



Perennial crops enhance the association between microbial biomass and soil organic carbon sequestration

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ABSTRACT

Perennial cropping systems are increasingly promoted for providing a wide range of ecosystem services in agriculture, including climate change mitigation through soil organic carbon (SOC) sequestration. However, the microbial mechanisms underlying SOC sequestration remain unresolved. We conducted a global meta-analysis of 84 peer-reviewed studies comprising 514 paired comparisons between perennial and annual cropping systems. Results showed that compared with annual cropping systems, perennial cropping systems simultaneously increased SOC and microbial biomass carbon (MBC) in the topsoil (0–30 cm) by 15% and 37%, respectively. The log response ratio of MBC was statistically associated with the log response ratio of SOC, explaining 51% of the variance in SOC response. A framework based on partial least squares path modeling demonstrated that increases in MBC were more strongly associated with SOC accrual than with a wide range of environmental factors. Overall, our findings provide evidence that increases in MBC are statistically associated with SOC accrual in perennial cropping systems, indicating a critical role of microbial processes in shaping the SOC accrual potential of perennial systems. These results underscore the need to integrate soil biological mechanisms into carbon management strategies and highlight the potential of adopting perennial crops for climate-smart cropping systems.

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1. Introduction

Soils constitute the largest terrestrial reservoir of organic carbon and play a vital role in regulating atmospheric carbon dioxide (CO₂) concentrations (Batjes, 2011; Goidts et al., 2009; IPCC, 2023). Perennial crops, with their generally greater biomass production, deeper root systems, higher resource use efficiency, and extended growing season, are considered to have greater potential than annual crops for enhancing soil organic carbon (SOC) storage (Beniston et al., 2014; Chen et al., 2022; DuPont et al., 2014). Thus, the transition from annual to perennial cropping systems is increasingly recognized as an effective strategy to increase SOC storage (Ledo et al., 2020; Siddique et al., 2023). For example, a long-term experiment in northern France showed that perennial crops significantly increased topsoil SOC stocks over five years (Ferchaud et al., 2016). Existing explanations have largely emphasized physical protection associated with minimal soil disturbance, but the fate of additional carbon inputs remains unclear (Pausch and Kuzyakov, 2018; Sprunger et al., 2019; Tripolskaja et al., 2024; Wu et al., 2024). Therefore, even where SOC increases are observed, the underlying biogeochemical pathways remain poorly understood. In particular, it is still uncertain to what extent SOC accrual reflects the direct retention of plant-derived carbon or the transformation and stabilization of carbon through microbial processes.

Soil microbial processes are fundamental to SOC accumulation, primarily through the transformation of organic matter into microbial metabolites and necromass, which subsequently stabilize as mineral-associated organic carbon (Geyer et al., 2020; Lange et al., 2015; Zhang et al., 2020). Microbial biomass carbon (MBC), as an indicator of the living microbial pool, provides insight into the potential of microorganisms to decompose organic matter and transform carbon resources to sustain microbial activity (Blagodatskaya and Kuzyakov, 2013; Ling et al., 2025; Xia et al., 2025; Zhang et al., 2020). Rather than serving solely as a positive indicator of SOC accrual, higher MBC may also represent a larger microbial biomass pool capable of decomposing organic matter, indicating greater potential for microbially mediated carbon turnover (Liang, 2025; Nascimento et al., 2025). This dual role may help explain the negative relationships observed in some cases between MBC and SOC, highlighting the importance of MBC in interpreting SOC change. Previous studies have shown that perennial cropping systems significantly increase MBC by 35%, highlighting the growing importance of this ecosystem in driving the microbial pathway (Ding et al., 2025; Sasse, 2023). However, the importance of the microbial pathway in SOC accumulation varies across different ecosystems (Nascimento et al., 2025). For example, MBC could explain 20% of the increase in SOC in croplands (Duan et al., 2021) and 42% in grasslands (Chang et al., 2025). In contrast, there was a negative correlation between MBC and SOC in temperate broadleaf forests (Craig et al., 2022). The inconsistent coupling between MBC and SOC often hinges on the balance between microbial anabolism and catabolism (Feng et al., 2024; Poyda et al., 2023). In perennial systems, where substrate supply is sustained, a shift toward anabolic pathways favors the production of microbial necromass, a key precursor for mineral-associated organic matter (Liang et al., 2017; Yue et al., 2024; Wu et al., 2024). Conversely, in resource-limited or high-stress environments, catabolic processes dominate to meet maintenance energy requirements, potentially decoupling MBC growth from SOC sequestration (Drotz et al., 2010; García et al., 2023). Although previous studies on SOC accumulation in perennial cropping systems have primarily focused on the pathways related to crop traits and management practices, it is still important to assess the contribution of microbial pathways to SOC sequestration.

While microbially driven increases in SOC turnover rates during the conversion from annual to perennial crops help explain SOC dynamics, the effects of this conversion often take a long time to become apparent, as changes in soil structure and microbial communities are strongly time-dependent, thereby influencing the long-term storage of SOC (Cotrufo et al., 2013; Schmidt et al., 2011). For example, during the

initial stage of orchard establishment, the pronounced increase in MBC content provides the foundation for SOC sequestration, likely resulting in a substantial contribution to SOC storage over time (Ding et al., 2025; Woolf and Lehmann, 2019). One possible explanation is that MBC increases quickly in response to initial carbon inputs, while a portion of this biomass is progressively transformed into microbial necromass and sequestered as SOC over the years (Cotrufo et al., 2013; Ni et al., 2021). This microbial carbon pump effect may explain how the initial microbial pathway is activated by changes in carbon inputs, and that the strength of the association between SOC and MBC is likely to evolve over time (Kuzyakov et al., 2000; Zhang et al., 2020). Within this time-dependent process, crop age reflects the cumulative effects of plant-derived carbon inputs, microbial necromass accumulation, and soil structural development following the establishment of perennial cropping systems (Ledo et al., 2020; Siddique et al., 2023; Sprunger et al., 2019). Meanwhile, climatic conditions and soil physicochemical properties provide important environmental constraints that shape microbial metabolism, organic matter decomposition, and the increased persistence of microbial-derived carbon through mineral association and occlusion in aggregate, thereby influencing the efficiency and direction of microbial biomass-derived carbon transformation into persistent SOC pools (Kleber et al., 2015; Zhang et al., 2020; Zhou et al., 2025). Therefore, examining how the relationship between MBC and SOC changes with crop age, and how this time-dependent relationship is further shaped by climatic conditions and soil physicochemical properties, can help link the observed patterns to the mechanisms underlying SOC formation and long-term stabilization in perennial cropping systems.

We studied the potential of perennial cropping systems, as compared to annual systems, to promote SOC accrual and the role of soil microorganisms in driving this response. We further assessed how environmental factors and time since conversion from an annual to a perennial cropping system regulate the contribution of MBC to SOC accumulation. Specifically, this study addresses the following objectives: (1) characterize changes in SOC and MBC during the transition from annual to perennial cropping systems; (2) quantify the association between MBC and SOC accumulation during this transition; and (3) determine how climate, crop age, and soil properties modulate the relationship between MBC and SOC, and identify the conditions that maximize the contribution of MBC to SOC accumulation.

2. Materials and methods

2.1. Data collection

We compiled a global database of peer-reviewed case studies reporting changes in SOC under annual and perennial cropping systems. The initial dataset was developed by Ledo et al. (2020), comprising 15 peer-reviewed studies on soil organic carbon under the transition from annual to perennial cropping systems. It was subsequently expanded by Siddique et al. (2023) through the inclusion of 36 additional studies. Building on these efforts, our dataset provides a more complete global perspective and incorporates MBC data wherever available, resulting in a more comprehensive assessment of SOC changes associated with land-use conversion from annual to perennial cropping systems. To develop a more comprehensive dataset, we conducted additional searches in Web of Science (<http://apps.webofknowledge.com/>) and Google Scholar (<https://scholar.google.com/>). We identified 33 additional publications published by January 2025. The data-screening process closely followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines and was summarized in a PRISMA-style flow diagram (Figure S1; PRISMA-P Group et al., 2015). The keyword combinations were directly adopted from Siddique et al. (2023), with minor formatting standardization for database compatibility. The search strategy included: (1) “soil organic carbon” OR “carbon stock” OR “soil carbon sequestration” OR “soil carbon” AND (2) “annual” OR “annual crop”, AND (3) “perennial” OR “perennial

crop". The database included only peer-reviewed literature and aimed to incorporate as many relevant studies as possible for further analysis.

To be eligible for inclusion in this meta-analysis, studies had to meet the following criteria: (1) soil and climatic conditions were similar between annual and perennial cropping systems; (2) a paired-site design was used, with each study having soil organic carbon data for both cropping systems; (3) studies with a duration of less than two years were excluded. To evaluate the contributions from MBC, we collected all reported data on MBC between annual and perennial cropping systems. Several factorial experiments were included in the database when their original purpose was to explore the differences between annual and perennial cropping systems. Based on the above criteria, a total of 84 studies were identified, resulting in 514 data points, including 108 data points from 24 studies that reported differences in MBC (Tables S4 and S6). The data were obtained from 132 experimental sites worldwide (Fig. 1A; Table S5). When data were only presented in graphical format, we digitized the values using either Grapher™ (<http://www.goldensoftware.com/products/grapher>) or WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer>), depending on the quality and format of the figures (Rohatgi, 2021). In this study, perennial cropping systems are defined as managed agricultural lands planted once and harvested over multiple years (Zhang et al., 2022), including both herbaceous and woody perennials. However, most cases involved herbaceous species and only three data points represented woody perennials with MBC data (Table S6). The changes in SOC from annual to perennial

cropping systems were used as one of the response variables. For studies that reported MBC, changes in MBC were also extracted and treated as a second response variable. A comparative analysis was then conducted to examine the relationship between changes in SOC and MBC.

2.2. Selection of Environmental, Soil, and Crop-Related Variables

Environmental information for each experimental site was extracted from the literature, including geographic location, latitude, longitude, and climate zone. Climate zone classifications (tropical, subtropical, and temperate) were derived from Siddique et al. (2023), who used the Global Agro-Ecological Zoning (GAEZ v4.0) database to categorize site-level thermal zones (FAO and IIASA, 2021). Additional climatic variables such as mean annual temperature (MAT), mean annual precipitation (MAP), and elevation were also extracted from the literature. Soil characteristics included pH, bulk density, and particle composition (i.e., the percentages of sand, silt, and clay). Soil pH was initially treated as a continuous variable and subsequently classified into three groups ($\text{pH} < 6.5$, $6.5 \leq \text{pH} \leq 7.5$, $\text{pH} > 7.5$) to assess the effects of acidic, neutral, and alkaline soils on SOC and MBC dynamics in perennial cropping systems (Siddique et al., 2023). Initial SOC was also included as a covariate to account for baseline differences. Missing soil data were supplemented using global databases, including SoilGrids (Hengl et al., 2017) and the Harmonized World Soil Database (FAO et al., 2012). Crop-related variables included photosynthetic functional type and crop

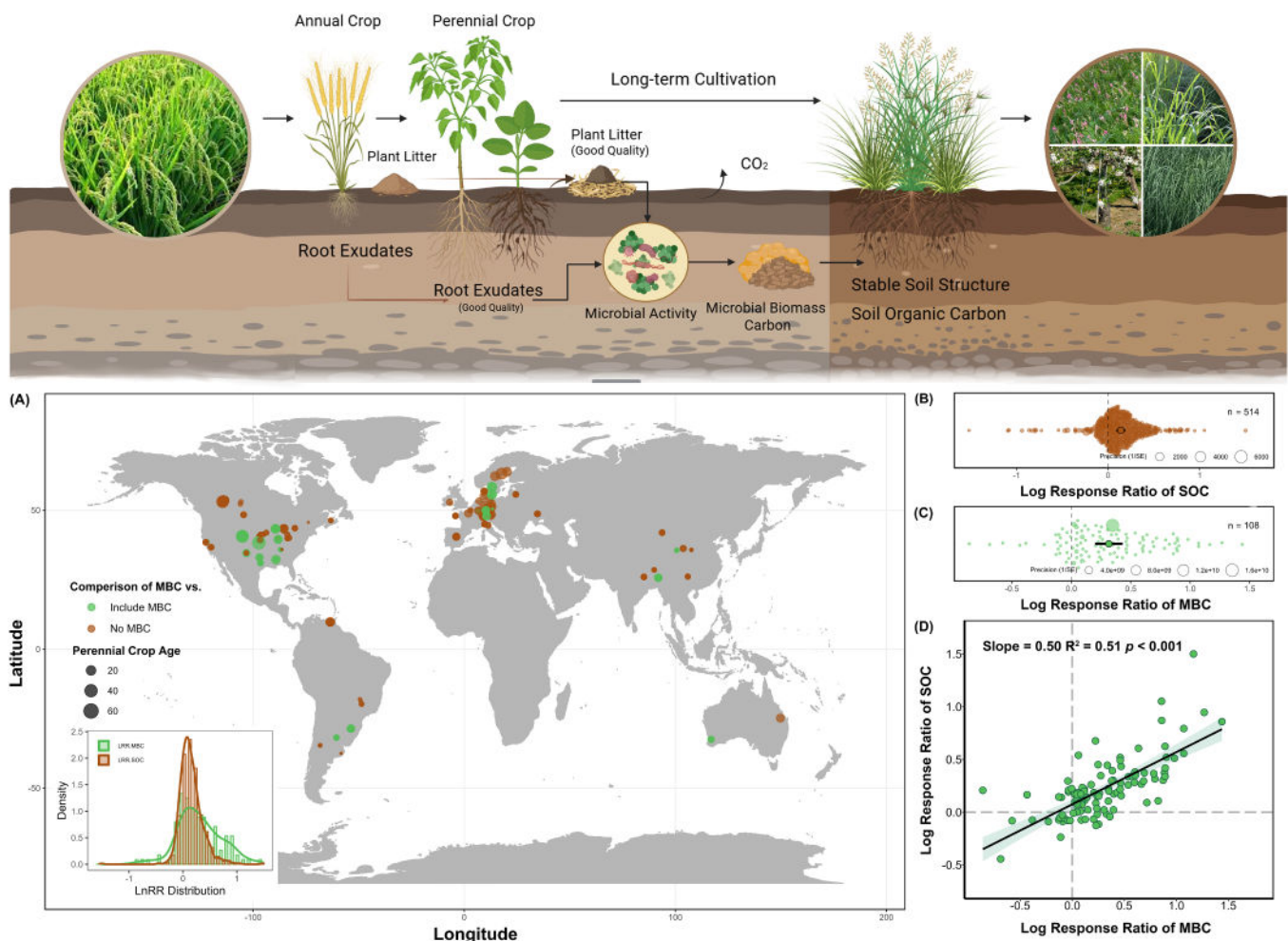


Fig. 1. (A) Global distribution of 84 studies (514 paired comparisons) included in the meta-analysis. Dot color indicates the presence of MBC data (green = with MBC; brown = without MBC); size indicates perennial crop age. The inset shows the distribution of the response for (B) SOC ($n = 514$) and (C) MBC ($n = 108$) under annual versus perennial systems, with means and 95% confidence intervals. Points are scaled by precision ($1/\text{SE}$). (D) Significant positive correlation between the responses of MBC and SOC (slope = 0.50, $R^2 = 0.51$, $p < 0.001$).

age in perennial species. Crop age was initially treated as a continuous variable and classified into three groups (< 5 years, 5–10 years, and > 10 years) to assess short-, medium-, and long-term effects of perennial cropping systems on SOC and MBC dynamics (Qin et al., 2016).

2.3. Calculation and standardization of data

To facilitate further analysis, all soil chemical and physical property data were standardized. SOC values originally reported in units such as “kg m⁻²,” “g m⁻²,” “t ha⁻¹,” “kg ha⁻¹,” or “percent” were uniformly converted to “Mg ha⁻¹.” Among all studies, most SOC data were reported directly as stock values, while the remaining were presented as SOC concentrations (e.g., “g kg⁻¹” or “mg g⁻¹”). For studies reporting SOC concentrations, SOC stocks were estimated using the corresponding bulk density (BD) and soil depth, with the final values expressed in Mg C ha⁻¹. This conversion ensured comparability across studies. Given the observed range of BD values in our dataset (0.93–1.64 g cm⁻³), the potential uncertainty introduced by this step is expected to be small. The calculation of SOC stocks followed the approach described by Goideits et al. (2009) and Guo and Gifford (2002), according to the following equation:

$$\text{SOC stock (Mg C ha}^{-1}\text{)} = \text{SOC} \times \text{BD} \times D \times 0.1 \quad (1)$$

where SOC is soil organic carbon concentration (g kg⁻¹), BD is bulk density (g cm⁻³), and D is soil depth (cm).

Variations in soil depth intervals associated with SOC measurements were substantial across the collected studies. To enhance the comparability of SOC data, we standardized observed SOC stocks to a common 0–30 cm depth following the methodology proposed by Batjes (2011) and Deng et al. (2014). The standardization of SOC was conducted according to the following equation:

$$\text{SOC}_{30} = \frac{1 - \beta^{30}}{1 - \beta^{d0}} \times \text{SOC}_{d0} \quad (2)$$

where SOC₃₀ represents the soil organic carbon stock (Mg C ha⁻¹) within the top 30 cm of the soil profile, β denotes the relative rate of SOC decline with increasing soil depth (fixed at 0.9786), d0 is the original sampling depth reported in individual studies (cm), and SOC_{d0} refers to the SOC stock measured at depth d0.

2.4. Meta-analysis

Meta-analysis was conducted to assess overall changes in MBC and SOC stocks following the transition from annual to perennial cropping systems, while regression analysis evaluated the relationship between changes in MBC and SOC induced by this transition. Random Forest modeling and correlation analyses were used to identify key environmental drivers. Building on this, we identified the specific ranges of environmental conditions, crop traits, and soil properties under which microbial contributions to SOC accumulation were most pronounced. Finally, partial least squares path modeling (PLS-PM) was used to reveal the structural relationships among MBC, SOC, and environmental variables, thereby clarifying the microbial processes governing SOC enhancement in perennial cropping systems.

All analyses and visualizations were conducted using R version 4.2.3 (R Core Team, 2023). A meta-analytic framework was applied to assess the effects of perennial cropping systems on SOC and MBC dynamics. The natural logarithm of the response ratio (lnRR) was used as the effect size metric for both SOC and MBC, calculated as the natural logarithm of the ratio between the mean value under perennial cropping systems ($\bar{X}_p$) and that under annual cropping systems ($\bar{X}_a$) (Alemu, 2014; Borenstein, 2009; Don et al., 2011):

$$\ln\text{RR} = \ln(\bar{X}_p) - \ln(\bar{X}_a) \quad (3)$$

The sampling variance (v) for each lnRR value was calculated based on the means, standard deviations (SD), and sample sizes (N) of both systems, using the following formula:

$$v = \frac{SD_p^2}{N_p \bar{X}_p^2} + \frac{SD_a^2}{N_a \bar{X}_a^2} \quad (4)$$

where SD_p and SD_a are the standard deviations for the perennial and annual cropping systems, respectively, and N_p and N_a are the sample sizes of the perennial and annual cropping systems, respectively (Wang et al., 2021; Zhou et al., 2018). In cases where only standard errors (SE) were provided, the corresponding SDs were calculated from the SEs and sample sizes (Hedges et al., 1999):

$$SD = SE \times \sqrt{N} \quad (5)$$

For ease of interpretation, results from the meta-analysis were back-transformed from lnRR values to percentage changes using the following formula:

$$\text{Percentage Change} = 100 \times [\exp(\ln\text{RR}) - 1] \quad (6)$$

Meta-analytic models incorporated inverse sampling variances as weights for individual studies. Missing SDs were imputed using a hot-deck method based on studies with similar mean values, implemented through the “metagear” package in R (Lajeunesse, 2016; Siddique et al., 2023). Multilevel mixed-effects meta-analytic models were fitted using the “metafor” package (Viechtbauer, 2010), with model parameters estimated by restricted maximum likelihood estimation. The model included two levels of random effects: a random intercept for study site to account for potential similarity among observations from the same site, and a random intercept for individual effect sizes nested within study site to account for potential non-independence among multiple effect sizes derived from the same site. The significance of moderator effects (i.e., the effects of study characteristics) was evaluated using omnibus Q_M tests. Effect sizes and model results were visualized using orchard plots generated by the “orchard” package (Nakagawa et al., 2023), showing overall mean effects and 95% confidence intervals.

Publication bias was assessed using funnel plots and Egger’s regression tests. A multilevel mixed-effects meta-regression model was fitted with SE and N as moderators, and the presence of bias was evaluated based on the deviation of the intercept from zero (Figure S2). Sensitivity analyses were conducted to test the robustness of the meta-analytic results by excluding studies with imputed standard deviations (Figure S3). The consistency of the overall trends before and after the exclusion was compared to assess the influence of imputed data on the findings. No conclusive evidence of publication bias was detected in the models fitted with either SE or N as moderators (Figure S2). In addition, sensitivity analysis demonstrated that the effect sizes remained stable after excluding studies with imputed standard deviations, indicating the robustness of the results (Figure S3).

2.5. Statistical analyses

To better understand the drivers influencing changes in SOC and MBC, a set of environmental and management-related covariates was included in the analysis. These variables included initial SOC, climatic zone, climatic variables (e.g., MAT and MAP), elevation, perennial crop age, soil particle composition, bulk density, soil pH, and photosynthetic functional types. Random forest analysis was performed to identify the most influential variables affecting changes in SOC and MBC and to select suitable moderators for regression analyses. Models were built using the “randomForest” package in R, with the number of trees set to 100 and other parameters set to default values (Liaw and Wiener, 2002). Variable importance was evaluated based on the increase in mean squared error following random permutation of each predictor variable. No fixed importance threshold was applied; instead, for each response

variable, predictors were ranked by the increase in mean squared error, and the three highest-ranked predictors were retained as candidate moderators for subsequent regression analyses. Pairwise Pearson correlation tests were conducted to examine the relationships between environmental factors (MAT, MAP, elevation, soil particle composition, bulk density, soil pH, and initial SOC) and the log response ratios of SOC and MBC. According to the Pearson correlation analysis, initial SOC was significantly positively correlated with the responses of MBC and SOC separately (Figure S4). Because initial SOC is mathematically coupled with changes in SOC, we only included it only in exploratory analyses and did not use it for our main inference (Slessarev et al., 2023). Coefficients of determination (R^2) and corresponding p -values (p) were calculated using the “Hmisc” package in R (Harrell, 2025). Significant correlations were visualized through heatmaps to detect potential multicollinearity among predictor variables. Structural equation modeling was performed using PLS-PM to explore the direct and indirect effects of environmental (MAT and MAP), soil (pH, BD, and soil particle composition), and crop (crop age) variables on the responses of SOC and MBC. All variables were standardized prior to analysis to ensure comparability of their effect sizes. The PLS-PM models were constructed and fitted using the “plsmp” package in R (Sanchez et al., 2024). Model goodness-of-fit was evaluated based on the Goodness-of-Fit index, and the significance of individual path coefficients was assessed using 500 bootstrap resamples to assess the uncertainty and significance of the estimated associations.

3. Results

Compared with annual cropping systems, perennial cropping systems increased SOC and MBC in the topsoil (0–30 cm) by 15% (95% confidence interval (CI)₉₅, 10–21%; $p < 0.001$; Fig. 1B) and 37% (CI₉₅, 22–54%; $p < 0.001$; Fig. 1C), respectively. The responses of MBC and SOC were positively correlated (slope = 0.50, $R^2 = 0.51$, $p < 0.001$; Fig. 1D). Random forest analysis indicated that the most important predictors differed between the responses of SOC and MBC. For SOC, the three highest-ranked predictors were climatic zone, crop age, and initial SOC; whereas for MBC, they were initial SOC, soil pH, and crop age (Fig. 2A and 2B). Although initial SOC was significantly correlated with both the responses of SOC ($R^2 = 0.088$, $p = 0.002$; Figure S4) and MBC ($R^2 = 0.161$, $p < 0.001$; Figure S4), its explanatory power was relatively low. Therefore, initial SOC was considered a supplementary soil property rather than a key background factor in our analysis, whereas climatic zone, crop age, and soil pH were selected as key environmental

factors for subgroup and regression analyses.

When grouped by climatic zone, the response of SOC significantly differed between tropical, subtropical, and temperate regions ($F = 11.76$, $p < 0.001$; Fig. 3A). Following the transition from annual to perennial cropping systems, SOC increased by 27% in subtropical regions and by 13% in temperate regions, with no significant change in tropical regions (Fig. 3A, Table S1). Similarly, the response of MBC differed significantly among climatic zones ($F = 10.41$, $p < 0.001$; Fig. 3B). Specifically, tropical regions showed a 92% increase in MBC (Fig. 3B, Table S2). In temperate and subtropical regions, MBC increased by 31% and 44%, respectively (Fig. 3B, Table S2). Regression analysis revealed a statistically significant positive relationship between the responses of MBC and SOC within each climatic zone (Fig. 4A). In tropical regions, the responses of MBC and SOC were positively correlated (slope = 0.35, $R^2 = 0.69$, $p = 0.01$; Fig. 4A). This was followed by subtropical regions, where a notable positive effect was observed (slope = 0.69, $R^2 = 0.62$, $p < 0.001$; Fig. 4A). In temperate regions, the relationship was statistically significant but explained less variation (slope = 0.38, $R^2 = 0.49$, $p < 0.001$; Fig. 4A).

The response of SOC to perennial cultivation changed over time ($F = 30.69$, $p < 0.001$; Fig. 3A). No significant change in SOC was observed for perennial crops younger than 5 years. In contrast, SOC increased by 12% and 29% in perennial crops cultivated for 5–10 years and over 10 years, respectively (Fig. 3A, Table S1). The response of MBC showed a similar pattern ($F = 19.26$, $p < 0.001$; Fig. 3B), indicating that MBC increased progressively with crop age, reaching 24% and 69% in crops cultivated for 5–10 years and over 10 years, respectively (Fig. 3B, Table S2). Significant positive correlations between the responses of MBC and SOC were consistently observed among different crop-age classes (Fig. 4B). The model showed moderate explanatory power and a clear positive relationship in crops older than 10 years (slope = 0.57, $R^2 = 0.55$, $p < 0.001$; Fig. 4B). In contrast, for perennial crops cultivated for 5–10 years, the model showed lower explanatory power (slope = 0.21, $R^2 = 0.16$, $p = 0.01$; Fig. 4B).

The SOC response differed significantly among soil pH categories, showing the greatest increase in alkaline soils (pH > 7.5; +24%), followed by neutral (6.5 ≤ pH ≤ 7.5; +15%) and acidic soils (pH < 6.5; +11%) ($F = 11.65$, $p < 0.001$; Fig. 3A, Table S1). MBC accumulation was most pronounced in neutral soils, with an average increase of 44% (Fig. 3B, Table S2). Meanwhile, acidic and alkaline soils showed average increases of 32% and 39% in MBC, respectively ($F = 9.27$, $p < 0.001$; Fig. 3B, Table S2). Regression analysis further revealed a consistent positive relationship between the responses of MBC and SOC across all

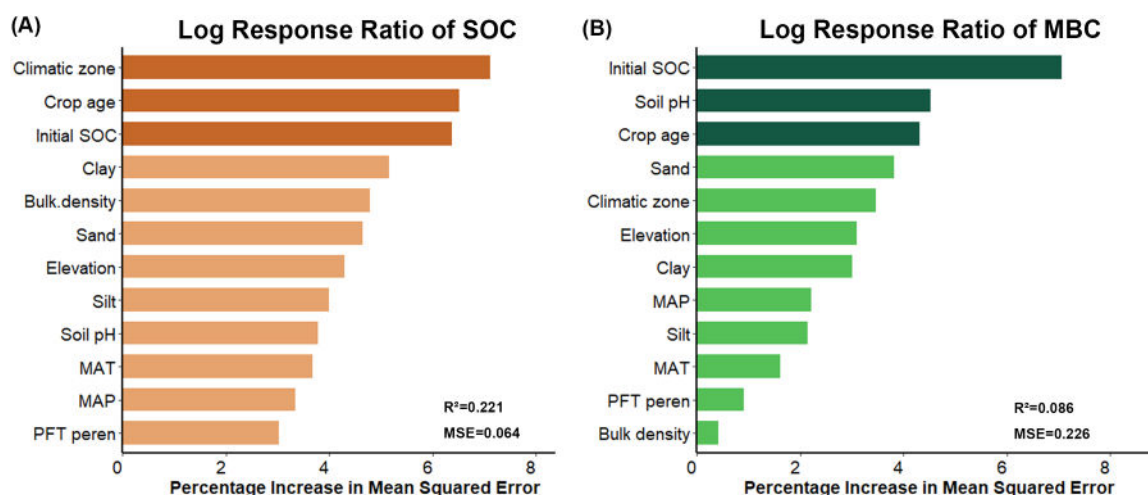


Fig. 2. (A) Variable importance for predicting the response of SOC based on the random forest algorithm. The most important predictors included climatic zone, crop age, and initial SOC. (B) Variable importance for predicting the response of MBC, showing that initial SOC, soil pH, and crop age ranked as the top three predictors. MAT: mean annual temperature; MAP: mean annual precipitation; PFT peren: perennial plant photosynthetic functional types; MSE: mean squared error.

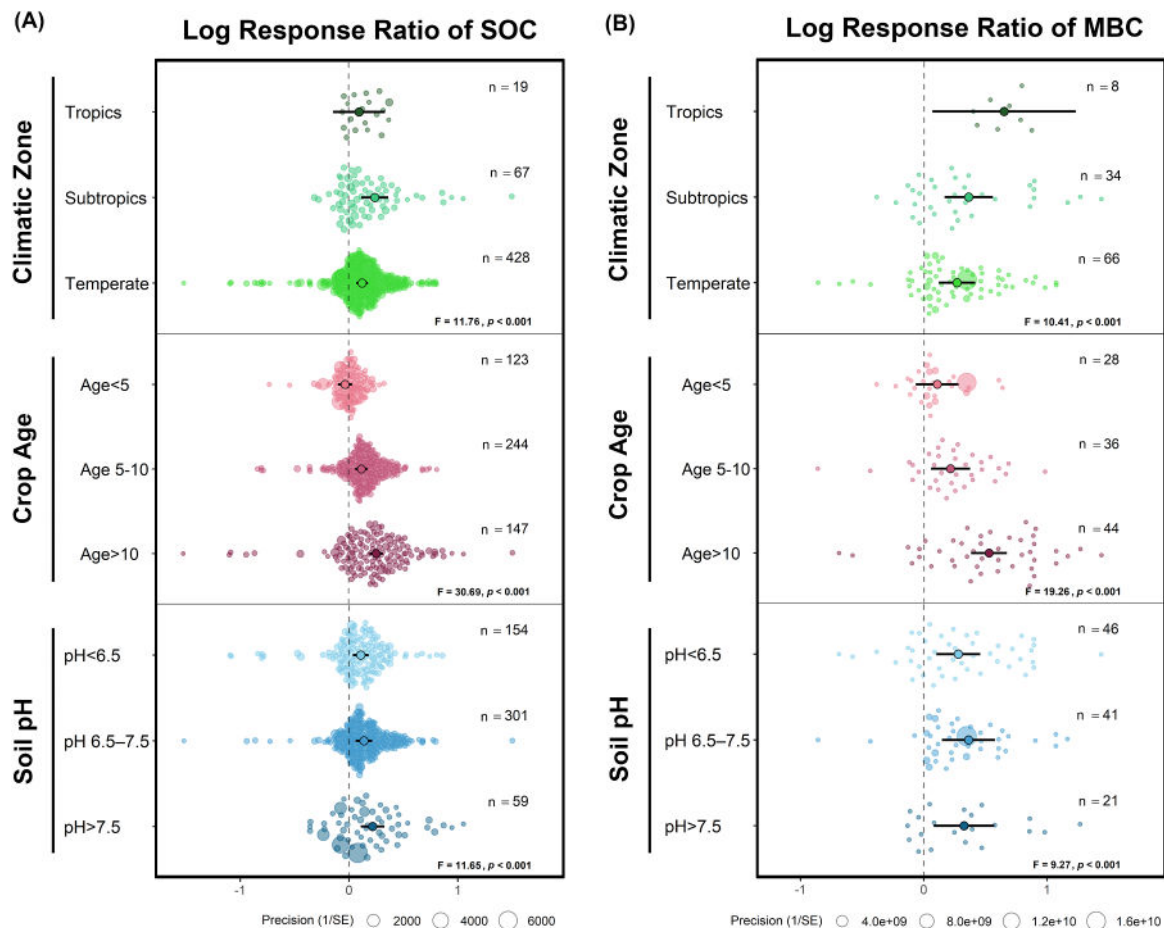


Fig. 3. Subgroup meta-analysis results showing the distributions of responses of (A) SOC and (B) MBC across different climatic zones (top panels), crop age classes (middle panels), and soil pH classes (bottom panels). Climate zone, crop age, and soil pH had significant effects on the responses of MBC and SOC (all $p < 0.001$). n : number of effect sizes; Precision (1/SE): inversely proportional to the standard error; larger circles represent more precise estimates.

soil pH categories (Fig. 4C). Under alkaline soil conditions, the relationship was more pronounced than in other soil environments (slope = 0.72, $R^2 = 0.67$, $p < 0.001$; Fig. 4C). Weaker, although still significant, relationships were observed in acidic soils (slope = 0.41, $R^2 = 0.66$, $p < 0.001$; Fig. 4C) and neutral soils (slope = 0.48, $R^2 = 0.43$, $p < 0.001$; Fig. 4C).

Regression analyses were conducted for three initial SOC categories: low ($< 50 \text{ Mg ha}^{-1}$), medium ($50\text{--}100 \text{ Mg ha}^{-1}$), and high ($> 100 \text{ Mg ha}^{-1}$) (Fig. 4D). Changes in MBC accounted for more variation in SOC under medium initial SOC (slope = 0.57, $R^2 = 0.62$, $p < 0.001$; Fig. 4D) than under either low initial SOC (slope = 0.33, $R^2 = 0.25$, $p < 0.001$; Fig. 4D) or high initial SOC (slope = 0.39, $R^2 = 0.37$, $p < 0.001$; Fig. 4D). However, the slopes for the responses of MBC and SOC did not differ significantly among low, medium, and high initial SOC levels ($F = 2.27$, $p = 0.11$; Table S3), suggesting that this relationship remains relatively consistent across different initial SOC levels.

PLS-PM revealed that climatic conditions, crop traits, and soil physicochemical properties jointly influenced the responses of MBC and SOC during the transition from annual to perennial cropping systems (Fig. 5). Pronounced positive effects were observed between the responses of MBC and SOC (path coefficient = 0.62, $p < 0.001$; Fig. 5). Climatic factors, including MAT and MAP, exerted a significant positive effect on the response of MBC (path coefficient = 0.27, $p < 0.01$; Fig. 5). Soil pH had a positive effect on the response of SOC (path coefficient = 0.25, $p < 0.001$; Fig. 5) but had a statistically insignificant influence on the response of MBC. Additionally, crop age had significant positive effects on the response of both MBC (path coefficient = 0.44, $p < 0.001$) and SOC (path coefficient = 0.21, $p < 0.01$; Fig. 5).

4. Discussion

4.1. Transitioning from annual to perennial cropping systems enhances the contribution of MBC to SOC

The transition from annual to perennial cropping systems promotes the accumulation of both SOC and MBC (Figs. 1B and 1C). This observed increase in SOC in perennial cropping systems is slightly lower than that reported in previous meta-analyses with limited sample size (e.g. Siddique et al., 2023). The notable increase in MBC reflects elevated microbial activity in perennial cropping systems, driven by greater plant carbon inputs that are likely transformed into microbial metabolites and necromass (Domeignoz-Horta et al., 2024; Georgiou et al., 2017; Pausch and Kuzyakov, 2018). For instance, herbaceous perennial crops such as switchgrass (*Panicum virgatum*) and alfalfa (*Medicago sativa*) generally produce litter with sustained inputs of labile carbon, such as soluble sugars and non-structural carbohydrates, which stimulate microbial metabolic activities and maintain higher MBC content over time (Börjesson et al., 2018; McGowan et al., 2019). In addition, by minimizing physical disturbance through reduced or no-tillage practices, perennial cropping systems may help maintain soil structure and microbial habitats, thereby allowing the initiation of microbial succession (Kierath et al., 2024). Moreover, perennial crops typically develop more extensive and deeper root systems, which enhance belowground carbon inputs and promote stable rhizosphere environments, further facilitating microbial successional processes (DuPont et al., 2010; Feng et al., 2024; Wang et al., 2021). This suggests that enhanced microbial activity following the conversion from annual to perennial crops is driven not

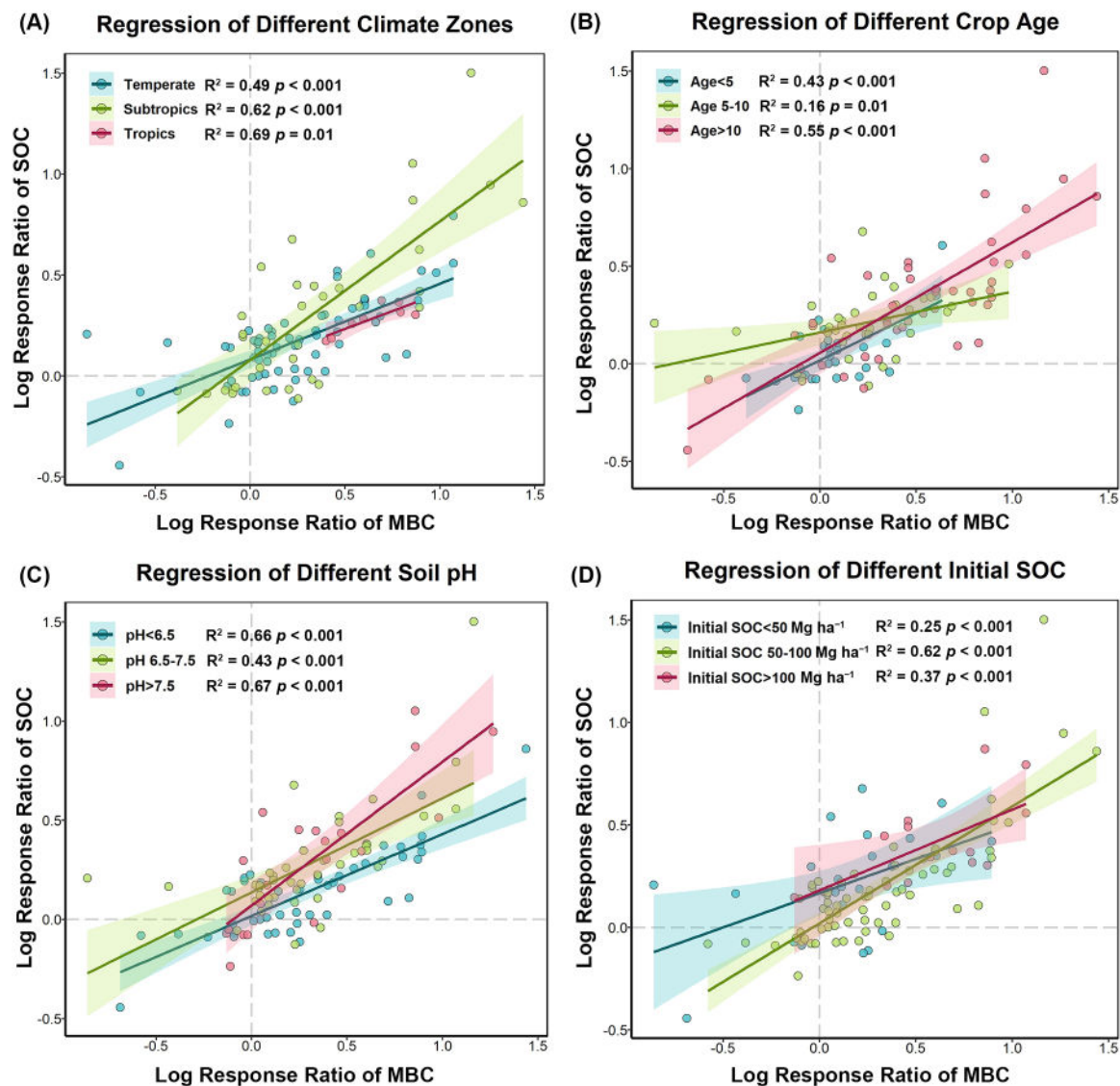


Fig. 4. Linear regression between the responses of MBC and SOC across (A) climate zones, (B) crop age classes, (C) soil pH, and (D) different initial SOC conditions. Detailed regression statistics are provided in Table S3 in the Supporting Information.

only by greater carbon inputs but also by improved soil functions.

In perennial cropping systems, MBC and SOC showed a positive association, indicating that higher microbial biomass coincides with greater SOC accumulation (Fig. 1D). Results from PLS-PM support this interpretation, showing that increases in MBC are significantly positively associated with SOC accumulation, and that both are influenced by environmental factors (Fig. 5). Compared with annual cropping systems, perennial cropping systems continuously supply organic substrates through litterfall and root exudates, thereby promoting microbial abundance and activity (Carvalho et al., 2017; Lehmann et al., 2011; Rubio et al., 2025; Sasse, 2023). The contribution of MBC to SOC accumulation varies under different land-use changes and is highly sensitive to plant carbon inputs (Deng et al., 2014). For instance, the increase in MBC explained only 38% of SOC accumulation in deforestation scenario (Wang et al., 2021), which is lower than the 51% observed in our study, suggesting that enhanced plant-derived carbon inputs under perennial cropping systems may strengthen the coupling between MBC responses and SOC accumulation during the conversion from annual to perennial cropping systems. A possible reason for these differences is that microbial activity is highly responsive to increases in carbon inputs, but shows a delayed response when carbon inputs

decline, creating a temporal mismatch between MBC and SOC accumulation (Feng et al., 2024; Sahani and Behera, 2001; Wang et al., 2021). The composition of carbon inputs in perennial systems is a critical determinant of the relationship between the responses of MBC and SOC (Liu et al., 2016; Zhang et al., 2025). Higher labile carbon inputs may be more readily transformed into microbial residues, which in turn contribute disproportionately to the formation of persistent SOC and enhance the explanatory power of MBC for SOC accumulation (Lehmann et al., 2011; Rubio et al., 2025). In this process, MBC partly reflects an increase in microbial carbon use efficiency, which helps explain the close relationship between MBC and SOC (Geyer et al., 2020).

The regression slope helps to evaluate how the log response ratio of MBC changes with the log response ratio of SOC, thereby indicating of the efficiency with which increases in MBC following conversion to perennial cropping systems contribute to SOC accumulation. The slope of the regression between the log response ratios of MBC and SOC is 0.50, indicating that the proportional increases in SOC and MBC are not directly proportional (Fig. 1D). This deviation from a 1:1 relationship likely reflects fundamental differences in their turnover characteristics: MBC represents a short-lived, highly dynamic carbon pool, whereas microbially derived SOC undergoes long-term stabilization through

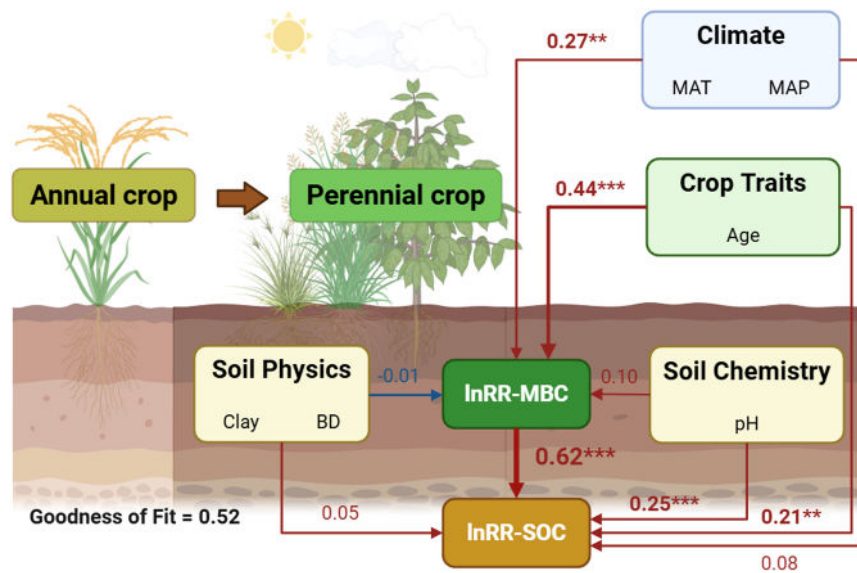


Fig. 5. Partial least squares path modeling (PLS-PM) illustrates the direct and indirect pathways influencing the responses of MBC and SOC during the transition from annual to perennial cropping systems. The model was validated using 500 bootstrap resamples, and the Goodness of Fit value was 0.52. Asterisks indicate significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). MAT: mean annual temperature; MAP: mean annual precipitation; BD: bulk density; *lnRR-MBC*: the log response ratio of MBC; *lnRR-SOC*: the log response ratio of SOC.

associations with soil minerals (Georgiou et al., 2017; Geyer et al., 2020; Woolf and Lehmann, 2019). Importantly, not all carbon inputs are ultimately retained as SOC; a substantial fraction is released to the atmosphere through microbial respiration (Liang, 2025; McFarlane et al., 2024). In the short term, this loss of carbon may be further amplified by the priming effect (Kuzakov et al., 2000). Moreover, some SOC originates from sources unrelated to MBC, such as plant residues or chemically recalcitrant compounds, and these inputs also contribute to SOC accumulation during the transition from annual to perennial cropping systems (Craig et al., 2022). Therefore, understanding the basis of the notable relationship between MBC and SOC in perennial cropping systems is essential for revealing the mechanisms of long-term SOC stabilization.

4.2. Abiotic and biotic factors control the relationship between MBC and SOC

The three most important predictors of SOC responses were climatic zone, crop age, and initial SOC, suggesting that SOC responses were mainly regulated by long-term environmental conditions, cumulative carbon inputs, and the baseline carbon pool (Fig. 2A). Climatic zone can influence environmental conditions such as plant productivity and organic matter decomposition rates (Lask et al., 2020). Crop age reflects the time-dependent cumulative effects of SOC accumulation driven by sustained root-derived carbon inputs after the establishment of perennial cropping systems, whereas initial SOC represents the pre-existing soil carbon status (Ericsson et al., 2013; Wu et al., 2024). In contrast, soil pH ranked highly among the important predictors of MBC responses, indicating that MBC was more sensitive to the current microbial growth environment and soil chemical conditions (Fig. 2B). Soil pH directly influences microbial community composition, enzyme activity, and nutrient availability, and thus MBC may be more strongly regulated by pH than SOC (McGowan et al., 2019). In addition, initial SOC and crop age were also important predictors of MBC, likely reflecting greater organic matter availability and more favorable rhizosphere conditions in older perennial crop systems, thereby supporting a more stable and functionally diverse microbial community (Feng et al., 2024; Hartmann and Six, 2022).

The PLS-PM showed that climatic factors, including MAT and MAP, exerted a significant positive effect on the response of MBC (Fig. 5),

suggesting that perennial cropping systems in warmer and wetter regions tend to enhance microbial proliferation and activity, thus promoting SOC accumulation (Boisvenue and Running, 2010; Moore et al., 2020; Zhou et al., 2018). Based on the climatic zone classification, perennial cropping systems in tropical regions showed a greater increase in MBC than those in subtropical and temperate regions. However, significant increases in SOC were only observed in subtropical and temperate regions (Figs. 3A and 3B). The relatively favorable moisture and soil conditions in these regions are more conducive to perennial crop cultivation, thereby promoting the accumulation of both MBC and SOC (Georgiou et al., 2022). Moreover, the regression slope between the responses of MBC and SOC was highest in subtropical regions, indicating a greater efficiency of MBC conversion into SOC (Fig. 4A; Table S1). This may reflect higher carbon inputs in subtropical regions compared to temperate regions. In addition, although tropical regions showed a greater increase in MBC and a significant coupling between MBC and SOC responses, their high carbon inputs did not result in significant SOC accumulation (Figs. 3 and 4A). This may be because microbial respiration is higher in tropical regions than in subtropical and temperate regions, offsetting potential SOC gains and resulting in significant SOC accumulation only in subtropical and temperate regions (Hartmann and Six, 2022; McFarlane et al., 2024).

The age of perennial systems may influence microbial activity, possibly through changes in root inputs, litter quality, soil properties, and microbiome composition (Cotrufo et al., 2013; Primieri et al., 2022). PLS-PM showed that crop age had significant positive effects on the responses of both MBC and SOC, with a stronger effect on MBC than on SOC (Fig. 5). The regression analysis supports a more effective contribution of MBC increases to SOC accumulation in long-term perennial systems with crop ages exceeding 10 years, whereas the coupling between MBC and SOC was weaker in systems aged 5–10 years than in the other crop-age groups (Fig. 4B). In short-term perennial systems, microbial processes may not yet have developed a stable linkage with carbon inputs, while the amount of carbon input may still be insufficient to sustain continuous SOC accumulation, with MBC–SOC relationship being particularly unstable in systems aged 5–10 years (Dutter et al., 2025; Lange et al., 2015; Zhang et al., 2020). As the duration of cultivation extends, continuously enhanced root-derived carbon inputs and aboveground litter returns collectively help improve soil structure and create a more stable environment for

microbial community establishment and functioning, thereby jointly enhancing SOC accumulation (Moore et al., 2020; Wu et al., 2024).

Soil physicochemical properties also played a critical role in regulating the responses of MBC and SOC. Soil pH, a key edaphic characteristic, exhibited a significant direct effect on SOC accumulation (Fig. 5). Subgroup analysis revealed that SOC increased more in alkaline soils than in other groups, whereas MBC increased more in neutral soils than in other groups (Figs. 3A and 3B). Regression analysis showed that MBC explained 67% of the variation in SOC in alkaline soils, with a higher regression coefficient than those observed under the other pH conditions (Fig. 4C). This finding suggests that the coupling between MBC and SOC is more pronounced in alkaline soils due to the favorable environment for microbial proliferation (Malik et al., 2018; Wen et al., 2025). The higher pH helps create a more favorable environment for microbial metabolism and stimulates the association of microbial residues with minerals (Zhou et al., 2012). The larger increase in MBC without a corresponding SOC gain in neutral soils may reflect a high-turnover but low-retention microbial C pathway rather than efficient SOC formation (Fig. 3). This decoupling may occur because enhanced microbial activity can also increase respiratory carbon loss, and because the retention of microbially processed carbon in SOC depends on stabilization processes such as aggregate protection (Dumbrell et al., 2010; Liang, 2025; Malik et al., 2018).

A suitable initial SOC level provides a favorable biochemical and physicochemical environment, such as accessible carbon sources, and is typically associated with higher soil fertility, improved aggregate structure, and greater water-holding capacity (Ferchaud et al., 2016; Georgiou et al., 2022; Ling et al., 2025). The relationship between the log response ratios of MBC and SOC was more pronounced at sites with relatively moderate initial SOC levels (Fig. 4D). Although the differences in the relationships between the log response ratios of MBC and SOC among initial SOC levels were not statistically significant, initial SOC was still significantly positively correlated with the responses of MBC and SOC separately (Figure S4C; Table S3). Moderate initial SOC levels can enhance microbial activity and metabolic processes, increase carbon input and availability, and subsequently promote the development of mineral-organic associations that facilitate carbon stabilization (Georgiou et al., 2022; Ledo et al., 2020). In such soils, sufficient SOC storage potential may remain before they approach carbon saturation, allowing microbial biomass-derived carbon to further contribute to SOC accumulation (Hou et al., 2023; Viscarra Rossel et al., 2024). This may partly explain why the relationship between the log response ratios of MBC and SOC appeared more pronounced at moderate initial SOC levels.

4.3. Limitations

Despite the valuable insights this study provides into the key drivers of SOC accumulation during the conversion from annual to perennial cropping systems, several limitations should be acknowledged. First, the dataset was dominated by herbaceous perennials, whereas only three observations were available for woody perennials. This limited sample size prevented a robust comparison between herbaceous and woody perennial systems. Therefore, the interpretation of the relationship between MBC and SOC accumulation primarily reflects herbaceous systems. Future studies with larger sample sizes should analyse herbaceous and woody perennial systems separately to determine whether their relationships between MBC and SOC accumulation differ. Second, this study focused primarily on microbial activity in topsoil. Given that the topsoil contains higher proportions of labile carbon, it remains uncertain whether subsoil microbial activity can effectively transform labile carbon into stable SOC pools. Third, this study did not directly quantify microbial respiratory carbon loss, which limits our ability to evaluate microbial carbon retention efficiency during the conversion from annual to perennial cropping systems. Previous studies have shown that perennial cropping may increase soil respiration, particularly during the

early stages of establishment, suggesting that enhanced microbial activity does not necessarily translate immediately into greater SOC retention (Hargreaves and Hofmockel, 2014). Fourth, the dataset was unevenly distributed across climatic zones, with tropical regions being particularly underrepresented. This uneven distribution limits the robustness and generalizability of climate-based comparisons and may bias interpretations of the climatic regulation of SOC and MBC. Moreover, although the dataset included 514 observations of SOC, there were only 108 paired observations on MBC and SOC. Future research should prioritize targeted sampling in tropical ecosystems and further investigate the stability of SOC in both topsoil and subsoil. Expanding high-resolution microbial datasets and integrating process-based tracking of microbial carbon fate are critical for improving the mechanistic understanding and predictive modeling of SOC sequestration.

5. Conclusion

This study systematically evaluated how climatic factors, crop traits, and baseline soil conditions regulate the simultaneous changes in SOC and MBC during the transition from annual to perennial cropping systems. The results show that perennial cropping systems significantly increased SOC and MBC levels. The random forest analysis and PLS-PM jointly revealed that changes in microbial biomass were closely associated with SOC accumulation in perennial cropping systems. Climatic zone, crop age, and soil pH were identified as key categorical drivers, while initial SOC exerted positive effects on changes in MBC and SOC. Specifically, the contribution of MBC to SOC accumulation was more pronounced under long-established perennial systems (older than 10 years), suggesting that crop age is a key dynamic factor differentiating the strength of SOC–MBC linkages across systems. Overall, these findings underscore the importance of incorporating microbial indicators, such as MBC, into SOC sequestration strategies and modeling frameworks in the context of land-use change and the development of climate-smart cropping systems, thereby promoting conditions that favor long-term SOC stabilization. This study adds to the growing body of evidence demonstrating that perennial cropping systems can contribute to climate-change mitigation through sustained carbon sequestration and advance progress towards multiple Sustainable Development Goals.

CRedit authorship contribution statement

Sheng Wang: Writing – review & editing. **Jiacong Zhou:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Bin Wang:** Writing – review & editing. **Jørgen Eivind Olesen:** Writing – review & editing. **Marshall D. McDaniel:** Writing – review & editing. **Ji Liu:** Writing – review & editing. **Yundi Bai:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Ji Chen:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization. **Peñuelas Josep:** Writing – review & editing. **Martínez-Núñez Carlos:** Writing – review & editing. **Imran Ahammad Siddique:** Writing – review & editing. **Yakov Kuzyakov:** Writing – review & editing. **Huanyuan Zhang-Zheng:** Writing – review & editing. **Pete Smith:** Writing – review & editing. **Ning Dong:** Writing – review & editing. **Kätterer Thomas:** Writing – review & editing. **Lennart Olsson:** Writing – review & editing. **Raúl Ochoa Hueso:** Writing – review & editing. **Carsten W. Mueller:** Writing – review & editing. **Kees Jan van Groenigen:** Writing – review & editing.

Ethics approval

Not applicable

Consent for publication

Not applicable

Consent to participate

Not applicable

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. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2026.110702](https://doi.org/10.1016/j.agee.2026.110702).

Data availability

<https://github.com/byd0856-dotcom/Meta-analysis-MBC-and-SOC.git>

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