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Soil microbial carbon use efficiency and the constraints

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Abstract

Background Microbial contributions to soil organic carbon formation have received increasing attention, and microbial carbon use efficiency is positively correlated with soil organic carbon storage.

Mainbody This work reviews the impact on microbial carbon use efficiency from six constraints, including plant community composition and diversity, soil pH, substrate quality, nutrient availability and stoichiometric ratios, soil texture and aggregates, water and thermal constraints, and external nutrient inputs. In general, the response of microbial carbon use efficiency showed large uncertainty to above constraints, including positive-, negative-, or non-correlation. However, some factors are biased, more likely to promote or inhibit carbon use efficiency. For example, external nutrient input (N, P, K, Ca) tended to promote carbon use efficiency, while climate warming showed more negative influence.

Conclusion Further, overwhelming works focused on single constraint, we suggest the importance to consider the synergistic influence of multiple environmental variables on microbial carbon use efficiency, special for the regulation mechanism of biological-environmental interactions.

Keywords Microbial carbon use efficiency, Environmental constraints, Soil pH, Climate warming, Stoichiometric ratio

Introduction

Loss of soil organic carbon (SOC) is known to accelerate climate warming, whereas store of more organic carbon into soils can help mitigate climate change. Microbial carbon use efficiency (CUE) is defined as the ratio of carbon consumed by microorganisms for their own growth to the sum of carbon consumed for both growth and respiration (Tao et al. 2023; Fig. 1), which is related to both carbon fixation and loss. Increasing studies propose that minor changes in soil microbial CUE have significant impacts on soil carbon storage and gas emissions (Domeignoz-Horta et al. 2020; García-Palacios et al. 2021; Tao et al. 2023). For example, a high soil microbial CUE implies more accumulation of microbial by-products and residues, which can increase soil carbon storage (Liang et al. 2017, 2019; Sokol et al. 2022). Theoretical analysis and empirical observations showed CUE over

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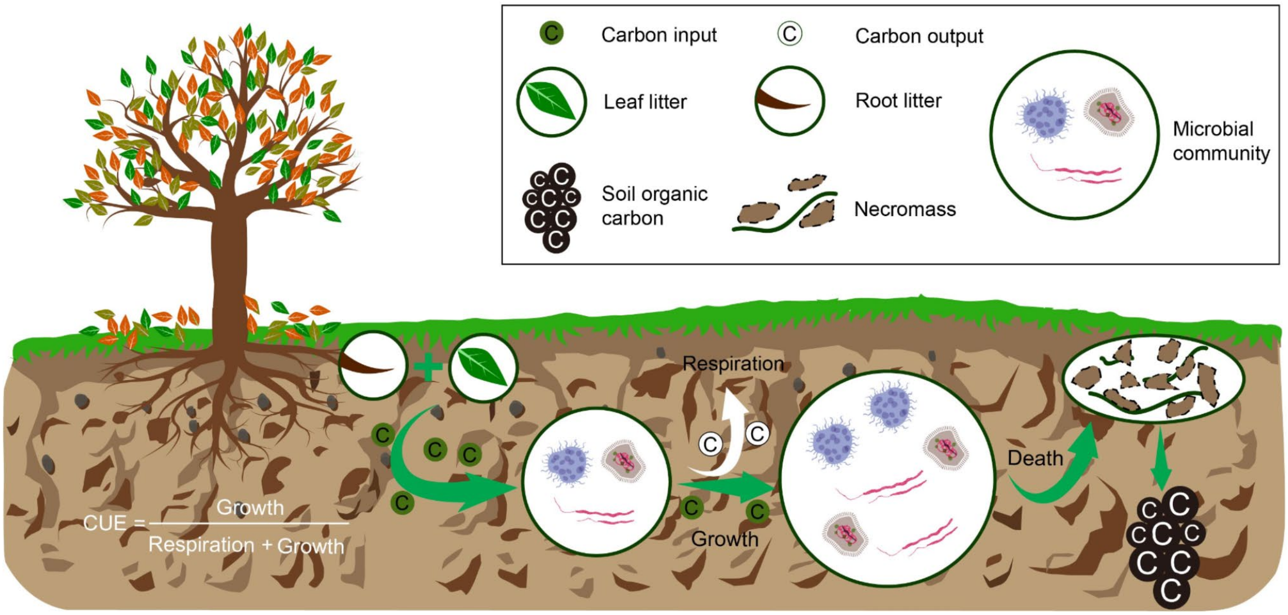

Fig. 1 Soil microbial carbon use efficiency. Plants primarily input carbon into the soil through root exudates and leaf litter. This litter serves as a carbon source for soil microorganisms, with a portion of the carbon released into the atmosphere through respiratory metabolism. Another portion is assimilated into microbial biomass. Upon death, these microorganisms form microbial residues, which contribute to the accumulation of soil organic carbon. Only a small amount of carbon is consumed for the secretion of extracellular enzymes and metabolic products (negligible). Therefore, microbial carbon use efficiency refers to the ratio of carbon consumed by microorganisms for their own growth to the sum of carbon consumed for both growth and respiration

a wide range of field conditions converges around 0.30 (Sinsabaugh et al. 2013). Changes in the abiotic and biotic factors, however, are acknowledged to have a significant impact on soil microbial CUE (Duan et al. 2023; Wang et al. 2023a; Xu et al. 2024).

Up to date, the limited reviews on microbial CUE mainly focused on the methodology, comparing the adaptation conditions and differences of various methods (Manzoni et al. 2012; Frey et al. 2013). For example, each method has its own set of benefits, drawbacks, and application range (Adingo et al. 2021). Some review paper also paid attention to the impact of a certain factor, such as warming (Zhang et al. 2022a), changes in plant types (Zhang et al. 2023a), and biological interactions in soil (Iven et al. 2023). However, the effects of the focused factors on microbial CUE are often multifaceted and unpredictable. A comprehensive analysis of multiple environmental factors remains scarce (Adingo et al. 2021). Here we emphatically discussed on the influences of abiotic and biotic factors on microbial CUE (Fig. 2). It is aimed to provide a comprehensive understanding of the response of microbial CUE to a changing environment, and highlights the focus to improve the prediction of microbial CUE.

Plant community composition and diversity

Currently, numerous studies have confirmed that plant species diversity significantly impacts the composition, activity, and biomass of soil microbial communities (Lu and Scheu 2021; Gottschall et al. 2022; Chen and Hu 2024). Plants shape soil conditions (water content, nutrient input) through litter and root inputs, which can promote microbial metabolism and potentially increase CUE (Iven et al. 2023). It indicates a positive correlation between plant community construction and soil CUE. The existence of plants has increased soil water content, thereby enhancing substrate diffusion and improving microbial CUE (Alvarez et al. 2017; Manzoni et al. 2012; Domeignoz-Horta et al. 2020). Higher plant species diversity and primary production increase the input of plant-derived carbon and nutrient content into the soil (Mori et al. 2020; Peng and Chen 2021). By this means, the resource supply for soil microbial communities is enhanced, promoting faster microbial growth, turnover, and higher CUE (Lange et al. 2015; Craig et al. 2022; Xiong et al. 2023). Duan et al. (2023) found that, with increasing tree species diversity and substrate availability, microbial CUE was also increased. The primary succession of vegetation is also accompanied by an increase in community richness. A study in the Hailuogou glacier retreat area revealed that, with the succession of vegetation, the ratio of oligotrophic to autotrophic microorganisms increased, and CUE gradually increased (Ma et al. 2023a). Moreover, the quantity and type of compounds secreted by plants are specific to plant species (Manzoni et al. 2012). Plants can provide energy sources for microorganisms by secreting labile carbon compounds (Hartmann et al. 2009), which may increase the CUE

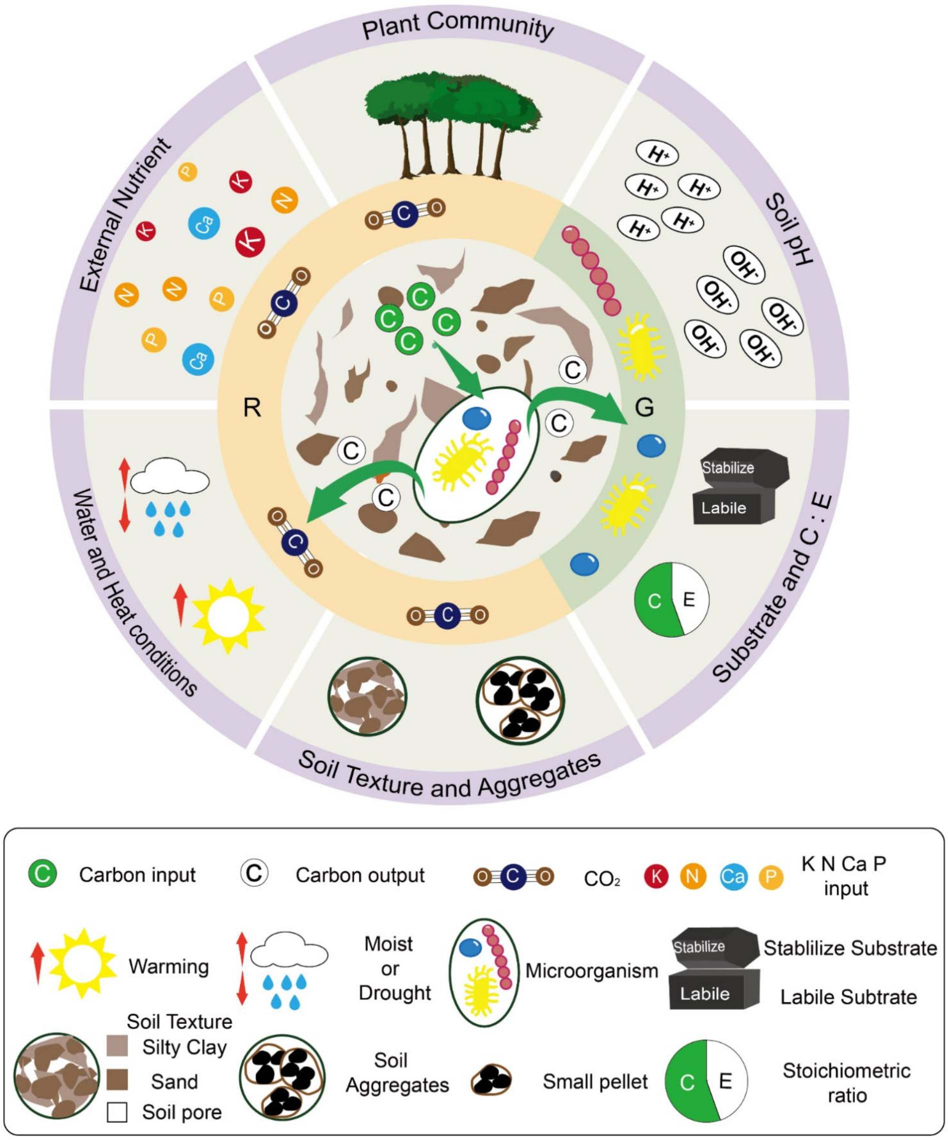

Fig. 2 Response of Soil Microbial Carbon Use Efficiency (CUE) to Different Factors. Microorganisms absorb carbon from the soil, with part of it used for growth(G) and the other part for respiration(R). The inner circle represents the proportion of carbon used for growth in the total carbon absorbed by microorganisms, which is called microbial carbon use efficiency (CUE). Six key factors are covered, starting from the top and proceeding clockwise: plant community composition and diversity; soil pH; substrate quality, nutrient availability and stoichiometric ratios (C: E represents the ratio of carbon (C) content to essential element (E) content in the substrate); soil texture (sand, loam, clay) and aggregates; water and thermal condition limitations (climate warming, drought, and humidity); external nutrient inputs (K, N, Ca, P)

of free-living microorganisms under carbon limitation. Therefore, in general, diverse plant systems have higher microbial biomass and lower respiration rates compared to monocultures (Anderson and Domsch 2010).

Moreover, plants can compete with microorganisms and affect microbial CUE. For example, the abundance of nitrate-reducing bacteria decreases with changes in plant nitrogen use efficiency (Moreau et al. 2015). Through indirect competition, plants may select the proliferation of fast-growing microbes or select for microbes with high investments in resource acquisition. Thus, the community-level CUE is reduced, but such an effect may additionally depend on the plant species involved and environmental context of the rhizosphere (Iven et al. 2023). Further, some plants even produce secondary metabolites (such as jasmonic acid and salicylic acid) (Watson et al. 2015) or utilize toxic compounds (such as indole glucosinolates) (Anthony et al. 2020) to inhibit related microorganisms, potentially reducing CUE. Contrary to the above view, Prommer et al. (2020) found in a diversity experiment in temperate grasslands that plant species richness had no significant effect on microbial CUE. Cascading effects of biotic interactions are widely known to introduce apparent stochasticity to microbial communities, which may be difficult to predict (Powell et al., 2016). When examining the interactions between microorganisms and plants, it's important to analyze specific conditions in detail.

Soil pH value

The soil pH value is a major factor influencing microbial CUE (Wu et al. 2023, 2024; Liu et al. 2024). Two mechanisms are now proposed influencing the microbial community composition and activity. Firstly, under low pH conditions, bacterial growth is suppressed, leading to decrease organic matter availability (Silva-Sánchez et al. 2019). Less resources resulted in a decreased CUE, indicating a close correlation between pH and CUE (Silva-Sánchez et al. 2019). Secondly, pH impacts microbial activity through cellular stress. For example, under low soil pH conditions, the solubility of toxic metals such as Al^{3+} increases, causing cellular stress and subsequently reducing microbial CUE (Wang et al. 2023a; Jones et al. 2019). Additionally, microorganisms in low pH environments may need to expend more energy to maintain pH balance, reducing the energy available for growth and thus decreasing microbial CUE (Wu et al. 2023). However, it was also found that the relationship between CUE and soil pH is not a simple positive linear one. With lime addition to agricultural soil, the overall relationship between CUE and pH followed a U-shaped (i.e., quadratic) curve (Schroeder et al. 2024). This suggested that CUE may reach its highest levels under acidic or alkaline pH conditions and be lowest under near-neutral soil conditions. Sinsabaugh et al. (2016) discovered a significant CUE minimum at a pH of 5.4 in a meta-analysis of global soils, which attributed to changes in the bacterial to fungal ratio.

Substrate quality, nutrient availability, and stoichiometric ratios

Numerous studies have demonstrated that the quality of carbon substrates, nutrient availability, and stoichiometric ratios regulate microbial CUE (Sinsabaugh et al. 2013; Mooshammer et al. 2014; Li et al. 2021). Complex organic compounds typically have lower carbon substrate quality due to their diverse types of chemical bonds and complex structures, requiring more enzymes for decomposition (Sinsabaugh et al. 2013). The incorporation of such low-quality carbon compounds into microbial biomass leads to microorganisms allocating more energy for enzyme production, reducing the energy available for growth and thus decreasing CUE values (Allison 2014). Such as highly oxidized chemicals like oxalic acid are to be integrated into biomass (Hervé et al. 2016). They necessarily consume significant amounts of reducing power (NADH), while generating a relatively minuscule amount of energy compared to glucose (Hervé et al. 2016). As a result, on oxalic acid or phenolic substances, the CUE of soil microbial communities is significantly smaller than on glucose (Frey et al. 2013). The degree of C reduction of the substrate (γS) is another important factor that affects the CUE of soil microorganisms. The γS of the main substrates utilized by microorganisms is usually within the range of 3–5, which is equivalent to the C reduction degree ($\gamma B \approx 4.2$) of soil microorganisms (Roels et al. 1980). When the γS of the substrate is less than 4.2, the microbial CUE is mainly limited by the reduction degree from the substrat. When the γS of the substrate is more than 4.2, the microbial CUE is higher (Roels et al., 1980; Gommers et al. 1988). It is worth noting that the responses of different microbial communities to substrate carbon quality were different. Compared with bacteria exposed to a carbon-rich environment, bacteria exposed to a carbon-limited environment can metabolize a wider range of substrates (von Stockar et al., 2013).

Substrate quality have a significant relative to soil depth. Since the surface soil receives more unstable carbon from surface litter and roots compared to deeper soil layers, this carbon is more readily available for efficient utilization (Zhang et al. 2023b). Deeper soil layers dominated by complex organic compounds lack readily available organic carbon in the form of plant debris and rhizodeposits. This suggesting that CUE may decrease with increasing soil depth. On one hand, under such conditions, it may reduce the decomposition of organic carbon in deeper soil layers (Agren and Bosatta 1987). On the other hand, as soil depth increases, the availability and quality of soil C substrates decrease. As organic carbon concentrations decrease, the benefits of organic carbon decomposition for microorganisms become smaller. The effect of soil depth on microbial CUE may be amplified by changes in organic matter quality, especially for compounds that require extensive enzymatic reactions for degradation (Agren and Bosatta 1987). Even if the microbial community possesses all the enzymes decomposing organic compounds, microorganisms must invest a significant amount of C and N in producing extracellular enzymes, thereby reducing microbial CUE. (Agren and Bosatta 1987; Manzoni and Porporato 2009). Zhang et al. (2023b) discovered that CUE decreased as soil depth in alpine grasslands on the Tibetan Plateau, microbial CUE showed significant negative correlation with microbial biomass-specific hydrolytic enzyme activity.

Under nutrient-limited conditions, microbial CUE decreases accordingly. Microorganisms adapt to nutrient-limited environments by altering their metabolic strategies with more energy in producing enzymes related to nutrient acquisition, which results in excess carbon overflow for respiration (Manzoni et al. 2012; Geyer et al. 2016; Mehnaz et al. 2019). Soil CUE decreased significantly due to phosphorus limitation (Mganga et al., 2022). High nutrient availability (simple SOM chemical structure and weak mineral-organic associations) is accompanied by high microbial CUE (Duan et al. 2023). Stoichiometric studies have shown that the C: N ratio can also significantly influence microbial CUE (Manzoni et al. 2012; Sinsabaugh et al. 2013; Takriti et al. 2018). At environments with a high C: N ratio (>10), microorganisms consume excess carbon through overflow respiration or producing other metabolites (such as proteins), thereby reducing CUE (Manzoni et al. 2012).

Soil texture and aggregates

Soil texture has an impact on soil water effects, with coarser-textured soils having lower water content compared to finer-textured soils. In theory, Microorganisms in coarser-textured soils may be more prone to diffusion limitations associated with low water content, resulting lower CUE (Butcher et al. 2020). However, contrary to expectations, the content of clay was negatively correlated with the content of CUE (Oliver et al. 2021). Studies have found that sandy soils have higher microbial CUE and lower biomass turnover times compared to clay soils (Li et al. 2021; Pei et al. 2021). A reasonable explanation is that clay content strongly affects the diffusivity of the matrix and the accessibility of microorganisms (Krull et al. 2003). Substrate are stabilized by interactions with clay mineral surfaces. (Krull et al. 2003; Li et al. 2020a). It is mean that higher clay content can better bind with the substrate, reducing its diffusivity. Additionally, higher clay content also has reduced the accessibility of substrates to microorganisms by physically protection (Li et al. 2020b).

Soil aggregates directly affect microbial growth and activities by providing diverse environments for microorganisms (Hattori, 1988). In return, microorganisms are usually involved in the formation of aggregates by binding between particles (Lehmann, J. et al. 2015). The reason that macroaggregates have a higher CUE than microaggregates is that microaggregates have higher carbon stability, making them more difficult for microorganisms to utilize. (Bimüller et al. 2016; Najera et al. 2020). The SOM of microaggregates is formed by primary particles of plant and microbial debris combined with humus substances or polysaccharide polymers. Humus substances or polysaccharide polymers can better protect organic matter from decomposition (Kimura et al. 2012; Denef et al. 2007). The low degradability of SOC in microaggregates reduces microbial mineralization (Tian et al. 2016), which may result in lower CUE. This conjecture has also been proved (Zhao et al. 2022; Li et al. 2024). Diverseness in soil aggregate structure also imply complex nutrient supplies, leading to in organic matter degradability and microbial CUE (Mo et al. 2021). Macroaggregates usually represent an important site of nutrient (e.g., N, P) accumulation (Green et al. 2005; Fonte et al. 2014). SOM has been proven to be more efficiently decomposed in N- and P-modified soils (Li et al., 2014). Therefore, compared with microaggregates, the SOM of macroaggregates appears to have higher degradability, leading to larger microbial CUE (Tian et al. 2016).

Constraints of water and thermal conditions

The constraints of soil water and thermal conditions have significant impacts on soil microbial CUE, particularly in the context of climate warming and changes in soil moisture (Classen et al. 2015; Tian et al. 2023; Liu et al. 2024). Climate warming lead to an increase in temperature, temperature increases often trigger other chain reactions, and their impact on CUE is multifaceted. Higher temperature, on one hand, can lead to an increase in CUE and accelerate SOM decomposition. A five-year experiment found that warming trigger fundamental changes in the physiology of microbial communities in tropical forest soil, increasing CUE (Nottingham et al. 2019). On a global scale, Ye et al. (2019) incorporated microbial CUE and the relationship between mean annual temperature (MAT) and enzyme kinetics-MAT into a SOC model. By datasets of measured respiration (including 110 dryland soils distributed globally and two mainlands to global-scale cross-biome datasets), this work found a positive CUE-MAT relationship. In other words, microbial CUE tends to increase with increasing MAT, possibly because the availability of plant carbon inputs is generally higher in warmer climates (Bardgett et al. 2008).

On the other hand, some studies have found that CUE is resistant to warming, because of thermal adaptability of microorganisms. Simon et al. (2020) conducted measurements of soil microbial growth, CUE, and respiration under three distinct temperature and atmospheric CO_2 levels, as well as summer drought conditions. The authors found the individual and combined effects of climate change treatments on microbial growth and respiration rate were significant. But microbial CUE at the community level remains almost stable regardless of treatment or season. Similarly, study have found that the CUE of temperate forest soil in the 0–40 cm depth did not change significantly in response to warming (Spohn et al. 2016a). This situation is also found in a 3.3-year warming experiment with a 4 °C increase in the 0–100 cm depth of alpine grassland soil on the Qinghai-Tibet Plateau (Zhang et al. 2023b) or a 2-year warming experiment with a 4 °C increase in the 0–100 cm depth of tropical forest soil (Nottingham et al. 2020). The response of microbial CUE to warming also varies at different soil depths, which may be due to the difference in substrate structure and microbial community. For a short-term (110-day) experiment on soil warming in alpine grassland, it was revealed that nitrogen limitation induced by warming reduced microbial CUE in the subsoil (30–40 cm), but not for the topsoil (0–10 cm) (Zhu et al. 2021). In another 4.5-year soil warming experiment with an increase of 4 °C, CUE was found to remain unchanged in the 0–60 cm depth, but decreased below 60 cm depth (Dove et al. 2021). In summary, the effect of climate warming on soil microbial CUE remains uncertain with complex enviroment of soil depth.

CUE is frequently reported to be reduced as the temperature increased (Frey et al. 2013; Rivkin and Legendre 2001; Wetterstedt and Agren 2011). The rate of maintenance respiration usually increases faster than the rate of new microbial biomass production under warming (Frey et al. 2013). Through a microbial-enzyme model to simulate the soil carbon response to a 5 °C temperature rise, it was found that CUE decreased under warming conditions (Allison et al. 2010). On a longer timescale, a 26-year soil warming experiment also revealed a decrease in CUE due to climate warming (Melillo et al. 2017). Shi et al. (2023) found through a 10-year forest soil warming experiment that soil warming led to increased non-biological adsorption of phosphorus. This condition lowered the availability of soil phosphorus, ultimately resulting in phosphorus limitation. To obtain the necessary phosphorus for growth, microorganisms increased the secretion of phosphatases, thereby reducing the carbon used for growth. Li et al. (2018) combined a microbial enzyme model with 22 years of carbon cycle measurements in Harvard Forest, using a probabilistic inversion method. They found that the increased temperature reduced CUE, and soil warming increased the temperature sensitivity of CUE. Notably, in an 11-year warming experiment, traditional tillage topsoil showed a 77% decrease in CUE due to warming, while CUE under conservation tillage increased by 29.1% (Wang et al. 2022). Microorganisms were regarded to effectively utilized richer and higher-quality substrates to build biomass during conservation tillage (Wang et al. 2022). In terms of most studies, the response of CUE to warming tends to decrease. However, considering the changes in microbial communities, the increase in carbon input, and the thermal adaptability of microorganisms that may be caused by warming, its specific response requires further analyzed.

Soil moisture regulates microbial activity through two primary physical mechanisms. The first one is the drying effect caused by low water potential. The decrease in extracellular water potential requires the accumulation of compatible solutes within microbial cells to balance the extracellular and intracellular water potentials (Rath and Rousk 2015; Rath et al. 2016). The second is the substrate diffusion limitation due to low water content (Herron et al. 2009). Substrate diffusion limitation is a physical constraint on soil microbial communities, limiting access of microbial communities to substrates (Weerts et al. 2001). But the influence of soil moisture on microbial CUE still needs to be specifically discussed. Study have found that drought conditions increased the fungal-to-bacterial ratio, thereby enhancing microbial CUE (Sun et al. 2022; Butcher et al. 2020). Similarly, in a short-term water stress event, CUE increases as osmoregulatory solutes and storage compounds are accumulated (Uhlırova, et al. 2005; Herron et al. 2009). However, in the long-term water stress event, CUE is reduced by repeated stress events, as the C costs for water stress responses become apparent (Tiemann and Billings 2011). Microorganisms also exhibit different responses under different humidity conditions, which further affect microbial CUE. Only under high humidity conditions, microbial species exhibit complementary effects by cross-feed shared resources (e.g., one species can utilize degradation products from neighboring species as substrates for growth). These effects enable more efficient growth, which may benefit microbial CUE (Domeignoz-Horta et al. 2020). In conclusion, when the interaction of microorganisms is not considered, short-term drought tends to reduce CUE, but the effect may be opposite under long-term drought.

External nutrient input

Most studies have found that under the condition of applying only N or adding N, P, and K simultaneously, CUE tends to increase (Poeplau et al. 2019; Zhang et al. 2022; Xu et al. 2024). The increase in CUE under N addition conditions can be attributed to several factors. First, it inhibits microbial respiration, which leads to an imbalance in the C: N ratio. This imbalance, in turn, enhances nitrogen utilization efficiency and reduces carbon investment in the production of extracellular enzymes for nitrogen acquisition. (Malik et al. 2020; Wang et al. 2023b; Yang et al. 2023). Second, some studies propose that the increase in CUE is not driven by stoichiometric imbalance. Instead, a decrease in the mineral protection of SOC increases the accessibility of microorganisms to carbon. (Feng et al. 2022). N induction led to changes in fungal composition, resulting in the production of more oxalic acid and causing changes in plant characteristics and community composition. Both of these aspects weakened mineral protection (Feng et al. 2022), organic matter is decomposed into smaller and more easily degradable molecular compounds, which are more conducive to microbial absorption and assimilation (Wallenstein and Weintraub 2008). Nitrogen-induced stress, such as soil acidification (Treseder 2008), may also trigger energy-intensive metabolic pathways or even directly cause microbial death (Jones et al. 2019; Horn et al. 2021), thus affecting microbial CUE.

Ma et al. (2023b) conducted a study examining the microbial CUE of soil layers after nitrogen fertilizer application. In contrast to previous findings, the authors observed that both short-term (2 years) and long-term (10 years) nitrogen addition did not significantly affect microbial CUE. It attributed to the slight increase in carbon allocation to microbial biomass production, which was insufficient to significantly change CUE (Ma et al. 2023b). In a similar study, Jiang et al. (2024) found that nitrogen fertilizer application in tropical forests did not affect the CUE of surface soil (0–10 cm). However, the CUE in deep soil (60–80 cm) increased by 25.5%, likely due to the decreased ratio of fungi to bacteria and the C: N ratio. In a 6-year nitrogen addition experiment, it was also found that the decrease in the ratio of fungi to bacteria in temperate grasslands led to a decrease in CUE (Riggs and Hobbie 2016).

Long-term fertilization (N, P, K) conditions enhanced microbial CUE (Li et al. 2021). Adding nitrogen and phosphorus to the soil likely reduces metabolic costs for microorganisms to acquire nutrients. It also eliminates the need for additional enzymes and enables more carbon to be used for growth, ultimately enhancing CUE (Manzoni et al. 2012; Spohn et al. 2016b). Xu et al. (2024) found that the microbial CUE in soil treated with mineral fertilizer (N, P, K) alone increased by 22% compared to unfertilized soil. Additionally, the addition of Ca can also influence soil microbial CUE. Ca addition, on one hand, can promote bacteria production and affect the microbial community. On the other hand, it enhances the stability of microbial by-products by increasing the binding of litter and microbial by-products, resulting in a 45% increase in CUE (Shabtai et al. 2023). In general, if the input of external nutrients does not significantly change the ratio of fungi to bacteria in the soil, it tends to increase microbial CUE.

Prospects

From a research perspective on soil microbial CUE, most current studies concentrate on single-site, single-factor impacts. These studies primarily examine changes in fungal and bacterial functional groups, carbon substrate quality, nutritional limitations, as well as the impacts of carbon, nitrogen, and phosphorus addition, organic fertilizer application, temperature rise, soil pH, moisture, aggregate size, and plant community composition and changes (Fig. 2). Given the complex interactions between soil, plants, and microorganisms, future research should pay more attention to the combined effects of multiple factors on soil microbial CUE.

In consideration of soil layers observed for soil microbial CUE, many studies concentrate primarily on the 0–15 (20) cm surface soil layer, overlooking the CUE at deeper soil depths. Moreover, further research should encompass other aspects, such as temperature sensitivity and substrate quality, across different soil depths. A comprehensive investigation is warranted to elucidate how the soil microbial CUE varies with the multi-factorial changes across soil profile.

As regards the types of ecosystems observed for soil microbial CUE, present studies cover diverse types of ecosystems. Study places significant focus on the comparison and analysis among different ecosystems, including farmland, grassland, shrubland and forest but blue carbon habitats, also, deserve more attention. Currently, the time range of studies tends to be short-term. Additionally, in compared to local study, comprehensive focus on a global scale is still limited, but necessary.

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L.X. and G.H. conceptualized this study; R.D., J.L., L.X., E.L., L.Z., M.Z. have participated in writing the original draft of manuscript.

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Data availability
Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
Leilei Xiao is an Associate Editor for Annals of Microbiology. The authors declare that they have no other competing interests.

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