

Microbial growth rate is a stronger predictor of soil organic carbon than carbon use efficiency

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The extent to which microbial processes control soil organic carbon (SOC) dynamics remains uncertain. Carbon use efficiency (CUE), that is, the fraction of assimilated carbon allocated to growth, has been used as a key parameter but its relationship with SOC reflects carbon partitioning rather than the absolute magnitude of microbial fluxes. The microbial growth rate could provide a more mechanistic link to SOC accumulation because it quantifies biomass production and reflects necromass formation. Here we combine a global ¹⁸O–H₂O dataset ($n = 268$ paired observations) with outputs from four land surface models to test whether growth rate predicts SOC more strongly than CUE. In the incubation experiments, growth rates are more closely associated with SOC than CUE, although soil properties and climate explain equal or greater variance. Models reproduce the stronger role of growth rate over CUE but tend to underestimate the abiotic controls. The models also emphasize CUE as the main predictor of the SOC-to-net primary production ratio, in contrast to observations, which indicates the soil's capacity to retain plant carbon inputs. Together, these findings identify the microbial growth rate as a diagnostic that can help bridge models with empirical data and guide a more balanced representation of microbial and mineral controls in SOC projections.

A key principle in soil carbon research is that carbon fluxes, rather than static pool sizes, are more directly linked to ecosystem function^{1,2}. Microorganisms exemplify this principle, where although microbial biomass typically accounts for less than 5% of total soil organic carbon (SOC)³, microbial residues (necromass) can contribute over 50% of SOC^{4,5}. This reflects their disproportionate and lasting contribution to long-term soil carbon sequestration. This enduring contribution arises from rapid cycling of microbial biomass, which regulates the fluxes of microbial carbon uptake, respiration, growth and death⁶. Therefore, microbial communities act as a biological pump actively shaping SOC dynamics⁷,

complementing the mineral pump that stabilizes organic matter through mineral interactions⁸.

However, in efforts to quantify microbial control over SOC dynamics, recent studies have focused on microbial carbon use efficiency (CUE), that is, the proportion of assimilated carbon allocated to growth, as a key parameter linking microbial activity to SOC. Several modelling studies suggest that CUE strongly affects SOC stocks^{9–11}, with Tao et al.¹² reporting that global variations in CUE exert a greater influence on SOC than any other model parameter. However, this claim remains contested. Subsequent work has highlighted methodological concerns such as equifinality in inverse modelling¹³ and the omission of

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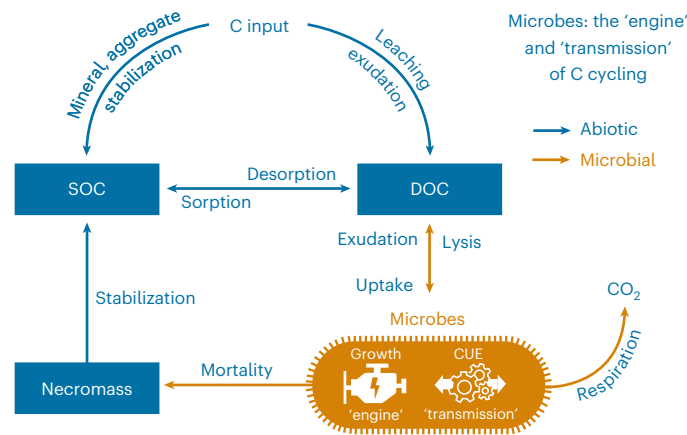


Fig. 1 | Conceptual model of microbial regulation of soil carbon cycling. This diagram uses a mechanical metaphor in which microbial growth rate functions as the ‘engine’ driving carbon fluxes, while CUE serves as the ‘transmission’ modulating the partitioning of carbon between biomass production and CO₂ release. Plant carbon inputs can contribute to SOC through mineral and aggregate stabilization, or enter the dissolved organic carbon (DOC) pool via leaching of soluble litter and root exudation. Exchanges between SOC and DOC occur through sorption and desorption. Microbes assimilate DOC and either respire carbon or allocate it to growth. Microbial exudation and lysis release dissolved organic matter back to the DOC pool, whereas stabilized microbial necromass contributes to SOC. The orange arrows represent microbially mediated cycling, while the blue arrows indicate physicochemical processes, including plant-derived inputs. For clarity, all arrows are drawn with equal thickness to represent pathways rather than quantified flux magnitudes.

key physicochemical stabilization processes¹⁴, while empirical studies found inconsistent SOC–CUE relationships^{15–22}. More fundamentally, CUE is a ratio property; it describes carbon partitioning between growth and respiration but does not capture the absolute magnitude of microbial carbon fluxes. Consequently, a high CUE does not necessarily result in greater SOC accumulation. If microbial biomass turns over rapidly, assimilated carbon may be quickly respired or recycled, limiting its contribution to long-term storage^{12,23}. Conversely, a low CUE does not necessarily limit SOC accumulation. When microbial processing is inefficient and decomposition rates are slow, organic carbon can still progressively accumulate over time depending on stabilization by mineral interactions^{24,25}. These scenarios highlight that CUE captures only part of the microbial influence on SOC and that the variability of SOC ultimately reflects both microbial process rates and the strength of physicochemical stabilization.

Microbial growth rate, which quantifies the gross rate of biomass production, offers a more mechanistic and process-based metric linking carbon assimilation to microbial biomass cycling and necromass formation²⁶. Accumulating evidence suggests that the growth rate may show a stronger association with SOC dynamics than CUE because the microbial growth rate reflects the production and cycling of microbial residues, which are key precursors to stable SOC¹⁸. Moreover, while both the microbial growth rate and CUE are ecologically meaningful properties, the growth rate is more plastic and responsive to environmental variation^{11,27,28}, whereas CUE is often more constrained across conditions^{11,27–29}.

In this study, we adopt an integrative framework, which is common in process-based models but less emphasized in experimental studies, in which microbial process rates such as uptake and growth, together with CUE, jointly regulate SOC dynamics. In this framework, microbial process rates act as the engine driving carbon fluxes, with CUE serving as the transmission that modulates their efficiency (Fig. 1). This highlights the microbial growth rate as the direct mechanistic link to SOC dynamics, with CUE operating as a secondary modulator^{30,31}.

In this study, we combine a global observational dataset derived from the ¹⁸O–H₂O labelling method, a robust and widely used approach for quantifying microbial growth rates and CUE^{32,33}, with outputs from four land surface models (ORCHIDEE-CENTURY, ORCHIDEE-MIMICS, JULES-RothC and CABLE-CASA). We ask whether the microbial growth rate is a stronger predictor of observed spatial variation in SOC than CUE or abiotic factors underpinning the mineral pump of SOC stabilization. In addition, we introduce a diagnostic framework that connects microbial observations with model outputs, offering a clearer way to evaluate model performance and improve predictions of soil carbon change.

Results

Observed SOC is more strongly linked to microbial growth than to CUE but even more to abiotic factors

Using 268 paired observations obtained via the ¹⁸O–H₂O labelling method across diverse ecosystems (Supplementary Fig. 1), we examined the relationships between SOC and microbial or ecosystem properties (Fig. 2). Bivariate regressions identified significant positive correlations between SOC and the microbial absolute growth rate (that is, microbial biomass production per unit soil mass per unit time; $R^2 = 0.371$, $P < 0.001$), microbial respiration rate ($R^2 = 0.269$, $P < 0.001$), microbial biomass ($R^2 = 0.285$, $P < 0.001$) and, to a much lesser extent, microbial CUE ($R^2 = 0.015$, $P = 0.046$). On the other hand, the microbial specific growth rate (that is, the microbial growth rate normalized to the microbial biomass; $R^2 < 0.001$, $P = 0.999$) and net primary production (NPP) (derived from MODIS; $R^2 < 0.001$, $P = 0.999$) showed no significant relationship with SOC. These results indicate that SOC covaries more strongly with microbial absolute growth and biomass than with CUE, specific growth rate or plant productivity.

Random forest regression confirmed these patterns: the microbial growth rate was a stronger predictor of SOC than CUE; however, the soil clay content and the mean annual temperature (MAT) explained comparable or even greater variation (Fig. 3a). Thus, while the growth rate provides a clearer microbial link to SOC than CUE, abiotic constraints remain equally or even more important.

The positive association between absolute microbial growth rate and SOC mainly reflected microbial biomass regulation by SOC availability: the absolute growth rate correlated with microbial biomass ($R^2 = 0.237$, $P < 0.001$), respiration ($R^2 = 0.381$, $P < 0.001$) and, to a lesser extent, specific growth rate ($R^2 = 0.219$, $P < 0.001$; Supplementary Fig. 2a). On the other hand, soil microbial CUE showed no significant relationship with microbial biomass ($R^2 = 0.015$, $P = 0.094$), a negative relationship with the microbial respiration rate ($R^2 = 0.245$, $P < 0.001$), a modest positive relationship with the specific microbial growth rate ($R^2 = 0.209$, $P < 0.001$) and a weak positive relationship with the absolute microbial growth rate ($R^2 = 0.119$, $P < 0.001$; Supplementary Fig. 2b). Together, these patterns indicate that the absolute microbial growth rate, or the associated respiration rate, captures SOC variation more consistently than microbial CUE, which is largely decoupled from both SOC and microbial biomass.

Because microbial growth rates were measured under controlled laboratory conditions, we examined their sensitivity to incubation temperature. Growth rates exhibited only weak temperature dependence, both in absolute terms ($R^2 = 0.02$, $P = 0.034$; Supplementary Fig. 3a) and when normalized by SOC to account for pool-size effects ($R^2 = 0.01$, $P = 0.142$; Supplementary Fig. 3b). These results indicate that the observed variation in microbial growth mainly reflects actual site differences rather than artefacts of incubation temperature.

Model simulations overemphasizes microbial traits relative to abiotic factors

We next tested whether four land surface models, that is, ORCHIDEE-CENTURY, ORCHIDEE-MIMICS, JULES-RothC and CABLE-CASA, reproduce the stronger SOC–growth link. Among them, only

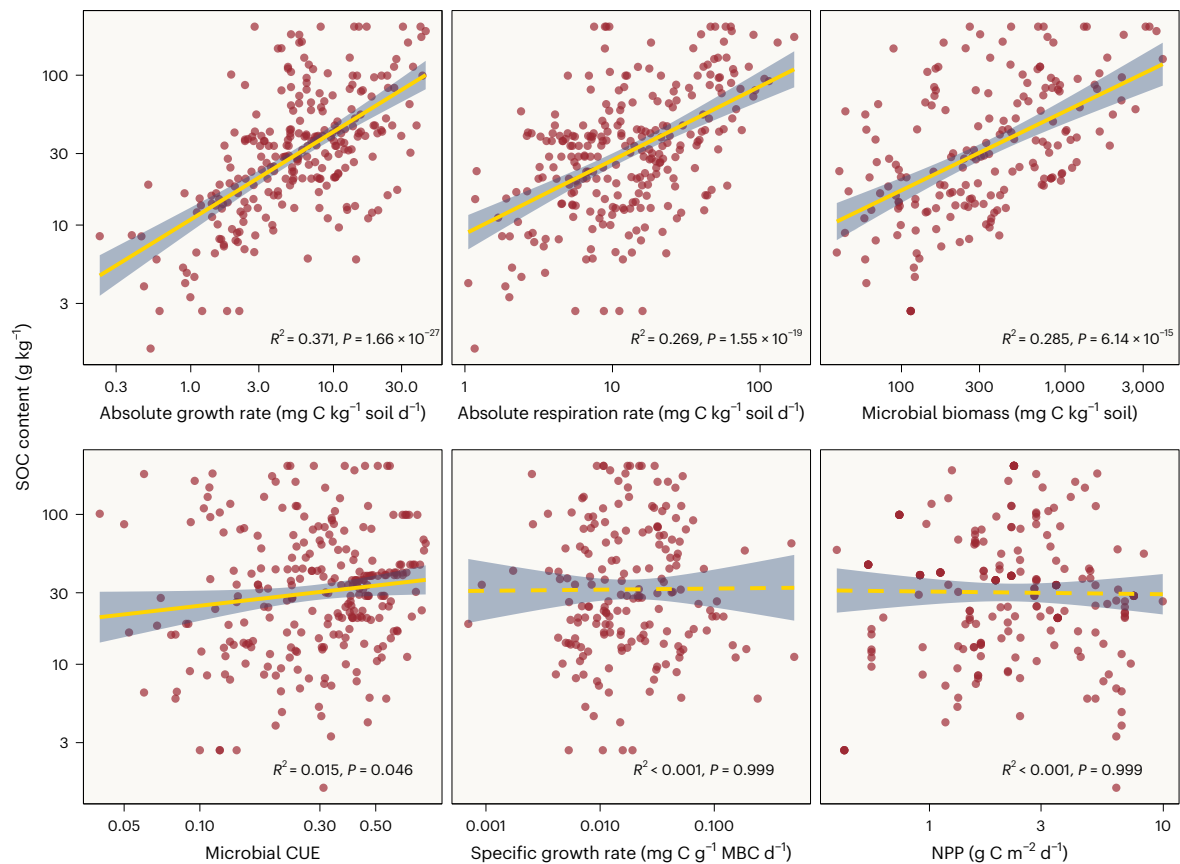


Fig. 2 | Relationships between SOC and microbial or ecosystem properties based on observational data. SOC versus absolute growth rate, absolute respiration rate, microbial biomass, microbial CUE, specific microbial growth rate and NPP. Both axes are log-transformed; linear regression analyses were performed on log-transformed data. The yellow lines represent the regression

fits; the solid lines indicate statistically significant relationships ($P < 0.05$), while the dashed lines indicate non-significant relationships ($P > 0.05$). The shaded bands denote the 95% confidence intervals around the regression estimates. All statistical tests were two-sided. MBC, microbial biomass carbon.

ORCHIDEE-MIMICS explicitly represents microbial processes; the others diagnose microbial properties indirectly under steady-state assumptions (Supplementary Fig. 4). The CUE values reported refer to system-level emergent CUE, not the fixed values assigned to the individual decomposition pathways in the model.

Simulations revealed large variability in emergent CUE across models, both in magnitude and spatial distribution (Fig. 4a–e). For example, CUE values in CABLE-CASA were narrowly constrained (0.15–0.25), whereas the other models produced broader ranges. On the other hand, microbial growth rates were more spatially consistent and tightly constrained (Fig. 4f–j). Correlations confirmed this pattern: growth rates were highly consistent across models ($\rho = 0.82–0.94$, $P < 0.001$), whereas CUE correlations were weaker and sometimes negative (Fig. 4k–m). SOC projections themselves showed moderate agreement across models ($\rho = 0.57–0.92$) and with the Harmonized World Soil Database (HWSD) ($\rho = 0.51–0.59$).

Direct regressions indicated that modelled microbial growth rates predicted SOC more strongly than CUE ($R^2 = 0.04–0.67$ versus 0.02–0.15; Supplementary Fig. 5). To test whether the microbial growth rate provides more information than plant inputs alone, we compared the SOC–growth and SOC–NPP relationships across the four models (Supplementary Figs. 5 and 6). In all models, the microbial growth rate was tightly correlated with NPP ($R^2 = 0.883–0.986$; Supplementary Fig. 6), reflecting the dominant role of plant inputs in driving the microbial growth rate within models. However, the strength of SOC–growth versus SOC–NPP associations differed among models. In ORCHIDEE-MIMICS, which has explicit microbial–mineral stabilization pathways, SOC was more strongly linked to growth ($R^2 = 0.668$,

$P < 0.001$; Supplementary Fig. 5b) than to NPP ($R^2 = 0.491$, $P < 0.001$; Supplementary Fig. 6b), indicating that explicit representation of microbial processes partially decouples SOC storage from inputs by incorporating microbial feedback and stabilization mechanisms. On the other hand, in the three models without explicit modelling of soil microbes (ORCHIDEE-CENTURY, CABLE-CASA and JULES-RothC), the SOC–growth and SOC–NPP relationships were very similar, which is consistent with SOC accumulation being largely input-driven. Across all models, CUE showed only weak ($R^2 = 0.073–0.190$) or negative ($R^2 = 0.348–0.467$) associations with NPP (Supplementary Fig. 6). Together, these results suggest that the microbial growth rate can capture both the magnitude of inputs and the modifying influence of microbial feedback, whereas CUE does not.

Random forest analysis supported these results (Fig. 3b and Supplementary Fig. 7): the growth rate was the most important microbial predictor of SOC, while CUE showed little explanatory power. Notably, microbial properties outweighed abiotic predictors such as clay content and MAT in all models, suggesting that current formulations overemphasize microbial control relative to physical drivers. Overall, while the microbial growth rate remains a more consistent predictor of SOC than CUE, the models tend to exaggerate microbial influence and underrepresent abiotic controls compared with observations.

SOC-to-NPP ratio observations highlight growth and physical factors whereas models emphasize CUE

To account for variation in carbon inputs, we normalized SOC according to NPP. This ratio (SOC-to-NPP), which represents soil carbon residence time under steady-state conditions, reflects the capacity of soils to

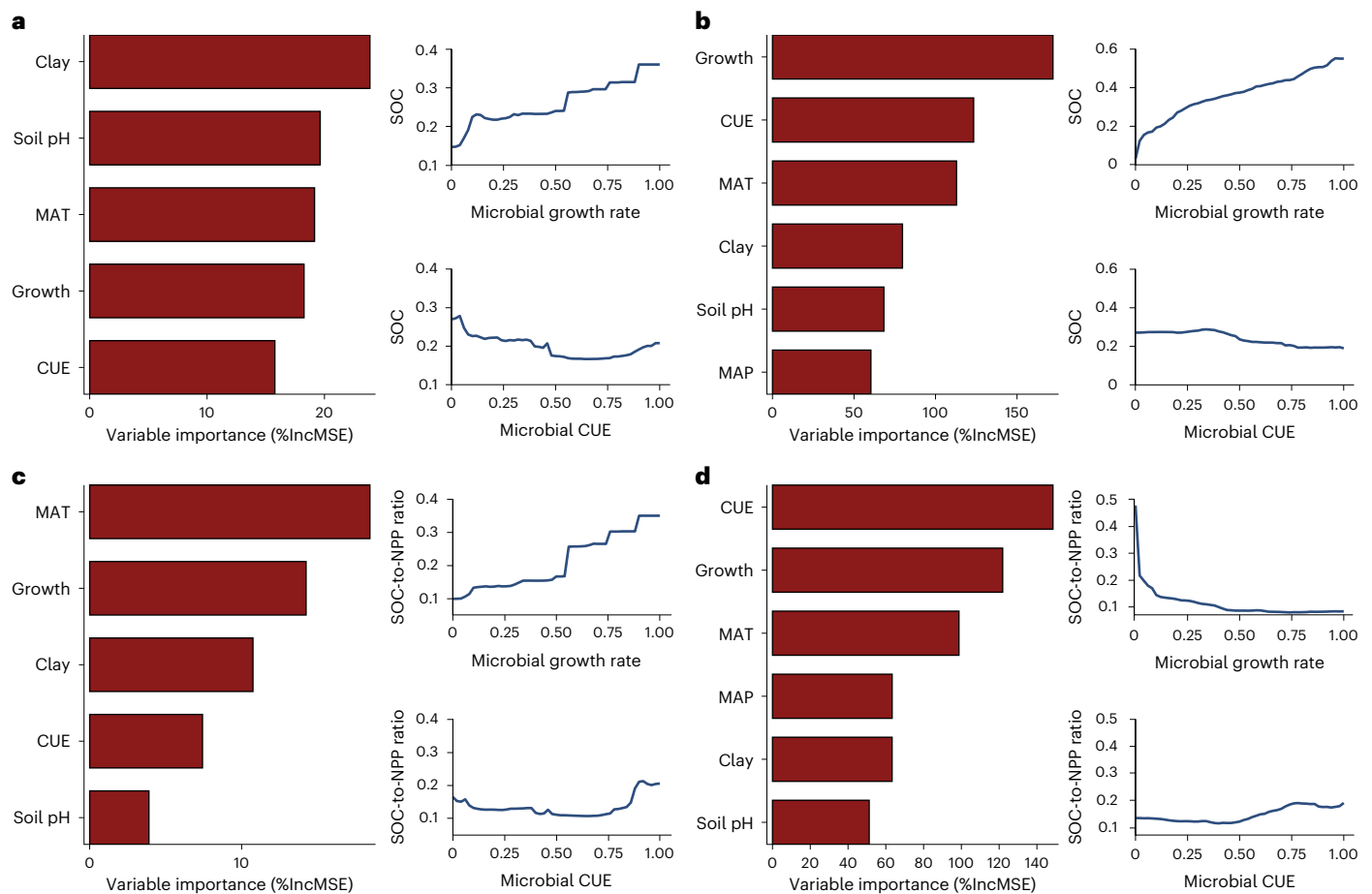


Fig. 3 | Variable importance of microbial and environmental factors for SOC and SOC-to-NPP. a, SOC in the observational data. **b**, SOC across four land surface models. **c**, SOC-to-NPP ratios in the observational data. **d**, SOC-to-NPP ratios across four land surface models. Variable importance was quantified using

random forest permutation importance, expressed as the percentage increase in mean squared error (%IncMSE). The partial dependence plots to the right of each panel show the marginal effects of the microbial growth rate (top) and microbial CUE (bottom) on SOC or SOC-to-NPP.

retain plant carbon inputs as SOC. We then used random forest analysis to identify the factors that regulate this ratio. In the observational dataset (using site-level MODIS NPP), microbial absolute growth rate and MAT emerged as the strongest predictors of SOC-to-NPP, whereas CUE had only a minor role (Fig. 3c). In contrast, model simulations showed the opposite pattern: CUE consistently ranked as the dominant predictor of SOC-to-NPP, exceeding microbial growth rate and environmental variables in importance (Fig. 3d). This strong effect of growth at low SOC-to-NPP values reflects model structure: low growth occurs in low-input, low-SOC regimes where SOC-to-NPP is extremely sensitive to small increases in NPP-driven growth. Moreover, across all models, microbial properties generally ranked above abiotic drivers for both SOC and SOC-to-NPP (Fig. 3b,d), whereas in observations, environmental factors such as MAT explained variance comparable to or greater than microbial growth (Fig. 3a,c). Together, the model-imposed coupling of microbial growth to NPP, which produces steep SOC-to-NPP sensitivity under low-input conditions, and the persistent overemphasis of microbial predictors relative to abiotic controls, explain a major part of the model–data mismatch.

We further explored microbial controls under changing inputs using elevated CO₂ simulations in ORCHIDEE-MIMICS and ORCHIDEE-CENTURY. In both models, the absolute change in SOC (Δ SOC) over the 300-year simulation after CO₂ doubling driven by stimulated plant productivity and increased carbon inputs, was primarily explained by changes in microbial growth rate (Δ Growth), with changes in CUE (Δ CUE) having a secondary role (Supplementary Fig. 8a). To

assess how efficiently additional plant inputs were converted into SOC, we normalized Δ SOC according to Δ NPP. This ratio (Δ SOC-to- Δ NPP) represents the sensitivity of SOC to changes in NPP and serves as a diagnostic of retention efficiency. Under this metric, the pattern was reversed: CUE became the strongest predictor of Δ SOC-to- Δ NPP in the models' simulations (Supplementary Fig. 8b).

Together, these results suggest that in models, microbial growth rates are closely tied to NPP and thus govern the magnitude of SOC accumulation, whereas CUE determines how much of the extra inputs due to elevated CO₂ are retained as SOC. This reflects model formulations, where microbial growth largely mirrors spatial and temporal variations in NPP and CUE is the result of coefficients partitioning NPP between respiration and retention in the soil compartments. In contrast, observational data show no strong link between CUE and SOC-to-NPP, implying that current models may oversimplify soil carbon cycling by overemphasizing microbial allocation and underrepresenting other mechanisms important in real ecosystems.

Discussion

By combining global observations with four land surface models, we show that the absolute microbial growth rate is more strongly associated with SOC dynamics than CUE. This stronger association reflects its mechanistic role in linking carbon assimilation to microbial biomass production and necromass formation, which is the key precursor of stable SOC^{6,26}. Because the growth rate integrates uptake and allocation processes, it serves as a more direct and quantifiable indicator of

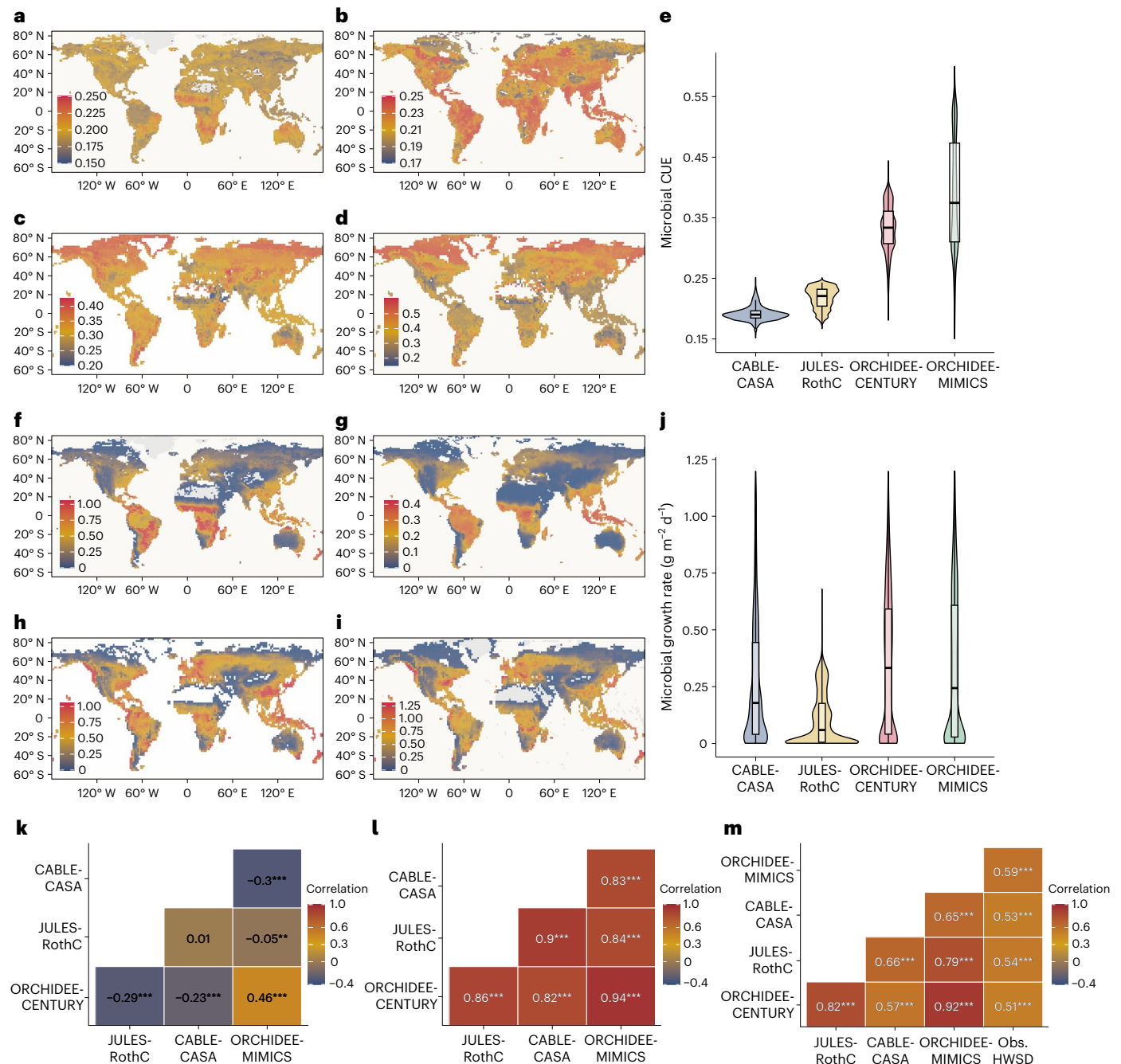


Fig. 4 | Spatial distributions, variability and correlations of microbial properties across four land surface models. a–e, Spatial maps and violin plots showing the distribution and variability of microbial CUE simulated by each model. **a**, CABLE-CASA. **b**, JULES-RothC. **c**, ORCHIDEE-CENTURY. **d**, ORCHIDEE-MIMICS. **e**, Microbial CUE. **f–j**, Spatial maps and violin plots for the microbial growth rate. **f**, CABLE-CASA. **g**, JULES-RothC. **h**, ORCHIDEE-CENTURY. **i**, ORCHIDEE-MIMICS. **j**, Microbial growth rate. Each violin plot reflects independently simulated grid cells for each model (CABLE-CASA: $n = 7,117$; JULES-RothC: $n = 7,367$; ORCHIDEE-CENTURY: $n = 4,762$; ORCHIDEE-MIMICS: $n = 4,666$),

which serve as independent spatial units of analysis. The box plots indicate the median (centre line), interquartile range (25th–75th percentiles) and whiskers extending to the most extreme values within 1.5× the interquartile range; outliers beyond this range are omitted for clarity. **k–m**, Spearman correlation of spatial patterns, showing model–model correlations for microbial CUE (**k**), model–model correlations for microbial growth rate (**l**) and correlations between simulated SOC and observed SOC from the HWSD database (Obs. HWSD) (**m**). The numerical values denote correlation coefficients; the asterisks indicate the significance level (** $P < 0.01$, *** $P < 0.001$). All correlation tests were two-sided.

microbial contributions to soil carbon cycling than the ratio-based metric of CUE^{16,27,34,35}. Notably, the correlation between the absolute microbial growth rate and SOC may partly reflect microbial adjustments in biomass in response to SOC availability because microbial biomass is known to scale with SOC across ecosystems³. However, the absolute growth rate is not simply a proxy for biomass. It also integrates the pace of microbial carbon assimilation and allocation, which are processes

not captured by biomass alone. This suggests that the absolute microbial growth rate provides mechanistically relevant information for understanding SOC dynamics.

Although many studies reported significant positive relationships between microbial CUE and SOC in both empirical observations and process-based models^{12,19,21,31,36}, our results suggest that the influence of CUE on SOC is more context-dependent than previously assumed^{19,31,36,37}.

In our global dataset of 268 observations obtained with the ^{18}O - H_2O labelling method (incubation times ≤ 48 h), CUE showed no significant relationship with SOC. Because this approach is relatively insensitive to incubation duration and includes a pre-incubation step that minimizes wet-up effects, these particular methodological artefacts^{37,38} are unlikely to explain the lack of correlation with SOC. Instead, the explanation is more fundamental: CUE is a ratio that describes the partitioning of assimilated carbon between growth and respiration but it does not capture the absolute fluxes of carbon through microbial biomass and necromass³⁹. Moreover, measured CUE represents a transient microbial property that fluctuates on hourly to daily timescales, whereas SOC changes over decades to centuries³¹. This temporal mismatch naturally weakens their association³⁷. Although microbial growth rate estimates are subject to the same incubation-related limitations as CUE, the relationship between growth rate and SOC is robust and less sensitive to experimental conditions. This is because the microbial growth rate quantifies the magnitude of carbon fluxes and is directly linked to SOC availability and microbial biomass. On the other hand, CUE compounds uncertainties from measurements of both growth and respiration while excluding biomass effects, which weakens its association with SOC in experimental contexts^{31,36,37}. These considerations highlight the limitations of relying on ratio-based metrics such as CUE to capture SOC dynamics in empirical evidence^{15,40}.

Model simulations partially support these conclusions by reproducing the stronger association between microbial growth rate and SOC than between CUE and SOC. However, they also diverge from observations by overemphasizing microbial controls relative to abiotic factors, a pattern that is consistent with Georgiou et al.⁴¹. In soil carbon models, SOC stocks are the result of input and output carbon fluxes (for example, decomposition), which in turn depend on rate constants that are tuned during model calibration. By contrast, emergent CUE is a by-product of these calibrated fluxes and is not directly constrained in the calibration process. Consequently, even though emergent CUE values differed widely among models, all four models produced similar SOC estimates^{42–44} (Fig. 4). This structural feature also explains why, in model simulations, microbial growth rate, as determined by decomposition rates and carbon allocation strategies, shows a stronger correlation with SOC than CUE and is also tightly linked to NPP. The link to NPP is a direct consequence of the equilibrium conditions these models attained; larger NPP implies larger carbon fluxes through all the model pools and thus a higher microbial growth rate. However, we also found important nuances in this coupling among models. In ORCHIDEE-MIMICS, the NPP–growth correlation was weaker ($R^2 = 0.88$ versus > 0.97 in the other models), reflecting its explicit representation of microbial feedbacks and stabilization processes, such as sorption, aggregation and dissolved losses, which reduce the direct control of NPP on SOC and partly decouple inputs from stocks^{45,46}. This agrees with expectations from microbial-explicit models, in which decomposition depends on both substrate and microbial biomass rather than substrate alone^{47,48}. Despite this nuance, all models still gave more weight to microbial properties than to abiotic factors, such as clay content and temperature, suggesting that current structures overemphasize microbial controls. Future models should better integrate microbial and abiotic drivers to capture SOC dynamics more realistically⁴⁶. Overall, while the strong growth–SOC link partly reflects model design, the microbial growth rate remains a useful diagnostic that integrates carbon inputs and allocation strategies, providing a benchmark for evaluating model realism.

Despite its central role in carbon cycling, the microbial growth rate is usually treated as an emergent property in soil carbon models—indirectly inferred as the product of CUE and decomposition (or carbon uptake) rate^{9,49,50}. This approach limits alignment with empirical evidence. A more process-based strategy is to explicitly simulate microbial carbon uptake and biomass production from measurable traits and environmental drivers⁵¹. Doing so would reduce structural uncertainty and promote more mechanistically grounded model development⁵². Recent advances in molecular techniques now make such

parameterization more feasible. Metagenomic and transcriptomic approaches can provide information on microbial growth potential and realized activity across taxonomic and biogeographical scales^{53,54}, offering a strong basis for model parameterization.

Our results reveal a clear mismatch between models and observations in the relationships between SOC/NPP and microbial properties. SOC/NPP, which represents soil carbon residence time under steady-state conditions^{55,56}, shows contrasting controls in the two approaches. In the observational data, SOC/NPP was strongly associated with the absolute microbial growth rate but only weakly with CUE. In contrast, models assigned a dominant role to CUE, especially under elevated CO_2 ($\Delta\text{SOC}/\Delta\text{NPP}$), even though emergent CUE was not a strong predictor of SOC stocks. This means that while CUE contributes little to explaining steady-state SOC, models emphasize its role in determining how efficiently new carbon inputs are retained under changing conditions or management initiatives. This discrepancy probably arises from structural assumptions in current models, where decomposition and substrate availability tightly constrain carbon cycling⁴⁸. Thus, models may overemphasize the role of microbial partitioning while underrepresenting physical stabilization. Therefore, future models should better integrate microbial and abiotic mechanisms to represent SOC dynamics more realistically, particularly under changing environmental conditions or management initiatives (for example, the ‘4 per mille’ initiative⁵⁷).

In conclusion, by integrating global ^{18}O - H_2O observations with four land surface models, we demonstrate that the microbial growth rate predicts SOC more consistently than CUE. Observations further reveal that abiotic factors, such as clay content and climate, explain equal or greater variation in SOC, highlighting strong physical constraints over microbial effects. Models capture the stronger role of microbial growth rate relative to CUE for SOC but they tend to overemphasize microbial controls at the expense of abiotic drivers. Together, these findings establish microbial growth rate as a process diagnostic linking models with observations and for rebalancing microbial and abiotic drivers in projections of soil carbon dynamics.

Methods

Observation data collection

We used the microbial growth rate and CUE observations compiled by Hu et al.^{16,58}, including 268 measurements obtained using the ^{18}O - H_2O labelling method. In this approach, microbial growth is quantified by tracking the incorporation of ^{18}O into DNA, which is then converted to gross biomass production ($\text{mg C kg}^{-1} \text{ soil h}^{-1}$), while microbial respiration is estimated from total CO_2 efflux. Alongside microbial CUE and the growth rate data, associated variables such as MAT, mean annual precipitation (MAP), SOC, incubation temperature and MBC were also extracted. In addition, the NPP for each site was derived from the MODIS data⁵⁹ based on the reported latitude and longitude.

Land surface model simulations

We conducted simulations using four land surface models, that is, ORCHIDEE-CENTURY, ORCHIDEE-MIMICS, CABLE-CASA and JULES-RothC, by equilibrating SOC stocks to the boundary conditions of the year 1700. The simulation protocol followed the guidelines of the TRENDY model intercomparison project⁶⁰, which standardizes the spin-up procedures for biogeochemical cycles under pre-industrial conditions. Each of the four models incorporates a distinct, widely used soil organic matter (SOM) module: ORCHIDEE-CENTURY⁶¹, ORCHIDEE-MIMICS⁶², CABLE-CASA⁶³ and JULES-RothC⁶⁴, respectively. ORCHIDEE-CENTURY and ORCHIDEE-MIMICS share an identical model structure except for their SOM modules, allowing us to isolate the effects of SOM representation on model outputs, an approach not feasible when comparing structurally distinct models.

All model outputs were aggregated to grid-cell averages by combining values across all plant functional types within each grid cell. To reduce interannual variability, we averaged all model outputs

over a 30-year period. Environmental drivers used in each model, including MAT, MAP, soil pH and clay content, were also extracted to assess their influence on spatial variation in SOC and microbial traits. For models that do not provide soil pH internally (for example, ORCHIDEE-CENTURY and JULES-RothC), we supplemented the missing values by extracting the corresponding pH from a global gridded dataset⁶⁵ at each cell, thereby ensuring consistent coverage across all models for the combined analyses.

Emergent CUE in land surface models

Among the four land surface models analysed, ORCHIDEE-CENTURY, CABLE-CASA and JULES-RothC do not explicitly simulate microbial biomass pools. Instead, they represent microbial processes implicitly through the partitioning of decomposed carbon into respiration (CO₂ release) and transfer to downstream carbon pools. To approximate microbial CUE in these models, we followed a flux-based approach^{37,66,67}, calculating the fraction of carbon retained in the receiving pool relative to the total flux from the donor pool. This fraction, representing the portion that was not respired, was used as a proxy for microbial CUE (see conceptual illustration in Supplementary Fig. 4). This flux-based CUE is not a direct microbial trait but rather a proxy inferred from carbon flow partitioning within the model structure. We define this metric as emergent CUE, representing a system-level carbon use efficiency that arises from the balance of carbon fluxes between pools and losses via respiration. Emergent CUE integrates microbial allocation behaviour and model structural assumptions and can be consistently applied across both microbial-explicit models (for example, MIMICS) and microbial-implicit models (for example, CENTURY, CASA, RothC), thereby facilitating comparison of modeled SOC retention and evaluation of microbial controls on soil carbon dynamics.

In cases where multiple upstream carbon fluxes contributed to a receiving pool, we estimated a flux-weighted average CUE as equation (1):

$$CUE_{\text{avg}} = \frac{\sum_{i=1}^n F_i CUE_i}{\sum_{i=1}^n F_i} \quad (1)$$

where F_i is the total carbon flux entering from upstream pool i and CUE_i is the fraction of that flux retained in the receiving pool (that is, not lost as CO₂). In this context, CUE_{avg} represents the overall efficiency with which incoming carbon is retained, averaged across all contributing fluxes.

Similarly, the total microbial growth, defined as the sum of retained carbon from all upstream fluxes, was calculated as equation (2):

$$\text{Growth}_{\text{total}} = \sum_{i=1}^n F_i CUE_i \quad (2)$$

CO₂ doubling experiment

To evaluate the response of soil carbon processes to elevated atmospheric CO₂, we conducted an additional experiment using ORCHIDEE-CENTURY and ORCHIDEE-MIMICS. Starting from the previously simulated steady-state SOC conditions, we doubled atmospheric CO₂ concentration and ran the models for an additional 300 years. We then compared SOC stocks, microbial growth rates, and CUE values before and after the CO₂ perturbation, computing the changes in each (ΔSOC , ΔGrowth , ΔCUE). Elevated CO₂ stimulated plant productivity, and consequently carbon inputs to the soil. The magnitude of this stimulation varied spatially, depending on interactions among water availability, temperature, atmospheric CO₂ concentration, and soil nutrient status.

Data analysis

We first examined the value ranges and spatial distributions of microbial CUE and the growth rate as predicted by four land surface models. Pairwise Spearman correlation analyses were conducted to assess

spatial consistency among these variables. To ensure comparability, all datasets were resampled to a common spatial resolution of two degrees, corresponding to the coarsest dataset (ORCHIDEE), using a grid-averaging approach before the spatial correlation analysis. Model performance was further evaluated by comparing model-predicted SOC with observed SOC from the HWSO database.

We explored the relationships between microbial properties (microbial growth rate, CUE, microbial biomass and respiration rate) and SOC using univariate linear regression analyses. Additionally, we examined how microbial growth rate and CUE correlated with other microbial properties.

To identify the primary microbial drivers of SOC variation across space and under elevated CO₂, we conducted two sets of random forest regression analyses. For the spatial analysis, we used microbial properties (growth rate and CUE), climate variables and soil properties as predictors, and SOC as the response variable. As the models produced broadly consistent results (Supplementary Fig. 8), this aggregation allowed a unified interpretation across models. Model outputs from the four land surface models were first min–max scaled (0–1 range) and then combined to ensure comparability (Supplementary Fig. 9).

Random forest models were implemented using the randomForest package (v.4.6-12)⁶⁸ in R (v.4.3.0), with 500 trees ($n\text{tree} = 500$) and the number of variables sampled at each split ($m\text{try}$) set to the square root of the number of predictors. Predictor importance was quantified using the percentage increase in mean squared error according to random permutation. Partial dependence plots were used to visualize the marginal effects of the microbial growth rate and CUE on SOC, isolating non-linear and interactive effects while averaging over other predictors.

To assess microbial controls on SOC response to elevated CO₂, we performed a second random forest analysis using simulation outputs from the two ORCHIDEE models. The response variable was the ratio of ΔSOC -to- ΔNPP , which serves as a diagnostic describing how efficiently additional plant carbon inputs (per unit increase in NPP) were converted into SOC. Predictors included baseline microbial growth rate and CUE, climate variables, soil pH and clay content. This analysis identified which microbial trait most strongly influenced SOC changes under elevated CO₂, independent of productivity effects.

All data processing and statistical analyses were conducted in R (v.4.3.0), and all analytical figures were produced using the ggplot2 package (v.3.5.2). The conceptual schematic presented in Fig. 1 was created in Microsoft PowerPoint 2019 and refined in Inkscape (v.1.3.2) using original graphical elements, without incorporating any third-party copyrighted material.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The global observational dataset is available via figshare at <https://doi.org/10.6084/m9.figshare.30070084.v1> (ref. 58). Simulation outputs from the four land surface models (ORCHIDEE-CENTURY, ORCHIDEE-MIMICS, CABLE-CASA and JULES-RothC) are also available via figshare at <https://figshare.com/s/95f8435036d7f6825a53> (ref. 69). All custom R scripts used for data processing, statistical analyses and figure generation are openly available via Zenodo at <https://doi.org/10.5281/zenodo.17800780> (ref. 70).

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Author contributions

X.H., G.M. and D.S.G. conceived and designed the study. J.H. provided the observational dataset. S.M., P.C., Y.-P.W., R.Z.A. and E.A. contributed to the initial development of the study concept and discussions. Y.C. and E.B. supplied the data that supported the preliminary exploratory analyses. P.C. and D.S.G. secured the project funding. All authors contributed to the writing, discussion and revision of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Data analysis Statistical analyses, including linear regression, Spearman correlation, and random forest regression, were performed using R software (version 4.3.3). The randomForest package (version 4.6-12) was used for machine learning analyses. Custom R scripts developed to process the data and perform analyses are available upon request. Model simulations were conducted following TRENDY project protocols, and data from four land surface models were aggregated and analyzed using standard R functions.

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Research sample	The research sample consists of 268 paired observations of microbial growth rate and CUE, collected from natural, undisturbed ecosystems globally. No experimental manipulations were applied to these samples.
Sampling strategy	No new sampling was performed. Observational sites were included based on data availability in published sources, representing a broad range of climatic and edaphic conditions.
Data collection	No primary data were collected by the authors. All observational data were obtained from previously published studies, and model outputs were generated using established TRENDY protocols.
Timing and spatial scale	Observational data span multiple years from 92 global sites. Model simulations were run to equilibrium under pre-industrial conditions and extended under elevated CO ₂ for 300 years.
Data exclusions	No data points were excluded from analyses. Missing values in the observational dataset were retained as gaps and not imputed.
Reproducibility	The analyses were conducted with transparent methods using publicly available data and standard modeling frameworks. Four independent land surface models were compared to verify consistency of findings. Model code and analysis scripts are available upon request.
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