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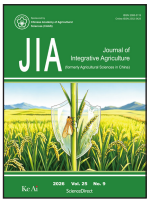

RESEARCH ARTICLE

Distinct decomposition dynamics of heterogeneous carbon components in cultivated agricultural soils controlled by flexible microbial substrate utilization strategy

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Highlights

- Plant debris dominates SOC mineralization, and microbial necromass controls stability.
- A shift from bacteria to fungi drives carbohydrates-to-lignin decomposition in C-rich soil.
- Actinomycetes dominate lignin and carbohydrates co-metabolism in C-starved habitats.
- Flexible substrate utilization strategy regulates the decomposition of heterogeneous SOC components.

Abstract

Improving soil organic matter (SOM) maintenance is crucial for terrestrial carbon (C) sequestration and ecosystem functioning. Conservation tillage favors SOM pool buildup; however, it remains unclear how the decomposition of heterogeneous components is manipulated by microbial substrate utilization strategy from the view of SOM stability. Here, a one-year microcosm incubation was conducted using surface soils developed under 12 years of conservation tillage (high-C soil) and maize residue removal (low-C soil). Temporal changes in lignin phenols, neutral sugars, and amino sugars in the soil were monitored along with microbial phospholipid fatty acids (PLFAs) and enzyme activities. Throughout incubation, lignin phenols declined more (20.8–26.3%) than the SOM (12.3–14.5%) and amino sugars (10.6–12.3%), highlighting the key role of plant debris in SOM mineralization, and complementarily, the greater contribution of microbial necromass to SOM stabilization. Moreover, the decomposition dynamics of neutral sugars and lignin were strongly influenced by C availability. In the low-C soil, these two types of compounds decomposed with similar temporal patterns and extents, and such substrate co-metabolism was dominantly mediated by actinomycetes. In contrast, in the high-C soil, a lower oxidases-to-carbohydrolases ratio regulated the sequential decomposition of labile neutral sugars followed by recalcitrant lignin. Such microbial substrate selectivity was associated with a shift in microbial community from bacterial dominance toward increased fungal contribution. Overall, our findings underscore the significant interplay between soil C availability and flexible microbial substrate utilization strategy in regulating decomposition of heterogeneous SOM components, as well as their distinct contributions in SOM turnover and stabilization.

Keywords: SOM decomposition, microbial necromass, lignin phenols, carbohydrates, microbial community, microbial substrate utilization strategy

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1. Introduction

Improving the accumulation and stabilization of soil organic matter (SOM) is crucial for sustaining soil functioning and enhancing agricultural ecosystems as carbon (C) sinks. However, the mechanisms controlling SOM turnover are still actively debated (Cotrufo *et al.* 2015; Lehmann *et al.* 2020), especially considering that SOM encompasses various components with distinct intrinsic biochemical properties and residence times from days to millennia (Trumbore 2000). The decomposition process of heterogeneous constituents could profoundly affect the preservation of SOM (Schmidt *et al.* 2011), and microbiota, as executors driving SOM turnover, play a pivotal role in the decomposition of various substrates in response to changing habitats (Schimel and Schaeffer 2012; Cotrufo *et al.* 2013; Jansson and Hofmockel 2018). Nevertheless, it remains unclear how microbial substrate utilization strategy regulates the coupled decomposition of distinct SOM components under varying C availabilities.

Plant inputs serve as the primary C source for SOM formation, through both microbial degradation and physical translocation pathways (Köegel-Knabner 2017). In the soil continuum model (SCM), SOM is termed as a mixture composed of plant-derived components and microbial products at different decay stages (Lehmann and Kleber 2015). Neutral sugars, originally derived from cellulose and hemicellulose in vascular plant debris (Kleber *et al.* 2007), constitute a readily available C source for microbial growth (Martens and Loeffelmann 2002; Gunina and Kuzyakov 2015). In contrast, lignin, with its complex aromatic structure (Martin *et al.* 1980; Martens 2000; Thevenot *et al.* 2010), could persist in soil as part of plant debris (Melillo *et al.* 1982), although specific microorganisms can depolymerize lignin and utilize its monomers as C and energy sources (Hall *et al.* 2020; Duran *et al.* 2024). Along with the decomposition of plant-derived components, microbial necromass, e.g., fungal chitin and bacterial peptidoglycan in cell walls, accumulates in soil as the byproducts of microbial growth and metabolism, contributing significantly to SOM stabilization (Zhang *et al.* 1999; Liang *et al.* 2017; Wang *et al.* 2020). Therefore, heterogeneous components within the SCM, regardless of plant and microbial origin, could be involved in soil organic carbon (SOC) turnover; whereas, how the distinct decomposition dynamics of these components are driven by functional microorganisms in different habitats warrants further exploration.

Microbial substrate utilization strategy varies with resource availability and determines the transformation of heterogeneous SOM components (McNichol *et al.* 2024). In soils with limited C availability, microbes may be compelled to allocate more C towards energy production to degrade biochemically resistant substrates, consequently reducing biomass accumulation (Malik *et al.* 2019). Comparatively, in C-rich environments, microorganisms tend to adopt energy-efficient metabolic strategy, preferentially utilizing labile substrates and maintaining a functionally optimal community structure (Gunina and Kuzyakov 2015; Huang *et al.* 2021). Such differentiation in resource utilization is closely linked to microbial community composition and metabolic potential, as certain microbial groups produce specialized enzyme systems tailored to degrade specific organic substrates (Wang *et al.* 2022). Bacteria generally prefer simple substrates (Brouns *et al.* 2016), whereas fungi, known for their lower metabolic nutrient requirements and a broader range of extracellular enzymes, are capable of decomposing recalcitrant biopolymers (de Boer *et al.* 2005). It has been recognized that microbial communities could dynamically reshape their metabolic strategy in response to altered substrate availability (Cao *et al.* 2024). However, how this flexible microbial substrate utilization strategy interacts with the distinct decomposition of heterogeneous SOM components remains poorly understood.

Intensive farmland use and the lack of organic inputs have caused severe soil degradation, particularly in the black soil region of Northeast China. In recent decades, conservation tillage has been implemented in maize cropping systems to restore degraded soil and improve SOC pool capacity (Teng *et al.* 2024). However, the resistance of the accumulated SOM to decomposition under improved C availability remains poorly understood. Therefore, by analyzing changes in SOC and its heterogeneous components during a microcosm incubation, combined with soil enzyme activities and microbial community composition assays, we aim to elucidate the roles of both plant- and microbial-derived components in controlling SOC decomposition processes, and the mediation of functional microorganisms across soils of different C levels. Our hypotheses are: (1) Microbial substrate utilization strategy is regulated by C availability, with plant-derived components being preferentially decomposed over microbial necromass; (2) under C limitation, lignin decomposition depends on co-metabolism with carbohydrates, mainly performed by generalists; whereas in soils that have undergone long-term maize residue return, divergent substrates follow a sequential decomposition pattern over time, driven by a functional group shift from bacterial to fungal dominance. This research provides foundational insights into how organic inputs influence SOC dynamics and microbial strategy, contributing to sustainable soil management in agroecosystems.

2. Materials and methods

2.1. Soil description and sampling

Soil samples for the microcosm incubation were collected from a long-term conservation tillage experimental field established in 2007, located in Lishu County, Jilin Province, China (43°19′N, 124°14′E). The region experiences a temperate semi-humid continental monsoon climate, with an annual mean precipitation of 614 mm and a mean annual temperature of 6.9°C. The soils are clay loams classified as Mollisols according to USDA Soil Taxonomy (Soil Survey Staff 2022). The experimental site has been under a long-term continuous maize (*Zea mays* L.) cropping system. Two treatments were included in this study: no-tillage without maize straw return (NT0), and no-tillage with 100% maize straw mulching (NT100) for 12 years. The annual maize straw return rate was equivalent to 7.5 t ha^{-1} yr^{-1}. The pH values of the soil samples from the NT0 and NT100 treatments were 6.82 and 6.86, respectively.

Soil samples from the 0–5 cm layer were collected for microcosm incubation, owing to its sensitivity to changes in agricultural management practices. Before sampling, surface litter and the organic layer were removed. Samples for each treatment were collected using the "S" sampling scheme, each comprising a composite of five soil cores. In the laboratory, visible root material was manually removed, and the fresh samples were passed through a 2-mm sieve. The homogenized samples were stored at 4°C for approximately one week before incubation. Soils sampled from the NT0 and NT100 treatments were designated as low-C and high-C soils, respectively.

2.2. Microcosm incubation of SOM decomposition

Soil samples (100 g) from each treatment were incubated in individual culture bottles, each with a soil depth of about 1.5 cm. Fertilizer was added once at the beginning of the experiment at rates consistent with field practices, corresponding to 240 kg N ha^{-1}, 110 kg P_2O_5 ha^{-1}, and 110 kg K_2O ha^{-1}. During the incubation, only sterilized water was added periodically to maintain soil moisture at 60% of the maximum water-holding capacity. Each culture bottle was covered with a perforated membrane to minimize moisture loss while allowing gas exchange. Soil incubation was conducted at 25°C in a light-shielded incubator, with three replicates per treatment sampled destructively at each time point (days 0, 7, 30, 60, 90, 120, 180, 240, and 360). Each collected soil sample was divided into four portions for analysis: (1) a fresh portion for dissolved organic carbon (DOC) analysis; (2) an air-dried portion for the analyses of SOC, amino sugar, lignin phenols, and neutral sugar; (3) a freeze-dried portion for phospholipid fatty acid (PLFA) analysis; and (4) the remaining portion was stored at –20°C for enzyme activity measurements.

2.3. Soil analyses

SOC and DOC analyses The SOC content was measured using an elemental analyzer (Elemental Analyzer System GmbH, Germany). DOC was extracted from 6 g of fresh soil using K_2SO_4 (1:5, w/v) through shaking, followed by centrifugation. The supernatant was then filtered through a 0.45 μm membrane, and the DOC concentration was determined using a TOC analyzer (Multi N/C 3100, Analytik Jena, Germany).

Soil amino sugar analysis Soil amino sugars concentrations were determined following Zhang and Amelung (1996). Soil samples (containing ca. 4 mg N) were hydrolyzed with 6 mol L^{-1} HCl, with inositol as an internal standard. After filtration, pH adjustment to remove impurities, and centrifugation, the supernatant was concentrated by rotary evaporation, and then extracted with methanol. The purified amino sugars were derivatized with hydroxylamine hydrochloride and 4-(dimethylamino) pyridine to form aldonitrile derivatives, followed by extraction with dichloromethane. Quantification was performed by gas chromatography (GC-7890B, Agilent, USA) equipped with a flame ionization detector (FID). Total amino sugars were calculated as the sum of glucosamine (GluN), muramic acid (MurN), and galactosamine (GalN), with the GluN/MurN ratio representing the relative contribution of fungal versus bacterial residues.

Soil lignin analysis Lignin phenols were quantified using the alkaline CuO oxidation method (Hedges and Ertel 1982). Soil samples (containing ca. 5 mg C) were mixed with CuO, glucose, ammonium iron (II) sulfate, and 2 mol L^{-1} NaOH, and digested under magnetic stirring. After centrifugation, the supernatant was acidified and kept in the dark to precipitate humic acids. Lignin phenols were then extracted using C_{18} solid-phase columns (Agilent Technologies Co., Ltd., USA) (Köegel-Knabner and Bochter 1985), derivatized with N,O-bis(trimethylsilyl)trifluoroacetamide (BSTFA), and quantified by gas chromatography (HP 6890A, Agilent, USA). Lignin concentration was calculated as the total of eight diagnostic phenols: vanillyl and syringaldehyde (aldehydes); vanillic acid, syringic acid, p-coumaric acid, and ferulic acid (acids); and acetovanillone and acetosyringone (ketones) (Köegel-Knabner 1986). Despite its limited specificity due to possible interference from non-lignin phenolic compounds (e.g., tannins and microbial polyphenols), the CuO oxidation method remains a key technique for measuring plant-derived biomarkers.

Soil neutral sugar analysis The extraction of soil neutral sugars was conducted as described by Zhang *et al.* (2007). Soil samples (containing ca. 4 mg C) were hydrolyzed with 4 mol L^{-1} trifluoroacetic acid (TFA). After adding the internal standard (inositol), the hydrolysates were filtered and centrifuged. The supernatant was concentrated by rotary evaporation and then freeze-dried. The purified neutral sugars were derivatized with hydroxylamine hydrochloride and 4-(dimethylamino) pyridine, followed by dichloromethane extraction. Quantification was performed using gas chromatography (HP 6890, Agilent, USA) equipped with a flame ionization detector (FID). Total neutral sugar concentration was calculated as the sum of eight monosaccharides: glucose, galactose, mannose, arabinose, xylose, ribose, rhamnose, and fucose. The hexose-to-pentose (GM/AX) ratio, where GM refers to the sum of galactose and mannose and AX refers to the sum of arabinose and xylose (Chantigny *et al.* 2000; Gunina and Kuzyakov 2015), reflects the extent to which microorganisms process plant-derived carbohydrates in soil (Oades 1984; Schmidt *et al.* 2015).

Soil PLFA extraction and analysis Soil microbial biomass and community composition were assessed using PLFA analysis, following Bossio *et al.* (1998). Phospholipids were extracted from 4 g of freeze-dried soil using a chloroform/methanol/phosphate buffer mixture (1:2:0.8), and isolated *via* solid-phase extraction. The phospholipids were then transesterified into fatty acid methyl esters and analyzed using gas chromatography (Agilent 7890B, USA) with MIDI peak identification software (version 4.5). Quantification was based on an internal standard (19:0), and total microbial biomass was calculated as the sum of all identifiable PLFA peaks (relative abundance>0.5%). Microbial functional groups were identified using diagnostic PLFAs (Willers *et al.* 2015; Joergensen 2022): the bacterial PLFAs included i13:0, a13:0, i14:0, i15:0, a15:0, i15:1ω6c, i16:0, i17:0, a17:0, i18:0, 14:1ω5c, 16:1ω7c, 16:1ω9c, 17:0 cyclo ω7c,

17:1ω8c, 18:1ω5, 19:0 cyclo ω7c, 20:1ω9c, and 22:1ω9c; the fungal PLFAs included 18:2ω6c, 18:2ω9c, and 16:1ω5c; and the actinomycete PLFAs included 10Me16:0, 10Me17:0, and 10Me18:0. The relative abundance of each group was expressed as the percentage of total PLFAs.

Soil extracellular enzyme activity determination The activities of two carbohydrolases, β-glucosidase (BG) and cellobiohydrolase (CB), two N-acquiring hydrolases, leucine aminopeptidase (LAP) and N-acetylglucosaminidase, and two oxidases, polyphenol oxidase (PPO) and peroxidase (PER), were measured following German *et al.* (2011). Briefly, soil samples (1.5 g) were suspended in 125 mL of 50 m mol L^{-1} sodium acetate buffer and homogenized. A 200 μL aliquot of the suspension was transferred to 96-well microplates in triplicate. For the carbohydrolases and N-acquiring hydrolases assays, 50 μL of 200 mmol L^{-1} substrate solution was added. Substrate controls, blanks, quenching controls, and fluorescence standards were included. After 5 h of incubation at 20°C, fluorescence was measured at 365 nm excitation and 450 nm emission. For the oxidases assays, 200 μL of suspension and 50 μL of 25 mmol L^{-1} dihydroxyphenylalanine (DOPA) were added to the reaction wells. Negative controls consisted of acetate buffer and L-DOPA. For the PER assay, 10 μL of 0.3% H_2O_2 was introduced into both the negative and blank wells. Absorbance was measured at 460 nm after 24 h of incubation at 20°C. The oxidases/carbohydrolases ratio, calculated as the sum of PPO and PER activities divided by the sum of BG and CB activities, indicates microbial investment in labile C acquisition, with lower values reflecting greater investment.

2.4. Statistical analyses

Empirical model fitting A double exponential equation was used to describe the SOM decomposition processes mathematically (Strukelj *et al.* 2018). The equation is:

$$Y_{(t)}=M_1e^{-k_1t}+M_2e^{-k_2t} \quad (1)$$

where $Y_{(t)}$ represents the SOC content at time t (d), M_1 is the size of the SOC pool decomposed at a rapid decomposition rate k_1 (d^{-1}), and M_2 is the size of the SOC pool decomposed at a slower decomposition rate k_2 (d^{-1}). The sum of M_1 and M_2 represents the total initial SOC content in the soil sample.

Decomposition rates of SOC and heterogeneous components The decomposition rate was defined as the reduction percentage (%) in SOC and the heterogeneous components during the entire incubation stage, as well as during the early and later stages, as determined by the empirical model. The formula is as follows:

$$\text{Reduction percentage (\%)}=\frac{C_0-C_1}{C_0}\times 100 \quad (2)$$

where C_0 is the content at the start of the stage, and C_1 is the content at the end of the corresponding stage (early, later, or the entire stage).

Statistical analyses Data normality was tested using the Shapiro-Wilk test, and the homogeneity of variances was assessed with Levene's test to meet the assumptions of parametric tests. A two-way repeated measures ANOVA was conducted to assess the individual and interactive effects of soil C level (treatment) and incubation time (time) on SOC, DOC, organic C components, and microbial community dynamics, followed by Tukey's HSD test for post hoc comparisons. One-way ANOVA with Tukey's test was performed to detect significant differences in the decomposition rates of SOC and its components within the same stage. Independent-sample *t*-tests were applied to compare SOC and component concentrations between the low-C and high-C soils. All statistical analyses were conducted using R (version 4.4.3), with statistical significance set at $P<0.05$.

Given the strong interplay between soil C availability and microbial substrate utilization strategy, partial least squares structural equation modeling (PLS-SEM) was employed to further elucidate the potential regulatory effect of microbial community structure and enzyme activity on neutral sugar and lignin decomposition under varying C availabilities. BG and CB were used to represent potential carbohydrolases activity, LAP and NAG as N-acquiring hydrolases activity, and PPO and PER as oxidases activity. The model fit was assessed using goodness-of-fit (GOF) statistics, and path coefficients along with explained variance (R^2) were estimated and validated through 5,000 bootstrap resampling using Smart PLS software.

3. Results

3.1. Temporal changes in SOC and DOC during the incubation

Maize straw mulching for 12 years significantly increased the SOC content to 21.2 g kg^{-1} compared to aboveground residue removal (17.4 g kg^{-1}) (Fig. 1-A). SOC decomposition in both soils followed a double-exponential model: a rapid decomposition stage during the first 90 days (early stage), followed by a slower decomposition from 90 to 360 days (later stage). After one-year incubation, SOC declined by 2.6 g kg^{-1} in the high-C soil and 2.5 g kg^{-1} in the low-C soil. The reduction percentage was significantly lower in high-C soil (12.3%) than low-C soil (14.5%) ($P<0.05$).

The DOC remained consistently higher in the high-C soil throughout the incubation (Fig. 1-B). The DOC decrease was 53.5 mg kg^{-1} in the high-C soil and 32.6 mg kg^{-1} in the low-C soil, with a larger reduction percentage in the high-C soil (23.4% *vs*. 20.8%), particularly during the early stage (19.6% *vs*. 13.4%).

3.2. Decomposition dynamics of SOM components

Throughout the incubation, lignin phenols declined by 20.8–26.3% (Fig. 2-B), and neutral sugars by 26.7–35.1% (Fig. 2-C). These reductions exceeded those observed in SOC ($P<0.05$; Fig. 3-C), but the decomposition dynamics of these components were significantly different between the two soils (Fig. 2-B and C).

In the low-C soil, neutral sugars and lignin phenols decreased by 26.7 and 26.3%, respectively, over the incubation (Fig. 3-C), with no significant differences in their reduction percentages during either the early or later stages (Fig. 3-A and B). In contrast, in the high-C soil, neutral sugars decreased more (35.1%) than lignin phenols (20.8%) (Fig. 3-C), primarily due to a higher reduction in the early

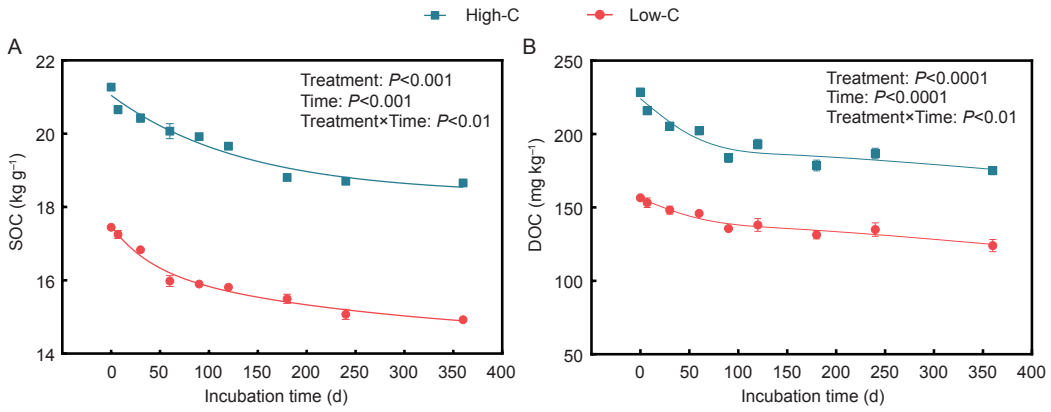

Fig. 1 Temporal changes in soil organic carbon (SOC) content (A) and dissolved organic carbon (DOC) content (B) during incubation in soils developed under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C). Error bars are SE (n=3). A double-exponential model was fitted to the SOC content (Y, g kg^{-1}) over time for both low-C and high-C soils. For the low-C soil: Y_l=10.63e$^{-0.01829t}$+6.83e$^{-0.0003396t}$ (R^2=0.96); for the high-C soil: Y_h=2.67e$^{-0.008071t}$+18.34e$^{-0.008057t}$ (R^2=0.93).

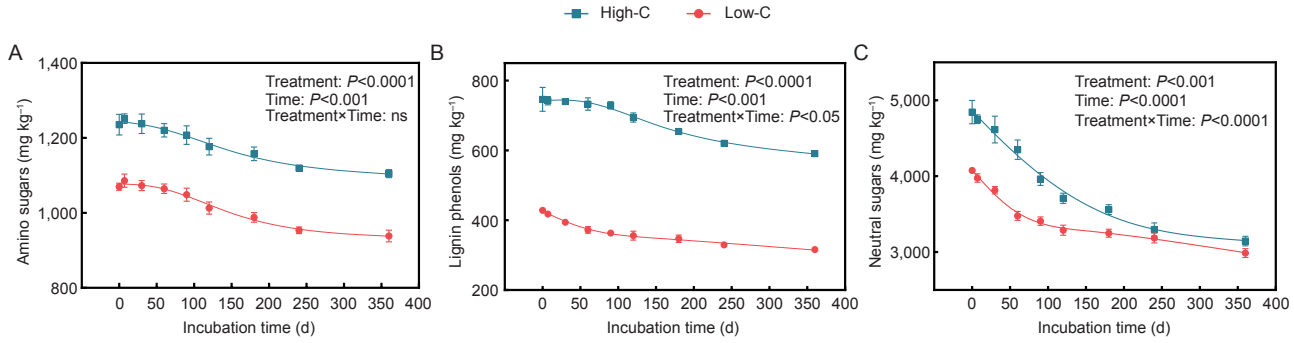

Fig. 2 Temporal changes in the concentrations of amino sugars (A), lignin phenols (B), and neutral sugars (C) during incubation in soils developed under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C). Error bars are SE (n=3).

stage (18.2% *vs*. 2.3%) (P<0.05; Fig. 3-A). In the later stage, the reductions in neutral sugars (20.7%) and lignin phenols (18.9%) were not significantly different (Fig. 3-B). In both soils, the GM/AX ratio of neutral sugars increased during the early stage and remained stable after 90 days (Fig. 4-A).

Although the absolute decline was larger in the high-C soil, the reduction percentage of amino sugars was significantly lower than in the low-C soil (10.6% *vs*. 12.3%) (Figs. 2-A and 3-C). The amino sugar reduction was lower than that of SOC, lignin phenols and neutral sugars (P<0.05; Fig. 3-C). The GluN/MurN ratio increased nonlinearly over time in both soils and was constantly higher in the high-C soil (Fig. 4-B).

By the end of incubation, the relative proportions of the heterogeneous components in SOC changed significantly (Fig. 3-C). In the low-C soil, the proportion of amino sugars in SOC increased by 2.6%, while those of lignin phenols and neutral sugars decreased by 13.9 and 14.3%, respectively. In the high-C soil, the proportion of amino sugars increased by 2.0%, with lignin phenols and neutral sugars declining by 9.3 and 25.8%, respectively.

3.3. Changes in PLFAs during the incubation

Total and individual PLFAs in soil declined over time (Fig. 5-A–D), but the relative abundances of the origin-specific PLFAs showed distinct temporal patterns (Fig. 5-E–G). Bacterial and fungal PLFAs remained consistently higher in the high-C soil (P<0.05; Fig. 5-E and F), whereas the actinomycete PLFA level was greater in low-C soil (P<0.05; Fig. 5-G). Bacterial PLFAs declined more rapidly in low-C soil (5.14%) than in high-C soil (4.65%) (P<0.05; Fig. 5-E). Fungal PLFAs increased until around 90–120 days and then decreased continuously (Fig. 5-F). Consequently, the fungi-to-bacteria PLFAs (F/B) ratio increased, peaking between 90 and 120 days (Fig. 5-H), with a greater increase in high-C soil (14.5%) compared to low-C soil (8.7%). Actinomycete PLFAs increased significantly throughout the incubation in both soils (P<0.05; Fig. 5-G).

3.4. Changes in enzyme activities during the incubation

During the incubation, carbohydrolases activity consistently exceeded oxidases activity in the high-C soil, whereas the opposite pattern occurred in the low-C soil (P<0.05; Fig. 6-A and B). Accordingly, the oxidases/carbohydrolases ratio was significantly lower in the high-C soil, particularly during the early stage (Fig. 6-C), and changed slowly during the later stage in both soils.

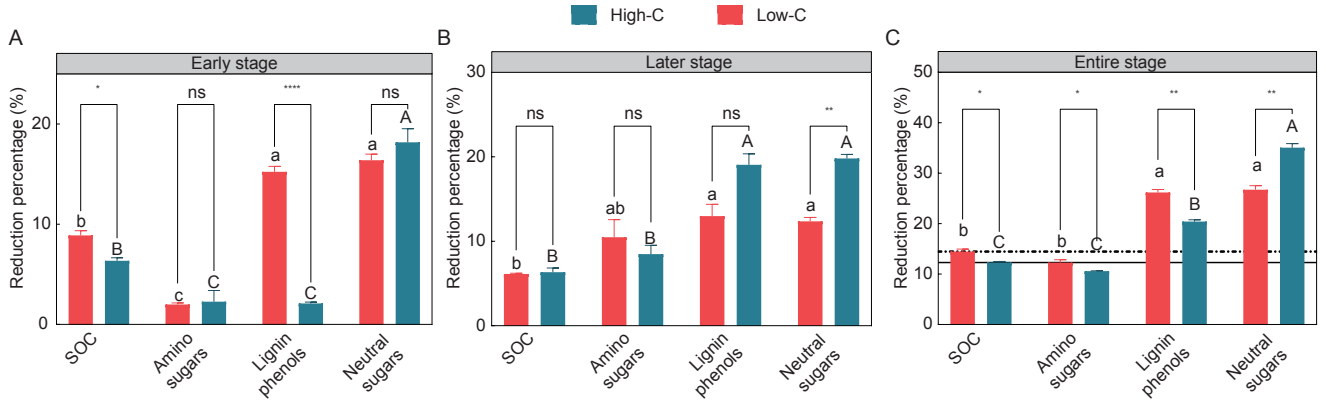

Fig. 3 Reduction percentages of soil organic carbon (SOC) and its components during incubation in soils developed under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C) during the early stage (0–90 days) (A), later stage (90–360 days) (B), and entire incubation period (0–360 days) (C), based on fitted double-exponential models. Asterisks (*) indicate significant differences between high-C and low-C soils for the same variable. Error bars are SE (n=3). Uppercase letters denote significant differences among variables in low-C soil, while lowercase letters indicate differences in high-C soil. Statistical significance is indicated as follows: ns, P>0.05; *, P<0.05; **, P<0.01; ***, P<0.001; ****, P<0.0001. In Fig. 3-C, the dashed black line represents the reduction percentage of SOC in low-C soil, while the solid black line represents the reduction percentage in high-C soil.

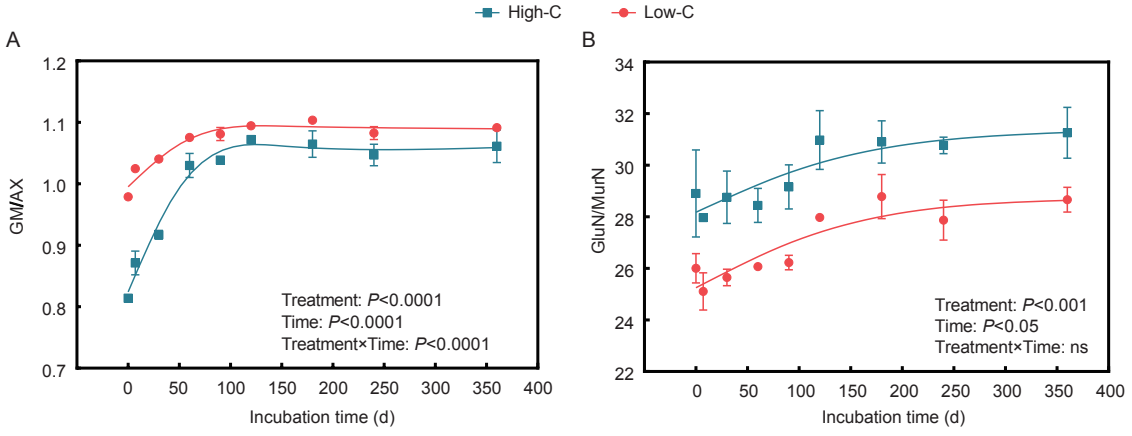

Fig. 4 Temporal changes in the ratio of hexose to pentose sugars (GM/AX) (A) and the ratio of glucosamine to muramic acid (GluN/MurN) (B) during incubation in soils under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C). Error bars are SE (n=3). Hexose is the sum of mannose and galactose, while pentose is the sum of arabinose and xylose.

3.5. PLS-SEM analysis

The PLS-SEM analysis revealed the pathways through which microbial community structure and enzyme activity regulated the dynamics of heterogeneous SOM components, which further influenced the SOC in soils with different C levels (Fig. 7-A–C). Separate PLS-SEM models were developed for the early and later decomposition stages of the high-C soil, and for the entire incubation stage in the low-C soil. In the high-C soil, during the early stage (Fig. 7-A), neutral sugars were significantly positively correlated with SOC, while the F/B ratio positively influenced carbohydrolases activity, which was negatively correlated with neutral sugars. In the later stage (Fig. 7-B), lignin phenols were positively correlated with SOC, and actinomycetes were negatively associated with neutral sugars. Additionally, neutral sugars were positively correlated with lignin phenols. In the low-C soil (Fig. 7-C), both lignin phenols and neutral sugars were positively correlated with SOC. Actinomycetes positively influenced the activities of carbohydrolases, oxidases, and N-acquiring hydrolases and showed a negative correlation with neutral sugars. Meanwhile, neutral sugars showed a significant positive correlation with lignin phenols.

4. Discussion

4.1. Divergent function of plant debris and microbial necromass in controlling the SOM decomposition process

During the decomposition of SOC in the incubation microcosm, the temporal declines in neutral sugars, lignin phenols, and amino sugars indicated the involvement of heterogeneous components in SOC mineralization (Fig. 2). However, their decomposition varied and differed from that of the total SOC (Fig. 3-C), inferring compound-specific transformation and multidimensional control on SOC turnover.

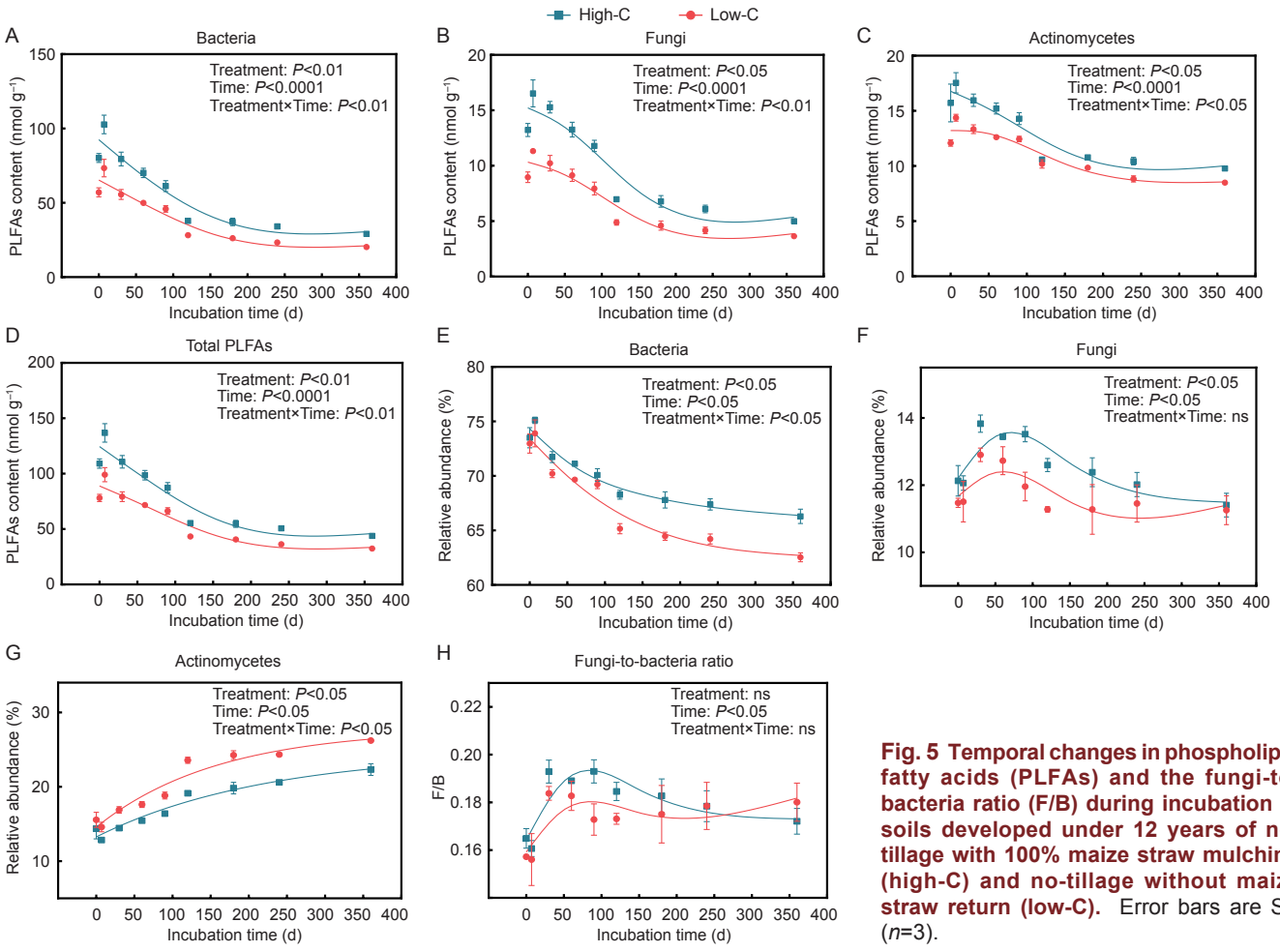

Fig. 5 Temporal changes in phospholipid fatty acids (PLFAs) and the fungi-to-bacteria ratio (F/B) during incubation in soils developed under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C). Error bars are SE (n=3).

Specifically, the decomposition rates of lignin phenols and neutral sugars were higher than those of SOC and amino sugars throughout the one-year incubation (Fig. 3-C), implying that plant-derived component degradation was dominantly responsible for SOC mineralization. Consistent with our finding, Barre *et al.* (2018) observed that lignin decomposed at a higher rate than microbial-derived compounds in soils with bare fallow for over 50 years, despite slow decomposition of certain plant-derived long-chain alkanes. On the contrary, Bahri *et al.* (2008) reckoned that lignin was relatively decomposition-resistant, as only a small portion (ca. 7%) of added lignin C was mineralized over a 44-week incubation. However, it was ignored in their study that the mineralization rate of the SOC was significantly lower (less than 2%) than that of lignin over the same duration. By re-comparing the decomposition degree between lignin and SOC, we highlighted that the plant-derived components, even with inherent chemical recalcitrance, can serve as C source for microbial metabolism, thereby driving soil humification and SOM stabilization. Therefore, plant debris in soil remained more active decomposition readiness than previously assumed. In addition, the degree of lignin decomposition reported by Bahri *et al.* (2008) was markedly lower than our results (7% after 44 weeks *vs*. 20–26% after 52 weeks of incubation), which was likely attributed to the absence of exogenous N addition in their incubation, as N deficiency could constrain the initial lignin decomposition (Huang *et al.* 2023).

Opposite to the active decomposition of lignin phenols, amino sugars declined more slowly than both lignin and SOC (Fig. 3-C), explicitly indicating the dominant role of microbial necromass in controlling SOC maintenance (Liang *et al.* 2017). Consequently, the contribution of plant lignin to SOC pool persistence decreased, while that of microbial necromass increased (Fig. 3-C), suggesting that the functional complementarity of microbial necromass and plant debris could coordinately manipulate SOC turnover and stabilization (Li *et al.* 2023). The selective retention of microbial necromass during SOC mineralization was likely associated with its stable chemical signature, i.e., the decomposition-resistance of peptidoglycan polymers in Gram-positive bacteria and chitin in fungal cell walls (Köegel-Knabner *et al.* 2008; Paul 2016). Particularly, the melanin in fungal cell walls, a relatively recalcitrant organic compound (Köegel-Knabner 2002), could furthermore explain the enhanced recalcitrance of fungal necromass than bacterial counterpart (Fig. 4-B). Furthermore, as N-containing compounds, microbial necromass interacts more intensively with minerals than plant debris, further reducing its accessibility to soil microorganisms (Grandy and Neff 2008; Kopittke *et al.* 2018). With the prolonged incubation, the temporal increase in the GM/AX ratio indicated enhanced microbial assimilation of carbohydrates for proliferation, and accordingly microbial necromass production (Fig. 4-A).

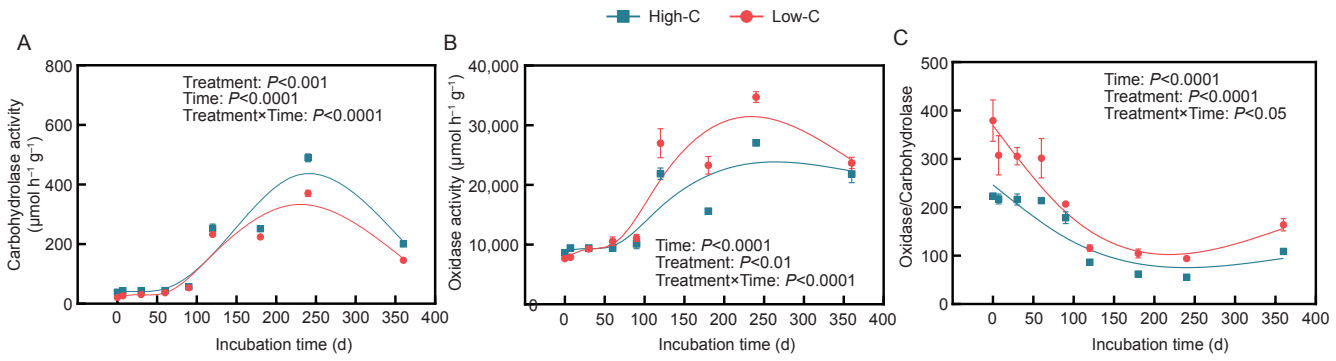

Fig. 6 Temporal changes in extracellular enzyme activities during incubation in soils developed under 12 years of no-tillage with 100% maize straw mulching (high-C) and no-tillage without maize straw return (low-C). Error bars are SE (n=3).

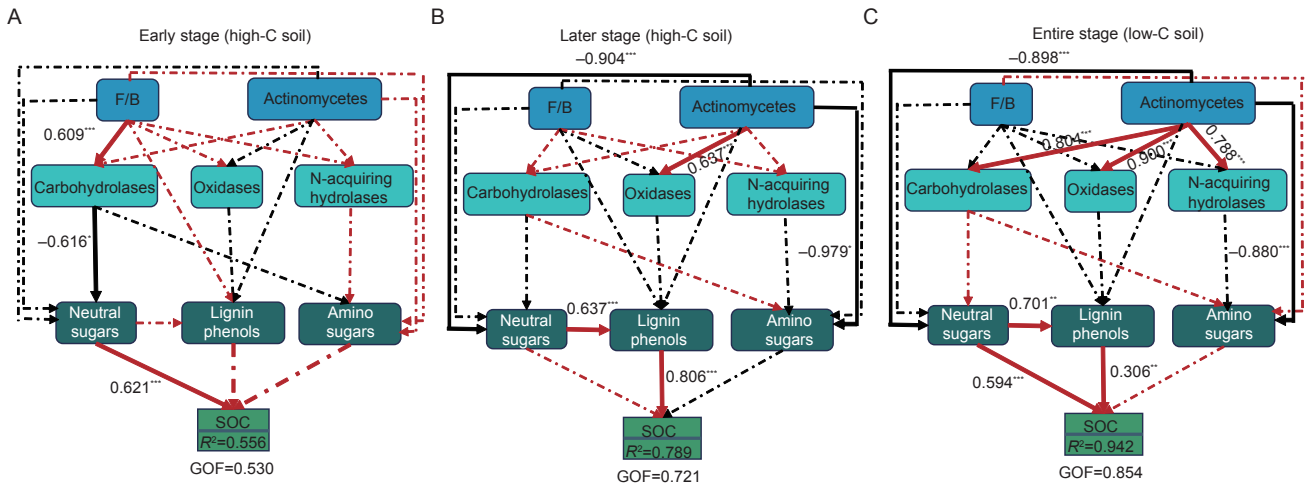

Fig. 7 Partial least squares structural equation models (PLS-SEM) illustrating how the fungi-to-bacteria ratio (F/B), actinomycetes abundance, and extracellular enzyme activities (carbohydrolases, oxidases and N-acquiring hydrolases) influence the retention of heterogeneous carbon components (amino sugars, neutral sugars and lignin phenols) in soils, thereby affecting soil organic carbon (SOC) content. Early stage (0–90 days) in soil developed under 12 years of no-tillage with 100% maize straw mulching (high-C) (A); later stage (90–360 days) in soil developed under 12 years of no-tillage with 100% maize straw mulching (high-C) (B); entire stage (0–360 days) in soil developed under 12 years of no-tillage without maize straw return (low-C) (C). Positive and negative path coefficients are shown in red and black, respectively, with nonsignificant paths in dashed lines. Statistical significance is indicated as follows: *, P<0.05; **, P<0.01; ***, P<0.001.

Therefore, in addition to the inherent decomposition resistance of microbial necromass, the re-synthesis of microbial cell walls during their proliferation could partially compensate the decomposed portion, further increasing the contribution of microbial necromass to SOC stabilization.

4.2. Flexible microbial substrate utilization strategy controlled distinct decomposition of heterogeneous SOM components

In our research, a decade of maize straw mulching favored SOC accumulation, corroborating the well-established view that conservation tillage practices promote C sequestration in agricultural ecosystems (Ma *et al*. 2025), thereby helping to mitigate the rise in atmospheric CO_2 (Liu *et al*. 2023). Although the accumulated SOC exhibited greater mineralization in the high-C soil than in the low-C soil (Fig. 1-A), its lower decomposition rate indicates that long-term maize residue return simultaneously enhanced SOC stability and increased SOC storage capacity (Fig. 3-C). In both incubated soils, the decomposition dynamics of microbial necromass changed simultaneously with that of SOC mineralization, i.e., a lower decomposition of amino sugars corresponded to lower SOC loss in the high-C soil and *vice versa* in the low-C soil (Fig. 3-C). This inferred a consistent role of microbial necromass retention in SOC stabilization across soils with varying C levels, linking microbial necromass resistance with SOC stabilization.

Comparatively, the decomposition of neutral sugars and lignin phenols in soil, both originally derived from plant inputs, depended strongly on C availability (Fig. 2-B and C), highlighting their distinct susceptibility involved in microbial decomposition of SOM. In the high-C soil, neutral sugars decomposed faster than lignin phenols (Fig. 3-C), indicating that microorganisms preferentially utilized labile carbohydrates with the improved substrate availability. However, this “sequential decomposition” pattern did not

occur in low-C soil, where lignin phenols and neutral sugars decomposed at comparable rates (Fig. 3-C), implying co-metabolism of the labile and recalcitrant components, i.e., carbohydrates could act as available C source to facilitate lignin decomposition (Kuzyakov *et al.* 2000; Schimel and Weintraub 2003). Similarly, in the later stage of incubation in the high-C soil, the decomposition rates of lignin phenols and neutral sugars converged (Fig. 3-B), confirming the weakened microbial substrate selectivity with the decline of C availability. Therefore, microbial survival strategy may play a more prominent role in controlling the transformation of SOM components than the distinct chemical signatures of plant-derived components (Fig. 8). Carbon-starvation in the low-C soil forced microbial communities less choosy about food, with all available components could be exploited to meet nutritional demands, irrespective of the metabolic costs involved (Kopittke *et al.* 2018; Gunina and Kuzyakov 2022). Yang *et al.* (2022) supported our findings by revealing that soils with low organic matter had a limited capacity to stabilize lignin, accompanied by significant losses of easily degradable unsaturated fatty acids. In contrast, increased C availability enhanced microbial selectivity for labile substrates, minimizing energy expenditure and maximizing metabolic efficiency, as carbohydrates degradation typically yields more energy relative to the investment required (Gunina and Kuzyakov 2022). This microbial "choosiness" under improved C availability was consistent with the "C source suppression effect", wherein microorganisms preferentially consumed simple C sources, limiting the utilization of complex substrates (Monod 1949).

Microbial group composition further modulated these substrate utilization patterns. Actinomycetes, consistent with their oligotrophic characteristics (Liu *et al.* 2018), were more abundant in low-C soil and increased temporally with the decomposition of both lignin and neutral sugars (Figs. 5-G and 7-C). As generalists, actinomycetes are equipped with a comprehensive array of extracellular enzymes, enabling efficient degradation of diverse, complex substrates (Bao *et al.* 2021; Chen *et al.* 2021), especially exploiting their competitive advantage in utilizing recalcitrant substrates when labile C was depleted (Louca *et al.* 2018). In contrast, both bacteria and fungi were more abundant in high-C soil (Fig. 5-E and F), indicating that these microbial groups occupied overlapping ecological niches, enabling their co-adaptation to C-enriched environments (López-Mondéjar *et al.* 2020). The rapid initial decomposition of neutral sugars (Fig. 2-C), corresponding with bacterial dominance and a lower oxidases/carbohydrolases ratio (Figs. 5-E and 7-C), reflecting the competitive advantage of bacteria as specialists in acquiring labile C sources (Reischke *et al.* 2014; Chen *et al.* 2021). As labile C was gradually consumed (Fig. 1-B), fungal abundance peaked, and the shift from bacterial to fungal dominance aligned with the sequential degradation of lignin (Figs. 2-B and 5-H), indicating that fungi possess a stronger competitive capacity for processing chemically stable component under reduced C availability. Although fungi are recognized as generalists capable of degrading both labile and recalcitrant substrates (Wang *et al.* 2021), our findings suggest that in substrate-rich habitats, ecological functional differentiation between bacteria and fungi reduces their direct competition. This, in turn, promotes complementary microbial functioning *via* collaborative utilization of multiple resources (Dini-Andreote *et al.* 2015; Schmidt *et al.* 2015). By the later stage, as labile C was mostly depleted (Fig. 1-B), microbial community shifted toward actinomycetes (Figs. 5-G and 7-B), similar to the pattern observed in the low-C

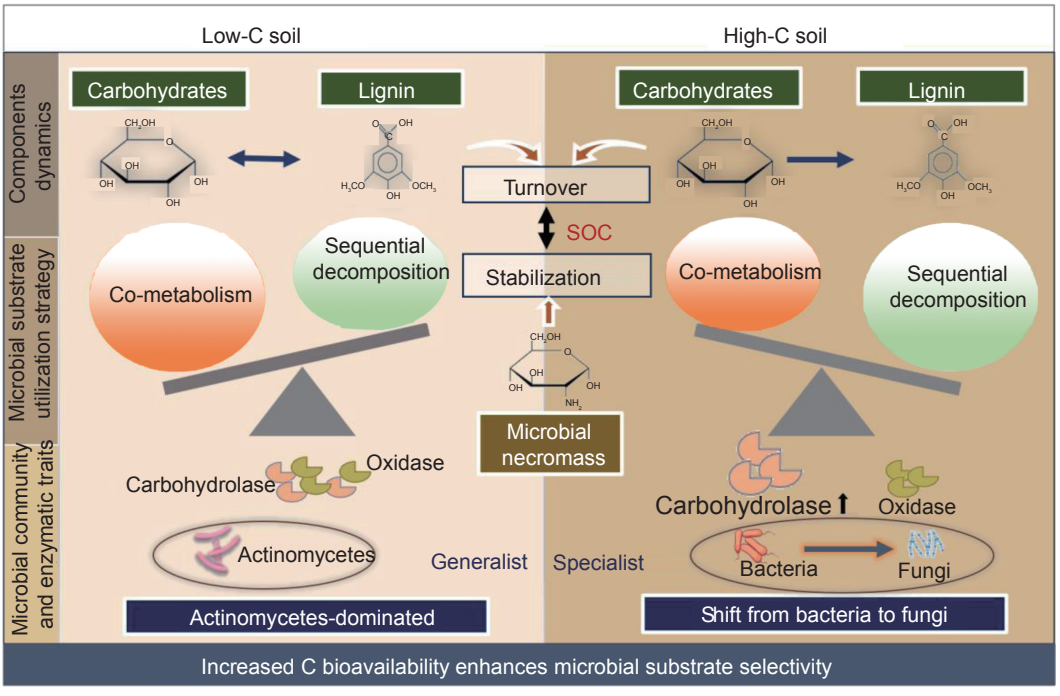

Fig. 8 Illustration on how the interplay between soil C availability and flexible microbial strategy regulating soil organic carbon (SOC) turnover and stability through divergent decomposition of different components.

soil (Fig. 7-C), re-affirming the generalist nature of actinomycetes which enables effective decomposition of recalcitrant substrates under C-limited conditions.

5. Conclusion

This study investigated the divergent roles of plant debris and microbial necromass in controlling SOM decomposition, with a focus on how microbial substrate utilization strategy altered under varying soil C availability. Plant-derived components were more prone to decomposition than microbial necromass, emphasizing the faster turnover of plant debris in SOC mineralization, whereas microbial necromass contribution to SOM stabilization through a compensatory effect. Soil C availability strongly modulated microbial substrate utilization strategy. Under C-starvation habitat, actinomycetes dominated SOM decomposition *via* the co-metabolism of carbohydrates and lignin, whereas in C-rich environment, sequential decomposition from labile to recalcitrant component indicated the enhanced microbial substrate selectivity. Bacteria preferentially utilized labile substrates, while fungi predominantly dominated recalcitrant lignin degradation as C availability declined. Herein, flexible microbial strategy regulated the distinct decomposition of heterogeneous SOM components, thereby regulating SOM turnover and stability. These findings highlighted the significant role of soil C availability in shaping microbial substrate utilization strategy, offering valuable insights for improving soil management and enhancing ecosystem resilience in conservation agriculture.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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