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Warming promotes accumulation of microbial- and plant-derived carbon in terrestrial ecosystems

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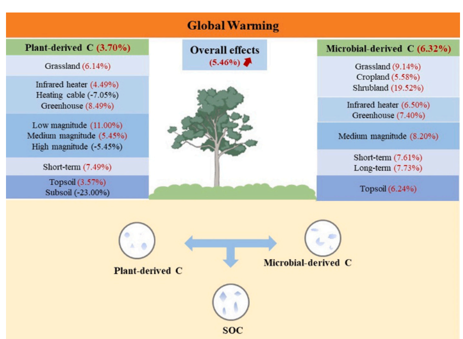
HIGHLIGHTS

- A meta-analysis on 142 articles was used to study the effect of experimental warming on organic carbon.
- Warming promotes the accumulation of microbial- and plant-derived carbon.
- Warming effects on different carbon sources vary with warming conditions and environment.

GRAPHICAL ABSTRACT

Schematic representation depicting of the effects of experimental warming on microbial-derived and plant-derived carbon. Red numbers indicate significantly positive effects (increase), and black numbers indicate significantly negative effects (decrease). Some drawing elements from BioRender (https://biorender.com/).



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ABSTRACT

The impact of global warming on soil carbon pools has been extensively investigated, however, there is still a lack of understanding regarding the specific response of microbial- and plant-derived carbon to warming. To address this knowledge gap, we conducted a comprehensive meta-analysis of 142 studies and evaluated 986 observations comparisons of different carbon source responses to warming. Our results revealed several key insights. Firstly, climate warming resulted in an average increase of 5.46 % in the terrestrial soil carbon pool. Specifically, microbial-derived carbon showed an average increase of 6.32 %, while plant-derived carbon

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Meta-analysis
Terrestrial ecosystems

exhibited an average increase of 3.70 %. Secondly, while warming duration and magnitude do not significantly affect the response of microbial-derived carbon to warming, they did impact the response of plant-derived carbon. Lastly, we observed that the response of different carbon sources to warming was affected by the specific environmental backgrounds:ecosystem and climatic zone types affect the response of warming to microbial-derived carbon, while differences in climatic region affect response of warming to plant-derived carbon. The variations in the response of different soil carbon sources to warming can be attributed to the nature of the carbon source themselves, as well as the complex transformations that occur between them through microbial metabolic processes and their interactions with soil mineral particles. We suggest that interactions at the soil-plant-microbe interface should be considered more carefully, and the response of ecosystems to warming should be observed from the perspective of soil organic carbon sources, so as to better understand the response of terrestrial ecosystems carbon cycle to global warming.

1. Introduction

Soil organic carbon (SOC) is the largest carbon pool in terrestrial ecosystems (>2344 Pg), exceeding the sum of atmosphere and plant carbon, and plays a vital role in regulating climate (Davidson et al., 2000; Jobbágy and Jackson, 2000; Köchy et al., 2015; Prietzel et al., 2016; Stockmann et al., 2013; Zhao et al., 2022b). It is worth nothing that soil organic carbon comes mainly form plant and microbial sources (Rocci et al., 2021; Whalen et al., 2022). Specifically, plant-derived carbon includes plant component carbon such as lignin, aboveground litter, root litter and exudates, and microbial-derived carbon includes microbial biomass carbon, microbial necromass and residues, as well as various chemical substances secreted by microorganisms (Angst et al., 2021; Liang et al., 2019; Liang and Balser, 2011). Microorganisms fix external inputs of carbon into soil organic carbon through decomposition and transformation while microorganisms obtain carbon and energy through metabolism (Liang et al., 2017; Schmidt et al., 2011); meanwhile, organic carbon interacts with soil minerals to promote the accumulation of SOC (Cotrufo et al., 2015; Sokol et al., 2018). Therefore, plant inputs and interactions with microorganisms play an important role in the formation and accumulation of soil organic carbon (Cotrufo et al., 2022; Sokol et al., 2022).

Global average surface temperature is rising globally (IPCC, 2021). Global warming affects above and belowground plant growth (Belay-Tedla et al., 2009; Sun et al., 2022), alters microbial decomposition dynamics and community structure (Fanin et al., 2022; Romero-Olivares et al., 2017), and influences the ability and capacity of belowground ecosystems to fix carbon, which in turn affects biogeochemical cycling processes in terrestrial ecosystems (Lu et al., 2013; Sun et al., 2022; Zhou et al., 2011). However, the response of SOC to global warming is still unclear, with more studies finding a decrease in SOC with increasing temperature (Cheng et al., 2017; Lu et al., 2013; Nottingham et al., 2019; Zeng et al., 2022), while others report the exact opposite result (Day et al., 2008), and others also finding that warming does not affect SOC (Bokhorst et al., 2010). This may be related to the fact that different sources of soil carbon respond differently to climate warming. It was found that plant responses to warming may lead to changes in plant carbon inputs to the soil, resulting in the accumulation of soil organic carbon (Day et al., 2008). A meta-analysis found that global warming increased plant leaf and aboveground carbon concentrations in terrestrial ecosystems (Sun et al., 2022), while a study found that warming promoted below-ground biomass growth in alpine meadow, leading to greater allocation of plant carbon of the subsurface (Zhu et al., 2021). However, it is also possible that more litter entering the soil may have priming effect, leading to a decrease in soil organic carbon content (Keiluweit et al., 2015; Luo et al., 2020). Also warming may directly stimulate lignin decomposition in alpine meadow soil, affecting the dynamics of the soil carbon pool (Feng et al., 2008). Warming affected microbial carbon use efficiency and microbial biomass (Allison et al., 2010; Li et al., 2019), altered soil enzyme activities (Chen et al., 2018; Suseela et al., 2014), and affected microbial abundance and community structure (Cheng et al., 2017; Wang et al., 2021c). Also, changes in substrate quantity and quality due to warming-induced litter inputs affect microbial carbon use efficiency, and complex interactions and constraints in the soil influence the accumulation and transformation of microbial-sourced carbon in the soil (Domeignoz-Horta et al., 2023; Hagerty et al., 2014; Melillo et al., 2017). The methodological variability among individual studies and the diversity of ecosystems resulted in a wide range of results on the response of different sources of carbon to global warming.

A number of methodological factors can influence the variable results of experimental warming on plant- or microbial-derived carbon. For example, the experimental duration and magnitude of warming is highly variable in experiments measuring carbon responses (Crowther et al., 2016; Lu et al., 2013), and this could influence the variation in the observed response. Short-term warming may promote the production of enzymes that lead to soil carbon loss (Chen et al., 2020a; Nottingham et al., 2019; Xue et al., 2016), while long-term warming may allow for adaptive change in microbes and plants that can mitigate soil carbon loss (Robinson et al., 2022). Furthermore, changes in soil organic carbon may vary with the magnitude of warming (Ma et al., 2017; Sun et al., 2022). Finally, experimental warming is implemented using a range of experimental methods, including the use of open-top chambers, infrared heaters or buried cables, which may influence the response of different sources of soil carbon sources (Chen et al., 2022; Duan et al., 2022).

The response of different carbon sources to warming may vary with the background conditions in which the experiment took place. Firstly, the content of carbon of microbial- and plant-derived may naturally vary in different environmental backgrounds (Whalen et al., 2022). Previous studies have shown that the average value of microbial-derived carbon in different ecosystems ranges from 33 %–63 %, with the lowest microbial-derived carbon in forest soils and the highest in grasslands (Liang et al., 2019; Wang et al., 2021a). Consequently, the response of different source carbons to warming experiments conducted in different environmental backgrounds can differ significantly. Warming experiments in alpine meadows revealed that warming promoted the accumulation of soil microbial sources of carbon and that bacterial derived of carbon increased more than fungal derived (Zhao et al., 2022a). Whereas warming had no effect on soil microbial community composition or biomass in temperate mountain forests (Schindlbacher et al., 2011), it greatly increased vegetation productivity in the northern hemisphere (Zhang et al., 2022b). Moreover, warming promoted the accumulation of lignin and microbial residues in temperate agro-ecosystem (Ma et al., 2022). Warming aggravates the soil water shortage in arid areas, inhibits the growth and activity of soil microorganisms (Malik et al., 2020), but promotes plant root growth (Li et al., 2021). In tropical forests, warming will lead to the increase of microbial carbon use efficiency, enhance the activity of hydrolase, and lead to soil carbon loss (Nottingham et al., 2019). The difference of environmental background leads to the difference of content and stability of soil microbial and plant-derived carbon pools, which urges us to comprehensively evaluate and analyze the response of different carbon sources to global warming.

In this study, we systematically searched the literatures and extracted data from 142 studies that applied experimental warming and measured response variables related to soil carbon and its source (microbial-, plant-derived). Overall, the objective of this study was to investigate the effects of experimental warming on soil microbial- and plant-derived carbon content (increase, decrease, unchanged) under different climatic backgrounds or different warming treatments.

2. Materials and methods

2.1. Data compilation

We began our literature collection efforts in April 2022 by using the Web of Science to search the literature from 1900 through September 2022 for global studies of the effects of experimental warming on plant-derived carbon and microbial-derived carbon. We specially used the

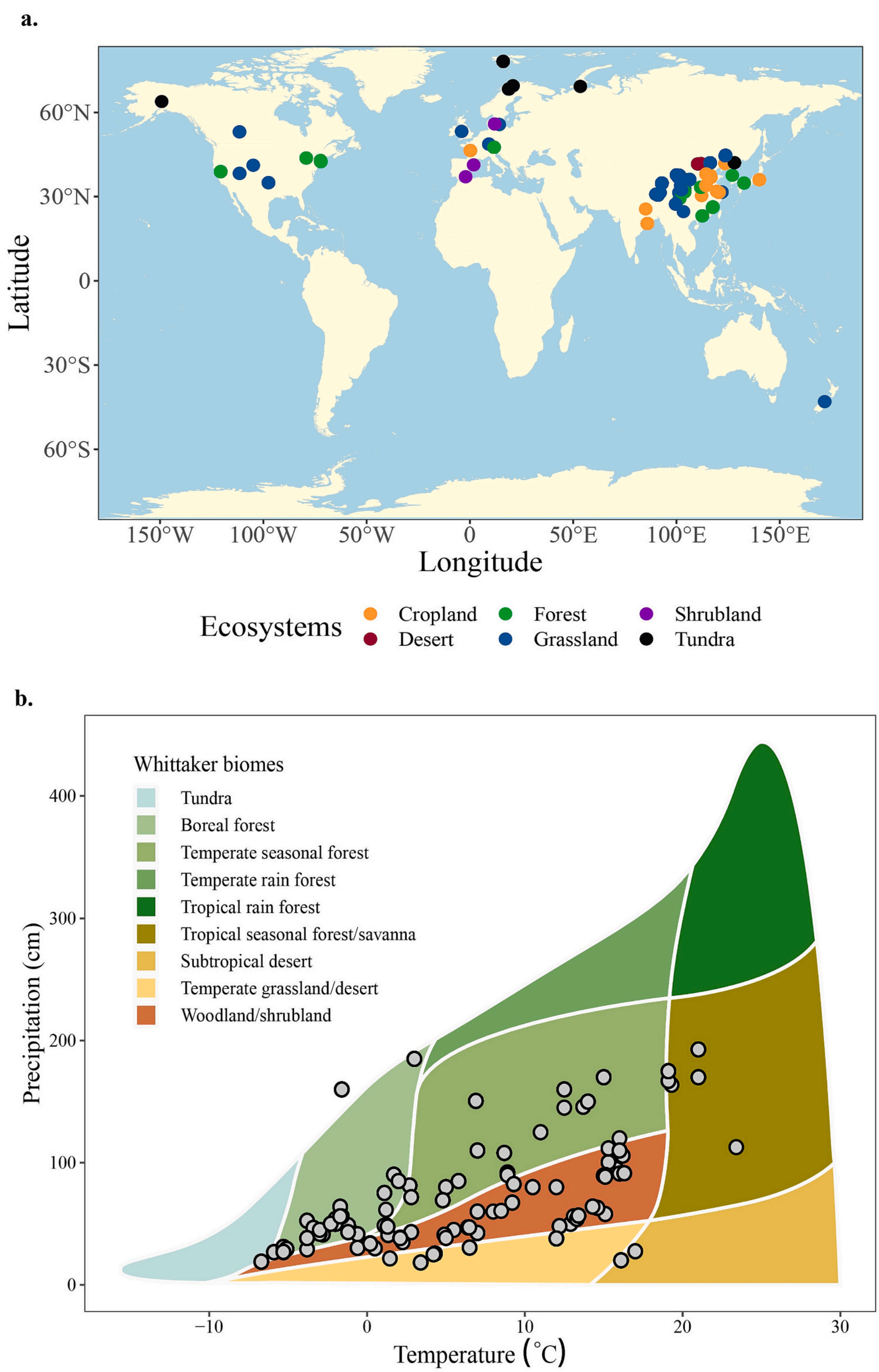

Fig. 1. a. Global distribution map of the 142 warming experiments analyzed here. b. Distribution of studies along temperature and precipitation gradients, overlaid with the different biome types as defined by Whittaker (1975).

following search terms with Boolean combinations: “microbial-derived SOC”, “microbial necromass”, “microbial biomass”, “microbial residue”, “microbial carbon”, “microbial-derived carbon”, “plant-derived SOC”, “plant-derived carbon”, “rhizosphere secretions”, “rhizosphere effect products”, “warm*”, “elevated temperature”, “temperature ris*”. In total, we identified 5890 papers from this search, which we then further screened by reading the title, and when appropriate, the abstracts and methods to determine whether the study fit our screening criteria. Our screening criteria were as follows: (1) the study needed to be experimental (not review) and in the field (not laboratory chambers or indoor greenhouse). We also excluded transplant experiments, which may change local environmental and microbial conditions; (2) experimental site, vegetation, and soil types were similar in control and treatment groups; (3) at least one index of plant-derived (i.e. fine root and aboveground biomass, litter C, cellulose, lignin, plant-derived compounds and root secretions) or microbial-derived carbon (i.e. microbial biomass carbon (MBC), amino sugars (GluN, MurN, GalN), microbial residues (including both fungal and bacterial residues), and phospholipid-derived fatty acid (PLFA, including both fungal and bacterial PLFA)) was reported; (4) means, standard deviation (SD, or standard error, SE), and sample sizes were directly provided or could be calculated based on the information provided. Our study focused on soil carbon from different sources, and we mainly recorded data related to soil carbon from different sources, and for soil-related variables (reported in the text), including pH, moisture, TN, C/N, and so on. Due to the focus of the study, we paid more attention to the results reported in 142 retrieved papers and synthesized and analyzed the data reported in the literature (Fig. 1). We extracted data from figures using WebPlotDigitizer4.2 software (Burda et al., 2017). All SE measurements were converted into SD. In all, we included data from 142 articles; we list all sources in the appendix (Supplementary Material 1).

To evaluate how different experimental warming methods influenced results, we categorized experiments based on duration, magnitude, and treatment type (Lu et al., 2013; Yan et al., 2019). For warming duration, we categorized studies as short-term (≤3 years), mid-term (3–6 years), or long-term (>6 years). For warming magnitude, we divided experiments into those that had a low magnitude of warming (≤1 °C), a medium magnitude of warming (1–3 °C), or a high magnitude of warming (>3 °C). We also categorized warming experiments into three types: ‘greenhouse’ (including open top chambers, closed top chambers and snow fences), ‘infrared heaters’ (including infrared heaters or lamps suspended above the ground), and ‘heating cables’ (including underground heating cables or pipes) (Table S1).

We also extracted geographical and environmental data from each study, including latitude and longitude, altitude, mean annual temperature (MAT), mean annual precipitation (MAP), ecosystem types, climate zones and regions. We classified study sites into dry (<400 mm) and humid (≥400 mm) categories based on their ambient precipitation levels, and into tropical (0–25°), temperate (25–50°), and boreal (> 50°) based on latitudes (Wang et al., 2022) (Table S1).

2.2. Statistical analyses

We calculated the effect size of the warming treatment on each response variable using the natural logarithm of the response ratio (lnRR) (Hedges et al., 1999) as:

$$\text{lnRR} = ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = ln(\overline{X}_t) - ln(\overline{X}_c) \tag{1}$$

where $\overline{X_t}$ and $\overline{X_c}$ were the average values of the variable of interest in the warming and control treatments, respectively. A positive or negative lnRR value indicates an increase or decrease of a particular carbon source in the warming treatment. Where the SE was reported in the study, we converted it to SD, using the following Eq. (2):

$$SD = \sqrt{n}*SE \tag{2}$$

For each study, we calculated the variance as:

$$\text{v} = \frac{\text{SD}_t^2}{\text{n}_t\text{X}_t^2} + \frac{\text{SD}_c^2}{\text{n}_c\text{X}_c^2} \tag{3}$$

where SD_t^2 and SD_c^2 are the standard deviations and n_t and n_c are the sample sizes in the warming and control treatments, respectively.

We considered the overall effect of the warming treatment on a given response variable to be significant if the 95 % confidence interval (CI) did not overlap with zero. Finally, we calculated the percentage change of a given variable as:

$$\text{Percentage change}(\%) = \left(e^{\text{lnRR}} - 1\right) \tag{4}$$

We used the “rma” function in the R package “metafor” Viechtbauer (2010) to calculate the weighted mean response ration and 95 % confidence intervals (CIs) to quantify the effect size of warming on microbial-derived and plant-derived carbon (Table S2). And we conducted subgroup analysis to measure categorical explanatory moderators (such as warming setting, magnitude, duration, depth, ecosystem, climatic region and zone) to measure their effects on different derived carbon (Tables S3,4). We used “lm” model to predict the relationship between warming and the variables (plot the correlation figure after taking the absolute value of the latitude). The relative importance of predictors on the response of different derived carbons to warming was also examined separately using the “glmulti” package to compare the effects of environmental factors and warming conditions on different source carbons (Chen et al., 2020b). Structural equation model was used to determine the direct and indirect effects on environmental factors and warming conditions on different source carbons conducted by “piecewiseSEM” package, and we used the Fisher’s C test (0 ≤ Fisher’s C/df ≤ 2 and $0.05 < P \leq 1$) to judge the goodness of the model results (Lefcheck and Freckleton, 2015).

We used the *maps* package to plot the distribution of sampling points (Fig. 1a) and the *plotbiomes* package to plot the Whittaker biomes (Fig. 1b). We used the *stat_cor* function in the *ggpubr* package to present the correlation coefficients (Pearson correlation) and *p*-values in the figures. To evaluate whether there was publication bias in our meta-analysis, we performed Egger regressions with funnel plots and normality tests with Q-Q plots for sensitivity analysis (Figs. S2–5). Relevant data and descriptions can be found in Supplementary Material 2.

3. Results

3.1. Geographical distribution of studies

Of the 142 relevant studies that we included in our meta-analysis, the majority were distributed across eastern Asia (mainly China), Europe, and North America (Fig. 1a). Despite this geographical bias, study sites were relatively well distributed across the major bioclimatic gradients of temperature and precipitation, covering most biome types globally (Fig. 1b). Mean annual temperature ranges from −6.7 to 23.4 °C and annual precipitation ranges from 183 to 1927 mm (Fig. 1b). Ecosystems include cropland, forest, grassland, desert, shrubland and tundra (Fig. 1a).

3.2. Effects of warming on different carbon sources

We found that warming had significant positive effects on microbial- and plant-derived carbon (Fig. 2). We found that warming effects on carbon from different sources depended on soil depth, warming duration, magnitude and warming methodology (Fig. 2). For example, warming effects on microbial-derived carbon were generally positive,

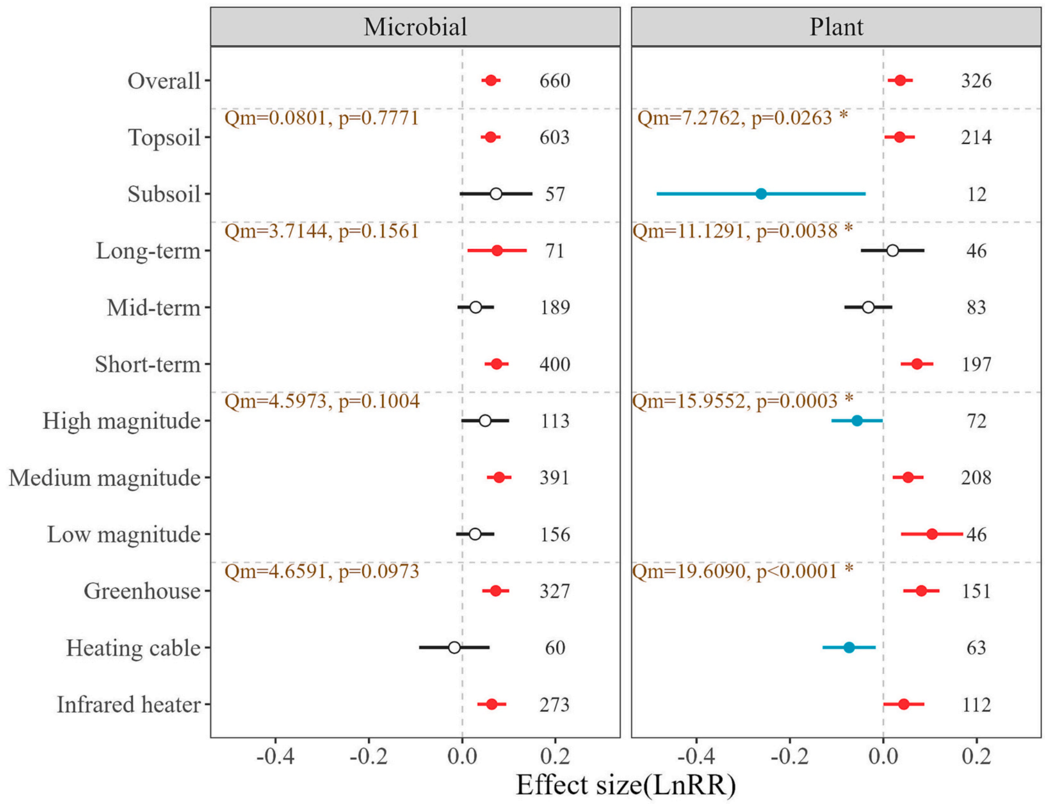

Fig. 2. Response of different derived carbon to warming conditions. Setting: (greenhouse, heating cable and infrared heater), magnitude (low magnitude [≤1 °C], medium magnitude [1– 3 °C], high magnitude [>3 °C]), duration (short-term [≤3 yr], mid-term [3– 6 yr], long-term [>6 yr]), depth (topsoil [0–30 cm], subsoil [>30 cm]). Solid red, blue and hollow black dots indicate significant positive, negative and non-significant effects, respectively. Numbers indicate the number of studies for each response.

but only significant for studies in the topsoil, over the short- and long-term, with medium magnitude, and conducted with greenhouse or infrared heaters. For plant-derived carbon, warming had positive effects in the topsoil, but negative effects in deeper soil (Fig. 2). Plant-derived carbon increased in short-term, but not in mid- or long-term studies. Plant-derived carbon increased when warming was low and medium in magnitude, but decreased in high magnitude warming treatments. In addition, plant-derived carbon increased with warming in greenhouse and infrared experiments, but decreased with warming in heating cable experiments. Plant-derived carbon decreases with increasing duration and magnitude of warming (Fig. 3), which is consistent with the results of subgroup analysis.

3.3. *Effects of warming on different source carbon in different environmental backgrounds*

Fig. 4 presents the results for the effects of warming on different derived carbon sources among regions and biomes. We found that microbial-derived carbon was not influenced by warming in cold regions, increased with warming in temperate regions, and decreased with warming in tropical regions. Likewise, we found that microbial-derived carbon increased with warming in both humid and arid environments,

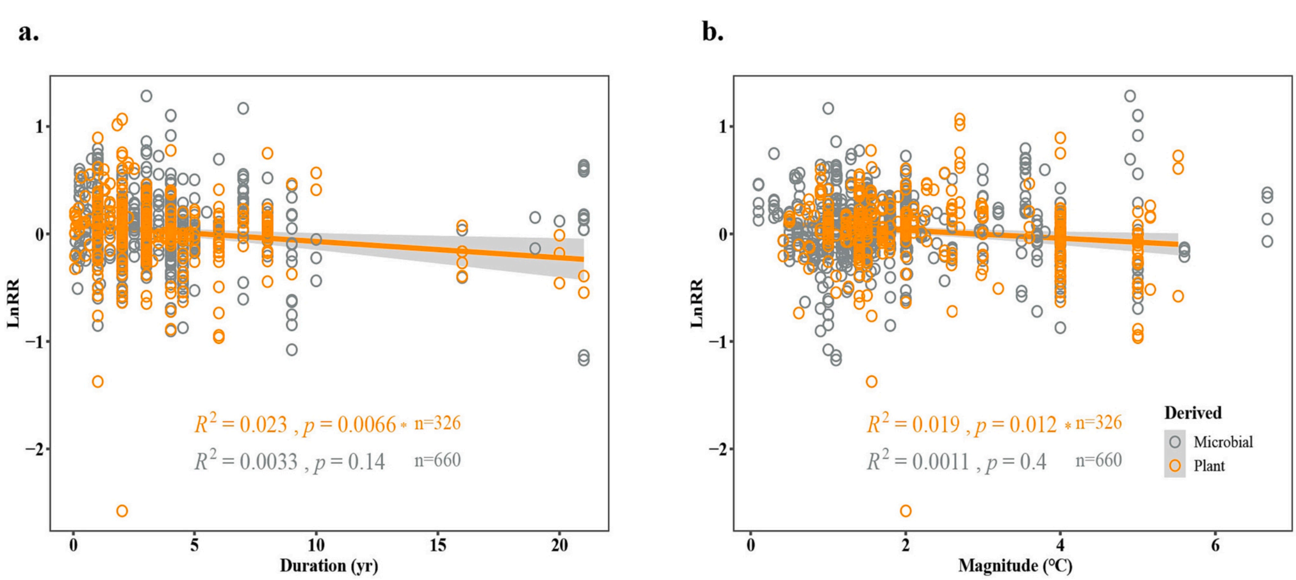

Fig. 3. Response of different derived carbon to warming in relation to the warming factors. (a) Duration (yr) and (b) magnitude (°C). Stars indicate significant effects

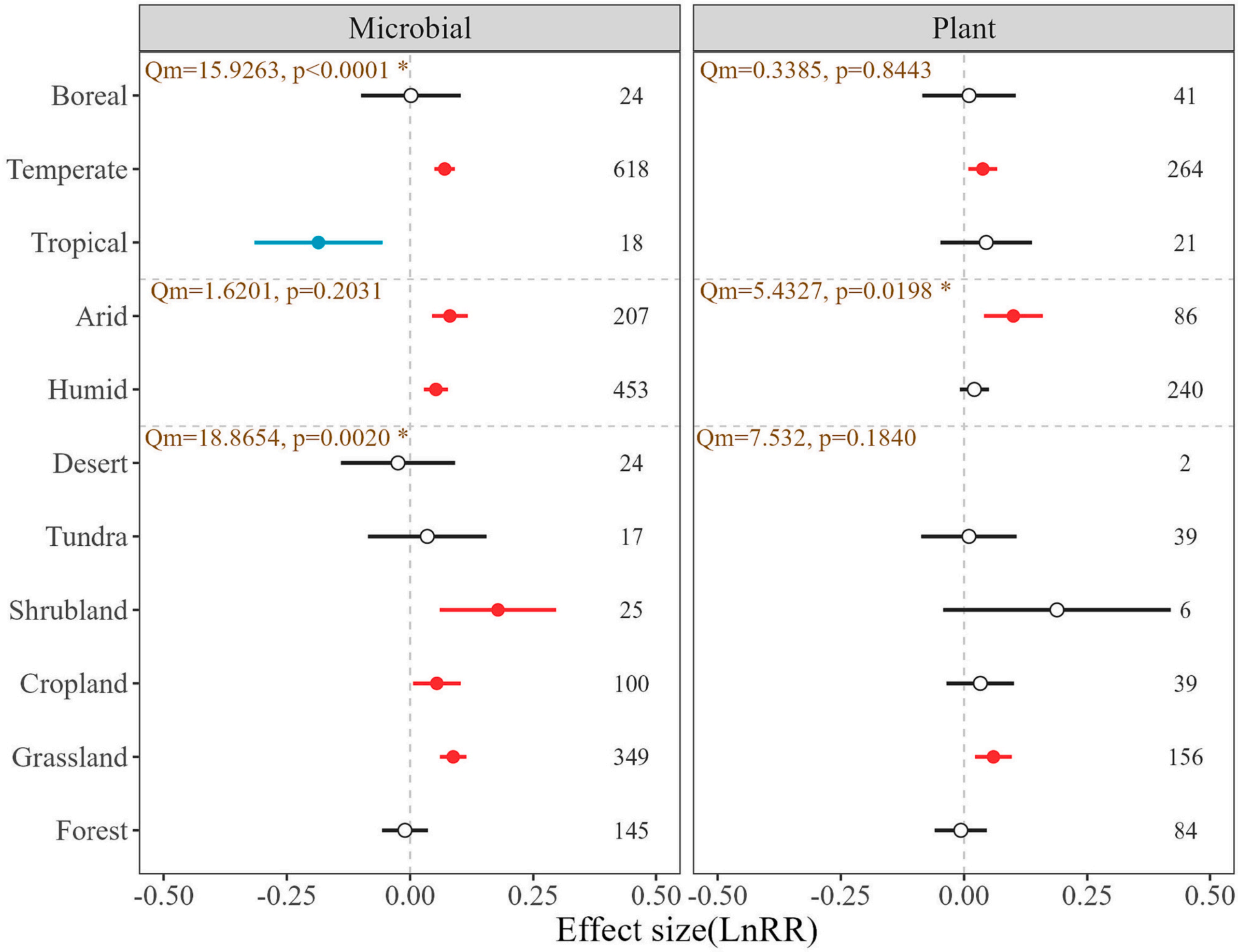

Fig. 4. Response of different derived carbon to warming in the different environmental backgrounds. Ecosystem types (forest, grassland, cropland, shrubland, tundra and desert), climatic regions (arid, humid) and climatic zones (boreal, temperate, tropical). Solid red, blue and hollow black dots indicate significant positive, negative and non-significant effects, respectively. Numbers indicate the number of studies for each response. The result of plant-derived carbon in deserts is not shown because of its extreme negative value (−0.6026, 95 % CI -1.6015 to 0.3964).

and only in shrublands, croplands and grasslands (not deserts, tundras or forests). Plant-derived carbon only increased with warming in temperate, arid and grassland experiments.

For geographic factors (Fig. 5, S1), we found a positive correlation between the magnitude of warming effects on different derived carbon and altitude, i.e., the higher the altitude, the lower the temperature, and the microbial- and plant-derived carbon accumulates under warming. For climatic factors (Fig. 6), warming leads to a decrease in microbial- and plant-derived carbon with increasing annual precipitation, while warming experiments at higher mean annual temperatures lead to a decrease in microbial-derived carbon, for example, in the tropics, where microbial-derived carbon responds negatively to warming (Fig. 4).

We found that for microbial-derived carbon, climate zone, mean annual temperature, ecosystem type, and altitude had a large effect on microbial-derived carbon under warming conditions, which is consistent with the results of previous subgroup and correlation analysis, and for plant-derived carbon, altitude, ecosystem type, soil depth, warming setting and duration, and climate region had a large effect on plant-derived carbon under warming conditions, which is consistent with the results of subgroup and correlation analysis (Fig. 7).

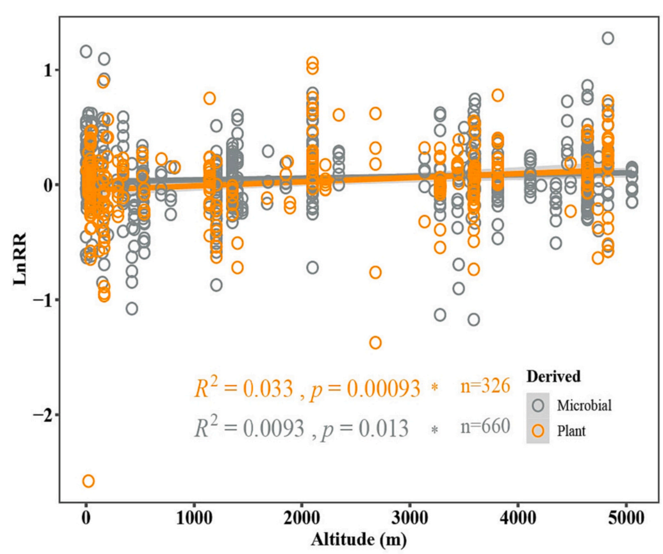

Fig. 5. Response of different derived carbon to warming in relation to the altitude (m). Stars indicate significant effects.

4. Discussion

Our results suggest that the both plant-derived and microbial-

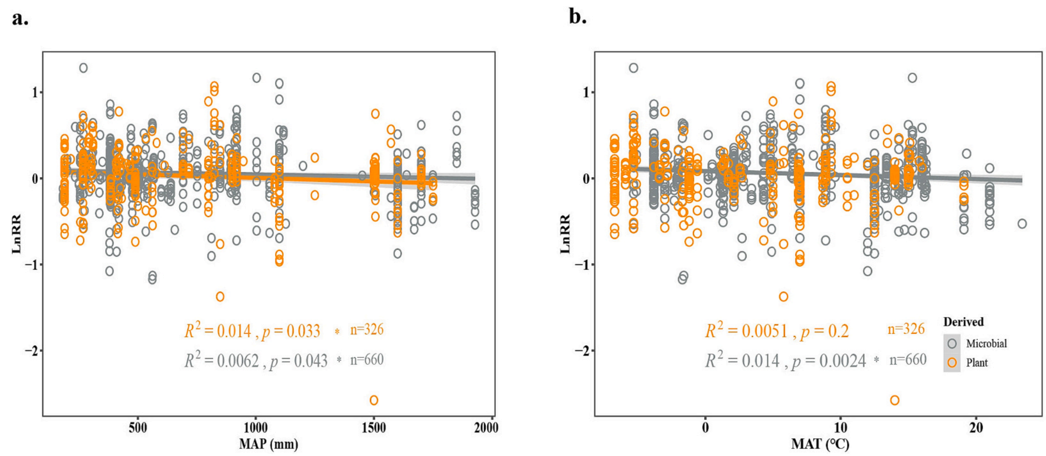

Fig. 6. Response of different derived carbon to warming in relation to the climatic factors. (a) MAP (mm) and (b) MAT (°C). Stars indicate significant effects.

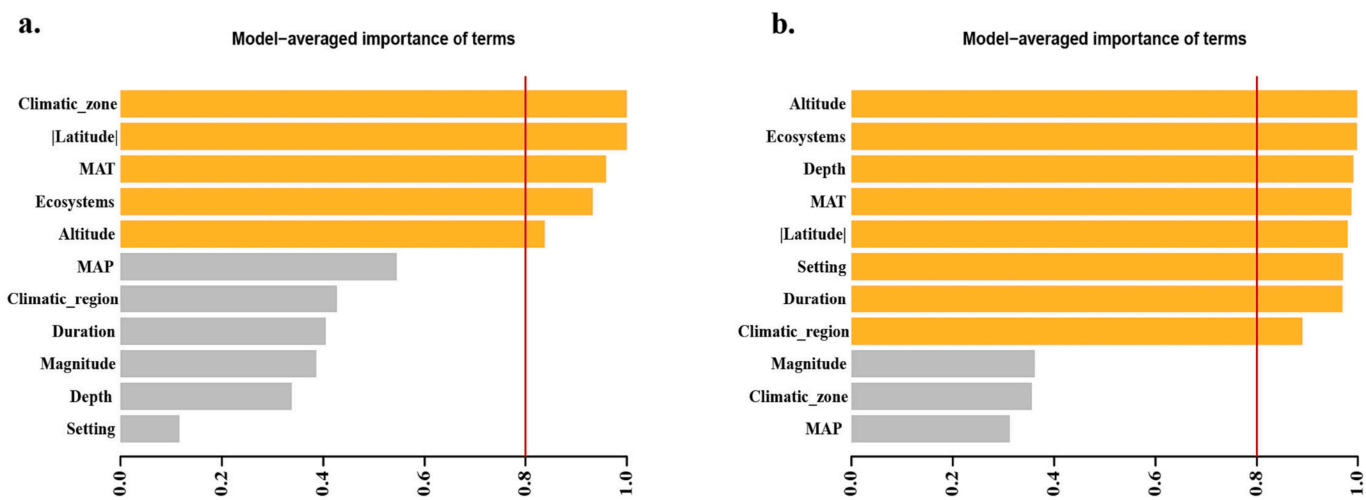

Fig. 7. Model importance of the predictors of the warming effects on (a) microbial-derived and (b) plant-derived carbon. The importance is based on the sum of Akaike weights derived from model selection. Cutoff is set at 0.8 (red solid line) to differentiate among the most important moderators (as showed by orange column).

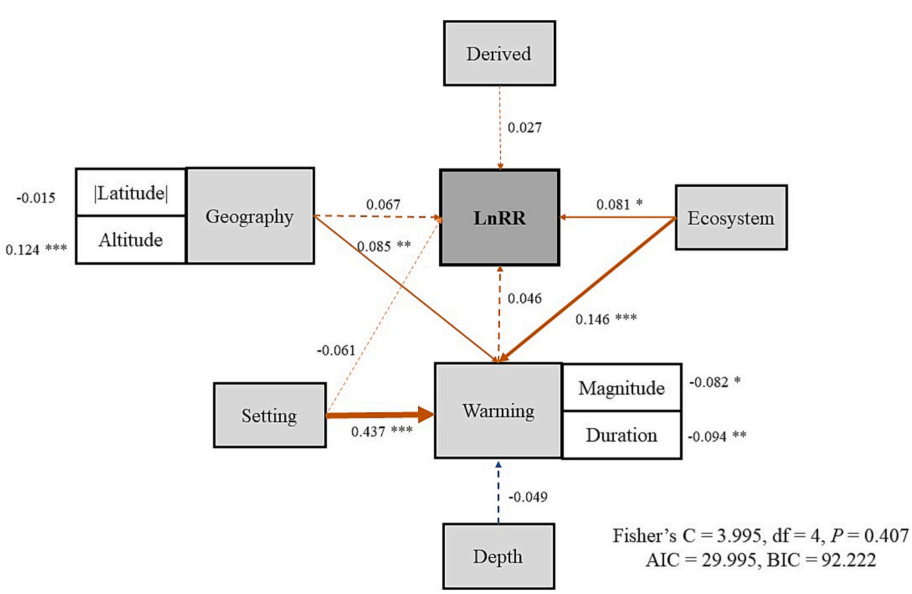

Fig. 8. Pathways of environmental and anthropogenic factors impacting the influence of warming on different derived carbon. PiecewiseSEM accounting for the direct and indirect effects of warming, geography, different derived, ecosystem type, depth and setting on the response of the warming on different derived carbon at the global scale. The geographical and warming were divided into composite variable. Numbers adjacent to measured variables are their coefficients with composite variables. Numbers adjacent to arrows are path coefficients. The solid and dash line represents the direct and indirect relationship, the red and blue line represents positive and negative relationship, respectively. The thickness of the arrow represents the strength of the relationship. Significance levels of each predictor are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

derived carbon increased significantly under experimental warming compared to control and that different sources may affect the carbon transformation during warming and influence the carbon cycle processes in different environmental and warming contexts. The response of soil carbon to warming is less influenced by carbon source, but can be directly influenced by ecosystem type, and warming setting can also indirectly influence the response of carbon to warming by affecting the warming effect, as well as ecosystem type (Fig. 8). Through the funnel plots we found that the results of the model for the warming effect on microbial- and plant-derived carbon were less influenced by publication bias and the Rosenthal fail safe number were greater than the critical values, and the conclusions were reliable (Fig. S2). However, as might be expected, we found considerable variation in the effect of experimental warming, depending on both the methodological details of the study (e.g., intensity and duration of the experiment) and the environmental background in which the study took place (e.g., temperature, precipitation). We suggest that future climate change studies should consider the input of plant- and microbial-derived carbon and their transformation relationship to better understand the dynamics of soil organic matter in the context of global climate change (Ma et al., 2017; Zhang et al., 2022a). In addition, as with most putative global-scale studies, the studies included in our meta-analysis were geographically biased (mainly located in Asia, South America and Europe), indicating the need for more concerted efforts in other parts of the world to evaluate the effects of global warming on soil organic carbon.

4.1. Warming increases microbial-derived carbon

According to the study, microbial biomass carbon, microbial structural components are categorized as microbial-derived carbon, such as cellular structural substances such as amino sugar (Angst et al., 2021; Whalen et al., 2022). We found that microbial-derived carbon was positively influenced by experimental warming, regardless of methodological and environmental background (Figs. 2,4). This may be related to the fact that microbes increase their growth and adaptation in warmer environments (Rijkers et al., 2022; Zhou et al., 2011). Climate warming increased microbial biomass carbon and abundance is consistent with previous studies (Chen et al., 2015; Ding et al., 2019; Ma et al., 2017; Sun et al., 2022). One reason for this could be that as soil temperature increases, microbial turnover increases, while the growth efficiency remains unchanged, leading to an increase in soil carbon pools (Hagerty et al., 2014; Hartley et al., 2021). Furthermore, at higher temperatures, microbes may invest more in metabolism than catabolism, leading to higher microbial biomass production and thus higher levels of microbial necromass accumulation (Table S2, MBC: LnRR = 0.0549, 0.0245–0.0852) (Angst et al., 2018). Indeed, the ‘microbial carbon pump’ theory emphasizes the positive role of microorganisms in soil organic matter storage (Cai et al., 2022; Wang et al., 2021b; Zhu et al., 2020). In addition, a large proportion of soil organic carbon comes from the microbes themselves and their residues after death (Wang et al., 2020; Whalen et al., 2022), which is one of the main sources of soil organic carbon (Liang et al., 2020). Compounds of microbial-derived play an important role in soil organic carbon stocks in both topsoil and subsoil (Angst et al., 2018), and are the direct source of 30–80 % of SOC in terrestrial ecosystems (Janzen, 2015; Whalen et al., 2022).

The microbial response to experimental warming is modulated by the environmental background of the experiments (Fig. 4) (Janzen, 2015). Specifically, we found that microbial-derived carbon increased in grassland, shrubland, and cropland as the experimental warming, whereas there was no significant change in microbial-derived carbon in forests (Fig. 4). This is similar to previous findings where warming significantly increase MBC in agricultural fields (Li et al., 2018), while grassland warming experiments showed increased microbial abundance and diversity (Sheik et al., 2011). Warming experiments of shrubland resulted in an increase in microbial abundance (Song et al., 2021), and with more litter entering the soil potentially becoming microbial food and contributing to the accumulation of MBC (DeMarco et al., 2014), while shrubification reduced the microbial decomposition efficiency and mineralization of soil organic carbon (Jia et al., 2022).

Simultaneously, the response of microbial-derived carbon to climate warming varied across climate zones (Fig. 4). Warming in the tropics has been shown to reduce microbial diversity and enhance respiration, releasing more CO_2 and causing microbial-derived carbon to decline significantly in the tropics (Nottingham et al., 2022), whereas in temperate soils warming promotes the accumulation of microbial residues (Fig. 4) (Ma et al., 2022). This may be related to the fact that microorganisms in tropical ecosystems are more sensitive to changes in litter inputs and higher MAT (Fig. 6, 7a) (Xu et al., 2013), which stimulate soil carbon decomposition. In conclusion, tropical warming leads to enhanced microbial respiration and a decline in diversity, resulting in increased soil carbon mineralization and ultimately a significant reduction in microbial-derived carbon content (He et al., 2019; Nottingham et al., 2022).

Our results also found that dry and wet environments did not significantly affect microbial-derived carbon at increasing temperature (Fig. 4, $p > 0.05$), but higher MAP may be detrimental to the accumulation of microbial-derived carbon (Fig. 6). However, compared to other factors, the effect of MAP on microbial-derived carbon may not be a major factor (Fig. 7), which may be related to the weaker impact of MAP on microbial and enzyme activity (Sinsabaugh et al., 2008).

4.2. Warming increases plant-derived carbon

Both the duration and magnitude of warming and soil depth were important factors influencing the response of plant-derived carbon to warming (Fig. 7). Greenhouse and infrared heater increase air/surface and soil temperatures, while the heating cable mainly increases soil temperature (Yan et al., 2022). Greenhouse and infrared heater increased the soil temperature by 1.65 and 1.95 °C, while the heating cable increased the soil temperature by 4.12 °C (Table S5). This result is consistent with the effect of warming magnitude (Fig. 2), which indicates that the higher the warming, the lower the plant-derived carbon content, but a certain range of warming promotes the accumulation of plant-derived carbon in the soil (Fig. 2). Meanwhile, warming increased the topsoil temperature by 2.45 °C and the subsoil temperature by 3.16 °C (Table S5), clearly warming the subsoil more and promoting the decomposition of plant-derived carbon in the subsoil (Fig. 2). Moreover, plant-derived carbon in the subsoil is more sensitive to temperature, and warming accelerate microbial decomposition, such as promotes lignin decomposition in the grassland subsoil (Jia et al., 2019; Ofiti et al., 2021). Furthermore, as warmer led to an increase in plant belowground biomass (Table S2, belowground biomass: LnRR = 0.0893, 0.0170–0.1617), the priming effect maybe result in greater carbon loss from plant-derived in the subsoil than their carbon input (John et al., 2002; Keiluweit et al., 2015). Therefore, if global warming continues to maintain higher growth tendency, it may negatively affect the carbon cycle in terrestrial ecosystems, leading to more soil carbon loss (Fu et al., 2015).

In terrestrial ecosystems, there was no significant difference in the response of plant-derived carbon to warming (Fig. 4). Experimental warming stimulated the growth of above- and belowground plants (Table S2, aboveground biomass: LnRR = 0.0759, 0.0259–0.1259; belowground biomass: LnRR = 0.0893, 0.0170–0.1617), leading to an increase in plant carbon pools (Day et al., 2008; Fu et al., 2014; Gao and Yan, 2019). It may be related to the increased activity of photosynthesis-related enzymes in plants due to warming, as well as the ability of plants to allocate more photosynthetically active products to their roots for nutrient acquisition (Chandregowda et al., 2023; Zhu et al., 2022). And the difference in climatic zones had no significant effect on plant-derived carbon (Fig. 4). However, soil moisture may affect the content of plant-derived carbon in the soil. The higher MAP, the lower the plant-derived carbon in the soil due to warming (Fig. 6a). In arid region, warming can promote the growth and downward distribution of plant roots (Engelhardt et al., 2021; Li et al., 2021), but measuring aboveground biomass may exaggerate the response of plant-derived carbon to warming, and there is a strong photodegradation process in arid zones, which results in plant litter material going directly into the atmosphere as CO_2 without participating in the belowground carbon cycling process (Asao et al., 2018; Huang and Li, 2017; Huang et al., 2017). Hence, subsequent studies need to do a better job of defining more detailed scales to determine the effects of climate warming on plant-derived carbon in different environmental backgrounds.

4.3. Implications between microbial-derived and plant-derived carbon to warming

Ecosystem type not only affects soil carbon pools by influencing the warming effect of artificial experiments but also can directly affect the stability of soil carbon pools (Fig. 8). Differences in ecosystem type leads to differences in the inputs of different carbon sources, and the response of community structure and species diversity to warming in different ecosystems may lead to differences in the dynamics of soil carbon pools (Bellè et al., 2022; Sardans et al., 2012; Trivedi et al., 2022).

Meanwhile, the conversion of microbial-derived and plant-derived carbon into soil organic carbon differs and there are differences between the responses to warming (Fig. 2). Microbial-derived carbon was mainly influenced by the ecosystem type and plant-derived carbon was mainly influenced by the warming conditions (Figs. 2, 4). The differences in influencing factors may be related to the conversion of carbon from different sources, and although warming increases both types of carbon and promotes carbon accumulation, we cannot be sure of the final form of carbon sequestered in the soil. And, plant-derived carbon and microbial-derived carbon eventually become stable sources of soil organic carbon through many complex decomposition and transformation processes (Barré et al., 2018; Kallenbach et al., 2016; Whalen et al., 2022). While the stability of soil organic carbon is related to a variety of factors, the accumulation and release of soil carbon pools are related to the carbon balance of the global ecosystem (Cotrufo et al., 2015; Walker et al., 2022). Different carbon sources ultimately form different proportions of soil organic carbon, with plant-derived carbon tending to form particulate organic carbon and microbial-derived carbon tending to form mineral-associated organic carbon, and different forms are associated with the stability of soil carbon pools (Benbi et al., 2014; Klink et al., 2022; Rocci et al., 2021; Sokol et al., 2018). In addition, the final proportion of soil organic carbon from different sources may differ due to the different processes of conversion of plant- and microbial-derived carbon to soil organic carbon (Lugato et al., 2021).

5. Conclusions

Combining the results of 142 experimental warming studies into a meta-analysis, we showed that (1) warming had a positive effect on microbial- and plant-derived carbon; (2) the response of microbial-derived carbon to warming was influenced by ecosystem type and climate zone; (3) the response of plant-derived carbon to warming was influenced by warming conditions and climatic region. We suggest that future studies will be needed to more deeply understand the transformation of plant- and microbial-derived carbon, and to explore the feedback regulation process and mechanisms influencing the interplay between soils, plants, and microbes. We also suggest that it may be useful to use different derived carbon sources as a factor to explain the differential responses of terrestrial ecosystems to warming, and to include these differences to better understand carbon turnover processes under global climate change.

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CRediT authorship contribution statement

The paper was coauthored by Huan Han, Congjuan Li, Ran Liu, Jinshi Jian, Madinai Abulimiti, Ping Yuan. Congjuan Li and Huan Han planned the study; Huan Han, Madinai Abulimiti and Ping Yuan collected the data; Huan Han and Madinai Abulimiti performed all data analyses; Huan Han, Congjuan Li wrote the first draft of the manuscript, and all authors contributed to the comments and revisions.

Declaration of competing 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

Data will be made available on request.

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