

Article

Increasing soil microbial necromass carbon under climate change in Chinese terrestrial ecosystems

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Abstract: Soil necromass carbon (C) has significant potential for C sequestration in combination with minerals. Warming and nitrogen (N) deposition affect necromass C; however, these effects vary greatly across different climate conditions, ecosystem types, and soil properties. However, the ways in which regional specificity affects the consequences of climate change on necromass C are still unknown. To address this, we synthesized 197 paired observations from 50 climate change studies to investigate these effects in China. Our results indicate that warming and N addition significantly increase necromass C accumulation by 17.26% and 8.5%, respectively. Warming strongly promotes necromass C sequestration, particularly in croplands, cool and semiarid regions, and areas with high soil organic carbon (SOC) content and loam soils. This study emphasizes the intricate interplay between climate change and necromass carbon (C) across diverse climate scenarios, ecosystem categories, and soil characteristics. It reveals that nitrogen (N) addition enhances necromass C accumulation under all climate conditions, with particularly notable effects in croplands, forests, soils rich in soil organic carbon (SOC), and those with clay or clay-loam textures. These findings offer vital perspectives on how climate change can impact the storage and turnover of necromass C.

Keywords: Microbial necromass carbon; Soil organic carbon; Climate change; Warming; N addition

1. Introduction

The stability and function of terrestrial ecosystems are greatly affected by climate change. Warming and nitrogen deposition are two relatively key influencing factors (Hu et al., 2023a; Luo et al., 2020a; Mou et al., 2021). According to the relevant content of the 6th phase of the coupled model comparison project, the middle and low latitude regions are more vulnerable to climate warming and increased nitrogen deposition, among which the situation in China is particularly fragile (Ferraro et al., 2015; Pohlmann et al., 2019; Simpkins, 2017). Although China's land area accounts for only 6.5% of the world's total land area, its soil organic carbon accounts for 10% to 31% of the world's total (Piao et al., 2022). Due to climate change, China may lose organic carbon faster than other

Academic Editor: Firstname Last-name

Received: date

Revised: date

Accepted: date

Published: date

Citation: To be added by editorial staff during production.

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regions (Luo et al., 2020a). Nitrogen and temperature will have certain impacts on soil microorganisms and the growth of plants. Plants and microorganisms are very crucial for the storage of organic carbon (Mou et al., 2021). More nitrogen deposition and global warming will alter the dynamics of organic carbon. It may cause changes in carbon storage and have an impact on ecosystem functions (Mou et al., 2021; Luo et al., 2020b).

The formation of soil organic matter is more influenced by the anabolic metabolism of microorganisms than by plant-derived substances (Liang and Balser, 2012; Xiao et al., 2023). In 2018, researchers such as Shao discovered that in the soil, microbial necrotic carbon (C) accounts for 10% - 50% of soil organic carbon. When these microbial necrotic carbon (C) combine with soil minerals, It is even less likely to be decomposed. Glucosamine is derived from the cell walls of bacteria, and lactic acid bactericidal acid is derived from the cell walls of fungi. Both are regarded as markers of carbon (C) sources in microbial necrotic blocks (Tian et al., 2021; Zhou et al., 2023).

Concern over the potential effects of climate change on microbial necrotic mass C has grown in recent years (Liang and Balser, 2012; Luo et al., 2020b; Tian et al., 2021). However, it is still unclear what causes carbon production in necrotic mass and how climate change affects it globally. Both nitrogen deposition and global warming increase the microbial turnover of soil organic carbon and plant-derived carbon input, though the dynamics of necromass C remain controversial (Hu et al., 2023a; Hu et al., 2023b; Tian et al., 2022; Mou et al., 2021; Murugan et al., 2014; Anning et al., 2021; Wang et al., 2022; Wang et al., 2023). Warming alters microbial turnover and necromass C accumulation, which speeds up necromass C dynamics (Ma et al., 2022). N deposition increases nutrition and decreases pH, which accelerates necromass C breakdown (Tian et al., 2022). It has been demonstrated that warming and nitrogen addition have beneficial effects on necromass carbon (Ma et al., 2022; Tian et al., 2022), neutral (Zhang et al., 2016; Zhang et al., 2022), and negative (Jing et al., 2019; Liang and Balser, 2015). likely linked to climatic conditions, ecosystem types, and soil properties (Li et al., 2024; Ma et al., 2018a; Zhou et al., 2023). Warming in cool regions causes more necromass carbon to build up than in warm regions (Jing et al., 2019; Ma et al., 2022). Adding nitrogen to clay soils helps carbon accumulate better than in sandy soils (Li et al., 2024; Ma et al., 2018a). This happens because clay holds water and nutrients better than sandy soil (Zhou et al., 2023). Grasslands react more to warming and nitrogen than forests do. Forests have more complex and stable ecosystems (Duan et al., 2023). Croplands face strong human interference. This makes it harder to predict how climate change affects necromass carbon (Duan et al., 2023). Current studies may not fully account for three factors: local climates, ecosystem types, and soil textures. These differences explain why necromass carbon responds differently to climate change. China's temperature patterns will change unevenly between 2030-2052. Average temperatures will rise 1.5°C overall (Shi et al., 2018). Northern areas will warm noticeably. Northeast areas might cool down significantly (Shi et al., 2018). Nitrogen deposition decreases from southeast to northwest. But North, Central, and Northeast China keep getting more nitrogen over time (van Groenigen et al., 2017; Yu et al., 2019). Together, these changes threaten necromass carbon storage.

China became the third-largest emitter in the world between 2009 and 2022, when its emissions increased from 7.71 billion tons to 11.48 billion tons (Xu et al., 2024). The continuous process of urbanization and industrialization emphasizes the potential risks of carbon (C) loss due to possible climate changes (Shi et al., 2014). It is essential to consider the regulatory roles of climate conditions, ecosystem types, and characteristics of the soil in the research area in order to gain a deeper comprehension of the effect on

necromass carbon of warming and nitrogen (N) deposition. In this regard, we gathered 208 paired observations from 50 published studies on warming and N addition in China. We proposed and investigated the following theories: (1) Warming is predicted to boost microbiological activity and decomposition rates, which will hasten the buildup of necromass C (Sun et al., 2020; Yang et al., 2023; Zhu et al., 2022). (2) N addition is anticipated to enhance nutrient cycling and encourage plant and microorganism growth (Duan et al., 2023; Anning et al., 2021). The role that necromass C plays in soil organic carbon (SOC) will therefore eventually rise (Li et al., 2024; Liao et al., 2022; Tian et al., 2017). (3) Climate variability, ecosystem types, and soil characteristics may affect necromass C dynamics under climate change (Hu et al., 2023; Piton et al., 2020; Wang et al., 2024; Gao et al., 2022; Li et al., 2022; Liao et al., 2022).

2. Materials and Methods

2.1 Data collection

The sources of the data were Google Scholar (scholar.google.com), Web of Science (<https://www.webofscience.com>), and the National Knowledge Infrastructure of China (<https://www.cnki.net/>). The search was limited to studies that looked at how microbial necromass accumulation was impacted by climate change, and it included papers that were published prior to October 2023 that addressed how climate change affected either amino sugars or microbial necromass. There were many different keyword combinations used, including ("global warming" OR "climate change" OR "warm" OR "warming" OR "elevated temperature" OR "nitrogen deposition" OR "nitrogen addition") AND ("microbial necromass" OR "fungal necromass" OR "bacterial necromass" OR "microbial residues" OR "amino sugars" OR "glucosamine" OR "muramic acid").

In order to mitigate publication bias, the following criteria were used to screen articles (Bai et al., 2019): (1) Research in China is required. (3°51'N–53°33'N, 73°33'E–135°05'E), (2) articles must include the contents of FNC and BNC or amino glucosamine and muramic acid, (3) each experiment must have control and treatment groups with a minimum of three replications, (4) control and treatment plots must be set up in a **consistent environment**, and (5) sample sizes, means, and the data must contain the standard deviations for the treatment and control groups. The following is how the standard deviation was determined if only the standard error was provided $SD = SE\sqrt{n}$. Implementing these criteria led to the selection of 50 articles on climate change, totaling 197 paired observations to analyze microbial necromass responses to climate change.

Additional information collected included latitude, longitude, elevation, **MAT**, **MAP**, soil pH, initial SOC content, soil total N, C/N ratio, microbial biomass C and N, soil texture, and treatment variation (e.g., the magnitude of warming, N addition level, and precipitation reduction). The data in the figures were obtained using the Web Plot Digitizer. The Global Aridity and **PET** Database (<https://cgiarcsi.community/data/global-aridity-and-pet-database>) served as the source of the aridity index. In the absence of soil texture data, the Harmonized World Soil Database v2.0 (<https://www.fao.org/soils-portal/data-hub>) was used to supplement the information. To further explore the regulatory mechanisms of microbial necromass under climate change through background conditions, ecosystem types were categorized into cropland, forest, and grassland. The aridity index was classified as semiarid ($AI \leq 0.65$) or humid ($AI > 0.65$) (Hao et al., 2021). Following the USDA soil texture classification system, data were further classified into clay, clay loam, and loam (Zhou et al., 2023). The MAT of the study sites was used to classify

the data into two climatic conditions: warm (subtropical and tropical climates) and cool (temperate and Mediterranean climates). (Bai et al., 2019). Initial SOC content was categorized as low (<12g C/kg) or high (>12g C/kg) (Du et al., 2020).

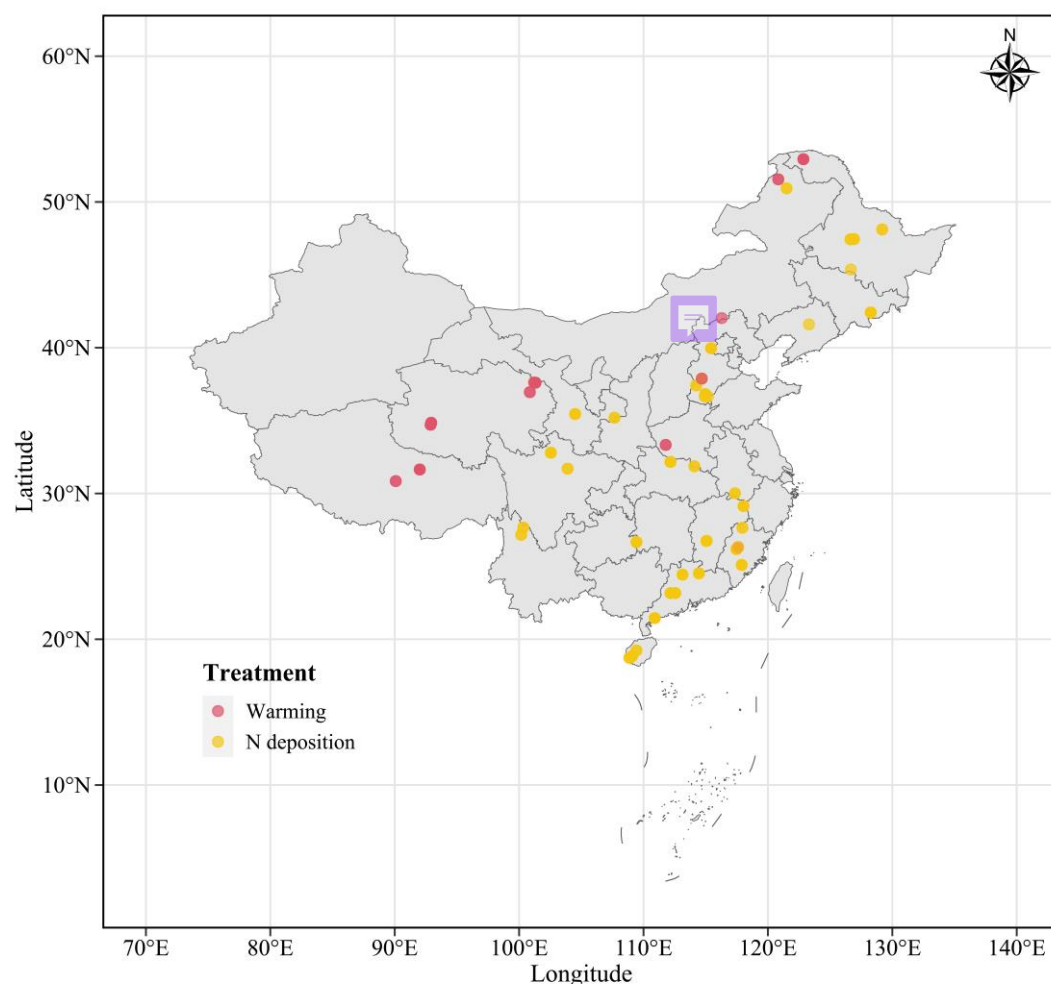


Fig. 1. Distribution of the microbial necromass C experimental sites used in the meta-analysis.

2.2 Microbial necromass calculation

The molar ratio of muramic acid to glucosamine in bacterial cells is 2:1, according to earlier studies (Gurevitch et al., 2018; Hedges et al., 1999; Ma et al., 2018b). The following formulas (1), (2), and (3) are employed to calculate, using this ratio, the C content of total necromass C (TNC), fungal necromass C (FNC), and bacterial necromass C (BNC):

$$(1) \text{ BNC} = \text{MurN} \times 45$$

$$(2) \text{ FNC} = \left(\frac{\text{GluN}}{179.17} - 2 \times \frac{\text{MurN}}{251.23} \right) \times 179.17 \times 9$$

$$(3) \text{ TNC} = \text{BNC} + \text{FNC}$$

The ratios specified in formulas (4), (5), and (6), respectively, are used to assess the roles that BNC, FNC, and TNC play in SOC (Zhou et al., 2023):

$$(4) \quad \text{Contribution of bacterial necromass C to SOC} = \frac{\text{BNC}}{\text{SOC}} \quad 149$$

$$(5) \quad \text{Contribution of fungal necromass C to SOC} = \frac{\text{FNC}}{\text{SOC}} \quad 150$$

$$(6) \quad \text{Contribution of total necromass C to SOC} = \frac{\text{TNC}}{\text{SOC}} \quad 151$$

2.3 Meta-analysis 152

According to Hedges et al. (1999), the ratio of natural logarithms was utilized, or $\ln\text{RR}_i$, to determine how microbial necromass C is affected by climate change.. The calculation formula is presented in equation (7): 153
154
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$$(7) \quad \ln\text{RR}_i = \ln\left(\frac{X_t}{X_c}\right) = \ln(X_t) - \ln(X_c) \quad 156$$

In this equation, $\ln\text{RR}_i$ represents the effect size, X_t is the mean of the treatment group, and X_c is the mean of the control group. The variance of $\ln\text{RR}_i$ is calculated using equation (8): 157
158
159

$$(8) \quad v_i = \frac{SD_t^2}{n_t X_t^2} + \frac{SD_c^2}{n_c X_c^2} \quad 160$$

where SD_t and SD_c represent the standard deviations of the treatment and control, respectively. n_t and n_c are the sample sizes for the treatment group and the control group, respectively. To enhance the accuracy of results, cases with greater variances were assigned lower weights, whereas those with lower variances received higher weights. The weight w_i for each case is calculated as shown in equation (9): 161
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163
164
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$$(9) \quad w_i = \frac{1}{v_i} \quad 166$$

The weighted effect size $\ln\text{RR}$ is calculated as per equation (10): 167

$$(10) \quad \ln\text{RR} = \frac{\sum(w_i \times \ln\text{RR}_i)}{\sum w_i} \quad 168$$

The standard error of $\ln\text{RR}$ ($S_{\ln\text{RR}}$) and 95% confidence intervals (95%CI) are computed using equations (11) and (12), respectively: 169
170

$$(11) \quad S_{\ln\text{RR}} = \sqrt{\frac{1}{\sum w_i}} \quad 171$$

$$(12) \quad 95\% \text{CI} = \ln\text{RR} \pm 1.96 \times S_{\ln\text{RR}} \quad 172$$

To directly reflect the effect size of climate change on microbial necromass C, the percent change is calculated using equation (13):

$$(13) \quad \text{Effect size} = (e^{\ln RR} - 1) \times 100\%$$

2.4 Statistical analysis

For all data analyses in this study, R version 4.3.1 was used. (Team, 2014). To assess how warming and N addition affect TNC, BNC, FNC, and their contribution to SOC, the "rma.mv" function from the "metafor" package was utilized to compute lnRR and 95%CI (Viechtbauer, 2010). Subgroup analyses were also performed to assess these impacts across different ecosystem types, MAT, AI, initial organic C content, and soil texture. To evaluate publication bias, Fail-Safe analysis and Egger's regression test were employed (Egger et al., 1997; Rosenberg, 2005). To examine the mechanisms underlying the impacts of warming and N addition on microbial necromass, structural equation modeling (SEM) was performed using the "lavaan" package (Oberski, 2014).

3. Results

3.1 Effect of climate change on microbial necromass C

The ways that climate change affected microbial necromass C varied noticeably. (Fig. 2). Warming led to increased TNC accumulation by 17.26%, BNC accumulation by 9.75%, and FNC accumulation by 19.78% ($p < 0.05$), whereas N addition also increased TNC, BNC, and FNC by 8.5%, 10.71%, and 8.52% ($p < 0.01$), respectively. Climate change caused changes in the FNC/SOC, BNC/SOC, and TNC/SOC ratios ranging from 1.5% to 18.77%; only warming substantially changed these contributions. ($p < 0.01$; Fig. 2).

Climate change effect on necromass C

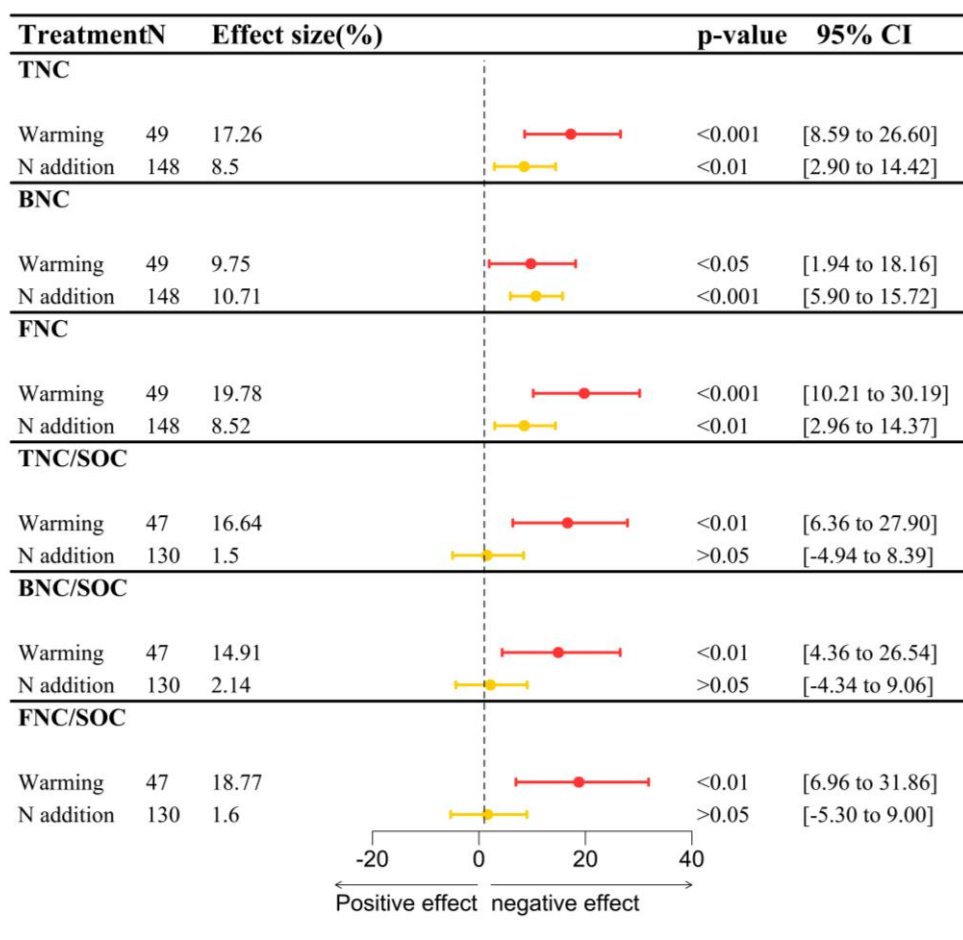


Fig. 2. Effect size and 95% confidence intervals of climate change effects on microbial necromass C and its contribution to SOC. TNC, total necromass C; BNC, bacterial necromass C; FNC, fungal necromass C; SOC, soil organic C. The closed and open symbols indicate significant and non-significant effects, respectively.

3.2 Response of microbial necromass C to climate change depending on climatic conditions, ecosystem types, and soil properties

Climate conditions influenced how microbial necromass C responded to climate change (Figs. 3a, b, c). In cool climates, warming and N addition increased TNC by 15.72% and 7.79%, respectively ($p < 0.05$). Both treatments also increased the BNC, TNC, and FNC contributions to SOC ($p < 0.05$). In warm climates, the addition of N accelerated the accumulation of TNC (10.58%), BNC (10.51%), and FNC (10.29%; $p < 0.01$). Only with the addition of N did the amount of microbial necromass C in humid sites rise noticeably ($p < 0.05$; Figs. 4a, b, c). In semiarid regions, N addition and warming both raised TNC by 11.20% and 15.11%, respectively ($p < 0.05$), despite the fact that only the addition of N markedly raised BNC.

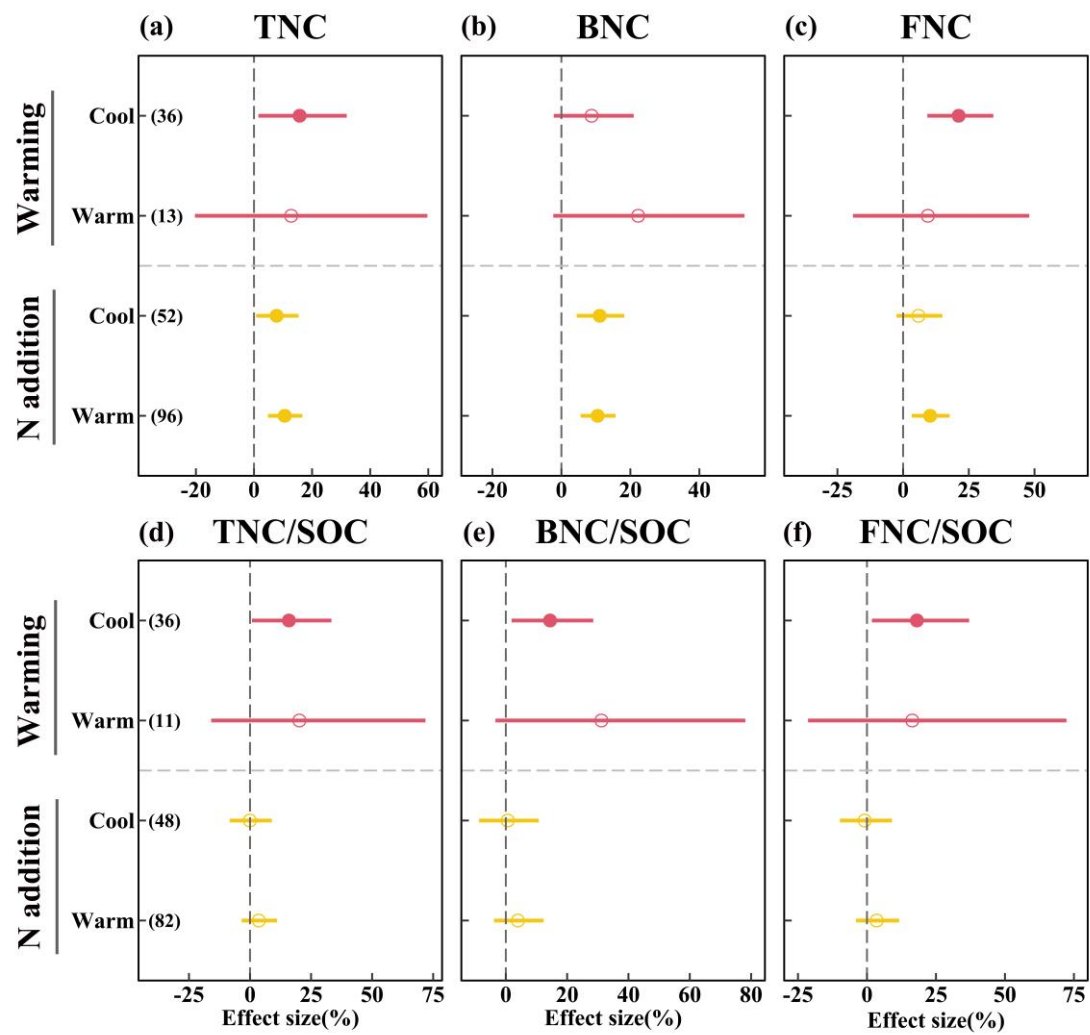


Fig. 3. The impact of climate change on microbial necromass C (a–c) and its role in SOC (d–f) are
 dependent on MAT. Soil organic carbon (SOC), bacterial necromass C (BNC), fungal necromass
 C (FNC), and total necromass C (TNC). The closed and open symbols indicate significant and
 nonsignificant effects.

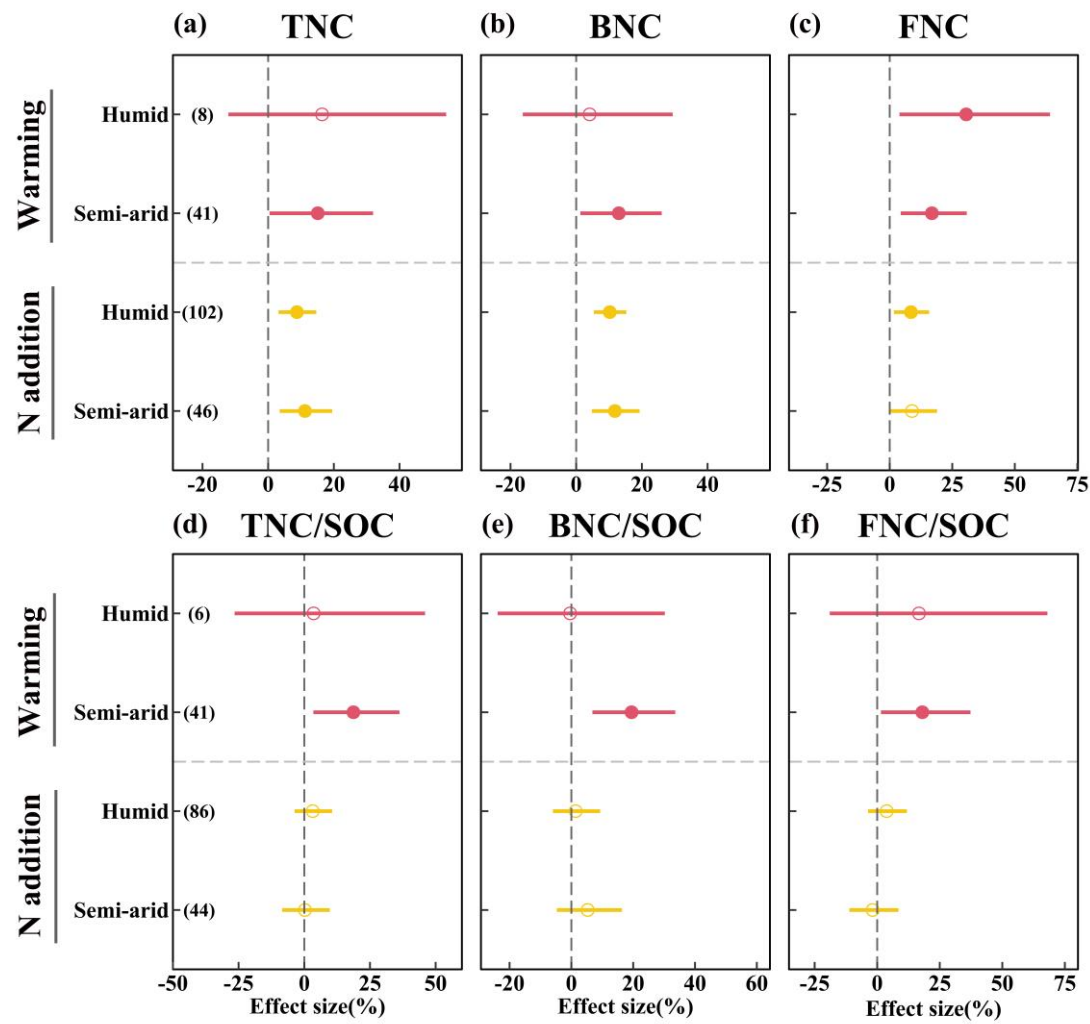


Fig. 4. The aridity index determines how climate change affects microbial necromass C (a–c) and how it contributes to SOC (d–f). Soil organic carbon (SOC), bacterial necromass C (BNC), fungal necromass C (FNC), and total necromass C (TNC). The closed and open symbols indicate significant and nonsignificant effects.

The necromass C responses to climate change varied across different ecosystem types (Figs. 5a, b, c). In croplands, warming increased TNC and FNC by 43.85% and 44.30% ($p < 0.05$), respectively. In grasslands, warming caused FNC to rise by 15.89% ($p < 0.05$). N addition increased TNC, BNC, and FNC in croplands and forests ($p < 0.05$). Furthermore, warming increased TNC and BNC contributions to SOC in grasslands by 18.22% and 18.35%, respectively ($p < 0.05$), however, in no ecosystem, the addition of N had an impact on these contributions (Figs. 5d, e, f).

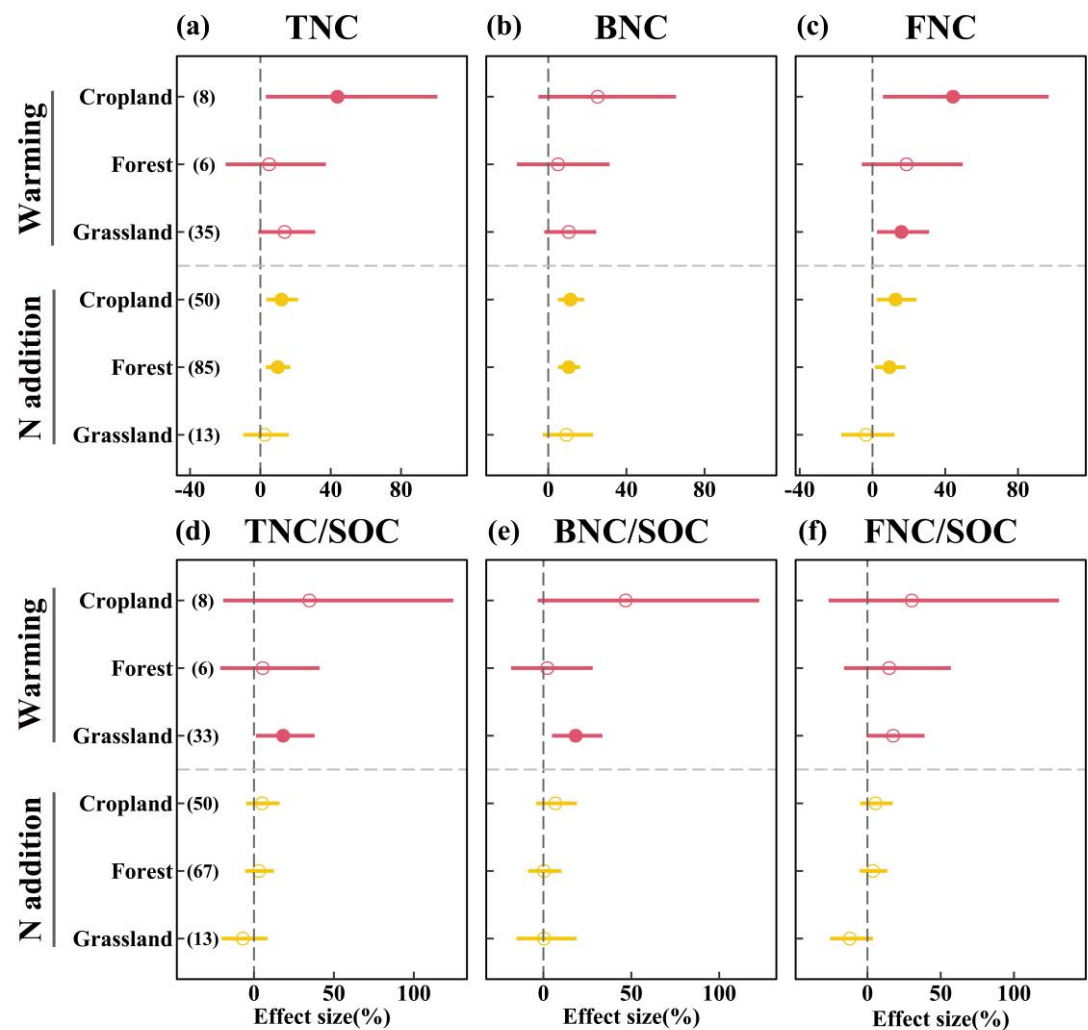


Fig. 5. Ecosystem type determines how climate change affects microbial necromass C (a–c) and how it contributes to SOC (d,e). TNC, total necromass C; BNC, bacterial necromass C; FNC, fungal necromass C; SOC, soil organic C. The closed and open symbols indicate significant and nonsignificant effects.

In soils where the starting SOC content is less than 12 g/kg, N addition only significantly increased BNC by 12.34% ($p < 0.01$). In soils with high initial SOC content (>12 g/kg), warming and N addition significantly enhanced microbial necromass C ($p < 0.05$; Figs. 6a, b, c). Warming increased TNC/SOC, BNC/SOC, and FNC/SOC by 15.96%, 15.11%, and 17.69%, respectively ($p < 0.05$), whereas N addition increased TNC/SOC, BNC/SOC, and FNC/SOC by 3.99%, 3.21%, and 3.51%, respectively ($p < 0.05$).

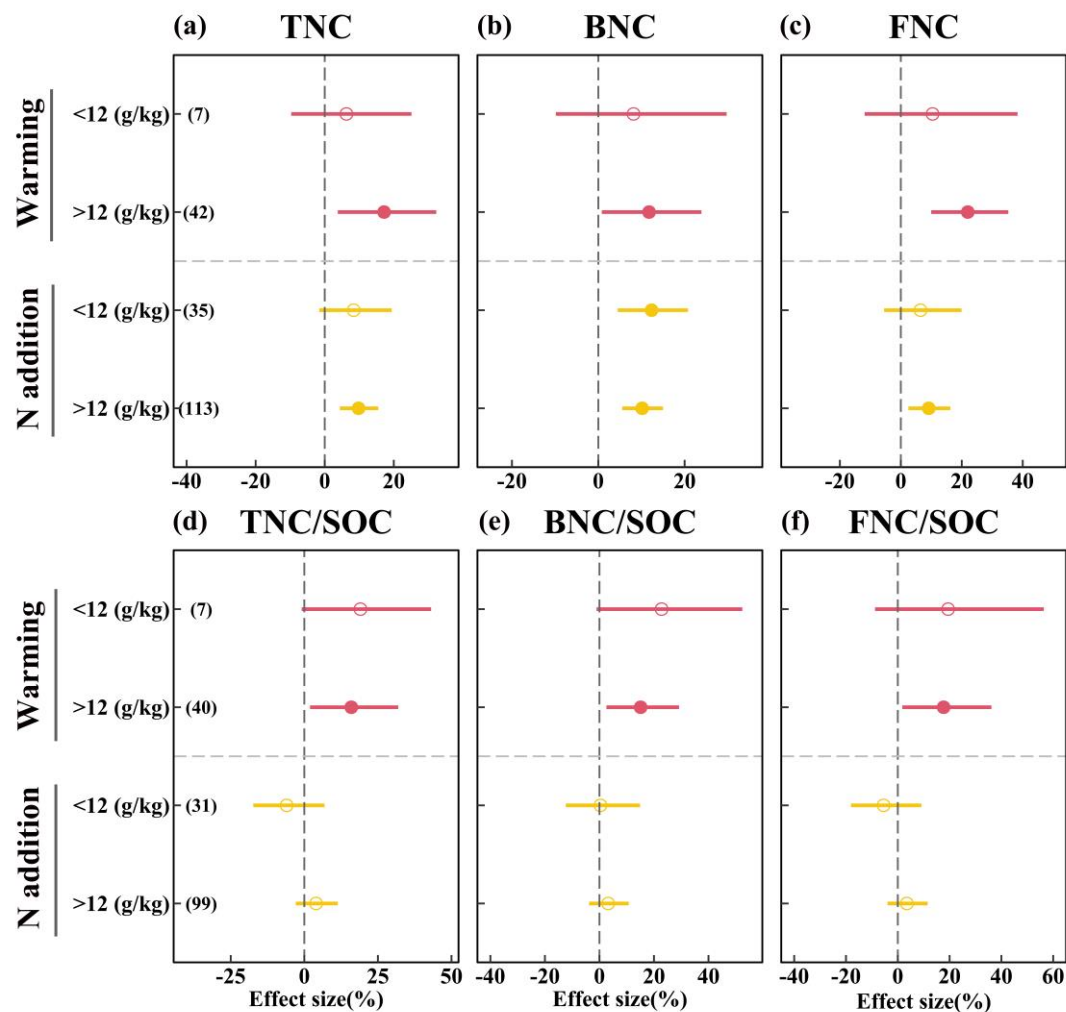


Fig. 6. SOC content determines how climate change affects microbial necromass C (a–c) and how it contributes to SOC (d–f). TNC, total necromass C; BNC, bacterial necromass C; FNC, fungal necromass C; SOC, soil organic C. The closed and open symbols indicate significant and non-significant effects.

Additionally, there were variations in how different soil textures affected how microbial necromass C responded to climate change factors (Figs. 7a, b, c). Microbial necromass C levels in loam soil increased with warming (TNC: 21.76%, BNC: 16.64%, and FNC: 34.99%), as did its contribution to SOC (TNC/SOC: 25.08%, BNC/SOC: 27.40%, and FNC/SOC: 36.53%) ($p < 0.05$). In clay soils, N addition led to an increase of 7.13% in TNC and 8.60% in BNC ($p < 0.05$). In clay loam soils, N addition significantly boosted TNC by 11.88%, BNC by 10.64%, and FNC by 11.91% ($p < 0.01$).

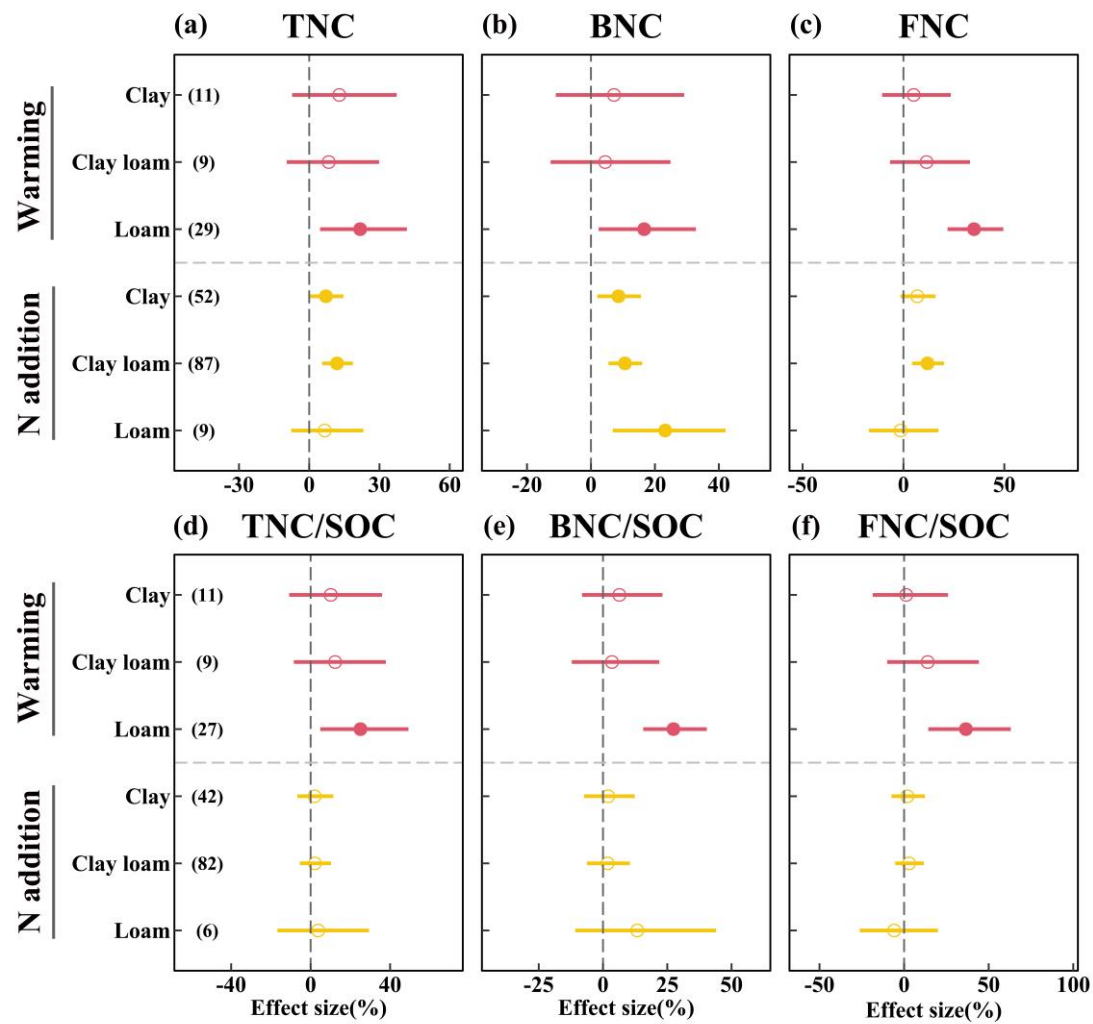


Fig. 7. Climate change effects on microbial necromass C (a–c) and its contribution to SOC (d–f) depend on soil texture. TNC, total necromass C; BNC, bacterial necromass C; FNC, fungal necromass C; SOC, soil organic C. The closed and open symbols indicate significant and nonsignificant effects.

3.3 Mechanisms of the impact of climate change on microbial necromass C

The SEM provided the best fit for the data, revealing diverse mechanisms through which climate change influences microbial necromass C (Fig. 8). Under warming, The correlation between SOC and muramic acid was significantly positive ($P < 0.05$), which significantly impacted the accumulation of TNC ($P < 0.001$). N addition positively influenced glucosamine (GluN) levels, which, in turn, affected TNC, thereby enhancing SOC ($P < 0.05$).

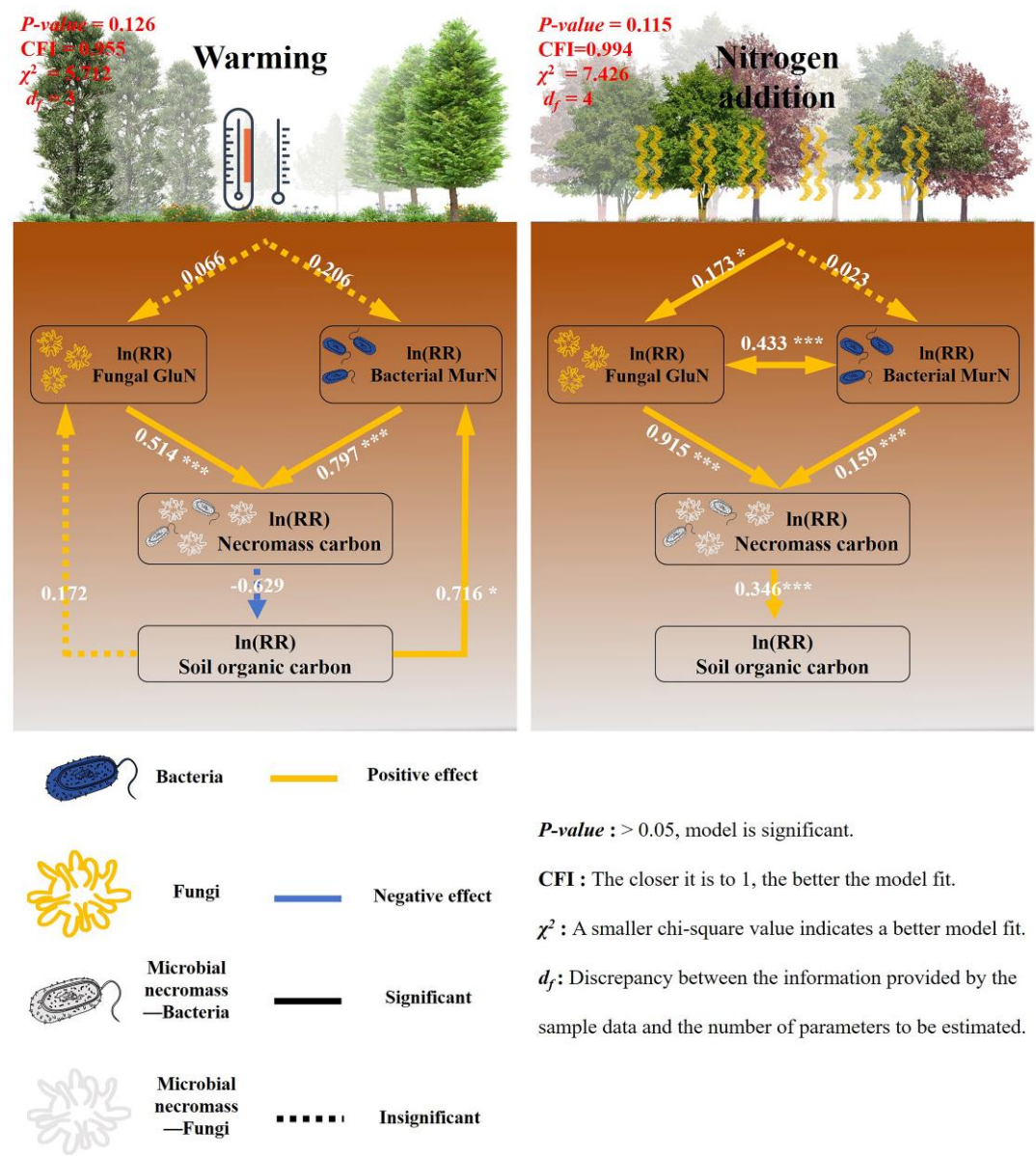


Fig. 8. Meta-analysis results of microbial necromass C response to climate change and the model results of expected causal relationships were obtained through structural equation modeling. Numbers on the arrows indicate standardized path coefficients, and asterisks mark their significance: * < 0.05; ** < 0.01; *** < 0.001.

4. Discussion

4.1 Response of microbial necromass C to climate change

4.1.1 Response of microbial necromass C to warming

According to our original theory, warming enhanced TNC's contribution to SOC, which encouraged its buildup (Figs. 2a, d). The 17.26% increase in TNC observed in our study differed from the unchanged TNC reported in a recent study (Fig. 2a) (Hu et al., 2023a). This difference might be because Hu et al.'s (2023) study had a small sample size, with only 23 samples, while our study had 49 samples. With more samples, our research probably gave a better estimate of how warming affects TNC, meaning their study might have underestimated the warming effect. Also, the different environmental conditions in our study sites could have played a role, as factors like soil texture and moisture can change how microbes respond to warming (Sun et al., 2020). The rises in TNC and TNC/SOC under warming might be connected to increases in BNC (Fig. 2; Fig. 8), showing that bacteria and fungi react differently (Yang et al., 2023; Zhu et al., 2022). Bacteria usually grow faster and are more active than fungi under warming, so they likely contribute more to TNC in SOC (Sun et al., 2020; Yang et al., 2023; Zhu et al., 2022).

4.1.2 Response of microbial necromass C to N addition

Our results indicated that N addition enhanced the accumulation of both necromass C and SOC (Fig. 2; Fig. 8). SEM analysis showed that N addition directly and indirectly increased levels of GluN and muramic (MurN) acid, both sources of necromass C, conforming to meta-analysis results (Fig. 8) (Hu et al., 2022). The positive correlation between GluN and MurN demonstrated the strong interaction between the bacterial and fungal communities under N addition (Fig. 8) (Anning et al., 2021). This interaction indicates not only a cooperative relationship between microbial groups but also potential shifts in community dynamics that could influence nutrient cycling (Anning et al., 2021; Wang et al., 2024). Furthermore, this interaction enhances nutrient assimilation by microorganisms (Wang et al., 2024). Nutrient enrichment also promotes plant and microbial growth, enhancing the efficiency of microbial carbon utilization, and enhancing both necromass C and SOC (Duan et al., 2023). These discoveries emphasize the considerable role of N addition in promoting necromass C and SOC sequestration, with greater accumulation observed under higher levels of N addition.

4.2 Background conditions regulating microbial necromass C under climate change

4.2.1 Background conditions regulating microbial necromass C under warming

Warming increased TNC in croplands (Fig. 5a). This effect could be stronger because of farming methods, which change the availability of nutrients and microbial activity (Hati et al., 2021; Hu et al., 2023a). Croplands have more disturbance than forests and grasslands because tillage spreads nutrients more evenly (Hati et al., 2021; Hu et al., 2023a). Warming makes microbes use more soil nutrients, but it also raises how much TNC adds to SOC.

In croplands, warming may create more opportunities for necromass C to bind with minerals, thereby promoting carbon sequestration. Warming increased TNC, BNC, and FNC in cool and humid areas (Figs. 3a, b, c). The climate in these areas plays a major role in necromass C accumulation (Ding et al., 2020). Temperature and moisture together

affect microbial activity (Pan et al., 2023). In cool and humid conditions, plants and microbes grow slower, but warming speeds up their carbon cycling (Liu et al., 2021; Zhang et al., 2015a). Cool and humid regions show stronger responses of necromass C to warming, so these areas need more study (Guo et al., 2018).

Warming affects necromass C differently depending on soil properties (Figs. 6a, b, c; Figs. 7a, b, c). Necromass C increased more in soils with high SOC or loam textures (Fig. 6a; Fig. 7a). This means soil texture and organic C may reduce warming's impact on microbial necromass. Earlier studies show loam soils help oxygen, water, and nutrients move better, which helps microbes grow (Gartzia-Bengoetxea et al., 2020; Li et al., 2024). Warming speeds up microbial activity, causing these soils to accumulate more necromass C (Mao et al., 2020; Zhou et al., 2023).

Warming increases necromass C (TNC, BNC, and FNC). This effect is strongest in croplands, cool humid areas, and soils with high SOC or loam textures. Climate, ecosystem type, and soil properties all affect how necromass C responds to warming. Warming speeds up microbial activity but can also help store more carbon, especially in soils good for microbial growth (Mao et al., 2020; Zhou et al., 2023).

4.2.2 Background conditions regulating microbial necromass C under N addition

Adding nitrogen increased necromass C in forests and croplands (Figs. 5a, b, c). Croplands need more nitrogen than other ecosystems because crops grow fast (Guo and Gifford, 2002). The extra nitrogen may boost necromass C through crop roots (Duan et al., 2023). Forests showed the strongest nitrogen shortage, with an average C/N ratio of 15.30. Adding nitrogen helps microbes break down material more easily, speeding up carbon cycling (Battistuzzi and Hedges, 2009).

Regardless of climate conditions, nitrogen (N) addition has been found to promote the accumulation of necromass carbon (C), and this effect is more evident in warm or semi-arid areas (as shown in Figures 3a, b, c and Figures 4a, b, c). High annual temperatures and a low aridity index indicate elevated microbial metabolic activity and soil permeability, which offer a conducive environment for microbial growth and turnover (Liang and Balser, 2012; Zhou et al., 2023). This demonstrates how microbial growth in warm or semiarid conditions can be stimulated by adding N, thereby increasing necromass C (Liao et al., 2022).

Necromass C was positively correlated with the sum of OC and TN contents when soil texture were silt loam and clay loam as well as when SOC content >3% (Figures 6a,b,c; Figures 7a,b,c), because increasing N resulted in an increase in fungal hyphal mass and binding material, promoting aggregation formation and protecting necromass C against microbial decomposition (Trivedi et al., 2017; Zhang et al., 2015b).

Furthermore, the addition of N further acidifies clay and clay loam (Nie et al., 2020), resulting in an upward trend in the ion concentrations of Fe^{2+} , Fe^{3+} and Al^{3+} (Li et al., 2024; Liao et al., 2022). This will promote the combination of microbial necromass C and soil minerals and enhance the soil's resistance to degradation (Tian et al., 2017). According to this relationship, nitrogen is an essential element for microbial necromass C, and it is also involved in soil texture to optimize carbon storage.

Necromass C increases with added nitrogen on forested lands (Bastin et al., 2013), cropland systems (Dale et al., 2007), and clay-textured soils that are high in organic

matter (Wang et al., 2015). To increase the amount of stored carbon in soils, farmers need to incorporate nitrogen because it helps build up necromass C. Therefore, researchers must study different methods for adding nitrogen onto soils, ecosystems and climates so they can best help store more carbon. Nitrogen addition also needs further research regarding its impacts on soil quality and ecological functions across a range of timescales given future changes in climatic conditions and management practices used by humans.

5. Conclusions

Our findings demonstrate how important climate, ecosystem types, and soil characteristics are in determining how warming and N addition affect necromass C. Warming is projected to promote significant necromass C sequestration, particularly in croplands, cool and semiarid regions, and areas with high SOC content and loam soils. N addition consistently enhances necromass C accumulation across all climate conditions, with especially pronounced effects in croplands, forests, soils with high SOC content, and clay or clay loam textures. Warming and N addition increase necromass C by affecting both bacterial and fungal necromass C, demonstrating how sensitively microbes are reacting to climate change. These findings demonstrate the importance of considering climate change and study site specificity when forecasting necromass C cycle feedbacks and formulating soil C sequestration plans.

Author Contributions: Y.P. and R.N.: Conceptualization, Investigation, Software, Methodology, Data Curation, Visualization, Writing—Original Draft. P.Z. and C.X. : Methodology, Writing—Review and Editing. Y.M. and M.Z.: Formal Analysis, Data Curation, Software. Y.W.: Conceptualization, Supervision, Writing—Review and Editing, Funding Acquisition, Validation. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financially supported by the National Key R&D Program of China (2023YFD2301500).

Acknowledgments: The authors would like to thank Lu Yang from the Chinese Academy of Forestry for his comments and suggestions to improve our paper.

Data Availability Statement: The data presented in this study are available upon request from the corresponding author. Conflicts of Interest: The authors declare no conflicts of interest.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Anning, D.K., Li, Z.L., Qiu, H.Z., Deng, D.L., Zhang, C.H., Ghanney, P., Shen, Q.R., 2021. Divergent Accumulation of Microbial Residues and Amino Sugars in Loess Soil after Six Years of Different Inorganic Nitrogen Enrichment Scenarios. *Appl. Sci.-Basel* 11, 5788. <https://doi.org/10.3390/app11135788>.
2. Bai, X.X., Huang, Y.W., Ren, W., Coyne, M., Jacinthe, P.A., Tao, B., Hui, D.F., Yang, J., Matocha, C., 2019. Responses of soil carbon sequestration to climate-smart agriculture practices: A meta-analysis. *Glob. Change Biol.* 25, 2591-2606. <https://doi.org/10.1111/gcb.14658>.
3. Battistuzzi, F.U., Hedges, S.B., 2009. A Major Clade of Prokaryotes with Ancient Adaptations to Life on Land. *Mol. Biol. and Evol.* 26, 335-343. <https://doi.org/10.1093/molbev/msn247>.
4. Ding, X.L., Chen, S.Y., Zhang, B., He, H.B., Filley, T.R., Horwath, W.R., 2020. Warming yields distinct accumulation patterns of microbial residues in dry and wet alpine grasslands on the Qinghai-Tibetan Plateau. *Biol. Fertil Soils* 56, 881-892. <https://doi.org/10.1007/s00374-020-01474-9>.

5. Du, Y.D., Cui, B.J., Zhang, Q., Wang, Z., Sun, J., Niu, W.Q., 2020. Effects of manure fertilizer on crop yield and soil properties in China: A meta-analysis. *Catena* 193, 104617. <https://doi.org/10.1016/j.catena.2020.104617>. 407
408
6. Duan, P.P., Wang, K.L., Li, D.J., 2023. Nitrogen addition effects on soil mineral-associated carbon differ between the valley and slope in a subtropical karst forest. *Geoderma* 430, 116357. <https://doi.org/10.1016/j.geoderma.2023.116357>. 409
410
7. Egger, M., Davey Smith, G., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple, graphical test. *Bmj* 315, 629-34. <https://doi.org/10.1136/bmj.315.7109.629>. 411
412
8. Ferraro, R., Waliser, D.E., Gleckler, P., Taylor, K.E., Eyring, V., 2015. Evolving Obs4MIPs to Support Phase 6 of the Coupled Model Intercomparison Project (CMIP6). *Bull. Amer. Meteorol. Soc.* 96, ES131-ES133. <https://doi.org/10.1175/bams-d-14-00216.1>. 413
414
415
9. Gao, C., Xu, L., Montoya, L., Madera, M., Hollingsworth, J., Chen, L., Purdom, E., Singan, V., Vogel, J., Hutmacher, R.B., Dahlberg, J.A., Coleman-Derr, D., Lemaux, P.G., Taylor, J.W., 2022. Co-occurrence networks reveal more complexity than community composition in resistance and resilience of microbial communities. *Nat. Commun.* 13, 3867. <https://doi.org/10.1038/s41467-022-31343-y>. 416
417
418
419
10. Gartzia-Bengoetxea, N., Virto, I., Arias-González, A., Enrique, A., Fernández-Ugalde, O., Barré, P., 2020. Mineral control of organic carbon storage in acid temperate forest soils in the Basque Country. *Geoderma* 358, 113998. <https://doi.org/10.1016/j.geoderma.2019.113998>. 420
421
422
11. Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. *Glob. Change Biol.* 8, 345-360. <https://doi.org/10.1046/j.1354-1013.2002.00486.x>. 423
424
12. Guo, X., Feng, J.J., Shi, Z., Zhou, X.S., Yuan, M.T., Tao, X.Y., Hale, L., Yuan, T., Wang, J.J., Qin, Y.J., Zhou, A.F., Fu, Y., Wu, L.Y., He, Z.L., Van Nostrand, J.D., Ning, D.L., Liu, X.D., Luo, Y.Q., Tiedje, J.M., Yang, Y.F., Zhou, J.Z., 2018. Climate warming leads to divergent succession of grassland microbial communities. *Nat. Clim. Chang.* 8, 813-818. <https://doi.org/10.1038/s41558-018-0254-2>. 425
426
427
428
13. Gurevitch, J., Koricheva, J., Nakagawa, S., Stewart, G., 2018. Meta-analysis and the science of research synthesis. *Nature* 555, 175-182. <https://doi.org/10.1038/nature25753>. 429
430
14. Hao, Z.G., Zhao, Y.F., Wang, X., Wu, J.H., Jiang, S.L., Xiao, J.N., Wang, K.C., Zhou, X.H., Liu, H.Y., Li, J., Sun, Y.X., 2021. Thresholds in aridity and soil carbon-to-nitrogen ratio govern the accumulation of soil microbial residues. *Commun. Earth Environ.* 2, 236. <https://doi.org/10.1038/s43247-021-00306-4>. 431
432
433
15. Hati, K.M., Jha, P., Dalal, R.C., Jayaraman, S., Dang, Y.P., Kopittke, P.M., Kirchhof, G., Menzies, N.W., 2021. 50 years of continuous no-tillage, stubble retention and nitrogen fertilization enhanced macro-aggregate formation and stabilisation in a Vertisol. *Soil Tillage Res.* 214, 105163. <https://doi.org/10.1016/j.still.2021.105163>. 434
435
436
16. Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150-1156. <https://doi.org/10.2307/177062>. 437
438
17. Hu, J.X., Du, M.L., Chen, J., Tie, L.H., Zhou, S.X., Buckeridge, K.M., Cornelissen, J.H.C., Huang, C.D., Kuzyakov, Y., 2023a. Microbial necromass under climate change and implications for soil organic matter. *Glob. Change Biol.* 29, 3503-3515. <https://doi.org/10.1111/gcb.16676>. 439
440
441
18. Hu, J.X., Huang, C.D., Zhou, S.X., Liu, X., Dijkstra, F.A., 2022. Nitrogen addition increases microbial necromass in croplands and bacterial necromass in forests: A global meta-analysis. *Soil Biol. Biochem.* 165, 108500. <https://doi.org/10.1016/j.soilbio.2021.108500>. 442
443
444
19. Hu, Q.Y., Liu, T.Q., Ding, H.N., Li, C.F., Tan, W.F., Yu, M., Liu, J., Cao, C.G., 2023b. Effects of nitrogen fertilizer on soil microbial residues and their contribution to soil organic carbon and total nitrogen in a rice-wheat system. *Appl. Soil Ecol.* 181, 104648. <https://doi.org/10.1016/j.apsoil.2022.104648>. 445
446
447
20. Jing, Y.L., Wang, Y., Liu, S.R., Zhang, X.D., Wang, Q.K., Liu, K., Yin, Y., Deng, J.F., 2019. Interactive effects of soil warming, throughfall reduction, and root exclusion on soil microbial community and residues in warm-temperate oak forests. *Appl. Soil Ecol.* 142, 52-58. <https://doi.org/10.1016/j.apsoil.2019.05.020>. 448
449
450
21. Li, C.N., Liao, H.J., Xu, L., Wang, C.T., He, N.P., Wang, J.M., Li, X.Z., 2022. The adjustment of life history strategies drives the ecological adaptations of soil microbiota to aridity. *Mol. Ecol.* 31, 2920-2934. <https://doi.org/10.1111/mec.16445>. 451
452
22. Li, Y.-Z., Bao, X.-L., Tang, S.-X., Xiao, K.-Q., Ge, C.-J., Xie, H.-T., He, H.-B., Mueller, C.W., Liang, C., 2024. Toward soil carbon storage: The influence of parent material and vegetation on profile-scale microbial community structure and necromass accumulation. *Soil Biol. Biochem.* 193, 109399. <https://doi.org/10.1016/j.soilbio.2024.109399>. 453
454
455
23. Liang, C., Balser, T.C., 2012. Warming and nitrogen deposition lessen microbial residue contribution to soil carbon pool. *Nat. Commun.* 3, 1222. <https://doi.org/10.1038/ncomms2224>. 456
457

24. Liang, C., Gutknecht, J.L.M., Balser, T.C., 2015. Microbial lipid and amino sugar responses to long-term simulated global environment changes in a California annual grassland. *FRONT MICROBIOL.* 6, 00385. <https://doi.org/10.3389/fmicb.2015.00385>.
25. Liao, C., Men, X., Wang, C., Chen, R., Cheng, X., 2022. Nitrogen availability and mineral particles contributed fungal necromass to the newly formed stable carbon pool in the alpine areas of Southwest China. *Soil Biol. Biochem.* 173, 108788. <https://doi.org/10.1016/j.soilbio.2022.108788>.
26. Liu, Z.W., Liu, X.X., Wu, X.L., Bian, R.J., Liu, X.Y., Zheng, J.F., Zhang, X.H., Cheng, K., Li, L.Q., Pan, G.X., 2021. Long-term elevated CO₂ and warming enhance microbial necromass carbon accumulation in a paddy soil. *Biol. Fertil. Soils* 57, 673–684. <https://doi.org/10.1007/s00374-021-01557-1>.
27. López-Fando, C., Pardo, M.T., 2012. Use of a partial-width tillage system maintains benefits of no-tillage in increasing total soil nitrogen. *Soil Tillage Res.* 118, 32–39. <https://doi.org/10.1016/j.still.2011.10.010>.
28. Luo, R.Y., Kuzyakov, Y., Liu, D.Y., Fan, J.L., Luo, J.F., Lindsey, S., He, J.S., Ding, W.X., 2020a. Nutrient addition reduces carbon sequestration in a Tibetan grassland soil: Disentangling microbial and physical controls. *Soil Biol. Biochem.* 144, 107764. <https://doi.org/10.1016/j.soilbio.2020.107764>.
29. Luo, Z.K., Luo, Y.Q., Wang, G.C., Xia, J.Y., Peng, C.H., 2020b. Warming-induced global soil carbon loss attenuated by downward carbon movement. *Glob. Change Biol.* 26, 7242–7254. <https://doi.org/10.1111/gcb.15370>.
30. Ma, L.X., Ju, Z.Q., Fang, Y.Y., Vancov, T., Gao, Q.Q., Wu, D., Zhang, A.P., Wang, Y.A., Hu, C.S., Wu, W.L., Du, Z.L., 2022. Soil warming and nitrogen addition facilitates lignin and microbial residues accrual in temperate agroecosystems. *Soil Biol. Biochem.* 170, 108693. <https://doi.org/10.1016/j.soilbio.2022.108693>.
31. Ma, T., Zhu, S.S., Wang, Z.H., Chen, D.M., Dai, G.H., Feng, B.W., Su, X.Y., Hu, H.F., Li, K.H., Han, W.X., Liang, C., Bai, Y.F., Feng, X.J., 2018a. Divergent accumulation of microbial necromass and plant lignin components in grassland soils. *Nat. Commun.* 9, 3480. <https://doi.org/10.1038/s41467-018-05891-1>.
32. Ma, Z.Q., Zhang, X.Y., Zhang, C., Wang, H.M., Chen, F.S., Fu, X.L., Fang, X.M., Sun, X.M., Lei, Q.L., 2018b. Accumulation of residual soil microbial carbon in Chinese fir plantation soils after nitrogen and phosphorus additions. *J. For. Res.* 29, 953–962. <https://doi.org/10.1007/s11676-017-0522-4>.
33. Mao, X.L., Van Zwieten, L., Zhang, M.K., Qiu, Z.T., Yao, Y.C., Wang, H.L., 2020. Soil parent material controls organic matter stocks and retention patterns in subtropical China. *J. Soils Sediments* 20, 2426–2438. <https://doi.org/10.1007/s11368-020-02578-3>.
34. Mou, Z.J., Kuang, L.H., He, L.F., Zhang, J., Zhang, X.Y., Hui, D.F., Li, Y., Wu, W.J., Mei, Q.M., He, X.J., Kuang, Y.W., Wang, J., Wang, Y.Q., Lambers, H., Sardans, J., Peñuelas, J., Liu, Z.F., 2021. Climatic and edaphic controls over the elevational pattern of microbial necromass in subtropical forests. *Catena* 207, 105707. <https://doi.org/10.1016/j.catena.2021.105707>.
35. Murugan, R., Loges, R., Taube, F., Sradnick, A., Joergensen, R.G., 2014. Changes in Soil Microbial Biomass and Residual Indices as Ecological Indicators of Land Use Change in Temperate Permanent Grassland. *Microb. Ecol.* 67, 907–918. <https://doi.org/10.1007/s00248-014-0383-8>.
36. Oberski, D., 2014. lavaan.survey: An R Package for Complex Survey Analysis of Structural Equation Models. *J. Stat. Softw.* 57, 1–27.
37. Pan, J.X., Peng, Y.F., Wang, J.S., Tian, D.S., Zhang, R.Y., Li, Y., Yang, L., Wang, S., Chen, C., Niu, S.L., 2023. Controlling factors for soil bacterial and fungal diversity and composition vary with vegetation types in alpine grasslands. *Appl. Soil Ecol.* 184, 104777. <https://doi.org/10.1016/j.apsoil.2022.104777>.
38. Piao, S.L., He, Y., Wang, X.H., Chen, F.H., 2022. Estimation of China's terrestrial ecosystem carbon sink: Methods, progress and prospects. *Sci. China-Earth Sci.* 65, 641–651. <https://doi.org/10.1007/s11430-021-9892-6>.
39. Piton, G., Legay, N., Arnoldi, C., Lavorel, S., Clément, J.C., Foulquier, A., 2020. Using proxies of microbial community-weighted means traits to explain the cascading effect of management intensity, soil and plant traits on ecosystem resilience in mountain grasslands. *J. Ecol.* 108, 876–893. <https://doi.org/10.1111/1365-2745.13327>.
40. Pohlmann, H., Müller, W.A., Bittner, M., Hettrich, S., Modali, K., Pankatz, K., Marotzke, J., 2019. Realistic Quasi-Biennial Oscillation Variability in Historical and Decadal Hindcast Simulations Using CMIP6 Forcing. *Geophys. Res. Lett.* 46, 14118–14125. <https://doi.org/10.1029/2019gl084878>.
41. Rosenberg, M.S., 2005. The file-drawer problem revisited: A general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* 59, 464–468. <https://doi.org/10.1554/04-602>.
42. Shao, P.S., He, H.B., Zhang, X.D., Xie, H.T., Bao, X.L., Liang, C., 2018. Responses of microbial residues to simulated climate change in a semiarid grassland. *Sci. Total Environ.* 644, 1286–1291. <https://doi.org/10.1016/j.scitotenv.2018.07.055>.

43. Shi, C., Jiang, Z.H., Chen, W.L., Li, L., 2018. Changes in temperature extremes over China under 1.5 °C and 2 °C global warming targets. *Adv. Clim. Chang. Res.* 9, 120-129. <https://doi.org/10.1016/j.accre.2017.11.003>.
44. Shi, P.J., Sun, S., Wang, M., Li, N., Wang, J.A., Jin, Y.Y., Gu, X.T., Yin, W.X., 2014. Climate change regionalization in China (1961-2010). *Sci. China-Earth Sci.* 57, 2676-2689. <https://doi.org/10.1007/s11430-014-4889-1>.
45. Simpkins, G., 2017. Progress in climate modelling. *Nat. Clim. Chang.* 7, 684-686. <https://doi.org/10.1038/nclimate3398>.
46. Sun, Y., Chen, H.Y.H., Jin, L., Wang, C.T., Zhang, R.T., Ruan, H.H., Yang, J.Y., 2020. Drought stress induced increase of fungi:bacteria ratio in a poplar plantation. *Catena* 193, 104607. <https://doi.org/10.1016/j.catena.2020.104607>.
47. Team, R.C., 2014. R: A language and environment for statistical computing. <https://www.r-project.org>.
48. Tian, J., Lou, Y.L., Gao, Y., Fang, H.J., Liu, S.T., Xu, M.G., Blagodatskaya, E., Kuzyakov, Y., 2017. Response of soil organic matter fractions and composition of microbial community to long-term organic and mineral fertilization. *Biol. Fertil. Soils* 53, 523-532. <https://doi.org/10.1007/s00374-017-1189-x>.
49. Tian, J., Zong, N., Hartley, I.P., He, N.P., Zhang, J.J., Powlson, D., Zhou, J.Z., Kuzyakov, Y., Zhang, F.S., Yu, G.R., Dungait, J.A.J., 2021. Microbial metabolic response to winter warming stabilizes soil carbon. *Glob. Change Biol.* 27, 2011-2028. <https://doi.org/10.1111/gcb.15538>.
50. Tian, P., Zhao, X.C., Liu, S.G., Wang, Q.G., Zhang, W., Guo, P., Razavi, B.S., Liang, C., Wang, Q.K., 2022. Differential responses of fungal and bacterial necromass accumulation in soil to nitrogen deposition in relation to deposition rate. *Sci. Total Environ.* 847, 157645. <https://doi.org/10.1016/j.scitotenv.2022.157645>.
51. Trivedi, P., Delgado-Baquerizo, M., Jeffries, T.C., Trivedi, C., Anderson, I.C., Lai, K., McNee, M., Flower, K., Singh, B.P., Minkey, D., Singh, B.K., 2017. Soil aggregation and associated microbial communities modify the impact of agricultural management on carbon content. *Environ. Microbiol.* 19, 3070-3086. <https://doi.org/10.1111/1462-2920.13779>.
52. van Groenigen, J.W., van Kessel, C., Hungate, B.A., Oenema, O., Powlson, D.S., van Groenigen, K.J., 2017. Sequestering Soil Organic Carbon: A Nitrogen Dilemma. *Environ. Sci. Technol.* 51, 4738-4739. <https://doi.org/10.1021/acs.est.7b01427>.
53. Viechtbauer, W., 2010. Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Softw.* 36, 1-48. <https://doi.org/10.18637/jss.v036.i03>.
54. Wang, C., Kuzyakov, Y., 2024. Mechanisms and implications of bacterial–fungal competition for soil resources. *ISME J.* 18, wrae073. <https://doi.org/10.1093/ismejo/wrae073>.
55. Wang, Q.C., Yang, L.M., Song, G., Jin, S.S., Hu, H.W., Wu, F.Z., Zheng, Y., He, J.Z., 2022. The accumulation of microbial residues and plant lignin phenols are more influenced by fertilization in young than mature subtropical forests. *For. Ecol. Manage.* 509, 120074. <https://doi.org/10.1016/j.foreco.2022.120074>.
56. Wang, Q.T., Zhang, Y., Zhang, P.P., Li, N., Wang, R.H., Zhang, X.J., Yin, H.J., 2023. Nitrogen deposition induces a greater soil C sequestration in the rhizosphere than bulk soil in an alpine forest. *Sci. Total Environ.* 875, 162701. <https://doi.org/10.1016/j.scitotenv.2023.162701>.
57. Wang, X.X., Zhou, L.Y., Fu, Y.L., Jiang, Z., Jia, S.X., Song, B.Q., Liu, D.Q., Zhou, X.H., 2024. Drought-induced changes in rare microbial community promoted contribution of microbial necromass C to SOC in a subtropical forest. *Soil Biol. Biochem.* 189, 109252. <https://doi.org/10.1016/j.soilbio.2023.109252>.
58. Xiao, K.Q., Zhao, Y., Liang, C., Zhao, M.Y., Moore, O.W., Otero-Fariña, A., Zhu, Y.G., Johnson, K., Peacock, C.L., 2023. Introducing the soil mineral carbon pump. *Nat. Rev. Earth Environ.* 4, 135-136. <https://doi.org/10.1038/s43017-023-00396-y>.
59. Xu, R.C., Tong, D., Xiao, Q.Y., Qin, X.Y., Chen, C.H., Yan, L., Cheng, J., Cui, C., Hu, H.W., Liu, W.Y., Yan, X.Z., Wang, H.X., Liu, X.D., Geng, G.N., Lei, Y., Guan, D.B., He, K.B., Zhang, Q., 2024. MEIC-global-CO2: A new global CO2 emission inventory with highly-resolved source category and sub-country information. *Sci. China-Earth Sci.* 67, 450-465. <https://doi.org/10.1007/s11430-023-1230-3>.
60. Yang, Y., Dou, Y., Wang, B., Xue, Z., Wang, Y., An, S., Chang, S.X., 2023. Deciphering factors driving soil microbial life-history strategies in restored grasslands. *iMeta* 2, e66. <https://doi.org/10.1002/imt2.66>.
61. Yu, G.R., Jia, Y.L., He, N.P., Zhu, J.X., Chen, Z., Wang, Q.F., Piao, S.L., Liu, X.J., He, H.L., Guo, X.B., Wen, Z., Li, P., Ding, G.A., Goulding, K., 2019. Stabilization of atmospheric nitrogen deposition in China over the past decade. *Nat. Geosci.* 12, 424-429. <https://doi.org/10.1038/s41561-019-0352-4>.
62. Zhang, B., Chen, S.Y., Zhang, J.F., He, X.Y., Liu, W.J., Zhao, Q., Zhao, L., Tian, C.J., 2015a. Depth-related responses of soil microbial communities to experimental warming in an alpine meadow on the Qinghai-Tibet Plateau. *Eur. J. Soil Sci.* 66, 496-504. <https://doi.org/10.1111/ejss.12240>.

63. Zhang, H., Guo, Y., Song, C., Song, Y., Wang, X., Sun, L., Gong, C., 2022. Six-year warming decreased amino sugar accumulation in the deep rhizosphere soil of permafrost peatland. *Appl. Soil Ecol.* 171, 104316. <https://doi.org/10.1016/j.apsoil.2021.104316>.
64. Zhang, H.J., Ding, W.X., Yu, H.Y., He, X.H., 2015b. Linking organic carbon accumulation to microbial community dynamics in a sandy loam soil: result of 20 years compost and inorganic fertilizers repeated application experiment. *Biol. Fertil. Soils* 51, 137-150. <https://doi.org/10.1007/s00374-014-0957-0>.
65. Zhang, W., Cui, Y.H., Lu, X.K., Bai, E., He, H.B., Xie, H.T., Liang, C., Zhang, X.D., 2016. High nitrogen deposition decreases the contribution of fungal residues to soil carbon pools in a tropical forest ecosystem. *Soil Biol. Biochem.* 97, 211-214. <https://doi.org/10.1016/j.soilbio.2016.03.019>.
66. Zhou, R.R., Liu, Y., Dungait, J.A.J., Kumar, A., Wang, J.S., Tiemann, L.K., Zhang, F.S., Kuzyakov, Y., Tian, J., 2023. Microbial necromass in cropland soils: A global meta-analysis of management effects. *Glob. Change Biol.* 29, 1998-2014. <https://doi.org/10.1111/gcb.16613>.
67. Zhu, Z.K., Fang, Y.Y., Liang, Y.Q., Li, Y.H., Liu, S.L., Li, Y.F., Li, B.Z., Gao, W., Yuan, H.Z., Kuzyakov, Y., Wu, J.S., Richter, A., Ge, T., 2022. Stoichiometric regulation of priming effects and soil carbon balance by microbial life strategies. *Soil Biol. Biochem.* 169, 108669. <https://doi.org/10.1016/j.soilbio.2022.108669>.

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