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RESEARCH ARTICLE

Global Synthesis of Fertilisation-Induced Changes in the Microbial Entombing Effect

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ABSTRACT

The microbial entombing effect refers to the accumulation and stabilisation of microbially derived carbon (C) in soils following the sustained production of microbial biomass and necromass. Fertilisation practices modify soil microbial activity and C cycling and consequently influence the microbial entombing effect, which has implications for global C sequestration. We conducted a global meta-analysis to evaluate the impact of fertilisation practices on the microbial entombing effect, focusing on microbial necromass C (MNC), microbial biomass C (MBC) and the microbial necromass accumulation coefficient (NAC = MNC/MBC) across 319, 1665 and 199 paired datasets, respectively. Overall, fertilisation increased MNC by 16.6%, primarily because of an overall increase in MBC (31.9%) rather than an increase in NAC. Inorganic fertiliser application resulted in a higher accumulation of MNC (14.7%) and MBC (24.9%) in croplands than in forests and grasslands. Combining nitrogen (N) and phosphorus (P) fertilisers with straw (NPS) exhibited the highest potential for global MNC accumulation (14,900 Tg), exceeding the global average by 10.6% under fertilisation. Combining N and P fertilisers with manure (NPM) resulted in the highest global MBC (660 Tg) and NAC (35.3). These findings highlight the necessity of combined organic–inorganic fertilisation strategies to enhance soil C sequestration by increasing the contribution of the microbial entombing effect. While mean annual temperature (MAT) played a key role in determining MBC, the initial pH (ipH) and initial soil organic C (iSOC) were the dominant factors influencing the microbial entombing effect. In alkaline soils, particularly those in Central and Western Asia, NPS and NPM fertilisation exhibited the greatest potential for enhancing MNC and NAC, respectively. This study provides mechanistic insights into the impacts of fertilisation on the microbial entombing effect and highlights the critical need for site-specific management to optimise soil C sequestration.

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1 | Introduction

Soil carbon (C) sequestration is crucial for sustaining soil health and food security and represents a pivotal nature-based solution to mitigating global warming (Lessmann et al. 2022; Olsson et al. 2019). Soil is the largest terrestrial reservoir of C, and even small shifts in soil C content can substantially influence atmospheric CO_2 levels and global C cycling (Davidson and Janssens 2006; Wang et al. 2022). The global potential for soil C sequestration through optimised agricultural management practices has been estimated at 0.44–0.68 Gt C/year (Lessmann et al. 2022). Among these practices, fertiliser management has been shown to be more effective in enhancing soil organic C (SOC) stocks than reduced tillage, crop rotation or residue incorporation (Lessmann et al. 2022). As soil C cycling is largely governed by microbial processes, understanding the impact of fertilisation on microbially driven soil C sequestration is essential for developing informed climate change mitigation strategies.

The entombing effect refers to the capture and stabilisation of C in soils via microbial processes, and it is driven by the continual production of microbial biomass and necromass (Liang and Zhu 2021). The concept of the 'microbial C pump' highlights the critical role of microbes in regulating soil C storage via the entombing effect (Liang et al. 2017; Zhu et al. 2020). Microorganisms decompose labile plant material and convert it into microbial biomass, which subsequently forms microbial necromass that contributes to the soil C pool (Liang et al. 2017). Notably, microbial necromass C (MNC) accounts for more than 50% of the SOC in croplands (Bernard et al. 2022; Sokol et al. 2022). Although microbial biomass C (MBC) accounts for only 1%–5% of SOC, it plays a central role in the continuous processing of organic C and in the generation of microbially derived compounds that accumulate in soils (Feng and Wang 2023). In this context, the microbial necromass accumulation coefficient (NAC) is key to understanding the transformation of microbial biomass into necromass (Han et al. 2024). Although NAC has been recognised as a valuable indicator of SOC dynamics, a comprehensive understanding of its role is lacking (Feng and Wang 2023). Therefore, the processes linking MBC generation and MNC accumulation must be better understood to optimise soil C storage and enhance C sequestration strategy effectiveness.

Fertilisation practices exert diverse effects on the formation of MBC and MNC across different ecosystems. Nitrogen addition has been shown to increase MNC in croplands but has a limited influence on fungal necromass and MNC in forest systems (Hu et al. 2022). Phosphorus addition suppresses MNC in alpine grasslands but increases MNC in subtropical forest soils, although it did not have a significant influence on MBC (Luo et al. 2022; Ma et al. 2023). In addition, fertilisation methods also have a significant influence on MBC and MNC. For instance, inorganic fertilisation alone had a minimal impact on both MBC and MNC, whereas combined inorganic–organic fertilisation increased MNC by 16.5%–17.1% in croplands (Li et al. 2024). This may be due to organic fertilisers causing the direct input of labile C that stimulates microbial growth and reproduction (Li et al. 2020; Li et al. 2024; Marschner 2003). To date, only one previous meta-analysis showed that NAC was the highest in croplands (28.2), followed by forests (26.8) and grasslands (21.1) (Han et al. 2024). However, studies on the differences in fertilisation effects across ecosystems are lacking, complicating efforts to identify consistent patterns and the drivers of the influence of fertilisation on the entombing effect.

The spatial heterogeneity of the microbial entombing effect is also influenced by edaphic and climatic factors (Angst et al. 2021; Arndt et al. 2022; Zhang et al. 2016). For example, a reduction in soil pH often increases the relative abundance of fungi, thereby increasing NAC (Han et al. 2024; Rousk et al. 2009). In soils with low initial SOC (iSOC) content, microorganisms exhibit high respiratory losses as they strive to acquire limiting nutrients, whereas in iSOC-rich soils, the turnover rate of living biomass and the retention of microbial necromass are elevated (Kumar and Pausch 2022). Key environmental variables, such as mean annual temperature (MAT) and mean annual precipitation (MAP), also play pivotal roles in soil C decomposition and microbial turnover (Donhauser et al. 2021; Hao et al. 2021). Notably, increased MAP has been associated with a decline in NAC (Han et al. 2024). Therefore, understanding the interactions between fertilisation practices and site-specific environmental conditions is critical for optimising microbial C accumulation. Although numerous individual studies have examined the effects of fertilisation on the microbial entombing effect, a comprehensive global synthesis is lacking.

Researchers typically quantify MNC by analysing soil-bound amino sugars as necromass biomarkers (Zhang and Amelung 1996). In particular, glucosamine (GluN) is derived from the cell walls of fungi and bacteria, whereas muramic acid (MurA) is specific to bacterial cells (Griepentrog et al. 2014). In bacterial biomass, GluN and MurA typically occur at a molar ratio of 2:1 (Joergensen 2018). Therefore, MNC is generally estimated from the combined content of GluN and MurA. In this meta-analysis, we collected MBC and MNC (or amino sugar) data from a variety of studies on fertilisation treatments across ecosystems to evaluate the global drivers of the effects of fertilisation on the microbial entombing effect. We hypothesise that (i) the microbial entombing effect, which is shaped by the fertilisation method, is strongly influenced by soil properties, with combined organic–inorganic fertilisation in croplands exerting the most positive effect; and (ii) variability in climate and initial soil conditions introduces substantial uncertainties in microbially derived C, with environmental factors playing pivotal roles in modulating the microbial entombment process.

2 | Material and Methods

2.1 | Data Collection

Data up to January 2024 were collected from the Web of Science (http://apps.webofknowledge.com/) and the China National Knowledge Infrastructure (https://www.cnki.net/). The search terms included combinations of (nitrogen OR phosphorus OR 'mineral fertiliser' OR 'inorganic fertiliser' OR manure OR compost OR straw) AND ('microbial necromass' OR 'fungal necromass' OR 'bacterial necromass' OR 'glucosamine' OR 'muramic acid' OR 'microbial biomass carbon' OR 'MBC'). Studies were selected based on the following inclusion criteria: (1) both fertilisation treatments and corresponding controls without fertilisation were reported; (2) data from different years within the

same study were treated as separate datasets; (3) in multifactorial studies, only treatments with and without fertilisation but not exposed to other global change drivers were considered; and (4) overlapping data from the same site across different publication years were treated as a single dataset. A total of 54 publications were selected for MNC, 329 for MBC and 31 for both MNC and MBC (Table S1). For sites lacking MBC data, missing values were supplemented using data from Han et al. (2024).

Fertilisation practices were classified into five categories: organic fertiliser application in croplands (CO), inorganic fertiliser application in croplands (CF), organic–inorganic fertiliser application in croplands (CFO), inorganic fertiliser application in forest ecosystems (FF) and inorganic fertiliser application in grassland ecosystems (GF). In addition to the experimental data, we collected supplementary information on experimental site details (longitude, latitude and elevation), MAT, MAP, initial soil pH (ipH), iSOC, changes in soil properties (e.g., pH and SOC) and management practices (e.g., fertilisation regime and duration). To assess the effects of organic fertiliser type on microbial necromass, organic inputs were categorised as manure (M) or straw (S). Inorganic fertilisers included nitrogen (N), phosphorus (P), potassium (K), nitrogen and phosphorus (NP), nitrogen and potassium (NK) and nitrogen, phosphorus and potassium (NPK). Among climatic factors, MAT was categorised into cool (≤10°C), warm (10°C–20°C) and tropical (>20°C) zones (Zhao et al. 2022). Soil ipH was classified as acidic (≤6), neutral (6–8) or alkaline (>8), and soil iSOC was classified as low (≤12 g/kg) or high (>12 g/kg) (Zhou et al. 2023). Experimental duration was categorised into three groups: ≤5, 5–10 and >10 years.

2.2 | Calculation of MNC and NAC

We calculated MNC and NAC as outlined by Hu et al. (2024) and Zhang et al. (2021) using the following equations:

$$\mathrm{MNC} = \mathrm{FNC} + \mathrm{BNC} \tag{1}$$

$$\mathrm{BNC} = \mathrm{MurA} * 31.3 \tag{2}$$

$$\mathrm{FNC} = 179.17 * 10.8 * \left(\frac{\mathrm{Glu}}{179.17} - 1.63 * \frac{\mathrm{MurA}}{251.23} \right) \tag{3}$$

$$\mathrm{NAC} = \frac{\mathrm{MNC}}{\mathrm{MBC}} \tag{4}$$

where FNC is fungal necromass C and BNC is bacterial necromass C. In the equations, the conversion factor from MurA to BNC is 45, with 251.23 denoting the molecular weight of MurA. Additionally, the conversion factor from GluN to FNC is 10.8, with 179.17 representing the molecular weight of GluN (Hu et al. 2024; Zhu et al. 2020).

2.3 | Data Analysis

The random effects model was used to assess the effects of fertilisation on microbial necromass and NAC based on the natural log response ratio ln(RR), variance (v) of ln(RR), 95% confidence interval (CI) and effect size (%), using the following equations:

$$\ln(\mathrm{RR}) = \frac{\ln(\mathrm{Xt})}{\ln(\mathrm{Xc})} \tag{5}$$

$$\mathrm{V} = \frac{\mathrm{s_t^2}}{\mathrm{n_t x_t^2}} + \frac{\mathrm{s_c^2}}{\mathrm{n_c x_c^2}} \tag{6}$$

$$\mathrm{W_i} = \frac{1}{\mathrm{V_i}} \tag{7}$$

$$RR_{++} = \frac{\sum (W_i * RR_i)}{\sum W_i} \tag{8}$$

$$95\,\%\,\mathrm{CI} = RR_{++} + 1.96 * \sqrt{\frac{1}{\Sigma \mathrm{w_i}}} \tag{9}$$

$$\text{Effect size}\,(\%) = \left(e^{RR_{++}} - 1\right) \times 100\,\% \tag{10}$$

where *Xt* and *Xc* represent the mean values of the fertilisation and nonfertilisation treatments, respectively; *St* and *Sc* represent the standard deviations of the fertilisation and nonfertilisation treatments, respectively; and *nt* and *nc* denote the sample sizes for the fertilisation and nonfertilisation treatments, respectively. The weighted mean response ratio (RR++) was calculated as the sum of the products of the response ratio and weighting factors for each experiment in the group. The fertilisation treatments were considered to have a significant influence on the target variables when the 95% CI did not overlap with zero.

2.4 | Statistical Analysis

To ensure data reliability, the frequency distributions of MNC, MBC and NAC were plotted, which showed that they followed a normal distribution (Figure S1). Publication bias was assessed based on a fail-safe analysis (Table S2). The average effect size and 95% bootstrapped CI were calculated using MetaWin 2.1. Treatment effects were deemed significant if the 95% CI did not include zero.

Differences in the ln(RR) values of MNC, MBC and NAC for different fertiliser types were examined using one-way analysis of variance, with Tukey's post hoc tests used to detect significant differences. These tests were performed using SPSS 20.0. Normality was confirmed using the Shapiro–Wilk test prior to significance testing. Linear regression analysis was employed to assess the relationships between MNC, MBC, NAC and their drivers using SPSS 20.0. Additionally, mixed-effects meta-regression models, implemented in R using the 'glmulti' package, were used to explore the influence of MAT, MAP, ipH, iSOC, fertilisation duration and the ln(RR) of soil pH, SOC and soil total N (TN) on MNC, MBC and NAC. Predictors with a cumulative Akaike weight exceeding 0.8 were considered significant (Terrer et al. 2016).

Boosted regression tree (BRT) analysis was used to quantify the relative importance of climate (MAT and MAP) and background

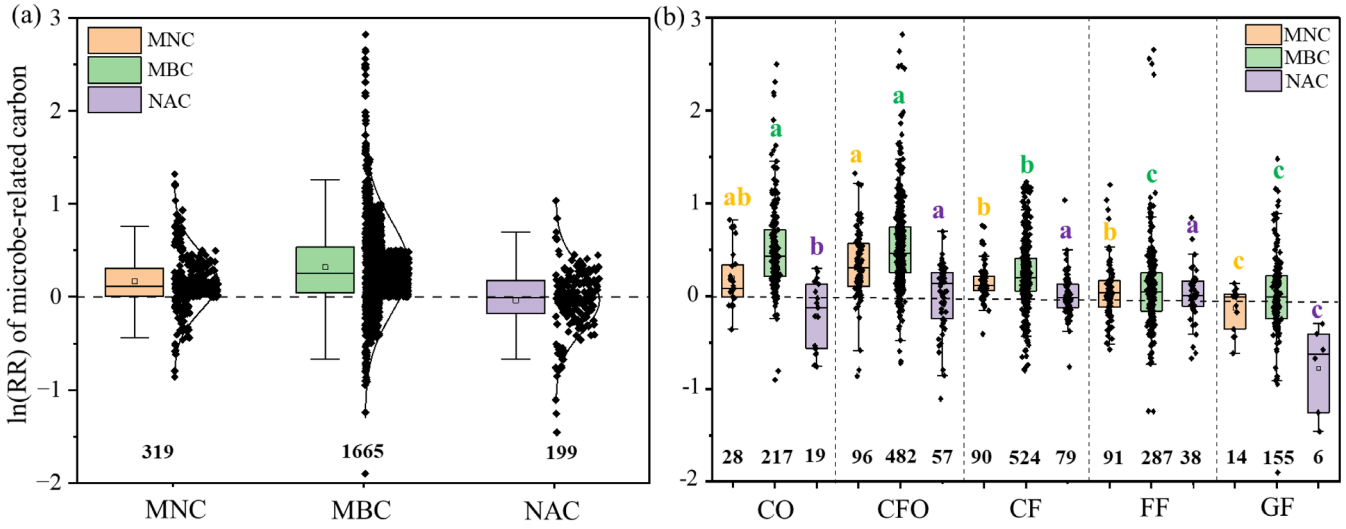


FIGURE 1 | (a) Responses of MNC, MBC and NAC to fertilisation at the global scale, and (b) their ecosystem-specific variations under different fertilisation regimes. Different lowercase letters indicate significant differences between ecosystems ($p < 0.05$). CF, inorganic fertiliser application in cropland; CFO, organic–inorganic fertiliser application in cropland; CO, organic fertiliser application in cropland; FF, inorganic fertiliser application in forest ecosystem; GF, inorganic fertiliser application in grassland ecosystem; ln(RR), natural log response ratio; MBC, microbial biomass C; MNC, microbial necromass C; NAC, microbial necromass accumulation coefficient.

soil properties (ipH and iSOC) for ln(RR) of MNC, MBC and NAC (Elith et al. 2008; Zhao et al. 2022). Due to limited global data, we excluded fertilisation duration and the ln(RR) of pH, SOC and TN from the BRT analysis. Gridded climate data (MAT and MAP) were sourced from the Climate Research Unit database (Harris et al. 2014), and soil ipH and iSOC were obtained from the SoilGrids database (Hengl et al. 2017). Random forest models, implemented in R (version 3.6.3) using the 'randomForest' package, were applied to predict grid-level relative changes (%) in MNC, MBC and NAC caused by fertilisation across croplands.

3 | Results

3.1 | Response of Entombing Effects to Fertilisation

Fertilisation significantly increased MNC and MBC by 16.6% and 31.9%, respectively ($p < 0.05$; Figure 1a and Figure S2). However, these effects varied across ecosystem types (Figure 1 and Figure S2). Inorganic fertilisation resulted in notably higher accumulations of MNC and MBC in croplands (CF) than in forests (FF) and grasslands (GF), with average increases of 14.7% and 24.9%, respectively ($p < 0.05$; Figure 1b). Furthermore, compared with CF, the CO and CFO treatments increased MNC by 30.1%–121.1% and MBC by 107.9%–116.7%, respectively ($p < 0.05$; Figure 1b and Figure S2). On a global scale, fertilisation did not significantly alter NAC compared with that in unfertilised controls (Figure 1a and Figure S2).

3.2 | Factors Affecting the Response of Entombing Effect to Fertilisation

The effect of fertilisation on soil microbial entombing processes was significantly influenced by climate and initial soil properties (Figure 2a). Soil MNC was negatively correlated with MAP ($p < 0.01$), whereas MBC was positively correlated with both MAP and MAT ($p < 0.05$; Figure 2a). The effects of fertilisation on MNC and NAC were predominantly regulated by soil ipH, whereas the effects on MBC were primarily driven by iSOC (Figure 2b–d). Additionally, increases in MNC were linked to increases in MBC, while increases in NAC were mainly associated with fertilisation-induced increases in soil pH (Figures 2a and 3a–c). These relationships varied across fertilisation treatments and ecosystems (Table S3). In addition, soil clay content was significantly correlated with MNC and MBC (Figure S3).

Compared with FF and GF, CF led to greater MBC accumulation and exhibited a more substantial increase in SOC content (average effect size: 13.9%) (Figure 3d). Fertilisation of alkaline soils resulted in the highest MNC accumulation (26.0% increase), whereas fertilisation of neutral soils reduced NAC by 26.9% ($p < 0.05$; Figure 4a,c). Under low iSOC conditions, fertilisation enhanced MBC accumulation by 46.0% ($p < 0.01$; Figure 4b). Moreover, warm environments favoured MBC accumulation, with a 33.6% increase, and the fertilisation effect became more pronounced in experiments lasting over 10 years (Figure 4b).

3.3 | Effects of Different Fertiliser Applications on Microbial Entombing Processes

Management practices had varying effects on soil C entombment across ecosystem types (Figure 5a–c). In croplands, the application of NP or NPK fertiliser increased MNC and MBC to 18.1%–19.2% and 27.1%–28.8%, respectively, compared with the application of N fertiliser alone (Figure 5a–c). Across different ecosystems, the combination of organic and inorganic fertiliser was the most effective method of promoting MNC, MBC and NAC (Figure 5a–c). Specifically, the application of

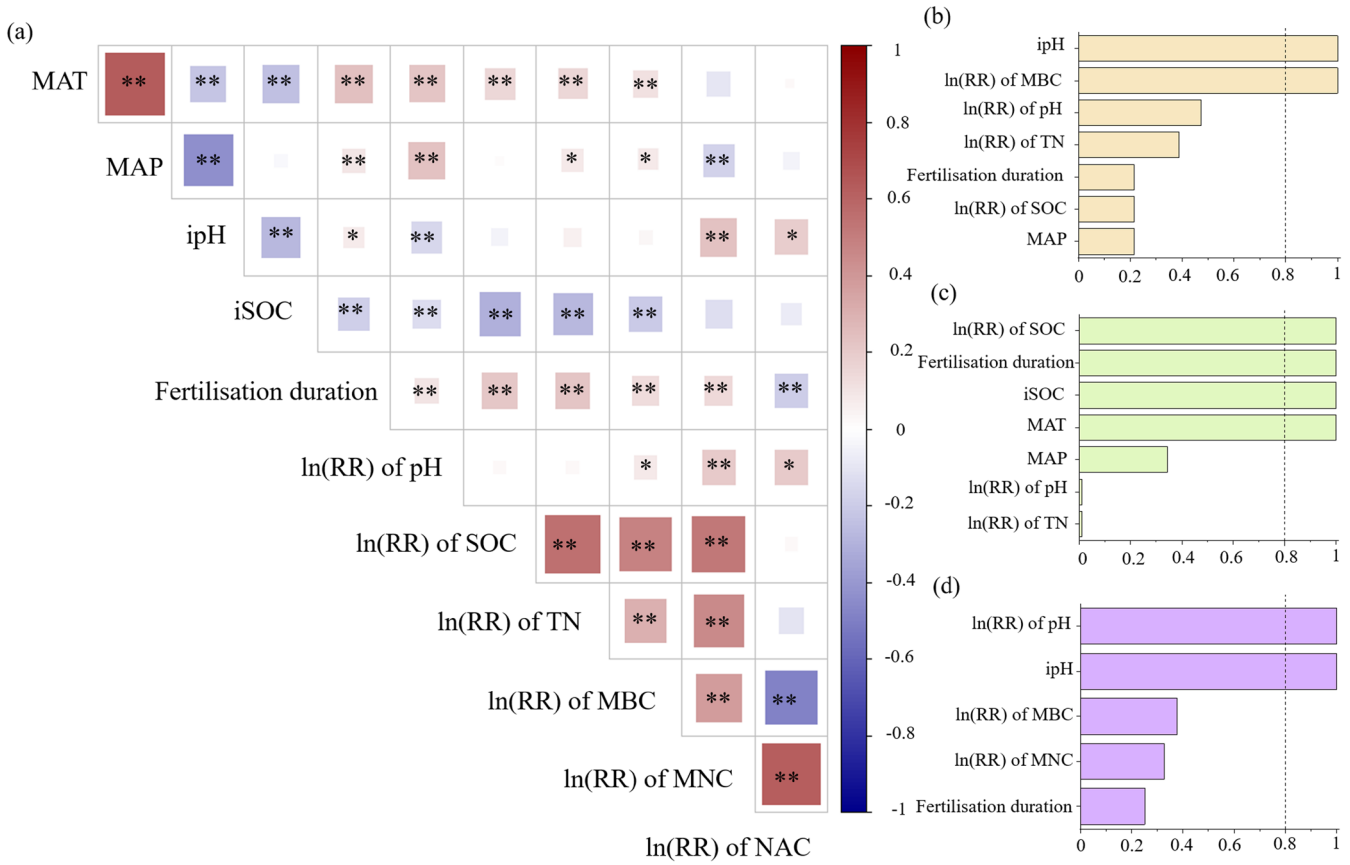


FIGURE 2 | Relationships between (a) MNC, MBC and NAC and climate factors (MAT and MAP), initial soil properties (ipH and iSOC) and management practice (fertilisation duration). Importance rank of influence of climate factors (MAT and MAP), initial soil properties (ipH and iSOC) and management practice (fertilisation duration) on (b) MNC, (c) MBC and (d) NAC. Red columns represent positive correlations, and blue columns represent negative correlations. Significant differences were identified using the least significant difference (LSD) multiple range test, with significance levels designated as $p < 0.05$ (*) and $p < 0.01$ (**). ipH, initial soil pH; iSOC, initial soil organic carbon content; MAP, mean annual precipitation; MAT, mean annual temperature; TN, total N.

NP fertiliser combined with straw (NPS) resulted in the highest MNC accumulation (14,900 Tg), which was 10.6% and 45.7% higher than the global fertilisation average and the nonfertilisation treatments, respectively (Figures 5a and 6). Additionally, NP fertiliser combined with manure (NPM) led to the highest MBC accumulation and the greatest NAC (Figure 5b,c). Under this management regime, MBC accumulation could potentially increase by 260 Tg (65.2% of the current global stock of 400 Tg), with NAC rising to 35.3.

We also identified optimal scenarios that combined management practices with specific climate and soil conditions (Figure 5d–f). NPS treatment under alkaline conditions (NPS-J) and NPM in cool climates with low iSOC and long-term fertilisation (NPM-C-L-L) were the most effective practices for increasing MNC and MBC, with average effect sizes of 63% and 78.4%, respectively. Meanwhile, NPM under alkaline conditions (NPM-J) had the most pronounced effect on NAC, showing an increase of 19.1%. Compared with the global average, optimal management practices had a greater impact on MBC in North America and Asia, whereas the highest potential for MNC accumulation and NAC enhancement in croplands was observed in Central and Western Asia (Figure 6a–c).

4 | Discussion

4.1 | Effect of Fertilisation on Microbial Entombing Across Ecosystems

Fertilisation had a significant positive impact on microbially derived C (Figure 1a), confirming the crucial role of essential nutrients in increasing microbial growth and promoting necromass accumulation (Liang et al. 2017). Through enhancing aboveground plant inputs, stimulating rhizodeposition and improving soil nutrient availability, fertilisation activated microbial communities and led to a substantial rise in MBC (Shi et al. 2024; Wang et al. 2024; Zhou et al. 2025). However, the increase in the ln(RR) of MNC was approximately half that of the ln(RR) of MBC (Figure 1a), indicating a decoupling between microbial biomass production and necromass accumulation. Although MNC predominantly accumulates from microbial turnover and cell death (Liu et al. 2010; Zhou et al. 2023), its stabilisation occurs over longer temporal scales than the rapid formation of living biomass. Long-term preservation of MNC in soil requires physical protection within soil aggregates and/or stabilisation through interaction with soil minerals (e.g., clay particles) to form organomineral complexes (Figure S3; Ye

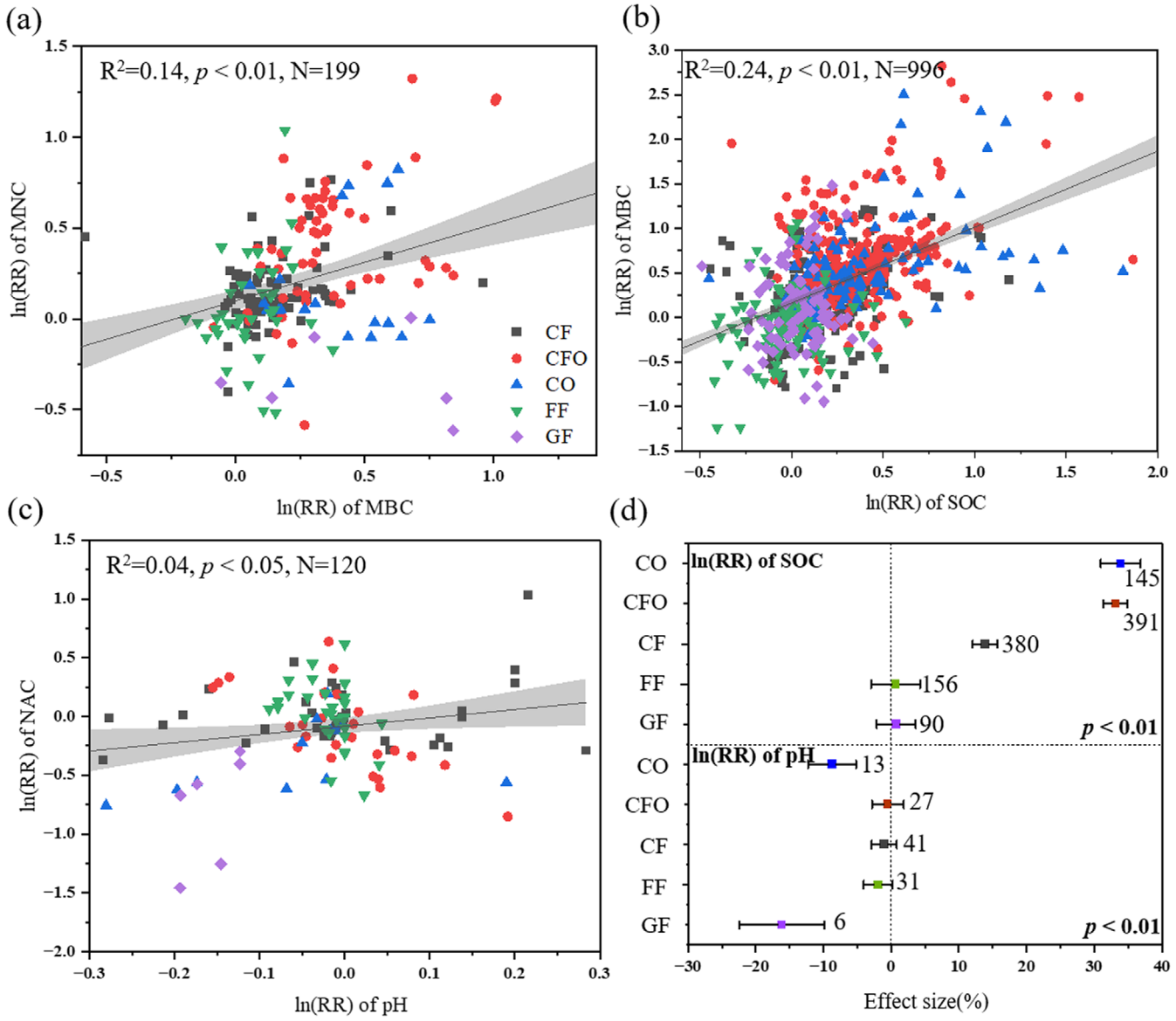


FIGURE 3 | Linear regressions between (a) MNC and MBC, (b) MBC and SOC and (c) NAC and pH (based on pooled data across all fertilisation treatments). (d) Effect sizes of different fertilisation treatments on SOC and pH in cropland, grassland and forest ecosystems. Significant differences between fertiliser treatments in (d) were identified with the LSD multiple range test, with significance levels set at $p < 0.05$ and $p < 0.01$. CF, inorganic fertiliser application in cropland; CFO, organic–inorganic fertiliser application in cropland; CO, organic fertiliser application in cropland; FF, inorganic fertiliser application in forest ecosystem; GF, inorganic fertiliser application in grassland ecosystem; MBC, microbial biomass C; MNC, microbial necromass C; NAC, microbial necromass accumulation coefficient.

et al. 2019; Ni et al. 2022). Additionally, substantial proportions of microbe-assimilated C are lost via respiration, which may further constrain necromass formation. Finally, while fertilisation increased the absolute abundances of both bacteria and fungi (Wu et al. 2022), it did not significantly alter the bacteria-to-fungi ratio (Ma et al. 2020; Figure S4), suggesting that microbial community structure remained relatively stable. The stability of microbial community structure may have contributed to the consistency of NAC. These findings indicate that the increase in necromass under fertilisation is primarily driven by the accumulation of microbial biomass, rather than by an increase in NAC.

The influence of fertilisation on C entombment varied across ecosystem types, which is consistent with our first hypothesis. Inorganic fertilisation led to a significantly greater accumulation of both MNC and MBC in croplands than in grasslands and forests (Figure 1b). The increase in MNC was closely associated with an increase in MBC, which in turn showed a positive correlation with changes in SOC (Figure 2a,b). In croplands, enhanced crop productivity and root biomass inputs under fertilisation contribute to higher SOC levels (Mandal et al. 2007). Conversely, in grasslands and forests, fertilisation often triggers a trade-off, where elevated aboveground biomass coincides with reduced plant diversity, and nutrient addition amplifies these effects (Harpole et al. 2016; Shi et al. 2024). Furthermore, in grassland ecosystems, N addition reduces the rate of root N exudation and leads to an increase in exudate C:N compared with that under no fertilisation (Li et al. 2021). This increase

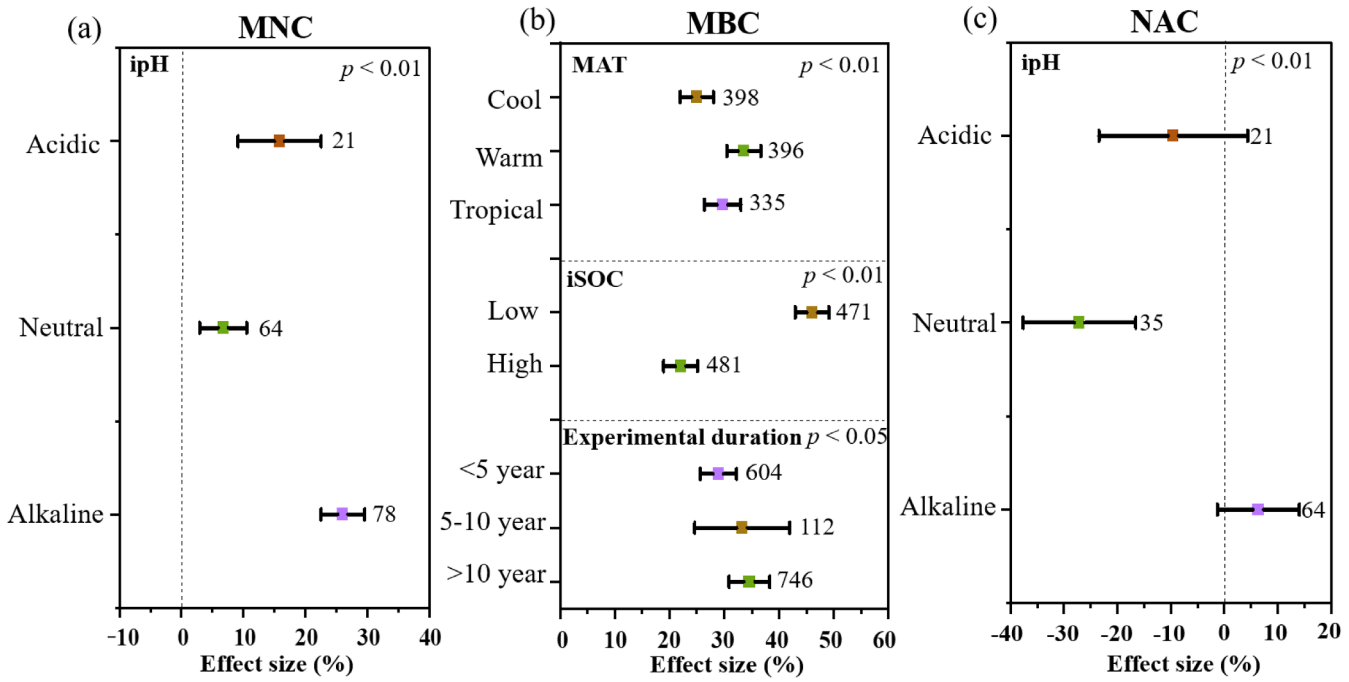


FIGURE 4 | Effect of fertilisation on (a) MNC, (b) MBC and (c) NAC under different environmental conditions. All results are presented as effect sizes (%) of the control soil (nonfertilisation treatment). Error bars are 95% CIs. Significant differences were determined using the LSD multiple range test, with significance thresholds established at $p < 0.05$ and $p < 0.01$. The number of observations is shown next to each bar. ipH, initial soil pH; iSOC, initial SOC content; MAT, mean annual temperature.

enhances soil microbial activity for N acquisition and may also prime the decomposition of otherwise persistent organic C (Kuzyakov 2002; Xiao et al. 2015), potentially offsetting the contribution of root-derived C to SOC formation (Sokol et al. 2019). Our meta-analysis revealed SOC did not significantly increase in these systems (Figure 3d), reflecting both positive and negative outcomes of fertilisation in grasslands and forests and underscoring the variability and uncertainty in SOC responses to fertilisation (Chu et al. 2023; Poeplau et al. 2019; Ye et al. 2018).

4.2 | Factors Controlling the Impact of Fertilisation on Microbial Entombing

The dynamic equilibrium of microbial C is regulated by the complex interplay of various factors (Luo et al. 2017). Climate variables, such as MAT and MAP, influence not only the soil microbial community composition but also the turnover of microbial C (Donhauser et al. 2021). Increased MAP stimulates plant growth, contributing to higher plant residue inputs that serve as C sources for soil microbes (Nielsen and Ball 2015). Concurrently, it stimulates microbial activity and accelerates the decomposition of soil organic matter and microbial necromass (Mason et al. 2022). These opposing mechanisms explain the contrasting effects of MAP on MBC and MNC (Figure 2a). Rising temperatures generally increase microbial metabolic activity, which is consistent with our observations of elevated MBC (Figure 2a) (Chander et al. 1998; Xu and Yuan 2017). However, the impact of climatic factors on NAC was minimal (Figure 2a), likely because NAC is more closely linked to soil microbial community dynamics and to edaphic properties, which are mainly controlled by nutrient availability and soil structure rather than climatic variables (Han et al. 2024; Liang and Zhu 2021). Fertilisation directly affects microbial growth, biomass turnover and C use efficiency by altering the availability of key nutrients, such as N and P, with immediate localised impacts on microbial processes (Kuzyakov and Xu 2013). In contrast, climatic factors, such as MAT and MAP, exert more indirect effects, primarily by modifying vegetation activity, soil moisture regimes or organic matter decomposition rates (Davidson and Janssens 2006). However, these climate-driven changes may not consistently affect the balance between microbial biomass and MNC, particularly in fertilised systems where nutrient inputs can override climatic variability (Fierer et al. 2009). Consequently, NAC showed relatively limited responsiveness to broader climatic fluctuations.

Changes in microbially derived C due to management practices are also shaped by the initial soil properties (Clayton et al. 2021). Our results indicate that the effects of fertilisation on MNC and NAC were primarily driven by soil pH, with the highest MNC accumulation observed in alkaline soils (Figure 4a,c). The decline in pH likely imposes selective pressure on microbial communities and suppresses enzyme activities, whereas a higher initial pH buffers the negative effects of fertilisation-induced acidification, allowing for increased MNC accumulation (Guo et al. 2021; Rousk et al. 2010; Sinsabaugh et al. 2008). In contrast, neutral soils, which provide optimal conditions for microbial growth, support rapid MBC synthesis and accelerated decomposition activities (Figure 4a; Fierer and Jackson 2006). The combination of low MNC accumulation and high MBC content in neutral soils causes reduced NAC. Unlike changes in MNC and NAC, those in MBC were primarily driven by the iSOC content (Figure 2c) because SOC serves as a direct source of organic matter for microbial growth and metabolism (Ge et al. 2019). Fertilisation

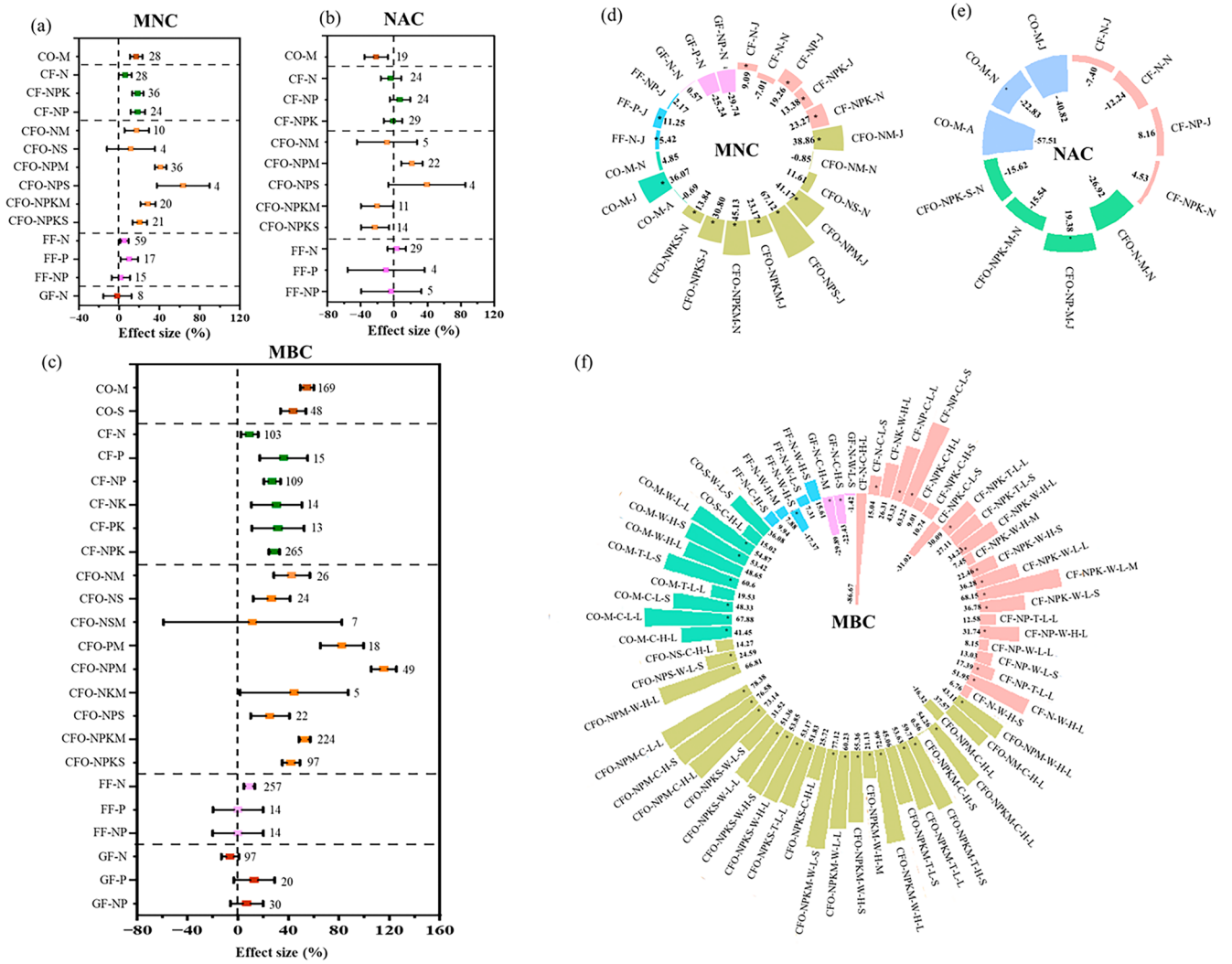


FIGURE 5 | Effect of (a–c) fertilisation practices and (d–f) their combination with specific climate and soil conditions on MNC, MBC and NAC. All results are presented as effect sizes (%) of the control soil (nonfertilisation treatment). Error bars are 95% CIs. The number of observations is shown next to each bar. CF, inorganic fertiliser application in cropland; CFO, organic–inorganic fertiliser application in cropland; CO, organic fertiliser application in cropland; duration of experiment (S, < 5 years; M, 5–10 years; L, > 10 years); FF, inorganic fertiliser application in forest ecosystem; GF, inorganic fertiliser application in grassland ecosystem; ipH (A, acidic; N, neutral; J, alkaline); iSOC (L, low; H, high); M, manure organic fertiliser; MBC, microbial biomass C; MNC, microbial necromass C; N, inorganic N fertiliser; NAC, microbial necromass accumulation coefficient; NP, inorganic N and P fertiliser; NPK, inorganic N, P and K fertiliser; NPM-C-L-L, NP fertiliser + manure with relatively cool temperature, low iSOC content and long-term fertilisation condition; NPM-J, NP fertiliser + manure under alkaline conditions; NPS-J, NP fertiliser + straw under alkaline conditions; S, straw organic fertiliser; soil MAT (C, cool; W, warm; T, tropical).

had a particularly strong effect in soils with low iSOC and significantly increased MBC by improving nutrient availability and stimulating organic matter transformation (Figure 4b) (Angers et al. 1992; He et al. 1997; Yuan et al. 2023). Overall, the effect of fertilisation on microbial C entombment is therefore highly dependent on the initial soil conditions.

4.3 | Carbon Sequestration Potential of Different Fertilisation Practices

A combined approach of organic and inorganic fertilisation was the most effective for enhancing soil C entombment (Figure 5a–c). Compared with N fertilisation alone, NP fertilisation enhances plant biomass and increases labile C inputs that fuel microbial activity (Zhran et al. 2021). As a crucial nutrient for phospholipid, nucleic acid and ATP production, P stimulates microbial growth (Johnston et al. 2019). The addition of straw promotes the microbial decomposition of complex compounds and the release of labile C, leading to greater microbial necromass accumulation, as observed in the NPS treatment (Figure 5a; Su et al. 2020). In contrast, manure provides a more balanced nutrient profile than straw, fostering microbial growth and turnover (Afonso et al. 2021; Zeng et al. 2007), which accounts for the higher MBC and NAC values observed in the NPM treatment (Figure 5b,c).

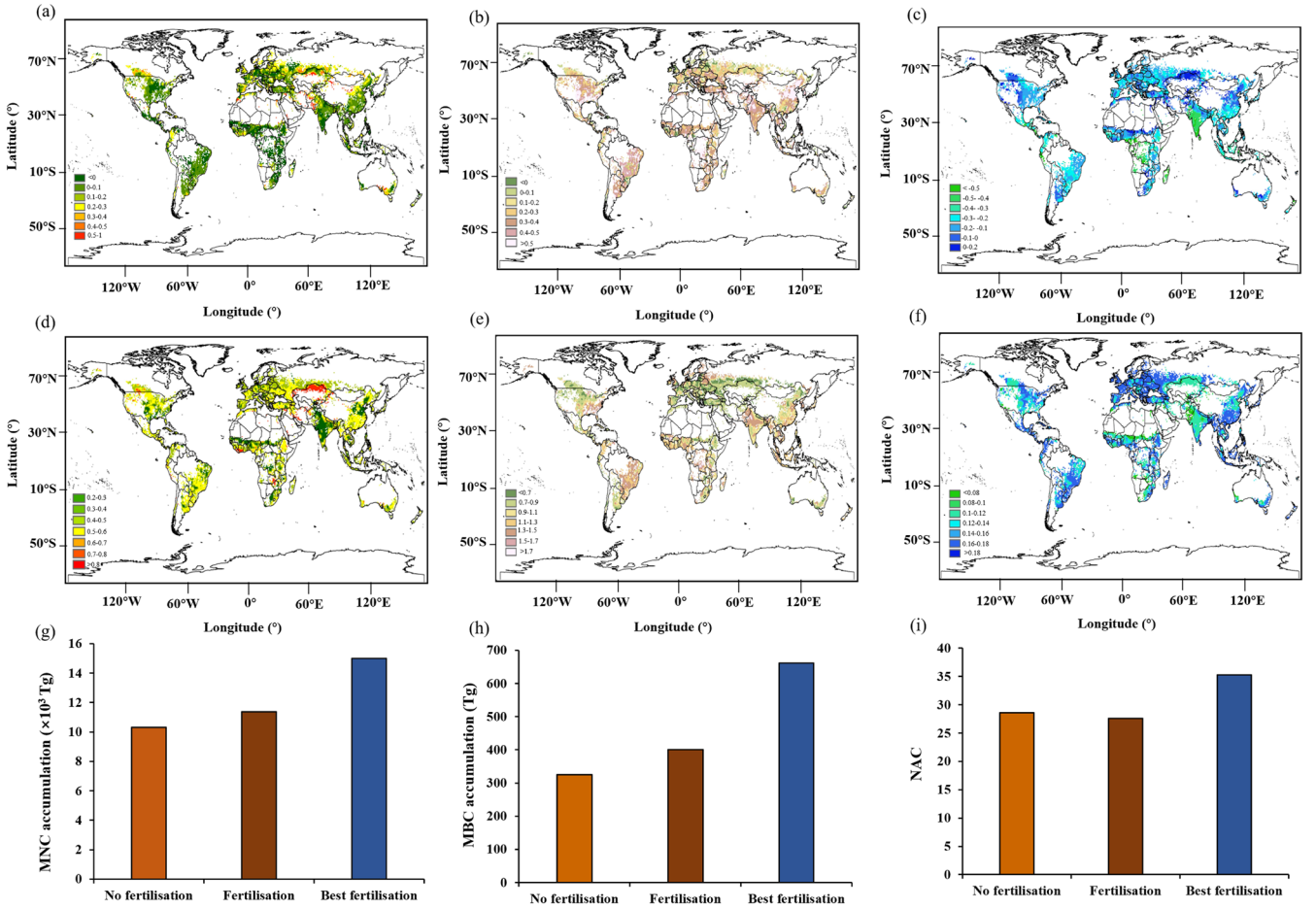


FIGURE 6 | Effect of (a–c) current fertilisation practices and (d–f) best management practices on the distribution of MNC, MBC and NAC and (g–i) the effect of no fertilisation, typical fertilisation and optimal fertilisation on the accumulation of MNC, MBC and NAC at topsoil. MBC, microbial biomass C; MNC, microbial necromass C; NAC, microbial necromass accumulation coefficient. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

In alkaline soils, both NPS and NPM treatments significantly enhanced MNC accumulation and increased NAC (Figure 5d,f). Alkaline environments can inhibit certain enzymes involved in organic matter decomposition (Drewnik 2006). The rapid decomposition of straw cellulose promotes microbial growth and necromass accumulation (Sinsabaugh et al. 2008; Six et al. 2006), whereas manure addition promotes the formation of organomineral complexes that protect microbial necromass. Geographically, regions such as Central and West Asia, which are characterised by carbonate-rich soils and low precipitation, are hotspots for MNC and NAC increases because of their alkaline soil conditions (Figure 6a,c). Predictions for croplands indicate higher MBC accumulation in North America and Asia (Figure 6b), where cold climates, low iSOC and long-term fertilisation create optimal conditions for MBC accumulation under NPM management. Cold temperatures slow microbial activity, decelerate organic matter decomposition and enhance microbial C use efficiency, leading to greater MBC accumulation (Davidson and Janssens 2006; Yuan et al. 2023). Long-term fertilisation further supports MBC buildup by providing sustained nutrient inputs (Zhang et al. 2017). These findings underscore the critical influence of site-specific fertilisation practices to maximise MNC, MBC and NAC and highlight the importance of tailored management strategies for optimising global soil C stocks.

4.4 | Implications and Uncertainty Analysis

As global agricultural expansion has continued, the optimisation of fertiliser management has become increasingly critical, particularly in intensively farmed regions. Converting forests and grasslands to croplands has led to significant reductions in SOC stocks, with reported declines of 24.5% and 22.7%, respectively (Huang et al. 2024). Our study revealed limited microbially driven C responses to fertilisation in forests and grasslands (Figure 1b), whereas increased microbial activity was observed in croplands under fertilisation, which enhances SOC accumulation through the greater microbial processing of crop residues and root biomass inputs (Mandal et al. 2007; Zhong et al. 2017). This suggests that cropland expansion promotes microbially driven soil C storage. However, excessive inorganic fertiliser use can result in soil acidification (Guo et al. 2010; Zhu et al. 2018), thereby diminishing the benefits of fertilisation for microbial necromass accumulation as the soil pH declines (Figure 4a). Conversely, combined organic and inorganic fertilisation more effectively stimulated microbial biomass production and

necromass accumulation (Figure 5a–c), highlighting the importance of implementing balanced fertilisation strategies in cultivated systems to maximise soil C sequestration and mitigate potential C loss.

Despite these findings, uncertainties remain due to data limitations. For example, insufficient data on soil clay content has hindered a detailed analysis of its influence on global microbial necromass stability (Table S4) despite its known effects on organomineral complex formation and soil aggregation (Figure S3; Ye et al. 2019; Ni et al. 2022). Additionally, the limited availability of grassland fertilisation data and the spatial bias of global fertilisation experiments—primarily concentrated in cropland ecosystems across Asia, Europe and North America, with sparse representation in Africa and South America—partially constrain the representativeness of our meta-analysis when assessing microbial responses to fertilisation. To improve global inference, future research should prioritise expanding empirical studies in these underrepresented regions.

5 | Conclusions

Fertilisation enhances microbial entombment processes by increasing MNC, primarily through greater MBC production, and does not significantly alter NAC. Inorganic fertilisers were more effective at increasing MBC and MNC when applied to croplands than when applied to grasslands or forests. Moreover, the combination of organic and inorganic fertilisation led to a more pronounced increase in microbial entombment than either fertiliser type alone. Although MAT significantly influenced MBC, ipH and iSOC were the dominant factors driving microbial entombment. Regionally, NP fertilisation combined with straw or manure under alkaline conditions, particularly in Central and Western Asia, effectively enhanced MNC and NAC, respectively. Conversely, NPM fertilisation in cooler climates, in low iSOC soils, and under long-term fertilisation regimes, especially in North America and Asia, was the most effective at increasing MBC. These findings underscore the positive impact of organic–inorganic fertilisation strategies on microbial entombment and emphasise the importance of considering initial soil conditions to improve predictions of the effects of fertilisation on microbial entombment and soil C sequestration.

Author Contributions

Haoran Fu: conceptualization, formal analysis, investigation, visualization, writing – original draft, writing – review and editing. **Hong Chen:** formal analysis, investigation, writing – original draft. **Zhengbo Ma:** formal analysis, investigation. **Guopeng Liang:** writing – review and editing. **Jing Tian:** writing – review and editing. **Wolfgang Wanek:** methodology, writing – review and editing. **David R. Chadwick:** writing – review and editing. **Davey L. Jones:** writing – review and editing. **Lianghuan Wu:** writing – review and editing. **Qingxu Ma:** conceptualization, visualization, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available at https://doi.org/10.6084/m9.figshare.29115149.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.