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Soil Biological Responses to Maize Residue Return in Subtropical Farmland

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Abstract Maize residue return has become an increasingly important agricultural practice for improving soil quality and promoting sustainable crop production in subtropical farmlands. As a major source of organic carbon and nutrients, returned maize residues influence a wide range of soil biological processes that are closely linked to ecosystem functioning and agricultural productivity. This review synthesizes current knowledge regarding the biological responses of subtropical agricultural soils to maize residue incorporation. Particular attention is given to the mechanisms of residue decomposition, changes in soil microbial biomass and community composition, and the responses of soil fauna and biodiversity. The review further examines how residue return affects soil enzymatic activities and nutrient cycling processes, including carbon, nitrogen, and phosphorus transformations. Evidence indicates that maize residue incorporation generally enhances microbial activity, stimulates beneficial functional groups, increases soil biological diversity, and promotes nutrient availability through accelerated biochemical processes. These biological improvements contribute to greater soil organic matter accumulation, enhanced aggregate stability, improved soil health, and increased ecosystem resilience. A case study from subtropical cropping systems is presented to illustrate the practical implications of residue management strategies for sustaining soil fertility and crop productivity. Despite significant advances, challenges remain in understanding long-term biological responses, microbial interactions, and the influence of climate variability on residue-mediated processes. Future research should integrate advanced molecular techniques, long-term field experiments, and ecosystem-scale assessments to better quantify the ecological benefits of maize residue return and support sustainable farmland management in subtropical regions.

Keywords Maize residue return; Soil microbial communities; Soil enzyme activity; Nutrient cycling; Subtropical farmland

1 Introduction

Sustainable intensification of crop production increasingly depends on practices that maintain or restore soil biological functioning while sustaining yields. Among these practices, returning crop residues to the soil is widely promoted as a strategy to rebuild soil organic matter, support nutrient cycling, and enhance long-term productivity under changing climates (Liu et al., 2023). In subtropical regions, where high temperatures and rainfall accelerate organic matter turnover, understanding how maize residue return shapes soil biological properties is critical for designing resilient, high-yielding systems (Li et al., 2024; Yang et al., 2024). Yet, the specific biological responses of subtropical soils to maize residue inputs, particularly in double-cropping systems, remain insufficiently characterized.

Maize residue return is a cornerstone of sustainable agriculture, as it recycles carbon (C) and nutrients, mitigates soil degradation, and helps reduce reliance on mineral fertilizers. A global meta-analysis showed that crop residue return combined with inorganic fertilizers significantly increases soil C, N, and P stocks across soil profiles, mitigates soil acidification in uplands, and raises grain yield, thereby contributing both to soil health and climate mitigation through deeper soil C sequestration (Liu et al., 2023). Long-term experiments also demonstrate that integrating straw return with chemical fertilizers markedly increases labile organic C fractions, microbial biomass C, and C-, N-, and P-cycling enzyme activities, indicating enhanced microbial functioning and improved ecological processes that underpin sustainable productivity (Liu et al., 2022). These findings highlight residue return as a key management lever to balance nutrient inputs, sustain grain yield, and restore soil biological quality.

Subtropical farmland ecosystems are characterized by warm, humid climates, high biological activity, and rapid C and nutrient turnover, which make soil processes highly sensitive to management. In a subtropical double-cropping maize system in South China, straw incorporation combined with optimized N fertilization increased soil organic C, total N, microbial biomass C, and enzyme activities, and significantly improved maize yield, illustrating the strong coupling between residue management, soil biology, and productivity under these climatic conditions (Yang et al., 2024). More broadly, studies in subtropical agricultural soils show that management practices such as intensive cultivation or organic inputs markedly alter microbial biomass and enzyme activities, with organic or residue-rich systems supporting higher microbial biomass and a greater suite of C-, N-, and P-cycling enzymes than conventionally managed or less-resourced soils. These ecosystem characteristics suggest that subtropical farmlands can rapidly respond, positively or negatively, to changes in residue management, making them ideal but complex targets for evaluating maize residue return effects.

Research on soil biological responses to residue return has advanced, but important knowledge gaps remain, especially for maize residues in subtropical systems. Long-term straw-return experiments in rice-wheat rotations show large increases in labile C pools, microbial biomass, and multiple hydrolase activities, with fungal communities particularly sensitive to residue-induced shifts in C composition and enzyme patterns (Liu et al., 2022). At the same time, metagenomic work on different residue-return strategies (chopped straw, compost, biochar) indicates that while overall microbial diversity may change little, functional genes involved in C, N, P, and S cycling and antibiotic resistance accumulate and are differentially modulated by residue forms, revealing complex microbiome-level responses that go beyond bulk biomass or activity measurements (Jiang et al., 2025). However, most studies focus on other crops or temperate/subtropical systems outside maize double-cropping; few explicitly characterize how maize residue return in subtropical farmlands reshapes soil microbial biomass, enzyme activities, and functional potentials through the profile. Addressing these gaps is essential to optimize maize residue management for soil health and yield in subtropical agriculture.

2 Mechanisms of Maize Residue Decomposition in Soil

2.1 Chemical composition and quality of maize residues

Maize residues are dominated by cellulose and hemicellulose, with lower proportions of lignin and proteins, but these fractions vary markedly among plant parts such as roots, stems, leaves and cob (Liu et al., 2022). Leaves of maize tend to have higher nitrogen (N), carbonyl and aryl C and lower lignin, making them more labile than stems and roots, which carry higher O-alkyl/di-O-alkyl C, lignin and C:N or lignin:N ratios (Liu et al., 2022). This internal heterogeneity means that the biochemical “quality” of maize residues is not uniform across the plant.

Organic C chemistry strongly regulates decomposition, with faster mass loss associated with O-alkyl and di-O-alkyl C and slower decay where phenolic and aromatic C and lignin accumulate. Fine-scale traits such as arabinoxylan substitution and cross-linking between hemicelluloses and lignin in maize cell walls also influence recalcitrance, so that roots rich in secondary walls and phenolic bridges decompose more slowly than primary-wall-rich leaves. Consequently, management that alters residue quantity and C:N while increasing lignin (e.g., high-yield, high-N systems) can raise residue recalcitrance even as N content increases.

2.2 Decomposition dynamics and carbon turnover processes

Maize residue decomposition typically shows an initial fast phase dominated by loss of labile C and nutrients, followed by a slower phase as more recalcitrant components control turnover (Huang et al., 2025). In field and incubation studies, maize residues lose around half their mass over a year, with decomposition rates declining sharply after the first month and cumulative C mineralization closely tied to loss of O-alkyl and di-O-alkyl C (Zhang et al., 2020). Within maize plants, leaves decompose earliest, while top stem parts and roots contribute more to slower C pools and longer C half-lives, favoring SOC accrual (Liu et al., 2022).

Microbial metabolism mediates the transformation of residue C into both CO_2 and stable SOC fractions. Residue inputs stimulate genes for degradation of labile to recalcitrant C and for N mineralization, promoting the formation of particulate and mineral-associated C pools enriched in plant-derived aliphatic structures (Zhang et al., 2020). Differences in residue chemistry alter not only decomposition rates but also enzyme profiles (e.g., cellulase, xylanase, laccase) and the efficiency with which enzymes convert complex cell walls into microbial products and persistent SOC. Conservation systems with surface-retained, high C:N maize residues slow decomposition and N release, shifting N supply later in the season and enhancing long-term soil N use efficiency and C storage (Barman et al., 2026).

2.3 Environmental factors regulating residue breakdown

Temperature and moisture critically regulate maize residue decomposition by modulating microbial activity and enzyme production. In saline-alkali soils, decomposition of maize leaves and stems shows distinct fast (0-15 d) and slow (15-90 d) stages, with warming from 15°C-25 °C and moderate wetting (20%-40% water holding capacity) accelerating early mass loss and CO_2 emissions, and higher moisture particularly enhancing breakdown of labile fractions (Auwal et al., 2021; Huang et al., 2025). Across soils, higher temperature and moisture generally increase SOC and residue decomposition, but the magnitude and temperature sensitivity ($Q_{10}\approx$ 1.4-1.7) depend on labile C supply and nutrient status (Auwal et al., 2021; Fang et al., 2022).

At broader scales, climate and edaphic factors structure microbial communities into ecological clusters that strongly predict maize residue-derived CO_2 fluxes (Zhao et al., 2021). Warmer, wetter, low-pH, high-organic-matter environments favor eco-clusters enriched in Actinobacteriota, Firmicutes and Sordariomycetes, which enhance residue decomposition. Locally, residue breakdown is initially driven by temperature and residue chemistry, with copiotrophic bacteria (e.g., Bacteroidetes, Firmicutes) dominating, and later by residue chemistry alone as more oligotrophic taxa (e.g., Acidobacteria, Chloroflexi) take over (Zhao et al., 2021; Huang et al., 2025). Nutrient availability further interacts with temperature: intermediate nutrient additions can minimize temperature sensitivity of straw mineralization, whereas low or high nutrient supply increase Q_{10} by altering extracellular enzyme activities (Auwal et al., 2021).

3 Effects of Maize Residue Return on Soil Microbial Communities

3.1 Changes in microbial biomass and activity

Maize residue return generally increases microbial biomass C and N and stimulates microbial activity by providing additional carbon substrates and nutrients. In Chinese Mollisols, surface application or incorporation of maize residue significantly increased microbial biomass C and N and altered the MBC/MBN ratio across maize growth stages, indicating enhanced microbial growth and shifts in C-N utilization patterns (Gao et al., 2021). Similarly, in double-cropping rice systems of southern China, residue returning under conventional or rotary tillage significantly increased microbial biomass C and N and the turnover rate of microbial biomass in both 0-10 and 10-20 cm layers, demonstrating that residue inputs accelerate microbial biomass production and cycling.

Residue return also promotes soil enzyme activities linked to C, N and P cycling, reflecting higher microbial functional activity. In a subtropical dual-maize system, straw returning combined with nitrogen fertilization significantly increased soil organic C, total N, microbial biomass C and key enzyme activities (e.g., urease, cellulase, sucrase, phosphatase), and these responses were associated with improved maize yield (Yang et al., 2024). Under a similar dual-cropping pattern, straw return with appropriate N rates enhanced urease, sucrase and cellulase activities and raised microbial biomass C, particularly at early vegetative stages, highlighting the importance of synchronized residue and N management for maintaining high microbial activity and soil fertility (Yang et al., 2022).

3.2 Responses of bacterial and fungal community structure

Maize residue return reshapes bacterial and fungal community composition and diversity, with fungi often showing stronger responses. In a subtropical maize dual-cropping system, straw returning significantly altered bacterial and fungal community composition and increased community diversity compared with traditional planting; dominant bacterial phyla included Proteobacteria, Acidobacteriota, Nitrospirae, Chloroflexi and Actinobacteriota, whereas Ascomycota and Mortierellomycota dominated fungi (Yang et al., 2022). In a wheat-maize rotation, maize residues strongly enriched several fungal genera (e.g., Fusarium, Epicoccum, Vishniacozyma, Cladosporium) in soils and on residues, while bacterial diversity and composition were relatively stable, indicating that fungal communities are more sensitive to residue inputs than bacteria (Cobo-Díaz et al., 2021).

Residue management also affects microbial network structure and assembly processes. In maize agroecosystems, tillage practices had stronger overall effects than residue retention, but residue retention significantly shifted fungal community composition and simplified both bacterial and fungal co-occurrence networks in the second year, suggesting altered interaction patterns under repeated residue inputs (Guan et al., 2022). Across multi-site maize systems, residue retention influenced both core and non-core bacterial and fungal communities, with core fungi shifting toward saprotroph-dominated assemblages and showing greater enrichment or depletion than core bacteria; deterministic processes became more important for core microbiome assembly under residue retention, highlighting structured selection by residue inputs (Guo et al., 2024).

3.3 Functional microorganisms involved in carbon and nutrient cycling

Residue return stimulates functional microbial groups and genes involved in carbon and nutrient transformations, which underpin soil organic carbon (SOC) sequestration. In a Mollisol incubated with maize residues, residue amendment increased microbial respiration, biomass C and the metabolic quotient, and expanded the assemblage of genes involved in C degradation from labile to recalcitrant compounds as well as N mineralization; these functional genes were closely associated with C and N accumulation in particulate and mineral-associated SOC pools, indicating that microbial metabolism transforms residue C and N into more stable soil pools. Metagenomic analysis of different residue-return strategies (chopped straw, compost, biochar) showed that chopped residues particularly enhanced microbial genes related to C, N, P and S cycling, while all residue forms modified the connectivity among nutrient-cycling pathways and led to accumulation of antibiotic resistance genes, suggesting profound functional re-organization of soil microbiomes under residue management (Jiang et al., 2025).

Specific taxonomic groups play key roles in residue decomposition and nutrient cycling. Non-dominant Actinobacteria, although representing only ~4%-5% of bacterial abundance, encoded about 16% of all carbohydrate-active enzymes in residue-amended paddy soils and maintained stable taxonomic and functional composition during straw decomposition; their contribution to plant residue degradation, supported by CAZyme, nitrogenase and antibiotic synthesis genes, became more pronounced in less fertile soils, underlining their importance in global C cycling (Bao et al., 2021). Multi-time-point analyses of bacterial and fungal communities in residue-amended Mollisols further showed tight associations between community composition and SOC fractions, where communities under residue treatments correlated positively with C and N in fine particulate and mineral-associated pools and with O-alkyl C, and negatively with aromatic C, linking microbial functional structure to the chemical nature and stability of SOC derived from residues.

4 Impacts of Maize Residue Return on Soil Fauna and Biological Diversity

4.1 Responses of soil mesofauna and macrofauna

Maize residue inputs provide energy and habitat that can rapidly alter mesofauna and macrofauna communities. In irrigated maize systems, six years of residue retention increased macrofauna abundance and diversity across depths, with particularly strong responses of earthworms and several predatory arthropod groups, and these faunal shifts covaried with higher soil C, N, moisture, aggregate stability and labile C indicators (Olayemi et al., 2022). Similarly, in a semi-arid maize-based system, combining residue retention with no-till produced a five-fold increase in earthworm abundance and biomass and shifted overall macrofauna community composition relative to tilled or residue-removed treatments, alongside improved aggregate stability and infiltration.

Functional responses of different faunal groups to residue inputs can be strongly stage-dependent and mediated by residue quality. A long-term litterbag study across residues of contrasting N, lignin and cellulose contents showed that labile, N-rich substrates initially stimulated both mesofauna (Collembola, Acari) and macrofauna (beetles, fly larvae), with macrofauna often preceding mesofauna in driving mass loss during early decomposition. Over time, dominance shifted within the macrofauna; beetles were key for lignin breakdown at intermediate stages, while ants became dominant decomposers in late stages when more protected cellulose remained, illustrating successional feedback loops between changing residue chemistry and faunal community structure. In maize systems, earthworms further mediate long-term residue-derived C distribution, with endogeic species especially enhancing incorporation of maize residue C into soil aggregates and SOC under no-till conditions.

4.2 Residue-mediated changes in soil food webs

Residue return reshapes soil micro-food webs by altering basal resources, stimulating microbes and nematodes, and modifying trophic interactions. In a wheat-maize rotation, long-term incorporation of maize straw or manure with mineral fertilizers increased fungal biomass and abundances of bacterivorous, plant-parasitic and omnivore-predatory nematodes, thereby enhancing nematode diversity and community stability and expanding the carbon “metabolic footprint” of higher trophic levels. A complementary 13-year experiment with straw incorporation in a rice-wheat system likewise found higher total, bacterivorous, plant-parasitic and omnivore-predatory nematodes, with increased Shannon diversity and maturity indices, indicating that residue inputs promote more complex and stable nematode-based food webs, particularly under low-fertility conditions (Chen et al., 2021).

Beyond nematodes, residue-based organic inputs can increase the overall complexity of soil micro-food web networks. In a 16-year subtropical field experiment comparing mineral fertilization with various levels of straw or manure substitution, high-level straw return increased microbial biomass and diversity and generated the most complex soil micro-food web co-occurrence networks, which were associated with the highest ecosystem multifunctionality (Li et al., 2023). In a similar wheat-maize rotation, integrating maize straw or manure with NPK strengthened bottom-up linkages from microbes to nematodes, with structural equation modeling indicating that microbial community changes propagated upwards to modify nematode community structure and carbon flow through the food web (Figure 1). At higher trophic levels, predator-prey cascades within nematode assemblages can also regulate microbial C pathways under residue return, with abundant omnivorous-predatory nematodes under no-till plus straw redirecting C towards fungi by suppressing fungivores and thereby amplifying fungal biomass and necromass formation (Zhang et al., 2020).

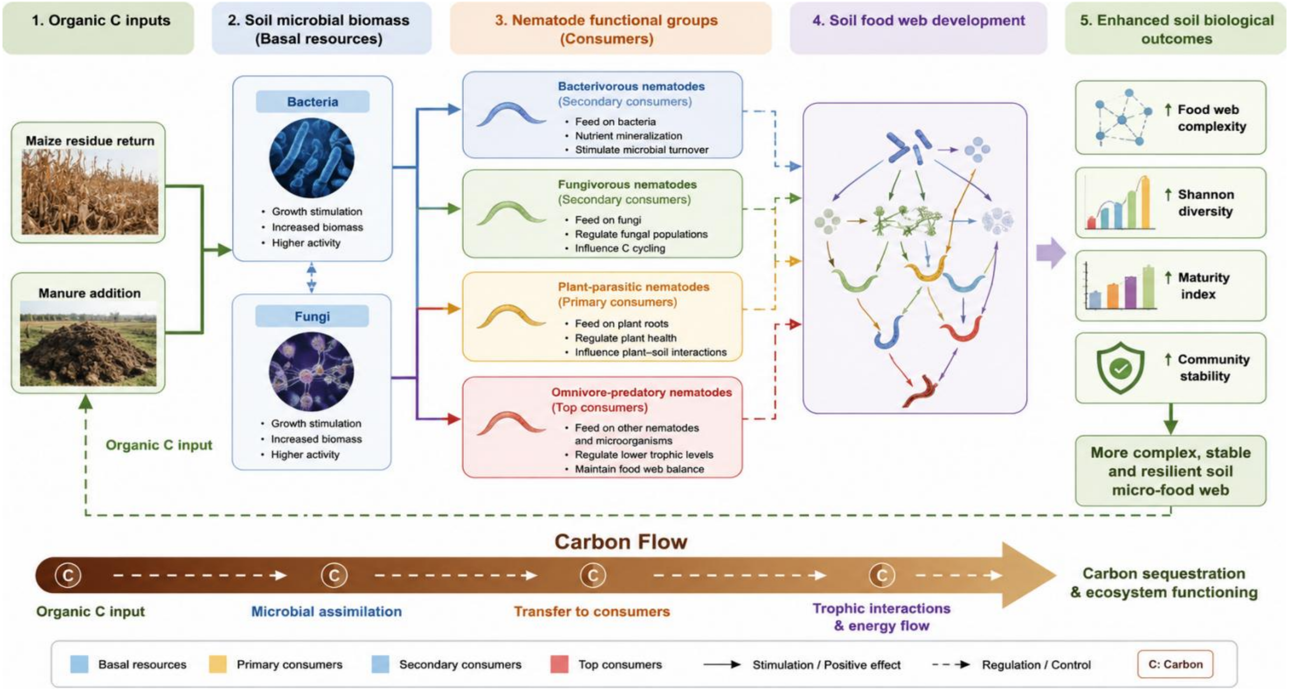

Figure 1 Conceptual framework illustrating how maize residue return influences soil microbial biomass, nematode trophic groups, and soil food web stability in subtropical agroecosystems

4.3 Biodiversity enhancement and ecological stability

Residue return contributes to belowground biodiversity and, through that, to ecosystem multifunctionality and stability. A large survey of 228 agricultural fields demonstrated positive relationships between multitrophic soil biodiversity (microbes, protists, invertebrates) and multiple functions including yield, nutrient provisioning and pathogen control, with soil network complexity (co-occurrence among trophic groups) strengthening the biodiversity-multifunctionality link (Jiao et al., 2021). Long-term substitution of mineral fertilizers by straw or manure further shows that organic residue inputs increase soil microbial biomass and diversity and the complexity of micro-food web networks, and these changes, in turn, enhance ecosystem multifunctionality, with fungal diversity emerging as a key trait associated with multiple simultaneous functions (Li et al., 2023).

Stability of soil biotic networks, rather than biodiversity per se, appears particularly important for maintaining multifunctionality in intensively managed systems. Along a disturbance gradient from pasture to maize cropland in subtropical soils, intensive management increased soil biota network complexity but decreased network stability; nevertheless, higher stability of entire soil biota networks, and especially of soil microfauna (nematodes, protozoa, arthropods), best predicted high soil multifunctionality (Long et al., 2025). Resource-enriched systems that combine mineral fertilizers with organic amendments can also increase potential cross-trophic interactions and thereby enhance stability of belowground functional traits and plant biomass, underscoring that biodiversity benefits depend on sufficient organic and nutrient resources to support multitrophic linkages. Integrating maize residue return within conservation-oriented systems (e.g., no-till, diversified organic inputs) therefore has the potential not only to increase soil faunal diversity but also to reinforce stable multitrophic networks that underpin resilient soil functions.

5 Soil Enzymatic Activities and Nutrient Transformation under Residue Return

5.1 Effects on carbon-cycling enzymes

Maize residue return strongly stimulates C-degrading enzymes, accelerating residue decomposition and formation of labile C pools. A global meta-analysis of straw return reported that hydrolytic C-degrading extracellular enzyme activities (e.g., β-glucosidase, cellulase) increased on average by 25% under straw incorporation, accompanied by substantial gains in dissolved, light-fraction, particulate and microbial biomass C, and a ~20% rise in soil organic carbon (SOC). Long-term fertilization combined with straw incorporation similarly enhanced cellulase, β-glucosidase, lignin peroxidase and manganese peroxidase activities and increased multiple labile organic C fractions and the carbon pool management index, indicating that residue-induced C-cycling enzymes are closely linked with improved soil C quality and storage (Zhang et al., 2020).

Residue form and mixing further modulate C-cycling enzymes and C stabilization. Short-term application of maize residue biochar altered β-glucosidase kinetic and thermodynamic traits, generally increasing catalytic efficiency (Vmax/Km) and decreasing activation energy and Q10, implying higher enzyme thermal stability and reduced temperature sensitivity of C turnover. Mixing maize with potato residues in field litterbags increased residue mass loss, enriched recalcitrant aromatic C, and was associated with greater β-glucosidase activity and shifts in bacterial keystone taxa, showing that residue mixtures can simultaneously accelerate decomposition and enhance stable C formation through enzyme-mediated pathways.

5.2 Regulation of nitrogen, phosphorus, and potassium cycling

Residue return strongly influences N-cycling enzymes and organic N transformations. In a Northeast China maize field, contrasting residue placements (no residue, surface retention, shallow and deep incorporation) differentially increased protease, N-acetyl-β-D-glucosaminidase, peptidase and urease activities across soil layers, and altered hydrolysable $NH4^+$ -N and amino acid N pools; redundancy analysis indicated that protease dominated soil organic N cycling under no-tillage and no-residue treatments, whereas peptidase and NAG became more important under incorporated residues (Su et al., 2024). In a long-term wheat system, fertilization plus straw increased N-acquiring enzymes (e.g., aminopeptidases) and was positively associated with dissolved and light-fraction C, suggesting tighter coupling between N-cycling enzymes and labile C under residue inputs (Zhang et al., 2020).

Phosphorus cycling is also regulated by residue return through changes in phosphatases and P availability within aggregates. Under a maize-wheat rotation on calcareous soil, increasing maize straw returning rates with fertilizer significantly enhanced acid and alkaline phosphomonoesterase and phosphodiesterase activities, particularly in <2 mm aggregates, and raised soil NO_3^--N and resin-P concentrations, while NH_4^+-N changed little (Lin et al., 2023). Across aggregates, phosphatase activities were strongly influenced by pH, NH_4^+-N, NO_3^--N, resin-P, soil organic matter and $CaCO_3$, indicating that residue-driven shifts in chemical environment and nutrient status jointly control P-mobilizing enzyme responses (Lin et al., 2023).

5.3 Interactions between enzyme activities and microbial processes

Residue return couples enzyme activities with microbial biomass, community structure and functional genes, thereby steering C and nutrient cycling. A global synthesis showed that stimulation of hydrolytic C-degrading enzymes under straw return was positively correlated with increases in microbial biomass C and SOC, and that climate, soil texture and straw management modulated these linkages, underscoring enzyme activities as keystone mediators between residue inputs and below-ground C pools. In a tropical maize conservation system, reduced tillage plus residue retention greatly increased β-glucosidase, β-galactosidase and glucosaminidase despite unchanged total SOC, suggesting that elevated C-cycling enzymes can enhance C turnover rates and potentially offset SOC accrual under warm conditions.

At finer scales, residue-induced enzyme changes track shifts in microbial community composition and nutrient limitation. A six-year maize-peanut intercropping and residue retention study found that residue retention significantly increased β-1,4-glucosidase activity and, together with intercropping, raised activities of N-acetylglucosaminidase+leucine aminopeptidase and alkaline phosphatase, altered enzyme C:N:P stoichiometric ratios, and alleviated microbial N limitation by improving soil N and P status and microbial biomass N and P. Experiments adding contrasting residues showed that increases in β-glucosidase, cellobiohydrolase, xylosidase and N-acetylglucosaminidase shortly after residue incorporation were associated with stimulated microbial growth, shifts in bacterial and fungal decomposer groups, and changes in C mineralization and N immobilization, demonstrating tight feedbacks between enzyme activities, microbial community assembly and C-N fluxes during residue decay.

6 Consequences for Soil Health and Ecosystem Functioning

6.1 Soil organic matter accumulation and carbon sequestration

Long-term maize residue return is a major pathway for soil organic matter (SOM) buildup and carbon sequestration in croplands. Across 238 trials in China, straw returning increased soil organic carbon (SOC) in upland systems by an average of 16.1%, with SOC gains closely controlled by total straw-C input and experiment duration. A crop-specific meta-analysis further showed that straw return in maize systems increased SOC by about 12%, with stronger effects under low initial organic matter and appropriate C/N of added inputs, underscoring the importance of matching residue inputs to soil conditions (Xin et al., 2024).

Profile studies in long-term maize systems indicate that residue return enhances both organic and inorganic C storage through the soil profile. In a Northeast China maize cropland, years of straw return increased SOC throughout 0-100 cm, with particularly large SOC stock gains (44%) in subsoil (20-60 cm), while also modifying soil inorganic carbon stocks in a depth-dependent manner. At the micro-scale, maize straw mulching in temperate cropland accelerated the accumulation of microbial residues, especially fungal-derived residues, and increased their contribution to SOM sequestration, indicating that residue-stimulated microbial processing is a key mechanism for long-term SOM stabilization.

6.2 Improvements in soil structure and aggregate stability

Residue return improves soil structure by promoting macroaggregate formation and aggregate-associated C storage. In a wheat-maize double-cropping system, 7 years of maize and/or wheat straw return increased the proportion of large macroaggregates by up to 32% and raised SOC in all aggregate size classes; intra-aggregate particulate and mineral-associated C stocks were strongly linearly related to cumulative C input, highlighting residue-driven aggregate C protection. A Chinese meta-analysis similarly found that straw return generally improved soil physical properties alongside SOC, supporting better structure under suitable tillage and residue rates (Xin et al., 2024).

Detailed aggregate studies show that continuous straw inputs alter both aggregate hierarchy and the quality of aggregate-protected C. In an oasis farmland with up to 20 years of straw return, SOC, particulate and mineral-associated C increased by 22%-64%, 5%-31% and 46%-226%, respectively, while microaggregates progressively converted to macroaggregates and mean weight diameter peaked after 10 years, indicating optimal structural stabilization at intermediate straw-return duration. Laboratory incubation with different maize residue components further revealed that residues enhance macroaggregate (>0.25 mm) formation and redistribute SOC toward larger aggregates and fine particles, suggesting dual physical and chemical pathways for aggregate-level C protection.

6.3 Implications for nutrient availability and crop productivity

Maize residue return improves nutrient status and can sustain or enhance crop yields when combined with appropriate fertilization. In a Mollisol monoculture maize system, straw mulching or deep ploughing increased SOC, total and available N and P in 0-40 cm soils; structural equation modeling showed that straw effects on yield were mediated mainly through improvements in total and available N, identifying N supply as the dominant control on maize productivity under residue return. Across China's uplands, a meta-analysis likewise indicated that straw returning improves multiple soil physicochemical properties that underpin nutrient retention, with management (C/N of exogenous inputs, straw rate, and tillage) strongly regulating the magnitude of C enhancement and associated fertility benefits (Xin et al., 2024).

Optimized residue-fertilizer strategies can maintain high maize yields while reducing mineral fertilizer inputs. In a long-term black soil experiment, maize straw return plus reduced NPK (SNPK) produced grain yields statistically similar to full NPK fertilization (~12.5 t/ha), both far exceeding PK or unfertilized controls, indicating that straw-derived organic N can partially substitute for inorganic N without yield penalty. Similarly, in a Mollisol, different maize straw return modes increased SOC and N and P availability at depth, and redundancy analysis identified SOC and N fractions as key drivers of yield, highlighting that well-managed residue return enhances both nutrient stocks and their crop availability.

7 Case Study: Biological Responses to Maize Residue Return in Subtropical Cropping Systems

7.1 Experimental design and site characteristics

A representative subtropical case study comes from a dual-cropping maize system at Guangxi University in Nanning, South China, where spring and autumn maize are grown each year under a humid subtropical monsoon climate with mean annual temperature around 21 °C -22 °C and precipitation near 1300 mm. The soils are clay loams with mildly acidic pH (~6.0-6.5) and moderate baseline SOC and total N, typical of intensively cultivated subtropical farmland (Yang et al., 2022). Field experiments used randomized plots comparing straw returning or incorporation with traditional planting (straw removed), combined with a gradient of N fertilization from 0 to 300 kg N ha^{-1} to capture interactive effects of residue C inputs and mineral N (Yang et al., 2024).

Soil sampling targeted the biologically active 0-20 cm layer and was synchronized with key maize growth stages. At jointing (V6) and maturity (R6), composite soil samples from each subplot were collected, sieved, and partitioned for microbial, enzymatic, and chemical analyses (Yang et al., 2024). Fresh subsamples were stored cold or frozen for microbial biomass and sequencing, whereas air-dried fractions were used to determine SOC, total N, and enzyme activities such as urease, cellulase, sucrase, catalase, and phosphatase (Yang et al., 2022). Parallel work in the same agro-climatic region extended this design over multiple years to assess cumulative effects of continuous straw returning with and without 250 kg N ha^{-} ^{1} on SOC, labile organic C, and major nutrients down to 40 cm depth, thereby linking short-term biological responses with medium-term soil quality and yield trends (Li et al., 2024).

7.2 Changes in soil microbial communities and enzyme activities

Under subtropical dual-maize, straw returning significantly increased SOC, total N, microbial biomass C, and the activities of urease, sucrase and cellulase relative to traditional planting, with strongest enzyme responses at V6, reflecting rapid utilization of fresh residue inputs during early crop growth (Yang et al., 2022; Yang et al., 2024). Optimal N rates (around 200-250 kg N ha^{-1}) with straw further enhanced enzyme activities and SOC relative to higher or zero N, indicating that balanced N supply supports an active, C-mineralizing microbial community without excessive N-driven inhibition or C/N imbalance (Yang et al., 2022; Yang et al., 2024). Over several years, continuous straw returning combined with 250 kg N ha^{-1} markedly increased SOC and labile organic C fractions in both 0-20 and 20-40 cm layers, demonstrating that repeated stimulation of microbial activity by residues ultimately translated into deeper C accumulation in this subtropical system (Li et al., 2024).

High-throughput sequencing revealed that straw returning reshaped bacterial and fungal communities, increasing diversity and altering dominant taxa compared with straw-removed plots (Yang et al., 2022). In straw-returned soils, bacterial communities were dominated by Proteobacteria, Acidobacteriota, Nitrospirae, Chloroflexi and Actinobacteriota, while fungi were dominated by Ascomycota and Mortierellomycota; co-occurrence network and redundancy analyses showed that SOC, total N and sucrase activity were closely associated with shifts in bacterial composition. Increasing N rate tended to reduce bacterial and fungal richness even as enzyme activities and SOC rose, highlighting a trade-off between nutrient-driven productivity and microbial diversity (Yang et al., 2022). Across years, straw plus N enhanced N, P and K status and maize yield, indicating that the observed microbial and enzymatic changes supported improved nutrient cycling and crop performance under subtropical conditions (Li et al., 2024).

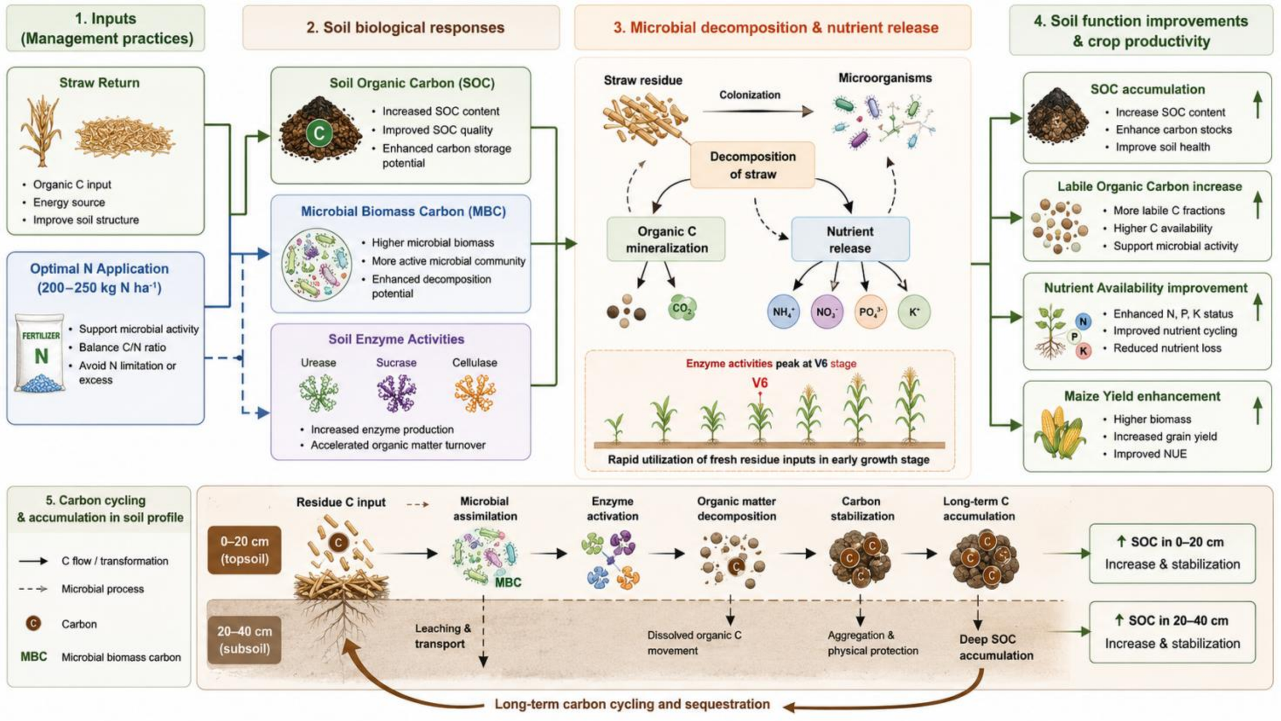

Figure 2 Mechanisms by which straw return and optimal nitrogen application enhance soil enzyme activities, microbial biomass, and soil organic carbon accumulation in subtropical dual-maize systems

7.3 Lessons learned and practical implications for residue management

The subtropical dual-maize case study shows that returning maize straw, particularly in combination with moderate to high N fertilization, is an effective strategy for improving soil biological functioning and fertility. Straw incorporation with about 200-250 kg N ha^{-1} increased SOC, total N, microbial biomass C, and multiple C- and N-cycling enzyme activities compared with straw removal or sub-optimal N, and these gains coincided with higher maize yields (Yang et al., 2024). Continuous straw returning with 250 kg N ha^{-1} over several years more than doubled SOC compared with the initial level and raised labile C and macronutrient pools throughout the upper 40 cm, demonstrating strong potential for C sequestration and nutrient build-up in humid subtropical soils (Li et al., 2024).

However, the experiments also emphasize the need to fine-tune N inputs and residue handling to avoid undesirable biological responses. Higher N fertilization reduced microbial richness despite enhancing enzyme activities and SOC, suggesting that excessive N may simplify microbial communities and potentially narrow functional redundancy (Yang et al., 2022). The close linkages between SOC, TN, enzyme activities, and microbial community composition indicate that monitoring both biochemical and molecular indicators is useful for guiding residue management in subtropical maize systems (Yang et al., 2022; Yang et al., 2024). Practically, the case study supports recommendations to retain or incorporate maize straw rather than remove it, couple residue return with balanced N rates near 200-250 kg/ha, and maintain multi-year continuity of these practices to realize cumulative gains in soil biological quality, nutrient availability, and yield under subtropical double-cropping maize (Li et al., 2024; Yang et al., 2024).

8 Challenges, Future Perspectives, and Conclusions

Current understanding of soil biological responses to maize residue return is constrained by methodological and design limitations. Many microbiome studies rely on single-site, single-depth or few-timepoint sampling, even though year-long, multi-depth monitoring shows that spatiotemporal variation can outweigh management effects, meaning residue impacts may be misinterpreted if sampling is sparse. Large-scale reciprocal transplant experiments on straw decomposition further reveal strong climatic controls and slow bulk-soil responses, highlighting that short-term or single-climate studies may not capture the full range of residue-microbiome interactions across subtropical regions.

Molecular approaches also face intrinsic biases and gaps. Culture-based methods miss most soil taxa, while DNA-based surveys detect genes but not necessarily their expression or functional contribution to fluxes. Reviews emphasize that sampling, storage, DNA extraction and sequencing strategies can distort community profiles, and that linking community composition or metagenomic potential to actual process rates (e.g., decomposition, N cycling) remains difficult, especially under dynamically changing residue and climate conditions.

High-throughput “omics” are transforming how soil biology under residue return can be assessed. Metagenomics, metatranscriptomics, metaproteomics and lipidomics allow direct characterization of unculturable soil microbes, their genes and functions, and have been widely applied to study rhizosphere processes, multi-trophic interactions and cropping system effects on microbial ecology. New sequencing platforms (Illumina, Ion Torrent, PacBio, Oxford Nanopore) and functional tools (GeoChip, stable-isotope probing, targeted metagenomics) provide deeper, longer reads and functional gene profiling to resolve residue-responsive taxa and pathways.

Culturomics, metabolic fingerprinting and microbiome biobanking complement sequence-based tools by preserving “whole microbiomes” and enabling the design of synthetic or native consortia tailored for residue decomposition and soil health enhancement (Clagnan et al., 2024). Integrated multi-omics pipelines, combined with functional screening and preservation strategies, are proposed as the basis for microbiome-based solutions (e.g., decomposer consortia, biofertilizers) that could be specifically adapted to subtropical maize systems.

Future work on maize residue return in subtropical farmland should prioritize designs that explicitly address spatiotemporal heterogeneity and climate interactions. Year-long, multi-depth, multi-field sampling demonstrates that temporal trends and field-specific factors dominate over management in shaping microbiomes, underlining the need for longer-term, replicated residue trials that integrate microbial composition, activity and soil C-N fluxes. Large geographic experiments and modeling under contrasting climates and fertility levels show that residue effects on aggregate-protected C and sequestration pathways differ with soil type and fertility, suggesting that residue strategies must be tailored to local conditions and evaluated over decadal scales.

Linking biology to function and management outcomes is another priority. Reviews of straw return identify major gaps around pathogen dynamics, allelopathy, and the balance between ecological benefits and potential risks, arguing for integrated assessments that couple biological indicators with yield and environmental metrics. Long-term and modeling studies in subtropical and dryland systems show that combining residue with optimized fertilization can increase SOC, improve aggregation, enhance microbial biomass and glomalin, and even deliver negative net greenhouse gas balances, pointing to residue-centered strategies as key to climate-smart, high-productivity maize systems that maintain resilient soil biota.

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