https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

Open Access Earth System Science Data Discussions

# Soil microbial necromass shapes global carbon stocks in agricultural and natural ecosystems

Jing-li Lu[a], Thomas W. Crowther[b], Manuel Delgado-Baquerizo[c], Wenjie Liu[a], Yamin Jiang[a], Hongyang Sun[d], Zhiqiang Wang[d, *]

[a] Center for Eco-Environment Restoration Engineering of Hainan Province, School of Ecology, Hainan University, Haikou, 570228, People's Republic of China;

[b] Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland;

[c] Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Seville, 41013, Spain;

[d] Sichuan Zoige Alpine Wetland Ecosystem National Observation and Research Station, College of Grassland Resources, Southwest Minzu University, Chengdu, 610041, People's Republic of China

* Corresponding author: Zhiqiang Wang

*E-mail address*: wangzq@swun.edu.cn

## Abstract

Soil carbon (C) plays an essential role in regulating global C cycle and climate. Microbial necromass is an important component of soil C, and yet the relative contribution of microbial necromass in shaping the global C stocks in agricultural and natural ecosystems worldwide remains virtually unknown. In this study, 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 and the FNC/BNC ratio, after accounting for other biotic and abiotic factors. Our results indicated that, in both agricultural and natural ecosystems, the contribution of FNC to SOC significantly exceeded that of BNC, with FNC contributing approximately twice as much as BNC to SOC. However, the contributions of FNC and BNC to SOC were markedly higher in agricultural ecosystems than those in natural ecosystems, with a contrasting trend in the FNC/BNC ratio. Soil physicochemical properties (C/N and clay) 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). The traditional paradigm is that SOC storage is primarily formed directly based on plant material (Zhu and Miller, 2003; von Lützow et al., 2008). However, emerging evidence demonstrates that the stable SOC pool is predominantly composed of microbially derived organic compounds rather than plant-derived residues, indicating that microbial necromass may in fact be a primary source of stable SOC (Kallenbach et al., 2016; Liang et al., 2017). Microbes generate biomass by degrading plant-derived C, which is subsequently stabilized as microbial necromass through interactions with minerals and various processes within soil aggregates (Liang et al., 2017). Although the living soil microbial biomass constitutes only about 2% of SOC, microbial necromass carbon (MNC) can contribute up to 50%–80% of SOC (Liang and Balser, 2011; Kallenbach et al., 2016; Liang et al., 2019). 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). In order to gain a comprehensive and in-depth understanding of the role of MNC in the global C cycle, many studies have focused on the relative contributions of fungal (FNC) versus bacterial necromass (BNC; Zhang et al., 2021; Zhou et al., 2023; Xu et al., 2024).

The distinct roles of fungi and bacteria in stabilizing and decomposing SOC, enable their necromass C to elucidate the kinetics of SOC storage and decomposition (Malik et al., 2016). To be more specific, the chemical composition and functional characteristics of fungi and bacteria differ considerably, which may also contribute to different mechanisms of SOC formation. 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). The intricate structures of chitin and β-glucans in fungal necromass make them more resistant to decomposition compared to the typically more degradable bacterial necromass, leading to differences in their C decomposition rates in soil (Xu et al., 2022). Wang et al. (2021a) suggested that the higher contribution of FNC to SOC (exceeding 65%) than BNC (32–36%) may be not only due to the slower decomposition rates of fungal cellular compounds but also attributable to the higher living fungal biomass relative to bacterial biomass in terrestrial ecosystems. Previous studies have also indicated that 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), and they were mainly affected by climatic and soil physicochemical factors (e.g., soil pH and clay content; He et al., 2020; Zhang et al., 2023). However, these studies on the relative contributions of fungal necromass carbon (FNC) and BNC to SOC, and their ratio (FNC/BNC), have predominantly focused on ecosystems categorized based on biotic communities and vegetation types, such as forests (Chen et al., 2020), with limited attention given to ecosystems classified by levels of human interference.

Terrestrial ecosystems can be broadly categorized into managed (agricultural) and natural ecosystems (Hobbs et al., 2011; Keith et al., 2022). The agricultural ecosystems, heavily reliant on human management, typically exhibit uniform plant litter influenced by agricultural activities (Bohan et al., 2013). In contrast, natural ecosystems, which are self-sustaining, display greater diversity in litter and root deposits, encompassing various plants and biological remains (Wu et al., 2019). Minimal human interference enhances fungal mycelial networks and stable soil aggregates, leading to higher FNC sequestration and contributions to SOC (Sanaullah et al., 2020; Sae-Tun et al., 2022). As key decomposers, fungi can break down cellulose and other complex organic compounds (Hättenschwiler et al., 2005). Choi et al. (2018) indicated that soil cellulose-degrading genes are associated with fungal activity and abundance. This suggests cellulose-rich soils may support higher fungal diversity and abundance. The low cellulose and chitin abundance in agricultural ecosystems might result from plant monoculture, while diverse plant inputs in natural ecosystems lead to rich soil cellulose content and higher fungal abundance and FNC (Song et al., 2022). These findings suggest that FNC and BNC accumulation respond differently to human interference and ecosystem characteristics, causing disparities in the FNC/BNC ratio across ecosystems. Therefore, understanding global patterns and drivers of FNC, BNC, and the FNC/BNC ratio in agricultural and natural ecosystems is crucial amid intensifying human activities and global changes.

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, and determine whether the influencing factors were consistent across these two ecosystem types.

## 2 Materials and methods

### 2.1 Data collection

To clarify the contributions of FNC and BNC to SOC and the FNC/BNC ratio at global scale, we compiled a comprehensive dataset from a range of peer-reviewed papers published before 2022 through the 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’. Data compilation was conducted following four stringent criteria to reduce bias from selected publications: (1) fungal and bacterial necromass (or glucosamine [GluN] and muramic acid [MurA]) had to be reported simultaneously for the same samples; (2) only data from agricultural and natural ecosystems (i.e., grasslands and forests) were used; (3) for natural ecosystems, we excluded the data from fertilized, polluted, treated, or anthropogenically disturbed sites; and (4) we only included data from the top 0–20 cm of the soil profile reported in the publications, with other depths or unspecified soil depths excluded from our dataset. In total, the final dataset consisted of 2094 observations from 486 sites worldwide (Figure 1) reported in 164 peer-reviewed papers. Among them, there were 1001 observations from agricultural ecosystems and 1093 observations from natural ecosystems.

We calculated the FNC and BNC based on the contents of fungal GluN and bacterial MurA using the following equations (Liang et al., 2019):

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

$$BNC = MurA \times 45,$$

where 9 is the conversion factor from GluN to FNC, and, 179.17 and 251.23 are the molecular weights of GluN and MurA, respectively; 45 is the conversion factor from MurA to BNC.

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. 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 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. 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 agro- and

https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

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 ($\chi^2$, $0 \leq \chi^2/\mathrm{df} \leq 2$), 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 Contributions of FNC and BNC to SOC and their ratio in agricultural and natural ecosystems

There were no significant differences in the contributions of FNC and BNC to SOC and the FNC/BNC ratio between forest and grassland ecosystems (*P* > 0.05; Figure S4). 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). The average FNC/BNC ratios for forests and grasslands were 2.80 and 3.58, respectively.

In contrast, our analysis revealed statistically significant disparities in the contributions of FNC and BNC to SOC and the FNC/BNC ratio in agricultural and natural ecosystems at the global scale ($P < 0.05$; Figure 2). Notably, the average contributions of FNC and BNC to SOC were substantially higher in agricultural ecosystems than in natural ecosystems ($P < 0.001$; see 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). Additionally, natural ecosystems exhibited a higher average FNC/BNC ratio of 3.22, surpassing the average of 2.61 observed in agricultural ecosystems (Figure 2c, Table 1).

### 3.2 Effects of driving factors on the contributions of FNC and BNC to SOC and the FNC/BNC ratio

To investigate the reasons behind the significant differences in the contributions of FNC and BNC to SOC and the FNC/BNC ratio between agricultural and natural ecosystems, we quantified the impact of four types of factors (geographical, climatic, soil physicochemical, and biotic) upon them. Soil physicochemical factors were the most important influence on the contributions of FNC and BNC to SOC in agricultural and natural ecosystems (Figures 3a–d, 4a–d). Specifically, in agricultural ecosystems, soil physicochemical factors accounted for 16% and 17% of variance in the contributions of FNC and BNC to SOC, respectively (Figures 3a, c). In comparison, soil physicochemical factors accounted for 20% and 24% of variance in the contributions of FNC and BNC to SOC in natural ecosystems, respectively

(Figures 3b, d). Conversely, geographical factors, rather than soil physicochemical 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).

These findings were further substantiated by the results obtained from the BRTs. These results indicated that soil physicochemical factors accounted for a substantial portion of the variance in the contributions of FNC and BNC to SOC in agricultural and natural ecosystems (Figures 4a–d), and geographical factors played a similar role in explaining the FNC/BNC ratio (Figures 4e, f). More precisely, soil physicochemical factors were identified as the primary contributors for the contributions of FNC and BNC to SOC, with their contributions amounting to 51% and 44% in agricultural ecosystems (Figures 4a, c), and 44% in natural ecosystems (Figures 4b, d), respectively. This underscores soil physicochemical factors as the primary influencers on the contributions of FNC and BNC to SOC in both ecosystems. Similarly, 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). In both ecosystems, the BRT models used to quantify the relative influence of the four types of factors on the contributions of FNC and BNC to SOC and the FNC/BNC ratio were all significant ($P < 0.001$), with explained model variances ranging from 23% to 66% (Figure 4). Although soil physicochemical factors were the primary factors influencing the contributions of FNC and BNC to SOC in both ecosystems, the response of the contributions to individual soil physicochemical factors was not entirely consistent between agricultural and natural ecosystems. Specifically, in the BRT models, the C/N ratio was the third most influential factor, following clay and SOC, influencing the contribution of FNC to SOC in agricultural ecosystems (Figure 4a). However, the C/N ratio emerged as the most important factor influencing the contribution of FNC to SOC in natural ecosystems and the contribution of BNC to SOC in both ecosystems (Figures 4b–d). Linear regression models indicated that the contributions of FNC and BNC to SOC decreased with increasing C/N ratio in both ecosystems (Figures S5g, S6g). 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 S7a).

The SEMs revealed similar results, indicating that soil physicochemical factors were the most influential factors for the contributions of FNC and BNC to SOC in both agricultural and natural ecosystems, and the factor can affect the contributions of FNC and BNC to SOC in two ecosystems both directly and indirectly (Figures 5a–d, 6a–d). Notably, the direct and standardized total effects of soil physicochemical factors on the contribution of FNC to SOC in natural ecosystem were both positive (Figures 6a, b). 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).

https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

## 4 Discussion

MNC is an important component of SOC (Ma et al., 2018), and its variations can influence the feedback effects on the C cycle and global climate change (Zhao et al., 2023). Our study indicated that the contributions of FNC to SOC were approximately twice those of BNC in agricultural and natural ecosystems. Although the contributions of FNC and BNC to SOC were significantly higher in agricultural ecosystems than in natural ecosystems, the FNC/BNC ratio was significantly higher in the latter. In addition, soil physicochemical properties and geographical factors were the most important predictors of the contributions of MNC (FNC and BNC) to SOC and the FNC/BNC ratio in the two ecosystems, respectively. These findings enhance our understanding of microbially mediated biogeochemical cycling processes under current and future climate scenarios.

### 4.1 Variation in the contributions of FNC and BNC to SOC and the FNC/BNC ratio in agricultural and natural ecosystems

With growing appreciation for the critical role of microbial necromass constituents in forming SOC, it is critical to understand the different drivers of this process across the globe. In this study, we found that the contribution of FNC to SOC significantly exceeded that of BNC, with the former contributing approximately twice as much as BNC to SOC in both agricultural and natural ecosystems (including forests and grasslands; Table 1). These findings were consistent with previous studies (Liang et al., 2019; Wang et al., 2021a; Zhang et al., 2023; Ding et al., 2024). On the one hand, this might be attributable to the various nutrient utilization strategies of the different microbial groups. Labile compounds in bacterial cell walls are preferentially utilized by microbes, resulting in a lower content of bacterial residue in soil (Hu et al., 2020). In contrast, fungi, with their more recalcitrant compounds (e.g., chitin), decompose slowly, allowing them to persist longer in soil. Over time, fungal residue contributes more significantly to SOC pools (Wang et al., 2021a). On the other hand, the thicker cell walls of fungi result in a lower surface area-to-volume ratio of their residual fragments, facilitating the easy formation of complex macromolecular aggregates (Zhao et al., 2023). This contributes significantly to the stability of fungal necromass and plays a crucial role in the accumulation of SOC. Additionally, the comparatively larger biomass of fungi may be a contributing factor to the predominance of FNC over BNC in terms of contributing to SOC in agricultural and natural ecosystems (He et al., 2020).

In the present study, their contributions were found to be consistently higher in agricultural ecosystems as compared to natural ecosystems, with respective values of 34.39% vs. 29.24% for FNC, and 15.65% vs. 14.02% for BNC (Figures 2a, b, Table 1). The higher contributions of FNC and BNC to SOC in agricultural ecosystems compared to natural ecosystems may be attributable to two main factors. First, owing to the diverse range of plant communities and minimal human interference in natural ecosystems, the content of plant-derived organic C significantly exceeds that in agricultural ecosystems impacted by farming activities, potentially resulting in a greater proportion of microbially derived C within SOC (Angst et al., 2021). Second, the concept of the microbial efficiency–substrate stability framework suggests that high-quality substrates (characterized by low C/N ratio) allow for greater accumulation of microbial residue because of a higher rate of microbial residue production (Castellano et al., 2015; Chen et al., 2020; Ni et al., 2020). In this study, the average C/N ratio in agricultural ecosystems was found to be significantly lower than in natural ecosystems—approximately one-third that of natural ecosystems (10.78 vs. 27.44). Therefore, the contribution of MNC (primarily from FNC and BNC) to SOC in agricultural ecosystems was significantly higher than that in natural ecosystems.

Significant differences in the FNC/BNC ratio were also observed between agricultural and natural ecosystems, with natural ecosystems exhibiting a higher FNC/BNC ratio (3.22 *vs*. 2.61; Figure 2c, Table 1). This finding is consistent with that of Wang et al. (2021a), providing additional confidence to the critical differences between these major microbial functional groups. The observed differences in the FNC/BNC ratio between agricultural and natural ecosystems may be attributable to the intrinsic characteristics of these two ecosystems. Zhou et al. (2023) suggested that soils with minimal human interference, such as those in natural ecosystems, tend to have higher FNC. Conversely, human interference (e.g., the application of organic fertilizers) is associated with an increase in BNC content in soil. Other studies have also demonstrated that minimizing soil disturbance can be advantageous for microbial growth, particularly fungi (Sanaullah et al., 2020; Sae-Tun et al., 2022). The mycelial networks of fungi contribute to the formation of more stable soil aggregates, which in turn promotes the sequestration of FNC (Sae-Tun et al., 2022). Furthermore, bacteria tend to dominate in soil with high nutrient content, such as agricultural ecosystems, while in soil with relatively lower nutrient levels, like natural ecosystems, fungi assume a dominant position owing to their enhanced and more extensive substrate degradation capabilities (Strickland and Rousk, 2010; Yu et al., 2022). Hence, comparatively speaking, natural ecosystems, characterized by minimal human interference and relatively lower nutrient levels, are more conducive to fungal growth and the accumulation of their necromass C, consequently resulting in a higher FNC/BNC ratio compared to agricultural ecosystems.

### 4.2 Important driving factors for the contributions of FNC and BNC to SOC and the FNC/BNC ratio

Our results indicated that soil physicochemical factors were key in determining the contributions of FNC and BNC to SOC (Figures 3a–d, 4a–d, 5a–d). Deng and Liang (2022) suggested that the potential contribution of microbial residue to the SOC pool was governed by the C/N ratio. This finding was corroborated by our results, which further indicated that the contributions of FNC and BNC to SOC decreased as the soil C/N ratio increased (Figures 4b–d, S5g, S6g). Several factors may account for the results. On the one hand, the soil C/N ratio regulates microbial community composition, thereby influencing the accumulation of FNC and BNC (Han et al., 2023). Specifically, a high C/N ratio often indicates a relative surplus of C and a limitation of N, which constrains microbial metabolism, reduces microbial turnover and biomass input, and consequently decreases the accumulation of FNC and BNC (Wu et al., 2025). On the other hand, under high C/N conditions, microbes tend to allocate more C to maintenance respiration or $CO_2$ release rather than biomass synthesis, leading to a lower efficiency of necromass production and diminished contribution to SOC (Liu et al., 2024). In addition, a high C/N ratio may also impair the binding capacity of microbial residues to soil minerals, thereby reducing their long-term stabilization and further weakening their contribution to SOC (Li et al., 2024). In contrast, soil clay content was the most predominant factor influencing the contribution of FNC to SOC in agricultural ecosystems (Figure 4a), and this contribution increased with increasing clay content (Figure S5g). Consistent findings have been reported by Six et al. (2006) and Liang et al. (2017), demonstrating that soils with higher clay and silt contents generally harbor greater quantities of microbial residues, particularly fungal-derived residues, due to the enhanced formation of stable organo-mineral complexes promoted by abundant fine soil particles. Moreover, agricultural management practices frequently disturb soil structure but 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 predictors of the FNC/BNC ratio in both agricultural and natural ecosystems (Figures 4e, f, 5f, 6f), and the FNC/BNC ratio increased with increasing elevation (Figure S7a). 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 two 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

https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

regions such as Africa, South America, and Australia (see Figure 1). Moreover, 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. Therefore, more 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.

## 5 Data availability

The data and R code for this manuscript are available at https://doi.org/10.6084/m9.figshare.28827386 (Lu, 2025).

## 6 Conclusions

Our results suggest that the contribution of FNC to SOC is significantly greater than that of 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 compared to agricultural ecosystems, primarily driven by geographical factors (elevation). Our results reveal consistent trends in the contributions of FNC and BNC to SOC, and the FNC/BNC ratio, which are indicative of ecosystem-level differences in C turnover and stabilization mechanisms across the globe. These insights are conducive to a better mechanistic understanding of the role of microbes in the C cycle in terrestrial ecosystems, and could inform strategies for C sequestration and sustainable land management strategies in the context of 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

## Acknowledgements

We are grateful for the data contributors and the scientific community which made the data accessible and useful for our study.

## Financial support

This work was supported financially by the National Natural Science Foundation of China (No. 32160291), the National Key Research and Development Program of China (No. 2021YFD2200403-04), the Natural Science Foundation of Hainan province (No. 423QN212), and the Hainan University Research start-up Fund (No. KYQD(ZR)22187).

## References

Angst, G., Mueller, K.E., Nierop, K.G., Simpson, M.J., 2021. Plant-or microbial-derived? A review on the molecular composition of stabilized soil organic matter. Soil Biol. Biochem. 156, 108189. https://doi.org/10.1016/j.soilbio.2021.108189

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J., 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437, 245–248. https://doi.org/10.1038/nature04038

Bohan, D.A., Raybould, A., Mulder, C., Woodward, G., Tamaddoni-Nezhad, A., Bluthgen, N., Pocock, M.J.O., Muggleton, S., Evans, D.M., Astegiano, J., Massol, F., Loeuille, N., Petit, S., Macfadyen, S., 2013. Networking agroecology: integrating the diversity of agroecosystem interactions. Adv. Ecol. Res. 49, 1–67. https://doi.org/10.1016/B978-0-12-420002-9.00001-9

Campitelli, E., 2022. *ggnewscale*: Multiple Fill and Colour Scales in '*ggplot2*'. R package version 0.4.8. https://CRAN.R-project.org/package=ggnewscale

Cao, Y., Ding, J., Li, J., Xin, Z., Ren, S., Wang, T., 2023. Necromass-derived soil organic carbon and its drivers at the global scale. Soil Biol. Biochem. 181, 109025. https://doi.org/10.1016/j.soilbio.2023.109025

Castellano, M.J., Mueller, K.E., Olk, D.C., Sawyer, J.E., Six, J., 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. Global Change Biol. 21, 3200–3209. https://doi.org/10.1111/gcb.12982

Chen, G., Ma, S., Tian, D., Xiao, W., Jiang, L., Xing, A., Zou, A., Zhou, L., Shen, H., Zheng, C., Ji, C., He, H., Zhu, B., Liu, L., Fang, J., 2020. Patterns and determinants of soil microbial residues from tropical to boreal forests. Soil Biol. Biochem. 151, 108059. https://doi.org/10.1016/j.soilbio.2020.108059

Choi, J., Bach, E., Lee, J., Flater, J., Dooley, S., Howe, A., Hofmockel, K. S., 2018. Spatial structuring of cellulase gene abundance and activity in soil. Front. Environ. Sci. 6, 107. https://doi.org/10.3389/fenvs.2018.00107

Crowther, T.W., Sokol, N.W., Oldfield, E.E., Maynard, D.S., Thomas, S.M., Bradford, M.A., 2015. Environmental stress response limits microbial necromass contributions to soil organic carbon. Soil Biol. Biochem. 85, 153–161. https://doi.org/10.1016/j.soilbio.2015.03.002

Cui, W., Li, R., Fan, Z., Wu, L., Zhao, X., Wei, G., Shu, D., 2023. Weak environmental adaptation of rare phylotypes sustaining soil multi-element cycles in response to decades-long fertilization. STOTEN. 871, 162063. https://doi.org/10.1016/j.scitotenv.2023.162063

Deng, F., Liang, C., 2022. Revisiting the quantitative contribution of microbial necromass to soil carbon pool: stoichiometric control by microbes and soil. Soil Biol. Biochem. 165, 108486. https://doi.org/10.1016/j.soilbio.2021.108486

Ding, Z., Mou, Z., Li, Y., Liang, C., Xie, Z., Wang, J., Hui, D., Lambers, H., Sardans, J., Peñuelas, J., Xu, H., Liu, Z., 2024. Spatial variation and controls of soil microbial necromass carbon in a tropical montane rainforest. STOTEN. 921, 170986. https://doi.org/10.1016/j.scitotenv.2024.170986

Fanin, N., Bezaud, S., Sarneel, J.M., Cecchini, S., Nicolas, M., Augusto, L., 2020. Relative importance of climate, soil and plant functional traits during the early decomposition stage of standardized litter. Ecosystems 23, 1004–1018. https://doi.org/10.1007/s10021-019-00452-z

Greenwell, B., Boehmke, B., Cunningham, J., Developers, G.B.M., 2022. *gbm*: Generalized Boosted Regression Models. R package version 2.1.8.1. https://CRAN.R-project.org/package=gbm

Han, B., Yao, Y., Wang, Y., Su, X., Ma, L., Chen, X., Li, Z., 2024. Microbial traits dictate soil necromass accumulation coefficient: A global synthesis. Global Ecol. Biogeogr. 33(1), 151–161. https://doi.org/10.1111/geb.13776

Hao, Z., Zhao, Y., Wang, X., Wu, J., Jiang, S., Xiao, J.,Wang, K., Zhou, X., Liu, H., Li, J., Sun, Y., 2021. Thresholds in aridity and soil carbon-to-nitrogen ratio govern the accumulation of soil microbial residues. Commun. Earth Environ. 2, 236. https://doi.org/10.1038/s43247-021-00306-4

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Rev. Ecol. Evol. S. 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

He, L., Rodrigues, J.L.M., Soudzilovskaia, N.A., Barceló, M., Olsson, P.A., Song, C., Tedersoo, L., Yuan, F., Yuan, F., Lipson, D.A., Xu, X., 2020. Global biogeography of fungal and bacterial biomass carbon in topsoil. Soil Biol. Biochem. 151, 108024. https://doi.org/10.1016/j.soilbio.2020.108024

Hobbs, R.J., Hallett, L.M., Ehrlich, P.R., Mooney, H.A., 2011. Intervention ecology: applying ecological science in the twenty-first century. BioScience 61, 442–450. https://doi.org/10.1525/bio.2011.61.6.6

Hollister, J. W., 2021. *elevatr*: Access Elevation Data from Various APIs. R package version 0.4.2. https://CRAN.R-project.org/package=elevatr/

Hu, Y., Zheng, Q., Noll, L., Zhang, S., Wanek, W., 2020. Direct measurement of the *in situ* decomposition of microbial-derived soil organic matter. Soil Biol. Biochem. 141, 107660. https://doi.org/10.1016/j.soilbio.2019.107660

Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nat. Commun. 7, 13630. https://doi.org/10.1038/ncomms13630

Kassambara, A., 2022. *ggpubr*: '*ggplot2*' Based Publication Ready Plots. R package version 0.5.0. https://CRAN.R-project.org/package=ggpubr

Keith, D.A., Ferrer-Paris, J.R., Nicholson, E., Bishop, M.J., Polidoro, B.A., Ramirez-Llodra, E., Tozer, M.G., Nel, J.L., Nally, R.M., Gregr, E.J., Watermeyer, K.E., Essl, F., Faber-Langendoen, D., Franklin, J., Lehmann, C.E.R., Etter, A., Roux, D.J., Stark, J.S., Rowland, J.A., Brummitt, N.A., Fernandez-Arcaya, U.C., Suthers, I.M., Wiser, S.K., Donohue, I., Jackson, L.J., Pennington, R.T., Iliffe, T.M., Gerovasileiou, V., Giller, P., Robson, B.J., Pettorelli, N., Andrade, A., Lindgaard, A., Tahvanainen, T., Terauds, A., Chadwick, M.A., Murray, N.J., Moat, J., Pliscoff, P., Zager, I., Kingsford, R.T., 2022. A function-based typology for Earth's ecosystems. Nature 610, 513–518. https://doi.org/10.1038/s41586-022-05318-4

Kock, N., 2015. Common method bias in PLS-SEM: A full collinearity assessment approach. International Journal of e-Collaboration (IJeC) 11, 1–10. https://doi.org/10.4018/ijec.2015100101

Körner, C., 2007. The use of 'altitude'in ecological research. Trends Ecol. Evol. 22(11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Lembrechts, J.J., van den Hoogen, J., Aalto, J., Ashcroft, M.B., De Frenne, P., Kemppinen, J., Kopecký, M., Luoto, Maclean, M.I.M.D, Crowther, T.W., Bailey, J.J., Haesen, S., Klinges, D.H., Niittynen, P., Scheffers, B.R., Van Meerbeek, K., Aartsma, P., Abdalaze, O., Abedi, M., Aerts, R., Ahmadian, N., Ahrends, A., Alatalo, J.M., Alexander, J.M., Allonsius, C.N., Altman, J., Ammann, C., Andres,C., Andrews, C., Ardö, J., Arriga, N., Arzac, A., Aschero, V., Assis, R.L., Assmann, J.J., Bader, M.Y., Bahalkeh, K., Barančok, P., Barrio, I.C., Barros, A., Barthe, M., Basham, E.W., BautersM., Bazzichetto, M., Marchesini, L.B., Bell, M.C., Benavides, J.C., Alonso, J.L.B., Berauer, B.J., Bjerke, J.W., Björk, R.G., Björkman, M.P., Björnsdóttir, K., Blonder, B., Boeckx, P., Boike, J., Bokhorst, S., Brum, B.N.S., Brůna, J., Buchmann, N., Buysse, P., Camargo, J.L., Campoe, O.C., Candan, O., Canessa, R., Cannone, N., ... Hik, D. S., 2022. Global maps of soil temperature. Global Change Biol. 28, 3110–3144. https://doi.org/10.1111/gcb.16060

Lenardon, M.D., Whitton, R.K., Munro, C.A., Marshall, D., Gow, N.A.R., 2007. Individual chitin synthase enzymes synthesize microfibrils of differing structure at specific locations in the *Candida albicans* cell wall. Mol. Microbiol. 66, 1164–1173. https://doi.org/10.1111/j.1365-2958.2007.05990.x

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Global Change Biol. 25, 3578–3590. https://doi.org/10.1111/gcb.14781

Liang, C., Balser, T.C., 2011. Microbial production of recalcitrant organic matter in global soils: implications for productivity and climate policy. Nat. Rev. Microbiol. 9, 75–75. https://doi.org/10.1038/nrmicro2386-c1

Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. 2, 17105. https://doi.org/10.1038/nmicrobiol.2017.105

Liu, X., Tian, Y., Heinzle, J., Salas, E., Kwatcho-Kengdo, S., Borken, W., Schindlbacher, A., Wanek, W., 2024. Long-term soil warming decreases soil microbial necromass carbon by adversely affecting its production and decomposition. Global Change Biol. 30(6), e17379. https://doi.org/10.1111/gcb.17379

Li, Y., Wang, S., Yang, Y., Ren, L., Wang, Z., Liao, Y., Yong, T., 2024. Global synthesis on the response of soil microbial necromass carbon to climate-smart agriculture. Global Change Biol. 30(5), e17302. https://doi.org/10.1111/gcb.17302

Luo, R., Kuzyakov, Y., Zhu, B., Qiang, W., Zhang, Y., Pang, X., 2022. Phosphorus addition decreases plant lignin but increases microbial necromass contribution to soil organic carbon in a subalpine forest. Global Change Biol. 28, 4194–4210. https://doi.org/10.1111/gcb.16205

Malik, A.A., Chowdhury, S., Schlager, V., Oliver, A., Puissant, J., Vazquez, P.G., Jehmlich, N., von Bergen, M., Griffiths, R., Gleixner, G., 2016. Soil fungal: bacterial ratios are linked to altered carbon cycling. Front. Microbiol. 7, 1247. https://doi.org/10.3389/fmicb.2016.01247

Ma, T., Zhu, S., Wang, Z., Chen, D., Dai, G., Feng, B., Su, X., Hu, H., Li, K., Han, W., Liang, C., Bai, Y., Feng, X., 2018. Divergent accumulation of microbial necromass and plant lignin components in grassland soils. Nat. Commun. 9, 3480. https://doi.org/10.1038/s41467-018-05891-1

Mou, Z., Kuang, L., He, L., Zhang, J., Zhang, X., Hui, D., Li, Y., Wu, W., Mei, Q., He, X., Kuang, Y., Wang, J., Wang, Y., Lambers, H., Sardans, J., Peñuelas, J., Liu, Z., 2021. Climatic and edaphic controls over the elevational pattern of microbial necromass in subtropical forests. Catena 207, 105707. https://doi.org/10.1016/j.catena.2021.105707

Ni, X., Liao, S., Tan, S., Peng, Y., Wang, D., Yue, K., Wu, F., Yang, Y., 2020. The vertical distribution and control of microbial necromass carbon in forest soils. Global Ecol. Biogeogr. 29, 1829–1839. https://doi.org/10.1111/geb.13159

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Wagner, H., 2020. *vegan*: Community Ecology Package. R package version 2.5.7. https://CRAN.R-project.org/package=vegan

Poggio, L., De Sousa, L.M., Batjes, N.H., Heuvelink, G., Kempen, B., Ribeiro, E., Rossiter, D., 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil 7, 217–240. https://doi.org/10.5194/soil-7-217-2021

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

Rosseel, Y. 2012. *lavaan*: An R package for structural equation modeling. J. Stat. Softw. 48, 1–36. https://doi.org/10.18637/jss.v048.i02

Sae-Tun, O., Bodner, G., Rosinger, C., Zechmeister-Boltenstern, S., Mentler, A., Keiblinger, K., 2022. Fungal biomass and microbial necromass facilitate soil carbon sequestration and aggregate stability under different soil tillage intensities. Appl. Soil Ecol. 179, 104599. https://doi.org/10.1016/j.apsoil.2022.104599

Sanaullah, M., Usman, M., Wakeel, A., Cheema, S.A., Ashraf, I., Farooq, M., 2020. Terrestrial ecosystem functioning affected by agricultural management systems:

A review. Soil Tillage Res. 196, 104464. https://doi.org/10.1016/j.still.2019.104464

Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci. Soc. Am. J. 70, 555–569. https://doi.org/10.2136/sssaj2004.0347

Song, A., Zhang, J., Xu, D., Wang, E., Bi, J., Asante-Badu, B., Njyenawe, M.C., Sun, M., Xue, P., Wang, S., Fan, F., 2022. Keystone microbial taxa drive the accelerated decompositions of cellulose and lignin by long-term resource enrichments. STOTEN 842, 156814. https://doi.org/10.1016/j.scitotenv.2022.156814

Spawn, S.A., Sullivan, C.C., Lark, T.J., Gibbs, H.K., 2020. Harmonized global maps of above and belowground biomass carbon density in the year 2010. Sci. Data 7, 112. https://doi.org/10.1038/s41597-020-0444-4

Strickland, M.S., Rousk, J., 2010. Considering fungal: bacterial dominance in soils–methods, controls, and ecosystem implications. Soil Biol. Biochem. 42, 1385–1395. https://doi.org/10.1016/j.soilbio.2010.05.007

von Lützow, M., Kögel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., Kalbitz, K., 2008. Stabilization mechanisms of organic matter in four temperate soils: Development and application of a conceptual model. J. Plant Nutr. Soil Sci. 171, 111–124. https://doi.org/10.1002/jpln.200700047

Wang, B., An, S., Liang, C., Liu, Y., Kuzyakov, Y., 2021a. Microbial necromass as the source of soil organic carbon in global ecosystems. Soil Biol. Biochem. 162, 108422. https://doi.org/10.1016/j.soilbio.2021.108422

Wang, B., Liang, C., Yao, H., Yang, E., An, S., 2021b. The accumulation of microbial necromass carbon from litter to mineral soil and its contribution to soil organic carbon sequestration. Catena 207, 105622. https://doi.org/10.1016/j.catena.2021.105622

Wang, Z., Zhao, M., Yan, Z., Yang, Y., Niklas, K.J., Huang, H., Mipam, T.D., He, X., Hu, H., Wright, S.J., 2022. Global patterns and predictors of soil microbial biomass carbon, nitrogen, and phosphorus in terrestrial ecosystems. Catena 211, 106037. https://doi.org/10.1016/j.catena.2022.106037

Wickham, H., 2016. *ggplot2*: elegant graphics for data analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org

Wu, H., Xiang, W., Ouyang, S., Forrester, D. I., Zhou, B., Chen, L., Ge, T., Lei, P., Chen, L., Zeng, Y., Song, X., Peñuelas, J., Peng, C., 2019. Linkage between tree species richness and soil microbial diversity improves phosphorus bioavailability. Funct. Ecol. 33, 1549–1560. https://doi.org/10.1111/1365-2435.13355

Wu, W., Feng, J., Wang, X., Xiao, J., Qin, W., Zhu, B., 2025. The response of soil microbial necromass carbon to global change: A global meta-analysis. Catena 249, 108693. https://doi.org/10.1016/j.catena.2024.108693

Xu, S., Song, X., Zeng, H., Wang, J., 2024. Soil microbial necromass carbon in forests: A global synthesis of patterns and controlling factors. Soil Ecol. Lett. 6(4), 240237. https://doi.org/10.1007/s42832-024-0237-3

Xu, Y., Sun, L., Gao, X., Wang, J., 2022. Contrasting response of fungal versus bacterial residue accumulation within soil aggregates to long-term fertilization. Sci. Rep. 12, 17834. https://doi.org/10.1038/s41598-022-22064-9

Yu, K., van den Hoogen, J., Wang, Z., Averill, C., Routh, D., Smith, G.R., Drenovsky, R.E., Scow, K.M., Mo, F., Waldrop, M.P., Yang, Y., Tang, W., Vries, F.T.D., Bardgett, R.D., Manning, P., Bastida, F., Baer, S.G., Bach, E.M., García, C., Wang, Q., Ma, L., Chen, B., He, X., Teurlincx, S., Heijboer, A., Bradley, J.A., Crowther, T. W., 2022. The biogeography of relative abundance of soil fungi versus bacteria in surface topsoil. Earth Syst. Sci. Data 14, 4339–4350. https://doi.org/10.5194/essd-14-4339-2022

Zhang, B., Zhu, S., Guo, L., Chen, G., Zhang, G., Li, J., 2025. Elevation-dependent distribution of soil microbial necromass carbon in *Pinus densata* Mast. forests. Appl. Soil Ecol. 209, 106049. https://doi.org/10.1016/j.apsoil.2025.106049

Zhang, Q., Li, X., Liu, J., Liu, J., Han, L., Wang, X., Liu, H., Xu, M., Yang, G., Ren, C., Han, X., 2023. The contribution of microbial necromass carbon to soil organic carbon in soil aggregates. Appl. Soil Ecol. 190, 104985. https://doi.org/10.1016/j.apsoil.2023.104985

Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329, 940–943. https://doi.org/10.1126/science.1192666

Zhang, X., Jia, J., Chen, L., Chu, H., He, J.S., Zhang, Y., Feng, X., 2021. Aridity and NPP constrain contribution of microbial necromass to soil organic carbon in the Qinghai-Tibet alpine grasslands. Soil Biol. Biochem. 156, 108213. https://doi.org/10.1016/j.soilbio.2021.108213

Zhao, X., Tian, P., Liu, S., Yin, P., Sun, Z., Wang, Q., 2023. Mean annual temperature and carbon availability respectively controlled the contributions of bacterial and fungal necromasss to organic carbon accumulation in topsoil across China's forests. Global Ecol. Biogeogr. 32, 120–131. https://doi.org/10.1111/geb.13605

Zhou, R., Liu, Y., Dungait, J.A., Kumar, A., Wang, J., Tiemann, L.K., Zhang, F., Kuzyakov, Y., Tian, J., 2023. Microbial necromass in cropland soils: A global meta-analysis of management effects. Global Change Biol. 29, 1998–2014. https://doi.org/10.1111/gcb.16613

Zhu, Y.G., Miller, R.M., 2003. Carbon cycling by arbuscular mycorrhizal fungi in soil–plant systems. Trends Plant Sci. 8, 407–409. https://doi.org/10.1016/S1360-1385(03)00184-5

**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 |

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

$^{\&}$Natural ecosystem includes forest and grassland;

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

$^{\#}$Within the same column, values with different capital letters indicate a significant difference in the same variable between forests and grasslands ($P < 0.05$, Wilcoxon rank-sum test).

https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

## 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

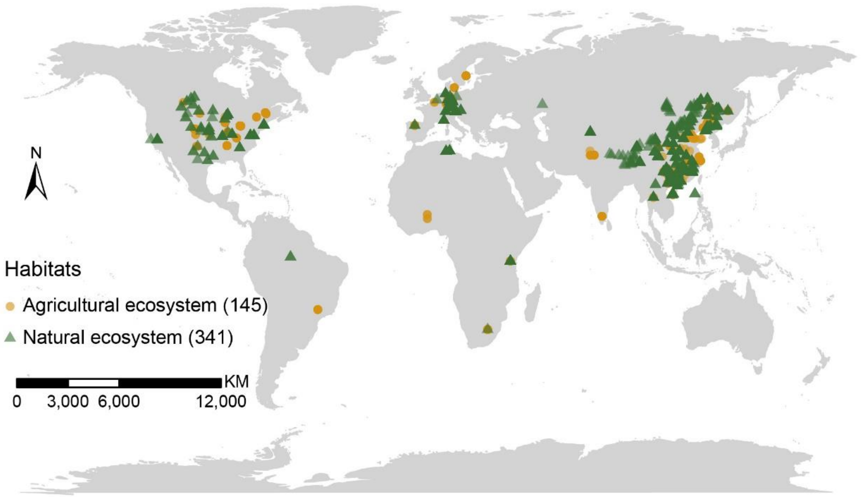
https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

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 S7.

**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 S7.

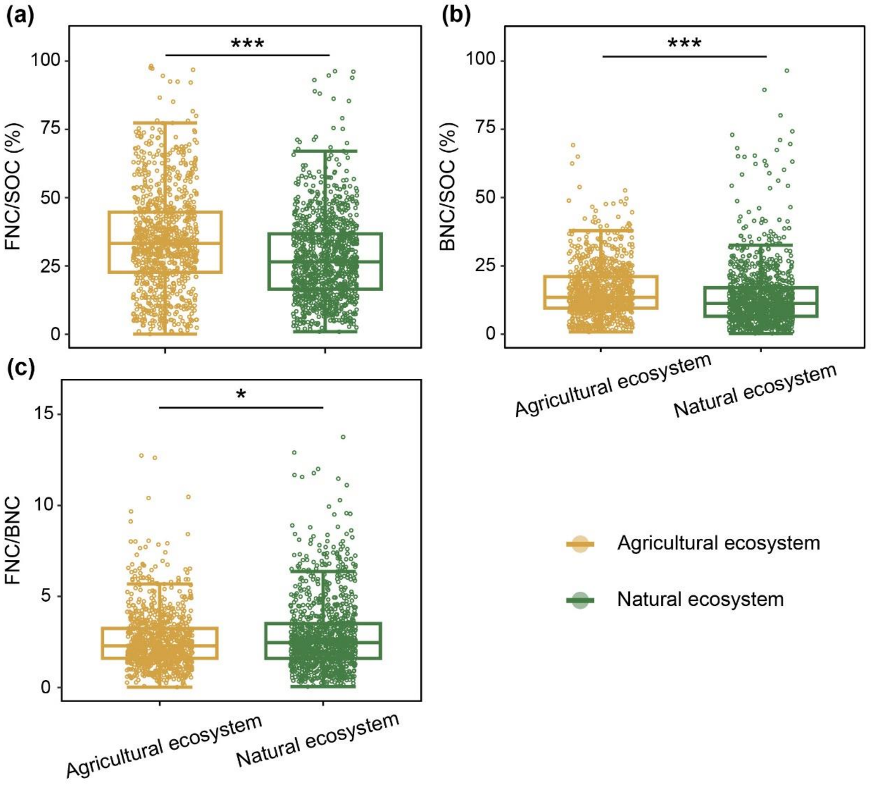
https://doi.org/10.5194/essd-2025-229
Preprint. Discussion started: 28 May 2025

762 **Figure 1.**



763

764 **Figure 2.**



765

**Figure 3.**

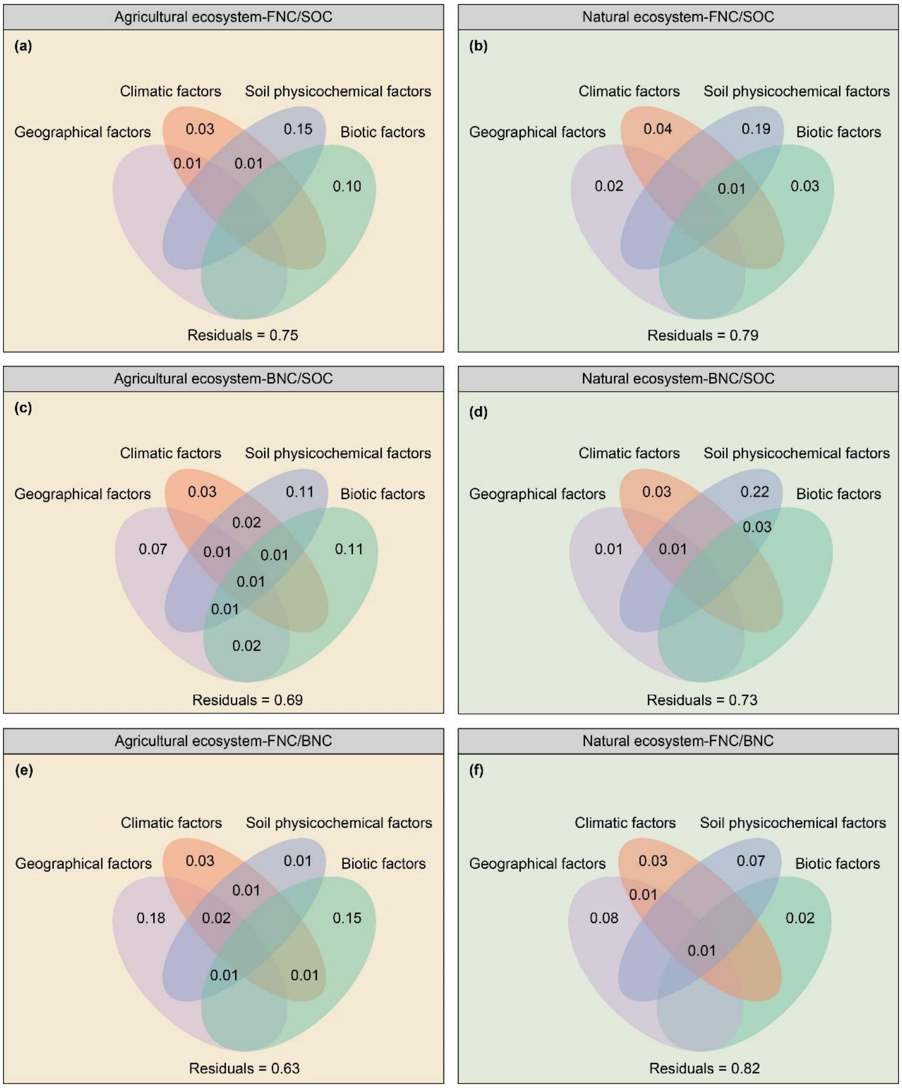

Agricultural ecosystem-FNC/SOC
(a)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.03
0.15
0.01
0.01
0.10
Residuals = 0.75
Natural ecosystem-FNC/SOC
(b)
Climatic factors
Soil physicochemical factors
Geographical factors
Biotic factors
0.04
0.19
0.02
0.01
0.03
Residuals = 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.**

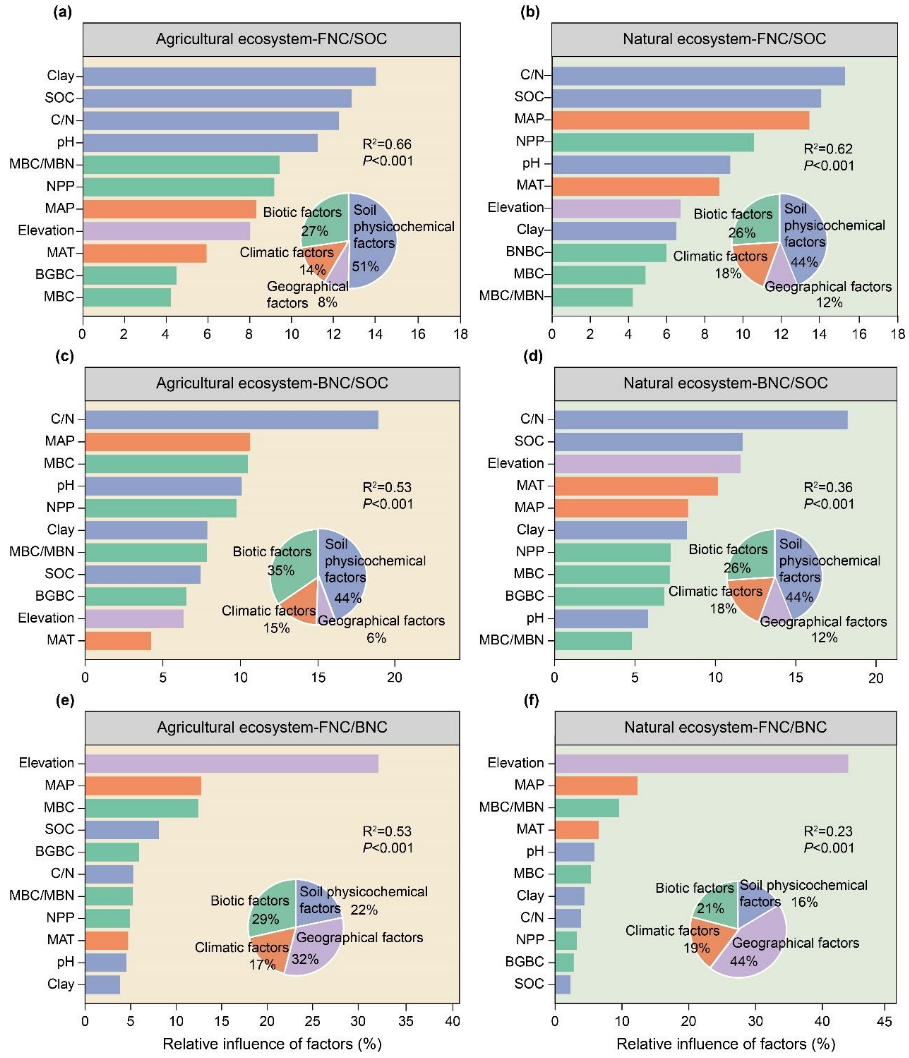

(a)
Agricultural ecosystem-FNC/SOC
Clay
SOC
C/N
pH
MBC/MBN
NPP
MAP
Elevation
MAT
BGBC
MBC
R²=0.66
P<0.001
Biotic factors 27%
Soil physicochemical factors 51%
Climatic factors 14%
Geographical factors 8%
0 2 4 6 8 10 12 14 16 18
(b)
Natural ecosystem-FNC/SOC
C/N
SOC
MAP
NPP
pH
MAT
Elevation
Clay
BNBC
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.**

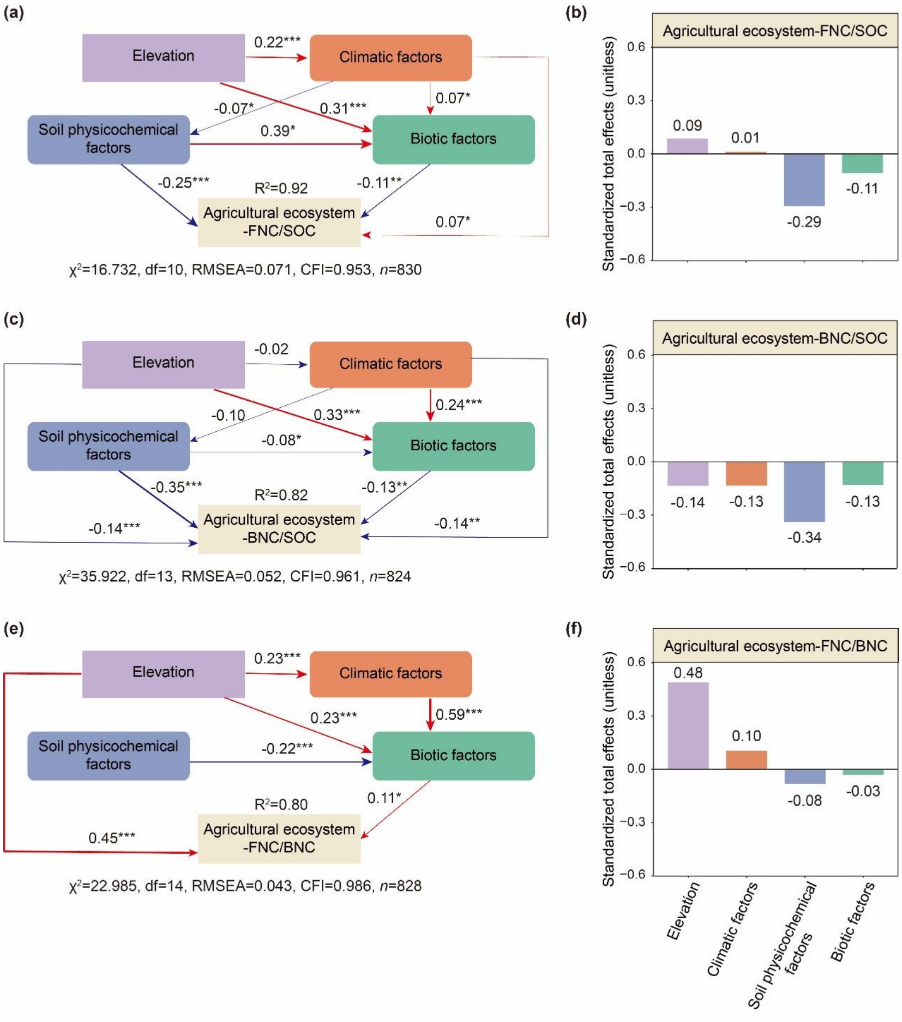
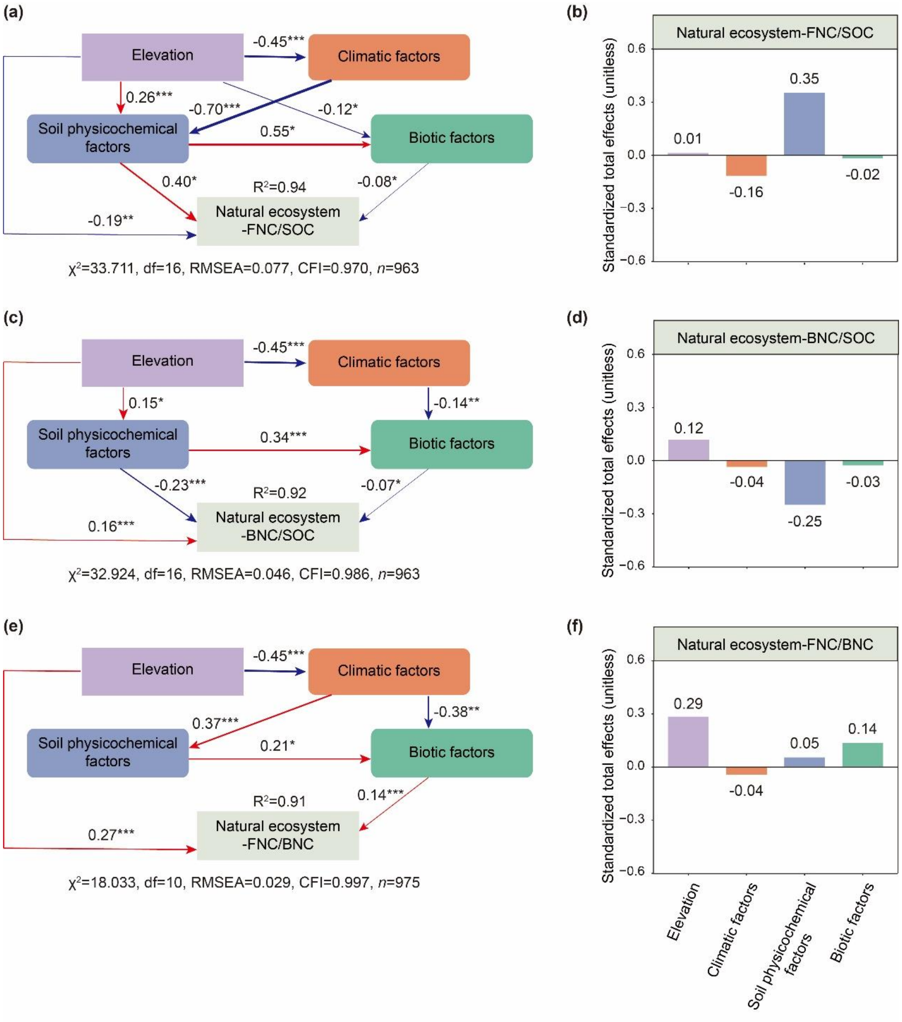

(a)
Elevation
0.22***
Climatic factors
-0.07*
0.31***
0.07*
Soil physicochemical factors
0.39*
Biotic factors
-0.25***
R²=0.92
-0.11**
Agricultural ecosystem -FNC/SOC
0.07*
χ²=16.732, df=10, RMSEA=0.071, CFI=0.953, n=830
(b)
Agricultural ecosystem-FNC/SOC
Standardized total effects (unitless)
0.6
0.3
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**
Agricultural ecosystem -BNC/SOC
-0.14***
-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
Climatic factors
-0.45***
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
Climatic factors
-0.45***
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)
0.6
0.3
0.0
−0.3
−0.6
0.12
-0.04
-0.25
-0.03
(e)
Elevation
Climatic factors
-0.45***
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)
0.6
0.3
0.0
−0.3
−0.6
0.29
-0.04
0.05
0.14
Elevation
Climatic factors
Soil physicochemical factors
Biotic factors