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PERSPECTIVE

Model formulation of microbial CO_2 production and efficiency can significantly influence short and long term soil C projections

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Models of soil C dynamics continue to be rapidly developed in a effort to improve projections of terrestrial C fluxes under a range of climate scenarios. Recently developed models of soil organic C (SOC) dynamics that incorporate microbes as the agents of decomposition [1–5] capture a greater number of relevant processes than their predecessors, but it remains unclear whether the mathematical formulations and parameterization of such models are accurate [6–9]. Different model structures, parameterizations, and functions describing responses to changing environmental conditions exert great influence on projections of SOC stocks and CO_2 flux [1, 4, 9]. Discrepancies between projections of SOC stocks from microbial models and current Earth system model (ESM) soil C modules, which can span two orders of magnitude, are highly sensitive to assumptions regarding microbial respiration and efficiency [1, 4, 6].

Although physical structure, chemical composition, and edaphic conditions ultimately govern the accessibility of decomposable SOC [10], physiology dictates the fate of C once it is liberated and taken up from SOC by microbes, regardless of its original composition. A fundamental component of microbial physiology, heterotrophic respiration, which is the conduit for C flow from SOC to the atmosphere and one of the largest potential positive feedbacks to climate warming, is often incorporated in models of SOC dynamics heuristically in a term for efficiency. Alternatively, microbial respiration can be formulated more mechanistically to reflect the fact that heterotrophic respiration in soils is largely mass specific when microbes are actively decomposing SOC [11]. Because heterotrophic microbial respiration influences how much of the C liberated from SOC is retained in the soil and how much is lost to the atmosphere, it is important to understand both the short and long term dynamical consequences of formulating respiratory losses differently in models used to project future climate. Despite all the recent effort to develop better models, to date nobody has determined if the widespread, heuristic formulation of respiratory C losses gives rise to different dynamics than the more physiologically grounded formulations of microbial respiration, over a range of time scales. Here, we address this question for the first time.

Typically in terrestrial modules of ESMs, e.g., the community land model (CLM), respiratory C loss from the soil is phenomenologically defined as 1 minus the fraction of C transferred between C pools [8]. The fraction lost in these transformations is attributed primarily to heterotrophic respiration of soil microbes. Recently proposed microbial modules that are candidates for replacing current CLM belowground dynamics [1, 3–5, 12] incorporate respiratory C losses via a term for efficiency, commonly referred to as C use efficiency (CUE), that is a scalar coefficient of the uptake component of C flux into the microbial biomass pool, B_C:

$$\frac{dB_C}{dt} = B_C[CUE \times U(S_C) - \lambda_B] \quad (1)$$

Hereafter, we refer to Eq. 1 as the CUE formulation. In the CUE formulation, λ_B prescribes losses from the microbial biomass C pool that include allocation to enzyme production, C excretion, death or any additional generic proportional losses, and $U(S_C)$ is the function defining C substrate (S_C) uptake, which is usually assumed to be of Michaelis-Menten form (i.e., substrate uptake rate is a saturating function of substrate availability).

The CUE formulation is conceptually rooted in the idea of microbial efficiency, which quantifies the partitioning of C flow through microbial biomass. Microbial efficiency is

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defined as the ratio of production or anabolism, P, to the sum of production and respiration (catabolism), R, $\frac{P}{P+R}$ [13], and quantifies the fraction of C liberated from SOC lost as CO_2 from the soil and the fraction remaining in microbial biomass. As an integrative metric, microbial efficiency reflects the context for the partitioning of C flow through microbes and is typically used to characterize growth conditional on environmental conditions. Consequently, microbial efficiency should not be considered an inherent physiological trait, but rather a derivative of microbial growth and respiratory demand. Although the fundamental definition of efficiency, $\frac{P}{P+R}$, is straightforward and intuitive, making the measurements to quantify efficiency presents a significant challenge because both P and R must be simultaneously quantified [14] with a high degree of accuracy over a range of relevant conditions. Furthermore, P and R can vary independently in response to changing edaphic conditions, changes in substrate availability and composition, and microbial life history. Modelers have circumnavigated the dearth of independent empirical observations of P and R by treating $\frac{P}{P+R}$ as a single parameter varying from 0 to 1, CUE, that indirectly prescribes respiratory C loss from heterotrophic soil microbes.

Incorporating respiration in this manner, with CUE multiplying the SOC substrate uptake function, is convenient but can result in some logical inconsistencies. For example, respiratory losses are directly influenced by C availability in the environment, not only by cellular demand, and respiratory losses remain a constant fraction of substrate uptake. Consequently, maintenance respiration is a function of uptake rate and vanishes if uptake ceases. Incorporating all respiratory losses as in Eq. 1 means that microbial biomass can persist indefinitely without respiratory costs as long as C uptake is zero, which is unrealistic [11]. Thus, prescribing that all respiratory C losses result from the product of CUE and uptake is inconsistent with constitutive or baseline respiration. Furthermore, though it is obvious that C enters microbial biomass prior to being respired, C lost as CO_2 in the CUE formulation is instantaneously respired as it is liberated from SOC, and is never depicted as having entered microbial biomass.

From basic physiology, we know that C must be taken into a cell before it is respired. Mathematically representing that respiratory C loss originates from an intracellular C pool necessitates the inclusion of a mass specific respiration rate (MSR; for simplicity it encompasses growth and maintenance respiration). This differs from the CUE formulation in that respiratory C losses only depend on microbial biomass, but C is lost via the same additional pathways as in the CUE formulation (e.g., allocation to enzyme production, C excretion—prescribed by λ_B in Eq. 1, and death). Aggregating mass specific growth and maintenance respiration into a single term results in no loss of generality because of linearity. Such a MSR term for maintenance respiration was recently incorporated by [11]. Dynamics with respiratory C losses prescribed in a mass specific manner assume the following generic form:

$$\frac{dB_C}{dt} = B_C[U(S_C) - MSR - \lambda_B], \tag{2}$$

which we refer to as the MSR formulation. The components of efficiency for the CUE formulation are defined as: $P = B_C \times CUE \times U(S_C)$, and $R = B_C \times (1-CUE) \times U(S_C)$, whereas for the MSR formulation: $P = B_C \times (U(S_C) - MSR)$, and $R = B_C \times MSR$. Thus, the aggregate metric of microbial efficiency reduces to CUE and $1 - \frac{MSR}{U(S_C)}$ for the CUE and MSR formulations, respectively.

A key difference between the two formulations of respiratory C loss is that, for a particular set of environmental conditions, CUE is assumed constant for the CUE formulation and MSR is assumed constant for the MSR formulation. Consequently, for a given set of environmental conditions, the CUE formulation dictates that efficiency is constant irrespective of substrate availability. In contrast, the MSR formulation portrays microbial efficiency as a function of both MSR and substrate availability, i.e., a dynamic aggregate resulting from the interaction between microbial physiology and environmental conditions. Consequently, variation and covariation in MSR and in substrate availability, which has been recently demonstrated in controlled experimental conditions [15], can independently influence efficiency in the MSR formulation. The two formulations of respiratory losses can be seen as opposite ends of a continuum, with all respiratory losses proportional to uptake for a pure CUE formulation and proportional to microbial biomass C for a pure MSR formulation. We focus on the opposite ends of the continuum to elucidate the most pronounced dynamical consequences of different mathematical formulations of microbial respiratory C loss.

Gross C fluxes can be made equivalent for the CUE and MSR formulations for any level of SOC, but it is unclear whether the values of CUE and MSR that result in equivalence are mutually consistent. Efficiency can also be equivalent for both formulations if $CUE = 1 - \frac{MSR}{U(S_C)}$, but such equivalence necessitates that the ratio of $\frac{MSR}{U(S_C)}$ is constant for all S_C. This underscores the fact that the CUE formulation treats efficiency as a pre-specified characteristic of microbes, rather than an emergent feature of microbial interactions with the environment, as in the MSR formulation. Explicitly including MSR in models may be more physiologically realistic, but it comes with a cost: measuring an additional parameter. The CUE formulation is appealing because CUE is an aggregate measure of efficiency, obviating the need to measure MSR, which is

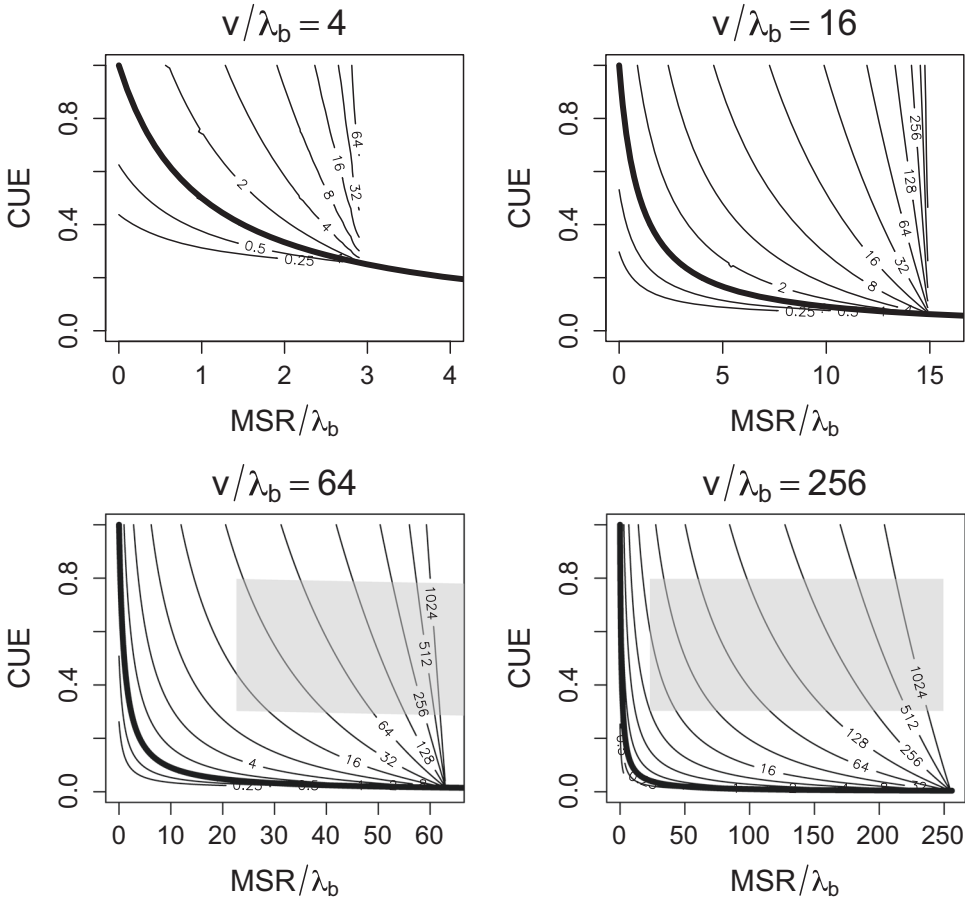

Fig. 1 Discrepancy in steady-state SOC pool sizes between the MSR and CUE formulations for four values of v/λ_B. Along the thick black line, $CUE = \frac{1}{MSR/\lambda_B+1}$ and thus $\hat{S}_C^{MSR}/\hat{S}_C^{CUE} = 1$. The contours depict the deviation in the steady state SOC pool sizes. The shaded region corresponds to the range of CUE and MSR/λ_B values from the literature. λ_B varies from 0.002 h^{-1} [2] to 0.0002 h^{-1} [1], and MSR varies from 0.045 to 0.240 h^{-1} [15, 17]

difficult in practice [14], and because it heuristically captures partitioning between anabolism and catabolism. The question of whether the more convenient, heuristic CUE and the more physiologically-based MSR formulations of respiratory C losses exhibit similar short term and long term dynamics has not been addressed, and needs to be answered before we continue moving forward with CUE-based microbial dynamics in soil biogeochemical modules of ESMs. Answering this question will tell us whether or not the more convenient CUE formulation faithfully portrays dynamics of a more physiologically realistic formulations of respiratory C losses from soil microbes.

Our goal here is to delineate the scenarios for which the CUE and MSR formulations of respiratory C loss result in significantly different soil C dynamics and when they agree. The different means of parsing C liberated from SOC into biomass and respired CO_2 represented by Eqs. 1 and 2 can result in significantly different long term microbial biomass C and SOC pool sizes, and in significantly different dynamical responses of microbial biomass C, and associated soil respiration. To see this, we must explicitly couple SOC substrate (S_C) dynamics to microbial biomass C dynamics. In the most abstract sense, the SOC decomposition process can be formalized with two general equations, one for SOC and one for microbial biomass C:

$$\begin{aligned} \frac{dS_C}{dt} &= I - B_C U(S_C) - S_C\lambda_S + B_C\lambda_B\varepsilon \\ \frac{dB_C}{dt} &= \begin{cases} B_C[CUE \times U(S_C) - \lambda_B]; & CUE \text{ formulation} \\ \text{or} \\ B_C[U(S_C) - MSR - \lambda_B]; & MSR \text{ formulation} \end{cases} \end{aligned} \tag{3}$$

The SOC pool increases as a function of external inputs, litter, (I) and C lost from microbial biomass (B_C) and decreases as a result of microbial uptake (U) and leaching (note we consider microbial biomass distinct from SOC throughout). Microbial uptake, $U(S_C)$, microbial respiration rate, MSR, and other losses, λ_B, are all mass specific rates, and ε is the fraction of C lost from microbes recycled back to the substrate pool. We only consider a single SOC pool to highlight dynamical differences between different formulations of respiratory C loss. Such differences will be independent of substrate particulars such as quality or recalcitrance because our focus is on the fate of C fate after it is taken up. For the comparison of interest here, we do not need to address varying propensities of acquisition for

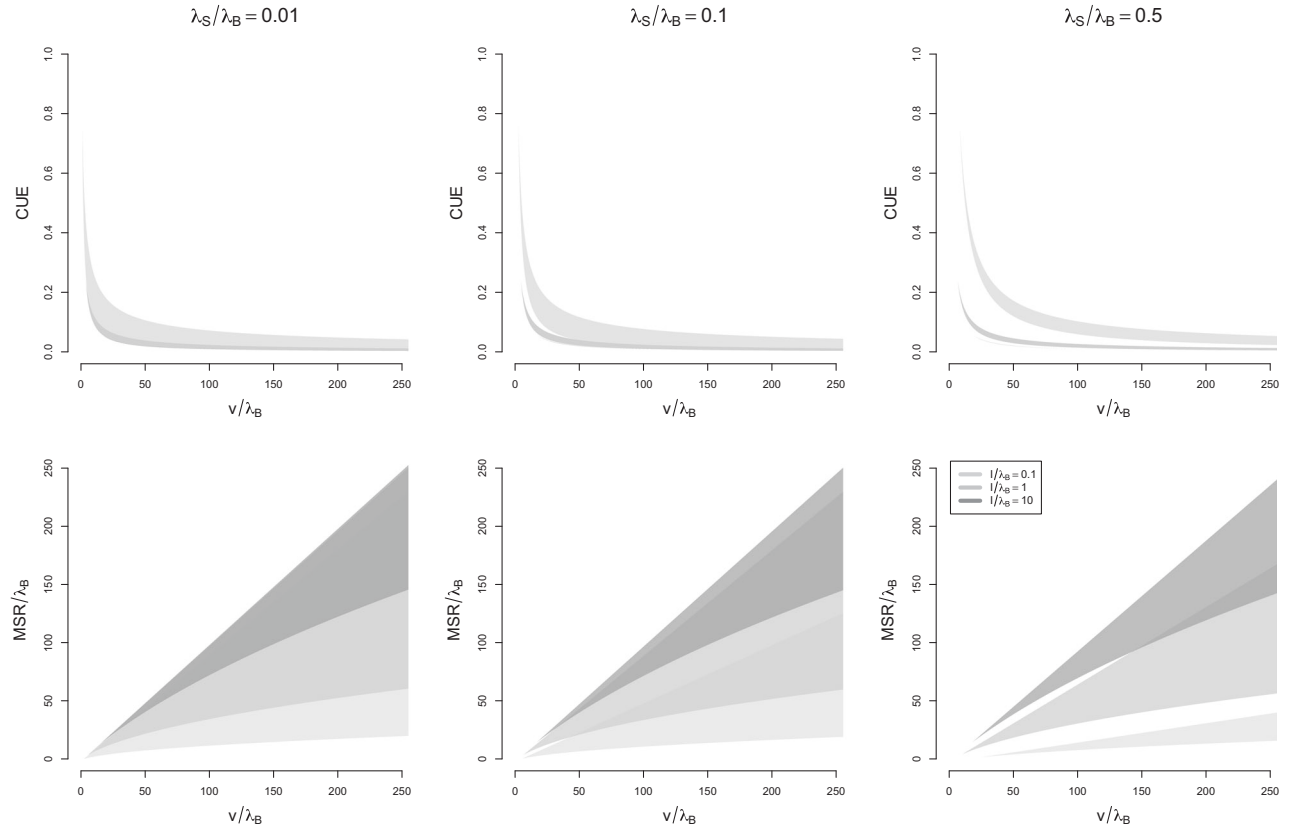

Fig. 2 Regions of parameter space consistent with biomass C to SOC ratios between 0 and 0.05. The λ_S/λ_B ratio reflects the relative loss rates from the SOC pool to non-respiratory loss rate from the microbial biomass pool, and the *x*-axis reflects the relative rates of maximum SOC uptake v and non-repiratory losses λ_B. Above the envelopes for CUE and below the envelopes for $\frac{MSR}{\lambda_B}$, $\hat{B}_C/\hat{S}_C > 0.05$. As the colors darken across envelopes, the relative magnitude of input rate to the SOC pool I increases relative to non-respiratory loss rate from microbial biomass λ_B

different substrates. Differences in SOC composition will certainly influences rates of acquisition and microbial growth rate, but because our focus is on how C that is already liberated is lost as CO_2, SOC chemistry will not influence the dynamical consequences of different mathematical formulations of microbial respiration. Although a soil enzyme C pool could have been explicitly included, we omitted enzymes for clarity. However, ε effectively prescribes that some C lost via λ_B increases the size of the substrate pool in a functionally similar manner to soil enzyme activity. The explicit inclusion of soil enzymes would shift C from either or both the SOC and biomass pools into an enzyme pool, but because soil enzyme C is usually assumed to be a small fraction of total soil C, the effect would be minimal. The same would hold for additional intermediate C pools, e.g., DOC [1].

The different formulations of respiratory C loss can result in three types of discrepancies: in equilibrium pool sizes for the same C pool, in the relative size of both C pools (biomass C and SOC), and in the response to perturbation, i.e., transient dynamics. For the first two, we examine equilibrium expressions for substrate C and biomass C:

$$\hat{S}_C = \begin{cases} U^{-1}\left(\frac{\lambda_B}{CUE}\right); & CUE \text{ formulation} \\ \text{or} \\ U^{-1}(MSR + \lambda_B); & MSR \text{ formulation} \end{cases}$$
$$\hat{B}_C = \begin{cases} \frac{I - U^{-1}\left(\frac{\lambda_B}{CUE}\right)\lambda_S}{\lambda_B\left(\frac{1}{CUE} - \varepsilon\right)}; & CUE \text{ formulation} \\ \text{or} \\ \frac{I - U^{-1}(MSR + \lambda_B)\lambda_S}{MSR + (1-\varepsilon)\lambda_B}; & MSR \text{ formulation} \end{cases} \quad (4)$$

It is clear from Eq. (4) that discrepancies between equilibrium pool sizes will occur if $\frac{\lambda_B}{CUE}$ is substantially different from $MSR + \lambda_B$. The standard assumption is that the uptake function $U(S_C)$ is of Michaelis–Menten form, $\frac{vS_C}{(K+S_C)}$ with v equaling maximum substrate uptake rate and K the half-saturation constant. Explicit and straightforward steady-state expressions for S_C in terms of the Michaelis-Menten

uptake kinetics can easily be obtained and are:

$$\hat{S}_C = \begin{cases} \frac{K}{\left(\frac{vCUE}{\lambda_B}-1\right)}; & CUE \text{ formulation} \\ \text{or} & \\ \frac{K}{\left(\frac{v}{MSR+\lambda_B}-1\right)}; & MSR \text{ formulation} \end{cases} \quad (5)$$

Steady state pool sizes ($\hat{S}_C$ in Eqs. 4 and 5) and microbial efficiency will be equal for both formulations if $CUE = \frac{1}{\frac{MSR}{\lambda_B}+1}$, but if $CUE \neq \frac{1}{\frac{MSR}{\lambda_B}+1}$ the steady state SOC pools for the two formulations will differ in size. Using the empirically observed and often assumed variation in CUE for soil microbes [1, 12, 14, 16], and recently quantified variation in MSR for a common soil microbe [15, 17], the potential for a discrepancy in steady-state SOC pool size between the two formulations can be assessed. In Fig. 1, the subset of parameter space corresponding to the assumed and empirically quantified ranges of CUE and MSR, shown as a shaded box, is superimposed on contour plots in which the contours denote the ratios of steady state SOC pool sizes for the CUE formulation relative to the MSR formulation. The lowest assumed value for λ_B found in the literature, 0.0002 h^{-1} [1], results in a discrepancy in SOC pool sizes of up to three orders of magnitude between the two formulations (the right edge of the shaded box in Fig. 1), whereas the highest assumed value, 0.05 d^{-1} [2], results in a less pronounced discrepancy (the left edge of the shaded box in Fig. 1) when combined with the lower portion of the empirical range for MSR, ≈0.05–0.2 h^{-1} [15, 17]. Smaller SOC pools for the MSR formulation relative to the CUE formulation are possible (lower left corner of each panel in Fig. 1, which corresponds to very low CUE and low MSR relative to λ_b), but the parameter space for this situation is restricted and is not supported by empirical evidence [18]. Thus, projections of microbial biomass C are likely to be significantly larger and projections of SOC are likely to be smaller using the CUE formulation with values in the current literature.

The two formulations also differ in how the steady state ratio of biomass C to SOC ($\hat{B}_C/\hat{S}_C$) varies as function of microbial physiology (Fig. 2). For ratios of v/λ_B above 50, lower values of CUE (≤0.2) than typically assumed, inferred from, or measured by experiments [1, 12, 15–17] are required for $\hat{B}_C/\hat{S}_C$ to be less than 0.05, the empirically observed upper limit [19]. This is especially true in environments characterized by large inputs to the SOC pool relative to non-respiratory losses from microbial biomass (darker envelopes in Fig. 2 corresponding to large values of I/λ_B). However, if v/λ_B is smaller in magnitude, assumed CUE values are consistent with $\hat{B}_C/\hat{S}_C \leq 0.05$. In contrast, for large ratios of maximum uptake rate to non-respiratory loss rate (high values of v/λ_B), the MSR formulation is more consistent with low ratios of microbial biomass C to SOC. The v/λ_B ratio will likely be large in soils though, because realized uptake that depends on substrate availability must compensate for both respiratory and non-respiratory C losses from microbes. The consistency across columns in Fig. 2 reflects the fact that as one component of microbial physiology changes, e.g., v/λ_B, another, efficiency in this case, must simultaneously change to constrain microbial biomass within reasonable limits. Although incorporating an additional SOC pool would expand the parameter range consistent with $\hat{B}_C/\hat{S}_C \leq 0.05$ for either model (sensu [4]), the qualitative differences between respiratory formulations, namely that the CUE formulation tends to generate greater microbial biomass C relative to SOC than the MSR formulation, will persist.

The discrepancies in steady state pool sizes for the CUE and MSR formulations are primarily the result of specific choices of parameter values. If the assumed values or the assumed ranges of values for CUE, MSR, non-respiratory loss rate (λ_B), and maximum substrate uptake rate (v) are incorrect, then discrepancies may be less distinct. Although the lowest assumed value for CUE in the soil literature is ≈0.3, aquatic microbes [13] and litterbag decomposition rates [12] are often characterized by CUE ≤ 0.2. Assuming a value ≤0.2 for CUE would indeed decrease the discrepancy in steady state soil C pool sizes, because lower values of CUE yield results more consistent with the MSR formulation and empirically observed ratios of $\hat{B}_C/\hat{S}_C$. This fact is interesting because [14] have argued that CUE values reported in the soil literature are likely to overestimate true efficiency. Additionally, because the ratio of biomass C to SOC considered here and in recent microbial models [1–5, 12] is best thought of as the ratio of microbial biomass C to SOC accessible for microbial breakdown and assimilation, the upper limit of 0.05 that is accurate for total SOC may be an underestimate when considering the available SOC pool [19]. If CUE ≤ 0.2 and the upper limit for the ratio of microbial biomass C to accessible SOC is higher than 0.05, the CUE model will produce steady state results more in line with empirical observations. However, this will not affect the comparison of the CUE and MSR formulations if both incorporate a single SOC pool.

Transient dynamics, i.e., responses to perturbations or varying environmental conditions such as temperature, also differ between the two formulations of respiratory C loss. For a dynamical system, e.g., Eq. 3 here, transient dynamics are typically characterized by linear stability analysis, which involves computing the eigenvalues of the the linearized system. The signs of the eigenvalues prescribe qualitative stability and the magnitudes of the eigenvalues prescribe the rate at which the system returns to steady-state. Both the CUE and MSR systems have eigenvalues with negative real parts and are thus stable in the dynamical sense

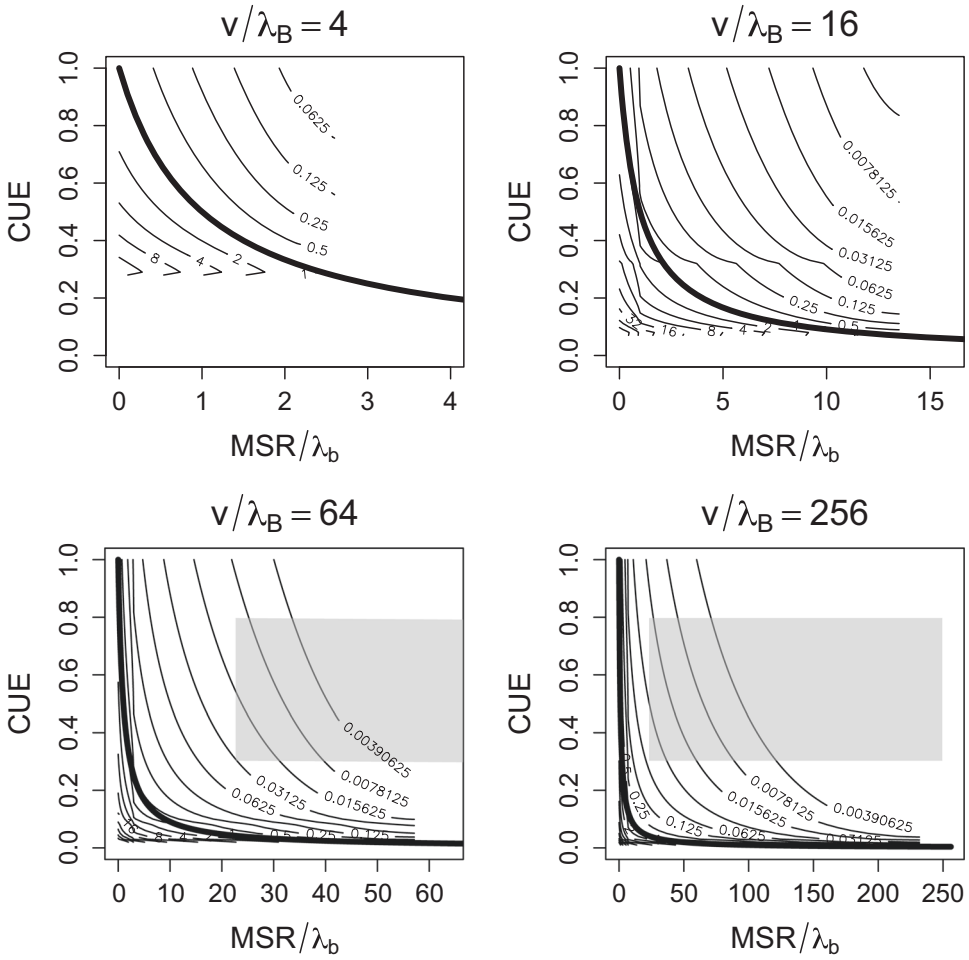

Fig. 3 Ratio of the largest eigenvalue for the MSR system to the largest eigenvalue for the CUE system. The region of microbe existence differs based on values of $\frac{I}{K\lambda_B}$, v/λ_B, λ_S/λ_B, and ϵ. For this particular figure, $\frac{I}{K\lambda_B} = 1$, $\lambda_S/\lambda_B = 0.1$, and $\epsilon = 0.2$. The shaded rectangle corresponds to the same parameter ranges as in Fig. 1. The thick black line corresponds to the ratio of eigenvalues for the case that steady state pools are equal for both formulations

(see Appendix for details). As with the discrepancy between steady-state SOC pool sizes, the difference in the eigenvalues for the two formulations depends on the relationship between CUE and $\frac{1}{\frac{MSR}{\lambda_B}+1}$. As above, if $CUE = \frac{1}{\frac{MSR}{\lambda_B}+1}$, pool sizes will be identical for both formulations, but the CUE formulation will almost always have a larger magnitude dominant eigenvalue, and as a result will be more responsive to perturbation than the MSR formulation (see Appendix). Thus, even if steady state pools sizes are identical for both formulations, transient dynamics, i.e., the responses to punctuated or continued perturbations, will differ between the two formulations of respiratory C loss. In Fig. 3, the subset of parameter space corresponding to the assumed and empirically quantified ranges of CUE and MSR, shown by a shaded box as in Fig. 1, is superimposed on contour plots in which the contours denote ratios of dominant eigenvalues for the CUE formulation relative to the MSR formulation. For the same ranges of CUE and $\frac{MSR}{\lambda_B}$ delineated in Fig. 1, the dominant eigenvalue of the CUE formulation is approximately an order of magnitude larger than the dominant eigenvalue for the MSR formulation.

In general, the CUE formulation is characterized by larger magnitude negative eigenvalues (the shaded box in Fig. 3 overlaps with ratios substantially smaller than 1), meaning that CUE formulations will both return to steady-state more quickly after a perturbation (a faster approach to steady state in Fig. 4a, c) and will track fluctuations in the environment more closely (smaller magnitude oscillations in Fig. 4b, d) given the parameter values widely used in the literaure. In contrast, the MSR formulation results in a slower and less damped approach to steady state (red lines vs. blue lines in Fig. 4a, c) because of relatively smaller magnitude negative eigenvalues, and less of a tendency to respond to high frequency environmental variation (red lines vs. blue lines in Fig. 4b), depicted here for illustrative purposes in response to variation in temperature (see Appendix for details). For larger values of $\frac{MSR}{\lambda_B}$, the sensitivity of the MSR formulation decreases (the magnitude of the real part of the dominant eigenvalue decreases in absolute value) due to increased respiratory loss, and can lead to much longer transient dynamics (compare the red lines in Fig. 4a, b to the red lines in to Fig. 4c, d). However, for smaller values of $\frac{MSR}{\lambda_B}$, the MSR formulation can more

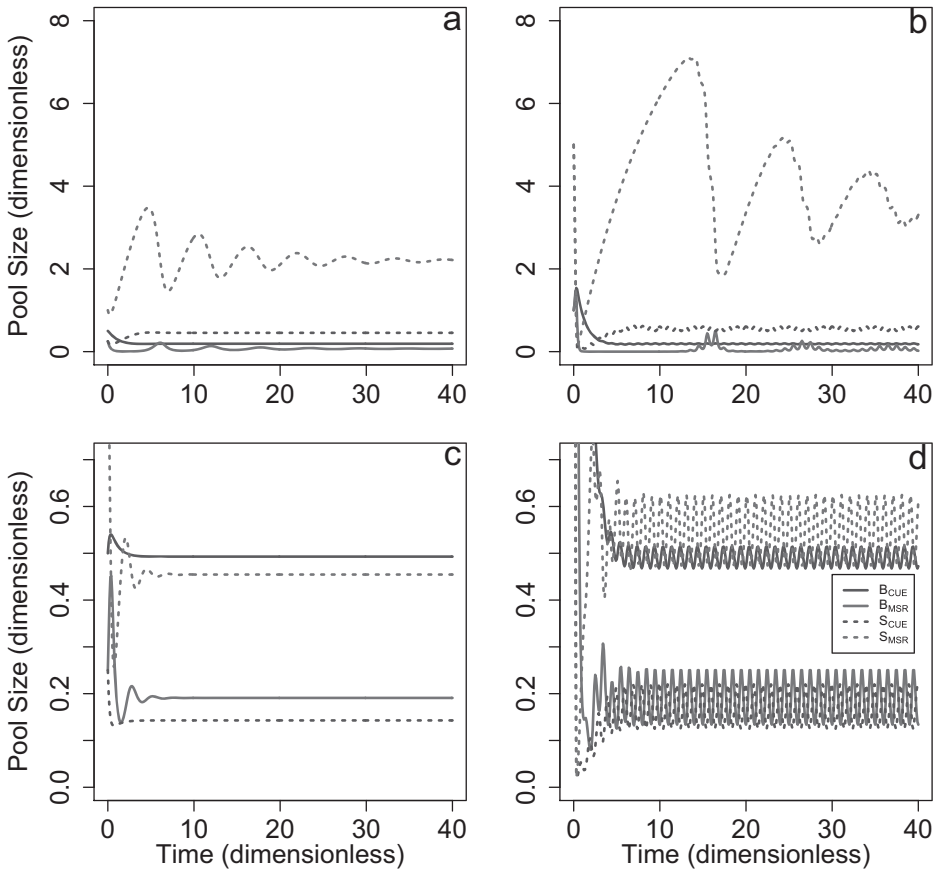

Fig. 4 Simulated SOC and microbial biomass C dynamics using dimensionless versions of equations 1 (CUE formulation) and 2 (MSR formuiation) presented in the Appendix. Simulations in panels **a** and **c** start at the same arbitrary initial conditions, and simulations in panels **b** and **d** start at the same arbitrary initial conditions. Inputs to the SOC pool, uptake, and loss are identical for all panels, $\frac{I}{K\lambda_B} = 1$, $v^{'} = \frac{v}{\lambda_B} = 16$, $\lambda_S^{'} = \frac{\lambda_s}{\lambda_B} = 0.1$, which are the same values for Fig. 3. In panels **a** and **b**, $CUE = 0.2$ and $\frac{MSR}{\lambda_B} = 10$, and in panels **c** and **d**, $CUE = 0.5$ and $\frac{MSR}{\lambda_B} = 4$. In panels **b** and **d**, environmental variation is implicitly incorporated by varying T sinusoidally over time, assuming Arrhenius dependence of v' on T, with amplitude and frequency identical for both formulations. The units for time and pool size are dimensionless. See Methods for details

closely track high frequency environmental variation (red lines in Fig. 4d) and will exhibit transient behavior similar to that of the CUE formulation. In general, prescribing respiratory losses solely as mass specific slows down the flow of C from SOC into the atmosphere relative to a CUE formulation because C must enter the biomass C pool and leave as CO_2 after a period time dictated by the value of MSR. Oscillatory behavior is known to be a feature of non-linear models of SOC dynamics [20], but whether long period oscillations exist in nature is unknown. Perhaps more importantly though, the difference in responsiveness can result in different steady-state pool sizes for the MSR formulation in the presence of environmental variation (the difference between in the red dashed lines in panels a and b and between panels c and d in Fig. 4). As a consequence, the CUE formulation will therefore not generate the potentially significant changes in SOC pool size in response to environmental variation that result from the MSR formulation.

The way that microbial respiration is formulated in models of SOC dynamics influences projections of terrestrial C fluxes. Different formulations of microbial respiration can generate discrepancies in steady-state SOC and microbial biomass C pool sizes of more than two orders of magnitude, depending on assumed relative rates of respiratory and non-respiratory losses for microbes reported in the literature. Contrasting formulations of microbial respiration can also drive divergent transient responses to environmental perturbations, with CUE formulations exhibiting a reduced propensity for transient SOC and microbial biomass C dynamics than formulations based on mass specific respiratory losses. Thus, the distinction between efficiency based respiratory losses and mass specific respiratory losses is not merely syntactic or semantic. However, because there is significant uncertainty regarding parameters that influence discrepancies between formulations (e.g., λ_B and v), it is currently impossible to quantify the exact magnitude of these discrepancies in both short and long-term dynamics. Regardless, the results presented here highlight the critical dependence of modeled SOC stock dynamics on respiratory and non-respiratory C losses from microbes, on the way these fluxes are represented mathematically, and the need to more accurately quantify both fluxes. As a consequence, the growing community of soil modelers must reassess how microbial soil respiration is formally incorporated in models, and the parameter values that prescribe microbial efficiency.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Mathematical appendix

To simplify analysis, we non-dimensionalized Eq. 3 to arrive at

$$\frac{dS_C^{'}}{d\tau} = I^{'} - B_C^{'}\frac{v^{'}S_C^{'}}{(1+S_C^{'})} - S_C^{'}\lambda_S^{'} + B_C^{'}\varepsilon$$

$$\frac{dB_C^{'}}{d\tau} = \begin{cases} B_C^{'}\left[CUE \times \frac{v^{'}S_C^{'}}{(1+S_C^{'})} - 1\right]; & CUE \text{ formulation} \\ \text{or} \\ B_C^{'}\left[\frac{v^{'}S_C^{'}}{(1+S_C^{'})} - MSR^{'} - 1\right]; & MSR \text{ formulation} \end{cases}$$

in which $S_C^{'} = \frac{S_C}{K}$, $B_C^{'} = \frac{B_C}{K}$, $\tau = \lambda_B t$, $I^{'} = \frac{I}{K\lambda_B}$, $v^{'} = \frac{v}{\lambda_B}$, $\lambda_S^{'} = \frac{\lambda_S}{\lambda_B}$, and $MSR^{'} = \frac{MSR}{\lambda_B}$.

The equilibria are given by

$$\hat{S}_C = \begin{cases} \frac{1}{(v^{'}CUE-1)}; & CUE \text{ formulation} \\ \text{or} \\ \frac{1}{\left(\frac{v^{'}}{MSR^{'}}-1\right)}; & MSR^{'} \text{ formulation} \end{cases}$$

$$\hat{B}_C = \begin{cases} \frac{I^{'} - \left(\frac{\lambda_S^{'}}{v^{'}CUE-1}\right)}{\left(\frac{1}{CUE}-\varepsilon\right)}; & CUE \text{ formulation} \\ \text{or} \\ \frac{I^{'} - \frac{\lambda_S^{'}}{\left(\frac{v^{'}}{MSR^{'}+1}-1\right)}}{MSR^{'}+1-\varepsilon}; & MSR \text{ formulation} \end{cases} \quad (6)$$

In the absence of life,

$$\hat{S}_C^{'} = \frac{I^{'}}{\lambda_S^{'}} = \frac{I}{\lambda_S}, \quad (7)$$

and for biota to persist, $v^{'} > CUE$ and $\lambda_S^{'} < I^{'}(v^{'}CUE-1)$ for the CUE formulation, and $v^{'} > MSR^{'}+1$ and $\lambda_S^{'} < I^{'}\left(\frac{v^{'}}{MSR^{'}+1}-1\right)$ for the MSR formulation.

The ratio of equilibrium SOC for the MSR formulation to equilibrium SOC for the CUE formulation is given by

$$\frac{\hat{S}_C^{'MSR}}{\hat{S}_C^{'CUE}} = \frac{(v^{'}CUE-1)}{\left(\frac{v^{'}}{MSR^{'}+1}-1\right)}. \quad (8)$$

The ratio will equal 1 if $CUE = \frac{1}{MSR^{'}+1}$, denoted by the bold line in the figure panels.

To address the discrepancy in the response to perturbation, we analyze the characteristic equation resulting from the determinants of the Jacobians for the two formulations. The Jacobian evaluated at the equilibrium for both systems assumes the general form

$$\hat{J}_X = \begin{bmatrix} \frac{-v^{'}\hat{B}_C^{'}}{\left(1+\hat{S}_C^{'}\right)^2} - \lambda_S^{'} & \frac{-v^{'}\hat{S}_C^{'}}{1+\hat{S}_C^{'}} + \epsilon \\ \frac{v^{'}\hat{B}_C^{'}X}{\left(1+\hat{S}_C^{'}\right)^2} & 0 \end{bmatrix} \quad (9)$$

in which $X = CUE$ or 1 and $\frac{-v^{'}\hat{S}^{'}}{1+\hat{S}^{'}} = \frac{1}{CUE}$ or $MSR^{'}+1$ for the CUE and MSR formulations, respectively. The eigenvalues for the associated characteristic equation are

$$\frac{-(A+\lambda_S^{'}) \pm \sqrt{(A+\lambda_S^{'})^2 + 4AX(\epsilon - B)}}{2} \quad (10)$$

in which $A = \frac{v^{'}\hat{B}_C^{'}}{\left(1+\hat{S}_C^{'}\right)^2}$ for both formulations and $B = \frac{1}{CUE}$ or $MSR^{'}+1$ for the CUE and MSR formulations, respectively. In the absence of life, we simply recover $\lambda_S^{'}$ as the only eigenvalue. Thus, the addition of living microbes to the soil system increases the absolute magnitude of the dominant eigenvalue, thereby decreasing return time to equilibrium and increasing system stability. The real parts of all eigenvalues for both formulations are negative, reflecting the stability of the steady-state. To most directly compare stability between formulations, we assume that the equilibria are the same for both, i.e $CUE = \frac{1}{MSR^{'}+1}$. The discrepancy in stability between the two formulations is most easily seen for the case of no recycling, $\varepsilon = 0$, because the only difference in the eigenvalues arises in the AXB term. For the CUE formulation, AXB simply reduces to A because $X = CUE$ and $B = \frac{1}{CUE}$, which also means that the response to perturbation is independent of CUE in the absence of recycling. For the MSR formulation, $AXB = A(MSR^{'}+1)$ because $X = 1$ and $B = MSR^{'}+1$. A is the same by assumption, which means that in the case of no recycling the return to identical equilibrium will be faster for the CUE formulation. In general, increased rates of recycling, $\varepsilon > 0$, promote a faster return to equilibrium and shorter duration transient dynamics. $MSR^{'} > 1$, which is substantiated in other work [18], is a sufficient condition to guarantee the same damped response to perturbation and longer transient dynamics of the MSR formulation as for the case of no recycling. The influence of CUE on stability is more severely constrained because both ε and CUE are bounded by 0 and 1, whereas $MSR^{'}$ can, and will often be significantly greater than 1.

Equations 3 were simulated with $I^{'} = 1$, $v^{'} = 16$, $CUE = [0.2,0.5]$, $MSR^{'} = [4,10]$, and $\lambda_S^{'} = 0.1$ to generate temporal trajectories of S_C and B_C. To simulate the response to temperature variation, we made the standard assumption that v exhibits an Arrhenius temperature dependence [1],

and incorporated variation in the following manner,

$$v'' = v'\alpha e^{\frac{-E_a}{R\left(288+5\sin\frac{\pi t}{2}\right)}}, \quad (11)$$

with $\alpha = 10^9$, $E_a = 50{,}000$ and $R = 8.134$.

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