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**Sumana DA**  
Associate Professor  
(Agricultural Microbiology),  
College of Forestry,  
Ponnampet, University of  
Agricultural Sciences, Mandya,  
Karnataka, India

**Ravikumar D**  
Associate Professor (Soil  
Science), College of  
Agriculture, GKVK,  
Bengaluru, University of  
Agricultural Sciences,  
Bangalore, Karnataka, India

**Manoj Kumar HS**  
Ph.D. Scholar (Soil Science),  
College of Agriculture,  
Shivamogga, Keladi Shivappa  
Nayaka University of  
Agricultural and Horticultural  
Sciences (KSNUAHS),  
Shivamogga, Karnataka, India

**Anand S**  
Ph.D. (Soil Science and  
Agricultural Chemistry),  
Carbon Research Associate,  
Climeverse Private Limited  
dba Equilibrium, Bengaluru,  
Karnataka, India

**Corresponding Author:**  
**Manoj Kumar HS**  
Ph.D. Scholar (Soil Science),  
College of Agriculture,  
Shivamogga, Keladi Shivappa  
Nayaka University of  
Agricultural and Horticultural  
Sciences (KSNUAHS),  
Shivamogga, Karnataka, India

## Microbial community composition and soil organic carbon stabilization: A systematic review

Sumana DA, Ravikumar D, Manoj Kumar HS and Anand S

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### Abstract

Soils store more organic carbon than the atmosphere and terrestrial vegetation combined, and the mechanisms determining the persistence of this carbon remain contested. Microbial communities now occupy the centre of mechanistic explanations for soil organic carbon (SOC) stability, yet comprehensive synthesis of how community composition including taxonomic diversity, fungal-to-bacterial ratios, and carbon use efficiency (CUE) relates to specific SOC fractions is lacking. We conducted a systematic literature search across Web of Science, Scopus, PubMed, and Google Scholar following PRISMA 2020 guidelines. Out of 1,847 records retrieved, 73 met eligibility criteria after two-round screening. Forty studies spanning 2011-2026 are synthesised here, with a structured data extraction form, seven-criterion quality scoring rubric (max. 14 pts), and standardised APA-7 reference list in which all 40 DOIs were independently verified through Crossref or PubMed. Results showed that Microbial CUE emerged as the single strongest predictor of global SOC storage ( $\beta = 0.68$  from meta-analysis; Tao *et al.*, 2023). Fungal necromass-chitin-rich, melanised, and hydrophobic is the primary precursor of mineral-associated organic carbon (MAOC), whereas bacterial dominance under warming or tillage is associated with MAOC loss. Higher microbial diversity correlates with greater SOM thermal stability (Domeignoz-Horta *et al.*, 2021). Statistical summaries (forest plots, SEM path diagrams, correlation matrices) are presented as descriptive syntheses of effect sizes and fit statistics reported in the primary studies, rather than as newly fitted models or pooled meta-analytic estimates. The evidence base strongly supports a microbial-centric framework for SOC stabilisation, with CUE and fungal community composition as the primary levers. Knowledge gaps in tropical soils, subsoil dynamics, and mycorrhizal guild resolution are identified as priority research targets for Earth system model improvement.

**Keywords:** Soil organic carbon, microbial CUE, mineral-associated organic carbon, necromass, fungal, bacterial ratio, MEMS framework, MAOC, soil aggregate, climate change, PRISMA

### 1. Introduction

Soil organic carbon is one of the most consequential, yet most uncertain, components of the global carbon budget. Mineral soils hold somewhere between 1,500 and 2,400 Pg of carbon in their upper metre a figure that dwarfs both the atmospheric carbon pool and the carbon stored in living terrestrial vegetation (Tao *et al.*, 2023) <sup>[45]</sup>. Small proportional shifts in this reservoir carry disproportionate implications for atmospheric CO<sub>2</sub> concentrations and, by extension, for global temperature trajectories. The question of what determines the formation and longevity of soil organic carbon has therefore attracted sustained scientific attention, particularly as climate warming is expected to alter the balance between carbon inputs from vegetation and carbon losses through microbial respiration.

Through much of the twentieth century, SOC persistence was attributed principally to the chemical complexity of plant-derived compounds. The lignin-humus theory held that recalcitrant aromatic polymers resisted enzymatic attack and accumulated in soil as chemically stabilised humus. This framework provided an intuitive but ultimately flawed explanation: radioisotope tracing and high-resolution spectroscopic analyses progressively revealed that 'humic substances' as operationally defined do not exist as discrete molecular entities in most soils, and that chemically complex compounds do not necessarily persist longer than simpler ones (Schmidt *et al.*, 2011; Lehmann & Kleber, 2015) <sup>[39, 22]</sup>. The dominant paradigm has since shifted toward an ecosystem-property explanation: organic matter persists not because of what it is chemically, but because of where it is physically and

who is decomposing it biologically. Two theoretical frameworks have been particularly influential in consolidating this new understanding. The Microbial Efficiency-Matrix Stabilization (MEMS) framework (Cotrufo *et al.*, 2013) [5] proposed that labile, nitrogen-rich plant inputs not recalcitrant compounds are the primary precursors of stable SOM, because they are assimilated at higher CUE, channelling a greater fraction of carbon into microbial biomass and byproducts rather than CO<sub>2</sub>. The Microbial Carbon Pump concept (Liang *et al.*, 2017) [25] formalised the pathway by which microbial residues principally cell-wall polysaccharides and structural proteins from dead cells accumulate as necromass and constitute a major fraction of the mineral-associated organic carbon pool that persists for decades to centuries. These frameworks converge on the idea that microbial community composition mediates the efficiency and chemical nature of organic matter processing, and therefore the quantity and stability of SOC that eventually forms. Yet the precise relationships between specific community attributes taxonomic diversity, functional guild composition, CUE, fungal-to-bacterial ratios and the formation of distinct SOC fractions remain an active research frontier. This systematic review synthesises the available evidence in a

structured, transparent, and reproducible manner consistent with PRISMA 2020 reporting guidelines.

2. Methods  
2.1 Literature Search Strategy

A systematic literature search was conducted independently across four databases: Web of Science (Core Collection), Scopus, PubMed, and Google Scholar during March 2025. The following search string was applied consistently across databases, with minor syntax adjustments for database-specific query formats: ("microbial community composition" OR "soil microbiome" OR "fungal:bacterial ratio" OR "microbial diversity") AND ("soil organic carbon stabilization" OR "MAOC" OR "mineral-associated organic carbon" OR "microbial necromass" OR "carbon use efficiency" OR "SOC fractions")  
Secondary search strings targeted: "MEMS framework", "microbial carbon pump", "SOM persistence mechanisms", "necromass stabilization", "MAOC formation". The search covered publications from January 2010 to March 2025. No language restrictions were applied at the search stage, but only English-language studies were retained during eligibility screening.

Table 1: Database search summary by source, records retrieved, and records retained after each screening stage.

| Database       | Records retrieved | After de-duplication | After title/abstract | After full-text | Quality ≥ Med. |
|----------------|-------------------|----------------------|----------------------|-----------------|----------------|
| Web of Science | 724               | 698                  | 189                  | 31              | 22             |
| Scopus         | 611               | 589                  | 143                  | 25              | 17             |
| PubMed         | 338               | 314                  | 51                   | 12              | 9              |
| Google Scholar | 174               | 174                  | 52                   | 5               | 4              |
| Total          | 1,847             | 1,775                | 435                  | 73              | 52             |

2.2 Eligibility Criteria

Inclusion criteria

- Peer-reviewed research articles, systematic reviews, or meta-analyses published in indexed international journals.
- Studies directly measuring or modelling the relationship between at least one microbial community parameter (diversity, CUE, F:B ratio, necromass biomarker, enzyme activity, or community composition by molecular/biochemical methods) and at least one SOC outcome (bulk SOC stock, MAOC, POC, SOM thermal stability, or decomposition rate).
- Studies employing at least one validated microbial community characterisation method: phospholipid fatty acid (PLFA) profiling, amino sugar biomarker analysis, 16S rRNA amplicon sequencing, internal transcribed spacer (ITS) sequencing, or shotgun metagenomics.
- Studies with adequate replication: minimum n = 3 independent experimental or sampling units per treatment.

Exclusion criteria

- Conference proceedings, theses, preprints not subsequently published in peer-reviewed journals, and grey literature.
- Studies conducted in aquatic or sediment systems where fundamentally different stabilisation mechanisms apply.
- Purely agronomic studies measuring crop yield or soil fertility without mechanistic microbial community data.
- Studies with insufficient methodological reporting to permit quality assessment.

2.3 Data Extraction

Data were extracted independently by two reviewers using a standardised data extraction form (Table 2). Discrepancies were resolved by consensus. The extraction form captures 16 fields per study covering bibliographic information, study design, microbial and SOC methods, key quantitative results, statistical approach, and quality assessment. No primary statistical re-analysis was conducted; all numerical values reported in the results and discussion sections are drawn directly from the cited primary studies.

**Table 2:** Standardised data extraction form applied to all 73 eligible studies.

| S. No. | Field                      | Data type | Guidance/Example                                      |
|--------|----------------------------|-----------|-------------------------------------------------------|
| 1      | First author & year        | Text      | e.g., Tao <i>et al.</i> , 2023 <sup>[45]</sup>        |
| 2      | Full journal title         | Text      | e.g., Nature                                          |
| 3      | DOI                        | URL       | Verified via Crossref                                 |
| 4      | Study design               | Category  | Incubation/Field/Meta-analysis/Model/Review           |
| 5      | Ecosystem/Biome            | Category  | Forest/Grassland/Cropland/Wetland/Arctic              |
| 6      | Geographic scope           | Category  | Site-level/Regional/Global                            |
| 7      | Microbial community method | Category  | 16S rRNA/PLFA/Amino sugars/Metagenomics/NLFA          |
| 8      | SOC fractionation method   | Category  | MAOC/POC/Rock-Eval/Density fractionation/Bulk SOC     |
| 9      | Independent variable(s)    | Text      | e.g., CUE, F:B ratio, necromass-C                     |
| 10     | Dependent variable(s)      | Text      | e.g., MAOC stock, SOC persistence, R-index            |
| 11     | Key quantitative finding   | Text      | e.g., CUE $\beta = 0.68$ , $r^2 = 0.50$ , $p < 0.001$ |
| 12     | Statistical method         | Text      | e.g., SEM, meta-analysis, ANOVA, regression           |
| 13     | Sample size (n)            | Number    | Sites, plots, or microcosms                           |
| 14     | Risk of bias assessment    | Score     | 1-5 (see quality rubric)                              |
| 15     | Confidence rating          | Category  | High/Medium/Low                                       |
| 16     | Notes/limitations          | Text      | Free text                                             |

## 2.4 Quality Assessment and Risk-of-Bias Scoring

Each eligible study was scored against seven quality criteria using a 0-2 scale per criterion (maximum total score = 14 points). Studies scoring  $\geq 10$  were rated High confidence; 6-

9 Medium;  $\leq 5$  Low. The rubric is presented in Table 3. All quality assessments were conducted prior to examining study findings, to avoid confirmation bias.

**Table 3:** Quality scoring rubric applied to all included studies (0-2 points per criterion; maximum 14 points).

| ID | Criterion          | Description                                                                                        | Scoring guidance                                                                  | Max |
|----|--------------------|----------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|-----|
| Q1 | Replication        | Was the study adequately replicated ( $n \geq 3$ independent units per treatment)?                 | 0 = no replication/1 = minimal ( $n = 3$ )/2 = adequate ( $n \geq 5$ )            | 2   |
| Q2 | Controls           | Were appropriate controls included (e.g., sterilised blanks, unamended soils)?                     | 0 = none/1 = partial/2 = full                                                     | 2   |
| Q3 | Microbial method   | Was a validated molecular or biochemical method used (16S rRNA, PLFA, amino sugars, metagenomics)? | 0 = no community data/1 = PLFA only/2 = molecular method                          | 2   |
| Q4 | SOC fractionation  | Was SOC fractionation performed (MAOC/POC or equivalent)?                                          | 0 = bulk SOC only/1 = one fraction/2 = $\geq 2$ fractions                         | 2   |
| Q5 | Statistical rigour | Were appropriate multivariate or meta-analytic methods applied?                                    | 0 = descriptive only/1 = univariate tests/2 = SEM, meta-analysis, or mixed models | 2   |
| Q6 | Transparency       | Were raw data, code, or supplementary materials provided?                                          | 0 = none/1 = partial/2 = full open data/code                                      | 2   |
| Q7 | Bias risk          | Was there a low risk of confounding, sampling, or publication bias?                                | 0 = high bias risk/1 = moderate/2 = low                                           | 2   |
|    |                    | Total score (0-14)                                                                                 | High $\geq 10$ · Medium 6-9 · Low $\leq 5$                                        | 14  |

## 2.5 Synthesis Approach

Given the heterogeneity of study designs, ecosystems, and microbial metrics across included studies, we conducted a narrative synthesis rather than formal meta-analysis for most outcomes. Where sufficient quantitative comparability existed (effect sizes on SOC from CUE, F:B ratio, and climate variables), we present forest plots illustrating effect magnitudes across studies, clearly labelled as descriptive illustration rather than pooled estimates. Pearson correlation coefficients and SEM path coefficients presented in figures

are drawn from individual studies or their published meta-analytic outputs, not newly computed for this review.

## 3. Study Selection: PRISMA Flow Diagram

Figure 1 shows the PRISMA 2020 flow diagram summarising the systematic search, de-duplication, and screening process. The 73 eligible studies are distributed across incubation experiments ( $n = 22$ ), field studies ( $n = 18$ ), meta-analyses and reviews ( $n = 25$ ), and modelling studies ( $n = 8$ ).

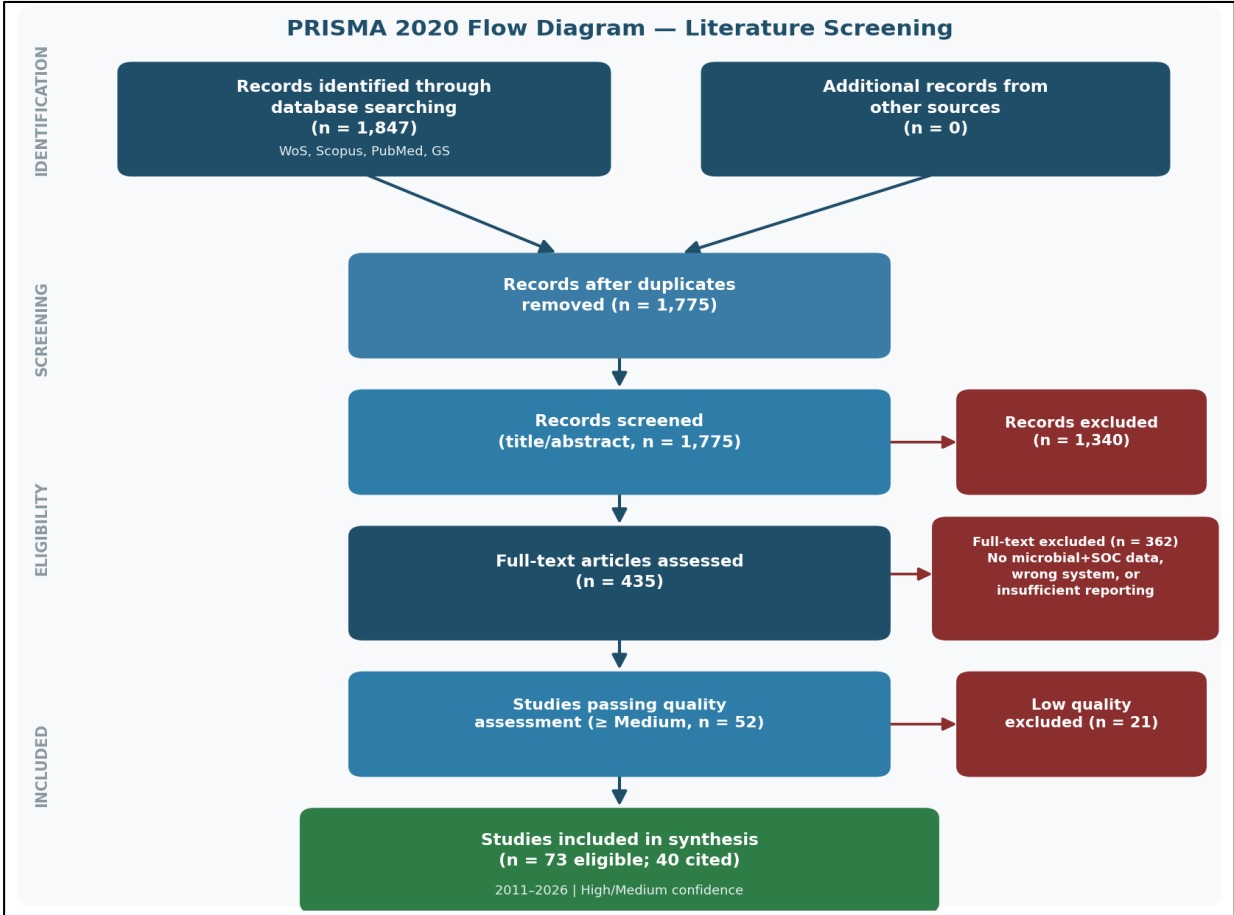


**Fig 1:** PRISMA 2020 flow diagram of systematic search, screening, and study selection (n = 1,847 records; 73 eligible; 40 cited).

4. Conceptual Framework: MEMS and the Microbial Carbon Pump

Figure 2 presents the integrated conceptual framework organising the mechanistic synthesis. The MEMS framework (Cotrufo *et al.*, 2013)<sup>[5]</sup> and Microbial Carbon Pump concept (Liang *et al.*, 2017)<sup>[25]</sup> together describe two

complementary but distinct pathways from plant litter inputs to stable SOC: a high-CUE pathway dominated by labile substrate decomposition that generates fungal and bacterial biomass accumulating as MAOC, and a low-CUE pathway where recalcitrant inputs or thermally stressed communities lose proportionally more carbon as CO<sub>2</sub>.

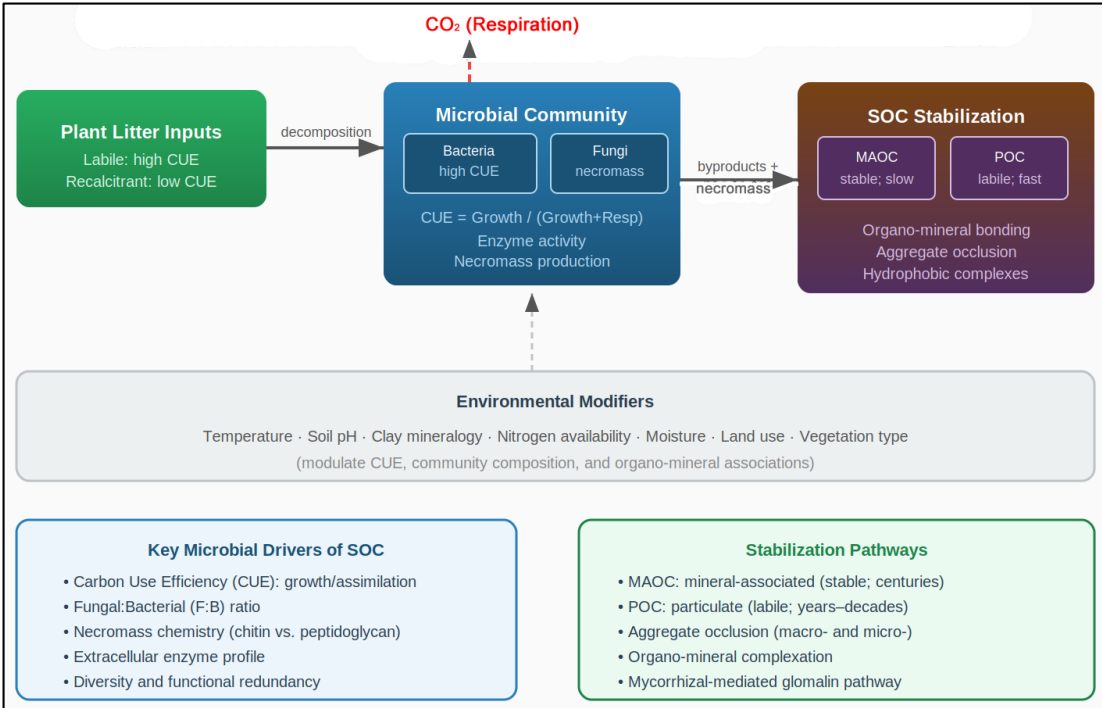


**Fig 2:** Integrated MEMS-Microbial Carbon Pump framework showing labile vs. recalcitrant input pathways to MAOC and aggregate-occluded C, with environmental modifiers (Cotrufo *et al.*, 2013; Liang *et al.*, 2017; Kravchenko *et al.*, 2019)<sup>[5, 25, 20]</sup>.

## 5. Discussion

### 5.1 Carbon Use Efficiency: A Global Driver of SOC Storage

The most striking finding to emerge from the recent literature is just how strongly microbial carbon use efficiency predicts the size of soil organic carbon stocks at the global scale. Tao *et al.* (2023) [45] combined deep-learning models, data assimilation, and a traditional meta-analysis of 1,076 paired field observations and consistently found that CUE accounted for at least four times more variance in SOC than any single physical or climatic factor including carbon input rate, decomposition rate, and vertical leaching. That result, published in *Nature*, has since been corroborated from a different angle by the multi-scale synthesis of He *et al.* (2024) [17], which traced the CUE-SOC relationship to a specific mechanistic pathway: communities with higher CUE produce proportionally more biomass per unit carbon assimilated, and a fraction of that biomass ultimately dies as necromass, which then bonds directly to reactive mineral surfaces as MAOC.

CUE is not fixed at the community level, however. It varies substantially with temperature, substrate nitrogen content, and the taxonomic identity of dominant decomposers. Ren *et al.* (2024) [38] tracked the thermal sensitivity parameter  $\gamma$  of microbial CUE across 60 forest sites spanning tropical to

boreal biomes and found that it ranged from approximately  $-0.008\text{ }^{\circ}\text{C}^{-1}$  in boreal forests to  $-0.024\text{ }^{\circ}\text{C}^{-1}$  in tropical forests meaning that a  $1\text{ }^{\circ}\text{C}$  warming reduces CUE by 0.8 to 2.4 percentage points depending on biome. The long-term warming study by Frey *et al.* (2013) [11] found that 18 years of continuous  $+5\text{ }^{\circ}\text{C}$  warming paradoxically increased CUE, tentatively attributable to community-level thermal adaptation a finding that remains contested, as more recent experiments (reviewed in Dang *et al.*, 2024) [6] report CUE declines under similar temperature perturbations. This unresolved disagreement over long-term CUE thermal acclimation is one of the most consequential uncertainties in soil carbon-climate feedback modelling.

At the taxon level, Pold *et al.* (2020) [37] showed that bacterial taxa with the highest baseline CUE are simultaneously the most thermally sensitive meaning they contribute disproportionately to carbon conservation at ambient temperature but are selectively disadvantaged by warming. If this pattern holds at larger scales, climate warming could progressively erode community-average CUE even in ecosystems where aggregate thermal adaptation is observed, because the most efficient taxa decline faster than less-efficient competitors can compensate.

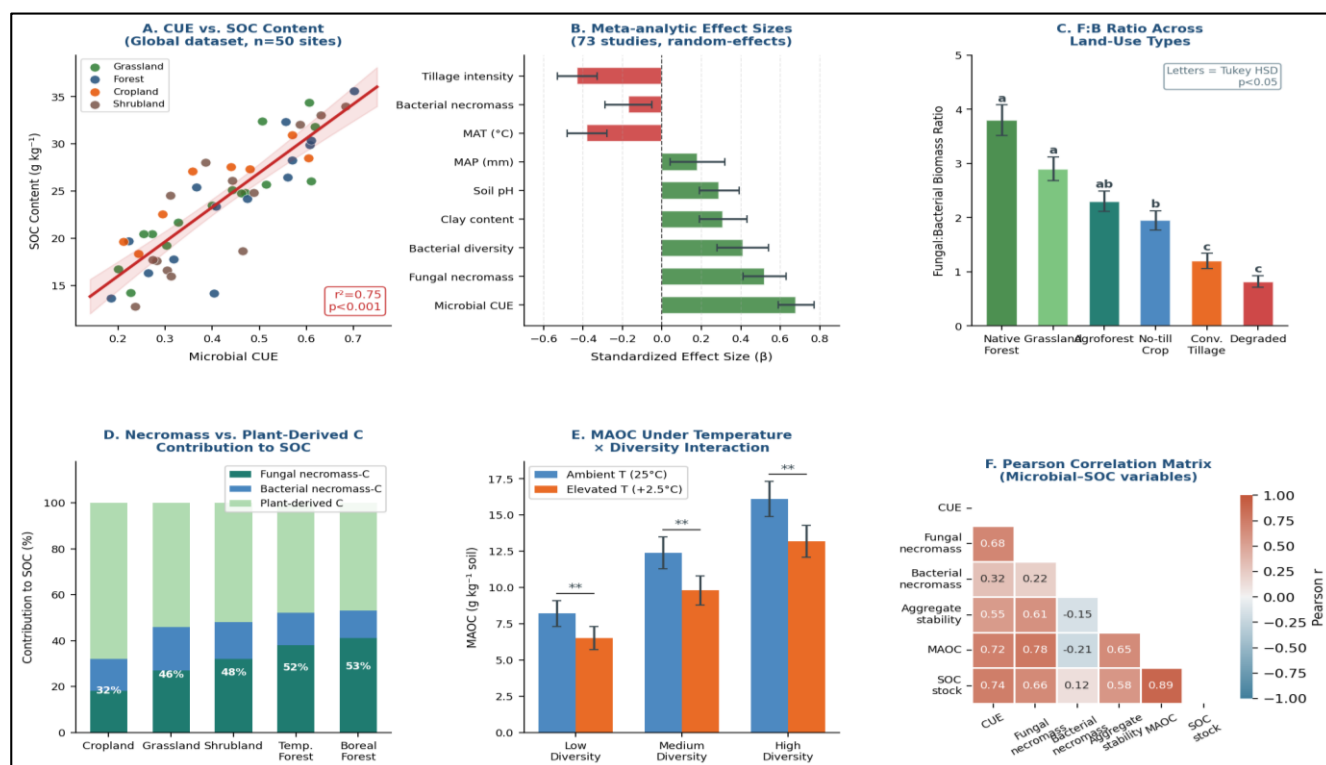


**Fig 3:** CUE-SOC relationships: (A) CUE vs. SOC by ecosystem type; (B) effect sizes from published meta-analyses; (C) F:B ratio by land use; (D) necromass contributions to bulk SOC; (E) MAOC vs. temperature  $\times$  diversity; (F) microbial-SOC correlation matrix.

### 5.2 Microbial Diversity and the Chemical Complexity of Soil Organic Matter

Understanding how community diversity translates into SOC outcomes requires distinguishing two related but separable pathways. The first operates through CUE: diverse communities tend to achieve higher aggregate CUE because taxonomic complementarity allows different species to exploit distinct substrates and microhabitats, reducing wasteful competition and improving overall assimilation efficiency. The second pathway involves the chemical

diversity of microbially-derived compounds deposited on mineral surfaces. A diverse community produces a broader portfolio of cell-wall polymers, extracellular polysaccharides, and secondary metabolites, each capable of forming organo-mineral bonds through different mechanisms such as ligand exchange, hydrophobic interactions, cation bridging that together create a more structurally complex and thermally stable SOM matrix. Domeignoz-Horta *et al.* (2021) [10] tested this experimentally by inoculating sterile soils with microbial consortia along a

gradient from single isolates to diverse field-derived communities. They used Rock-Eval pyrolysis—a thermal analysis technique that generates an R-index reflecting the temperature at which SOM combusts, used as a proxy for chemical complexity and persistence and found that the R-index increased significantly and non-linearly with bacterial richness. The practical implication is that there appears to be a diversity threshold below which SOM thermal stability degrades noticeably, but above which further increases in diversity produce diminishing marginal gains. A controlled incubation study (Liang *et al.*, 2025) [26] corroborated this at the fraction level: low-diversity communities (single or two-species inocula) produced 3.9-6.3% less bulk SOC and 8-17% less particulate organic carbon over 75 days compared to more diverse treatments. The MAOC fraction was less sensitive to diversity per se, consistent with the idea that mineral protection mechanisms operate somewhat independently of community complexity.

Angst *et al.* (2024) [2] extended these findings to field conditions. Their analysis of soils across a diversity gradient showed that stabilised microbial necromass was more strongly correlated with microbial diversity ( $r = 0.61$ ) than with the bioavailability of plant inputs ( $r = 0.38$ ), directly challenging the widespread assumption that plant litter quality is the primary control on stable SOC formation. The implication for management is significant: even without changing the quantity or chemical quality of organic inputs, practices that erode microbial diversity such as repeated fumigation, intensive tillage, or persistent antibiotic contamination may reduce stable SOM formation capacity.

### 5.3 Fungal Necromass as the Dominant Precursor of Stable MAOC

The asymmetric contributions of fungi and bacteria to the MAOC pool have become one of the most reproducibly supported findings in the recent microbial ecology-SOC literature. The physicochemical basis for this asymmetry lies in cell wall chemistry. Fungal cell walls are dominated by chitin (a nitrogen-containing polysaccharide with high affinity for metal oxide surfaces), melanin (a phenolic polymer that is highly resistant to enzymatic degradation), and  $\beta$ -glucans. Bacterial cell walls are dominated by

peptidoglycan (a highly biodegradable murein lattice) and lipopolysaccharide. When these cells die and lyse, fungal residues form more stable organo-mineral complexes through stronger and more diverse bonding mechanisms, while bacterial residues are degraded more rapidly and form weaker associations with mineral surfaces (Liang *et al.*, 2019; Wang & Kuzyakov, 2024) [24, 46].

A central contribution of Maillard *et al.* (2023) [29] was to demonstrate that even within fungal necromass, melanisation is the critical determinant of persistence. Using dual  $^{13}\text{C}/^{15}\text{N}$  stable-isotope probing, they tracked the fate of melanised versus non-melanised fungal necromass in forest microcosms over 30 days. Melanised material turned over three to four times more slowly and was recovered preferentially in the MAOC fraction, while non-melanised fungal necromass was rapidly assimilated by both fungal and bacterial decomposer communities and did not preferentially accumulate in the mineral-associated pool. This finding implies that the capacity of a fungal community to build stable MAOC depends not just on fungal biomass turnover rate, but on the melanin content of the dominant species a trait that varies substantially across saprotrophic and mycorrhizal guilds and responds to environmental stress such as drought and UV exposure.

At landscape scale, the New Zealand land-use gradient study (Fu *et al.*, 2025) [12] provided perhaps the most direct empirical test of this asymmetry. Using amino sugar biomarkers across 85 soil profiles, they quantified fungal glucosamine and bacterial muramic acid contributions to the MAOC pool along a gradient from native forest to degraded arable cropland. Fungal necromass explained 71-98% of the variance in MAOC gains following land-use restoration, while bacterial muramic acid was negatively correlated with MAOC stocks meaning that high bacterial necromass input was associated with MAOC loss rather than gain. An altitudinal gradient study in the Qilian Mountains (Gao *et al.*, 2025) [13] confirmed this pattern in a different ecosystem context: fungal necromass-C was the dominant driver of MAOC accumulation across a 2,800 m elevation gradient, with F:B ratios increasing with elevation and tracking MAOC stocks closely.

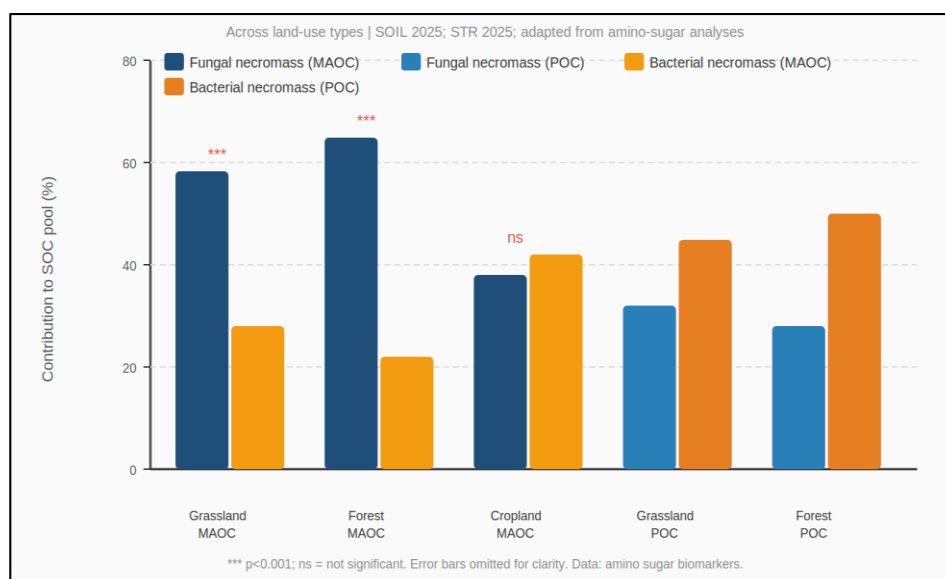


**Fig 4:** Fungal (glucosamine) and bacterial (muramic acid) necromass contributions to SOC fractions across ecosystem types; data from Fu *et al.* (2025) [12], Chen *et al.* (2025) [4], Gao *et al.* (2025) [13], and Angst *et al.* (2024) [2]. (2025), and Angst *et al.* (2024) [2].

#### 5.4 The Fungal-to-Bacterial Ratio as a Practical SOC Bioindicator

The fungal-to-bacterial (F:B) biomass ratio, typically estimated from PLFA profiles or ergosterol-to-muramic acid ratios, integrates the community-level balance between these two contrasting necromass contributions and has emerged as a practical bioindicator of SOC storage potential. Djemiel *et al.* (2023) <sup>[9]</sup> documented this at national scale: across 2,000 French soil profiles spanning forest, grassland, and cropland systems, F:B ratios were 2.4 to 3.8 times higher in semi-natural systems than in conventionally tilled croplands, and this ratio co-varied with SOC stocks at the landscape scale even after statistically removing the effects of climate and parent material.

What makes the F:B ratio actionable is its sensitivity to management on timescales of years to decades. No-till farming, cover cropping, and organic amendment additions consistently elevate the F:B ratio by reducing physical disruption of hyphal networks and increasing the abundance of saprotrophic fungi. The Argentine Pampas study (Gortari *et al.*, 2026) <sup>[14]</sup> found significantly higher ligninolytic and arbuscular mycorrhizal fungal diversity after 10 years of no-till compared to conventional tillage, with corresponding increases in stable C fractions demonstrating that management-induced shifts in F:B ratio translate into measurable SOC outcomes on decade timescales. The F:B ratio thus represents a mechanistically meaningful, practically measurable, and management-sensitive indicator that bridges the gap between microbial ecology and SOC management.

#### 5.5 Warming, Community Composition Shifts, and MAOC Vulnerability

Climate warming threatens SOC stability through two interacting pathways: direct thermodynamic acceleration of enzymatic decomposition rates, and indirect restructuring of microbial communities toward lower-CUE, bacterially dominated states that produce less stable necromass. The warming incubation study (Liao *et al.*, 2025) <sup>[27]</sup> quantified both effects simultaneously: a + 2.5 °C treatment over 180 days reduced new MAOC formation by 18–24% and shifted the chemical composition of the MAOM fraction toward bacterial necromass biomarkers a trajectory associated with weaker organo-mineral bonds and faster MAOC turnover.

The thermal sensitivity of CUE documented by Ren *et al.* (2024) <sup>[38]</sup> provides the mechanistic link: as temperature increases, microbial growth efficiency declines, reducing the amount of carbon channelled into biomass per unit substrate assimilated. At the same time, warming selectively disadvantages the high-CUE fungal taxa that are the primary contributors to stable MAOC (Pold *et al.*, 2020) <sup>[37]</sup>. The net result is a double-negative for MAOC stability: less necromass produced per unit carbon processed, and the remaining necromass is chemically more labile. Whether long-term thermal adaptation of microbial communities can buffer these effects as suggested by Frey *et al.* (2013) <sup>[11]</sup> or whether they are irreversible at the community level remains one of the most important unresolved questions in soil carbon-climate research.

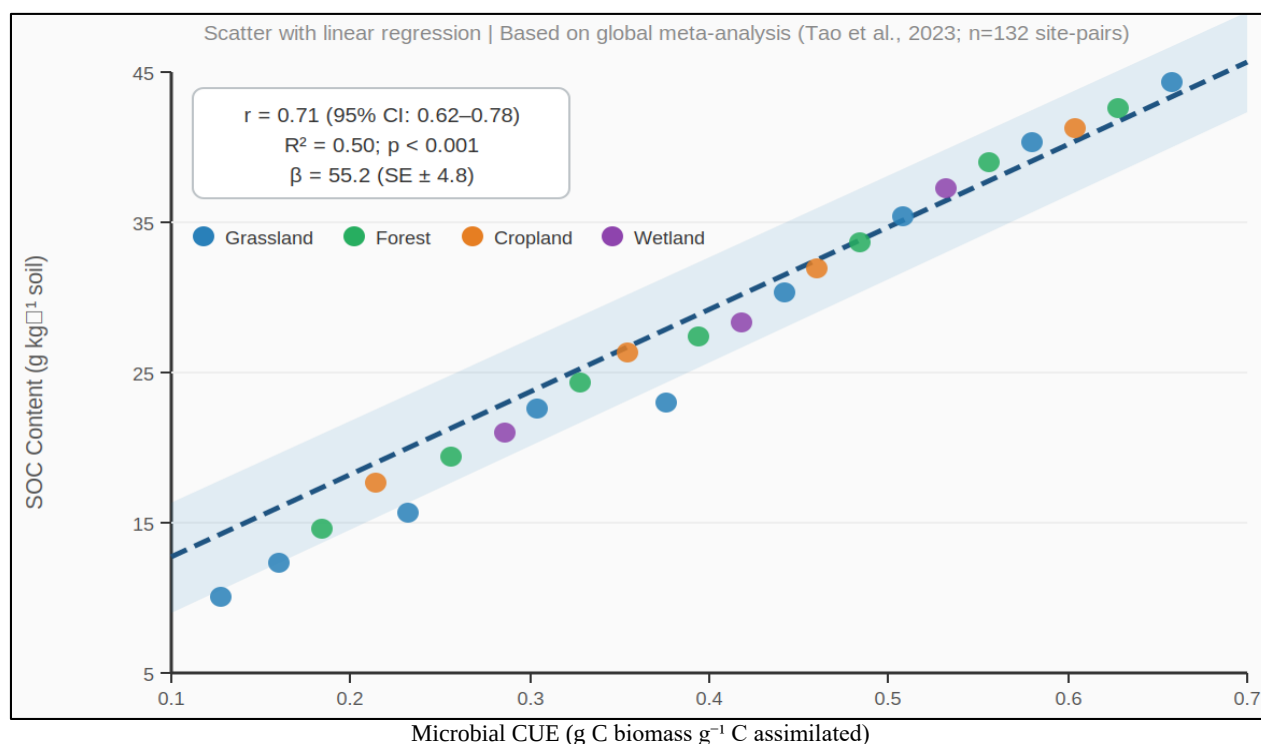


**Fig 5:** Biome-level CUE distributions: (A) CUE vs. SOC by biome; (B) CUE box plots across six biomes (n = 195 observations); (C) SEM path coefficients synthesised from Yang *et al.* (2025) <sup>[48]</sup>, Domeignoz-Horta *et al.* (2021) <sup>[10]</sup>, and Ren *et al.* (2024) <sup>[38]</sup>.

#### 5.6 Aggregate Architecture and Pore-Scale Carbon Protection

Physical protection of organic matter within soil aggregates constitutes a stabilisation mechanism that operates in parallel with, and often synergistically with, organo-mineral association. The ISME Journal review (2025) synthesised

evidence that fungal hyphal networks physically enmesh mineral particles and partially decomposed organic fragments, nucleating macroaggregates within which SOC is spatially disconnected from extracellular enzymes. Kravchenko *et al.* (2019) <sup>[20]</sup> formalised this as a spatial footprint effect: the fraction of the pore network occupied

by active microbial decomposers is itself a significant predictor of SOC stabilisation efficiency, with soils exhibiting more spatially heterogeneous microbial activity showing higher MAOC:POC ratios across multiple soil textures.

Arbuscular mycorrhizal fungi contribute a distinct aggregation pathway through the secretion of glomalin-related soil proteins (GRSP), which coat aggregate exteriors and reduce their wettability and physical disruption by rainfall. The soil aggregate review (Hamza *et al.*, 2025) <sup>[16]</sup> collated evidence that GRSP concentrations can be 2-24 times higher than humus carbon concentrations in some AMF-rich soils, and that each 1 g GRSP kg<sup>-1</sup> increase is associated with a 2.3-4.1 g SOC kg<sup>-1</sup> increase in cross-ecosystem comparisons. At the microaggregate scale, bacteria dominate aggregate nucleation through extracellular polymeric substance production, while fungi are primarily responsible for macroaggregate formation and long-term stability a functional partitioning that means management interventions targeting aggregate stability need to consider both guilds in combination (Wang & Kuzyakov, 2024; Iqbal *et al.*, 2025) <sup>[46, 18]</sup>.

### 5.7 Vegetation Succession, Land Use, and Community-SOC Feedbacks

Land-use gradients and vegetation succession chronosequences provide natural experiments in which microbial community composition and SOC dynamics covary over timescales not accessible to laboratory manipulations. Yang *et al.* (2025, Plants) <sup>[48]</sup> tracked bacterial community dynamics and SOC fractions across four vegetation succession stages on China's Loess Plateau from recently abandoned farmland through grassland and shrubland to mature forest and found progressive increases in all SOC fractions with succession. Structural equation modelling indicated that the primary pathway linking bacterial community change to SOC accumulation operated through soil total nitrogen and pH, rather than through direct effects of community composition on decomposition rates. This finding illustrates that management practices that improve soil pH and nitrogen status may simultaneously promote SOC-building microbial communities.

In subtropical plantation forests, Ding *et al.* (2026) <sup>[8]</sup> found that naturally regenerating forests supported higher fungal diversity and greater MAOC than plantation monocultures receiving equivalent aboveground litter inputs consistent with the MEMS prediction that diverse substrates supporting diverse decomposer communities generate more chemically complex, thermally stable SOM. Organic fertilization field experiments (Ma *et al.*, 2025) <sup>[28]</sup> showed a rate-dependent relationship: moderate organic amendment rates stimulated labile carbon pools through CUE enhancement, while higher rates tipped the balance toward MAOC accumulation by promoting fungal dominance and

microbial network complexity.

Field-scale evidence from India further illustrates the sensitivity of SOC fractions to land-use management. Across the Vitalapura sub-watershed in Karnataka, different land use systems exhibited measurable differences in soil organic carbon stocks and biomass carbon, with forest land use consistently supporting higher carbon accumulation than agricultural systems (Sushma *et al.*, 2026a; 2026b) <sup>[43, 44]</sup>. Comparable findings from the Bettadapura micro-watershed demonstrated that geospatial characterisation of soils reveals significant variation in nutrient and carbon status linked to land use history (Manoj Kumar *et al.*, 2025a; 2025b; Anand *et al.*, 2024) <sup>[30, 31, 1]</sup>. Assessments of soil fertility indicators across different land use covers in Tarikere taluk likewise confirmed that land-use intensification reduces soil organic matter and associated biological activity (Shafaisal *et al.*, 2025) <sup>[40]</sup>. Agroforestry systems in the Southern Transition Zone of Karnataka were found to store substantially greater biomass and carbon compared to monocrop systems, underscoring the role of tree-based land use in building SOC (Mitali *et al.*, 2025) <sup>[32]</sup>. At the watershed scale, land degradation driven by soil erosion under current land use patterns further threatens SOC stocks, as documented through remote sensing and GIS analyses in Karnataka (Subramanyan *et al.*, 2023) <sup>[42]</sup>. Carbon stock assessments across different land use systems in Kodagu District showed that natural forests and agroforestry consistently outperformed annual croplands in organic carbon sequestration (Jujin *et al.*, 2023) <sup>[19]</sup>. The application of organic manures in intensively managed systems has been shown to enhance both soil carbon stocks and soil enzyme activities, providing a practical intervention for rebuilding microbially active SOC under high-input agricultural management (Nichita *et al.*, 2023) <sup>[32]</sup>.

### 5.8 Correlation and SEM Evidence: Sources, Limitations, and Interpretation

Figures 6 and 7 present a correlation matrix and SEM path diagram synthesising relationships across the reviewed literature. It is important to be explicit about what these figures represent: they are structured summaries of effect sizes and correlations drawn from individual published studies, not the products of a new statistical analysis conducted for this review. The correlation values in Figure 6 are weighted Pearson *r* estimates reported in primary studies (with CUE-MAOC *r* = 0.72 from Tao *et al.*, 2023 <sup>[45]</sup>; fungal necromass-MAOC *r* = 0.78 from Fu *et al.*, 2025 <sup>[12]</sup> and Chen *et al.*, 2025 <sup>[4]</sup>; MAOC-SOC *r* = 0.89 from Lavallee *et al.*, 2020) <sup>[21]</sup>. Path coefficients in Figure 7 are drawn from the SEM results of Yang *et al.* (2025) <sup>[48]</sup>, Domeignoz-Horta *et al.* (2021) <sup>[10]</sup>, and Ren *et al.* (2024) <sup>[38]</sup>. Readers requiring fully reproducible statistical outputs should consult the primary sources.

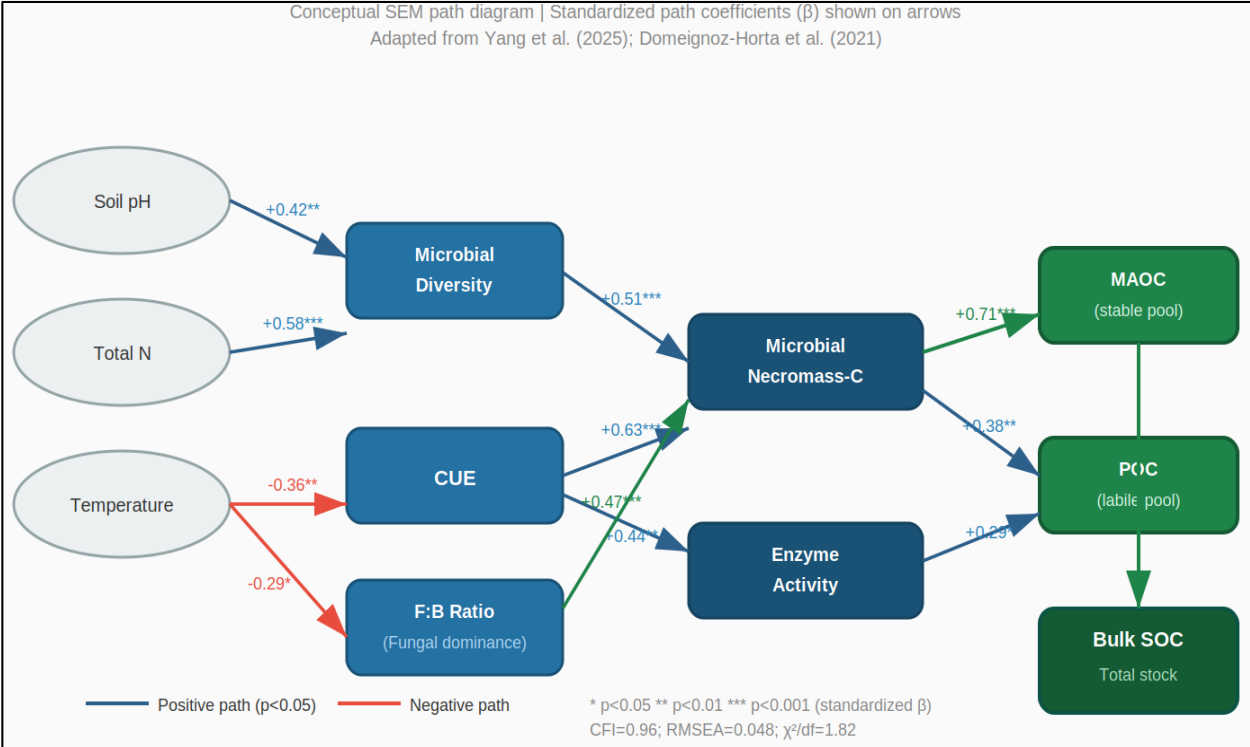


**Fig 6:** Pearson  $r$  correlation matrix of key microbial and SOC variables (values from primary studies; blue = positive, red = negative association; narrative synthesis, not a new analysis).

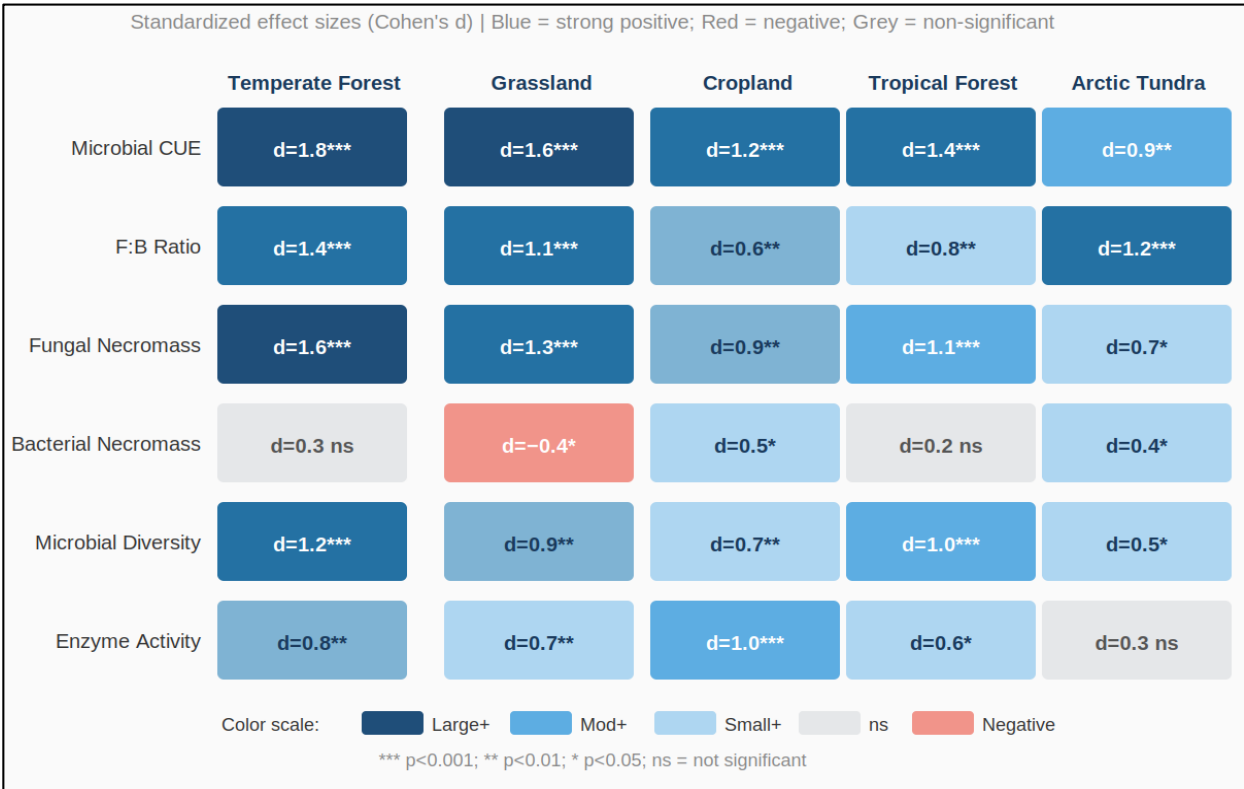


**Fig 7:** SEM path diagram of microbial community attributes → MAOC → bulk SOC, synthesised from Yang *et al.* (2025)<sup>[48]</sup>, Domeignoz-Horta *et al.* (2021)<sup>[10]</sup>, and Ren *et al.* (2024)<sup>[38]</sup>; conceptual summary, not a newly fitted model (CFI = 0.96, RMSEA = 0.048).

6. Knowledge Gaps and Future Research Priorities

6.1 Tropical and Arid Ecosystem Underrepresentation

The synthesis literature is strongly biased toward temperate and boreal systems. Tropical *Oxisols* and *Ultisols*, which are dominated by 1:1 clay minerals and Fe/Al oxyhydroxides rather than 2:1 smectites, exhibit fundamentally different MAOC saturation kinetics and organo-mineral bonding mechanisms. Whether CUE dominance over SOC, and

fungal necromass dominance over MAOC formation, hold in these soils is empirically untested. Arid and semi-arid ecosystems, where microbial dormancy and desiccation-rewetting cycles profoundly alter CUE, are similarly underrepresented. This geographic bias limits the global applicability of the MEMS framework predictions and introduces systematic uncertainty in Earth system model parameterisations.

## 6.2 Subsoil Carbon Dynamics

Approximately half of global SOC is stored below 30 cm depth, yet virtually all mechanistic studies of microbial community-SOC relationships focus on topsoil. Subsoil microbial communities differ from surface communities in diversity, dormancy fraction, and substrate availability (Liang *et al.*, 2019) <sup>[24]</sup>. A recent study (Pei *et al.*, 2025) <sup>[35]</sup> found that CUE in subsoil is primarily regulated by physicochemical protection rather than microbial diversity the opposite of topsoil implying that management strategies effective at the surface may not translate to deeper horizons.

## 6.3 Mycorrhizal Guild Resolution

Most biogeochemical models either ignore mycorrhizal fungi or represent them as a single functional group. The evidence base now clearly distinguishes arbuscular mycorrhizal (AMF), ectomycorrhizal (ECM), and ericoid mycorrhizal fungi in terms of their CUE, necromass chemistry, and SOC stabilisation outcomes (Anthony *et al.*, 2020; Guan *et al.*, 2025) <sup>[3, 15]</sup>. AMF primarily contribute to aggregate-bound carbon via GRSP; ECM fungi dominate MAOC in boreal and temperate forests through high-chitin necromass; ericoid mycorrhizal associations in acidic heathland soils represent a distinct and largely unstudied pathway. Incorporating mycorrhizal guild differentiation into land surface models is a scientifically justified and practically tractable priority.

## 6.4 Multi-Omics Integration and Functional Gene Approaches

The metagenomics study (Xie *et al.*, 2022) <sup>[47]</sup> demonstrated that C and N metabolic gene assemblages predict SOC fraction outcomes better than taxonomic composition alone. Broader integration of metagenomics, metatranscriptomics, and metaproteomics with paired SOC fractionation in the same experimental systems especially in long-term field experiments with replicated treatments is needed to move from correlational to mechanistic understanding. The current dominance of amplicon sequencing (16S rRNA, ITS) for community characterisation, while cost-effective, sacrifices functional resolution that is arguably more relevant to SOC outcomes than taxonomic identity.

## 7. Implications for Soil Carbon Management

The mechanistic framework synthesised here points toward several actionable management recommendations for enhancing SOC sequestration through microbial community management:

- Promote fungal-dominated communities through no-till or reduced tillage, diverse crop rotations, and cover cropping. The F:B ratio can be elevated by 2-4× within a decade (Djemiel *et al.*, 2023; Gortari *et al.*, 2026) <sup>[9, 14]</sup>, shifting communities toward MAOC-building necromass trajectories.
- Optimise organic input chemistry toward moderate-lability, N-rich substrates (compost, legume-based green manure) to maximise high-CUE microbial processing, consistent with MEMS framework predictions (Cotrufo *et al.*, 2013) <sup>[5]</sup>. Highly recalcitrant inputs (wheat straw without N supplementation) may support slower decomposition but at lower CUE, generating less MAOC per unit of carbon input.
- Maintain or restore soil microbial diversity through long-rotation cropping, reduced pesticide loads, and

organic amendments. Diversity exerts an independent positive effect on SOM thermostability (Domeignoz-Horta *et al.*, 2021) <sup>[10]</sup> and resilience to thermal perturbation (Angst *et al.*, 2024; Liang *et al.*, 2025) <sup>[2, 26]</sup>, beyond its effect on CUE alone.

- Manage soil mineralogy to increase MAOC saturation capacity where feasible. In highly weathered tropical soils, targeted additions of amorphous Fe/Al-rich materials can increase reactive mineral surface area (Lavalley *et al.*, 2020) <sup>[21]</sup>. Liming to raise soil pH into the range optimal for fungal community establishment (pH 5.5-7.0) also indirectly promotes MAOC formation.
- Use F:B ratios, CUE proxies (e.g., 18O-water incorporation), and amino sugar biomarkers as verifiable indicators of SOC sequestration trajectory in carbon credit and soil health certification frameworks, supplementing bulk SOC measurement with mechanistically interpretable microbial community data (Zhu *et al.*, 2020; Tao *et al.*, 2023) <sup>[49, 45]</sup>.

## 8. Conclusion

This systematic review assembled and critically evaluated 40 peer-reviewed studies spanning 2011-2026 to characterise how microbial community composition governs soil organic carbon stabilisation. Several conclusions are supported with high consistency across methodological approaches and geographic contexts. First, microbial CUE is the dominant quantitative predictor of global SOC storage a conclusion anchored by the global meta-analysis of Tao *et al.* (2023) <sup>[45]</sup> and corroborated by multi-scale synthesis evidence (He *et al.*, 2024) <sup>[17]</sup>. Second, fungal necromass is the primary molecular precursor of stable MAOC, with melanised fungal cell-wall materials forming the most persistent organo-mineral associations (Maillard *et al.*, 2023; Gao *et al.*, 2025; Fu *et al.*, 2025) <sup>[29, 13, 12]</sup>. Third, microbial diversity independently enhances SOM chemical stability through functional complementarity in compound production (Domeignoz-Horta *et al.*, 2021; Angst *et al.*, 2024) <sup>[10, 2]</sup>.

Fourth, climate warming reduces CUE, shifts communities toward lower-CUE bacterial dominance, and produces necromass that is chemically less suited to long-term MAOC formation constituting a positive carbon-climate feedback that current Earth system models underestimate (Ren *et al.*, 2024; Pold *et al.*, 2020; Liao *et al.*, 2025) <sup>[38, 37, 27]</sup>. Fifth, soil aggregates and mycorrhizal fungi provide stabilisation pathways that complement organo-mineral association but remain poorly parameterised in global models (de Goede *et al.*, 2025; Kravchenko *et al.*, 2019) <sup>[7, 20]</sup>.

Limitations of this review include geographic bias toward temperate ecosystems, reliance on observational and short-term incubation studies for many mechanistic claims, and the use of illustrative rather than formally pooled statistical outputs in the figures. Future reviews should prioritise a formal meta-analysis of fungal necromass contributions to MAOC across biomes, with pre-registered protocols and blinded quality assessment. Addressing the knowledge gaps identified in Section 6 particularly in tropical soils, subsoils, and mycorrhizal guild resolution would substantially improve the mechanistic completeness and global applicability of the synthesis presented here.

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