

PERSPECTIVE

Dilemmas in Linking Microbial Carbon Use Efficiency With Soil Organic Carbon Dynamics

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Microbial carbon use efficiency (CUE), the proportion of substrate carbon that soil microorganisms assimilate for growth out of total uptake, is an important parameter affecting soil organic carbon (SOC) (Tao et al. 2023). Although CUE decreases as more carbon is used for respiration, the relationships between CUE and SOC are variable. For example, Wang et al. (2021) reported a positive relationship between CUE and SOC along a forest transect in eastern China, whereas CUE was negatively related to SOC across six temperate forests in USA (Craig et al. 2022). Since CUE can effectively integrate changes in soil microbial community composition and physiology, this parameter has been increasingly incorporated into models to represent microbially mediated SOC dynamics (Tao et al. 2023). However, poor understanding of the relationship between CUE and SOC, as well as the factors driving this relationship (e.g., temperature), may result in unrealistic predictions of SOC (Luo et al. 2024).

There are two competing hypotheses regarding how microbial metabolic pathways drive the relationships between CUE and SOC. First, a higher CUE suggests a stronger ability for SOC sequestration due to increased microbial biomass formation and associated necromass accumulation (Liang, Schimel, and Jastrow 2017; Wang et al. 2021). Second, a higher CUE is often accompanied with larger microbial metabolic activity, which will stimulate SOC decomposition due to the enhanced energy and nutrient requirements (Allison, Wallenstein, and Bradford 2010). There are increasing debates on these two

competing hypotheses, which have contributed to advancing the understanding of CUE and its relationship with SOC (Tao et al. 2023). Here, we provide three emerging issues that can help understanding the relationships between CUE and SOC (Figure 1).

First, CUE can be estimated by several methods, including ^{13/14}C labeling, ¹⁸O-H₂O labeling, stoichiometric models, calorimetry, and metabolic flux analysis. However, various methods are usually based on different concepts, assumptions, and microbial processes, likely leading to uncertainties on understanding CUE and its relationship with SOC. For example, Tao et al. (2023) revealed a positive relationship between CUE and SOC at a global scale without considering the CUE estimation methods. However, when their results are categorized by various CUE estimation methods, there was a negative relationship between CUE and SOC calculated using the stoichiometry model and a positive relationship for studies using labeling (He et al. 2024). Based on the assumptions of the stoichiometric model, soil microorganisms will likely invest more resources (e.g., the production of extracellular enzymes) to acquire nutrients in relatively C-rich environments, resulting in a negative relationship between CUE and SOC (He et al. 2024). In contrast, the labeling methods consider microbial biomass production as a proxy for microbial growth, likely leading to a positive correlation between CUE and SOC since a greater microbial biomass typically supports more

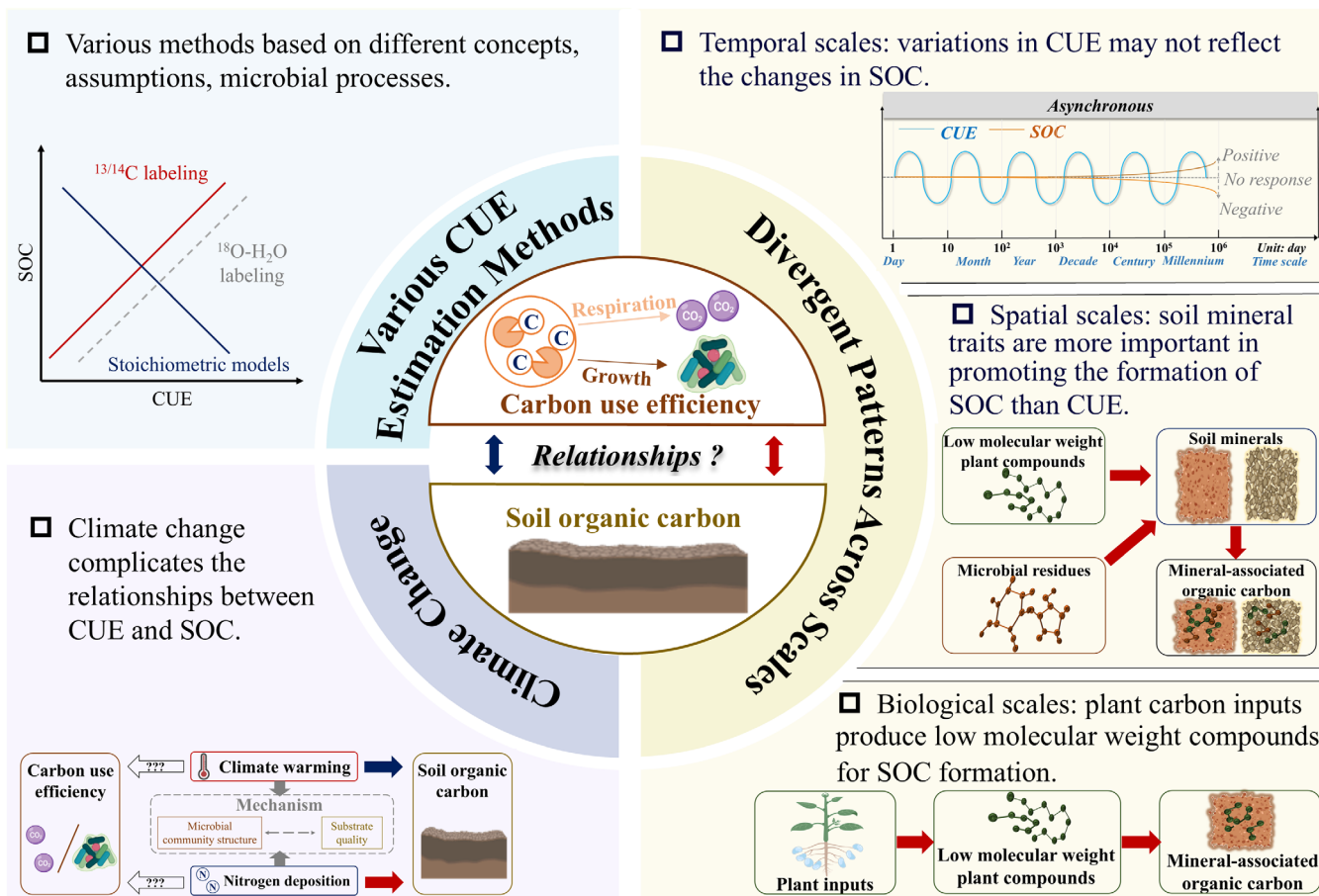


FIGURE 1 | Three fundamental uncertainties to explore the relationships between carbon use efficiency and soil organic carbon. In the upper left section, the red solid line indicates a significant positive relationship, the blue solid line indicates a significant negative relationship, and the gray dashed line indicates a non-significant relationship. In the remainder of the figure, the red single (or double) arrows indicate positive effects, the blue single (or double) arrows indicate negative effects, and the gray arrows indicate uncertain effects. CUE, carbon use efficiency; SOC, soil organic carbon.

microbial residues in SOC (Wang et al. 2021). Furthermore, a significant positive relationship between CUE and SOC was observed under $^{13/14}\text{C}$ labeling rather than $^{18}\text{O}-\text{H}_2\text{O}$ labeling methods (Luo et al. 2024). This is because extra $^{13/14}\text{C}$ substrate addition is more likely to trigger increased microbial biomass than ^{18}O substrate. Therefore, understanding the limitations of various CUE estimation methods can be beneficial in examining the relationships between CUE and SOC.

Second, the relationship between CUE and SOC displays divergent patterns and is influenced by different factors across various temporal, spatial and biological scales, complicating their relationships.

- i. Regarding temporal scales, CUE is a dynamic metric that responds within days or weeks to rapid changes in environment (Allison, Wallenstein, and Bradford 2010). For instance, Ren et al. (2024) showed responses of CUE to temperature gradients within a one-day incubation. Conversely, it may take years to document significant changes in SOC, such as the stabilization of microbial necromass within soil aggregates or its association with minerals (Liang, Schimel, and Jastrow 2017). Hence,

short-term variations in CUE may not necessarily reflect the long-term changes in SOC.

- ii. Across spatial scales, the relationships between CUE and SOC depend on the stabilization of microbial residues with minerals via adsorption, occlusion, and aggregation (He et al. 2024). Indeed, soil mineral traits usually define the upper limit for mineral-associated organic carbon stocks and play more important roles than CUE in determining SOC dynamics across spatial scales.
- iii. Regarding the biological scales, SOC is the balance of plant-derived carbon inputs and microbially-mediated decomposition. Plant carbon inputs can directly produce low molecular weight compounds (e.g., root exudates) or be indirectly converted into low molecular weight compounds through extracellular enzymes for SOC formation, which operates independently of microbial transformation (Liang, Schimel, and Jastrow 2017). For example, experimental warming and nitrogen addition significantly changed SOC content by altering net primary productivity, while CUE remain constant (Knorr et al. 2024). Therefore, plant productivity has been suggested as a more significant factor than CUE in explaining SOC dynamics.

Third, the relationships between CUE and SOC are becoming more complicated under climate change. Knorr et al. (2024) reported that warming decreased SOC content, but the effect of warming on CUE was still under debate due to the differing temperature sensitivities of microbial growth and respiration (Ren et al. 2024). Moreover, numerical simulations revealed that the relationships between CUE and SOC were largely dependent on the relationships between CUE and temperature (Luo et al. 2024). In addition, long-term warming or nitrogen deposition could suppress CUE by reducing substrate quality, as the decomposition of low-quality substrates requires more energy. In return, low-quality substrates may shift microbial communities towards K-strategists, which may increase CUE (Ren et al. 2024). Altogether, climate change may affect the substrate quality and microbial communities in unpredicted ways, complicating the relationships between CUE and SOC.

To better understand the relationships between CUE and SOC, we recommend three potential solutions. (i) CUE estimation methods, including experimental procedures and relevant terminologies, should be standardized to facilitate the wider comparison across studies. It is essential to understand the advantages and disadvantages of the various methods before choosing the appropriate method for individual studies. New techniques for more accurate CUE estimations are also required. (ii) A better understanding of specific SOC pools that are more responsive to environmental changes, such as soil necromass or labeled SOC compositions, will help reveal the relationships between CUE and SOC. For example, by using microbial biomarkers and isotope labeling techniques (Craig et al. 2022), researchers will likely offer insights into the role of CUE on SOC variations across temporal scales. (iii) Enhancing the understanding of CUE in terms of the depth and breadth of temporal resolutions (e.g., high-frequency and long-term measurements), various spatial scales (e.g., various ecosystems, climate zones, and soil depths) and multi-factor climate change simulation experiments (e.g., experimental warming, nitrogen addition and precipitation manipulation), will help elucidate the relationships between CUE and SOC across a range of biotic and abiotic variables.

In many current models, higher CUE was hypothesized to cause SOC accumulation. However, SOC may or may not increase with increasing CUE, highlighting the large uncertainties in these models. For example, a negative relationship between CUE and SOC was found in a microbial-enzyme model, where a decrease in CUE was associated with a reduction in microbial biomass and extracellular enzymes, leading to an increase in SOC (Allison, Wallenstein, and Bradford 2010). Given the complexity of the various microbial metabolic pathways involved in CUE, it might be useful to consider the measurable components of CUE as the core framework in future models, like microbial respiration and growth. In addition, the interaction between various microbial metabolic processes and environmental variables can be characterized by kinetics, which can help reveal the changes in CUE and its relationship with SOC. The huge databases derived from the recent advancements in metagenomics and probe-based technologies may provide unique opportunities to develop an alternative parameter for CUE. For example, the temperature sensitivity of CUE is positively correlated with the abundance of functional genes associated with labile carbon components decomposition, while it is negatively correlated with the abundance

of functional genes related to recalcitrant carbon decomposition, as determined by metagenomic sequencing (Ren et al. 2024). In addition, to better understand CUE variations and their driving factors, models can be designed with CUE as an output that is constrained by the observational data, which may offer another opportunity to better reveal the relationships between CUE and SOC (Allison 2025). From this standpoint, more paired observations on CUE and SOC can help optimize the model parameters, ultimately enhancing the robustness of the model predictions.

In summary, there are still large uncertainties on the relationships between CUE and SOC across (1) different CUE estimation methods, (2) various temporal, spatial and biological scales, and (3) multiple climate change scenarios. These uncertainties call for further efforts to re-examine the relationships between CUE and SOC to better represent microbial processes in the current modeling frameworks. In particular, developing advanced estimation methods and model simulations for CUE requires interdisciplinary research that involves extensive collaboration among mathematicians, soil microbiologists, ecologists, and modelers.

Author Contributions

Jiacong Zhou: conceptualization, funding acquisition, visualization, writing – original draft, writing – review and editing. **Yiqi Luo:** conceptualization, writing – review and editing. **Ji Chen:** conceptualization, funding acquisition, methodology, project administration, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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