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Research article

The conversion of croplands to wetlands alters soil organic carbon by regulating soil particulate and microbial necromass carbon

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ABSTRACT

Natural wetlands store 20–30 % of soil organic carbon (SOC), and conversion of croplands to wetlands is thus an effective strategy for SOC restoration. However, the contribution of microbial necromass carbon to SOC change during this conversion process remains unclear. We collected samples of topsoil (0–20 cm) and subsoil (40–60 cm) from croplands, rewetlands (i.e., rewetting croplands) and natural wetlands in 20 different sites in Baiyangdian Lake to compare the changes of SOC fractions (particulate organic carbon, POC; minerals associated organic carbon, MAOC) and the microbial contribution to SOC. Both SOC and POC in the topsoil gradually decreased from croplands to wetlands, and the proportion of MAOC to SOC increased. The content of microbial necromass carbon (MNC) mirrored the decline in SOC, yet its contribution to SOC in the topsoil remained stable at 16.0 %–19.6 %. The relative contribution of MNC to POC gradually decreased in converting croplands to wetlands across the topsoil and subsoil, while its contribution to MAOC gradually increased in the subsoil. Depth-dependent regulation of SOC fractions was observed, with conversion indirectly affecting soil microbe and necromass accumulation through regulating soil properties, thereby influencing SOC fractions in the topsoil. In contrast, in the subsoil, soil properties had a more direct impact on SOC fractions, with microbial effects being less apparent. This study confirms the critical role of MNC in regulating SOC and its fractions during converting croplands to wetlands, and highlights the potential to enhance SOC stability.

Nomenclature

SOC	soil organic carbon
POC	particulate organic carbon
MAOC	mineral-bound organic carbon
MBC	microbial biomass carbon
MNC	Microbial necromass carbon
FNC	fungal necromass carbon
BNC	bacterial necromass carbon
MBN	microbial biomass nitrogen
MBP	microbial biomass phosphorus
SWC	soil water content

1. Introduction

Enhancing and protecting soil organic carbon (SOC) storage and its stability is a highly effective strategy for reducing atmospheric CO_2 levels and mitigating global warming (Yang et al., 2022; Ren et al., 2023). It is particularly noteworthy that natural wetlands, despite covering only 5–8 % of the global land surface, store about 20–30 % of the world's SOC (Wang et al., 2024; Ren et al., 2023; Mitsch et al., 2013). Regrettably, the reclamation and cultivation of these areas have become the primary drivers of global wetland loss over recent decades, resulting in significant carbon emissions (Lugato et al., 2021; Liu et al., 2023a; Wang et al., 2024; Fluet-Chouinard et al., 2023; Hu et al., 2017). In response to this challenge, the restoration of croplands to their

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original wetlands state has become a promising solution for bolstering environmental conservation and the capacity for SOC sequestration (Liu et al., 2024a; Ding et al., 2019; Zhang et al., 2023).

However, the complexity inherent of SOC and its various fractions introduce ambiguity regarding the effectiveness of rewetting croplands (i.e., conversion of croplands to wetlands) in augmenting SOC content and ensuring its long-term stability (Chojnacka et al., 2023; An et al., 2021). SOC can be classified into two crucial fractions: particulate organic carbon (POC) and mineral-associated organic carbon (MAOC), based on their formation pathway and protection mechanism (Angst et al., 2023; Hansen et al., 2024). POC is primarily derived from plant residue fragmentation and microbial biomass, and protected by physical occlusion (Zou et al., 2023; Wu et al., 2023). Conversely, MAOC is formed through the sorption of microbial necromass and its decomposition products onto soil mineral surfaces (Zhu et al., 2020; Zou et al., 2023; Chang et al., 2024), conferring higher resistance to microbial decomposition and thus contributing to its greater stability (Martens et al., 2023; Heckman et al., 2023; Zhu et al., 2019). The distinct formation and persistence mechanisms of POC and MAOC suggest that they may respond differently to environmental changes (Wu et al., 2023; Angst et al., 2023).

As one of the main sources of both POC and MAOC, soil microbial necromass carbon (MNC) has garnered significant attention due to its responsiveness to environmental changes. Previous studies showed that MNC can account for 54 % of POC sources and 11 % of MAOC sources in cropland soils (Zou et al., 2023), and it contributes to 29 % of SOC in wetlands globally (Cao et al., 2023). The production and accumulation of MNC are modulated by environmental factors and soil microbial communities, leading to variable contributions across different ecosystems (Wang et al., 2021a; Zou et al., 2023; Cao et al., 2023), and MNC is highly depth-dependent because of the difference of plant input, soil nutrients and soil mineral deposits between topsoil and subsoil (He et al., 2022). However, there is a notable knowledge gap concerning the specific contributions of MNC to MAOC and POC among wetlands, rewetting croplands, and croplands. Therefore, it is essential to investigate the contributions of various SOC fractions during the transition from croplands to wetlands for accurately evaluating the carbon sequestration benefits associated with wetland restoration efforts.

Cultivation and tillage in croplands can alter soil structure, properties, nutrient availability, as well as the quality and quantity of organic matter input from plants. These alterations may profoundly influence the abundance, community composition, and metabolic activities of soil microbes, and subsequently impact the accumulation of MNC and its contribution to SOC fractions (Cao et al., 2023; Wang et al., 2024; Liu et al., 2023b). A previous study confirmed that reforestation, as a form of land-use transition, can enhance the contribution of MNC to SOC compared to natural forests, potentially due to the nutrient-rich conditions left by prior agricultural practices that foster rapid microbial turnover (Zhang et al., 2023). Given the unique moisture and nutrient conditions of wetlands, along with the disruptions caused by human tillage, the impact of converting croplands to wetlands on MNC and its contribution to SOC remains unclear. This uncertainty may lead to MNC accumulation and contribution that deviate from the natural succession of the ecosystem, thereby complicating our ability to predict and assess the carbon sequestration capacity of restored wetlands (Wang et al., 2024; Zhang et al., 2023). Therefore, it is crucial to investigate whether the levels of MNC and its contribution to SOC revert to those in natural wetlands after the rewetting of croplands, and to assess whether they are influenced by the legacy effects of previous agricultural activities.

Here we compared MNC and its contributions to SOC at different soil depths in croplands, rewetlands and natural wetlands, and analyzed the mechanism influencing MNC and SOC fractions during the ecological transition from croplands to wetlands. Considering that the restoration from croplands to wetlands is a reverse process of wetland reclamation, we hypothesize that: (1) SOC would restore to the similar levels with natural wetlands by regulating POC rather than MAOC due to the difference in their stability; (2) MNC and its contribution to SOC may decrease because decreasing soil nutrients and increasing soil moisture could limit microbial biomass; and (3) the effects of this land-use conversion on MNC and its contribution to SOC fractions is depth-dependent. This study provides critical insights for accurately evaluating the carbon sequestration benefits associated with wetland restoration efforts by clarifying how SOC components and microbial drivers shift during the conversion from farmland to wetland, and directly support the optimization of wetland management strategies.

2. Materials and methods

2.1. Study area

The study site is located in Baiyangdian (115°45′-116°07′ E, 38°44′-38°59′ N), the largest lake group in North China Plain, and consisting of 143 small lakes with a total area of 366 km^2 (Tian et al., 2024b). The average annual temperature in this region is 12.2 °C and the annual precipitation is 529.7 mm, which belongs to the warm temperate sub-humid continental monsoon climate (Tian et al., 2024b). In Baiyangdian, natural wetlands are dominated by common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), and croplands are used for a rotation of wheat and corn cultivation (Wang et al., 2021b). The soil type is mainly silty loam with a low degree of soil agglutination (Wang et al., 2021b). The croplands are managed artificially through irrigation and fertilization during the growing season, with soil cultivation extending to a depth of no more than 40 cm (Wang et al., 2022). Additionally, natural wetlands may experience flooding during periods of abundant rainfall. Since 2018, the government has carried out ecological replenishment and returning part of croplands to wetlands. Therefore, croplands, rewetlands (i.e., rewetting croplands) and natural wetlands in this region are adjacent, which is an ideal platform to explore how converting croplands into wetlands affects SOC fractions and its determinants. We expect that the response patterns of SOC fractions to land-use change can be broadly applicable to wetland restoration and agricultural management practices worldwide.

2.2. Field sampling

In 2023, we sampled soils in 20 sites in Baiyangdian. At each site, we selected a cropland, a rewetland (restored from a cropland to a wetland) and a natural wetland that were adjacent (Fig. 1). To ensure comparability between rewetlands and their natural counterparts, our selection of natural wetlands was restricted to platform reed wetlands, deliberately excluding flooded wetlands. We set up a 2 m × 2 m plot at each site for each land-use type, and collected five samples of the topsoil (0–20 cm deep) and the subsoil (40–60 cm deep). The five soil samples of the same depth were mixed to form one composite sample. The selection of the soil depths was based on the typical tillage depth in this region, which generally does not exceed 40 cm, and aligns with the conventional soil layer divisions used in previous studies (Chen et al., 2021a; He et al., 2022). We collected vegetation samples in September 2023, dried and measured biomass, which was used as reference data for plant carbon input.

2.3. Soil physicochemical properties measurements

We used chloroform-fumigation extraction procedure to measure microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and microbial biomass phosphorous (MBP) (Fierer et al., 2003; Vance et al., 1987; Brookes et al., 1985; Li et al., 2025) with a liquid measurement module of TOC analyzer (Analytikjena, multiN/C 3100, Germany), continuous-flow analyzer (AA3; Bran + Luebbe GmbH, Hamburg, Germany) and ultraviolet spectrophotometer at 880 nm. For fumigation, 5 g of the fresh soil sample was placed in a sealed container in dark and fumigated with chloroform vapor at room temperature for

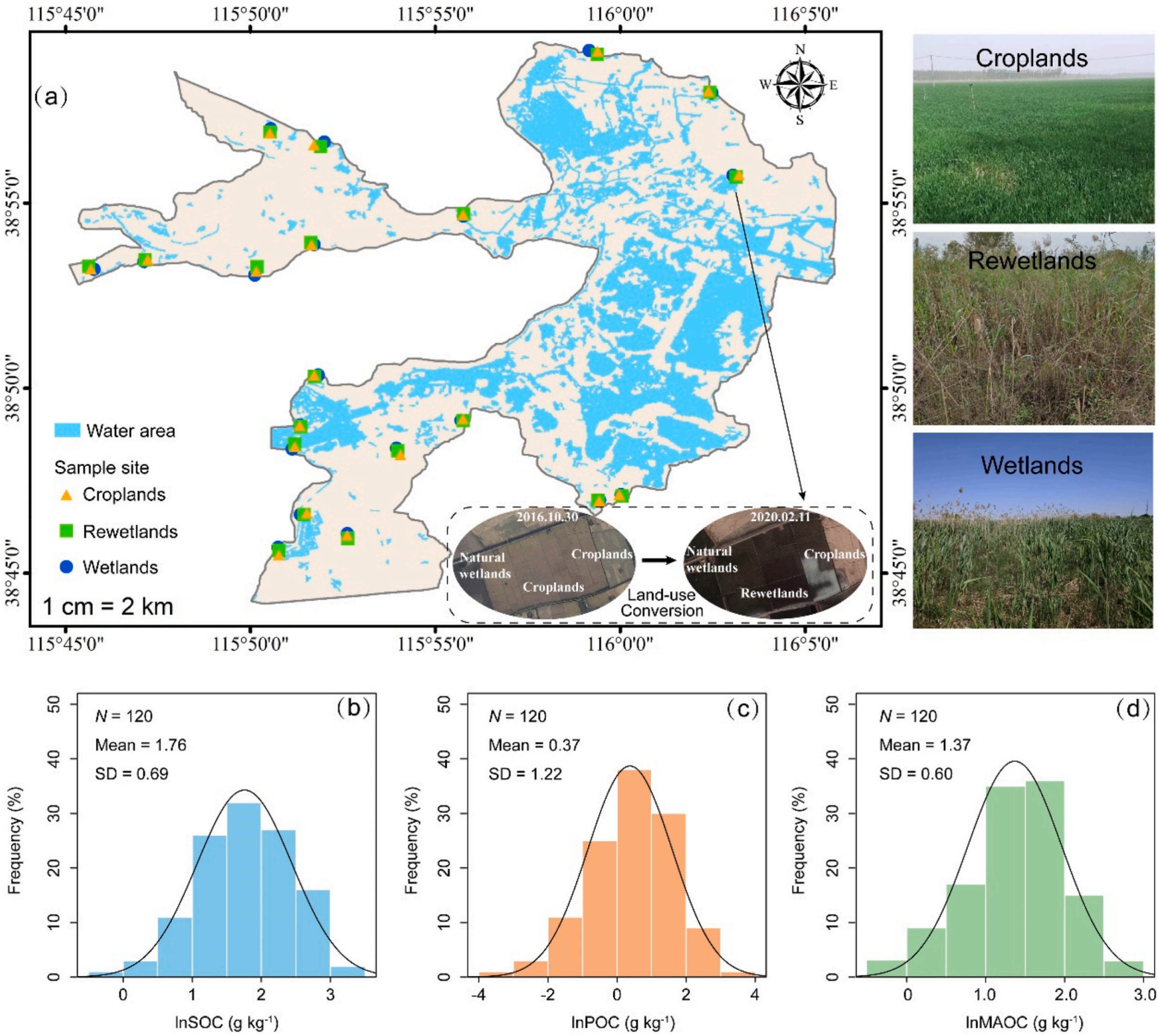

Fig. 1. Geographic distributions and landscape of the sampling sites (a) and frequency distributions of SOC (b) and POC (c) and MAOC (d) across the three land-use types in Baiyangdian. Two remote-sensing images provide an example of pre- and post-conversion of the land, with landscape photos taken in April 2023.

24 h. After fumigation, the soil was dried in a fume hood to remove residual chloroform. Unfumigated control samples were prepared in the same way but without chloroform exposure (Brookes et al., 1985; Vance et al., 1987; Fierer et al., 2003). Subsequently, these soil samples were extracted with 0.05 M Na_2SO_4 to obtain a solution for measuring MBC and MBN, and with 0.5 M $NaHCO_3$ to obtain a solution for measuring MBP. MBC (mg g^{-1}) was calculated as the difference in TOC of fumigated and unfumigated subsamples, divided by a correction factor (kEC) of 0.45 (Beck et al., 1997). MBN was calculated by assessing the differences of total dissolved nitrogen between the fumigated and the unfumigated samples, using an extraction efficiency factor of 0.54 (Brookes et al., 1985). Similarly, MBP was determined by examining the variations of total dissolved phosphorus between the fumigated and the unfumigated samples, applying an extraction efficiency factor of 0.4 (Brookes et al., 1985). The NO_3^--N and NH_4^+-N contents were measured by continuous-flow analyzer (AA3; Bran + Luebbe GmbH, Hamburg, Germany). In addition, we measured soil pH and electric conductivity (EC) by mixing soil and water with a ratio of 1:5, the soil water content and bulk density by ring knife method.

2.4. Determination of SOC fractions

We separated particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions from bulk soils using a fractionation method based on particle size (Lavallee et al., 2020; Liu et al., 2022). Briefly, ~10 g of air-dried bulk soils (<2 mm) was dispersed with sodium hex metaphosphate solution and then passed through a 53-μm sieve. The material passing through the sieve was the MAOM fraction, while the remaining material on the sieve was the POM fraction. POM and MAOM fractions were thoroughly washed with deionized water, oven dried at 60 °C and, weighed. The average recovery rate of the soil was 98.3 %. POC and MAOC contents were determined via a high-temperature combustion method using a solid measurement module of TOC analyzer (Analytikjena, multiN/C 3100, Germany), and converted into concentrations (in the units of mg g^{-1} soil), given the weight percentage of each fraction. SOC concentration was calculated as the sum of the concentration of POC and MAOC. Prior to measurement, we added 10 % HCl to each soil sample to remove inorganic carbon, and then washed it three times with deionized water to neutralize residual acidity (Bisutti et al., 2004; Liu et al., 2024b).

2.5. Soil amino sugar analyses and MNC calculations

We determined MNC based on the amino sugars. The analysis of amino sugars, such as GluN and MurA, were performed by high-performance liquid chromatography (HPAEC-PAD), following the methodology outlined by Indorf et al. (2013). Briefly, we hydrolyzed 0.5 g soil sample with 2 mL of 6 M HCl at 105 °C for 8 h and the solution was dried thoroughly using N_2 gas after cooling to room temperature. Add 5 mL deionized water to extract amino sugars, and adjust the pH of the solution to neutral, then centrifuge at 12,000 rpm for 10 min, and the upper aqueous phase was retained and filtered through a 0.22 μm membrane for measurement the content of GluN and MurA by an ion chromatograph (ThermoFisher, ICS5000, American).We determined bacterial necromass carbon (BNC) based on the MurA content and fungal necromass carbon (FNC) based on GluN content (Liang et al. 2017, 2019). Microbial necromass C (MNC) is the sum of BNC and FNC. BNC and FNC were calculated using the following formulas:

$$BNC = MurA \times 45$$

$$FNC = \left(\frac{GluN}{179.2} - \frac{MurA}{251.2}\right) \times 179.17 \times 9$$

where the number 45 indicates the conversion ratio from MurA to BNC (Appuhn and Joergensen, 2006; Joergensen, 2018), 179.2 and 251.2 represent the molecular weights of GluN and MurA, respectively, while the value 9 denotes the conversion ratio of fungal GluN to FNC (Joergensen, 2018; Appuhn and Joergensen, 2006).

2.6. Statistical analyses

Analysis of variance (ANOVA) with repeated measures was used to test the effects of land-use types (croplands, rewetlands and wetlands) and soil depth on SOC and its associated fractions (POC, MAOC, MNC, FNC, BNC), with soil depth as a within-subject factor. When a significant effect was found, post hoc test (*t*-test for depth and Duncan test for land-use) was used for multiple comparisons. Before analysis, all the data were tested and transformed to ensure the normality and homogeneity of variance. We calculated the responses ratio (RR) of microbial necromass carbon (BNC, FNC and MNC) to land-use conversion as (Hedges et al., 1999): $RR = \ln(X_i/X_j) = \ln(X_i)\text{-}\ln(X_j)$, among which X_i and X_j are the value of the rewetland or wetland and cropland. A positive value of RR indicated an increase of the variable in the rewetland or wetland than cropland soils, and *vice versa*. We performed linear regressions of MNC to POC and MAOC, and used the slope of the regression equation to indicate the contribution of MNC to POC and MAOC (the increase in MNC with the increase in unit POC and MAOC). The relationships between the soil properties and SOC fractions were assessed using Spearman's correlation, and Mantel test. We conducted a random forest model to explore the relative importance of explanatory variables on MNC. We developed structural equation models to reveal the mechanisms of how conversion of croplands to wetlands affected SOC fractions by the Partial Least Squares Path Model (PLS-PM) in R 4.3.3.

3. Results

3.1. Changes of SOC, POC and MAOC

In all the three land-use types, SOC, POC and MAOC contents in the topsoil were significantly higher than those in the subsoil (all $p < 0.001$, Fig. 2). Specifically, in the topsoil, SOC and POC contents in croplands were significantly higher than those in wetlands, with intermediate values observed in rewetlands. Conversely, in the subsoil, there were no significant difference of SOC and POC contents among the three land-use types (Fig. 2a and b). Land-use conversion had no significant effect on the MAOC content in either the topsoil or the subsoil (Fig. 2c). The proportion of MAOC to SOC was significantly higher than the proportion of POC to SOC in both the topsoil and the subsoil in all three land-use types (Fig. 2d and e). Land-use conversion had a marginally significant effect on the proportion of MAOC to SOC and POC to SOC ($F = 2.59$, $p = 0.084$). The proportion of MAOC to SOC in the topsoil tended to be significantly lower in croplands than in rewetlands, while the proportion of POC to SOC tended to be higher (Fig. 2d and e).

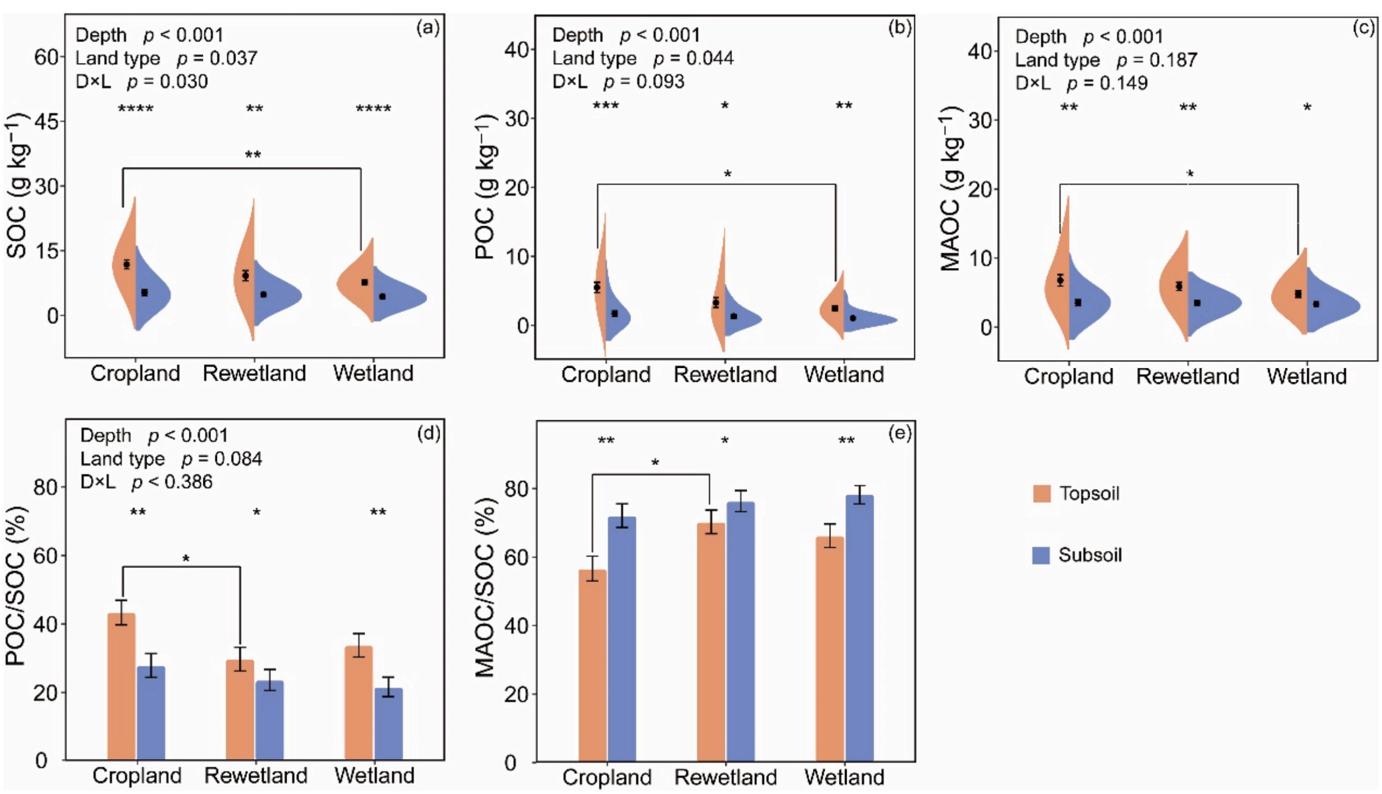

Fig. 2. Contents of soil organic carbon (SOC), particulate organic carbon (POC) and mineral associated organic carbon (MAOC) in croplands, rewetlands and wetlands. *, **, *** represent $p < 0.05$, $p < 0.01$ and $p < 0.001$ for post-hoc tests (*t*-test for depth and Duncan test for land-use), respectively. Mean ± se are shown (n = 20).

The conversion of croplands to rewetlands led to a 25 % reduction of SOC in the topsoil, with POC accounting for 71 % of the reduction and MAOC contributing for 29 % (Fig. 4a). In the subsoil, there was an 8 % reduction in SOC, where POC represented 95 % of the reduction and MAOC 5 % (Fig. 4a). Additionally, conversion of croplands to wetlands led to a greater decline in SOC, with reductions of 41 % in the topsoil and 17 % in the subsoil (Fig. 4c). POC contributed to 60 % and 76 % of the decrease in the topsoil and subsoil, respectively, while MAOC contributed to 40 % and 24 % of the decrease in the topsoil and subsoil, respectively (Fig. 4c).

3.2. Changes of BNC, FNC and MNC and their proportions to SOC

The BNC, FNC and MNC contents were significantly higher in the topsoil than in the subsoil (all $p < 0.001$, Fig. 3). Land-use conversion exerted a marginally significant effect on the BNC content ($p = 0.066$, Fig. 3a). The BNC content in the topsoil tended to be higher in croplands than in rewetlands and wetlands (Fig. 3a). In the topsoil, the FNC and MNC contents in croplands were significantly higher than those in rewetlands and wetlands, but in the subsoil, they did not differ significantly among these three land-use types (Fig. 3b and c).

Averaged across the three land-use types, BNC accounted for 4.32 % of SOC, which was significantly lower than the contribution of FNC

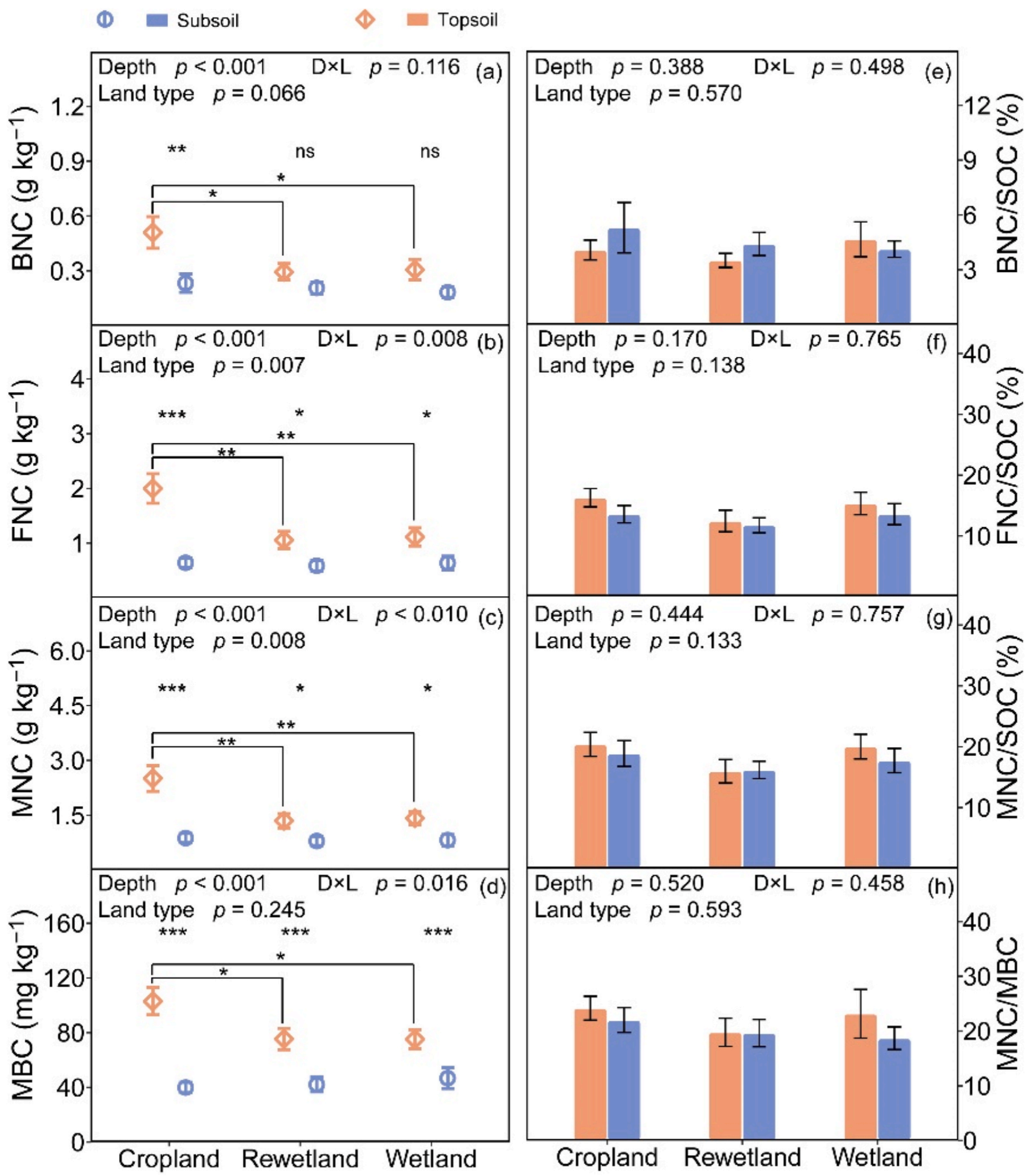

Fig. 3. Content of soil bacterial necromass carbon (BNC), fungal necromass carbon (FNC), microbial necromass carbon (MNC) and microbial biomass carbon (MBC) and their ratios to soil SOC in croplands, rewetlands and wetlands. *, **, *** represent $p < 0.05$, $p < 0.01$ and $p < 0.001$ for post-hoc tests (t-test for depth and Duncan test for land-use), respectively. Mean ± se are shown (n = 20).

(14.21 %; $p < 0.01$, Fig. 2e and f). The proportions of BNC, FNC and MNC to SOC did not change with the land-use conversion, and they showed no significant difference between the topsoil and the subsoil (all $p > 0.05$, Fig. 3e, f, g).

Land-use conversion induced a different influence on the MBC content in the topsoil and subsoil ($p < 0.05$, Fig. 3d). The MBC content in croplands was significantly higher than that in rewetlands and wetlands in the topsoil ($p < 0.05$), whereas no significant differences were observed in the subsoil ($p > 0.05$, Fig. 3d). The ratio of MNC to MBC (the accumulation rate of MNC) showed no significant difference among the three land-use types and between the two soil depths (all $p > 0.05$, Fig. 3h).

The responses ratio (RR) of BNC, FNC and MNC to land-use conversion in the topsoil were significantly lower than 0, indicating a substantial decrease from croplands to wetlands (Fig. 4b). Conversely, the 95 % confidence interval value of RR overlapped with zero in the subsoil, suggesting that the response of BNC, FNC, and MNC to land-use conversion is not significant (Fig. 4b). Corresponding with the conversion of croplands to rewetlands, RR of BNC, FNC, and MNC were significantly less than 0 in the topsoil, while the 95 % confidence interval of RR overlapping with zero in the subsoil (Fig. 4d).

3.3. Linear regression among MNC and POC and MAOC

To compare the contributions of MNC to MAOC and POC in returning cropland to wetland, we performed linear regressions of MNC to POC and MAOC. The slope of the regression equation indicated the increase in MNC with the increase in unit POC and MAOC; that is, the input of MNC to MAOC and POC pool. In the topsoil, POC had a significant positive relationship with MNC in both croplands and rewetlands, but the slope of the linear regression was significantly higher in croplands (0.27, Fig. 5a) than in rewetlands (0.18, Fig. 5c). There was no significant relationship between POC and MNC in wetlands ($p > 0.05$, Fig. 5e). In the topsoil, MAOC was significantly positively related to MNC in all three land-use types, and the slope of the linear regression was 0.25 for croplands, 0.23 for rewetlands and 0.29 for wetlands (Fig. 5). In the topsoil, the relative contribution of MNC to POC gradually decreased during the conversion of croplands to wetlands. In the subsoil, POC had a positive relationship with MNC and POC in croplands and rewetlands (the slopes of the regressions were 0.18 and 0.08 for croplands and rewetlands; Fig. 5g–i), but not in wetlands ($p > 0.05$, Fig. 5k). In the subsoil, a significant positive correlation between MAOC and MNC was noted across all three land-use types, with regression slopes of 0.17 for croplands, 0.29 for rewetlands, and 0.33 for wetlands (Fig. 5h–j, l). This suggests that as the conversion from cropland to wetland progresses, the relative contribution of MNC to the POC pool in the subsoil diminishes, while its contribution to the MAOC pool increases gradually.

3.4. Relationships of MNC with biotic and abiotic factors

MNC was significantly correlated with both biotic factors (MBC and MBN) and abiotic ones (soil moisture and soil NO_3^--N content; all $p < 0.05$; Fig. S3). Soil NO_3^--N and MBC were the most important factors influencing MNC, followed by MBN and soil moisture in the topsoil (Fig. 6a). Specifically, in the topsoil, MNC was positively associated with soil NO_3^--N ($p < 0.001$; Fig. 6c), MBC ($p < 0.001$; Fig. 6d) and MBN ($p < 0.001$; Fig. 6f), and negatively associated with soil moisture ($p < 0.001$; Fig. 6e). Different from the topsoil, the most likely drivers of subsoil MNC were soil NO_3^--N and MBC (Fig. 6b), despite significant correlations of MNC with soil moisture and MBN (all $p < 0.05$; Fig. 6b). Soil NO_3^--N and MBC were positively correlated with MNC in the subsoil ($p < 0.001$; Fig. 6c and d). The biotic and abiotic variables explained 61.42 % and 44.26 % of the total variance of MNC in the topsoil and subsoil,

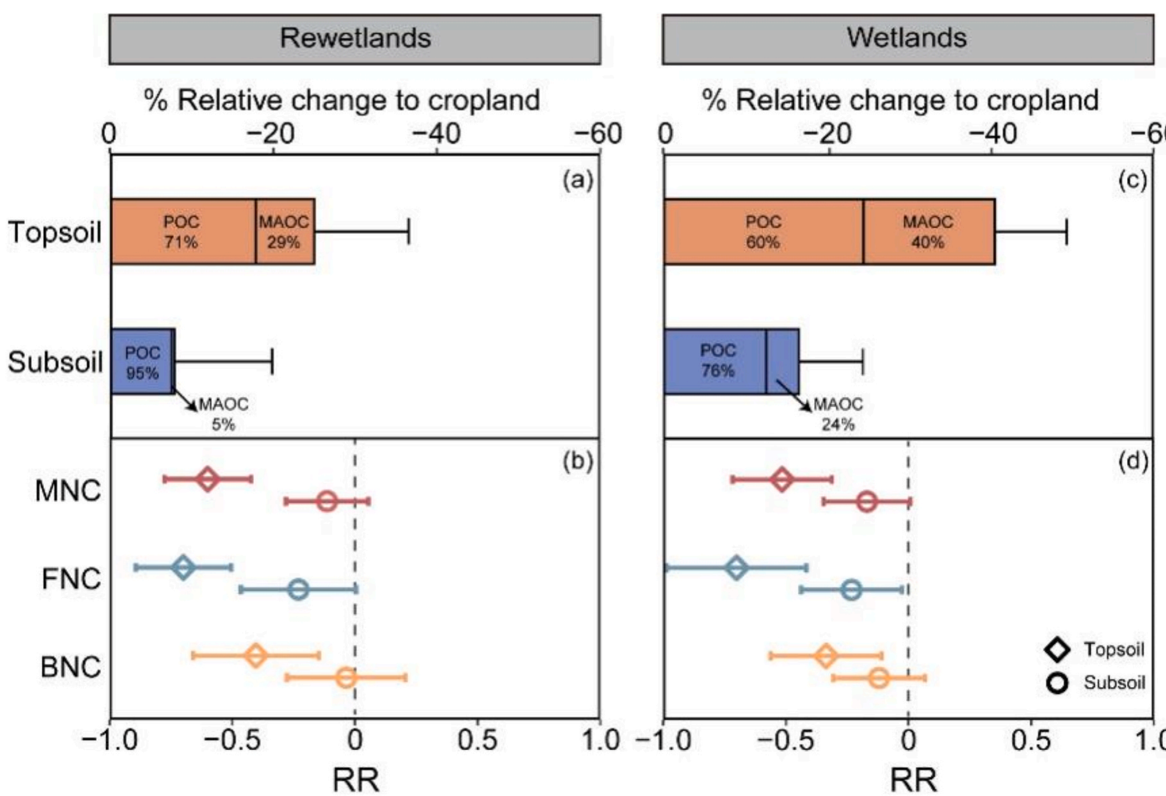

Fig. 4. The relative change of SOC in rewetlands and wetlands to croplands driven by land-use conversion (a, c), the labeled number indicated the contribution of POC or MAOC to SOC change. RR indicates the response ratio of microbial necromass carbon in rewetlands and wetlands relative to croplands (b, d). Solid dots represent values of RR and bars represent the 95 % confidence interval. If the 95 % confidence interval value of RR does not overlap with zero, the response is considered to be significant.

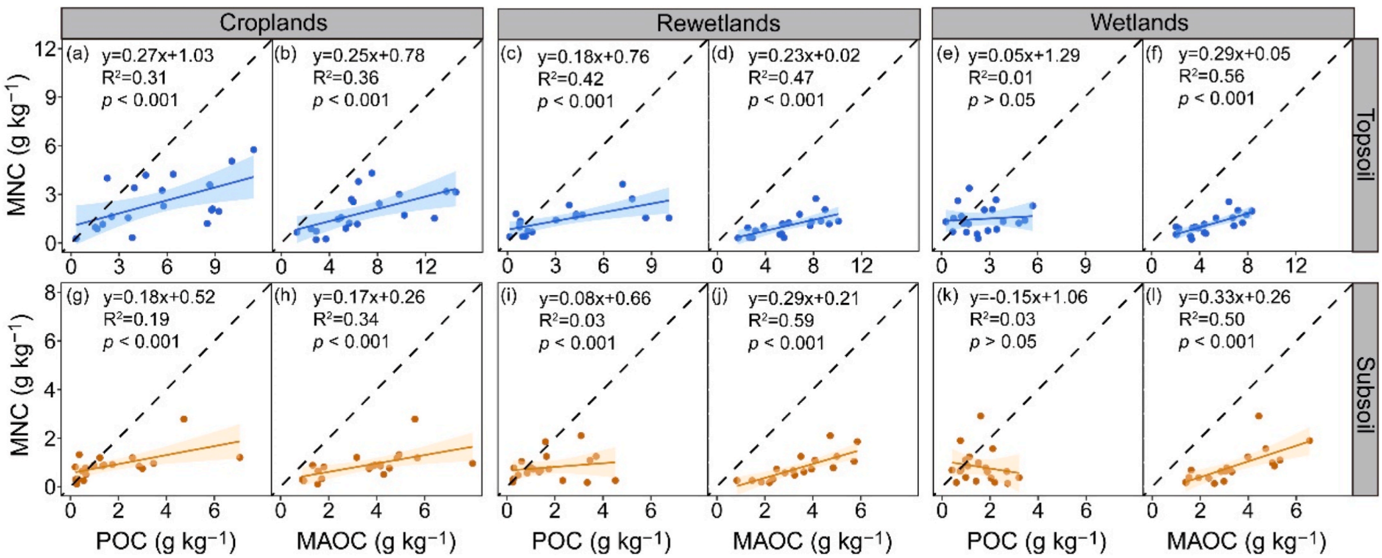

Fig. 5. Linear regressions of soil organic carbon fractions (POC and MAOC) with microbial necromass carbon (MNC) in croplands, rewetlands and wetlands. Blue and yellow symbols represent data points in the topsoil and subsoil, respectively. The solid lines were fitted by ordinary least-squares regressions, and the shadow areas corresponded to 95 % confidence intervals. The linear fitting equation, R^2 and p values were given. n = 20.

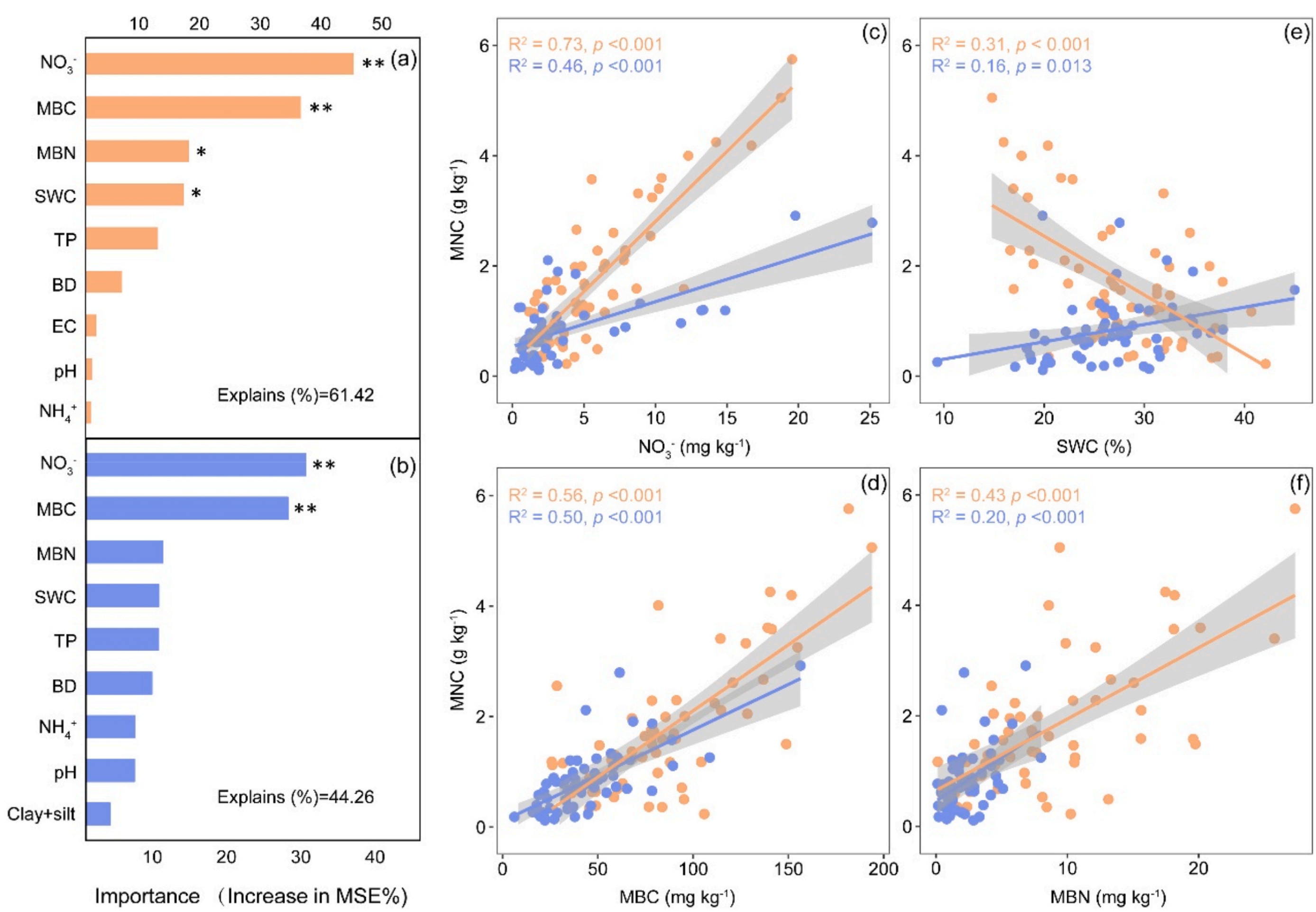

Fig. 6. Relationships of MNC with potential drivers. The relative importance of biotic and abiotic variables in influencing MNC in the topsoil (a) and the subsoil (b) revealed by random forest model. Mean squared errors (MSE) show the importance of main predictors. The explanatory percentage (Explains, %) is the total effect of all variables for MNC. * and ** indicates significance at the $p < 0.05$ and $p < 0.01$ level. (c) (d) (e) (f) are the relationship of MNC with NO_3^--N content, soil moisture, MBC and MBN, respectively, the yellow and blue indicates topsoil and subsoil.

respectively.

3.5. Regulation of SOC fraction by MNC

In the topsoil, both MNC and soil microbes could directly positively affect SOC fraction, and conversion of croplands to wetlands indirectly affected SOC fraction by regulating soil properties, specifically soil NO_3^--N content and soil moisture (Fig. 7a). In contrast, within the subsoil, SOC fraction was directly positively affected by MNC and directly negatively affected by soil abiotic properties (soil NO_3^--N content and silt + clay fraction), and conversion of croplands to wetlands indirectly affected SOC fraction by regulating soil abiotic properties and also soil microbes (Fig. 7b–d). Soil microbes did not exert a direct influence on subsoil SOC fraction, but had an indirect influence via MNC (Fig. 7b–d).

4. Discussion

Contrary to the common assumption that cropland cessation or wetland restoration could increase SOC (Ding et al., 2019, Wang et al., 2024), our findings indicate that SOC and POC decreased during conversion of croplands to wetlands, especially in the topsoil (Fig. 2). The low SOC content in wetland mainly because of our selection of natural wetlands was restricted to platform reed wetlands, deliberately excluding flooded wetlands. Since SOC is influenced by both plant input and microbial necromass, the observed variations of SOC fractions are likely associated with environmental conditions, management strategies, and plantation species (Li et al., 2012; Zhang et al., 2023). Therefore, the observed decrease in SOC and POC following conversion of croplands to wetlands could be attributed to reduced litter input and MNC. Our results provide direct evidence that MNC reduced from croplands to wetlands in the topsoil, which aligns with the trend observed in plant biomass across the three land-use types (Table S1). In addition, our study demonstrates that conversion of croplands to wetlands has little effect on SOC and its fractions in the subsoil, likely because there was no significant variation of soil water content in the subsoil among the three land-use types (Table S1), and the typical tillage depth does not exceed 40 cm in the North China Plain (Wang et al., 2022; Tian et al., 2016). The decrease of SOC and POC further led to an increased proportion of MAOC to SOC following conversion of croplands to wetlands, indicating that the stability of SOC could be enhanced by cropland rewetting, as MAOC is known to be more stable than POC (Chen et al., 2021b; Li et al., 2023).

FNC was much higher than BNC in all three land-use types, with an average contribution of 79 % and 76 % to MNC in the topsoil and subsoil, respectively (Fig. 3). This finding is consistent with previous studies (Cao et al., 2023; Ding et al., 2019; Wang et al., 2021a), because fungi

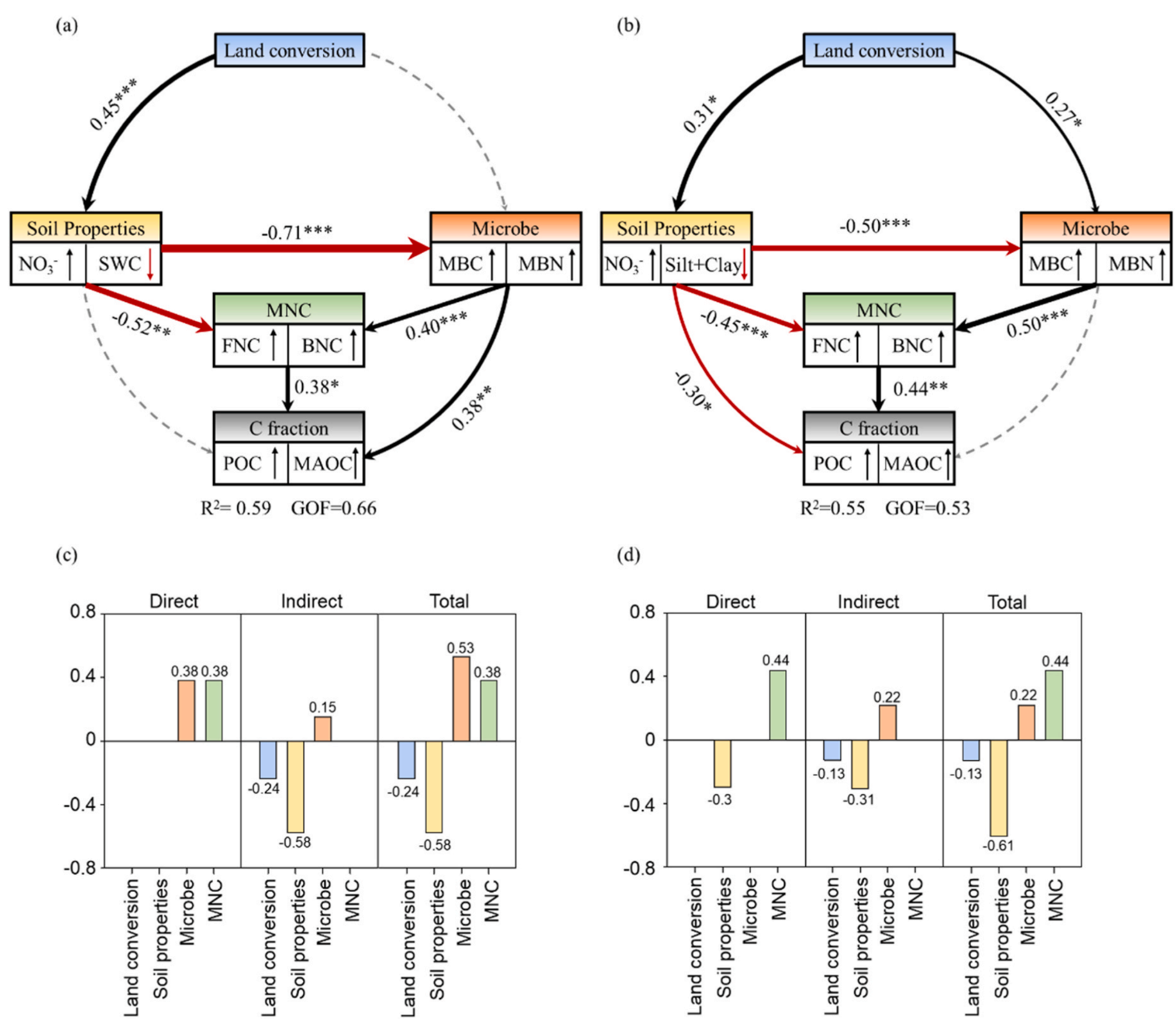

Fig. 7. Structural equation models (SEM) revealing the direct and indirect effects of biotic and abiotic factors on microbial necromass C in the topsoil (a) and subsoil (b). Land conversion means cropland converting to wetland. Black and red solid arrows indicate positive and negative associations, respectively. Dotted lines represent pathways that are not significant. Numbers adjoining the arrows indicate significant standardized path coefficients. The arrow width is proportional to the strength of the association. The multiple-layer rectangles indicate the first component from the PCA of mineral and microbial properties, and the vertical arrows within it represent the positive relationships between adjacent variables and the corresponding PC1. (c) and (d) are the standardized effects of each variable.

generally possess a larger biomass than bacteria, and FNC is more resistant to decomposition due to the lower lability of GluN in fungal residues compared to MurA in bacterial residues (Wang et al., 2021a; Cao et al., 2023, Hou et al., 2024). Consistent with our hypothesis, MNC, BNC and FNC significantly decreased in the topsoil during conversion of croplands to wetlands. This finding contrasts with a previous study reporting that MNC increased during peatland restoration in Northeast China (Ding et al., 2019). The differential response of MNC to land-use conversion in our study compared to that in peatlands may be attributed to the different plant carbon inputs and substrate availability (He et al., 2022; Ding et al., 2019). The higher plant litter inputs in croplands compared to rewetlands and wetlands, providing more carbon substrates for microbial transformation (Zhang et al., 2023; Wang et al., 2024; Prommer et al., 2020). The higher soil nutrient availability in croplands, caused by fertilization, supports greater microbial biomass compared to rewetlands and wetlands. This is corroborated by the random forest model, which indicates that the NO_3^--N content explained 45 % of the variation of MNC in the topsoil. Additionally, a positive correlation between MNC and microbial biomass was observed (Fig. 6). However, no differences were detected in the accumulation rate of MNC (MNC/MBC, Fig. 3h) across the three land-use types, which may be attributed to the similar trends of MNC and MBC in the three land-use types, suggesting the similar turnover rates of microorganisms (Zhang et al., 2021). In the subsoil, MNC, FNC, and BNC did not change during conversion of croplands to wetlands, possibly because microbial activity and turnover are constrained by higher soil moisture and limited input of plant-derived carbon.

The average contributions of MNC to SOC were found to be 19.63 % in croplands, 15.96 % in rewetlands, and 17.71 % in wetlands, which were lower than those of globally farmland and wetland soils (Cao et al., 2023; Wang et al., 2021a). In Baiyangdian, high soil moisture may limit the decomposition of plant-derived carbon and microbial activity, thereby reducing the contribution of MNC to SOC (Liu et al., 2023a; Mpamah et al., 2017; Tian et al., 2024a). Additionally, soil pH has a negative effect on amino sugar accumulation, and the alkaline soil conditions in our study could explain the lower contribution of MNC to SOC (Zou et al., 2023; Ni et al., 2020; Niu et al., 2023). The conversion of croplands to wetlands did not alter the proportion of BNC, FNC, and MNC to SOC, presumably due to the concurrent decrease of BNC, FNC, MNC and SOC. SOC was significantly positively correlated with MNC among the three land-use types (Fig. S2), indicating that the variation of the SOC response to land-use conversion was at least partially caused by MNC, emphasizes the importance of microbe-derived carbon in sequestering SOC during conversion from croplands to wetlands.

The relative contribution of MNC to POC decreased in both topsoil and subsoil during conversion of croplands to wetlands, while the relative contribution of MNC to MAOC increased in the subsoil (Fig. 5). One plausible explanation for this shift is that the gradual increase in soil moisture content from croplands to wetlands could have limited the formation of soil aggregates, thereby reducing the protection for microbial necromass in the POC fraction (Liu et al., 2024a). Furthermore, minerals such as iron and aluminum in wetlands could be leached into the subsoil, providing additional binding sites for MNC and enhancing the relative contribution of MNC to MAOC during conversion of croplands to wetlands in the subsoil. The decline in the relative contribution of MNC to POC may be a contributing factor to the decrease in POC/SOC and the concurrent increase in MAOC/SOC in the topsoil. This implies that the sequestration of MNC within POC is diminished during transition from croplands to wetlands. When considering changes in SOC and its fractions due to land-use conversion, as well as the associated alterations in MNC response ratios, we can infer a potential pathway where the decrease in SOC during cropland conversion to wetlands is linked to the decrease in MNC levels, resulting in reduced MNC sequestration in POC, subsequently leading to a decrease in POC and ultimately SOC. In the subsoil, a similar trend of reduced MNC sequestration in POC is noted, although the low MNC content does not lead to substantial changes. This pathway aligns with findings from studies on forest management and nitrogen enrichment (Chen et al., 2024; Li et al., 2023).

The response of SOC fractions to land-use conversion of croplands to wetlands are modulated by soil properties and microbial characteristics, with the impact pathway being depth-dependent (Fig. 7). In the topsoil, land-use conversion of croplands to wetlands primarily restricts the activity and growth of soil microbe by reducing soil nutrients (NO_3^--N) and increasing soil moisture, thereby reducing the accumulation of microbial residues, and finally negatively affecting SOC fractions (Figs. 6 and 7). The pathway by which soil properties affect MNC was consistent with previous studies (Cao et al., 2023; Wang et al., 2021a; Cui et al., 2020). In the subsoil, soil properties and MNC directly impact SOC fractions, mainly due to the binding sites provided by silt + clay (Zhu et al., 2024). The microbial activity in the subsoil is diminished (He et al., 2022), and its direct influence on SOC fractions has disappeared. Our study advances current understanding by quantifying microbial-derived carbon's role and demonstrating the critical importance of POC in SOC storage during land-use conversion. Future research should prioritize analyzing how shifts in microbial diversity, community structure and functional gene expression collectively regulate SOC transformation pathways and minerals interactions during land-use conversion.

5. Conclusion

Our study reveals that conversion of croplands to wetlands does not result in an increase in SOC and its fractions in the topsoil or subsoil. Instead, it tends to return to levels similar to those in natural wetlands, primarily through regulation of POC rather than MAOC. Our study further highlights the pivotal role of MNC in regulating SOC and its fractions. The reduction in MNC led to less MNC being sequestered in POC, subsequently caused a decrease in POC and, subsequently, in SOC during the process of converting croplands to wetlands. This finding underscores the critical contribution of microbial-derived carbon to SOC sequestration during this land-use transition. The findings demonstrate that SOC fractions accumulation depends on soil nutrient availability and soil moisture during croplands to wetlands conversion. To optimize SOC fractions sequestration in rewetlands, we propose that maintaining optimal nutrient levels and soil moisture to facilitate SOC stabilization mechanisms.

CRediT authorship contribution statement

Qian-Wei Li: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation. **Qi Guo:** Methodology, Investigation, Data curation. **Jun-Qin Gao:** Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Jia-Tao Zhu:** Investigation. **Di Du:** Writing – review & editing, Writing – original draft. **Ling-Ke Zhang:** Investigation. **Hua-Bing Liu:** Investigation. **Fei-Hai Yu:** Writing – review & editing. **Qiang Wang:** Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126704.

Data availability

The authors do not have permission to share data.

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