed that the reductions in microbial biomass with root exclusion became larger as experimental duration went longer (Figs. 3c and 4), lacking a saturating response and suggesting that root effects on microorganisms is lasting and deepening. Long-term root exclusion leads to a shift in microbial utilization from labile C pools to recalcitrant C pools in soils (Pisani et al. 2016; Wu et al. 2018). Given that fungi have high ability of utilizing recalcitrant C compounds as described above (Strickland and Rousk 2010; Meng et al. 2020), significant inhibitions in fungi with root exclusion (Fig. 2b) is likely unable to meet the microbial C needs for growth, and ultimately decreasing microbial biomass over time. Furthermore, the long-term root exclusion has less compensation effect from dead roots, because nearly 92% fine roots and 80% coarse roots are decomposed beyond three-year according to global root decomposition rate (Silver and Miya 2001). This time-dependent effect of root litter indicates that the root importance on soil microorganisms would be underestimated by short-term experiments. Thus, more long-term experiments conducted in forest ecosystems are urgently needed to gain insights into microbial responses to root exclusion at the global scale.

Although factors controlling the responses of microbial biomass to aboveground litter removal and root exclusion differed, we did observe that the greater influence of belowground litter inputs on the soil microbial biomass than aboveground litter inputs is consistent across diverse forest biomes (expect boreal forests) and treatment durations (Fig. 4). Similarly, 35.7% studies, which simultaneously removing aboveground and belowground litters, showed that the effects of roots on microbial biomass are larger than that of aboveground litter in temperate forests (Wang et al. 2017a; vanden Enden et al., 2018) and sub/tropical forests (Wang et al. 2017b; Wu et al. 2018; Liu et al. 2019). We thus emphasize that C allocation should be considered when projecting microbe-derived soil C changes in response to climate change and forest managements in forest ecosystems.

However, the generally weak accounts of variations in microbial biomass under litter exclusion by all variables considered here point to the complex nature of microbial responses to litter exclusion. Climatic variables individually accounted for 24% of the overall variations in microbial biomass under aboveground litter removal, whereas the experimental duration and DOC explained 50.2% of changes in microbial biomass under root exclusion. Although litter exclusion significantly influences soil temperature and soil moisture (Xu et al. 2013; Zhang et al. 2020), which may alter microbial responses due to their close linkages (Wang et al. 2019; Rasmussen et al. 2020), we did not observe these soil properties influence microbial response to litter exclusion based on our limited number of observations (Table S1). This finding further brings a challenge to describe the effects of multiple drivers on the response ratio of microbial biomass, which is similar to many other meta-analysis studies that lacking sufficient associated measurements (Ren et al. 2017; Yang et al. 2020). Therefore, microbial community and soil property responses should be examined simultaneously under the context of removing litters in future experimental research. Despite above-mentioned limitations, our study is the first meta-analysis elucidating litter roles in the microbial community and providing a global picture for understanding the relative importance of above- versus belowground litter in regulating the microbial community in forest ecosystems.

Conclusions

To our knowledge, this current meta-analysis study is the first global syntheses to quantitatively evaluate the roles of above- and belowground litter on the soil microbial community in forest ecosystems. Our synthesis showed that root litter was stronger than aboveground litter for microbial biomass worldwide. More importantly, the root effect amplified over time, but effect of aboveground litter was dependent on climate (i.e., forest biomes). Furthermore, removing litter from above- and belowground shifted the microbial community structure in the opposite direction, which could have profound but different effects on the global soil C cycle. These findings highlight the importance and different roles of aboveground and root litters, which should be fully considered when predicting microbe-mediated processes and establishing forest management strategies with a changing climate.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40663-021-00318-8.

Additional file 1: Fig. S1. The root removal effect on microbial biomass by trenching and girdling methods. The numbers in the right of figure represents the number of case studies. **Fig.S2.** Effects of ALR and RE on dissolved organic carbon. The numbers in the right of figure represents the number of case studies. ALR, above-ground litter removal; RE, root exclusion. **Table S1.** Correlation coefficients of the effect size of sol microbial biomass and F/B ratio to above-ground litter removal (ALR) and root exclusion (RE) with climatic variables and soil properties

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Authors' contributions

YJ designed the study, data preparation, analysis, and wrote the paper. QW provided the paper editing. PT and WL participated in the data preparation and processing. ZS and HY provided suggestion to improve the paper quality. All the authors read and approved the final manuscript.

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Availability of data and materials
The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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