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Spatiotemporal variability in divergent accrual of particulate and mineral-associated organic carbon by vegetation restoration on the Loess Plateau

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ABSTRACT

Vegetation restoration is a promising climate mitigation strategy, with considerable potential for enhancing soil organic carbon (SOC) sequestration. However, knowledge on the effects of vegetation restoration on different SOC fractions remains poorly characterized. We conducted a regional synthesis to quantify how vegetation restoration, the most typical and successful agricultural land-use change on the Loess Plateau, affects particulate (POC) and mineral-associated organic carbon (MAOC). We found that vegetation restoration significantly increased SOC by 66 %, higher than the global average estimate (<45 %), with a much greater increase in POC (103 %) than in MAOC (48 %), which resulted in an increased proportion of POC in SOC but decreased that of MAOC. Moreover, the accrual of POC and MAOC was greater for conversion to forest and shrubland than to grassland, and for artificial restoration than for natural restoration, and for legume species than for non-legume species, respectively. Notably, the accrual of POC and MAOC showed divergent spatial and temporal dependencies. Spatially, the response of MAOC increased significantly, whereas that of POC showed no significant change with the latitude. With increasing soil depth, the response of POC and MAOC gradually decreased, but was always positive across the whole 0–400 cm profile. Temporally, the response of POC and MAOC increased significantly with time since restoration, and the increase in POC was more pronounced than that in MAOC and the accrual occurred approximately 2.5 years post-restoration. Collectively, our findings show a stronger accrual of POC relative to MAOC after vegetation restoration, along with their spatial and temporal dependencies, which underscore the importance of multi-pool management of SOC for accurately predicting the soil C sink potential in restored ecosystems.

1. Introduction

The United Nations (UN) has designated 2021–2030 as the 'UN Decade on Ecosystem Restoration' to accelerate global ecosystem restoration and contribute to the attainment of the Sustainable Development Goals (Edrisi and Abhilash, 2021). Vegetation restoration by

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abandonment of cropland, afforestation and reforestation, prohibition of grazing, etc., has also become an important strategy for carbon (C) sequestration, climate change mitigation and the restoration of ecosystem functions (Ascenzi et al., 2025; Beillouin et al., 2023; Strassburg et al., 2020). Recent estimate suggests that forest and grassland restoration decreased the global warming potentials by 328 % and 158 %, respectively (He et al., 2024). Consequently, these climate benefits depend largely on the soils, which constitute the largest C reservoir in terrestrial ecosystems with an estimated 1500 Pg C, where even minor fluctuations in soil organic C (SOC) could result in profound feedback for global C cycling and climate change (Crowther et al., 2019). Therefore, investigating the response of SOC to vegetation restoration is essential for developing policies to mitigate climate change and underpinning the implementation of the UN Decade on Ecosystem Restoration.

Soil organic carbon has been physically fractionated into particulate- (POC) and mineral-associated organic C (MAOC) with different compositions, formation pathways and environmental persistence, which enables a better understanding of SOC formation and stabilization mechanisms (Angst et al., 2023; Manzoni and Cotrufo, 2024). Specifically, POC is mainly composed of plant-derived compounds and free or occluded within soil aggregates, whereas MAOC is mainly comprised of plant- and microbe-derived microscopic organic molecules and is protected from decomposition through association with soil minerals and protection within micropores and microaggregates (Lavallee et al., 2020; Cotrufo et al., 2022; Sokol et al., 2022). The different properties of these two fractions may result in divergent fates under human activity or global change, ultimately affecting the enduring stabilization and sequestration of SOC (Georgiou et al., 2024; Wu et al., 2023; Díaz-Martínez et al., 2024). For example, recent estimate has indicated that the global MAOC and POC storages are 975 and 330 Pg C, with mean turnover times of 129 and 23 years, respectively (Zhou et al., 2024). Consequently, the separation of SOC into POC and MAOC enables more accurate prediction of the mechanisms underlying the SOC response to environmental change, which can be a potentially meaningful framework for improving Earth system models and informing land management for efficient C sequestration (Islam et al., 2022; Zhou et al., 2024).

Vegetation restoration can differentially affect SOC fractions through direct inputs of litter, roots and their exudates or indirect changes in soil physicochemical properties and microbial communities given the different formation mechanisms of POC and MAOC (Lavallee et al., 2020; Bai and Cotrufo, 2022; Liao et al., 2023). Previous studies have reported positive (Mendham et al., 2004; Li et al., 2023b), negative (Zhang et al., 2023; Santos et al., 2020), or neutral (Yang et al., 2023a; Hu et al., 2021) effects due to differences in the formation mechanisms of POC and MAOC and variations in restoration types and methods, climate, soil properties and restoration durations (Eze et al., 2023; Li et al., 2023b; Zhai et al., 2024). In addition, the magnitude of such positive effects also differed between POC and MAOC, with the increase in POC being greater (Mendham et al., 2004; Liao et al., 2023) or smaller (Li et al., 2023b) than that in MAOC. This divergent response of POC and MAOC to vegetation restoration might ultimately alter the SOC composition and affect the stability of SOC in fragile restoration ecosystems (Zhao et al., 2025b). Hence, identifying large-scale patterns of soil POC and MAOC responses to vegetation restoration could reconcile and explain previous inconsistent findings and is critical for accurately assessing soil C dynamics and reducing uncertainties in model predictions of terrestrial C-climate feedbacks.

The Loess Plateau covers a total area of 6.24×10^5 km^2, of which approximately 68 % is subject to soil erosion, being one of the most severely eroded areas in the world while simultaneously undergoing extensive vegetation restoration (Wang et al., 2021; Yang et al., 2023b). For example, the Grain for Green Program, initiated in 1999 to reconvert croplands to forestlands, shrublands and grasslands, has been recognized as the most typical and successful agricultural land-use change on the Loess Plateau, achieving the dual objectives of soil conservation and ecological rehabilitation (Fu et al., 2017). Soil erosion decreased from 1013 t·km^{-2}·a^{-1} in 1991–1995 to 595 t·km^{-2}·a^{-1} in 2011–2015 (Jin et al., 2021), and vegetation coverage increased from 32 % in 1999 to 71 % in 2020 (Yang et al., 2023b). These large-scale vegetation restoration measures on the Loess Plateau considerably promoted soil SOC sequestration (Li et al., 2022; Yang et al., 2023b), while the spatial and temporal variations of POC and MAOC and their relationships with climatic and edaphic factors remained unclear, which greatly hampered our ability to assess soil C dynamics after vegetation restoration and to accurately predict the long-term C sink potential of restored ecosystems.

To address this knowledge gap, we conducted a regional synthesis examining the effects of vegetation restoration on POC and MAOC on the Loess Plateau, using a regional dataset of 784 observations from 33 publications (Table S1; Fig. S1). We aimed to answer the following questions: (1) How do POC and MAOC respond to vegetation restoration in terms of magnitude and direction? (2) How does the spatiotemporal variability of the responses manifest? (3) How do plant, soil and biological properties drive these responses? Answering these questions will advance our understanding of the effects of vegetation restoration on SOC dynamics in fragile semi-arid restoration ecosystems and provide insights into future priorities for ecological restoration research and management strategies.

2. Materials and methods

2.1. Data compilation

We searched for peer-reviewed publications in Web of Science (Core Collection, http://apps.webofknowledge.com/) and China National Knowledge Infrastructure (http://www.cnki.net) up to Apr 2024. The following terms were used, revegetation OR rehabilitation OR reconstruction OR reclamation OR vegetation restoration OR afforestation OR land use conversion OR land use change and "particulate organic matter" OR "POM" OR "mineral-associated organic matter" OR "MAOM" OR "particulate organic carbon" OR "POC" OR "mineral-associated organic carbon" OR "MAOC" OR "light fraction" OR "heavy fraction" and "Loess Plateau". This search resulted in 394 publications as shown in Appendix Table S1.

We screened these publications according to the following criteria: (1) The experiment was conducted under field conditions with paired control cropland and vegetation restoration treatments at the same location. (2) The controls were established based on space (unrestored plots compared with adjacent restored plots) or time (pre-restoration compared with post-restoration). (3) For studies with multifactorial experiments, only treatments with the control and vegetation restoration alone were selected. (4) Paired results from the same publication with different locations, restoration types, methods, durations, and soil depths were considered independent experiments. (5) The soil was dispersed using sodium hexametaphosphate, sodium polytungstate, sodium iodide, sonication, or shaking with glass beads to adequately break down the aggregates (Liu et al., 2025). Then, the SOC fractions were separated by density, size or their combination approaches, with MAOC defined as the fraction smaller than 50–63 μm when separated by size, or heavier than 1.6–1.85 g cm^{-3} when separated by density (Lavallee et al., 2020). In addition, when one study reported both light (<1.6–1.85 g cm^{-3}) and heavy POC (>1.6–1.85 g cm^{-3} and >50–63 μm), the sum was considered the overall POC (Rocci et al., 2021; Wu et al., 2023). (6) The studies must report on at least two of the target variables (i.e., SOC, POC or MAOC (g kg^{-1} bulk soil)). (7) If the results from the same experiment were reported in different publications, only one dataset was retained. (8) The mean, standard deviation (SD) or standard error (SE) or coefficient of variation (CV), and sample size (n) of the control and vegetation restoration treatments could be directly obtained or calculated. We followed the preferred reporting items for meta-analysis (PRISMA) guidelines (Fig. S2) for reviewing, searching, and selecting the dataset. Finally, 784 paired observations from 33 studies were included in our regional dataset for the Loess Plateau (Fig. S1). All original publications and reasons for exclusion are provided in Appendix Table S1.

We also extracted information on geographic location and experimental design (i.e., restoration types, methods, and durations, species type and soil depth) from each selected publication. Moreover, we collected other ancillary data associated with climatic, soil physical, chemical, and biological properties, including mean annual temperature (MAT), mean annual precipitation (MAP), aboveground (ANPP), belowground (BNPP) and litter biomass, total nitrogen (TN), soil pH, soil mineral N (NH_4^+ and NO_3^-), dissolved organic C (DOC), dissolved organic nitrogen (DON), microbial biomass C (MBC), microbial biomass nitrogen (MBN), easily oxidized organic C (EOC), total (TP) and available (AP) phosphorus, soil moisture (SM), soil bulk density (BD), soil clay content, β-1,4-glucosidase (BG), N-acetyl-β-D-glucosaminidase (NAG), leucine aminopeptidase (LAP), alkaline phosphatase (ALP) and peroxiredoxin (PERX) activities. For each publication, we extracted the mean, SD or SE or CV, and n directly from tables, text, and supplementary files or indirectly from graphs using WebPlotDigizer (https://automeris.io/WebPlotDigitizer/).

2.2. Effect size calculation

To estimate the effect of vegetation restoration on individual variables for each case study, we calculated the natural logarithm of the response ratio (*lnRR*):

$$\ln RR = \ln(X_t/X_c)$$

where X_t and X_c are the mean values of the variables in the vegetation restoration and control treatments, respectively. The variance (*v(lnRR)*) for each *lnRR* was calculated as follows:

$$v(\ln RR) = \frac{SD_t^2}{n_t X_t^2} + \frac{SD_c^2}{n_c X_c^2}$$

where SD_t and SD_c are the standard deviations of the vegetation restoration and control treatments, respectively, and n_t and n_c are the number of replicates of the vegetation restoration and control treatments, respectively.

The mean weighted response ratio ($lnRR_{++}$) was calculated as follows:

$$\ln RR_{++} = \frac{\sum_{i=1}^{m} w_i \ln RR_i}{\sum_{i=1}^{m} w_i}$$

where *m* represents the number of comparisons in the group and $lnRR_i$ is the effect size of the *i*-th study. The weight of the *i*-th study (w_i) was calculated as follows:

$$w_i = \frac{1}{v(\ln RR)_i}$$

$$v(\ln RR)_i = v(\ln RR) + \tau^2$$

where $v(lnRR)_i$ represents the variance of study (i), v indicates the variance within a study, and τ^2 is the variance between studies.

To facilitate interpretation and comprehension, the mean weighted *lnRR* was expressed as a percentage change (%):

$$Percentage\ change(\%) = \left(e^{\ln RR_{++}} - 1\right) \times 100$$

2.3. Statistical analyses

All statistical analyses were performed in R language version 4.3.2 (v4.3.2; http://www.r-project.org/). We conducted multilevel random-effect meta-analyses without any moderators to estimate the overall mean effect size of vegetation restoration on individual variables using *rma.mv* function in the *metafor* package (Viechtbauer, 2010). Since we usually extracted multiple effect sizes from the same study, which resulted in correlations among these effect sizes. We thus accounted for non-independence among effect sizes by setting both the study identity and observation identity as random effects. Moreover, since multiple treatments are often compared with a single control (i.e., shared control) in the same study, we accounted for these repeated measures in a variance-covariance matrix (Lajeunesse, 2011).

Multilevel mixed-effect meta-analyses with moderators were then developed using the same random effects structure as the above random-effect model. The categorical moderators included in the model were restoration type and method, forest type, legume type, and species type. Each categorical moderator was divided into subgroups as shown in Table S2. We used restricted maximum likelihood estimation to fit the above models and to calculate the mean weighted effect sizes and 95 % confidence intervals (CIs) using the *rma.mv* function in the *metafor* package (Viechtbauer, 2010). The effect of vegetation restoration was considered significant when the 95 % CIs did not overlap with zero. We performed the omnibus test (Q_M) to examine the significance of between-group differences for each categorical moderator in the mixed-effects model. Then, the post-hoc paired tests for each categorical moderator were performed using the *linearHypothesis* function in the *car* package.

Linear mixed-effect models were performed to examine the relationships between the response ratios of the SOC, POC or MAOC and soil background properties (MAT, MAP, initial soil pH and clay content), and the response ratios of the plant properties (ANPP, BNPP, and litter biomass), soil physicochemical (pH, SM, BD, TN, TP, AP, NH_4^+, NO_3^-, DOC, DON, EOC, MBC and MBN), and biological properties (BG, NAG, LAP, ALP and PERX).

$$\ln RR = \beta_0 + \beta_1 x + \beta_{study} + \theta$$

where β_0, β_1, β_{study}, and θ are the intercept, slope coefficient, random effect, and sampling error, respectively, and x indicates the background soil properties, and the response ratios of the plant properties, soil physicochemical, and biological properties. The "study" was set as random effect to account for the autocorrelation among observations from the same study. We conducted the analysis using the restricted maximum likelihood estimation in the lme4 package (Bates et al., 2015). We then bootstrapped the fitted coefficients by 1000 iterations to calculate the 95 % bootstrapped CIs. The relationship was considered significant when the 95 % bootstrapped CIs of the slope did not overlap zero.

2.4. Robustness test

We evaluated robustness of the results using the following approach. Firstly, we calculated the bias-corrected effect sizes using the delta method to account for the small sample size bias (Lajeunesse, 2015), and compared these to uncorrected *lnRR* (Fig. S2). Secondly, the funnel plot was carried out and the asymmetry was assessed by Egger's regression test (Egger et al., 1997). Rosenberg fail-safe number was calculated to further evaluate whether the potential publication bias affected our results when asymmetry was detected (Rosenberg, 2005). Finally, we conducted a sensitivity analysis of the results by performing leave-one-out analysis. Based on the above analysis, we found that the funnel plots were asymmetric for SOC, POC and MAOC ($P < 0.05$; Fig. S3). However, the Rosenberg fail-safe numbers for these all metrics were much larger than 5 n + 10, which is considered the threshold for a robust mean effect size (Table S3). Furthermore, the sensitivity analysis based on leave-one-out analysis showed that the results were unlikely to be driven by a single influential observation and study by removing any observation or study (Figs. S4 and S5). Overall, there was no evidence of publication bias for all of the variables, and our results were robust.

3. Results

3.1. Effects of vegetation restoration on POC and MAOC

Across the whole dataset, vegetation restoration significantly increased the POC, MAOC, and SOC contents by 102.89 % (95 % CI = 62.96–152.60 %, $P < 0.05$), 47.72 % (95 % CI = 23.42–76.82 %, $P < 0.05$) and 65.96 % (95 % CI = 40.03–96.68 %, $P < 0.05$), respectively (Fig. 1), indicating that the positive effect of vegetation restoration on POC was greater than that on MAOC. Moreover, vegetation restoration significantly increased the proportion of POC in SOC (POC:SOC) by 23.15 % (95 % CI = 6.37–42.57 %, $P < 0.05$) but decreased the proportion of MAOC in SOC (MAOC:SOC) by 10.62 % (95 % CI = −15.49 to −5.47 %, $P < 0.05$) (Fig. S6). In addition, the response ratios of POC were significantly positively correlated with those of MAOC (Fig. 1).

The effects of vegetation restoration on SOC, POC, and MAOC accrual varied among the type and method of restoration and legume type (Q_M = 8.15–60.92, $P < 0.05$), with stronger positive effects observed for conversion to forests and shrublands than to grasslands, and for artificial restoration than for natural restoration, and for legume species than for non-legume species, respectively (Tables S4 and S5; Fig. 2). In addition, the stronger positive effect of legume-associated restoration was predominantly observed in forest conversion scenarios. Furthermore, forest type significantly influenced the response of POC to vegetation restoration ($Q_M = 8.14$, $P = 0.0043$) rather than that of SOC and MAOC (Q_M = 0.76–2.20, $P > 0.05$), with stronger positive effects observed for conversion to pure forests than to mixed forests (Tables S4 and S5; Fig. 2). Our further investigation of common restoration species on the Loess Plateau revealed that the positive effects on POC induced by *Robinia pseudoacacia* and *Hippophae rhamnoides* were stronger than those induced by *Caragana korshinskii* (Tables S4 and S5; Fig. 2).

3.2. Spatiotemporal variability of POC and MAOC accrual

The responses of total and fractional SOC to vegetation restoration were spatially and temporally dependent (Fig. 3). Spatially, the response ratios of SOC and MAOC increased significantly, whereas the response ratio of POC did not change significantly with the latitude. Moreover,

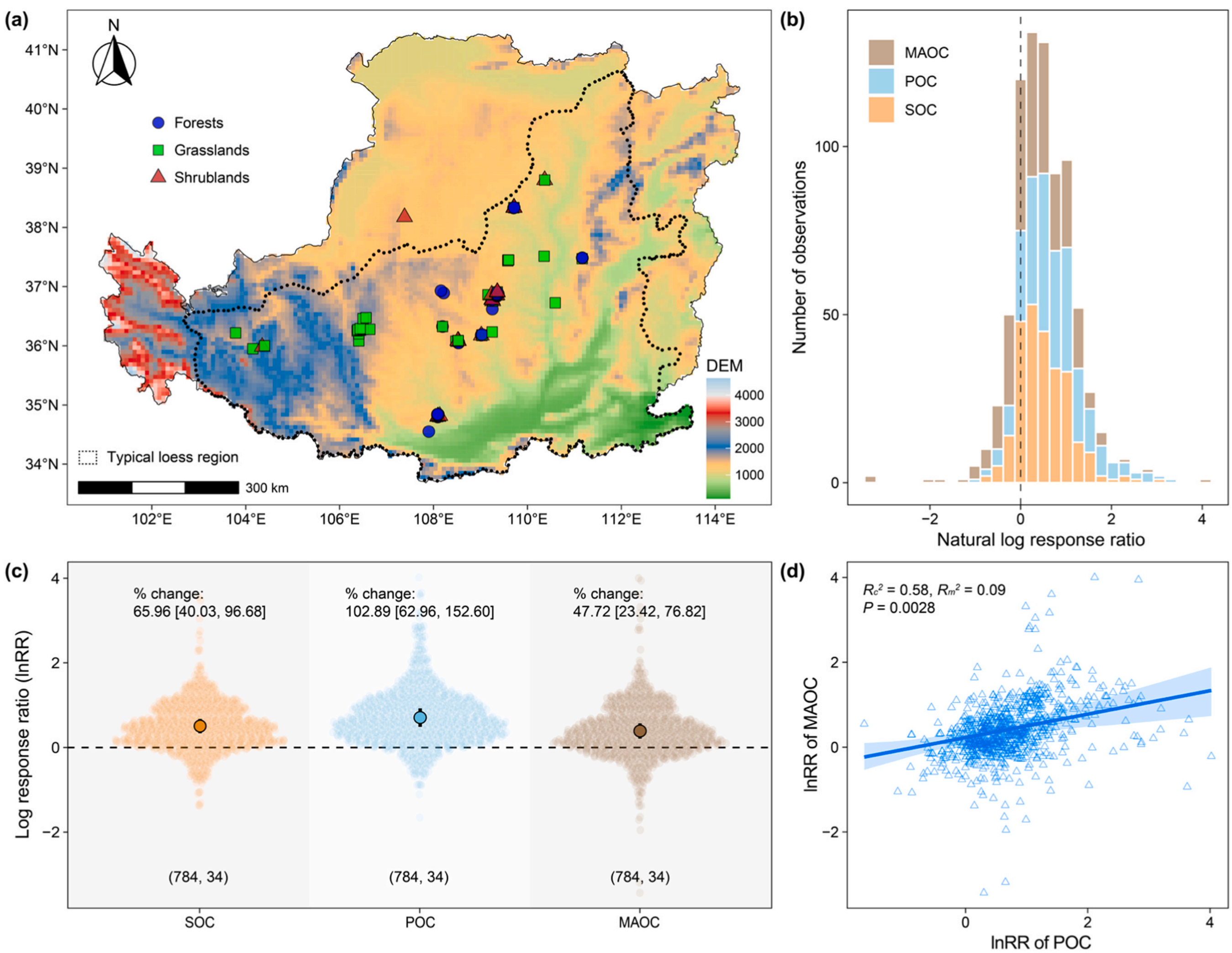

Fig. 1. The responses of SOC, POC and MAOC to vegetation restoration. (a) Geographical distribution of vegetation restoration studies with POC and/or MAOC data included in this meta-analysis. (b) Histogram of effect size. The effect size was calculated as the log response ratio (*lnRR*). (c) The overall mean effect of vegetation restoration to SOC, POC and MAOC. Each point represents an effect size. The values on the top side were converted from *lnRR* to weighted mean percentage change (%). The circles with error bars show the over mean effect size along with the 95 % confidence interval (CIs). Filled symbols represent statistical significance when the 95 % CIs do not overlap with zero ($P < 0.05$). The numbers in parentheses show the sample sizes and study numbers. (d) The relationships of the response ratio of POC to the response ratio of MAOC. The conditional and marginal R^2 and P values were then calculated based on the linear mixed effects model with the study set as random effect. SOC, soil organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon.

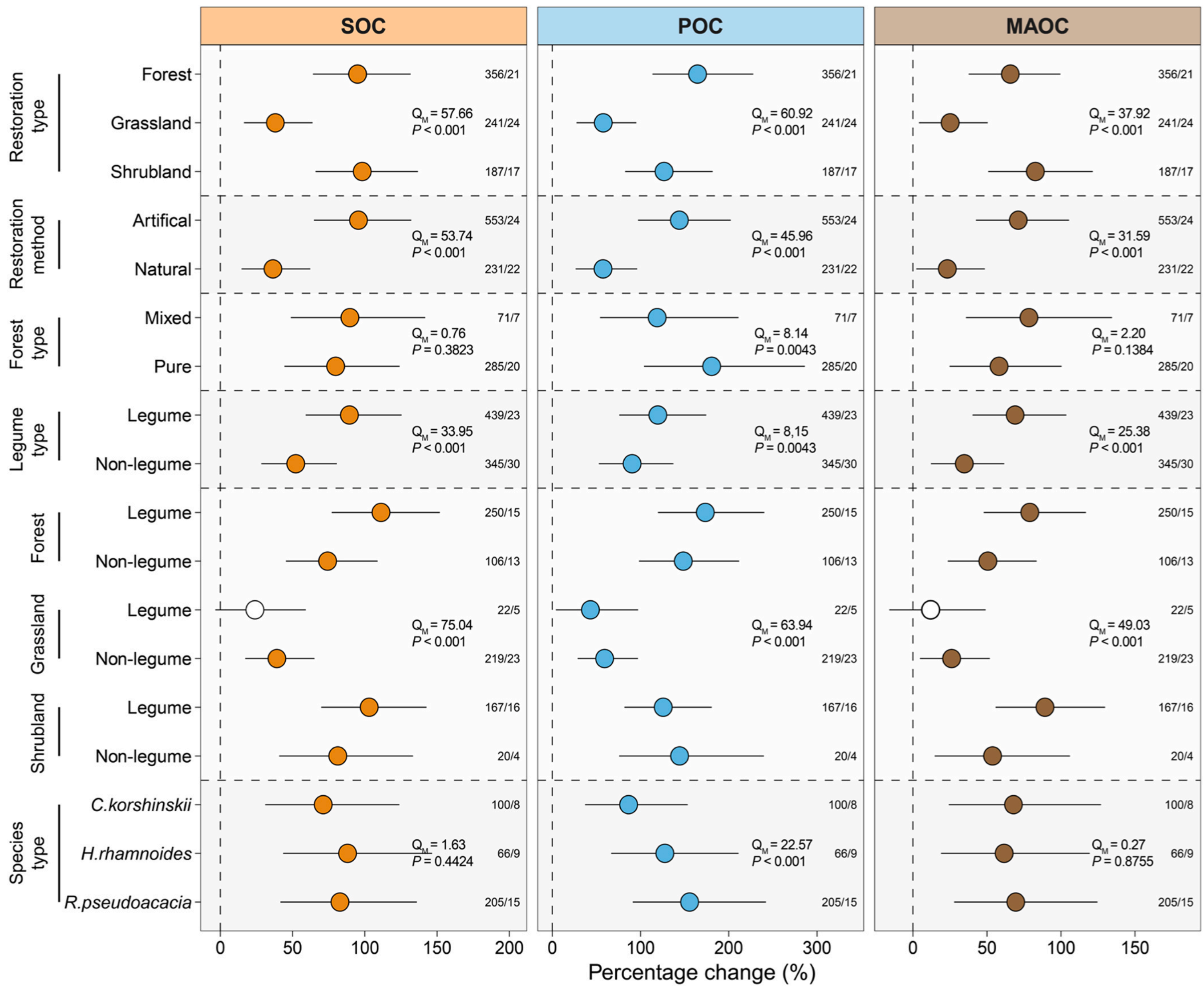

Fig. 2. The responses of SOC, POC and MAOC to vegetation restoration as affected by moderators. These moderators included vegetation restoration type and method, forest type, legume type, and species type. Detailed subgroup information and estimate are provided in Tables S2 and S4, respectively. The circles with error bars show the weighted mean percentage change (%) along with the 95 % confidence interval (CIs). Filled symbols represent statistical significance when the 95 % CIs do not overlap with zero ($P < 0.05$). The numbers on the right side of each panel denote the sample sizes and study numbers. Q_M is the heterogeneity of the weighted mean effect size associated with the moderator, with $P < 0.05$ indicating a significant difference among different subgroups under the same moderator. SOC, soil organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon.

with the increase in soil depth, the response ratios of total and fractional SOC initially decreased and then remained constant below 20 cm but was always greater than zero across the whole profile (0–400 cm). Notably, the response ratios of SOC and POC within the top 200 cm and those of MAOC within the top 100 cm were significant.

Temporally, the response ratios of total and fractional SOC increased significantly with time since restoration, and the increase in POC was more pronounced than that in SOC and MAOC (Fig. 3). Moreover, the response ratio of POC:SOC was significantly positive associated, whereas the response ratio of MAOC:SOC was not significantly associated with time since restoration (Fig. S7). In addition, although the mean response ratios of total and fractional SOC were negative within approximately the first 2.5 years post-restoration, these values were not statistically significant (Fig. 3). However, they became positive starting at approximately 2.5 years post-restoration, indicating that total and fractional SOC were initially maintained at control levels and that progressively significant soil C benefits started at that point.

3.3. Drivers of POC and MAOC accrual in response to vegetation restoration

The effects of vegetation restoration on total and fractional SOC accrual were regulated by soil and environmental background properties and changes in plant, soil physicochemical, and biological properties (Figs. 4 and 5). For example, the response ratios of SOC, POC and MAOC were negatively correlated with initial SOC levels (Fig. 4). The response ratios of SOC and POC rather than MAOC were positively linked to MAT or MAP. Additionally, the response ratios of SOC, POC and MAOC were positively associated with changes in plant properties such as aboveground, root and litter biomass, soil physicochemical properties such as moisture, TN, AP, DOC, DON, EOC, MBC and MBN, and soil biological properties such as BG and LAP enzyme activities. However, they were negatively associated with changes in soil physicochemical properties such as BD and soil pH (Fig. 5).

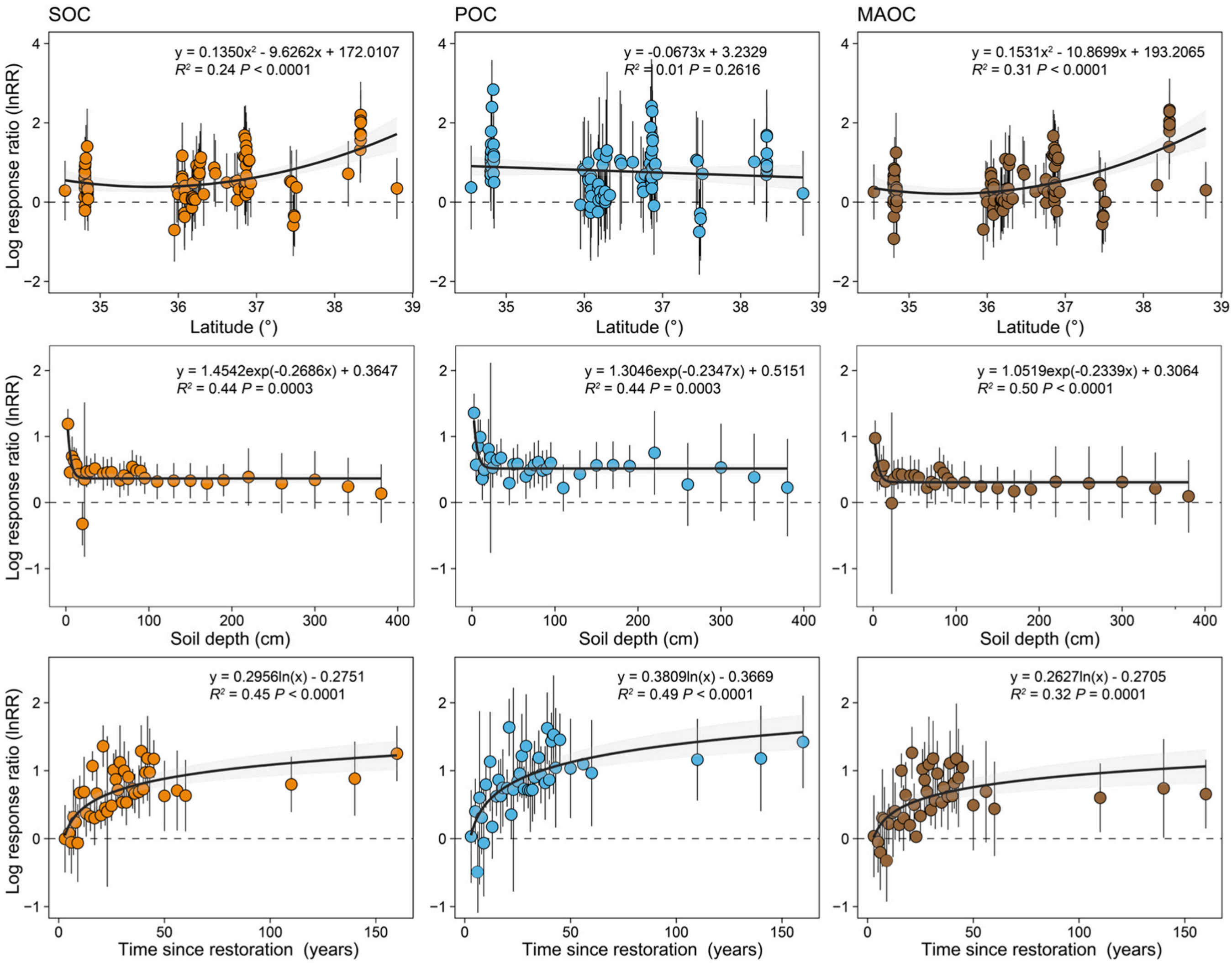

Fig. 3. The relationships between the response ratio of SOC, POC, and MAOC to vegetation restoration and latitude, soil depth, and time since restoration. The restoration effects were expressed as the mean response ratios with 95 % confidence interval (CIs) based on multilevel random-effects meta-analyses. Vegetation restoration effects were considered significant when the 95 % CIs do not overlap with zero ($P < 0.05$). SOC, soil organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon.

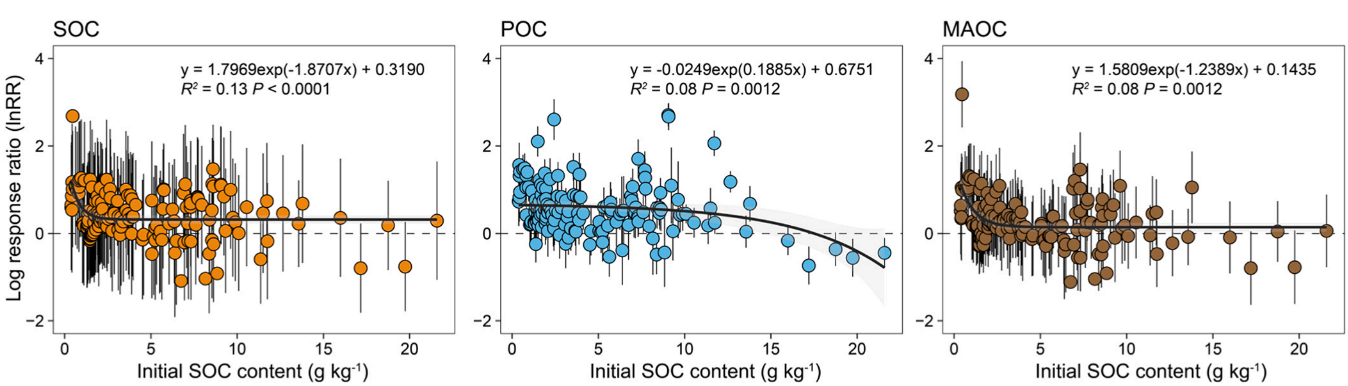

Fig. 4. The relationships between the response ratio of SOC, POC, and MAOC to vegetation restoration and initial SOC content. The restoration effects were expressed as the mean response ratios with 95 % confidence interval (CIs) based on multilevel random-effects meta-analyses. Vegetation restoration effects were considered significant when the 95 % CIs do not overlap with zero ($P < 0.05$). SOC, soil organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon.

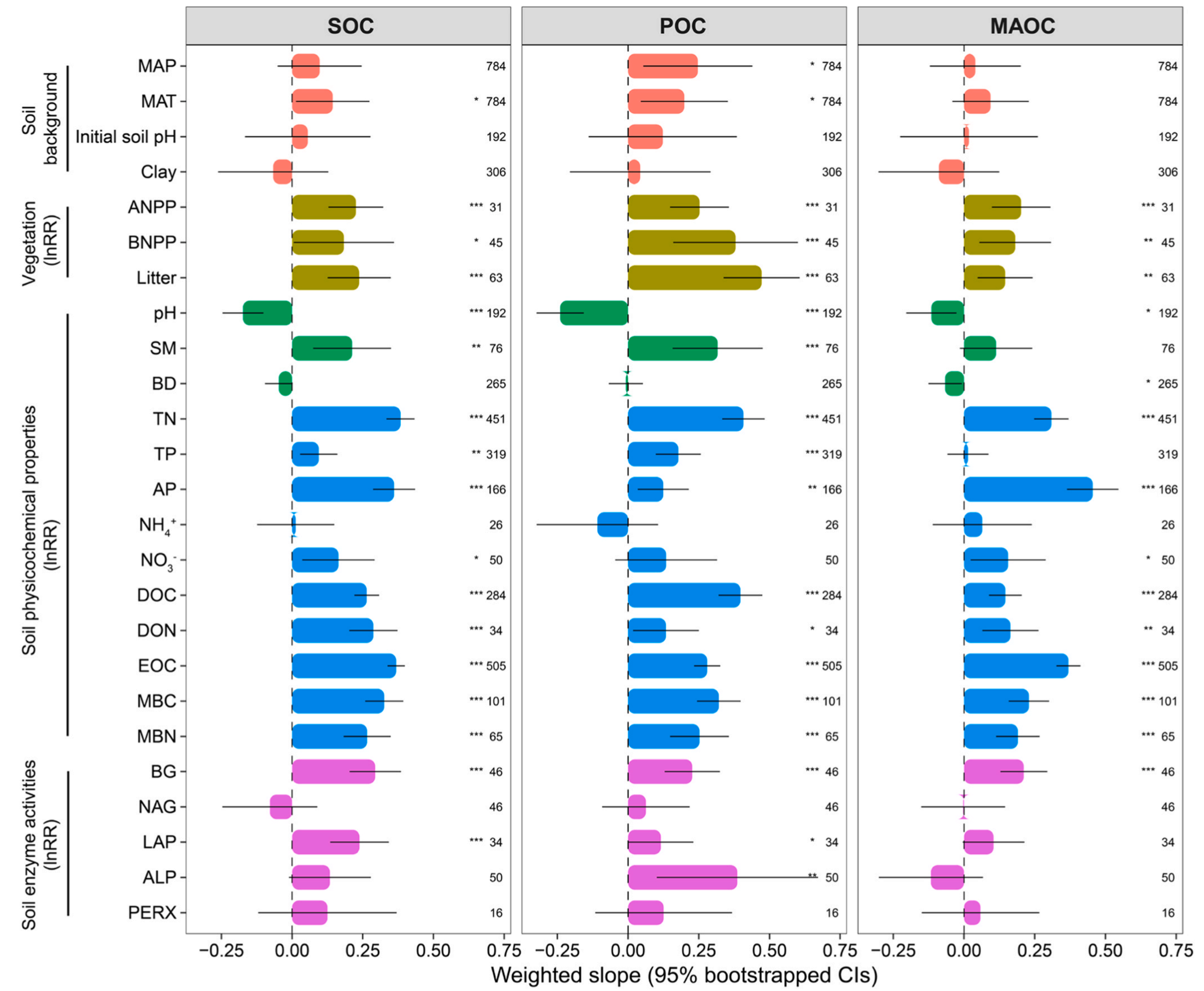

Fig. 5. The relationships between the response ratios of SOC, POC and MAOC and soil background properties, and the response ratios of vegetation properties, soil physical, chemical, and biological properties. The weighted slope was calculated based on the linear mixed effects model with the study set as random effect. We then bootstrapped the fitted coefficients by 1000 iterations to calculated the 95 % bootstrapped confidence intervals (CIs). The relationship was considered significant when the 95 % CIs did not overlap zero ($P < 0.05$). ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. The sample size for each variable is shown on the right. MAT, mean annual temperature; MAP, mean annual precipitation; Clay, soil clay content; ANPP, aboveground biomass; BNPP, root biomass; Litter, litter biomass; pH, soil pH; SM, soil moisture; BD, bulk density; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; NH4 + , ammonium; NO3-, nitrate; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; EOC, easily oxidized organic carbon; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; BG, β-1,4-glucosidase; NAG, N-acetyl-β-D-glucosaminidase; LAP, leucine aminopeptidase; ALP, alkaline phosphatase; PERX, peroxiredoxin.

4. Discussion

4.1. POC is more sensitive than MAOC in response to vegetation restoration

Our results demonstrated that vegetation restoration significantly increased the SOC by 65.96 % on the Loess Plateau (Fig. 1), which was higher than the global average estimate (< 45 %; Eze et al., 2023; Zhang et al., 2024; Ascenzi et al., 2025). However, vegetation restoration altered the SOC fractions, with a more pronounced increase in POC (102.89 %) than in MAOC (47.72 %) (Fig. 1), suggesting that the response of POC to vegetation restoration was more sensitive than that of MAOC. This finding was consistent with those from other regions, such as the Karst region (Lan, 2021), the Tibetan Plateau (Wang et al., 2025), and global scale (Zhang et al., 2024). This might be attributed to the following potential mechanisms.

Firstly, POC is primarily composed of relatively undecomposed light fragments of plant-derived (Lavallee et al., 2020; Cotrufo et al., 2022). Vegetation restoration significantly increased aboveground litter and root biomass, which could directly increase POC (Fig. S8; Cotrufo et al., 2022; Luo et al., 2023). However, MAOC is formed by direct adsorption of depolymerized POC products (e.g., DOC) or root secretions, and by the binding of microbial necromass formed by microbial *in vivo* turnover with minerals (Lavallee et al., 2020; Cotrufo et al., 2022). The formation process is more complex and energy-intensive (Rocci et al., 2021). In addition, below-ground C inputs contribute more effectively than above-ground C inputs to MAOC formation (Sokol and Bradford, 2019; Villarino et al., 2021; Wu et al., 2023). However, vegetation restoration on the Loess Plateau or at the global scale has resulted in greater increases in above-ground litter biomass than in below-ground root biomass (Fig. S8; Luo et al., 2023), which might be more conducive to POC rather than MAOC accumulation. Furthermore, litter quality gradually decreases (increasing C:N and lignin concentrations) with time since restoration (Prescott and Vesterdal, 2021; Liu et al., 2023; Zhang et al., 2023). The inputs of low-quality organic matter to soils are not readily utilized by microbes, and are expected to result in low microbial substrate use efficiency and assimilation metabolism, which is favorable for the formation of POC rather than MAOC according to the Microbial Efficiency-Matrix Stabilization (MEMS) framework (Cotrufo et al., 2013; Angst et al., 2023).

Secondly, the accumulation of SOC contributed by plant C inputs due to vegetation restoration may be greater than its loss (Kimmell et al., 2023; Zheng et al., 2024). Plant C inputs provide energy and C sources for soil microorganisms and thus promote microbial growth and activity, which accelerates SOC decomposition and CO_2 release through the priming effect (Philippot et al., 2024). Since the stability and turnover times of POC are lower than those of MAOC, such decomposition processes are likely to preferentially lead to the loss of POC (Mendham et al., 2004; Villarino et al., 2021; Yu et al., 2023). While the mineral adsorption of depolymerized POC products, and the increased microbial *in vivo* turnover and residue formation due to enhanced microbial activity and abundance in the process might promote MAOC accrual (Cotrufo et al., 2022; Angst et al., 2023; Zhai et al., 2024). However, plant C inputs (e.g., oxalic acid in root secretions) could also contribute to the direct dissolution of organo-mineral complexes or to indirect MAOC decomposition through microbial mobilization with the priming effect (Keiluweit et al., 2015; Jilling et al., 2021). Indeed, a global meta-analysis showed that although exogenous C input significantly increased the MAOC content, it also significantly enhanced MAOC decomposition (Zhang et al., 2022). Case studies have also shown that MAOC but not POC content is the strongest predictor of soil priming effects (Hao et al., 2024b). Moreover, the increased soil aggregation caused by vegetation restoration could promote the accrual of occluded POC and protect it from microbial decomposition (Chen et al., 2022; Kimmell et al., 2023). For example, previous study demonstrated that POC accrual and its aggregate protection were the key mechanisms underlying the accrual and stability of SOC during vegetation restoration (Chen et al., 2022).

Thirdly, the Loess Plateau is one of the most erosion-intensive regions around the world, and this erosion leads to substantial loss of SOC (Fu et al., 2017). The limited transport capacity of runoff results in the preferential transport of fine particles (usually associated with MAOC) during the soil erosion process, which results in the erosion-driven total loss of SOC being dominated by MAOC rather than POC (Li et al., 2023a; Liu et al., 2024), irrespective of vegetation coverage (Li et al., 2024).

Collectively, our results indicate that vegetation restoration-induced changes in total and fractional SOC on the Loess Plateau depend on a balance between accumulation and loss (decomposition and erosion), where accumulation outweighs loss, with greater promotion of POC than MAOC. This divergent accrual of POC and MAOC eventually resulted in an increase in the proportion of POC and a decrease in the proportion of MAOC in SOC (Fig. S6). Our findings were similar to previous global meta-analyses on the effects of direct return of crop residues or N input-induced increases in plant biomass on SOC fractions, all of which found that crop/plant residue inputs contributed more to POC than to MAOC (Hu et al., 2023; Tang et al., 2023; Wooliver and Jagadamma, 2023; Wu et al., 2023).

4.2. Moderators associated with vegetation restoration on POC and MAOC

Our results indicated that the type and method of restoration, and legume type affected POC and MAOC accrual after vegetation restoration on the Loess Plateau (Fig. 2). Specifically, stronger positive effects were observed for conversion to forests and shrublands than to grasslands, and for artificial restoration than for natural restoration, and for legume species than for non-legume species, respectively. These differences may be linked to variations in plant and soil physicochemical and biological properties following specific types of restoration.

Firstly, litter and root biomass were greater under forest and artificial restoration (mostly fast-growing plants and forest) than under grassland and natural restoration on the Loess Plateau (Dong et al., 2023; Liu et al., 2023; Hao et al., 2024a), which was the most direct reason for the increase in POC and MAOC (Fig. 5). Secondly, compared with grassland and natural restoration, forest and artificial restoration resulted in greater decreases in pH and BD, and greater increases in soil moisture and nutrients (Fig. S9). Our linear mixed models showed that the response ratios of POC and MAOC were significantly negatively correlated with the response ratios of pH and BD, and positively related to the response ratios of soil moisture and nutrients (Fig. 5). The reduction in soil pH and BD and the increase in soil moisture under afforestation in semi-arid alkaline soils (Hong et al., 2018; Jin et al., 2022) could provide better habitat for microbes and stimulate microbial activity, which would increase litter/root decomposition and thus promote POC accumulation (Fig. 5; Su et al., 2023; Zhai et al., 2024), while the increase in microbial activity and turnover promoted necromass formation, which contributed to MAOC accumulation (Fig. 5; Cotrufo et al., 2022; Sha et al., 2023). Thirdly, lower C/N ratios of litter and roots due to the N-fixing capacity of legumes, especially under legume afforestation could accelerate their decomposition and incorporation into POC (Fig. S10; Cotrufo et al., 2022; Dong et al., 2023), while increased microbial substrate use efficiency due to increased soil N availability was favorable for MAOC formation (Cotrufo et al., 2013). Fourthly, forest/artificial restoration on the Loess Plateau results in greater soil aggregation than grassland/natural restoration (Yao et al., 2019; Dong et al., 2022), which protects POC and MAOC from decomposition (Chen et al., 2022). Previous studies also demonstrated that artificial afforestation had more effective capacity for soil C sequestration than that of naturally restored grassland because of the greater return of plant biomass, incorporation of legume species, and soil aggregation (Chen et al., 2022; Dong et al., 2022; Yang et al., 2023a). Finally, afforested lands on the Loess Plateau's restored ecosystems showed significantly greater benefits in reducing runoff and sediment than grasslands, according to recent meta-analysis (Jia et al., 2025), which could further reduce erosion losses of POC and MAOC.

4.3. Spatiotemporal variability of POC and MAOC accrual

The responses of total and fractional SOC to vegetation restoration on the Loess Plateau were spatially dependent, and SOC and MAOC showed stronger positive effects at higher latitudes than at lower latitudes, while POC had weak relationship along the latitudinal gradient (Fig. 3). The stronger accrual of SOC and MAOC at higher latitudes may be attributed to the effect of lower initial SOC levels outweighing the effects of MAT, MAP and plant biomass (Fig. 4 and S11). At high latitudes, low temperatures and precipitation can slow microbial decomposition but also restrict plant growth and C input (Hartley et al., 2021; Kong et al., 2022), and their impact on MAOC may be weakened by mineral protection (Angst et al., 2023; Georgiou et al., 2024). However, vegetation restoration on C-poor soils at high latitudes on the Loess Plateau can rapidly improve soil environment and provide greater potential for SOC accumulation (Huang et al., 2024; Zhao et al., 2025b; Zheng et al., 2024), and thus the effects may outweigh those of MAT, MAP and plant biomass. We found that the responses of total and fractional SOC were significantly negatively correlated with initial SOC levels (Fig. 4). This finding also confirmed the C saturation hypothesis that the accrual potential of SOC and its fractions decreases with increasing initial SOC levels under changing environmental conditions or land management practices, as less saturated SOC-poor soils have higher C sequestration capacities compared to SOC-rich soils (Georgiou et al., 2022; Huang et al., 2024).

In addition, our linear mixed models revealed significant positive correlations between MAT, MAP and the response ratio of POC, but a relatively weak relationship with the response ratio of MAOC (Fig. 5).

These findings might suggest that vegetation restoration in warmer or wetter regions of the Loess Plateau is more favorable for POC accumulation, which is in line with previous meta-analysis that reported an enhanced positive response of POC to plant inputs (cover crops) in regions with higher MAT (Wooliver and Jagadamma, 2023). The higher plant biomass and warmer and humid environments in lower latitude regions (Fig. S12; Yang et al., 2023b) could increase the incorporation of decomposed litter and roots into the soil for conversion to POC (Huang et al., 2024; Schwieger et al., 2025), thereby partially offsetting the negative effects of higher initial SOC levels on POC accumulation in the region. Although high temperature and moisture generally increase microbial decomposition of POC due to its instability (Lugato et al., 2021), the exogenous C input associated with vegetation restoration may exceed the decomposition of POC (Hu et al., 2021; Huang et al., 2024). Therefore, vegetation restoration largely moderated the divergent accrual patterns of POC and MAOC along the latitudinal gradient, with stronger decoupled accumulation patterns of POC and MAOC in the restored ecosystems at lower latitudes of the Loess Plateau (Figs. S7 and S13).

As expected, our results indicated that the response of total and fractional SOC to vegetation restoration on the Loess Plateau decreased with increasing soil depth (Fig. 3). The most pronounced C accumulation occurred in the top 20 cm, which was attributed primarily to greater litter and root inputs to the surface layer (Hicks Pries et al., 2023; Yang et al., 2023a). Previous study also showed that 56 % of the root biomass, 65 % of the POC, and 56 % of the MAOC were allocated to the top 0–60 cm profile during 160 years of vegetation restoration on the Loess Plateau (Yang et al., 2023a). Notably, the restoration effects were positive throughout the whole 400 cm profile, with significant response ratios of SOC and POC in the top 200 cm profile and those of MAOC in the top 100 cm profile (Fig. 3). Inputs of deep roots and secretions, vertical transport of shallow DOC, and microbial residue accumulation contribute to the accumulation of POC and MOAC in deep soil (Song et al., 2020; Hicks Pries et al., 2023). Although deep soil C supply might lead to deep soil C loss through priming effects (Bernal et al., 2016; Shahzad et al., 2018), deep soil C accumulation due to vegetation restoration on the Loess Plateau were greater than microbial decomposition. However, this accumulation did not change the relative proportions of POC and MAOC in SOC (Fig. S7), whereas C accumulated in deep soils may be more stable given deep soil burial and lower microbial activity (Chaopricha and Marín-Spiotta, 2014; Hicks Pries et al., 2023).

In addition, we found a significant positive correlation between the response ratios of total and fractional SOC and the time since restoration

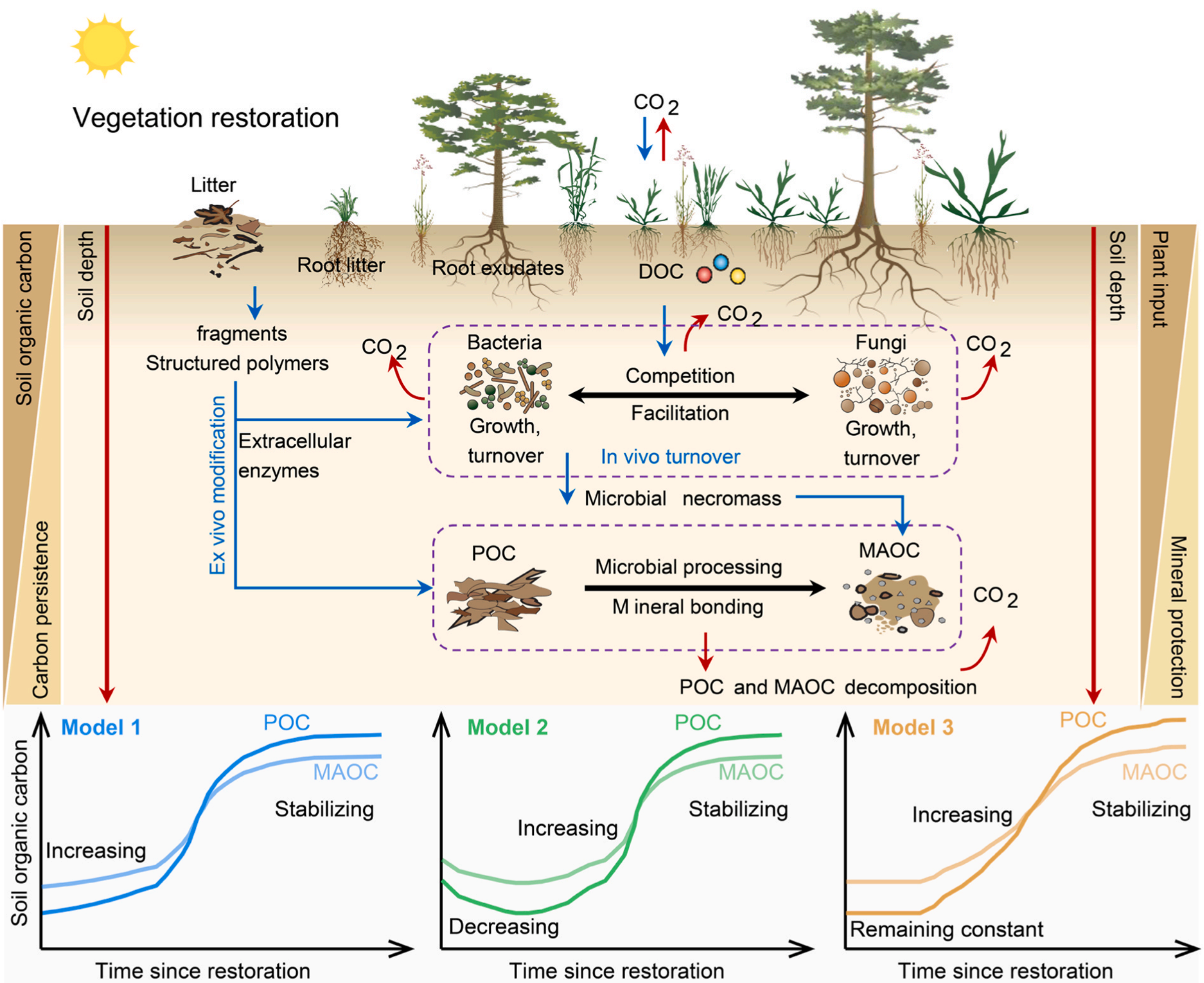

Fig. 6. Conceptual framework illustrating the response of SOC to vegetation restoration, and its dynamic patterns along the time since restoration. POC is primarily composed of relatively undecomposed light fragments of plant-derived that are free or occluded within aggregates according to the mechanistic framework for the formation of SOC fractions, while MAOC is formed by direct adsorption of depolymerized POC products (e.g., DOC) or root exudates, and by the binding of microbial necromass formed by microbial *in vivo* turnover with minerals (Bai and Cotrufo, 2022). The lower panel represents the SOC dynamics with vegetation succession on the Loess Plateau, i.e., the "increasing first and then stabilizing" (Model 1) and the "decreasing first, increasing later, and stabilizing eventually" (Model 2) (Deng and Shangguan, 2025) and the 'remaining constant first, increasing later, and stabilizing eventually' (Model 3, this study).

(Fig. 3), demonstrating progressively intensifying C sequestration benefits with increasing duration of restoration. This pattern supports the dynamic disequilibrium theory, which proposes that soils evolve toward SOC accumulation at a stable state after disturbance (e.g., land use change) and global change (e.g., climate warming) (Luo and Weng, 2011; Huang et al., 2024). With the increase in time since restoration, the gradual increase in litter and root inputs and improvement in soil quality (Liao et al., 2023; Sha et al., 2023; Su et al., 2023) could promote POC and MAOC accrual. Additionally, although the mean response ratios were negative in the short term (within the first 2.5 years post-restoration), they were not significant (Fig. 3), which may suggest that SOC accumulation due to plant C inputs was counterbalanced by microbial decomposition in the short term. This seems to be inconsistent with two recently proposed models of SOC dynamics with vegetation succession, namely, the "increasing first and then stabilizing" model (Model 1) and the "decreasing first, increasing later, and stabilizing eventually" model (Model 2) (Deng and Shangguan, 2025). Therefore, our results led us to propose a third model (Model 3) for SOC dynamics with vegetation succession on the Loess Plateau, i.e., the 'remaining constant first, increasing later, and stabilizing eventually' model (Fig. 6).

Moreover, the accrual-time relationship was logarithmic rather than linear with time since restoration (Fig. 3), indicating decelerated SOC accrual in the later restoration stages over the long term. With vegetation succession, the quality of plant C inputs gradually decreases (increasing C:N and lignin concentrations) (Prescott and Vesterdal, 2021; Liu et al., 2023), and the rate of litter decomposition progressively slows down, thereby the SOC accumulation after vegetation restoration mainly occurs within the early successional stage (Liu et al., 2023; Xu et al., 2024). Furthermore, the inputs of organic matter of low-quality (higher C:N ratios) would be favorable for the formation of POC rather than MAOC based on MEMS framework (Cotrufo et al., 2013; Angst et al., 2023). Alternatively, the current perspective suggests that the accrual of MAOC has a saturation threshold due to the limited mineral surface area for binding, whereas POC could accumulate continuously under sustained plant inputs (Lugato et al., 2021; Georgiou et al., 2022; Angst et al., 2023). Overall, the magnitude of POC accrual was consistently greater than that of MAOC with time since restoration on the Loess Plateau (Fig. 3), which ultimately contributed to a gradual increase in the proportion of POC in SOC (Fig. S7).

4.4. Limitations and implications for future research

Our study still has several limitations. Data limitations hindered accurate assessment of vegetation restoration effects. For example, approximately 89 % of the total and fractional SOC data were from the 0–100 cm soil profile in our whole dataset, with fewer records from beyond 100 cm. Moreover, the majority of studies sampled soils within 50 years after vegetation restoration, the lack of long-term observations post-restoration might limit the accurate assessment of the temporal dynamics of SOC. In addition, soil erosion contributes to SOC losses, which may lead to an underestimation of vegetation restoration effects. Despite the above limitations, our study still provides important insights into the effects of vegetation restoration on POC and MAOC on the Loess Plateau.

Depth-dependent variations in SOC remain understudied but hold substantial potential. For example, the Loess Plateau of China is the largest and deepest loess depositional area in the world, with an estimated average loess thickness of 92.2 m (Zhu et al., 2018). Our results showed that deep-rooted vegetation restoration could contribute to accumulation of total and fractional SOC across the whole 0–400 cm profile, with significant accumulation observed at least at depths of 100–200 cm (Fig. 3). Moreover, the SOC in deep soils is generally more stable and less saturated than topsoil due to inhibition by physical isolation (e.g., burial) and chemical processes (e.g., mineral binding as MAOC), and is important but often overlooked C pools (Chaopricha and Marín-Spiotta, 2014; Georgiou et al., 2022; Hicks Pries et al., 2023).

However, deep-rooted vegetation restoration on the Loess Plateau has led to excessive depletion of deep soil water, resulting in the ecological risk of "water for carbon", which limits the continued accrual of SOC and the sustainability of vegetation restoration (Jia et al., 2020; Li et al., 2021). This desiccation of deep soil moisture but enrichment of nutrients may have complex implications for POC and MAOC, which need to be further evaluated. Future studies will necessitate the development of water-budget-driven vegetation restoration frameworks that concurrently elucidate soil moisture-carbon conversion efficiency and optimize their coupling mechanisms to achieve climate-smart SOC sequestration strategies (Gao et al., 2018).

Additionally, vegetation restoration on the Loess Plateau contributed to a greater increase in POC than in MAOC, leading to an increase in the proportion of POC in SOC (Fig. 1 and S6). The POC is generally considered to be more labile than MAOC (Lavallee et al., 2020; Georgiou et al., 2024; Zhou et al., 2024) and an increase in POC:SOC ratio is accompanied by a decrease in SOC stability (Li et al., 2023b; Zhao et al., 2025a; Liu et al., 2022; Oladele and Adetunji, 2021). Moreover, our results demonstrated that changes in POC:SOC ratio were significantly and positively correlated with changes in labile SOC fractions (DOC and MBC) (Fig. S14), suggesting an increase in easily decomposable SOC fractions in restored soils (Sun et al., 2023; Su et al., 2023). Hence, the stronger accrual of POC may reduce SOC stability, which is consistent with previous studies (Zhao et al., 2025b; Li et al., 2023b; Wu et al., 2023; Liu et al., 2025). Additionally, there may be a saturation upper limit for MAOC accrual due to the limited mineral surface area for binding, whereas POC can accumulate continuously (Lugato et al., 2021; Georgiou et al., 2022; Angst et al., 2023). The appropriate management of restoration ecosystems could maintain large POC pools, such as thick litter/organic horizons, for decades to centuries (Angst et al., 2023). In addition, POC and MAOC are inter-connected, with POC serving as a direct precursor of MAOC (Angst et al., 2023; Cotrufo et al., 2022), and high proportion of POC in SOC may contribute to the formation of MAOC (Cotrufo et al., 2022; Liu et al., 2025). Therefore, increased POC not only contributes to SOC accrual but also provides a foundation for MAOC formation. Overall, future restoration studies should focus not only on SOC dynamics but also on the relative changes of POC and MAOC, including validation of characterizing SOC stability through the POC:SOC ratio. These findings will help to improve land management of restoration ecosystem and help recalibrate SOC research to be less narrowly focused on SOC, which will be key to unlocking and maintaining them as sustainable C sinks (Angst et al., 2023).

5. Conclusion

Our meta-analysis conducted a regional synthesis to examine the effects of vegetation restoration on total SOC and its two classical functional fractions, POC and MAOC, on the Loess Plateau. We found that vegetation restoration significantly increased POC more than MAOC, which led to an increase in the proportion of POC in SOC and a decrease in the proportion of MAOC in SOC. The accrual effects of POC, and MAOC were stronger for conversion to forests and shrublands than to grasslands, and for artificial restoration than for natural restoration, and for legume species than for non-legume species, respectively. Moreover, the restoration effects were spatially and temporally dependent. Spatially, the response ratios of SOC and MAOC increased significantly, whereas the response ratio of POC did not change significantly with latitude. With the increase in soil depth, the response ratio of total and fractional SOC gradually decreased, but was always positive across the whole 0–400 cm profile. Temporally, the response ratio of total and fractional SOC increased significantly with time since restoration, and the increase in POC was more pronounced than that in SOC and MAOC. Our findings highlight that partitioning and evaluating the responses of distinct SOC fractions (POC and MAOC) is potentially meaningful framework that enables a better understanding and accurate prediction of SOC dynamics, which will be key to unlocking and maintaining them as a sustainable C sink in restored ecosystems.

CRediT authorship contribution statement

Xiaorong Wei: Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Yufei Yao:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Data curation. **Jian Liu:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition. **Mingan Shao:** Writing – review & editing. **Liping Qiu:** Writing – review & editing, Supervision. **Jing Xiao:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Weibo Kong:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation.

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.2025.109856.

Data availability

The data that support the findings of this study are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.28600205.

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