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META-ANALYSIS

Contrasting Exogenous and Endogenous Soil Microbial Carbon Use Efficiencies Under Global Changes

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Keywords: carbon input | drought | global changes | microbial endogenous carbon use efficiency | microbial exogenous carbon use efficiency | nutrient inputs | warming

ABSTRACT

Aim: Microbial carbon use efficiency (CUE) is one of the key indicators for the formation and release of soil carbon. CUE can be divided into exogenous CUE (CUE_{ex}, efficiency in using external carbon sources measured by e.g. ^{13}C or ^{14}C labeling) and endogenous CUE (CUE_{en}, efficiency in using internal carbon sources measured by ^{18}O labeling). Global changes strongly influence CUE, which response depends on the carbon source. However, the effect size and drivers of CUE_{ex} and CUE_{en} responses to global changes remain unclear, leading to large uncertainties when forecasting terrestrial carbon cycling. We aimed to quantify the magnitude and direction of microbial CUE_{ex} and CUE_{en} responses to global changes.

Location: Global.

Time Period: 2011–2024.

Major Taxa Studied: Soil microorganisms.

Methods: Database containing 213 paired microbial CUE_{ex} and 155 paired microbial CUE_{en} data was integrated and meta-analysed to assess the impacts of global change factors on microbial CUE. Additional information gathered encompassed latitude, longitude, climate, plant properties, soil properties, microbial properties and experimental conditions.

Results: We found that CUE_{ex} decreased with absolute latitude, while CUE_{en} showed the opposite trend. Warming reduced CUE_{ex} and CUE_{en} by 3.6% and 16.5%, respectively. Drought increased CUE_{ex} by 7.9%, but decreased CUE_{en} by 14.3%. Nutrient inputs consistently decreased CUE_{ex} by 5.0%–17.1%, while nitrogen and nitrogen combined with phosphorus and potassium inputs increased CUE_{en} by 25.5% and 43.1%, respectively. Aridity index, soil pH and cation exchange capacity were the main factors influencing microbial CUE_{ex}. In contrast, microbial respiration and growth rates, followed by microbial biomass, were the major predictors of microbial CUE_{en}.

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Main Conclusions: Biogeochemical models should account for the opposite spatial patterns of microbial CUE_{ex} and CUE_{en}, as well as their respective specific drivers under global changes, to accurately predict microbial responses to various carbon sources.

1 | Introduction

The Earth and its ecosystems are currently facing multifaceted challenges arising from global change factors including warming, droughts, anthropogenic nutrient inputs (nitrogen (N), phosphorus (P) and potassium (K)) and non-native plant invasions. These factors impact the soil organic carbon (SOC) feedback to changing global conditions (Walker et al. 2018). Soil microorganisms play a critical role in the regulation of soil C dynamics in response to the global changes listed above through their physiological mechanisms, such as vivo turnover and ex vivo modification (Liang et al. 2017). While previous studies have focused on the role of soil microorganisms in the decomposition of organic matter, it has increasingly been recognised that microorganisms also facilitate soil C sequestration through anabolic processes (Wieder et al. 2013; Zhu et al. 2022). Therefore, the C use efficiency (CUE) of soil microorganisms, defined as the efficiency of microorganisms in converting organic C inputs to biomass C, has been recognised as a critical indicator of microbial anabolism related to soil C sequestration (Tao et al. 2023). Thus, an accurate quantification of the responses of microbial CUE to global changes is therefore critical for the prediction of microbial involvement in the formation, transformation and stabilisation of soil C under various environmental stimuli.

Soil microorganisms not only utilise exogenous C from plant litter for their growth but also endogenous C from soil organic matter. Microbial CUE is divided into two categories based on its C source: microbial exogenous CUE (CUE_{ex}) and microbial endogenous CUE (CUE_{en}). Microbial CUE_{ex} is measured using the stable ^{13}C isotope labeling approach, which tracks the incorporation of exogenous C into microbial phospholipid fatty acids (Brant et al. 2006). Notably, microbial CUE_{ex} gradually declines as the substrate is consumed and can also confound the C absorbed into cells with the C bound to biomass (Geyer et al. 2019). In contrast, microbial CUE_{en} is quantified without substrate addition using ^{18}O-labelled water. This approach is based on the incorporation of ^{18}O from ^{18}O-labelled water into microbial DNA during cell growth and then uses a DNA/microbial biomass carbon (MBC) ratio to calculate the MBC formed and compares that to total CO_2 production to calculate microbial CUE_{en} (Spohn et al. 2016). This technique assumes that water is the only source of oxygen required for microbial growth. It is important to distinguish between CUE_{ex} and CUE_{en}, as traditional biogeochemical models often assume a fixed or temperature-dependent microbial CUE without accounting for these differences (Allison et al. 2010). It remains unclear whether the magnitudes and spatial patterns of microbial CUE_{ex} and CUE_{en} are consistent due to differences in the quality of exogenous and endogenous C.

Global changes have been shown to impact microbial CUE by altering the stability and resilience of microorganisms (Cavicchioli et al. 2019; Zhang et al. 2022). Specifically, warming stimulates microbial activities, resulting in an energy distribution shift that prioritises respiration over microbial growth. Consequently, microbial CUE_{ex} and CUE_{en} tend to decrease with increasing temperature (Allison et al. 2010; Ruan et al. 2023). However, the long-term effects of continuous warming on microbial CUE_{ex} and CUE_{en} remain uncertain due to the "thermal adaptability" of microbial growth and respiration (Dove et al. 2021). Drought reduces soil water availability, limiting the diffusion and uptake of exogenous C by microbes. This leads to increased respiration relative to microbial growth, lowering microbial CUE_{en} (Herron et al. 2009). Conversely, drought promotes microbial absorption of exogenous C to sustain growth, resulting in increased CUE_{ex} (Tiemann and Billings 2011). The responses of microbial CUE to nutrient inputs are elusive because theoretically N and P inputs tend to make microbes allocate more assimilated C to biomass synthesis and increase microbial CUE (Liu et al. 2025). However, some studies actually showed that nutrient inputs led to increased soil microbial activity, resulting in accelerated microbial decomposition and decreased CUE in decomposer communities (Hu et al. 2022; Luo et al. 2020). These conflicting results indicate that the individual and partially contradictory outcomes caused by global changes have led to uncertainties regarding their overall impacts on microbial CUE. Therefore, understanding the magnitudes and directions of microbial CUE_{ex} and CUE_{en} responses to global changes is critical for better comprehending microorganism-mediated soil C cycling.

Assessing the effect sizes of driving factors on microbial CUE provides precise insights into soil C dynamics under global changes. Microbial CUE is influenced by extrinsic (e.g., climatic and edaphic properties) and intrinsic (e.g., microbial communities) factors (Widdig et al. 2020; Zhang et al. 2022). Inconsistencies in prior studies may result from site-specific climate, soil properties and microbial communities. Low aridity indices favour exogenous carbon decomposition, which sustains microbial respiration and decreases microbial CUE_{ex} (Cao et al. 2019). Conversely, high aridity indices (above 0.65) enhance microbial extracellular enzyme activities, facilitating endogenous carbon decomposition through hydrolysis or oxidation, which further reduces microbial CUE_{en} (Conant et al. 2011). Soil pH significantly influences microbial community structure. Alkaline soil results in a faster decomposition rate of soil organic matter, releasing more organic acids than acidic soil. Microorganisms exposed to exogenous C input must produce new reverse transporters or alter their metabolism to accommodate extra organic acids, negatively affecting microbial CUE_{ex} (Barberán et al. 2017). Soil acidification increases cation exchange capacity, disrupting microbial cell structures and enzyme functions while weakening microbial assimilation capacities (Auger et al. 2013). Additionally, soil microorganisms must balance organic C uptake for biomass production and respiration and absorb adequate nutrients to meet basic life needs, maintaining the reduced power and energy required for metabolic processes (Müller et al. 2021). Consequently, to fully comprehend the factors driving microbial CUE_{ex} and CUE_{en} in response to ecosystem changes on a global scale, it is crucial to integrate previous experimental findings conducted under different environmental conditions.

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While many studies have investigated microbial CUE responses to environmental changes, a comprehensive global analysis remains lacking. To address this gap, 213 paired microbial CUE_{ex} and 155 paired microbial CUE_{en} datasets were integrated and analysed in a meta-analysis to assess the impacts of global change factors on microbial CUE. The objectives of this study were to (1) determine the global spatial patterns of microbial CUE_{ex} and CUE_{en}, (2) quantify the magnitude and direction of microbial CUE_{ex} and CUE_{en} responses to global changes and (3) identify the key biological and abiotic factors influencing microbial CUE_{ex} and CUE_{en} under global changes. Achieving these goals is expected to provide a theoretical foundation for improving soil C sequestration and reducing greenhouse gas emissions mediated by microorganisms in response to global changes.

2 | Materials and Methods

2.1 | Database Collection

To examine the impacts of global change factors on microbial CUE, we compiled a comprehensive dataset by surveying peer-reviewed literature published until December 2024 from the Web of Science (http://apps.webofknowledge.com), Google Scholar (https://scholar.google.com), and China National Knowledge Infrastructure (CNKI, http://www.cnki.net/). Search keywords included "microbial carbon use efficiency" and various global change factors such as warming, elevated temperature, elevated carbon dioxide, drought, precipitation, fertilisation, land use, plant invasion, etc. To minimise publication bias, the following criteria were adopted: (a) Microbial CUE had to be reported for 0–30 cm soil. (b) The experiment had to use a pairwise design, with both control and at least one global change factor treatment. (c) The control and treatment plots had to be established under the same abiotic and biotic conditions. (d) When the same research results were presented in multiple publications, only one representative data pair was selected. (e) The mean microbial CUE could be extracted from figures or tables.

Two approaches were employed to estimate microbial CUE: the ^{13}C-labelled substrate approach (microbial CUE_{ex}) and the ^{18}O-labelled water approach (microbial CUE_{en}). Additionally, the extracellular enzyme-based stoichiometric model was not included, as it did not directly capture specific C partitioning. Due to limited data, the incorporated global change factors encompassed warming, drought, N input, P input, NP input, NPK input and C input.

In total, 368 paired microbial CUE data were collected, comprising 213 paired microbial CUE_{ex} and 155 paired microbial CUE_{en}. Additional information gathered encompassed latitude, longitude, climate, plant properties, soil properties, microbial properties and experimental conditions. Climate data included mean annual temperature (MAT), mean annual precipitation (MAP) and aridity index. Plant attributes covered net and gross primary productivity. Soil properties included pH, bulk density, cation exchange capacity, texture (sand, silt, clay), SOC and total nitrogen (N). Microbial properties included MBC, growth rate, respiration rate and phospholipid fatty acid content. Experimental conditions involved nutrient input rates, experimental duration, warming temperature, water stress intensity, substrate number, incubation time and temperature.

2.2 | Data Preparation

Data presented in the figures were extracted using Getadata Graph Digitizer 2.26 (http://getdata-graph-digitizer.com). The MAT, MAP and aridity indices were directly recorded from papers or extracted from WorldClim (https://worldclim.org/). Most studies were concentrated in three regions (Figure 1a): East Asia, North America and Western Europe. The experimental sites were situated in the latitude range of −33.93° to 68.35° and the longitude range of −93.39° to 150.66°. The MAT, MAP and aridity indices range from −3.30°C to 23.20°C, 281.00 mm to 1938.00 mm, and 0.20 to 3.52, respectively. Soil properties were obtained directly from literature or the Harmonised World Soil Database v 1.2 (HWSD). The nutrient input rate (presented as g kg^{-1} soil in laboratory incubations) was converted to kg $^{-1}ha^{-1}$ yr^{-1} after correcting for soil bulk density. Detailed site data on climate and soil texture are shown in Supporting Information Table S1.

To comprehensively examine the impacts of climate, vegetation, soil properties and experimental conditions on effect sizes, we grouped the data into categories based on various criteria. Experimental sites were categorised in two ways: first, based on MAT into cool (< 10°C) and warm (> 10°C) zones (Bai et al. 2019); second, based on aridity indexes into semi-arid (≤ 0.65, including semi-arid and dry sub-humid) and humid (> 0.65) zones (Zhou et al. 2023). Net primary productivity was classified as low (< 400 g C $m^{-2}yr^{-1}$), medium (400–800 g C $m^{-2}yr^{-1}$) and

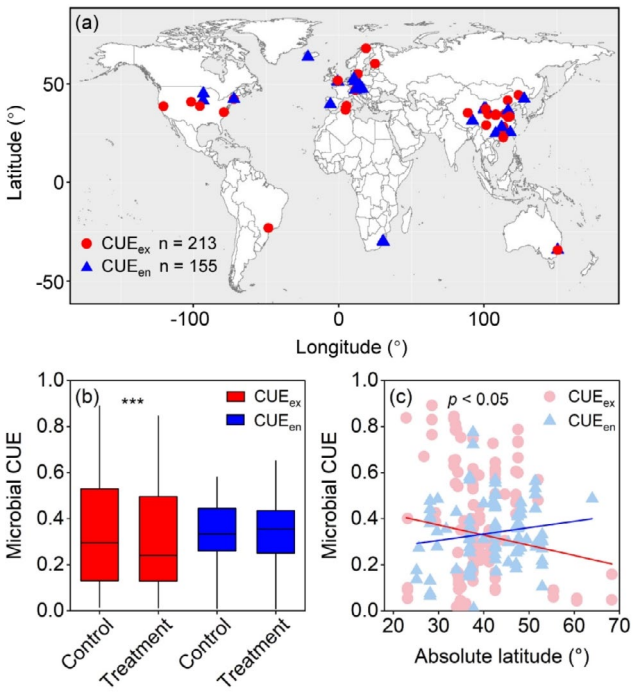

FIGURE 1 | Location of sites and the distribution of microbial exogenous carbon use efficiency (CUE_{ex}) and endogenous carbon use efficiency (CUE_{en}) in this meta-analysis. (a) Spatial distribution of experimental sites. (b) Box plots of microbial CUE under control and global change treatments. (c) Linear relationship between microbial carbon use efficiency (CUE) without global changes and absolute latitude. Solid lines within the box plots represent medians. The bottom and top edges of the boxes represent the 25th and 75th percentiles, respectively.

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high (> 800 g C $m^{-2} yr^{-1}$). Initial SOC was categorised as poor/low (< 12 g kg^{-1}) and moderate/rich (> 12 g kg^{-1}), while initial soil pH was classified as acidic (≤ 6), neutral (6–8) and alkaline (> 8) (Du et al. 2020). The experimental incubation duration to measure CUE was grouped as short-term (< 2 days), medium-term (2–7 days) and long-term (> 7 days) (Zhou et al. 2023).

2.3 | Meta-Analysis

The natural log of the response ratio (ln (*RR*)) and inverse variance weight were utilised to assess the effects of global change factors on microbial CUE. The calculation of ln (*RR*) was calculated as follows:

$$RR = Y_t / Y_c \tag{1}$$

$$\mathrm{Ln}(RR) = \mathrm{Ln}\left(Y_t\right) - \mathrm{Ln}\left(Y_c\right) \tag{2}$$

where Y_t and Y_c represent the means of microbial CUE under global change factors and control, respectively.

In cases of heterogeneity between treatments ($p \leq 0.05$ and $I^2 > 50\%$), a random effects model was applied for analysis; otherwise, a fixed effects model was employed. When literature provided only a standard error (SE), it was converted into a standard deviation (SD) using the following equation:

$$\mathrm{SD} = \mathrm{SE} \times \sqrt{n} \tag{3}$$

For datasets with missing SD (35%) data, it was derived from the mean by the coefficient of variation for all datasets (Cai et al. 2021).

The variance (*V*) of *Y* was calculated as follows:

$$V = \frac{\mathrm{SD}_t^2}{n_t Y_t^2} + \frac{\mathrm{SD}_c^2}{n_c Y_c^2} \tag{4}$$

where SD_c and SD_t represent the SD of microbial CUE under global change factors and control, respectively, while n_c and n_t represent sample numbers for microbial CUE under global change factors and control, respectively.

To assign a greater weight to entries with lower variance, the weighting factor (W_{ij}) was calculated for individual comparisons between the control and treatment (where $i = 1, 2, ..., m$; $j = 1, 2, ..., ki$), with *m* being the number of groups (e.g., the global change factors) and *ki* being the number of comparisons in group *i*. W_{ij} was calculated using the following equation:

$$W_{ij} = \frac{1}{V_{ij}} \tag{5}$$

To identify significant differences in effect sizes, the SE of RR_{++} and the 95% confidence interval (CI) were calculated as follows:

$$RR_{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij} RR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij}} \tag{6}$$

$$\mathrm{S}\left(\mathrm{RR}_{++}\right) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{k_i} W_{ij}}} \tag{7}$$

$$95\%\,\mathrm{CI} = RR_{++} \pm 1.96 S\left(RR_{++}\right) \tag{8}$$

If the 95% CI does not overlap with zero, the effect of global change factors on microbial CUE was considered significant.

The percentage change in soil microbial CUE effect size was calculated using the following formula:

$$\text{Effect size} = \left(e^{RR_{++}} - 1\right) \times 100\% \tag{9}$$

2.4 | Statistical Analysis

To ensure the data quality, the normality of effect sizes of global change factors on microbial CUE was tested for Gaussian distribution before data processing (Supporting Information Figure S1). Effect sizes were calculated using MetaWin 2.1 software (https://www.metawinsoft.com). Before the analyses, some factors were not considered to avoid autocorrelation. Specifically, the aridity index was adopted to represent climate instead of MAP. SOC was used as an indicator of soil fertility rather than soil total *N*. Silt plus clay content (soil fine particles) was employed as an indicator of soil texture instead of considering sand, silt and clay content. Biotic and abiotic factors were classified into five groups (climate, plant, experimental conditions, soil properties and soil microbial indices). Stepwise regression was performed to select factors in each group using the "fastDummies" package version 1.6.3 in R version 4.2.2. Finally, eleven variables (MAT, aridity index, net primary productivity, soil pH, SOC, soil fine particles, soil cation exchange capacity, MBC, microbial growth rate, microbial respiration rate and incubation time) were retained for subsequent random forest analysis. The "randomForest" package was used to quantify the effect of each predictor variable on the effect sizes (Hao et al. 2021).

3 | Results

3.1 | Global Spatial Patterns of Microbial CUE_{ex} and CUE_{en} Without Global Changes

The median microbial CUE_{ex} was 0.30 (ranged widely from 0.01 to 0.89), while the median microbial CUE_{en} was 0.33 (ranged widely from 0.01 to 0.77, Figure 1b). The global microbial CUE_{ex} and CUE_{en} exhibited contrasting patterns with absolute latitude (Figure 1c). Specifically, microbial CUE_{ex} decreased with absolute latitude (trending towards colder ecosystems), whereas microbial CUE_{en} increased with absolute latitude ($p < 0.05$).

3.2 | The Effects of Global Changes on CUE_{ex} and CUE_{en}

Global changes decreased microbial CUE_{ex} by 5.6% and increased microbial CUE_{en} by 0.8% (Figure 1b). Specifically, warming, P, NP and NPK inputs decreased microbial CUE_{ex} by 3.6%, 17.1%, 10.0% and 5.3%, respectively. Conversely, drought increased microbial

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CUE_{ex} by 7.9% (Figure 2a). In contrast, N and NPK inputs elevated microbial CUE_{en} by 25.5% and 43.1%, respectively, whereas warming, drought and C input reduced microbial CUE_{en} by 16.5%, 14.3% and 32.1%, respectively (Figure 2b).

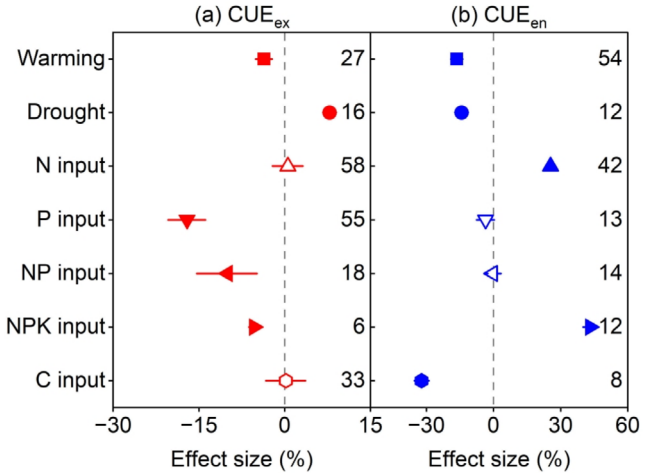

FIGURE 2 | Effects of global change factors on microbial exogenous carbon use efficiency (CUE_{ex}, a) and endogenous carbon use efficiency (CUE_{en}, b). Filled and open symbols reflect significant and non-significant effects of global change factors on microbial CUE, respectively. Error bars are 95% CIs. Sample sizes are indicated on the right side. N, P and K represent nitrogen, phosphorus and potassium deposition, respectively. Plant inv. means plant invasion. C input means carbon input.

The effects of global changes on microbial CUE_{ex} and CUE_{en} exhibited opposite trends (Figure 3). In cool regions, global changes decreased microbial CUE_{ex} by 4.2% but increased CUE_{en} by 8.2%. Similarly, in semi-arid sites, microbial CUE_{ex} declined by 9.8%, whereas CUE_{en} rose by 7.0%. In carbon-rich soils, global changes reduced CUE_{ex} but enhanced CUE_{en}. The effect sizes of microbial CUE_{ex} also diminished with higher soil pH and cation exchange capacity, while those of microbial CUE_{en} increased. Furthermore, microbial CUE_{ex} decreased by 7.4%, whereas CUE_{en} increased by 6.0% in soils with fine particles exceeding 50%.

3.3 | Predicted Driving Factors of Global Changes on Microbial CUE_{ex} and CUE_{en}

The results of random forest analysis revealed that the aridity index was the strongest predictor of the effect sizes of global changes on microbial CUE_{ex} (Increase in mean squared error (%IncMSE) of 10.9%), followed by soil pH (7.1%) and cation exchange capacity (5.4%) (Figure 4a). For microbial CUE_{en} under global changes, the most important predictors were microbial respiration rate (18.3%) and microbial growth rate (16.2%), followed by MBC (13.9%) (Figure 4b). Effect sizes of global changes on microbial CUE_{ex} increased with the aridity index, while effect sizes decreased with soil pH and cation exchange capacity (Figure 4c–e). Effect sizes of global change factors on microbial CUE_{en} were positively correlated with MBC and microbial growth rate, but negatively correlated with microbial respiration rate (Figure 4f–h).

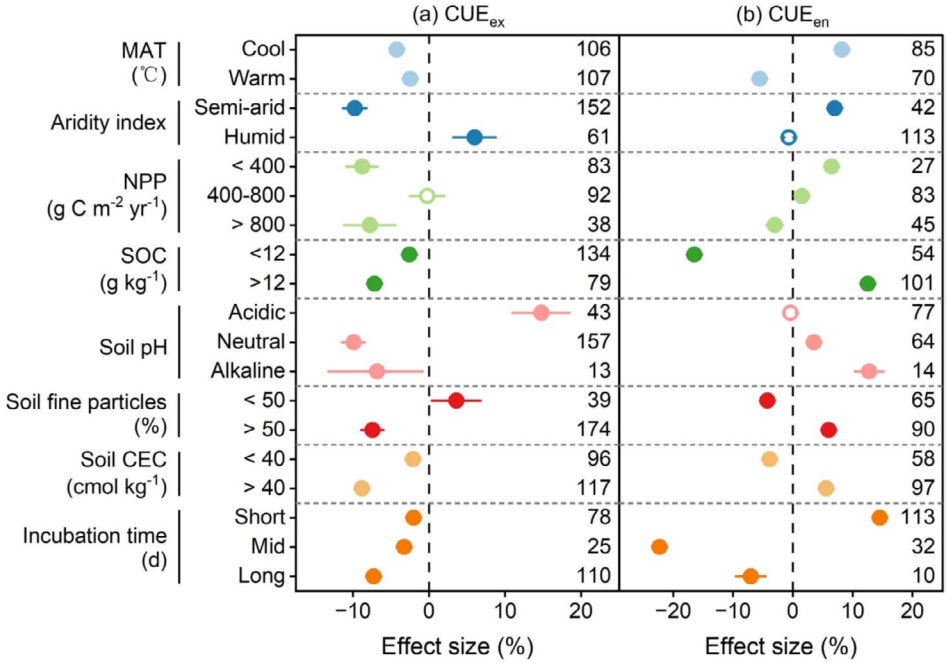

FIGURE 3 | Effects of climate, plant, experiment and soil chemical properties predictors on microbial exogenous carbon use efficiency (CUE_{ex}, a) and endogenous carbon use efficiency (CUE_{en}, b). The climate category encompasses mean annual temperature (MAT) and aridity index. The plant category includes net primary production (NPP). The experiment category involves incubation time. Soil chemical properties include soil organic carbon (SOC), soil pH, soil fine particles (silt plus clay) and soil cation exchange capacity (CEC). Error bars are 95% CIs. Sample sizes are indicated on the right side. MAT was classified as cool (< 10°C) and warm (> 10°C). The aridity index was classified as semi-arid (≤ 0.65) and humid (> 0.65). Soil pH was classified as acidic (< 6), neutral (6–8) and alkaline (> 8). Incubation time was classified as short (< 2 days), mid (2 ≤ time ≤ 7 days) and long (> 7 days).

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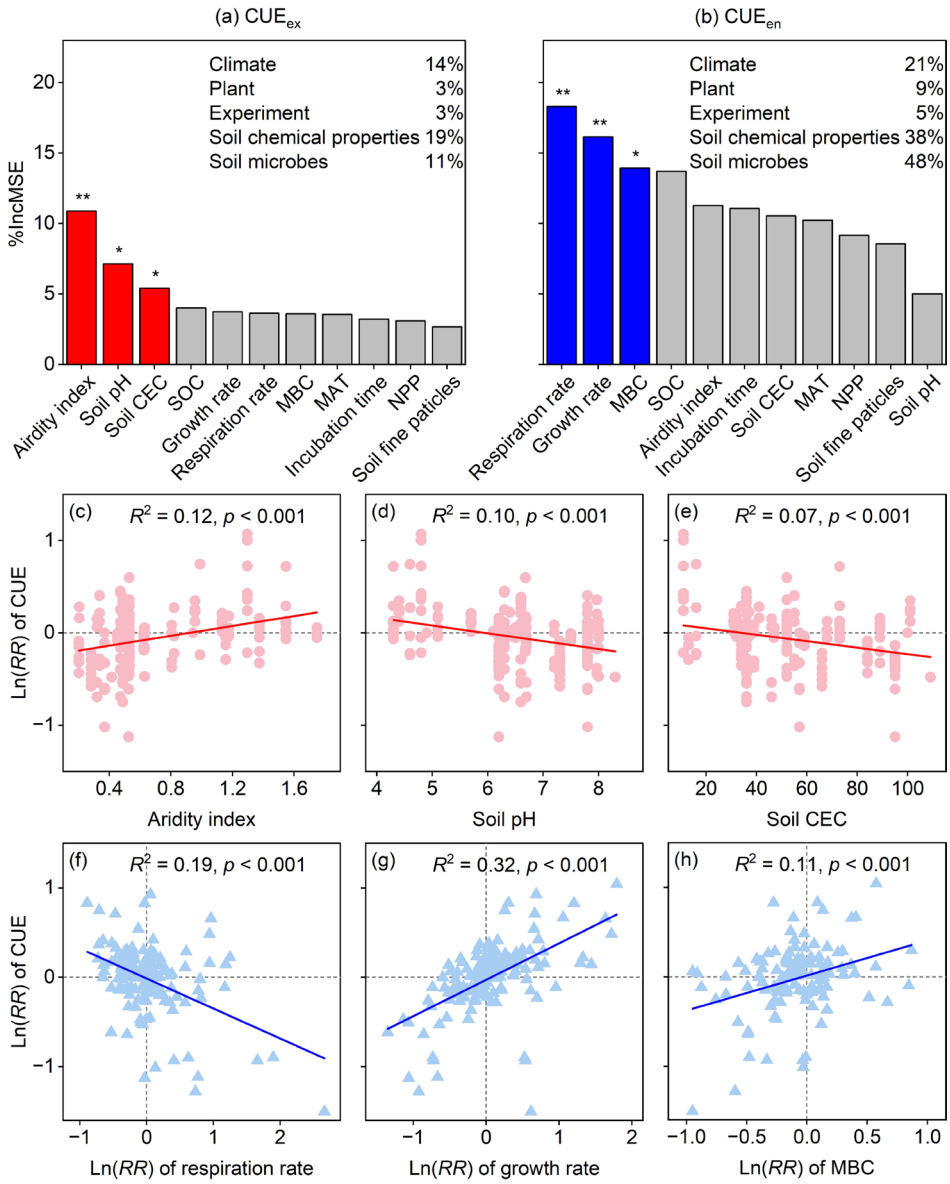

FIGURE 4 | Relative effects (%) of climate, plant, experimental approach, soil properties and microbial indices on microbial exogenous carbon use efficiency (CUE_{ex}, a) and endogenous carbon use efficiency (CUE_{en}, b) under global changes. Linear relationship between Ln(*RR*) of microbial CUE_{ex} and the aridity index (c), soil pH (d) and soil cation exchange capacity (CEC, e). Linear relationship between Ln(*RR*) of microbial CUE_{en} and effect size of microbial respiration rate (f), microbial growth rate (g) and MBC (h). Predictors include parameters of climate, plant, experiment, soil chemical properties and soil microorganisms. Climate includes mean annual temperature (MAT) and aridity index. Plant includes net primary production (NPP). The experiment includes incubation time. Soil chemical properties include soil organic carbon (SOC) content, pH, fine particles (silt plus clay particles) and CEC. Soil microorganisms include MBC, microbial growth rate and microbial respiration rate. The asterisk represents the significant impact of predictors on microbial CUE, with * and ** representing significance levels at $p < 0.05$ and $p < 0.01$, respectively. IncMSE represents the increase in mean squared error. The regression line is significant at levels $p < 0.001$.

4 | Discussion

4.1 | The Opposite Global Spatial Patterns of Microbial CUE_{ex} and CUE_{en}

Our findings revealed that the microbial CUE_{ex} and CUE_{en} were 0.30 and 0.33, respectively. This is similar to the average microbial CUE value (0.35) reported by Zhang et al. (2024), but both are lower than previously reported parameters (0.6, Figure 1b) (Manzoni et al. 2012). This indicates that the microbial CUE values used in C kinetic models may be overestimated, likely due to insufficient consideration of microbial nutrient limitations in natural ecosystems (Sinsabaugh et al. 2013). Nutrient limitation can lower CUE by uncoupling catabolism and anabolism through energy spillover pathways and by increasing the production of extracellular enzymes and polysaccharides (Russell and Cook 1995). Additionally, recalcitrant C sources, shaped by stochastic oxidative and condensation reactions in the environment, may further reduce CUE by raising the costs of extracellular and intracellular catabolism (Blagodatskaya and Kuzyakov 2008). Notably, microbial CUE_{ex} decreased with increasing absolute latitude

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(from 22.83° to 68.35°), while CUE_{en} exhibited the opposite trend (Figure 1c). Conventionally, biogeochemical models represent microbial CUE as a constant value or a function of temperature, and this simplification overlooks the spatial and substrate-specific variability in CUE (Manzoni et al. 2012). For instance, Steinweg et al. (2008) documented a reduction of approximately 0.009 in microbial CUE for every 1°C rise in temperature. Similarly, Allison et al. (2010) incorporated this linear correlation between microbial CUE and temperature into their microbial-enzyme model. Specifically, the failure to distinguish between the utilisation efficiencies of exogenous and endogenous carbon in current models may lead to inaccuracies in predicting soil carbon dynamics. However, our results question the notion that microbial CUE remains constant or diminishes linearly with temperature in biogeochemical models. Incorporating the dynamic changes in CUE_{ex} and CUE_{en} into models would not only capture microbial responses to environmental changes more accurately but also improve simulations of soil carbon cycling. This enhancement is crucial for increasing the reliability of carbon cycle predictions under future climate change scenarios.

The observed global trends of microbial CUE_{en} aligned with the assumptions of previous models, potentially due to the facilitation of organic matter decomposition and enhanced respiration at higher temperatures, resulting in diminished CUE_{en} at lower latitudes (Liu et al. 2019; Razavi et al. 2017). The decline in microbial CUE_{ex} with absolute latitude may be ascribed to two underlying mechanisms. Firstly, microbial communities in high-latitude regions often entered dormancy owing to low temperatures. Microbial growth rates were contingent on the availability of organic matter and nutrients within the soil matrix, and the introduction of exogenous carbon could alleviate carbon limitation in microorganisms (Joergensen and Wichern 2018). This stimulus could reactivate dormant soil microbial communities, elevate their metabolic respiration rates and consequently reduce microbial CUE_{ex} (Blagodatskaya and Kuzyakov 2013). Secondly, exogenous organic materials typically possessed higher carbon-to-nitrogen ratios compared to soil organic matter. Soils in high-latitude regions generally had lower available nitrogen levels than those in low-latitude regions. When exogenous organic materials were introduced into the soil, microorganisms may have preferentially decomposed soil organic matter to access nitrogen. This process could have inhibited the assimilation of exogenous carbon by soil microorganisms and subsequently decreased microbial CUE_{ex} (Mason-Jones et al. 2018; Zhou et al. 2022). Overall, our findings emphasised that the contrasting spatial patterns of microbial CUE_{ex} and CUE_{en} should be considered in biogeochemical models to enhance the accuracy of soil C dynamics predictions.

4.2 | Global Changes Diminished Microbial CUE_{ex} While Enhancing CUE_{en}

Warming reduced both microbial CUE_{ex} and CUE_{en}, whereas drought increased CUE_{ex} and decreased CUE_{en} (Figure 2). Wang et al. (2021) documented the negative effects of warming on microbial CUE and attributed this phenomenon to climate-induced changes in plant–soil–microbial interactions. Physiologically, microbial respiration is thought to be more temperature-sensitive than microbial growth, and higher temperatures may increase maintenance costs and energy demands, ultimately reducing microbial CUE (Allison et al. 2010; Manzoni et al. 2012). A recent study has indicated that the reduction in microbial CUE associated with MAT is primarily driven by microbial growth rather than respiration (Ren et al. 2024). Our findings support this conclusion by demonstrating that warming resulted in decreases in the microbial growth rates (Supporting Information Figure S2). Soil moisture is critical in regulating the osmotic potential and substrate diffusion, ultimately affecting microbial growth, dormancy and mortality (Schimel et al. 2007). Generally, drought would reduce the utilisation of C and energy resources to synthesise organic osmolytes, which disrupt the water potential in microbial cells and lead to cell damage (Simon et al. 2020). This slows down or even stops microbial growth, while respiration processes continue (Sinsabaugh et al. 2013). Drought leads to a faster increase in microbial respiration compared to microbial growth, resulting in a decline in microbial CUE_{en} (Figure 3 and Supporting Information Figure S2). Meanwhile, drought increases the fixation and adsorption of extracellular enzymes, which reduce their efficacy or completely deactivate them, and decrease organic matter decomposition (Alster et al. 2013). Under drought conditions, exogenous C inputs provide energy sources for originally starved microorganisms, promoting their absorption of exogenous C for sufficient growth and resulting in an increase in CUE_{ex} (Ullah et al. 2021).

We also observed a consistently negative impact of nutrient inputs on microbial CUE_{ex} (Figure 2a). Firstly, the exogenous nutrient inputs combined with exogenous C may have increased the abundance of bacteria that preferentially decompose simple C substrates, leading to further decomposition of exogenous litter by microorganisms to sustain their respiration requirements (Guillaume et al. 2016). Secondly, N and NPK inputs altered microbial activity and decreased microbial biomass by 17% and 19%, respectively (Supporting Information Figure S2). These factors may have resulted in reduced uptake and utilisation of labelled exogenous C by microorganisms, decreasing microbial CUE_{ex}. Conversely, N and NPK inputs significantly increased microbial CUE_{en} (Figure 2b), aligning with previous studies that demonstrated microbial CUE_{en} increases with higher levels of soil available nutrients (Widdig et al. 2020; Zhang et al. 2022). Exogenous nutrient inputs enhance soil nutrient availability, allowing microbes to direct more energy towards synthesising their biomass instead of producing enzymes for nutrient acquisition (Liu et al. 2025). However, P and NP inputs had no significant effects on microbial CUE_{en}, likely due to the irrelevance of microbial phosphatase activities to microbial CUE_{en} (Morris et al. 2022). The interactions between N and P inputs inhibited soil N oxidase ability in converting C compared to N input alone (Widdig et al. 2020). Furthermore, N input escalated microbial growth by decreasing the relative abundance of metabolism-related microbial genes; however, N combined with P input attenuated this effect (Leff et al. 2015) (Supporting Information Figure S2). Taken together, our results emphasise the different roles of global changes on microbial CUE_{ex} and CUE_{en} and recommend that these findings be incorporated into biogeochemical models to more accurately predict the soil carbon cycle.

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4.3 | Microbial CUE_{ex} and CUE_{en} Regulated by Different Factors

Our findings indicated that climate and soil chemical properties were the primary regulators of microbial CUE_{ex} under global changes (Figures 4a and 5). The aridity index emerged as the most critical factor determining microbial CUE_{ex}. Although exogenous C provided energy for microorganisms, microbial respiration was more temperature-sensitive than microbial growth under high temperatures and drought (Frey et al. 2013). Soil drought induced by warming also reduced soil available water, thereby limiting the ability of microorganisms to absorb exogenous C by constraining its migration and diffusion (Manzoni et al. 2012). Our additional findings, which showed that the effect of N, P and NPK inputs on microbial CUE_{ex} increased with the drought index, highlighted the critical role of drought in influencing CUE_{ex} (Supporting Information Figure S3). Furthermore, soil pH and cation exchange capacities were found to play essential roles in determining microbial CUE_{ex} under global changes. The response of microbial CUE_{ex} to these changes decreased with higher soil pH and cation exchange capacities (Figure 4d,e). At higher soil pH levels, exogenous C decomposes more rapidly, releasing additional organic acids. Microbes need to synthesise new reverse transport proteins or alter their metabolism to adapt to the increased production of organic acids, which results in greater consumption of organic C allocated for energy production (Barberán et al. 2017). Additionally, alkaline soil can adversely affect microbial diversity and bacterial populations, thereby reducing the utilisation of exogenous C (Wang et al. 2018) (Figure 3). While soil cation exchange is crucial for nutrient cycling and plant growth, high levels can increase harmful metal ions, such as Al^{3+}, which are toxic to microbial cell structures and enzymes, thereby reducing microbial CUE_{ex} (He et al. 2021).

Unlike microbial CUE_{ex}, CUE_{en} was dominated by microbial properties (Figures 4b and 5). It is directly controlled by intrinsic microbial characteristics, particularly their growth rate, respiration rate and microbial biomass C (Hu et al. 2022). The effect sizes of global changes on microbial CUE_{en} increased with the microbial growth rate and decreased with the microbial respiration rate (Supporting Information Figure S3). Microbial DNA synthesis is a critical process underpinning cell division and growth and thus plays a pivotal role in determining CUE_{en} (He et al. 2024). DNA replication requires significant energy and resources, including nucleotides and associated enzymes, which are derived from carbon sources within microbial cells (Qu et al. 2020). This process represents a substantial portion of carbon allocated towards biomass synthesis, directly influencing CUE_{en} (Cavicchioli et al. 2019). Another important aspect is the role of microbial diversity and functional traits in determining CUE_{en} (Anthony et al. 2020). High microbial

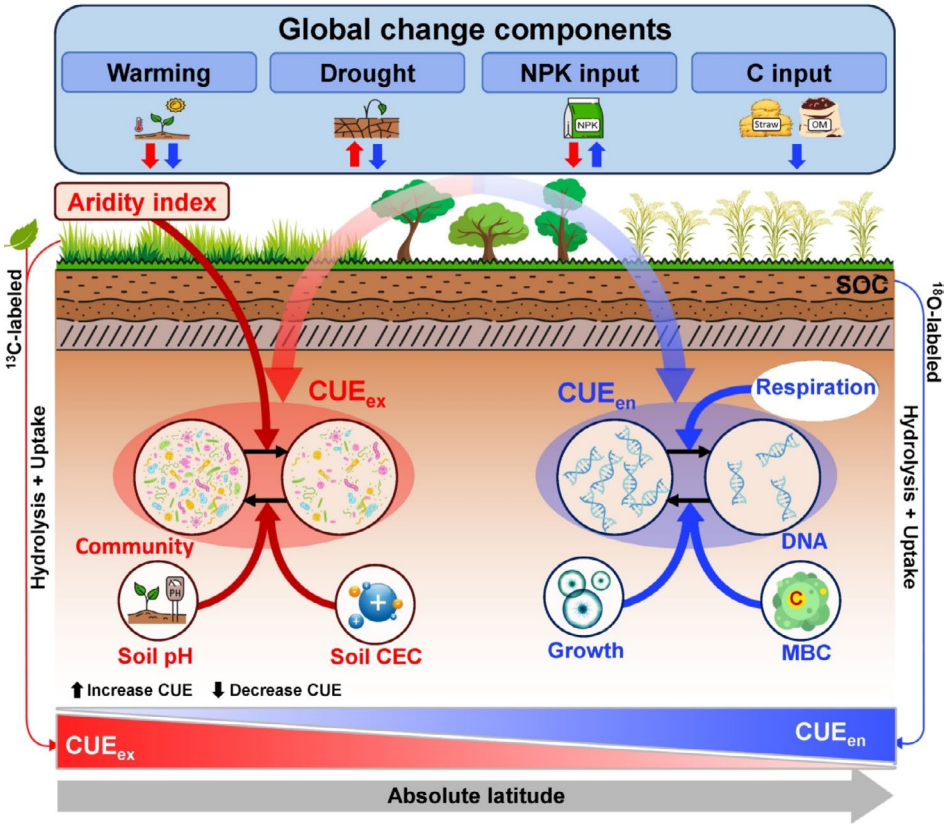

FIGURE 5 | Mechanisms underlying the changes of microbial exogenous carbon use efficiency (CUE_{ex}) and endogenous carbon use efficiency (CUE_{en}) in response to global changes. Downward arrows represent decreased microbial CUE. Nutrient inputs include nitrogen (N), phosphorus (P) and potassium (K) input. C inputs include straw and organic matter (OM) inputs. Community means microbial community. DNA represents deoxyribonucleic acid. Soil CEC represents soil cation exchange capacity. Respiration means microbial respiration rate. Growth means microbial growth rate. MBC represents microbial biomass carbon. The grey horizontal arrow represents absolute latitude. Red and blue long triangles at the bottom illustrate the changes in microbial CUE_{ex} and microbial CUE_{en} with absolute latitudes, respectively.

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diversity can buffer environmental stress by promoting functional redundancy, ensuring that essential processes such as DNA synthesis and respiration are maintained (He et al. 2024). Environmental factors, while important, exerted their effects on CUE_{en} primarily through indirect pathways. For example, drought or temperature stress can alter microbial activity and community composition, reducing growth rates or shifting metabolic strategies (Tian et al. 2024; Zheng et al. 2019). However, these changes are ultimately mediated by the biological responses of microorganisms. Overall, understanding the respective major controls of microbial CUE_{ex} and CUE_{en} is essential for comprehensively understanding CUE and predicting C cycling.

4.4 | Potential Uncertainties and Future Research Directions

The present study underscored the significance of global changes in the regulation of microbial CUE_{ex} and CUE_{en}. However, the methods and environmental variables employed in this research were not devoid of uncertainties. One major issue was that the ^{13}C-labelled substrate and ^{18}O-labelled water techniques captured different aspects of microbial metabolism, which led to significant differences in microbial growth and CUE. While dual labeling (^{13}C and ^{18}O) methods have been used to study the priming effects of soil C, there remains a need to explore the relationships between microbial CUE_{ex} and microbial CUE_{en} using dual labeling methods. Furthermore, the complexity of microbial CUE responses to global changes poses another challenge, which varies depending on substrate concentrations, types, incubation times and other factors. The standardisation of substrates used in microbial uptake studies could help to reduce the variability of microbial CUE measurements. Future research should focus on elucidating the responses of microbial CUE to interactions between different global change factors.

5 | Conclusions

This study found contrasting spatial patterns in microbial CUE_{ex} and CUE_{en}: microbial CUE_{ex} decreases and microbial CUE_{en} increases with absolute latitude. Therefore, biogeochemical models should consider these opposite spatial patterns to precisely represent the responses of microorganisms to various carbon sources. Additionally, decreased precipitation led to greater microbial CUE_{ex} and reduced microbial CUE_{en}, while nutrient inputs decreased microbial CUE_{ex}, and N and NPK inputs increased microbial CUE_{en}. The aridity index, soil pH and soil cation exchange capacity regulate microbial CUE_{ex}, whereas the microbial respiration rate, growth rate and biomass carbon regulated microbial CUE_{en}. These findings may assist in identifying optimal scenarios and driving factors for improving microbial CUE, while providing new insights into enhancing biogeochemical models to more accurately predict soil carbon cycling under global changes.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code used in this study are available at https://doi.org/10.6084/m9.figshare.28357832.

References

Allison, S. D., M. D. Wallenstein, and M. A. Bradford. 2010. "Soil-Carbon Response to Warming Dependent on Microbial Physiology." *Nature Geoscience* 3, no. 5: 336–340. https://doi.org/10.1038/ngeo846.

Alster, C. J., D. P. German, Y. Lu, and S. D. Allison. 2013. "Microbial Enzymatic Responses to Drought and to Nitrogen Addition in a Southern California Grassland." *Soil Biology and Biochemistry* 64: 68–79. https://doi.org/10.1016/j.soilbio.2013.03.034.

Anthony, M. A., T. W. Crowther, D. S. Maynard, J. van den Hoogen, and C. Averill. 2020. "Distinct Assembly Processes and Microbial Communities Constrain Soil Organic Carbon Formation." *One Earth* 2, no. 4: 349–360. https://doi.org/10.1016/j.oneear.2020.03.006.

Auger, C., S. Han, V. P. Appanna, S. C. Thomas, G. Ulibarri, and V. D. Appanna. 2013. "Metabolic Reengineering Invoked by Microbial Systems to Decontaminate Aluminum: Implications for Bioremediation Technologies." *Biotechnology Advances* 31, no. 2: 266–273. https://doi.org/10.1016/j.biotechadv.2012.11.008.

Bai, X., Y. Huang, W. Ren, et al. 2019. "Responses of Soil Carbon Sequestration to Climate-Smart Agriculture Practices: A Meta-Analysis." *Global Change Biology* 25, no. 8: 2591–2606. https://doi.org/10.1111/gcb.14658.

Barberán, A., H. Caceres Velazquez, S. Jones, and N. Fierer. 2017. "Hiding in Plain Sight: Mining Bacterial Species Records for Phenotypic Trait Information." *MSphere* 2, no. 4: e00237-00217. https://doi.org/10.1128/msphere.00237-17.

Blagodatskaya, E., and Y. Kuzyakov. 2013. "Active Microorganisms in Soil: Critical Review of Estimation Criteria and Approaches." *Soil Biology and Biochemistry* 67: 192–211. https://doi.org/10.1016/j.soilbio.2013.08.024.

Blagodatskaya, E., and Y. Kuzyakov. 2008. "Mechanisms of Real and Apparent Priming Effects and Their Dependence on Soil Microbial Biomass and Community Structure: Critical Review." *Biology and Fertility of Soils* 45, no. 2: 115–131. https://doi.org/10.1007/s00374-008-0334-y.

Brant, J. B., E. W. Sulzman, and D. D. Myrold. 2006. "Microbial Community Utilization of Added Carbon Substrates in Response to Long-Term Carbon Input Manipulation." *Soil Biology and Biochemistry* 38, no. 8: 2219–2232. https://doi.org/10.1016/j.soilbio.2006.01.022.

Cai, A., G. Liang, W. Yang, et al. 2021. "Patterns and Driving Factors of Litter Decomposition Across Chinese Terrestrial Ecosystems." *Journal of Cleaner Production* 278: 123964. https://doi.org/10.1016/j.jclepro.2020.123964.

Cao, Z., Y. Jia, Y. Cai, et al. 2019. "Past Aridity's Effect on Carbon Mineralization Potentials in Grassland Soils." *Biogeosciences* 16, no. 18: 3605–3619. https://doi.org/10.5194/bg-16-3605-2019.

Cavicchioli, R., W. J. Ripple, K. N. Timmis, et al. 2019. "Scientists' Warning to Humanity: Microorganisms and Climate Change." *Nature Reviews Microbiology* 17, no. 9: 569–586. https://doi.org/10.1038/s41579-019-0222-5.

14668238, 2025, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70027 by Cornell University, Wiley Online Library on [08/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Conant, R. T., M. G. Ryan, G. I. Ågren, et al. 2011. "Temperature and Soil Organic Matter Decomposition Rates–Synthesis of Current Knowledge and a Way Forward." *Global Change Biology* 17, no. 11: 3392–3404. https://doi.org/10.1111/j.1365-2486.2011.02496.x.

Dove, N. C., M. S. Torn, S. C. Hart, and N. Taş. 2021. "Metabolic Capabilities Mute Positive Response to Direct and Indirect Impacts of Warming Throughout the Soil Profile." *Nature Communications* 12, no. 1: 2089. https://doi.org/10.1038/s41467-021-22408-5.

Du, Y., B. Cui, Q. zhang, Z. Wang, J. Sun, and W. Niu. 2020. "Effects of Manure Fertilizer on Crop Yield and Soil Properties in China: A Meta-Analysis." *Catena* 193: 104617. https://doi.org/10.1016/j.catena.2020.104617.

Frey, S. D., J. Lee, J. M. Melillo, and J. Six. 2013. "The Temperature Response of Soil Microbial Efficiency and Its Feedback to Climate." *Nature Climate Change* 3, no. 4: 395–398. https://doi.org/10.1038/nclimate1796.

Geyer, K. M., P. Dijkstra, R. Sinsabaugh, and S. D. Frey. 2019. "Clarifying the Interpretation of Carbon Use Efficiency in Soil Through Methods Comparison." *Soil Biology and Biochemistry* 128: 79–88. https://doi.org/10.1016/j.soilbio.2018.09.036.

Guillaume, T., D. Maranguit, K. Murtilaksono, and Y. Kuzyakov. 2016. "Sensitivity and Resistance of Soil Fertility Indicators to Land-Use Changes: New Concept and Examples From Conversion of Indonesian Rainforest to Plantations." *Ecological Indicators* 67: 49–57. https://doi.org/10.1016/j.ecolind.2016.02.039.

Hao, Z., Y. Zhao, X. Wang, et al. 2021. "Thresholds in Aridity and Soil Carbon-To-Nitrogen Ratio Govern the Accumulation of Soil Microbial Residues." *Communications Earth & Environment* 2, no. 1: 236. https://doi.org/10.1038/s43247-021-00306-4.

He, M., X. Xiong, L. Wang, et al. 2021. "A Critical Review on Performance Indicators for Evaluating Soil Biota and Soil Health of Biochar-Amended Soils." *Journal of Hazardous Materials* 414: 125378. https://doi.org/10.1016/j.jhazmat.2021.125378.

He, X., E. Abs, S. D. Allison, et al. 2024. "Emerging Multiscale Insights on Microbial Carbon Use Efficiency in the Land Carbon Cycle." *Nature Communications* 15, no. 1: 8010. https://doi.org/10.1038/s41467-024-52160-5.

Herron, P. M., J. M. Stark, C. Holt, T. Hooker, and Z. G. Cardon. 2009. "Microbial Growth Efficiencies Across a Soil Moisture Gradient Assessed Using 13C-Acetic Acid Vapor and 15N-Ammonia Gas." *Soil Biology and Biochemistry* 41, no. 6: 1262–1269. https://doi.org/10.1016/j.soilbio.2009.03.010.

Hu, J., C. Huang, S. Zhou, and Y. Kuzyakov. 2022. "Nitrogen Addition to Soil Affects Microbial Carbon Use Efficiency: Meta-Analysis of Similarities and Differences in 13C and 18O Approaches." *Global Change Biology* 28, no. 16: 4977–4988. https://doi.org/10.1111/gcb.16226.

Joergensen, R. G., and F. Wichern. 2018. "Alive and Kicking: Why Dormant Soil Microorganisms Matter." *Soil Biology and Biochemistry* 116: 419–430. https://doi.org/10.1016/j.soilbio.2017.10.022.

Leff, J. W., S. E. Jones, S. M. Prober, et al. 2015. "Consistent Responses of Soil Microbial Communities to Elevated Nutrient Inputs in Grasslands Across the Globe." *Proceedings of the National Academy of Sciences* 112, no. 35: 10967–10972. https://doi.org/10.1073/pnas.1508382112.

Liang, C., J. P. Schimel, and J. D. Jastrow. 2017. "The Importance of Anabolism in Microbial Control Over Soil Carbon Storage." *Nature Microbiology* 2: 17105. https://doi.org/10.1038/nmicrobiol.2017.105.

Liu, M., H. Lin, and J. Li. 2025. "Are There Links Between Nutrient Inputs and the Response of Microbial Carbon Use Efficiency or Soil Organic Carbon? A Meta-Analysis." *Soil Biology and Biochemistry* 201: 109656. https://doi.org/10.1016/j.soilbio.2024.109656.

Liu, Q., X. Xu, H. Wang, E. Blagodatskaya, and Y. Kuzyakov. 2019. "Dominant Extracellular Enzymes in Priming of SOM Decomposition Depend on Temperature." *Geoderma* 343: 187–195. https://doi.org/10.1016/j.geoderma.2019.02.006.

Luo, R., Y. Kuzyakov, D. Liu, et al. 2020. "Nutrient Addition Reduces Carbon Sequestration in a Tibetan Grassland Soil: Disentangling Microbial and Physical Controls." *Soil Biology and Biochemistry* 144: 107764. https://doi.org/10.1016/j.soilbio.2020.107764.

Manzoni, S., P. Taylor, A. Richter, A. Porporato, and G. I. Ågren. 2012. "Environmental and Stoichiometric Controls on Microbial Carbon-Use Efficiency in Soils." *New Phytologist* 196, no. 1: 79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x.

Mason-Jones, K., N. Schmücker, and Y. Kuzyakov. 2018. "Contrasting Effects of Organic and Mineral Nitrogen Challenge the N-Mining Hypothesis for Soil Organic Matter Priming." *Soil Biology and Biochemistry* 124: 38–46. https://doi.org/10.1016/j.soilbio.2018.05.024.

Morris, K. A., A. Richter, M. Migliavacca, and M. Schrumpf. 2022. "Growth of Soil Microbes Is Not Limited by the Availability of Nitrogen and Phosphorus in a Mediterranean Oak-Savanna." *Soil Biology and Biochemistry* 169: 108680. https://doi.org/10.1016/j.soilbio.2022.108680.

Müller, A. L., W. Gu, V. Patsalo, J. S. Deutzmann, J. R. Williamson, and A. M. Spormann. 2021. "An Alternative Resource Allocation Strategy in the Chemolithoautotrophic Archaeon *Methanococcus maripaludis*." *Proceedings of the National Academy of Sciences* 118, no. 16: e2025854118. https://doi.org/10.1073/pnas.2025854118.

Qu, L., C. Wang, and E. Bai. 2020. "Evaluation of the ^{18}O-H_2O Incubation Method for Measurement of Soil Microbial Carbon Use Efficiency." *Soil Biology and Biochemistry* 145: 107802. https://doi.org/10.1016/j.soilbio.2020.107802.

Razavi, B. S., S. Liu, and Y. Kuzyakov. 2017. "Hot Experience for Cold-Adapted Microorganisms: Temperature Sensitivity of Soil Enzymes." *Soil Biology and Biochemistry* 105: 236–243. https://doi.org/10.1016/j.soilbio.2016.11.026.

Ren, C., Z. Zhou, M. Delgado-Baquerizo, et al. 2024. "Thermal Sensitivity of Soil Microbial Carbon Use Efficiency Across Forest Biomes." *Nature Communications* 15, no. 1: 6269. https://doi.org/10.1038/s41467-024-50593-6.

Ruan, Y., Y. Kuzyakov, X. Liu, et al. 2023. "Elevated Temperature and CO_2 Strongly Affect the Growth Strategies of Soil Bacteria." *Nature Communications* 14, no. 1: 391. https://doi.org/10.1038/s41467-023-36086-y.

Russell, J. B., and G. M. Cook. 1995. "Energetics of Bacterial Growth: Balance of Anabolic and Catabolic Reactions." *Microbiological Reviews* 59, no. 1: 48–62. https://doi.org/10.1128/mr.59.1.48-62.1995.

Schimel, J., T. C. Balser, and M. Wallenstein. 2007. "Microbial Stress-Response Physiology and Its Implications for Ecosystem Function." *Ecology* 88, no. 6: 1386–1394. https://doi.org/10.1890/06-0219.

Simon, E., A. Canarini, V. Martin, et al. 2020. "Microbial Growth and Carbon Use Efficiency Show Seasonal Responses in a Multifactorial Climate Change Experiment." *Communications Biology* 3, no. 1: 584. https://doi.org/10.1038/s42003-020-01317-1.

Sinsabaugh, R. L., S. Manzoni, D. L. Moorhead, and A. Richter. 2013. "Carbon Use Efficiency of Microbial Communities: Stoichiometry, Methodology and Modelling." *Ecology Letters* 16, no. 7: 930–939. https://doi.org/10.1111/ele.12113.

Spohn, M., E. M. Pötsch, S. A. Eichorst, D. Woebken, W. Wanek, and A. Richter. 2016. "Soil Microbial Carbon Use Efficiency and Biomass Turnover in a Long-Term Fertilization Experiment in a Temperate Grassland." *Soil Biology and Biochemistry* 97: 168–175. https://doi.org/10.1016/j.soilbio.2016.03.008.

Steinweg, J. M., A. F. Plante, R. T. Conant, E. A. Paul, and D. L. Tanaka. 2008. "Patterns of Substrate Utilization During Long-Term Incubations at Different Temperatures." *Soil Biology and Biochemistry* 40, no. 11: 2722–2728. https://doi.org/10.1016/j.soilbio.2008.07.002.

14668238, 2025, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.70027 by Cornell University, Wiley Online Library on [08/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Tao, F., Y. Huang, B. A. Hungate, et al. 2023. "Microbial Carbon Use Efficiency Promotes Global Soil Carbon Storage." *Nature* 618: 981–985. https://doi.org/10.1038/s41586-023-06042-3.

Tian, J., J. A. J. Dungait, R. Hou, et al. 2024. "Microbially Mediated Mechanisms Underlie Soil Carbon Accrual by Conservation Agriculture Under Decade-Long Warming." *Nature Communications* 15, no. 1: 377. https://doi.org/10.1038/s41467-023-44647-4.

Tiemann, L. K., and S. A. Billings. 2011. "Changes in Variability of Soil Moisture Alter Microbial Community C and N Resource Use." *Soil Biology and Biochemistry* 43, no. 9: 1837–1847. https://doi.org/10.1016/j.soilbio.2011.04.020.

Ullah, M. R., Y. Carrillo, and F. A. Dijkstra. 2021. "Drought-Induced and Seasonal Variation in Carbon Use Efficiency Is Associated With Fungi: Bacteria Ratio and Enzyme Production in a Grassland Ecosystem." *Soil Biology and Biochemistry* 155: 108159. https://doi.org/10.1016/j.soilbio.2021.108159.

Walker, T. W., C. Kaiser, F. Strasser, et al. 2018. "Microbial Temperature Sensitivity and Biomass Change Explain Soil Carbon Loss With Warming." *Nature Climate Change* 8, no. 10: 885–889. https://doi.org/10.1038/s41558-018-0259-x.

Wang, C., D. Liu, and E. Bai. 2018. "Decreasing Soil Microbial Diversity Is Associated With Decreasing Microbial Biomass Under Nitrogen Addition." *Soil Biology and Biochemistry* 120: 126–133. https://doi.org/10.1016/j.soilbio.2018.02.003.

Wang, C., L. Qu, L. Yang, et al. 2021. "Large-Scale Importance of Microbial Carbon Use Efficiency and Necromass to Soil Organic Carbon." *Global Change Biology* 27, no. 10: 2039–2048. https://doi.org/10.1111/gcb.15550.

Widdig, M., P.-M. Schleuss, L. A. Biederman, et al. 2020. "Microbial Carbon Use Efficiency in Grassland Soils Subjected to Nitrogen and Phosphorus Additions." *Soil Biology and Biochemistry* 146: 107815. https://doi.org/10.1016/j.soilbio.2020.107815.

Wieder, W. R., G. B. Bonan, and S. D. Allison. 2013. "Global Soil Carbon Projections Are Improved by Modelling Microbial Processes." *Nature Climate Change* 3, no. 10: 909–912. https://doi.org/10.1038/nclimate1951.

Zhang, Q., J. Feng, X. Li, Y. Chen, J. P. Schimel, and B. Zhu. 2024. "Effect of Field Warming on Soil Microbial Carbon Use Efficiency—A Meta-Analysis." *Soil Biology and Biochemistry* 197: 109531. https://doi.org/10.1016/j.soilbio.2024.109531.

Zhang, Q., W. Qin, J. Feng, and B. Zhu. 2022. "Responses of Soil Microbial Carbon Use Efficiency to Warming: Review and Prospects." *Soil Ecology Letters* 4, no. 4: 307–318. https://doi.org/10.1007/s42832-022-0137-3.

Zheng, Q., Y. Hu, S. Zhang, et al. 2019. "Growth Explains Microbial Carbon Use Efficiency Across Soils Differing in Land Use and Geology." *Soil Biology and Biochemistry* 128: 45–55. https://doi.org/10.1016/j.soilbio.2018.10.006.

Zhou, J., T. Guillaume, Y. Wen, et al. 2022. "Frequent Carbon Input Primes Decomposition of Decadal Soil Organic Matter." *Soil Biology and Biochemistry* 175: 108850. https://doi.org/10.1016/j.soilbio.2022.108850.

Zhou, R., Y. Liu, J. A. J. Dungait, et al. 2023. "Microbial Necromass in Cropland Soils: A Global Meta-Analysis of Management Effects." *Global Change Biology* 29, no. 7: 1998–2014. https://doi.org/10.1111/gcb.16613.

Zhu, Z., Y. Fang, Y. Liang, et al. 2022. "Stoichiometric Regulation of Priming Effects and Soil Carbon Balance by Microbial Life Strategies." *Soil Biology and Biochemistry* 169: 108669. https://doi.org/10.1016/j.soilbio.2022.108669.

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