

assessing the spatial variations in MNC and their contribution to SOC in forest soils is critical for improving SOC projections and management under different climate scenarios (Zhu et al., 2020).

Amino sugars (AS) in cell walls, including glucosamine (GluN) in fungal cell walls and muramic acid (MurA) in bacterial cell walls, have been widely applied to indicate MNC because they persist in soils after cell death, are absent in plant litter, and contribute little to living microbial biomass (Amelung et al., 2001; Glaser et al., 2004; Joergensen, 2018; Wu et al., 2023). Several studies have employed AS concentrations to estimate MNC in soils (Wang et al., 2021a; Wang et al., 2021b; Li et al., 2022, 2023). MNC is generally composed of a high percentage of fungal necromass C (FNC), usually > 65%, and a low percentage of bacterial necromass C (BNC) because fungi are the principal decomposers of complex substrates that are dominant in forest soils (Wang et al., 2021a). Changes in the FNC/BNC ratio can affect their contribution to MNC and further affect SOC sequestration. Several recent studies have explored the spatial patterns of MNC content, its contribution to SOC storage (often indicated by the MNC/SOC ratio), its composition (FNC and BNC), and its driving factors on a global scale (Ni et al., 2020; Wang et al., 2021; Dai et al., 2022; Cao et al., 2023). For example, Wang et al. (2021) synthesized a global data set to explore the patterns of MNC, MNC/SOC, and FNC/BNC in three ecosystems (forest, cropland, and grassland) across different soil depths and found that MNC contributed to 35% of the SOC in forest soils. Hao et al. (2021) reported that climate governs the accumulation of AS based on 268 data points from five ecosystem biomes (temperate forest, subtropical forest, tropical forest, temperate grassland, and subtropical grassland), with higher AS concentrations in the temperate zone than those in the subtropical zone. Cao et al. (2023) analyzed necromass-derived soil organic carbon and its drivers on a global scale, encompassing various terrestrial ecosystems and wetlands, including forest, bareland, wetland, shrubland, grassland, cropland, and tundra. They explored differences in necromass-derived SOC among different ecosystems. However, relatively few studies have explored the patterns of FNC/BNC in forests, although it is important to understand the spatial patterns of MNC (Ni et al., 2020; Wang et al., 2021). In addition, despite these advancements, the geographical patterns of MNC, MNC/SOC, and FNC/BNC and their dependence on forest biomes and forest types are still debated. For example, Dai et al. (2022) reported a significantly higher soil AS content in mixed forests than that in coniferous forests, whereas Zhu et al. (2022) reported no significant differences between them. Therefore, there is an urgent need to conduct an updated global synthesis using data from a large number of forest

sites to examine the spatial patterns of MNC, MNC/SOC, and FNC/BNC in forest soils, as well as their driving factors.

A series of driving factors for MNC, MNC/SOC, and FNC/BNC have been examined by previous studies. These driving factors included climatic factors, such as mean annual temperature (MAT) and precipitation (MAP), and soil properties, such as soil pH, texture, and mineralogy (Amelung et al., 1999; Wang et al., 2021). Specifically, MAT and MAP can indirectly affect microbial necromass accumulation, mainly by altering microbial processes (i.e., microbial biomass, microbial C-use efficiency, and turnover rate), the quantity and quality of plant C inputs, and soil properties (Liang et al., 2019). In addition, soil acidity is an important driver of microbial community structure, with fungi being more acid-tolerant than bacteria, leading to increased fungal biomass dominance in acidic soils (Strickland and Rousk, 2010), which could thus affect the accumulation of soil microbial necromass. However, the long-term stabilization of microbial necromass is strongly regulated by soil texture due to the physical protection of soil aggregates (Six et al., 2000) or chemical binding to organo-mineral complexes against further degradation by microbes (Singh et al., 2017). Furthermore, microbial necromass accumulation is significantly affected by soil nitrogen (N; Ni et al., 2021). Microbial necromass comprises proteins, nucleic acids, fungal chitin, glycoproteins, and bacterial peptidoglycans, which account for over 60% of soil N (Schulten and Schnitzer, 1997). In N-rich soils, low “N starvation signal” reduces the microbial consumption of soil stable C (e.g., MNC) and promotes the preferential utilization of glucose, which leads to microbial necromass accumulation in soils (Fang et al., 2018; Perveen et al., 2019; Ni et al., 2021). In contrast, under N limitation, plants and microorganisms may send higher “N starvation signal” to stimulate microorganisms to produce more extracellular enzymes to decompose microbial necromass to obtain N sources (Ni et al., 2021), which decreases soil microbial necromass accumulation. Microbial necromass production is regulated by three physiological traits: microbial growth rate, microbial C-use efficiency, and microbial biomass turnover rate (Liang et al., 2019). However, there is limited understanding of how MNC responds to environmental factors, and the empirical relationships among climate, plants, soil, and microbial necromass in forests at wide geographical scales remain incomplete. Furthermore, whether the dominant factors affecting MNC, MNC/SOC, and FNC/BNC differ across forest biomes or types remain unexplored.

In this study, we conducted a comprehensive global data synthesis to explore the spatial patterns of MNC, MNC/SOC, and FNC/BNC in the surface soils (0–20 cm) of forests and their controlling factors based on 1704 data points (562 for MNC, 580 for MNC/SOC, and 562 for FNC/BNC) from 66

articles across 93 forest sites. We tested how forest biomes, forest types, microbial biomass C, climate, and soil physicochemical properties (mainly soil texture, pH, and N content) affected the magnitudes of MNC, MNC/SOC, and FNC/BNC in the surface 0–20 cm soils. We hypothesized that:

1) MNC, MNC/SOC, and FNC/BNC values would be higher in regions with higher MAT and MAP (e.g., tropical and subtropical forests) than those in regions with lower MAT and MAP (e.g., boreal and temperate forests), because higher MAT and MAP can lead to faster microbial turnover and accumulation of MNC, particularly FNC.

2) MNC, MNC/SOC, and FNC/BNC values would be higher in mixed and broadleaved forests than those in coniferous forests because mixed species promote litter decomposition rate, and broadleaved species have higher quantity and quality of litter inputs as well as faster litter decomposition rates than coniferous forests.

3) Soil physicochemical properties, such as soil N content, soil pH, and soil texture, can directly affect MNC, MNC/SOC, and FNC/BNC in forest soils. It is because forest soils with different levels of soil N content could lead to variations in plant productivity and C inputs, and soils with different soil clay content could provide different levels of MNC storage potential.

2 Materials and methods

2.1 Data collection

The concentrations of AS and microbial necromass in soils were partially based on the data published by Ni et al. (2020), Wang et al. (2021), and Hao et al. (2021), and the concentration database was updated by incorporating peer-reviewed journal articles from the Web of Science (available at the website Web of Science) and the China National Knowledge Infrastructure (available at the website cnki.net) published before 2023. We searched the papers from the Web of Science in English. The search terms were “amino sugars,” “microbial necromass,” and “microbial residue.” We also used Chinese keywords, such as “微生物残体” (Chinese of microbial necromass) and “氨基糖” (Chinese of amino sugars), to search the papers from the China National Knowledge Infrastructure. Raw data were obtained from tables or extracted from published figures using GetData Graph Digitizer software. Only data from ≤ 20 cm soil layers in forests were considered, whereas those from the litter layer, O layer, and soils deeper than 20 cm were not included in this study.

We obtained 1704 data points (562 for MNC, 580 for MNC/SOC, and 562 for FNC/BNC) from 66 articles across 93 forest sites that met the specified criteria (Supplementary Table S1). The latitude ranged from 4.5°S to 52.25°N, and

the MAT ranged from -5.4 to 26°C . To explore the dependence of MNC, MNC/SOC, and FNC/BNC on climate, soil physicochemical properties, and microbial biomass C, we collected the following information from previous publications: MAP, MAT, SOC, total nitrogen (N), microbial biomass C (MBC), soil clay content, silt content, sand content, and soil pH. We collected the information of forest biomes from the literature, which were given as “boreal forest,” “temperate forest,” “subtropical forest,” “tropical forest,” and “mediterranean forest.” If the forest biome information were not given, we extracted the biome information from the biome inventory website: DRYAD (Fischer et al., 2022). Finally, the forest biomes were grouped as subtropical and tropical, boreal, Mediterranean, and temperate forests. Owing to the limited data on subtropical and tropical biomes, the data from these biomes were merged into a single (sub-)tropical forest category for our analysis. The forest types included broadleaved, coniferous, and mixed forests.

2.2 Calculations

If the study did not directly provide MNC data, we calculated it using the following methods: The BNC was calculated by directly multiplying the concentration of MurA by a conversion factor of 45 (Eq. (1); Appuhn and Joergensen, 2006). FNC was calculated by multiplying the concentration of fungal GluN by a conversion factor of nine (Eq. (2); Appuhn and Joergensen, 2006; Joergensen, 2018). Fungal GluN was calculated by subtracting bacterial GluN from total GluN, and bacterial GluN was estimated based on the bacterial MurA with a molar GluN to MurN ratio of 2:1 in bacteria, using molecular weights of 179.17 and 251.23 g/mol for GluN and MurA, respectively (Eq. (3); Engelking et al., 2007). The MNC was estimated as the sum of the FNC and BNC (Eq. (4); Joergensen, 2018). The MNC/SOC ratio represents the contribution of microbial necromass to SOC content (Liang et al., 2019). The FNC/BNC ratio was also calculated to indicate the relative abundance of FNC compared with BNC.

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

$$\text{FNC} = \text{Fungal GluN} \times 9 \quad (2)$$

$$\text{Fungal GluN} = (\text{total GluN}/179.17 - 2 \times \text{MurA}/251.23) \times 179.17 \quad (3)$$

$$\text{Total MNC} = \text{BNC} + \text{FNC} \quad (4)$$

2.3 Statistical analysis

The Wilcoxon test was used to assess the differences between the two groups of forest biomes and forest types. Linear and nonlinear regressions (exponential curves or

Gaussian curves according to the distributions of data points) were conducted to analyze the relationships of MNC and MNC/SOC with latitude, MAT, MAP, soil clay content, soil pH, and soil N content. All meta-regressions were performed using Sigmaplot v15.0 (Systat Software Inc., San Jose, California, USA).

3 Results

3.1 MNC, MNC/SOC, and FNC/BNC in different forest biomes and forest types

Our results showed that across all sites, MNC in surface 0–20 cm soils in forests globally ranged from 0.22 to 132.95 g kg⁻¹, with average and standard error of 19.04 ± 0.79 g kg⁻¹ ($n = 562$). Considering different forest biomes, MNC contents in surface 0–20 cm soils were 59.06 ± 2.59, 24.14 ± 1.37, 13.71 ± 0.46, and 4.03 ± 0.67 g kg⁻¹ for boreal ($n = 8$), temperate ($n = 283$), (sub-)tropical ($n = 238$), and Mediterranean ($n = 33$) forests, respectively (Fig. 1a). The MNC content followed the order of boreal > temperate > (sub-)tropical > Mediterranean forests, with significantly higher values in boreal forests than those in other forests (Fig. 1a). The contribution of MNC to SOC (i.e., MNC/SOC) in surface 0–20 cm soils in forests globally ranged from 1.21% to 100%, with an average and standard error of 42% ± 1%.

In addition, MNC/SOC values in surface 0–20 cm soils were 17% ± 0%, 45% ± 1%, 43% ± 1%, and 16% ± 1% in boreal, temperate, (sub-)tropical, and Mediterranean forests, respectively (Fig. 1b). The MNC/SOC ratio was significantly higher in (sub-)tropical and temperate forests than that in boreal and Mediterranean forests (Fig. 1b). Our results showed that across all sites, FNC/BNC in surface 0–20 cm soils in forests ranged globally from 0.17 to 14.5, with average and standard error of 3.23 ± 0.09. For forest biomes, FNC/BNC in surface 0–20 cm soil was 6.25 ± 0.63, 4.06 ± 0.14, 2.23 ± 0.06, and 2.52 ± 0.13 for boreal, temperate, (sub-)tropical, and Mediterranean forests, respectively, with significantly higher values in boreal forests than those in other forests (Fig. 1c).

Considering different forest types, MNC content in surface 0–20 cm soils was significantly higher in mixed forests (23.64 ± 1.25 g kg⁻¹) than those in coniferous forests (22.78 ± 2.4 g kg⁻¹) and in broadleaved forests (15.88 ± 0.69 g kg⁻¹) ($p < 0.01$; Fig. 1d). The MNC/SOC was 45% ± 1%, 42% ± 2%, and 40% ± 2% in broadleaved, coniferous, and mixed forests, respectively (Fig. 1e), with significantly higher values in broadleaved forest than those in coniferous forest ($p = 0.04$; Fig. 1e). In addition, the FNC/BNC was 3.27 ± 0.11, 3.10 ± 0.20, and 3.06 ± 0.25 in broadleaved, coniferous, and mixed forests, respectively (Fig. 1f). There were no significant differences among the forest types. Results from two-way analysis of variance (ANOVA) showed that the

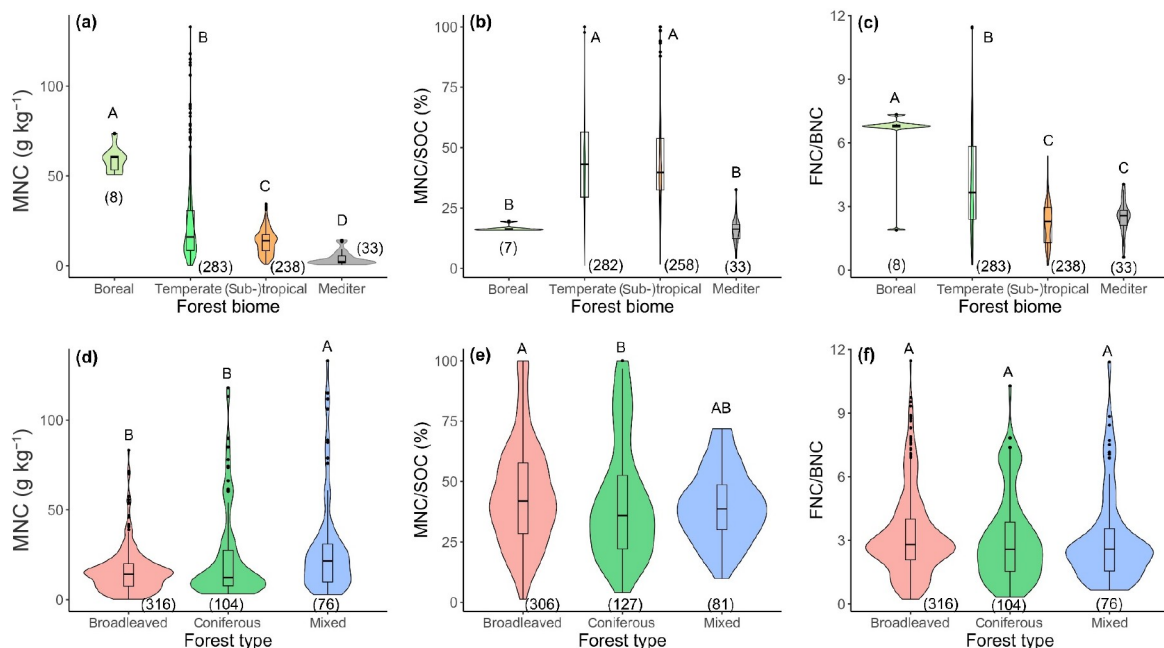


Fig. 1 Variations in microbial necromass carbon (MNC), its contribution to soil organic carbon (MNC/SOC), and the ratio of fungal necromass carbon to bacterial necromass carbon (FNC/BNC) in 0–20 cm surface soils across forest biomes (a–c) and forest types (d–f). The shapes of the violin represent the distribution pattern of the corresponding data. The upper and lower ends of boxes denote the 0.25 and 0.75 percentiles, respectively. The solid line and cross in the box mark the median and mean of each data set, respectively. Solid dots denote outliers. Numbers in the parentheses represent the number of data. The different lowercase letters indicate significant differences between groups.

effect of forest biome ($p < 0.001$) and the interaction between forest biome and forest type ($p < 0.001$) was significant for MNC (Fig. 2a). In the Mediterranean forest, the MNC in coniferous forests was significantly higher than that in broad-leaved forests (Fig. 2a, $p < 0.01$). In (sub-)tropical biome, MNC in mixed forests was significantly higher than that in broadleaved forests ($p = 0.05$), whereas in temperate biome, MNC in mixed forests was significantly higher than that in broadleaved ($p = 0.01$) and coniferous forests ($p = 0.02$) (Fig. 2a). Furthermore, two-way ANOVA showed no interaction between forest biome and forest type on MNC/SOC or FNC/BNC (Fig. 2b–2c). The effect of forest biome was significant for the MNC/SOC ratio ($p < 0.01$), and the effect of forest type was marginally significant for the MNC/SOC ratio ($p = 0.09$, Fig. 2b). Specifically, MNC/SOC in broadleaved forests was significantly higher than that in coniferous and mixed forests in temperate biome (Fig. 2b). For FNC/BNC, the effects of both forest biome ($p < 0.01$) and forest type ($p < 0.01$) were significant (Fig. 2c).

3.2 Correlations of MNC, MNC/SOC, FNC/BNC with latitude and climate

Regarding climate variables, MNC was significantly and positively correlated with latitude across all sites ($r^2 = 0.09$, $p < 0.01$), in (sub-)tropical forests ($r^2 = 0.08$, $p < 0.01$), and in Mediterranean forests ($r^2 = 0.63$, $p < 0.01$) (Fig. 3a). Additionally, MNC showed a significant negative correlation with MAT across all sites ($r^2 = 0.28$, $p < 0.01$), temperate forests ($r^2 = 0.14$, $p < 0.01$), (sub-)tropical forests ($r^2 = 0.34$, $p < 0.01$), and Mediterranean forests ($r^2 = 0.59$, $p < 0.01$) (Fig. 3b). Moreover, MNC was significantly negatively correlated with MAP across all sites ($r^2 = 0.03$, $p < 0.01$) and in (sub-)tropical forests ($r^2 = 0.15$, $p < 0.01$) but was significantly positively correlated with MAP in Mediterranean forests ($r^2 = 0.62$, $p < 0.01$) (Fig. 3c). In terms of MNC/SOC, there was no significant correlation with latitude across all sites in temperate, (sub-)tropical, or Mediterranean forests (Fig. 3d). For MAT, it first increased and then decreased across all sites ($r^2 = 0.11$, $p < 0.01$), in temperate ($r^2 = 0.07$, $p < 0.01$), and in (sub-)tropical forests ($r^2 = 0.07$, $p < 0.01$) (Fig. 3e). In

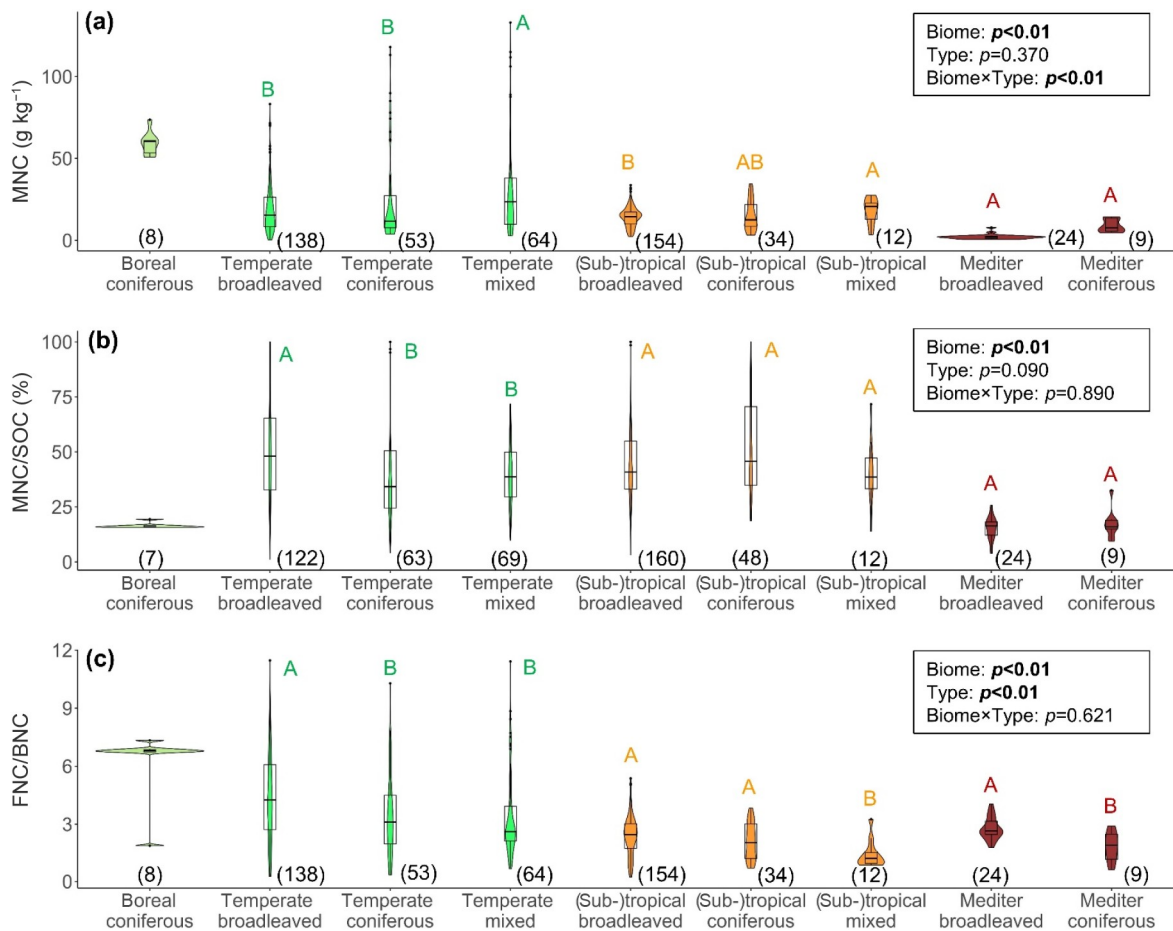


Fig. 2 Variations in MNC (a), its contribution to SOC (MNC/SOC) (b), the ratio FNC/BNC (c), in 0–20 cm surface soils across forest types in different forest biomes. The shapes of the violin represent the distribution pattern of the corresponding data. The upper and lower ends of boxes denote the 0.25 and 0.75 percentiles, respectively. The solid line and cross in the box mark the median and mean of each data set, respectively. Solid dots denote outliers. Numbers in the parentheses represent the number of data. The different capital letters indicate the significant differences between the two groups in each forest biome.

addition, MNC/SOC first increased and then decreased with MAP across all sites ($r^2 = 0.02$, $p < 0.01$) and decreased nonlinearly with MAP in (sub-)tropical forests ($r^2 = 0.04$, $p < 0.01$) (Fig. 3f). FNC/BNC was positively related to latitude across all sites ($r^2 = 0.14$, $p < 0.01$) but negatively correlated with latitude in the Mediterranean forests ($r^2 = 0.31$, $p < 0.01$) (Fig. 3g). FNC/BNC was negatively correlated with MAT across all sites ($r^2 = 0.17$, $p < 0.01$) but was positively correlated with MAT in (sub-)tropical ($r^2 = 0.13$, $p < 0.01$) and Mediterranean forests ($r^2 = 0.11$, $p = 0.02$) (Fig. 3h). In addition, FNC/BNC was negatively correlated with MAP across all sites ($r^2 = 0.17$, $p < 0.01$) and in Mediterranean forests ($r^2 = 0.11$, $p = 0.02$) but positively correlated with MAP in temperate ($r^2 = 0.13$, $p < 0.01$) and (sub-)tropical forests ($r^2 = 0.11$, $p = 0.02$) (Fig. 3i).

3.3 Correlations of MNC, MNC/SOC, FNC/BNC with MBC and soil properties

The MBC data were available only for temperate and (sub-)tropical forests in the data set. MNC was consistently positively correlated with MBC across all sites ($r^2 = 0.67$, $p < 0.01$), temperate forests ($r^2 = 0.66$, $p < 0.01$), and (sub-)tropical forests ($r^2 = 0.53$, $p < 0.01$; Fig. 4a). However, no significant correlation was found between MNC/SOC and MBC, regardless of whether the forests were temperate or (sub-)tropical (Fig. 4b). FNC/BNC was negatively correlated with MBC in (sub-)tropical forests ($r^2 = 0.11$, $p = 0.02$) but positively correlated with MBC in temperate forests ($r^2 = 0.13$, $p < 0.01$) (Fig. 4c).

Regarding soil properties, MNC was significantly negatively correlated with soil clay content in temperate forests ($r^2 =$

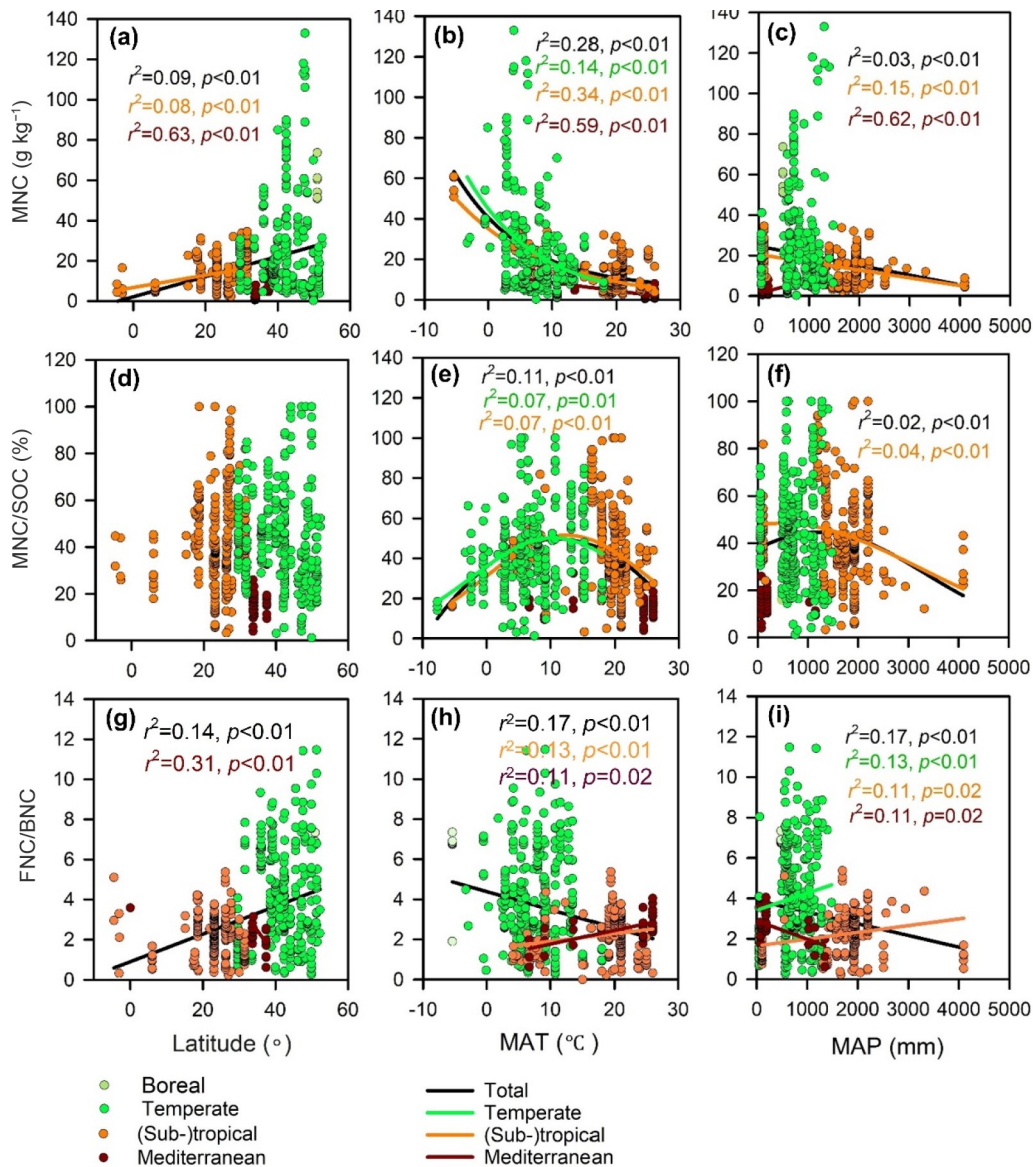


Fig. 3 Relationships of MNC (a–c), ratio MNC/SOC (d–f), ratio FNC/BNC (g–i), in 0–20 cm surface soils in boreal (light green), temperate (green), (sub-)tropical (orange), and Mediterranean (dark red) forests with latitude, mean annual temperature (MAT), and mean annual precipitation (MAP). r^2 values and linear regression lines are shown for significant relationships at $p < 0.05$.

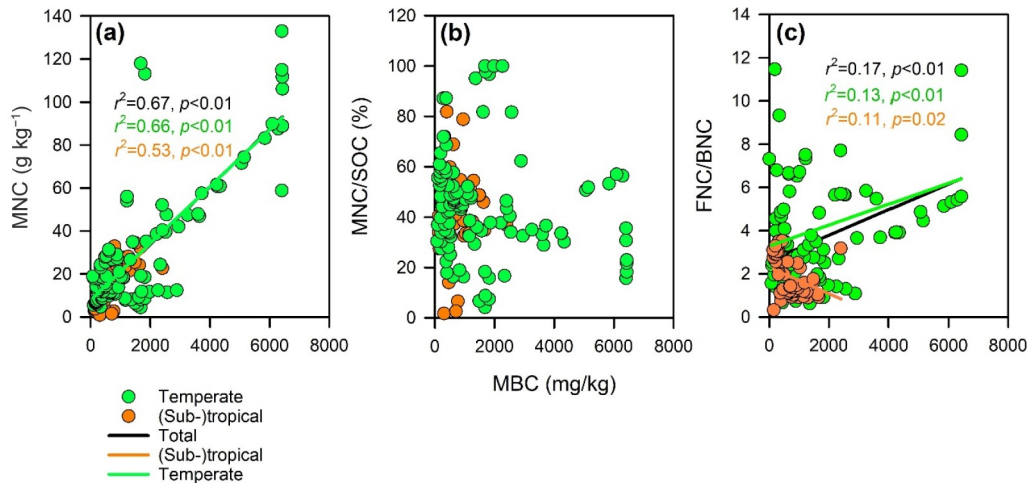


Fig. 4 Relationships of MNC (a), ratio MNC/SOC (b), ratio FNC/BNC (c), with microbial biomass carbon (MBC) in 0–20 cm surface soils in temperate (green) and (sub-)tropical (orange) forests. r^2 values and linear regression lines are shown for significant relationships at $p < 0.05$.

0.03, $p = 0.02$) (Fig. 5a). It was also significantly positively correlated with soil pH across all sites ($r^2 = 0.01$, $p = 0.01$), in temperate ($r^2 = 0.03$, $p < 0.01$), and (sub-)tropical forests ($r^2 = 0.14$, $p < 0.01$) (Fig. 5b); however, it was significantly negatively correlated with soil pH in Mediterranean forests ($r^2 = 0.56$, $p < 0.01$) (Fig. 5b). In addition, MNC was significantly positively correlated with soil N content across all sites ($r^2 = 0.01$, $p = 0.01$), in boreal ($r^2 = 0.01$, $p = 0.01$), temperate ($r^2 = 0.03$, $p < 0.01$), (sub-)tropical ($r^2 = 0.14$, $p < 0.01$), and Mediterranean forests ($r^2 = 0.56$, $p < 0.01$) (Fig. 5c). MNC/SOC was significantly negatively correlated with soil clay content in (sub-)tropical forests ($r^2 = 0.09$, $p < 0.01$) (Fig. 5d), with soil pH across all sites ($r^2 = 0.04$, $p < 0.01$) (Fig. 5e) and with soil N content in temperate forests ($r^2 = 0.10$, $p < 0.01$) and (sub-)tropical forests ($r^2 = 0.14$, $p < 0.01$) (Fig. 5f). FNC/BNC was negatively correlated with the soil clay content in the (sub-)tropical forests ($r^2 = 0.12$, $p < 0.01$) (Fig. 5g). FNC/BNC was positively correlated with soil pH across all sites ($r^2 = 0.01$, $p = 0.02$), temperate ($r^2 = 0.02$, $p = 0.02$), and Mediterranean forests ($r^2 = 0.33$, $p < 0.01$) (Fig. 5h) but negatively correlated with soil pH in (sub-)tropical forests ($r^2 = 0.10$, $p < 0.01$). In addition, FNC/BNC was positively correlated with the soil N content across all sites ($r^2 = 0.16$, $p < 0.01$), temperate forests ($r^2 = 0.09$, $p < 0.01$), and Mediterranean forests ($r^2 = 0.16$, $p = 0.04$) (Fig. 5i).

4 Discussion

4.1 Average MNC, MNC/SOC, and FNC/BNC in forest 0–20 cm soils

By comparing our study with the previous studies, we found the MNC value in our study ($19.04 \pm 0.79 \text{ g kg}^{-1}$) was higher than that reported in Wang et al. (2021) (17.16 g kg^{-1} in top

0–20 cm soils) and Cao et al. (2023) (13.05 g kg^{-1}); and the MNC/SOC ($42\% \pm 1\%$) was higher than that in Wang et al. (2021) (35%) and lower than that in Cao et al. (2023) (49%). For FNC/BNC, the average value in the present study (3.23 ± 0.09) was higher than those reported in Ni et al. (2020) (2.73 in 0–20 cm soils) and Wang et al. (2021) (2.83 in 0–20 cm soils). In addition, the average MNC and MNC/SOC values in temperate and (sub-) tropical forests in the present study were similar to those reported by Cao et al. (2023). However, this study showed higher average MNC and lower MNC/SOC in boreal forests than those reported by Cao et al. (2023). Although there were no data on MNC and MNC/SOC for Mediterranean forests in Cao et al. (2023), our study allows for a direct comparison of Mediterranean forests with other forest biomes. Therefore, compared to Cao et al. (2023), we gathered a more extensive data set covering diverse forest biomes. Consequently, our study delves into greater detail regarding the patterns and drivers of MNC in forest ecosystems.

Recent research has pointed out that “the composition of microbial necromass does not equal that of microbial biomass” and “the quantity and persistence of microbial necromass is governed by microbial death pathways, not only the initial biomass composition” (Camenzind et al., 2023). Nevertheless, our results suggest that microbial necromass and microbial biomass in forest soils are highly correlated over a wide geographic scale (Fig. 4a), which suggested the quantity of microbial biomass could be an important predictor of microbial necromass accumulation in forest soils.

4.2 Forest biome-dependent MNC, MNC/SOC, and FNC/BNC in forest soils

Representing the largest data set to date, this synthesis

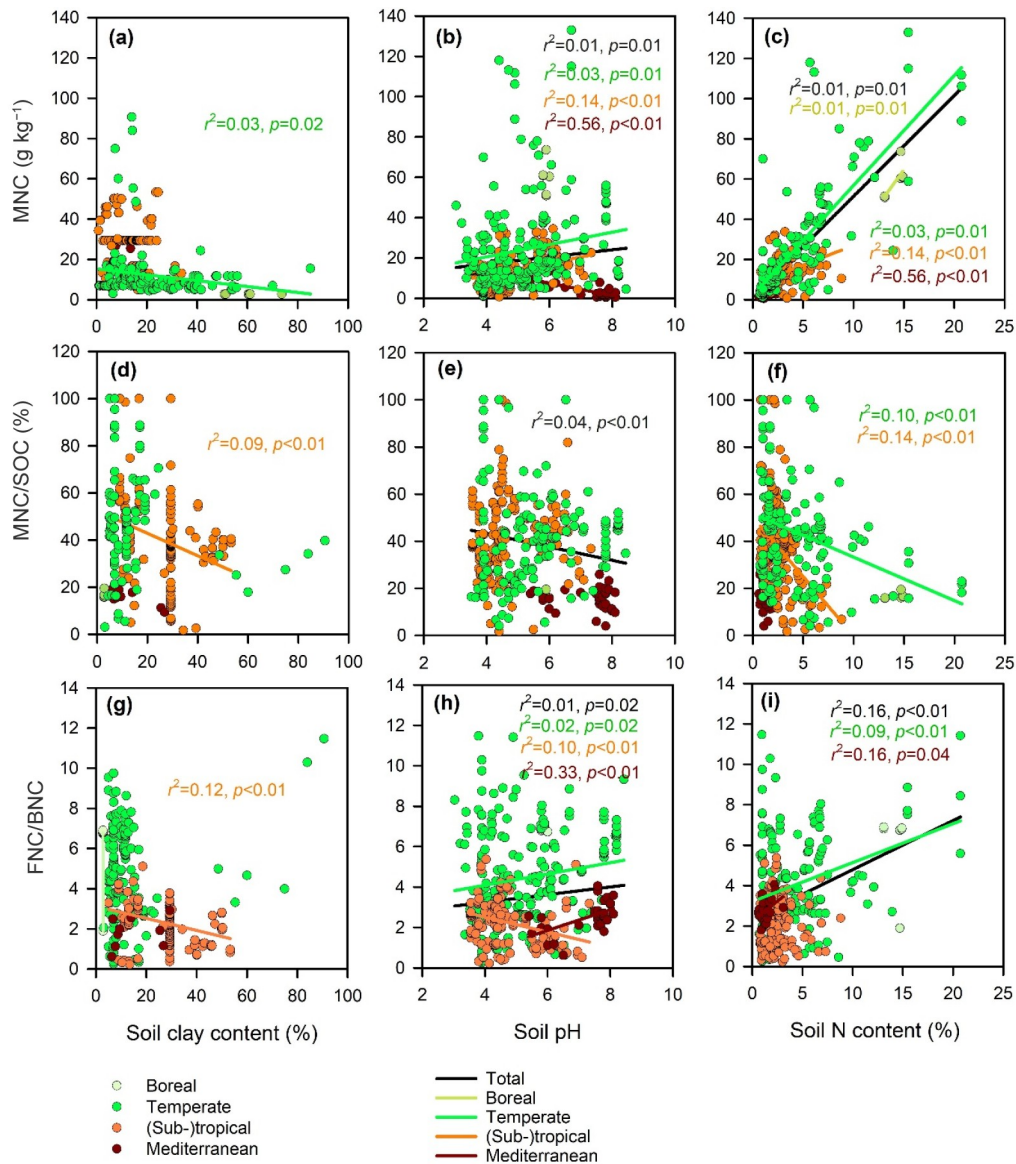


Fig. 5 Relationships of MNC (a–c), ratio MNC/SOC (d–f), ratio FNC/BNC (g–i), in 0–20 cm surface soils in boreal (light green), temperate (green), (sub-)tropical (orange), and Mediterranean (dark red) forests with soil clay content (%), soil pH, and soil N content. r^2 values and linear regression lines are shown for significant relationships at $p < 0.05$.

showed relatively higher MNC and FNC/BNC, and lower MNC/SOC ratios in boreal forests than those in other forest biomes (Fig. 1a, 1b, 1c). Because boreal forests are known to have low MAT, and thus low primary and secondary productivity, this pattern could be attributed to slow MNC decomposition and high accumulation of both MNC and non-microbial-necromass SOC (e.g., plant-derived SOC) in boreal forests in cold weather (Chen et al., 2020). This supports the idea that boreal forest soils function as net terrestrial C sinks in the global C cycle. Chen et al. (2020) linked higher MNC and lower MNC/SOC in boreal forests than those in tropical forests to temperature and soil N factors. This synthesis also showed relatively higher FNC/BNC ratios in boreal forests than those in other forest

biomes (Fig. 1c), which is consistent with the results reported by Chen et al. (2020). Previous studies have reported that FNC plays an important role in the stabilization and accumulation of SOC because very high fungal biomass (up to 600 kg ha⁻¹) derived from tannin-rich plant roots is associated with abundant ectomycorrhizae in boreal forests (Wallander et al., 2004; Adamczyk et al., 2019). The ratio of fungal to bacterial biomass in boreal forests (5.03) has also been reported to be higher than that in temperate forests (4.92) and tropical/subtropical forests (2.22) (He et al., 2020a), which could lead to a high FNC/BNC ratio in boreal forests. However, in this study, the data points in boreal forests were relatively low, with only eight for MNC and seven for MNC/SOC, suggesting the need for more compre-

hensive studies in boreal forest biomes. Hao et al. (2021) also found limited data from boreal regions and suggested that future studies should focus on improvements in data collection and accurate estimation of microbial residue accumulation.

Additionally, the patterns and controlling factors of MNC in Mediterranean forests have not been studied by previous global data syntheses (Chen et al., 2020; Ni et al., 2020; Wang et al., 2021; Dai et al., 2022; Cao et al., 2023). This study obtained 33 data points for MNC, MNC/SOC, and FNC/BNC in Mediterranean forests, and the results showed the lowest MNC and MNC/SOC in the Mediterranean forests among the forest biomes. Mediterranean forest has a unique climate with marked seasonality and severe summer droughts. Under such climatic conditions, plants have developed adaptive mechanisms to overcome Mediterranean summer drought, such as long-lived and hard leaves (sclerophylly), which cannot only reduce the quantity of litter but also produce low-quality litter and subsequently decelerate litter decomposition processes (Rutigliano et al., 2004; Incerti et al., 2011). In addition, the unique climatic conditions of Mediterranean forests can stress soil microbial communities (Aponte et al., 2010; Grosso et al., 2018), resulting in the decoupling of microbial biomass, activity, and SOC (Lucas-Borja et al., 2012). The stressed microbial communities, together with reduced litter inputs and decelerated litter decomposition, could at least partially explain the lower MNC and MNC/SOC values in the Mediterranean forests than those in other forest biomes.

We found significant differences in the spatial patterns and controlling factors of MNC between (sub-)tropical and temperate forests (Figs. 1a, 1b, 1c, 3, 4, 5). Specifically, MNC and FNC/BNC in temperate forests were significantly higher compared to (sub-)tropical forests (Fig. 1a, 1c), suggesting the cold environments in temperate forest support the accumulation of MNC and FNC. We also found both MNC in (sub-)tropical and temperate forests nonlinearly decreased with MAT (Fig. 3b), suggesting temperature plays an important role in regulating the accumulation of forest MNC in top 20 cm soils. However, MNC in temperate forests were not related to MAP, contrasting with that in (sub-)tropical forests (Fig. 3c). In addition, we found total soil N was one of the most important controlling factors affecting MNC both in (sub-)tropical and temperate forests (Fig. 5c). Temperate forests are often N-limited (Aber et al., 1998; Brumme and Khanna, 2008), which could explain the predominant role of total soil N in the MNC. For example, Chen et al. (2020b) found significant increases in microbial residues (AS) and mineral associated organic C after 6 years of N addition in two temperate forests, suggesting that N is an important factor affecting MNC in temperate forests. This effect is likely because a higher total N content promotes MNC formation by enhancing available nutrients for living microbial

organisms (Geisseler and Scow, 2014). For example, Liao et al. (2022) found that N availability and mineral particles contributed to the formation of fungal necromass in a newly formed stable carbon pool in the alpine regions of Southwest China. Therefore, the data in our study can be used to manage soil microbial necromass carbon to mitigate climate change in forests.

In addition, our results showed MNC in temperate forest decreased with soil clay content (Fig. 5a), which did not support the opinion that soils with higher clay content often have higher MNC and MNC/SOC because fine soil particles have a smaller pore diameter and more surface sites that can stabilize microbial necromass or metabolites by forming organo-mineral bonds (Six et al., 2006). The amount of MNC in soils can be controlled by its production and stabilization (Buckeridge et al., 2022). Our global data synthesis, for the first time, indicates that the amount of MNC in soils is controlled by both the production and retention/stabilization in (sub-)tropical forests but is predominantly produced in temperate forests. Although previous large-scale studies have identified temperature and soil N (or soil C/N) as the two major factors affecting MNC in forests (Chen et al., 2020; Deng and Liang, 2022; Zhu et al., 2022), this study provides a clear understanding of the correlations among microbial necromass C, MAT, soil clay content, soil total N, soil pH, and MBC, further confirming the critical role of MAT in regulating MNC in different forest biomes (Doetterl et al., 2015; Ni et al., 2020). This could be attributed to the fact that soil microbial communities are the main drivers of soil necromass degradation (Maillard et al., 2023), and MAT directly affects the communities and thus affects the accumulation of MNC.

The ratio of fungal to bacterial biomass was reported to be strongly affected by climatic and edaphic factors, and its value in temperate forests (4.92) was reported to be two times greater than that in tropical/subtropical forests (2.22) (He et al., 2020a), which led to higher FNC/BNC in temperate forests than that in (sub-)tropical forests. The higher FNC/BNC in temperate forests could also partially explain the higher MNC in temperate forests than that in (sub-)tropical forests. Although temperate forests have a higher MNC than (sub-)tropical forests, MNC has not been found to be the primary driver of SOC persistence in temperate forests (Craig et al., 2022), which may explain why MNC/SOC did not differ between the two forest biomes.

4.3 Forest type impacts on soil MNC are biome-dependent

Different forest types (i.e., broadleaved, coniferous, and mixed forests) exhibit varying plant species compositions, which can affect the quality of litter inputs (Huang et al., 2011; Zhou et al., 2019), soil microbial communities (Hackl et al., 2005; Wang et al., 2016), litter decomposition rates

(Prescott et al., 2000; Zhang et al., 2008), and the heterogeneity of SOC chemical components (Wang et al., 2016; Wang et al., 2023). Therefore, variations in these factors further influence MBC and MNC accumulation in soils (Shao et al., 2017; Dai et al., 2022). This study revealed a significant interaction between forest biome and forest type for MNC ($p < 0.01$), with highest MNC in mixed forest (Figs. 1d, 2a). Analyses of the differences in MNC among different forest types have also been reported in previous studies (Dai et al., 2022; Zhu et al., 2022). For example, Dai et al. (2022) reported significantly higher soil amino sugar content in mixed forests ($n = 3$) than that in coniferous forests ($n = 4$) in a Chinese forest, which is consistent with the global distribution patterns ($n = 38$ for mixed and $n = 64$ for coniferous forests). Zhu et al. (2022) found no significant difference in total AS content in soils among the three forest types, but did not provide the sampling number for each type of forest. Our global synthesis supports the idea that tree species mixtures promote microbial necromass accumulation in soils (Dai et al., 2022; Wang et al., 2022). However, the ratio of MNC/SOC was not found the highest in mixed forest (Figs. 1e, 2b), which suggested that the higher SOC content in mixed forest is not due to higher MNC accumulation in mixed forest compared with monocultures.

Generally, MNC is composed of a high percentage of fungal necromass biomass (> 65%) and a low percentage of bacterial necromass biomass (32%–36%) because fungi are the principal decomposers of complex substrates dominant in forest soils (Wang et al., 2021a). Recent research has found that the pine-oak mixed forest had higher network topological features of fungi but lower links and average degrees of bacteria than pure forests (Huo et al., 2023). Therefore, MNC in mixed forests should be higher because of more fungal biomass contributions than that in pure forests. However, this notion was not supported by either our results or previously reported findings (Ni et al., 2020), yet mixed forests with higher MNC had lower FNC/MNC than broadleaved and coniferous forests (Figs. S1c, S1d and S2). Given that soil N content was the predominant factor affecting MNC across forest types, the higher MNC in mixed forests was possibly due to the higher soil N content than those in broad-leaved and coniferous forests (Fig. S3). In addition to forest biomes and types, we believe that other factors, which were not analyzed in this study, play important roles in MNC production and accumulation, such as the soil food web (Kou et al., 2023) and the role of soil earthworms (He et al., 2020b; Angst et al., 2022).

5 Conclusions

In summary, this study highlights the significant impacts of forest biome and forest type on MNC content, MNC/SOC

ratio, and FNC/BNC ratio in the 0–20 cm soils of forests. Specifically, MNC was higher in boreal and temperate forests than that in (sub-)tropical and Mediterranean forests and higher in mixed forests than that in broad-leaved and coniferous forests. Additionally, MNC/SOC was higher in temperate and (sub-)tropical forests than that in boreal and Mediterranean forests and higher in broadleaved forests than that in coniferous forests. Based on regression analyses, climate, MBC, soil pH, and soil total N were identified as the important factors affecting MNC. Notably, our results suggest that the MNC content in soils was mainly controlled by both the production and retention/stabilization processes in (sub-)tropical forests and was predominantly controlled by production in temperate forests, which has not been reported in previous large-scale studies. This global synthesis, with the largest number of forest sites covered to date, is necessary for understanding the patterns and controlling factors of soil MNC and its contribution to SOC in forests. Nevertheless, the results presented in this synthesis are subject to potential uncertainties stemming from variations in sampling times, analytical methods, and the potential influence of site-specific MNC and AS conversion factors observed in different studies. Future research employing standardized measurement methods to address these potential data gaps will prove valuable in the ongoing monitoring and management of microbial necromass carbon in forest ecosystems.

Abbreviations

MNC, microbial necromass carbon; SOC, soil organic carbon; FNC/BNC, fungal-to-bacterial necromass carbon ratio; AS, amino sugars; GluN, glucosamine; MurA, muramic acid.

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

The data set used will be made available after acceptance.

Acknowledgments

This study was financially supported by the National Natural Science Foundation of China (42122054, 42192513, and 42321004), Guangdong Basic and Applied Basic Research Foundation (2021B1515020082), Key Platform and Scientific Research Projects of the Guangdong Provincial Education Department (2020KCXTD006), and Guangdong Provincial Key Laboratory of Soil and Groundwater Pollution Control (No. 2023B1212060002).

Author contributions

SX and JJW designed this study. SX and XYS searched the papers and collected the data, and SX analyzed the data. SX and JJW prepared the manuscript. HZ revised and commented on the initial draft and final manuscript.

Electronic supplementary material

Supplementary material is available in the online version of this article at <https://doi.org/10.1007/s42832-024-0237-3> and is accessible for authorized users.

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