Microbial necromass contribution to topsoil organic carbon storage of natural and agricultural ecosystems

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Abstract

Microbial necromass is an important component of soil carbon (C). Yet, the relative contribution of microbial necromass in shaping the global C stocks in agricultural and natural ecosystems worldwide remains virtually unknown. Here, we compiled data on fungal and bacterial necromass along with soil organic carbon (SOC) from the 0–20 cm soil layer across 486 study sites (145 agricultural and 341 natural ecosystems) to evaluate the relative contribution of fungal necromass C (FNC) and bacterial necromass C (BNC) to SOC. Our results indicated that, on average, FNC is two times more important than BNC in explaining SOC in both agricultural and natural ecosystems. The contributions of FNC and BNC to SOC were markedly higher in agricultural ecosystems compared with natural ecosystems, with a contrasting trend in the FNC/BNC ratio. Soil physicochemical properties (soil C/N ratio and clay content) were the most important predictors of the contributions of FNC and BNC to SOC in both ecosystems, while geographical factor (elevation) was the most important predictor of the FNC/BNC ratio. Our study enhances the current level of understanding regarding microbially mediated biogeochemical cycling and SOC dynamics, underscoring the critical role of microbial necromass in the global C cycle.

Keywords: agricultural ecosystems, bacterial necromass carbon, fungal necromass carbon, microbial necromass carbon, natural ecosystems

1 Introduction

As the largest carbon (C) pool in the terrestrial biosphere, soil organic carbon (SOC) plays a pivotal role in shaping the global C cycle and climate system (Bellamy et al., 2005; Crowther et al., 2015). In brief, plant inputs provide the primary carbon source to soils, and microbial processing transforms these inputs into microbial necromass that can persist over long turnover times (Cotrufo et al., 2013; Angst et al., 2021). Although the living soil microbial biomass typically constitutes only about 2% of SOC (a ratio referred to as the microbial quotient; Anderson & Domsch, 1989; Liu et al., 2023), microbial necromass has been shown to contribute more than half and up to approximately 80% of SOC, depending on soil type and analytical methods (Liang & Balser, 2011; Kallenbach et al., 2016; Liang et al., 2019). In other words, microbial necromass C (MNC) constitutes a substantial and critical component of stable SOC (Ma et al., 2018), and its dynamics are increasingly recognized for their role in regulating the terrestrial carbon cycle and climate feedbacks (Zhao et al., 2023). As such, there is growing scientific attention on the forces driving the accumulation of MNC and its contribution to SOC (Liang et al., 2017; Ni et al., 2020; Luo et al., 2022; Zhou et al., 2023). To gain a comprehensive understanding of MNC in the global C cycle, recent research has highlighted the distinct roles of fungal and bacterial necromass, revealing their contrasting responses to environmental and anthropogenic drivers. For instance, studies have shown that the accumulation and contribution of MNC are sensitive to factors such as aridity, primary productivity, agricultural management practices like tillage and fertilization, as well as key soil properties including pH and clay content (Zhang et al., 2021; Zhou et al., 2023; Xu et al., 2024).

Despite these advances, it remains unclear whether these organism-specific mechanisms translate into systematic differences in necromass contributions between ecosystems under varying degrees of human interference, such as agricultural versus natural systems.

With the distinct roles of fungi and bacteria in decomposing organic matter and stabilizing organic carbon in soil, the relative contribution to SOC of fungal and bacterial necromass C could be used to track the dynamics of SOC storage (Malik et al., 2016). The cell walls of fungi primarily consist of chitin (a nitrogen-containing polysaccharide) and β-glucans, whereas bacterial cell walls are mainly composed of peptidoglycan—a complex of sugars and amino acids (Lenardon et al., 2007). As bacterial amino sugars are readily degradable, while fungal chitin and -glucans are more recalcitrant, fungal necromass generally exhibits a longer turnover time in soil compared to bacterial necromass (Xu et al., 2022). Wang et al. (2021a) reported that the contribution of fungal necromass carbon (FNC) to SOC exceeded 65%, considerably higher than that of bacterial necromass carbon (BNC, 32–36%). This pattern is likely attributed to the slower decomposition rate and stronger mineral-associative capacity of fungal necromass. Furthermore, greater fungal biomass and higher turnover rates may enhance the input flux of fungal necromass (Klink et al., 2022). The contributions of FNC and BNC to SOC depended on the type of ecosystems (Wang et al., 2021a; Cao et al., 2023; Xu et al., 2024). However, few studies on fungal and bacterial necromass carbon and their contribution to SOC has been reported for ecosystems under human interference (Zhou et al., 2023).

Terrestrial ecosystems can be broadly categorized into managed (agricultural) and natural ecosystems (Hobbs et al., 2011; Keith et al., 2022). The agricultural ecosystems are typical of plant litter derived from single crops under intensive human management (Bohan et al., 2013), a context that typically leads to bacterial-dominated soil communities (van Der Heijden et al., 2008). In contrast, natural ecosystems display greater diversity in plant litter and root deposits (Wu et al., 2019). In such ecosystems, fungal mycelial networks and stable soil aggregates are enhanced, leading to higher FNC contributions to SOC (Sanaullah et al., 2020; Sae-Tun et al., 2022). While bacteria are undoubtedly vital decomposers, fungi play a distinct and often dominant role in the initial breakdown of complex plant polymers such as cellulose and lignin. This functional prominence stems from their potent enzymatic machinery and hyphal growth form, which enable physical penetration and decay of solid organic matter (de Boer et al., 2005). As key decomposers, fungi are thus critical in processing cellulose and other complex organic compounds (Hättenschwiler et al., 2005). Accordingly, as demonstrated by Choi et al. (2018), soil cellulose-degrading genes are frequently linked to fungal activity and abundance. Rather than implying higher cellulose concentration per se, diverse plant inputs increase the chemical heterogeneity of plant-derived polymers (e.g., cellulose, hemicelluloses, and lignin), which broadens decomposer niches and often favors fungal communities in litter horizons (Hättenschwiler et al., 2005; Štursová et al., 2012). In contrast, agricultural monocultures tend to reduce fungal diversity unless mitigated by management practices (Chen et al., 2020). Reflecting this context dependence, cellulose-rich inputs can enrich saprotrophic fungi in arable soils (Clocchiatti et al., 2021), whereas bacteria may contribute substantially in mineral soils or under specific microhabitat and land management conditions (Štursová et al., 2012; Choi et al., 2018). Due to distinct chemical properties and organo-mineral stabilization pathways, fungal and bacterial necromass exhibit differing turnover times, making the FNC/BNC ratio a mechanistic tracer of SOC formation (Angst et al., 2021; Kleber et al., 2021). Therefore, elucidating the global distribution and drivers of FNC, BNC, and their ratio across agricultural and natural ecosystems is essential for predicting management-induced shifts in SOC under varying climatic and soil conditions (Zhang et al., 2021; Zhou et al., 2023; Xu et al., 2024).

In order to explore the global patterns and drivers of FNC, BNC and the FNC/BNC ratio in agricultural and natural ecosystems, we compiled data from 486 study sites worldwide. The aims of this study were: (1) to quantify the contributions of FNC and BNC to SOC and the FNC/BNC ratio in agricultural and natural ecosystems; and (2) to investigate the primary driving factors influencing the contributions of FNC and BNC to SOC and the FNC/BNC ratio.

2 Materials and methods

2.1 Data collection

We compiled a comprehensive dataset following the stepwise workflow. (1) We collected peer-reviewed papers published from 1996 to 31 December 2022 from Web of Science (http://apps.webofknowledge.com), Google Scholar (http://scholar.google.com), and the China National Knowledge Infrastructure (http://cnki.net), using the keywords: ‘amino sugars’, ‘microbial necromass’, ‘microbial residue’, ‘fungal residue’, and ‘bacterial residue’. Records from different databases were merged and deduplicated to form an initial compilation. (2) We then filtered the compiled studies to include only those focusing on topsoil, defined as the 0–20 cm layer. Studies reporting deeper or unspecified sampling depths (e.g., 0–30 cm) were excluded to ensure spatial comparability. (3) Full texts were assessed to confirm the presence of paired fungal and bacterial residue data from the same sample—specifically, glucosamine (GluN) and muramic acid (MurA), or directly reported FNC and BNC values—to enable consistent cross-study calculation of the FNC/BNC ratio. Studies lacking either biomarker were excluded from ratio analyses, though those directly reporting the FNC/BNC ratio were retained. (4) Eligible observations were classified into agricultural ecosystems (including dry land, irrigated cropland, and submerged paddy) or natural ecosystems (forest and grassland) based on study metadata. (5) For natural ecosystems, data from fertilized, polluted, experimentally treated, or otherwise anthropogenically disturbed sites were excluded. In total, the final dataset consisted of 2094 observations from 486 sites worldwide (145 agricultural and 341 natural sites; Figure 1) reported in 164 peer-reviewed papers. Of these observations, 1001 were from agricultural ecosystems, and 1093 from natural ecosystems. Among the 341 natural sites, 195 were forests and 146 were grasslands. For agricultural sites, we used Google Earth Engine with the LGRIP30 V1 dataset to classify agricultural ecosystem into dry land and irrigated cropland, and we overlaid the JRC surface-water seasonality layer to extract submerged paddy from the irrigated class (LGRIP30 irrigated value = 2 and JRC seasonality ≥ 1). We ultimately classified 145 samples of agricultural ecosystems into 32 dry land, 72 irrigated, and 41 submerged paddy sites.

We calculated the FNC and BNC based on amino sugar concentrations following widely used conversion factors, correcting total GluN for its bacterial share using MurA:

$$FNC = \left(\frac{GluN}{179.17} - 2 \times \frac{MurA}{251.23}\right) \times 179.17 \times 9 \qquad \text{Equation 1}$$

where 9 (unitless) is the conversion factor from GluN to FNC. To estimate fungal-derived GluN, we subtracted the bacterial share of GluN assuming an empirical GluN:MurA molar ratio of 2:1 for bacterial residues. 179.17 and 251.23 are the molecular weights of GluN and MurA, respectively. And their units are all g/mol. The unit of FNC is mg/kg.

$$BNC = MurA \times 45 \qquad \text{Equation 2}$$

where 45 (unitless) is the conversion factor from MurA to BNC. The unit of BNC is mg/kg.

Additional information including site geographic location (latitude and longitude), topographical condition (elevation), climatic factors (mean annual temperature [MAT] and mean annual precipitation [MAP]), soil physicochemical properties (pH, SOC, total nitrogen [TN], clay content, and soil temperature), and biotic (microbial and plant) factors were recorded. Specifically, biotic factors included microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), MBC/MBN, net primary production (NPP), and belowground biomass C density (BGBC). The data of topographical condition (elevation) was classified as geographical factor in this study. When MAT and MAP were unavailable in the original articles, we extracted them from the global climate layers of WorldClim (http://www.worldclim.org/) with a grid precision of 30 × 30 arc sec according to geographic location. Missing elevation data were extracted using the *elevatr* package v.0.4.2 (Hollister, 2021) in the R environment. We acquired the data on annual mean soil temperature from the study of Lembrechts et al. (2022), while other absent soil physicochemical data were extracted from the Harmonized World Soil Database (https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/) and SoilGrids 2.0 (Poggio et al., 2021; https://www.soilgrids.org/) using ArcGIS 10.3. We supplemented missing climatic and soil variables using high-resolution, globally interpolated datasets to ensure consistent spatial coverage across all sites. After retrieving missing value from gridded data, we typically calibrate them against field-reported values via a field-anchored bias correction (i.e., a site- or region-specific “delta” adjustment) to minimize errors introduced by gridded data. While the use of such data introduces inherent uncertainties, these databases are widely adopted in global-scale ecological analyses and provide the most feasible approach for a unified assessment. In addition, the data on NPP and BGBC were acquired from the studies of Zhao and Running (2010) and Spawn et al. (2020), respectively. Missing MBC and MBN data were acquired using a

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global database with a high resolution of 30 × 30 arc sec (Wang et al., 2022).

2.2 Statistical analysis

All the statistical analyses were performed using R v4.1.3 (R Core Team, 2021). Initially, the Shapiro–Wilk test was employed to assess the normality of our data, followed by the application of Levene's test to evaluate the homogeneity of variances across different groups. To detect the significant differences in the contributions of FNC and BNC to SOC, and the FNC/BNC ratio between agricultural and natural ecosystems, as well as between forest and grassland ecosystems, the Wilcoxon rank sum test was conducted. Kruskal–Wallis and Dunn's post hoc tests were used to assess the significant differences of the contributions of FNC and BNC to SOC, and the FNC/BNC ratio among dry land, irrigated cropland, and submerged paddy. We used Spearman's rank correlation coefficient to explore the connections between the 16 variables considered in this study, including geographical and climatic factors, soil physicochemical properties, and biotic factors. Since there was a strong positive correlation between MAT and soil temperature (Figure S1), soil temperature was excluded from our subsequent analyses. Linear regressions between different factors and the contributions of FNC and BNC to SOC and the FNC/BNC ratio were performed. Dots and smoothing curves were drawn using the *geom_point* and *geom_smooth* functions, respectively, in the *ggplot2* package v.3.4.0 (Wickham, 2016).

Variation partitioning analysis was conducted using the *vegan* package v.2.5.7 (Oksanen et al., 2020) to evaluate the effects of four types of factors on the contributions of FNC and BNC to SOC and the FNC/BNC ratio in agricultural and natural ecosystems at global scale. We used a variance inflation factor threshold of 3.3 to eliminate those variables that were strongly correlated and avoid multicollinearity (Figure S2; Kock, 2015; Fanin et al., 2020). Following factor selection, boosted regression trees (BRTs) were used to partition independent influences of geographical (elevation) and climatic (MAT and MAP) factors, soil physicochemical properties (pH, clay, C/N, and SOC), and biotic factors (NPP, BGBC, MBC, and MBC/MBN) on the contributions of FNC and BNC to SOC and the FNC/BNC ratio with the *gbm* package v.2.1.8.1 (Greenwell et al., 2022).

Utilizing the selected factors, we performed structural equation models (SEMs) to quantify the effects (direct, indirect and both) of four types of factors on the contributions of FNC and BNC to SOC and the FNC/BNC ratio using *lavaan* package v.0.6.19 (Rosseel, 2012). According to the previously reported potential causal relationships between explanatory and response variables (Wang et al., 2021a, 2021b; Li et al., 2024), we established the *priori* structural equation models for agricultural and natural ecosystems, respectively (Figure S3). The SEMs were fitted via maximum likelihood estimation, with non-significant paths iteratively pruned through stepwise exclusion, followed by model evaluation using modification indices and goodness-of-fit criteria. The fit indices included degrees of freedom (df), chi-square (χ^2, $0 \leq \chi^2/df \leq 2$), comparative fit index ($CFI > 0.9$), and root mean square error of approximation ($RMSEA < 0.08$), which were used to assess the adequacy of the SEM.

Map, box, bar, bubble, and lollipop charts were plotted with the *ggplot2* package v.3.4.0 (Wickham, 2016). To enhance map visualization, the *ggnewscale* package v.0.4.8 (Campitelli, 2022) was necessary alongside the *ggplot2* package v.3.4.0 (Wickham, 2016). Similarly, the *ggpubr* package v.0.5.0 (Kassambara, 2022) was an additional necessity when creating lollipop charts.

3 Results

3.1 Fungal and bacterial necromass contribution to SOC in agricultural and natural ecosystems

Our analysis revealed statistically significant disparities in the contributions of FNC and BNC to SOC in agricultural and natural ecosystems at the global scale ($P < 0.05$; Figure 2a, b). Notably, the average contributions of FNC and BNC to SOC were substantially higher in agricultural ecosystems than in natural ecosystems ($P < 0.001$; Figures 2a, b). For FNC, the average contribution was 34.39% in agricultural ecosystems, versus 29.24% in natural ecosystems. BNC contributed an average of 15.65% to SOC in agricultural ecosystems, compared to 14.02% in natural ecosystems (Table 1). Our results also indicated that the contributions of FNC to SOC were approximately twice those of BNC in agricultural and natural ecosystems (Table 1).

The contributions of FNC and BNC to SOC indicated no significant difference between dry land and irrigated cropland ($P > 0.05$), whereas both differed significantly from submerged paddy ($P < 0.05$; Figure S4a, b). In detail, across dry land, irrigated cropland, and submerged paddy, the mean contributions of FNC to SOC were 37.77%, 35.35%, and 22.82%, respectively, whereas those of BNC were 17.34%, 15.95%, and 10.55% (Table 1). Moreover, there were no significant differences in the contributions of FNC and BNC to SOC between forest and grassland ecosystems ($P > 0.05$; Figure S5). Specifically, FNC contributed, on average, 29.11% to SOC in forests and 26.75% in grasslands, while BNC contributed 13.48% in forests and 14.34% in grasslands (Table 1).

3.2 Ratios of fungal and bacterial necromass in agricultural and natural ecosystems

Our results indicated that, at the global scale, the soil FNC/BNC ratio differs significantly between agricultural and natural ecosystems ($P < 0.05$; Fig. 2c), with a higher ratio in natural ecosystems (3.22) than in agricultural ecosystems (2.61; Table 1).The FNC/BNC ratio did not differ significantly among dry land, irrigated cropland, and submerged paddy ($P > 0.05$; Figure S4c), with average FNC/BNC ratios of 2.87, 2.51, and 2.62, respectively (Table 1). Similarly, there was no significant difference in the FNC/BNC ratio between forest and grassland ecosystems ($P > 0.05$; Figure S5), and the average FNC/BNC ratios for forests and grasslands were 2.80 and 3.58 (Table 1), respectively.

3.3 Associations of abiotic and biotic factors with microbial necromass parameters

Soil physicochemical factors were the most important influence on the contributions of FNC and BNC to SOC across both ecosystem types (Figures 3a–d, 4a–d).

Specifically, they explained 16% and 17% of the variance in the contributions of FNC and BNC to SOC in agricultural ecosystems, respectively (Figures 3a, c), and 20% and 24% in natural ecosystems (Figures 3b, d). BRTs corroborated this pattern, with soil physicochemical factors showing the highest relative influence (51% for FNC, and 44% for BNC) in agricultural systems and 44% in natural systems (Figures 4a–d). All BRT models were significant ($P < 0.001$), with explained variance 36–66%. While soil factors dominated overall, responses to individual variables differed between ecosystems. In detail, in agricultural systems, the C/N ratio ranked third for FNC after clay and SOC (Figure 4a), whereas C/N was the top predictor for FNC in natural systems and for BNC in both ecosystems (Figures 4b–d). Consistently, linear models showed declines in the contributions of FNC and BNC with increasing C/N in both ecosystems (Figures S6g, S7g). SEMs yielded convergent results, indicating both direct and indirect pathways (Figures 5a–d, 6a–d). Notably, the direct and total effects of soil physicochemical factors on FNC were negative in agricultural but positive in natural ecosystems (Figures 5a, b, 6a, b), whereas the effects on BNC were negative in both ecosystem types (Figures 5c, d, 6c, d).

Our results indicated that geographical factors were the most important contributors to explain the FNC/BNC ratio in both agricultural and natural ecosystems, accounting for 21% and 10% of the explained variance in the FNC/BNC ratio, respectively (Figures 3e, f). The results of the BRTs suggested that geographical factors played a similar role in explaining the FNC/BNC ratio (Figures 4e, f). In the BRT models, geographical factors emerged as the primary influencers of the FNC/BNC ratio in agricultural and natural ecosystems, accounting for 32% and 44% of the variance in each case, respectively (Figures 4e, f). To be more specific, elevation was the most significant geographical factors influencing the FNC/BNC ratio in both ecosystems (Figures 4e, f). Moreover, the FNC/BNC ratio in agricultural and natural ecosystems show significantly increased with an increase elevation (Figure S8a). The results of SEMs also indicated that geographical factors were the most influential factors for the FNC/BNC ratio in agricultural and natural ecosystems, exerting both direct and indirect effects on this ratio (Figures 5e, 6e), with the standardized total effect being positive (Figures 5f, 6f).

4 Discussion

4.1 Fungal necromass contributes two times more to SOC than bacterial necromass

Our results show that in agricultural ecosystems, FNC/SOC ranged from 0.09% to 97.53% (mean ± SE: 34.39 ± 0.67%), and BNC/SOC ranged from 0.81% to 65% (15.65 ± 0.33%). In natural ecosystems, FNC/SOC ranged from 0.92% to 96.29% (29.24 ± 0.51%), and BNC/SOC ranged from 0.25% to 89.45% (14.02 ± 0.36%) (Table 1). The FNC/BNC ratio ranged from 0.02 to 12.74 (2.61 ± 0.06) in agricultural ecosystems and from 0.12 to 44.24 (3.22 ± 0.11) in natural ecosystems (Table 1). Despite substantial variability at the individual sample level, the mean contribution of FNC was approximately twice that of BNC in both ecosystem types. Moreover, the mean FNC/BNC ratio was significantly higher in natural ecosystems than in agricultural ecosystems ($P < 0.05$; Figure 2). Although this general pattern has been reported in previous studies (Liang et al., 2019; Wang et al., 2021a; Zhang et al., 2023; Ding et al., 2024), the systematic differences in the magnitude of these contributions between agricultural and natural ecosystems—and their underlying drivers—have remained poorly understood. Our study not only confirms the broad pattern but also elucidates these ecosystem-level disparities and their environmental determinants. Consistent with our finding that the contribution of fungal necromass carbon (FNC) to SOC exceeded that of bacterial necromass carbon (BNC) in both ecosystem types (Table 1), the predominance of fungal necromass may be attributed to its more recalcitrant cell wall composition (e.g., chitin) and slower decomposition rate (Wang et al., 2021a). Our BRT and SEM analyses further identified soil clay content and C/N ratio as key drivers of FNC accumulation (Figs. 4a, 5a), reinforcing the importance of organo-mineral associations in the stabilization of fungal-derived carbon.

Additionally, our study reveals previously unreported disparities between ecosystem types, for example, the contributions of both fungal and bacterial necromass carbon (FNC and BNC) to SOC were significantly higher in agricultural ecosystems, while the FNC/BNC ratio was substantially elevated in natural ecosystems. The higher contributions of FNC and BNC to SOC in agricultural ecosystems may be attributable to two main factors. First, natural ecosystems typically receive larger and more heterogeneous plant-derived carbon inputs than agricultural systems. These inputs expand the plant-derived SOC pool and can dilute the relative contribution of microbial necromass to SOC, thereby resulting in a lower perceived contribution of microbial necromass in natural ecosystems (Angst et al., 2021; Kleber et al., 2021). Second, the significantly lower soil C/N ratio in agricultural ecosystems (10.78) compared to natural ecosystems (27.44) reflects relative nitrogen enrichment, largely resulting from anthropogenic fertilization (Castellano et al., 2015; Chen et al., 2020). This nitrogen-rich environment can enhance microbial carbon use efficiency and alleviate nutrient limitation, thereby promoting the production and accumulation of microbial necromass (Liang et al., 2017). Supporting this mechanism, we found that the contributions of both FNC and BNC to SOC decreased significantly with increasing soil C/N ratio in both agricultural ecosystems (FNC/SOC: $R = -0.27$, $P < 0.001$; BNC/SOC: $R = -0.29$, $P < 0.001$) and natural ecosystems (FNC/SOC: $R = -0.17$, $P < 0.001$; BNC/SOC: $R = -0.35$, $P < 0.001$; Figures S6g, S7g). These results further underscore that a lower soil C/N ratio—often indicative of higher nitrogen availability—is a key driver of microbial necromass accumulation. It should be noted that although in situ plant residues in agricultural systems (e.g., cereal straw) may have high C/N ratios, the overall soil C/N ratio is reduced by management practices such as mineral fertilization and the incorporation of low C/N organic amendments.

Furthermore, nutrient-rich conditions prevalent in agricultural systems (e.g., due to fertilization) often select for bacterial-dominated communities, as many bacteria exhibit *r*-strategist traits that support rapid growth under high resource availability. In contrast, natural ecosystems—characterized by lower nutrient availability and greater resource heterogeneity—tend to favor fungal dominance, since fungi often function as *K*-strategists with higher efficiency in decomposing complex organic matter under resource-limited conditions (Strickland & Rousk, 2010; Yu et al., 2022). This shift in microbial community composition is observed in our results, which show a significantly higher FNC/BNC ratio in natural ecosystems across our global dataset (Figure 2c, Table 1). A high FNC/BNC ratio signifies a fungal-dominated decomposition pathway. Fungal necromass—rich in recalcitrant compounds such as chitin—is more resistant to decay, and fungal hyphae play a key role in the formation of stable soil aggregates that physically protect organic matter from degradation (Lenardon et al., 2007). This pathway promotes the formation of stable, long-turnover SOC pools essential for long-term carbon sequestration (Six et al., 2006; Lehmann et al., 2020). Furthermore, fungi generally exhibit higher carbon use efficiency than bacteria, meaning a larger proportion of assimilated carbon is allocated to biomass production (and subsequently necromass) rather than being respired as CO_2 (Wang & Kuzyakov, 2024). Thus, the fungal-driven pathway characteristic of natural ecosystems represents a highly efficient conversion of plant litter into persistent soil organic matter (Kallenbach et al., 2016; Malik et al., 2016). Conversely, the lower FNC/BNC ratio observed in agricultural ecosystems reflects a bacterial-dominated pathway, accelerated by practices such as tillage and nutrient amendments. This pathway is associated with faster carbon cycling and greater carbon loss through respiration. Although microbial necromass can accumulate under these conditions—sometimes contributing more significantly to a reduced total SOC pool—the resulting carbon is often less stabilized (Zhou et al., 2023). Therefore, the FNC/BNC ratio serves not merely as a descriptive metric, but as a functional biomarker that elucidates fundamental differences in the stability and persistence of SOM between managed agricultural systems and natural ecosystems.

Notably, as major components of agricultural ecosystems, both dryland and irrigated croplands exhibited significantly greater contributions of FNC and BNC to SOC than submerged paddy soils, although the FNC/BNC ratio did not differ significantly among these three systems (Figure S4). This pattern may reflect similar aeration regimes in dryland and irrigated systems (predominantly oxygenated), leading to comparable decomposition–transformation–mineral association pathways and, thus, similar net contributions of fungal and bacterial residues to SOC (Ghezzehei et al., 2019). By contrast, persistent or periodic flooding in paddy soils induces anoxia, suppresses aerobic decomposition, and shifts metabolic pathways (e.g., denitrification and methanogenesis), potentially suppressing fungal activity or dominance and altering the relative accumulation and turnover of fungal and bacterial necromass (Qiu et al., 2017), resulting in contributions that differ significantly from—and are lower than—those in the other two systems. Flooding can suppress fungi yet also enhance the joint retention of both fungal and bacterial necromass via slower decomposition and mineral protection, yielding unchanged ratios but altered totals or compositional pathways (Chen et al., 2021; Gao et al., 2024).

4.2 Driving factors of the change in fungal and bacterial necromass contribution to SOC and their ratio

Deng and Liang (2022) suggested that the potential contribution of microbial necromass to the SOC pool was governed by the C/N ratio. This finding was confirmed by our results (Figures 4b–d). As elaborated in *Section 4.1*, high N availability (i.e., low soil C/N ratio) promotes the production and accumulation of microbial necromass (Wu et al., 2025). Consequently, the contributions of both FNC and BNC to SOC decreased with increasing soil C/N ratio (Figures S6g, S7g). In agricultural ecosystems, high soil N levels primarily result from fertilization (Chen et al., 2020). In contrast, natural ecosystems experience minimal anthropogenic disturbance, N often acts as the key limiting factor for microbial activity (Elser et al., 2007). Under N-limited conditions, microbes (both fungi and bacteria) allocate more energy and C resources to the synthesis of N-acquiring enzymes (e.g., proteases and chitinases). This shift in metabolic strategy reduces the C allocated to biomass synthesis, thereby diminishing the amount of C ultimately converted into microbial necromass (Mooshammer et al., 2014; Liu et al., 2024). Thus, although microbial community composition differs between natural and agricultural ecosystems, the regulatory role of soil C/N ratio in shaping their structure and function remains consistent (Han et al., 2024). In our study, soil clay content was identified as the predominant factor governing the contribution of FNC to SOC in agricultural ecosystems (Figure 4a), with this contribution increasing concomitantly with clay content (Figure S6d). This suggests that soils with higher clay and silt contents generally accumulate greater amounts of microbial residues, particularly those derived from fungi, which can be attributed to the promotion of stable organo-mineral complex formation by abundant fine soil particles (Six et al., 2006 and Liang et al., 2017). Furthermore, although agricultural management practices often disturb soil structure, they simultaneously enhance clay enrichment and aggregate formation, thereby providing effective physical protection for the long-term stabilization of fungal-derived C (Chen et al., 2020; Mou et al., 2021; Zhou et al., 2023).

On the contrary, geographical factor (elevation) was identified as the most influential predictor of the FNC/BNC ratio in both agricultural and natural ecosystems (Figures 4e, f, 5f, 6f), with the ratio increasing significantly with elevation (Figure S8a). Increasing elevation typically leads to decreased temperature, and increased precipitation (Körner, 2007), conditions favoring fungi over bacteria due to higher enzymatic capabilities and resource-use efficiency of fungi under the environments (Chen et al., 2020; Yu et al., 2022; Zhang et al., 2025). High elevation also results in slower soil development, which can reduce the availability of soil nutrients (Guerrero-Ramírez et al., 2020). This in turn increases environmental stress and restricts bacterial activity, thereby favoring the accumulation and conversion of fungal residues into necromass (Li et al., 2024). Our study further demonstrated that although elevation had a direct effect on the FNC/BNC ratio, it also indirectly influenced the ratio by modulating climatic factors, soil physicochemical properties, and biological factors (Figures 5e, 6e). This may explain why elevation is always integrate other environmental factor effects in the studies of MNC (Cui et al., 2023; Zhang et al., 2025).

4.3 Limitations and uncertainties

Although the present study provides important insights on global patterns and drivers of soil microbial necromass in agricultural and natural ecosystems, we must clarify three limitations. First, the limited data available on microbial characteristics, such as microbial community composition, enzymatic activities, and the content of soil aggregates and minerals hinder exploration of the drivers of soil microbial necromass. Second, it is undeniable that our dataset is unevenly distributed, primarily concentrating on the Northern Hemisphere, with sparse or nearly no data from other regions such as Africa, South America, and Australia (Figure 1). Additionally, the natural ecosystems in this study were limited to forests and grasslands, excluding other natural habitats such as wetlands and deserts. The uneven distribution of data may reduce the universality of MNC as a key driver of soil carbon pools in global terrestrial ecosystems. Furthermore, the compiled studies employed varied methodologies regarding sampling time, depth, and laboratory protocols. While such heterogeneity is an inherent challenge in global meta-analyses, it likely introduces additional variability and may constrain the direct comparability of certain data points. Therefore, more standardized data from these important areas and biomes are clearly required, and further investigation is warranted to fill the data gaps regarding the contribution of MNC to SOC in terrestrial ecosystems.

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5 Data availability

The data and R code for this manuscript are available at https://doi.org/10.6084/m9.figshare.28827383 (Lu, 2025).

6 Conclusions

Our results indicate that, on average, fungal necromass carbon (FNC) contributes approximately twice as much to soil organic carbon (SOC) as bacterial necromass carbon (BNC) in both agricultural and natural ecosystems. The relative contributions of FNC and BNC to SOC were found to be higher in agricultural ecosystems—an effect that is mediated by differences in soil physicochemical factors. The FNC/BNC ratio was significantly higher in natural ecosystems than in agricultural ecosystems, albeit with a modest effect size, and was primarily driven by geographical factors—particularly elevation. Our findings demonstrate that, despite considerable variability among individual sampling sites, statistically significant differences exist between agricultural and natural ecosystems in the contributions of fungal and bacterial necromass carbon (FNC and BNC) to soil organic carbon (SOC), as well as in the FNC/BNC ratio, at a global scale. These results underscore a potential fundamental divergence in the pathways and mechanisms of carbon turnover and stabilization between these two broad ecosystem types. These insights provide novel evidence that ecosystem management type (agricultural versus natural) is a key determinant of the pathways through which microbial necromass contributes to the global soil organic carbon (SOC) pool. Future studies that integrate microbial community composition with necromass dynamics across a broader range of biomes will be essential to predict ecosystem-specific responses of this critical carbon pool to global change.

Author contributions

JL performed the data analysis and prepared the original draft. TC and MDB contributed to manuscript review and editing. WL and HS contributed to data collection. YJ contributed to data analysis. ZW supervised the project and contributed to the original draft.

Competing interests

The contact author has declared that none of the authors has any competing interests.

Disclaimer

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Table 1. Summary of the contributions of fungal necromass carbon (FNC) and bacterial necromass carbon (BNC) to SOC and the FNC/BNC ratio in agricultural and natural ecosystems at the global scale investigated in this study.

Ecosystem	**FNC/SOC (%)**		**BNC/SOC (%)**		**FNC/BNC**	
	Range	Mean± SE	Range	Mean± SE	Range	Mean± SE
Natural ecosystem[&] (*N* = 341)	0.92–96.29	29.24 ± 0.51 b*	0.25–89.45	14.02 ± 0.36 b	0.12–44.24	3.22 ± 0.11 a
***Forest* (*N* = 195)**	0.92–96.29	29.11 ± 0.63 A[#]	0.94–96.47	13.48 ± 0.43 A	0.22–11.56	2.80 ± 0.07 A
***Grassland* (*N* = 146)**	0.96–93.89	26.75 ± 0.74 A	0.25–89.45	14.34 ± 0.60 A	0.05–44.24	3.58 ± 0.22 A
Agricultural ecosystem[%] (*N* = 145)	0.09–97.53	34.39 ± 0.67 a	0.81–65.00	15.65 ± 0.33 a	0.02–12.74	2.61 ± 0.06 b
***Dry land* (*N* = 32)**	3.01–96.81	37.77 ± 1.15 A[#]	0.81–65.00	17.34 ± 0.65 A	0.13–9.12	2.87 ± 0.12 A
***Irrigated cropland* (*N* = 72)**	0.09–97.25	35.35 ± 0.73 A	1.18–62.47	15.95 ± 0.38 A	0.02–12.74	2.51 ± 0.06 A
***Submerged paddy* (*N* = 41)**	4.96–97.53	22.82 ± 1.55 B	1.48–30.97	10.55 ± 0.66 B	0.31–10.40	2.62 ± 0.16 A

Note: *N* refers to the number of study sites;

[&] Natural ecosystem includes forest and grassland;

[%] Agricultural ecosystem includes dry land, irrigated cropland, and submerged paddy;

[*] Within the same column, values with different lowercase letters indicate a significant difference in the same variable between agricultural and natural ecosystems (Wilcoxon rank sum test; $P < 0.05$);

[#] Within the same column, values with different capital letters indicate a significant difference in the same variable between forests and grasslands (Wilcoxon rank sum test), as well as between dry land, irrigated cropland, and submerged paddy (Kruskal–Wallis and Dunn's post hoc tests; $P < 0.05$).

Figure legends

Figure 1. Global distribution of the sites used in this study. Ecosystem types are distinguished by distinct shapes and colors, with the numbers in parentheses indicating the number of study sites for each ecosystem type.

Figure 2. Comparison of the contributions of MNC to SOC and their ratio in agricultural and natural ecosystems. Colors indicate different ecosystems types. Significance levels: ***$P < 0.001$ and *$P < 0.05$.

Figure 3. Variations in the contributions of MNC to SOC and their ratio explained by four types of factors in agricultural and natural ecosystems. Colors indicate different types of factors.

Figure 4. Relative influence of different factors on the contributions of MNC to SOC and their ratio in agricultural and natural ecosystems. MAT, mean annual temperature; MAP, mean annual precipitation; MBC, microbial biomass carbon; SOC, soil organic carbon; C/N, the ratio of SOC to total nitrogen (TN); MBC/MBN, the ratio of MBC to microbial biomass nitrogen (MBN); NPP, net primary production; BGBC, belowground biomass carbon density. Colors indicate different types of factors.

Figure 5. The influence pathways of four types of factors on the contributions of MNC to SOC and their ratio in agricultural ecosystems. Direct and indirect effects (**a, c, e**) and the standardized total effects (**b, d, f**) of different factors on the contributions of MNC to SOC and their ratio of agricultural ecosystems are shown. Standardized path coefficients representing the effect sizes of potential causal factors are indicated by numbers adjacent to arrows. The width of arrows is proportional to the potential causal effect between variables. The red arrows indicate positive effects, and the blue arrows indicate negative effects. The numbers adjacent to boxes of response variables denote the explained variance (R^2). Right-angled rectangles denote single variables, whereas rounded rectangles represent composite variables. Colors indicate different types of factors. Significance levels: ***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$. The *priori* models are shown in Figure S3.

Figure 6. The influence pathways of four types of factors on the contributions of MNC to SOC and their ratio in natural ecosystems. Direct and indirect effects (**a, c, e**) and the standardized total effects (**b, d, f**) of different factors on the contributions of MNC to SOC and their ratio of natural ecosystems are shown. Standardized path coefficients representing the effect sizes of potential causal factors are indicated by numbers adjacent to arrows. The width of arrows is proportional to the potential causal effect between variables. The red arrows indicate positive effects, and the blue arrows indicate negative effects. The numbers adjacent to boxes of response variables denote the explained variance (R^2). Right-angled rectangles denote single variables, whereas rounded rectangles represent composite variables. Colors indicate different types of factors. Significance levels: ***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$. The *priori* models are shown in Figure S3.

Figure 1.

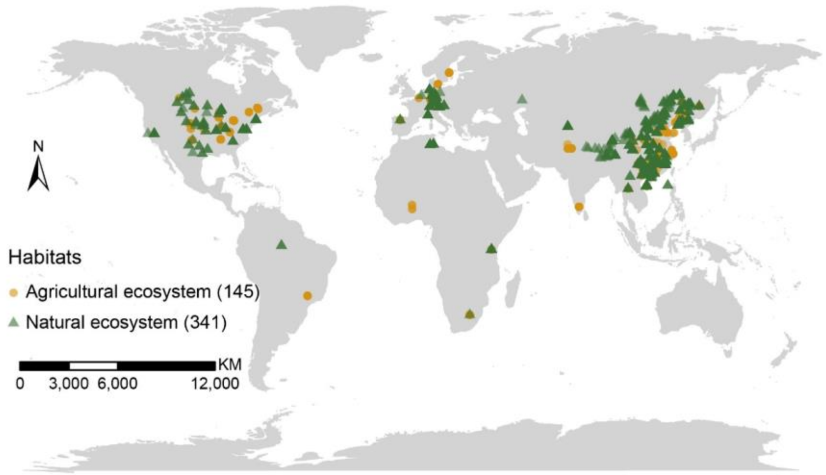

N
Habitats
● Agricultural ecosystem (145)
▲ Natural ecosystem (341)
KM
0
3,000
6,000
12,000

Figure 2.

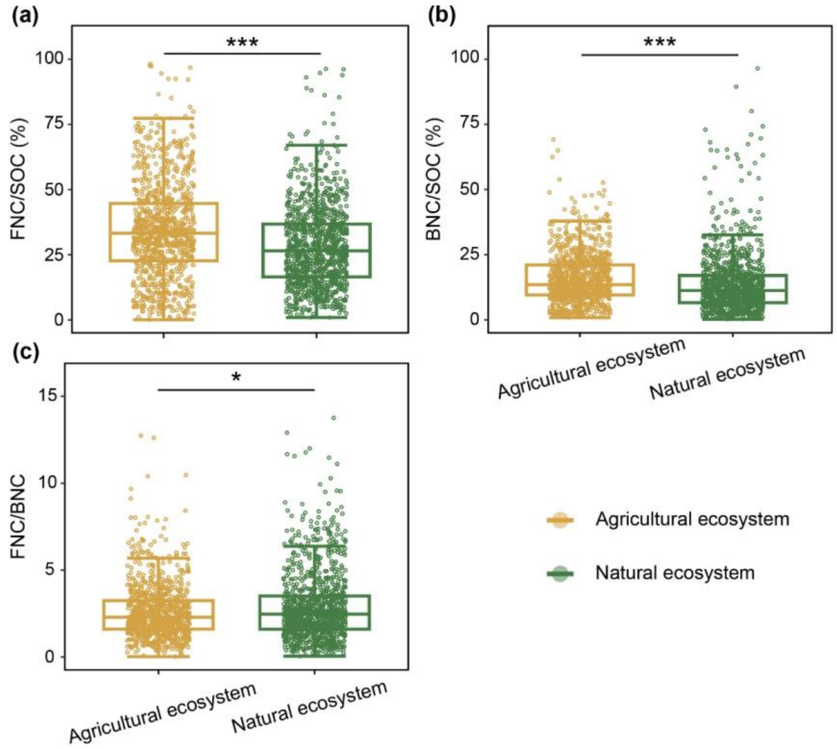

(a)
***
100
75
50
25
0
FNC/SOC (%)
(b)
***
100
75
50
25
0
BNC/SOC (%)
Agricultural ecosystem
Natural ecosystem
(c)
*
15
10
5
0
FNC/BNC
Agricultural ecosystem
Natural ecosystem
Agricultural ecosystem
Natural ecosystem

Figure 3.

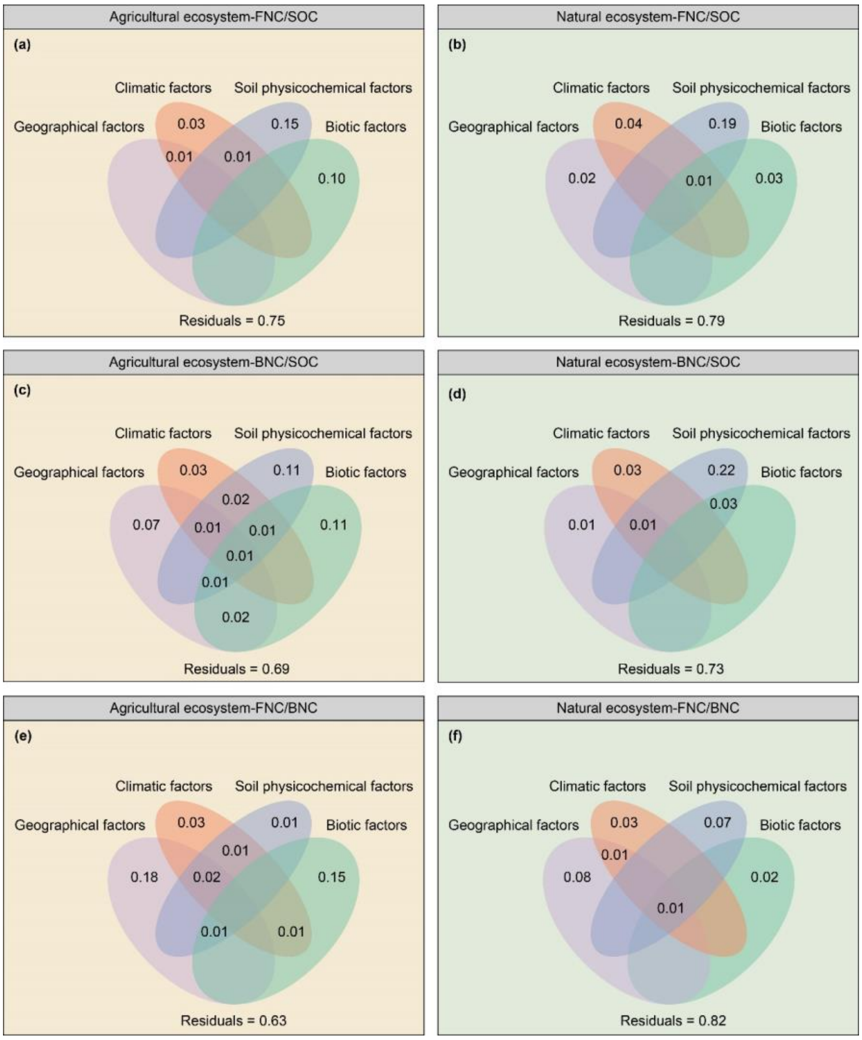

Agricultural ecosystem-FNC/SOC
(a)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.15
0.01
0.01
0.10
Residuals = 0.75
Natural ecosystem-FNC/SOC
(b)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.04
0.19
0.02
0.01
0.03
Residuals = 0.79
Agricultural ecosystem-BNC/SOC
(c)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.11
0.02
0.07
0.01
0.01
0.11
0.01
0.01
0.02
Residuals = 0.69
Natural ecosystem-BNC/SOC
(d)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.22
0.03
0.01
0.01
Residuals = 0.73
Agricultural ecosystem-FNC/BNC
(e)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.01
0.01
0.18
0.02
0.15
0.01
0.01
Residuals = 0.63
Natural ecosystem-FNC/BNC
(f)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.07
0.01
0.08
0.02
0.01
Residuals = 0.82

Figure 4.

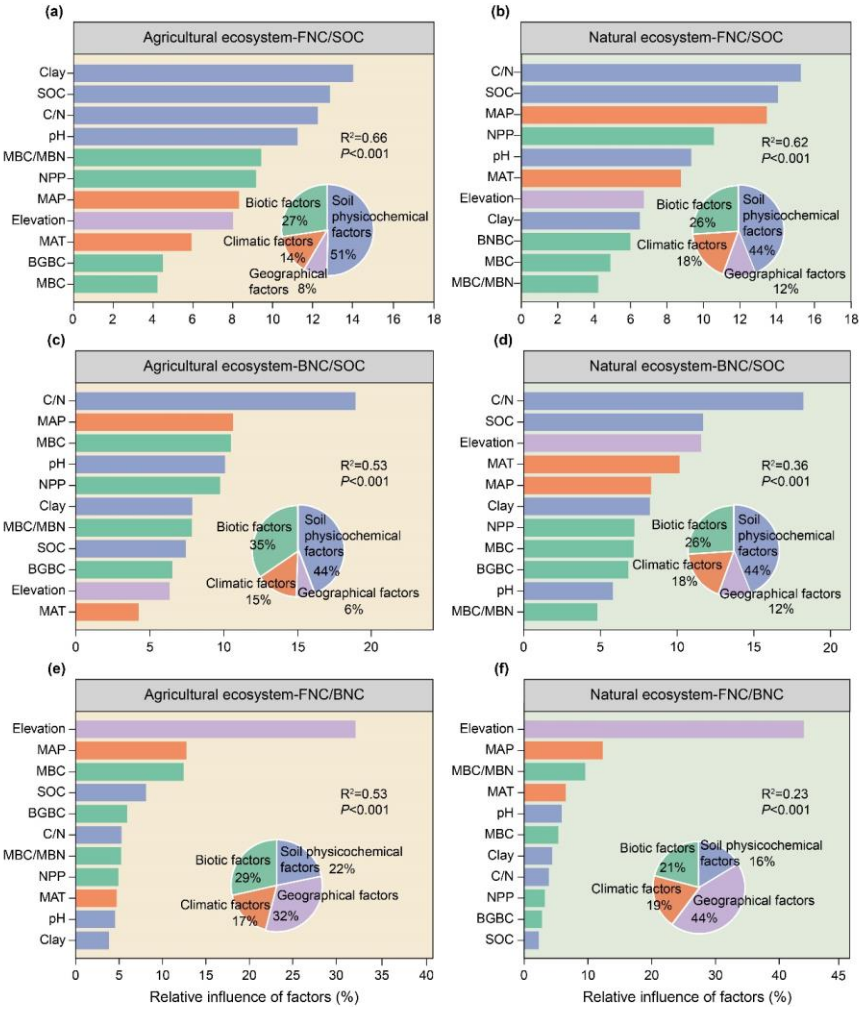

(a)
Agricultural ecosystem-FNC/SOC
Clay
SOC
C/N
pH
MBC/MBN
NPP
MAP
Elevation
MAT
BGBC
MBC
R²=0.66
P<0.001
Biotic factors 27%
Soil physicochemical factors 51%
Climatic factors 14%
Geographical factors 8%
0 2 4 6 8 10 12 14 16 18
(b)
Natural ecosystem-FNC/SOC
C/N
SOC
MAP
NPP
pH
MAT
Elevation
Clay
BNBC
MBC
MBC/MBN
R²=0.62
P<0.001
Biotic factors 26%
Soil physicochemical factors 44%
Climatic factors 18%
Geographical factors 12%
0 2 4 6 8 10 12 14 16 18
(c)
Agricultural ecosystem-BNC/SOC
C/N
MAP
MBC
pH
NPP
Clay
MBC/MBN
SOC
BGBC
Elevation
MAT
R²=0.53
P<0.001
Biotic factors 35%
Soil physicochemical factors 44%
Climatic factors 15%
Geographical factors 6%
0 5 10 15 20
(d)
Natural ecosystem-BNC/SOC
C/N
SOC
Elevation
MAT
MAP
Clay
NPP
MBC
BGBC
pH
MBC/MBN
R²=0.36
P<0.001
Biotic factors 26%
Soil physicochemical factors 44%
Climatic factors 18%
Geographical factors 12%
0 5 10 15 20
(e)
Agricultural ecosystem-FNC/BNC
Elevation
MAP
MBC
SOC
BGBC
C/N
MBC/MBN
NPP
MAT
pH
Clay
R²=0.53
P<0.001
Biotic factors 29%
Soil physicochemical factors 22%
Climatic factors 17%
Geographical factors 32%
0 5 10 15 20 25 30 35 40
Relative influence of factors (%)
(f)
Natural ecosystem-FNC/BNC
Elevation
MAP
MBC/MBN
MAT
pH
MBC
Clay
C/N
NPP
BGBC
SOC
R²=0.23
P<0.001
Biotic factors 21%
Soil physicochemical factors 16%
Climatic factors 19%
Geographical factors 44%
0 10 20 30 40 45
Relative influence of factors (%)

Figure 5.

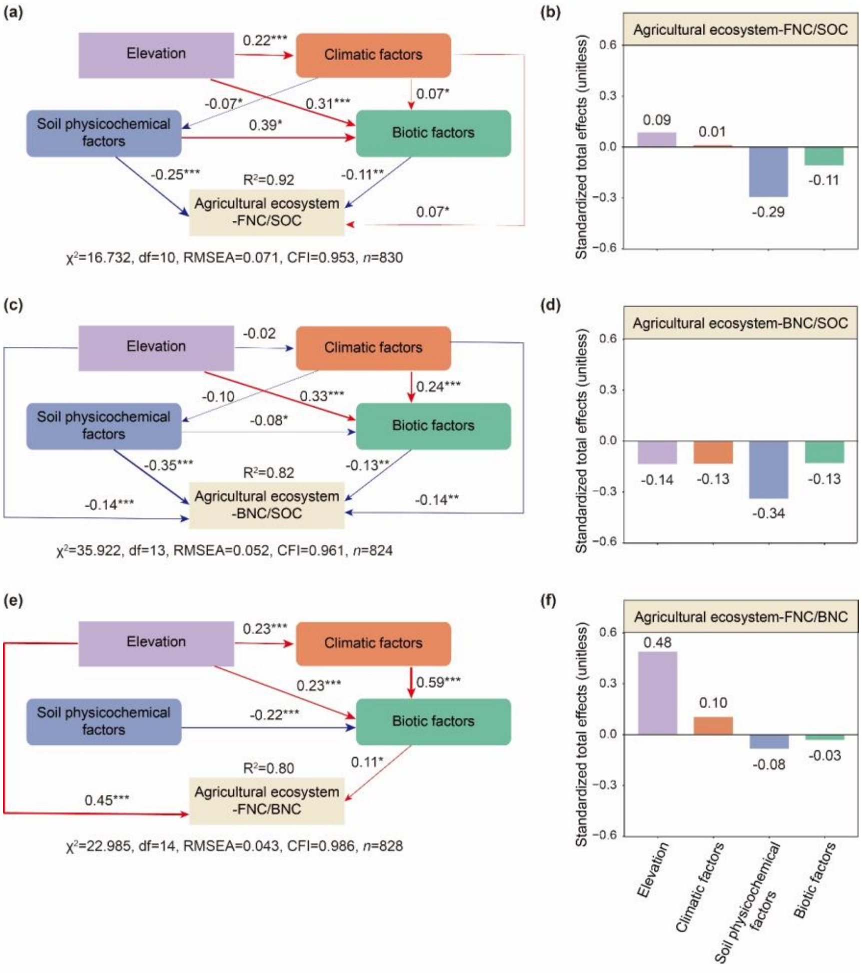
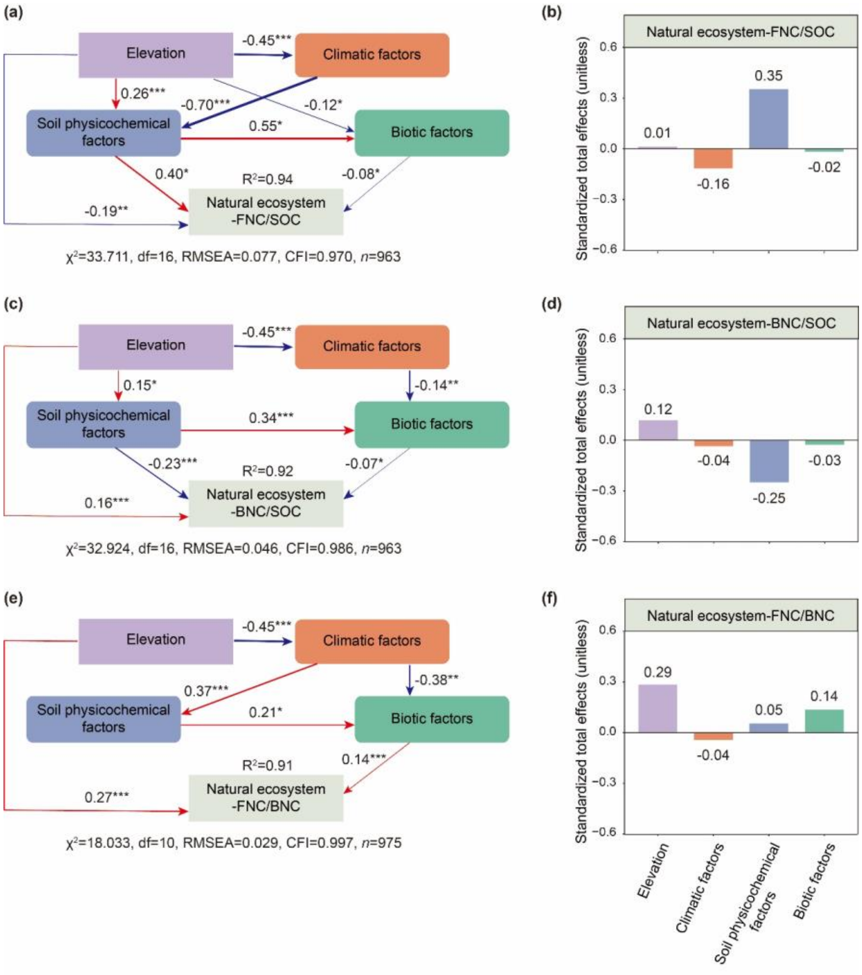

(a)
Elevation
0.22***
Climatic factors
-0.07*
0.31***
0.07*
Soil physicochemical factors
0.39*
Biotic factors
-0.25***
R²=0.92
-0.11**
Agricultural ecosystem -FNC/SOC
0.07*
χ²=16.732, df=10, RMSEA=0.071, CFI=0.953, n=830
(b)
Agricultural ecosystem-FNC/SOC
Standardized total effects (unitless)
0.6
0.3
0.0
-0.3
-0.6
0.09
0.01
-0.29
-0.11
(c)
Elevation
-0.02
Climatic factors
-0.10
0.33***
0.24***
Soil physicochemical factors
-0.08*
Biotic factors
-0.35***
R²=0.82
-0.13**
-0.14***
Agricultural ecosystem -BNC/SOC
-0.14**
χ²=35.922, df=13, RMSEA=0.052, CFI=0.961, n=824
(d)
Agricultural ecosystem-BNC/SOC
Standardized total effects (unitless)
0.6
0.3
0.0
-0.3
-0.6
-0.14
-0.13
-0.34
-0.13
(e)
Elevation
0.23***
Climatic factors
0.23***
0.59***
Soil physicochemical factors
-0.22***
Biotic factors
R²=0.80
0.11*
0.45***
Agricultural ecosystem -FNC/BNC
χ²=22.985, df=14, RMSEA=0.043, CFI=0.986, n=828
(f)
Agricultural ecosystem-FNC/BNC
Standardized total effects (unitless)
0.6
0.3
0.0
-0.3
-0.6
0.48
0.10
-0.08
-0.03
Elevation
Climatic factors
Soil physicochemical factors
Biotic factors

Figure 6.


(a)
Elevation
-0.45***
Climatic factors
0.26***
-0.70***
-0.12*
Soil physicochemical factors
0.55*
Biotic factors
0.40*
R²=0.94
-0.08*
-0.19**
Natural ecosystem -FNC/SOC
χ²=33.711, df=16, RMSEA=0.077, CFI=0.970, n=963
(b)
Natural ecosystem-FNC/SOC
Standardized total effects (unitless)
0.6
0.3
0.0
-0.3
-0.6
0.01
-0.16
0.35
-0.02
(c)
Elevation
-0.45***
Climatic factors
0.15*
-0.14**
Soil physicochemical factors
0.34***
Biotic factors
-0.23***
R²=0.92
-0.07*
0.16***
Natural ecosystem -BNC/SOC
χ²=32.924, df=16, RMSEA=0.046, CFI=0.986, n=963
(d)
Natural ecosystem-BNC/SOC
Standardized total effects (unitless)
0.12
-0.04
-0.25
-0.03
(e)
Elevation
-0.45***
Climatic factors
0.37***
-0.38**
Soil physicochemical factors
0.21*
Biotic factors
R²=0.91
0.14***
0.27***
Natural ecosystem -FNC/BNC
χ²=18.033, df=10, RMSEA=0.029, CFI=0.997, n=975
(f)
Natural ecosystem-FNC/BNC
Standardized total effects (unitless)
0.29
-0.04
0.05
0.14
Elevation
Climatic factors
Soil physicochemical factors
Biotic factors