Weaker soil carbon–climate feedbacks resulting from microbial and abiotic interactions

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Supplementary methods

The DEB based microbial model

Soil carbon dynamics involve many complex mechanisms, including, but not limited to, aggregation dynamics \(^1\), microbial population dynamics \(^2\), turbation dynamics \(^3,4\), redox chemistry \(^5\) and soil erosion \(^6\). Here we highlight that even a simple accounting of the interactions between polymeric SOM, monomeric DOM, microbial populations, and mineral surfaces will result in much more realistic predictions of soil carbon dynamics than many existing soil carbon models could do. Therefore, we formulate the DEB microbial model for one microbe, one enzyme, one polymeric SOM compound, one DOM compound, and one mineral surface, and reversible mineral adsorption of enzymes and DOM (although Figure S1 considers many microbes are degrading many substrates in the presence of different mineral surfaces). Our model structure assumes (1) enzymes lose their catalysis capability when adsorbed to a mineral surface \(^7\); (2) DOM becomes bio-unavailable when adsorbed to a mineral surface \(^8\); and (3) microbial metabolism can be described by the dynamic energy budget (DEB) theory \(^9\). With these assumptions, the model governing equations are:

\[
\begin{align*}
\frac{dS}{dt} &= I_S - F_S + \gamma_{BI}B + f_E \gamma_{EE}E \\
\frac{dC}{dt} &= I_C + F_S - F_C + \gamma_{BI}X + (1 - f_E) \gamma_{EE}E \\
\frac{dX}{dt} &= Y_X F_C - (\kappa - g + \gamma_{BI})X
\end{align*}
\]
\[
\frac{dB}{dt} = (g - \gamma_B)B \tag{4}
\]

\[
\frac{dE}{dt} = p_E B - \gamma_E E \tag{5}
\]

\[
R_{CO2} = (1 - Y_X) F_C + \left[ m + g \left( \frac{1}{Y_B} - 1 \right) + p_E \left( \frac{1}{Y_E} - 1 \right) \right] B + F_r \tag{6}
\]

All essential symbols are explained in Table S1. In our model, we assume that mineral adsorption and desorption can be described by the Langmuir isotherm \(^{10}\), such that the Equilibrium Chemistry Approximation kinetics can be used to describe the substrate uptake process involving multiple interacting components \(^{11}\):

\[
F_S = \frac{ESV_{E,max}}{k_E S + \frac{E}{k_{ES}} + \frac{M}{k_{ME}}} \tag{7}
\]

for enzymatic degradation of SOM, and

\[
F_C = \frac{zBCV_{B,max}}{k_B C + \frac{zB}{k_{BC}} + \frac{M}{k_{MC}}} \tag{8}
\]

for microbial uptake of DOM.

In the DEB theory, the DOM assimilation flux \(Y_X F_C\) changes the microbial reserve pool \(X\). Meanwhile, a parallel flux \((\kappa - g)X\) is exported from the reserve pool \(X\) to support microbial maintenance \(mB\). The residual from maintenance cost is used to support structural growth \(gB\) and enzyme production \(p_E B\). The flux of carbon overflow is represented by \(F_r\), which is zero when the microbe can efficiently use the carbon flux \((\kappa - g)X\) for metabolism (maintenance, growth, and enzyme production). These assumptions lead to the relationship

\[
(\kappa - g)X = \left( m + \frac{g}{Y_B} + \frac{p_E}{Y_E} \right) B + F_r \tag{9}
\]

To obtain the specific cell growth rate \(g\) and the specific enzyme production rate \(p_E\), we assume these two processes have the same priority and access the total productive reserve flux \(j_X = (\kappa - g)X/B - m\) in proportion to their potential rates: \(g_p\)
and $p_{E,p}$. The potential rates $g_p$ and $p_{E,p}$ are computed using the method of synthesizing unit for single reserve $^{12}$:

$$g_p = \left( \frac{1}{g_{\text{max}}} + \frac{1}{j_X Y_B} \right)^{-1}$$  \hfill (10)

and

$$p_{E,p} = \left( \frac{1}{p_{E,\text{max}}} + \frac{1}{j_X Y_E} \right)^{-1}$$  \hfill (11)

Accordingly, the actual specific growth rate and actual specific enzyme production rates are

$$g = g_p \min \left( \frac{j_X}{g_p/Y_B + p_{E,p}/Y_E}, 1 \right)$$  \hfill (12)

and

$$p_E = p_{E,p} \min \left( \frac{j_X}{g_p/Y_B + p_{E,p}/Y_E}, 1 \right)$$  \hfill (13)

**Steady state solution**

*Plastic microbial model*

We solve for the steady state solution (indicated by superscript “*”) of the model (Eqs. (1)-(6)) under the assumption of constant carbon input rates and model parameters and $Y_B = Y_E$ (this latter equality is not necessary, but it is helpful for a clear presentation of our results). By first setting all temporal derivatives of Eqs. (1)-(5) to zero, then by adding Eqs. (1) and (2), one finds

$$F_C = I_s + I_c + \gamma_{B1} \left( B^* + X^* \right) + \gamma_E E^*$$  \hfill (14)

From Eqs. (3)-(5), one has

$$F_C = \frac{\kappa X^*}{Y_X}$$  \hfill (15)

and from Eq. (5), one has

$$E^* = \frac{p_E}{\gamma_E} B^*$$  \hfill (16)
By substituting Eqs. (15) and (16) into Eq. (14), one obtains

\[
\left(\frac{\kappa}{Y_x} - \gamma_{B1}\right)X^* - \left(\gamma_{B1} + p_E\right)B^* = I_s + I_c
\]  

(17)

By solving together Eq. (9) (note \(F_r = 0\)) and (17), one finds

\[
B^* = \frac{I_s + I_c}{\left(\frac{\kappa}{Y_x} - \gamma_{B1}\right)\frac{m + g}{Y_B} + p_E - \gamma_{B1}}\left(\frac{\kappa}{Y_x} - \gamma_{B1}\right)A - \gamma_B
\]  

(18)

where

\[
A = \frac{m + \gamma_B/Y_B}{\kappa - \gamma_{B1}}
\]  

(20)

From Eq. (9) (with \(F_r = 0\)), one has

\[
X^* = AB^* = \frac{I_s + I_c}{\frac{\kappa}{Y_x} - \gamma_{B1} - \gamma_B/A}
\]  

(21)

By combining Eqs. (8), (16), (20), and (21), one obtains

\[
\frac{\kappa}{Y_x} A = \frac{zC^*V_{B,\text{max}}}{k_{BC} + C^* + zB^* + \frac{k_{BC}}{k_{MC}} M}
\]  

(22)

which, after reorganization, can be rewritten as

\[
\left(zV_{B,\text{max}} - \frac{\kappa}{Y_x} A\right)C^* = \frac{\kappa}{Y_x} A \left(k_{BC} + zB^* + \frac{k_{BC}}{k_{MC}} M\right)
\]  

(23)

From Eq. (23), one then obtains

\[
C^* = \frac{\kappa}{zV_{B,\text{max}} - \frac{\kappa}{Y_x} A} \left(k_{BC} + \frac{k_{BC}}{k_{MC}} M\right) + \frac{\kappa}{zV_{B,\text{max}} - \frac{\kappa}{Y_x} A} zB^*
\]  

(24)

Combining with Eq. (18) gives
\[ C^* = \frac{k_{BC} + k_{BC} M}{k_{MC} z V_{B,\text{max}} Y_X - 1} + \frac{I_S + I_C}{V_{B,\text{max}} A \kappa} \left( \frac{K}{Y_X - \gamma_{B1}} - A - \gamma_B \right) \]  

(25)

Under steady state, Eq. (1) leads to

\[ F_S = I_S + \gamma_{B1} B^* + f_E \gamma_E E^* \]  

(26)

Merging Eq. (24) and Eq. (7), one has

\[ \left( I_S + \gamma_{B1} B^* + f_E \gamma_E E^* \right) \left( k_{ES} + S^* + E^* + \frac{k_{ES}}{k_{ME}} M \right) = E^* S^* V_{E,\text{max}} \]  

(27)

By aid of Eq. (16), one can solve \( S^* \) from Eq. (7)

\[ S^* = \frac{\frac{I_S}{B} + \gamma_{B1} + f_E p_E}{\gamma_E \frac{V_{E,\text{max}}}{V_{E,\text{max}}} - \left( \frac{I_S}{B} + \gamma_{B1} + f_E p_E \right)} \left( k_{ES} + \frac{p_E}{\gamma_E} B^* + \frac{k_{ES}}{k_{ME}} M \right) \]  

(28)

We now have the steady state solution as Eqs. (16), (19), (21), (25), and (28). The steady state respiration is

\[ R_{CO2} = I_C + I_S \]  

(29)

Combining Eqs. (15), (19), and (29), we can derive the apparent carbon use efficiency

\[ CUE^* = 1 - \frac{R_{CO2}}{F_C} = 1 - I_C + I_S Y_X \frac{Y_{B1}}{K_A} \]  

(30)

Here we defined \( CUE^* \) as the ratio between retained microbial carbon (including microbial biomass and extracellular enzymes) and the microbial DOM uptake. In this definition, we consider respiration as the only carbon loss, being consistent with models such as CENTURY\textsuperscript{13}.

By further introducing Eq. (19) into Eq. (30), the apparent \( CUE^* \) is found as only a function of microbial characteristics

\[ CUE^* = \left( 1 + \frac{1}{A Y_{B1}} \right) \frac{Y_{B1}}{\kappa} Y_X \]  

(31)

By defining total SOM as the sum of all organic carbon, one also has

\[ \frac{dSOM}{dt} = I_C + I_S - R_{CO2}^* = I_C + I_S - \frac{R_{CO2}^*}{SOM^*} SOM^* \]  

(32)

where \( SOM^* \) is the equilibrium carbon storage defined as
\[ SOM^* = B^* + X^* + S^* + C^* + E^* \]  

(33)

Therefore, the carbon turnover time can be computed as

\[ \tau = \frac{SOM^*}{R_{CO_2}^*} = \frac{SOM^*}{I_C + I_S} \]  

(34)

**Rigid microbial model**

For a rigid microbe, the reserve pool is zero, giving

\[ Y_X F_C = \left( m + \frac{g}{Y_B} + \frac{p_E}{Y_E} \right) B^* \]  

(35)

By aid of Eq. (14) (with \( X^* = 0 \)) and Eq. (16), one can find

\[ B^* = \frac{(I_S + I_C) Y_X}{m + \gamma_{BL} \left( \frac{1}{Y_B} - Y_X \right) + p_E \left( \frac{1}{Y_E} - Y_X \right)} \]  

(36)

which, when combined with Eq. (8), leads to

\[ C^* = \frac{\left( m + \gamma_{BL} \frac{p_E}{Y_E} \right) \left( k_{BC} + zB^* + \frac{k_{BC} - M}{k_{MC}} \right)}{Y_X z V_{B,max} - \left( m + \gamma_{BL} \frac{p_E}{Y_B} \right)} \]  

(37)

The solutions of \( S^* \) and \( E^* \) have a similar form to that of the plastic microbes.

The revised apparent carbon use efficiency is found as

\[ CUE^* = \frac{Y_{BL} + p_E}{m + \gamma_{BL} + \frac{p_E}{Y_E}} Y_X \]  

(38)

Also, it can be verified that the steady state solution for the rigid microbe is equivalent to a plastic microbe with \( \kappa \to \infty \).

**Transient CUE**

For the main text, we defined transient carbon use efficiency as

\[ CUE(t, \Delta t) = 1 - \frac{\int_{t-\Delta t/2}^{t+\Delta t/2} R_{CO_2} dt}{\int_{t-\Delta t/2}^{t+\Delta t/2} r_{CO_2} dt} \]  

(39)

Depending on \( \Delta t \), we can compute \( CUE(t, \Delta t) \) at different temporal scales for a transient simulation.

**Parameterizing the temperature responses**
We categorized the temperature-dependent processes in our model into three groups: (i) equilibrium reactions, (ii) non-equilibrium reactions, and (iii) enzyme activity (i.e., fraction of enzymes that are inactivated through denaturation). Equilibrium reactions include mineral adsorption ($k_{ME}$ and $k_{MC}$), enzyme-SOM binding ($k_{ES}$), microbe-DOM binding ($k_{BC}$), and microbial maintenance $m$. Non-equilibrium reactions (or forward reactions here) include enzymatic degradation of SOM ($V_{E,max}$), microbial assimilation of DOM ($V_{B,max}$), and reserve turnover ($K$).

Below we describe our rationale for parameterizing the temperature dependence of these different processes.

Considering a generic reaction

$$S + E \leftrightarrow C \rightarrow E + P$$

the forward and backward reaction rates, using the Eyring’s transition state theory are computed as

$$k_1^+ = \frac{k_BT}{\hbar} \exp\left(-\frac{\Delta G_1^+}{RT}\right)$$  \hspace{1cm} (41-a)$$

$$k_1^- = \frac{k_BT}{\hbar} \exp\left(-\frac{\Delta G_1^-}{RT}\right)$$  \hspace{1cm} (41-b)$$

$$k_2^- = \frac{k_BT}{\hbar} \exp\left(-\frac{\Delta G_2^+}{RT}\right)$$  \hspace{1cm} (41-c)$$

where $k_B$ and $\hbar$ are, respectively, the Boltzmann constant and the Plank constant. $R$ is the ideal gas constant.

Under quasi-steady-state, one has the dissociation parameter (aka affinity parameter for MM kinetics)

$$K = \frac{k_2^- + k_1^-}{k_1^+} = \exp\left(-\frac{\Delta G_2^+ - \Delta G_1^+}{RT}\right) + \exp\left(-\frac{\Delta G_1^- - \Delta G_1^+}{RT}\right)$$  \hspace{1cm} (42)$$

with the enzyme-substrate binding described as

$$S + E \leftrightarrow C$$  \hspace{1cm} (43)$$
We note the affinity parameters for both enzyme-substrate complex formation (assuming $k_1^* < k_2^*$) and Langmuir adsorption are in the form of Eq. (42). Therefore, their temperature dependence is of the form

$$K_{EQ}(T) = K(T_0) \exp \left( \frac{-\Delta G_{EQ}}{RT} \left( \frac{1}{T} - \frac{1}{T_0} \right) \right)$$  \hspace{1cm} (44)$$

where $T_0$ (K) is the reference temperature where the reference reaction constant $K(T_0)$ is defined. $\Delta G_{EQ}$ is the Gibbs free energy (i.e. activation energy) of the equilibrium reaction.

The temperature dependence for non-equilibrium reactions (as represented by $k_2^*$) are in the form of Eq. (41-c), such that

$$K_{NEQ} = K_{NEQ}(T_0) \frac{T}{T_0} \exp \left( -\frac{\Delta G_{NEQ}}{RT} \left( \frac{1}{T} - \frac{1}{T_0} \right) \right)$$  \hspace{1cm} (45)$$

where the reference reaction constant $K_{NEQ}(T_0)$ is defined at temperature $T_0$. $\Delta G_{NEQ}$ is the Gibbs free energy of the non-equilibrium reaction.

Enzyme activity refers to the reversible transition between an enzyme’s active state and its inactive state as a function of temperature (although there are other factors, such as pH and ionic strength, affecting this transition). Our model considers the activities of the exoenzyme ($E$), transporter for DOM assimilation ($zB$), and enzyme that exports the reserve pool to support cell metabolism (described by parameter $\kappa$). Since the enzyme is a protein, we parameterize the active fraction as

$$f_{act} = \frac{1}{1 + \exp \left( \frac{-n\Delta G_E}{RT} \right)}$$  \hspace{1cm} (46)$$

According to Murphy et al.\(^{17}\)

$$\Delta G_E = \Delta H^* - T\Delta S^* + \Delta C_p \left[ (T - T_h^*) - T \ln \left( T/T_h^* \right) \right]$$  \hspace{1cm} (47)$$

where

$$\Delta C_p = -46.0 + 30 \left( 1 - 1.54n^{-0.268} \right) N_{CH}$$  \hspace{1cm} (48)$$
Using information provided by Ratkowsky et al.\textsuperscript{18}, we designed a method to identify sets of parameters $\Delta H^*, n, N_{CH}$ that result in reasonable temperature responses. When real data are available, our method is essentially the same as methods used previously\textsuperscript{19}.

There have been debates regarding whether enzyme denaturation is sufficient to explain the occurrence of optimal temperature in enzyme catalysis\textsuperscript{19-21}. Our results suggest that reversible enzyme denaturation can result in optimal temperature for enzyme catalysis and carbon decomposition.

**Microbial model with static CUE**

Assuming CUE holds at the steady state value (i.e., Eq. (31) for plastic microbe and Eq. (38) for rigid microbe, respectively), the model by Eqs. (1)-(6) can be converted into a model that is similar to that in Allison et al.\textsuperscript{22}, which was used as a prototype to improve global soil carbon modeling\textsuperscript{23}. The microbial dynamics in the converted model is in the form

$$\frac{dMIC}{dt} = F_C \text{CUE}^* - \gamma B_1 MIC - \frac{\beta_E}{1+A} MIC$$ \hspace{1cm} (49)

where $MIC = B + X = (1 + A)B$, such that the microbe must have a fixed ratio between its metabolic reserve and structure biomass. Here $\beta_E$ is the enzyme production rate at steady state.

Accordingly, the carbon uptake rate is

$$F_C = \frac{MIC}{1+A} \frac{2V_{B,\text{max}}}{k_{BC}(1 + \frac{C}{k_{BC}} + \frac{Z}{k_{BC} + A + \frac{M}{k_{MIC}}})}$$ \hspace{1cm} (50)

The enzymatic degradation is still described by Eq. (7), while transient SOM, DOM, enzyme concentrations and CO$_2$ from respiration are:

$$\frac{dS}{dt} = I_S - F_S + \frac{\gamma B_1}{1+A} MIC + f_E \gamma E E$$ \hspace{1cm} (51)

$$\frac{dC}{dt} = I_C + F_C - F_C + \gamma B_1 \frac{A}{1+A} MIC + (1 - f_E) \gamma E E$$ \hspace{1cm} (52)

$$\frac{dE}{dt} = \frac{\beta_E}{1+A} MIC - \gamma E E$$ \hspace{1cm} (53)

$$R_{CO2} = (1 - \text{CUE}^*) F_C$$ \hspace{1cm} (54)
The CUE-static microbial model by Eqs. (49)-(54) has numerically identical steady solution as the plastic DEB model (i.e., CUE-prognostic model) under constant temperature forcing (see Figures S7-S10).

When $\kappa \to \infty$, one finds $A = 0$. We thence obtain the rigid microbe model with static CUE, which differs from the rigid microbe model with prognostic CUE because its enzyme production rate $p_E$ is dynamically determined through DEB theory \(^9\) and the synthesizing unit method \(^12\).

**Transient model simulations**

For transient simulations, it may occur that the maintenance cost exceeds the export flux from the reserve pool. To account for this situation, we compute the actual specific maintenance rate as

$$m = \min \left[ m_0, \left( \kappa - g \right) \frac{X}{B} \right]$$

Accordingly we compute the mortality as density dependent \(^24\)

$$\gamma_{B1} = \frac{\gamma_{B1}}{\gamma_{B1} + B} \left( \frac{B}{\gamma_{B1} + B} \right)$$

The Monod term in Eq. (56) is introduced to prevent a microbe from dying out, so that carbon decomposition can still proceed at a very low rate even when microbes are outcompeted by mineral surfaces for DOM.

All transient model simulations were obtained using an adaptive ODE solver modified from the algorithm by Broekhuizen et al. \(^25\) The growth rates and enzyme production rates were calculated using the Brent's method \(^26\) by iteratively solving Eqs. (9)-(13). Numerical solutions were verified by comparing to steady-state solutions and found very accurate (Figure S3).

**Intrinsic decomposition rate and emergent temperature sensitivity**

Intrinsic decomposition is a concept adopted by the turnover pool based models \(^13\). Although our model does not support this concept, we derived surrogate intrinsic decomposition rates for what the “equal-carbon” method \(^27\) labels as “labile” and “recalcitrant” carbon by applying that method to our numerical incubation experiments. We applied the equation
to both the “labile” and “recalcitrant” carbon. Here $C$ denotes a carbon pool. The intrinsic decomposition rate $k_{\text{intrinsic}}$ is defined as the maximum decomposition rate derived from the incubation experiment (Figure S6). $f(T)$ is the nonlinear temperature response function whose values vary between zero and one (Figures S6).

**Multi-microbe model for microbial community dynamics**

We extended the one-microbe model to include multiple microbes for an additional demonstration of the effect of microbial plasticity and microbial community dynamics. This is achieved by extending the substrate dynamics into

$$\frac{dS}{dt} = I_S - \sum_{i=1}^{N} F_{S,i} + \sum_{i=1}^{N} \left( \gamma_{B,i} B_i + f_{E,i} \gamma_{E,i} E_i \right)$$

and

$$\frac{dC}{dt} = I_C + \sum_{i=1}^{N} \left( F_{S,i} - F_{C,i} \right) + \gamma_{B,i} X_i + (1 - f_{E,i}) \gamma_{E,i} E_i$$

where all microbes are described with the same dynamics as in the one-microbe model.

We added extra microbes starting from the reference microbe by increasing the optimal temperature by 0.5 K while maintaining the shape of temperature dependence of the reversible enzyme deactivation. Therefore, the $n$-th microbe in a model has its temperature optimum at $(n-1)*0.5+290$ K, while its enzyme activation temperature response curves has the same shape as the reference microbe.

**Supplemental discussion**

We were not able to find a single dataset sufficiently comprehensive to calibrate and evaluate each component of our model. However, we identified fourteen predictions from our model that are qualitatively consistent with empirical findings (Table S2). Like other microbe-explicit models, our model can also simulate the priming effect, but we did not include that in Table S2 and leave it for future investigations.

**Effect of microbial community structure**
We conducted a 100-year 4-K warming experiment using the multi-microbe model configured with one, three, and five microbes and temperature forcing of diurnal variability. We find, for the plastic model, that the reference microbe dominates the respiration signal even after 100-year 4-K warming (i.e., the plots of respiration rates from three and five microbe model vs. that from the single microbe model are on the $y=x$ line; see Figure S11e and S11f). The rigid microbial model indicated small change in microbial community structure (i.e., the plots of respiration rates from three and five microbe models vs. that from the single microbe model are slightly off the $y=x$ line; see Figure S11b and S11c). This contrast supports the idea that a reserve pool enhances microbial plasticity under environmental change and our assentation that a static-CUE model tends to predict stronger carbon-climate feedbacks (Figure 3). In addition, when the transient temporal variability was removed from the forcing temperature, we found that warming enhanced microbial community shift, indicating that laboratory incubation could potentially exaggerate the warming effect when compared to the same soil in the field where it experienced more abundant temporal variability (result not shown).

Effect of static $Q_{10}$

Although both field experiments and our results challenge the use of static $Q_{10}$, we here discuss its effect on the temperature perturbation simulations. We obtained the static-$Q_{10}$ model based on the static-CUE model, but kept the CUE at the value as predicted by the plastic DEB model (i.e., the prognostic CUE model) at the reference temperature (i.e., 290 K). We multiplied $V_{b,\text{max}}$ and $V_{E,\text{max}}$ with $Q_{10}^{(T-T_{\text{ref}})/10}$ to account for the temperature effect. The $Q_{10}$ value was calculated by ensuring the static-$Q_{10}$ model and the plastic DEB model predict the same equilibrium total soil carbon stock in the 4-K cooling experiment forced by yearly constant temperature (Figure S14). The resulting $Q_{10}$ is 1.703. We also calculated another $Q_{10}$ (1.09, a value at the low end of the often-used range [1, <10]) by ensuring the static-$Q_{10}$ model and the plastic DEB model produced the same equilibrium total soil carbon stock in the 4-K warming experiment forced by yearly
constant temperature. We did not report the experiments for the rigid-DEB model, because they did not change the conclusion that, similar to the static-CUE model, the static-$Q_{10}$ model also tends to overestimate the response of soil carbon stocks to global warming.

We compared the simulated responses of total soil carbon stocks to temperature perturbations for the mineral surface area of 1000 g C eqv. We did not report the experiment for 2000 g C eqv, as that required a new $Q_{10}$ value and also did not change our conclusion that soil carbon models should not use static-$Q_{10}$ to represent the bulk decomposition temperature sensitivity, no matter whether the model is microbe explicit or implicit.

Our comparison revealed three features with the use of static $Q_{10}$: (1) there is a much smaller effect of the temporal variability in temperature forcing on the simulated total carbon stocks (solid lines in Figure S14); (2) more variability in forcing data resulted in smaller soil carbon stocks (solid lines in Figure S14); and (3) just like the static-CUE model, the static-$Q_{10}$ model over-predicted the carbon-climate feedbacks but underestimated its variability (Figure S15). Therefore, we suggest new earth system models should avoid the use of static $Q_{10}$ for carbon-climate feedback projections.

*Potential extension to include moisture effects*

While we have not considered the moisture effect here, we contend that the moisture effect is also non-multiplicative. When not accounting for factors such as water-controlled aggregation, erosion, and abiotic chemistry, moisture will affect microbial biogeochemistry through three processes: (1) diffusion between microbes and the substrates; (2) transport of substrates from one place to another; and (3) microbial physiology. Resolving the first two processes requires a reactive transport model 44 and some modification of the substrate uptake process 11, whereas less is known to resolve the third process. Microbes deal with water stress in various ways, such as osmoregulation, dormancy, and drought-induced extracellular enzyme production. A recent study has indicated that including these physiological responses are critical to predict the effect of moisture on soil carbon dynamics 45. We are working diligently on these aspects and will report our results elsewhere.
Effect of trophic dynamics

Soil is a home for many organisms, including microflora, microfauna, plants, and animals. Accordingly, a complete description of soil carbon dynamics would ideally require a model to resolve the trophic dynamics between all those organisms. Unfortunately, all existing soil carbon models that we are aware of are insufficient to resolve trophic dynamics and their effects on soil carbon dynamics. Among those, the DFW (dynamic food web) model resolves many aspects of trophic dynamics \(^46\), but lacks many climate-relevant dynamics, such as moisture and temperature controls on decomposition. The ECOSYS model \(^47\), arguably one of the most mechanistic soil biogeochemical models, only resolves the interactions between autotrophic and heterotrophic microbes, whose bulk effect is also empirically represented in some land models, such as the community land model (CLM) that we have intensively contributed to \(^44,48\). Existing empirical measurements \(^49-51\) show that, at least in temperate soils, trophic dynamics have a smaller effect on carbon dynamics than on nutrient dynamics. Moreover, many laboratory experiments studying decomposition only characterize bacteria and fungi \(^52,53\). Given the limited empirical data available for characterizing trophic interactions and that our model reproduced many empirically observed phenomenon, we contend that our assertion that both temperature sensitivity and CUE are dynamic rather than static are quite robust.

References


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Supplemental tables

Table S1. Symbol explanations and default model parameters. The activation energy for mineral adsorption is based on Conant et al. 27, while that for maintenance respiration is based on Brown et al. 28 Mineral adsorption parameters are based on Mayes et al. 10 Enzyme activation parameters are based on Ratkowsky et al. 18 The yield rates are specified semi-arbitrarily, but our major conclusions that both CUE and temperature sensitivity are hysteretic and static CUE and static-Q10 models predict higher carbon-climate feedbacks are rather insensitive to their values. Other parameters are estimated to (1) simulate the emergent responses listed in Table S2 and (2) ensure microbial biomass is only a few percent (<3% in our reference simulation) of total SOM 29.

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<tr>
<th>Model parameter</th>
<th>Units</th>
<th>Definition</th>
<th>Default Value</th>
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<td>$f_E$</td>
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<td>Fraction of decayed extracellular enzyme contributing to SOM</td>
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<td>$k_{MC}$</td>
<td>g C</td>
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<td>Affinity parameter for enzymatic SOM degradation</td>
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<td>$k_{ME}$</td>
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<td>Affinity parameter for mineral surface adsorption of enzymes</td>
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<td>Symbol</td>
<td>Unit</td>
<td>Description</td>
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<tr>
<td>$\Delta G_{kMC}$</td>
<td>kJ mol$^{-1}$</td>
<td>Gibbs energy for DOM-mineral adsorption affinity parameter</td>
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<td>kJ mol$^{-1}$</td>
<td>Gibbs energy for enzyme-SOM affinity parameter</td>
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<td>$\Delta G_k$</td>
<td>kJ mol$^{-1}$</td>
<td>Gibbs energy for reserve export</td>
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<td>kJ mol$^{-1}$</td>
<td>Gibbs energy for maintenance</td>
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<td>$\Delta H^*$</td>
<td>J mol$^{-1}$</td>
<td>Enthalpy change at $T_H^*$</td>
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<td>$I_{SC}$</td>
<td>year$^{-1}$</td>
<td>External carbon input rate</td>
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<td>$M$</td>
<td>g C eqv</td>
<td>Mineral surface sites</td>
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<td>$N_{CH}$</td>
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<td>Average number of non-polar hydrogen atoms per amino acid residue</td>
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<tr>
<td>$\Delta S^*$</td>
<td>J K$^{-1}$mol$^{-1}$</td>
<td>Entropy change at $T_S^*$</td>
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<td>Reference temperature</td>
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<td>$T_H^*$</td>
<td>K</td>
<td>Convergence temperature for enthalpy</td>
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<td>Convergence temperature for entropy</td>
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<td>$V_{B,\text{max}}$</td>
<td>day$^{-1}$</td>
<td>Maximum processing rate of DOM assimilation</td>
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</tr>
<tr>
<td>$V_{E,\text{max}}$</td>
<td>day$^{-1}$</td>
<td>Maximum processing rate of enzymatic SOM degradation</td>
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<tr>
<td>$Y_E$</td>
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<td>Yield rate of enzyme from reserve metabolites</td>
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<tr>
<td>$Y_B$</td>
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<td>Yield rate of structural biomass from reserve metabolites</td>
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<tr>
<td>$Y_X$</td>
<td>None</td>
<td>Yield rate of reserve metabolite from DOM assimilation</td>
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<td>$\kappa$</td>
<td>day$^{-1}$</td>
<td>Metabolic turnover rate for plastic microbe ($\infty$ for rigid microbe)</td>
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</tr>
<tr>
<td>$0 \gamma_{B1}$</td>
<td>day$^{-1}$</td>
<td>Reference mortality rate</td>
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<tr>
<td>$1 \gamma_{B1}$</td>
<td>g C</td>
<td>Half saturation population for density dependent mortality</td>
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<tr>
<td>$\gamma_E$</td>
<td>day$^{-1}$</td>
<td>Enzyme turnover rate</td>
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<td>day$^{-1}$</td>
<td>Population growth rate</td>
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<td>$j_X$</td>
<td>day$^{-1}$</td>
<td>Total productive reserve flux</td>
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<tr>
<td>$p_E$</td>
<td>day$^{-1}$</td>
<td>Enzyme production rate</td>
<td></td>
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<tr>
<td>$B$</td>
<td>g C</td>
<td>Microbial structural biomass</td>
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<tr>
<td>$C$</td>
<td>g C</td>
<td>Monomeric organic carbon</td>
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</tr>
<tr>
<td>$E$</td>
<td>g C</td>
<td>Extracellular enzyme</td>
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Other symbols
<table>
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<tr>
<th>Symbol</th>
<th>Unit</th>
<th>Description</th>
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<tr>
<td>$S$</td>
<td>g C</td>
<td>Polymeric organic carbon</td>
</tr>
<tr>
<td>$X$</td>
<td>g C</td>
<td>Microbial reserve biomass</td>
</tr>
<tr>
<td>$F_C$</td>
<td>g C day$^{-1}$</td>
<td>DOM uptake</td>
</tr>
<tr>
<td>$F_R$</td>
<td>g C day$^{-1}$</td>
<td>Carbon overflow</td>
</tr>
<tr>
<td>$I_S$</td>
<td>g C day$^{-1}$</td>
<td>SOM external input rate, equals to $I_{S_{fSOM}}$</td>
</tr>
<tr>
<td>$I_C$</td>
<td>g C day$^{-1}$</td>
<td>DOM external input rate, equals to $I_{S_{fDOC}}$</td>
</tr>
<tr>
<td>$R_{CO2}$</td>
<td>g C day$^{-1}$</td>
<td>Respiration rate</td>
</tr>
<tr>
<td>$CUE^*$</td>
<td>None</td>
<td>Apparent CUE for steady state model</td>
</tr>
<tr>
<td>$CUE(t, \Delta t)$</td>
<td>None</td>
<td>Transient CUE at time $t$ defined at temporal window $\Delta t$</td>
</tr>
<tr>
<td>$\gamma_{B1}$</td>
<td>day$^{-1}$</td>
<td>Mortality rate</td>
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Table S2. Example model predicted responses consistent with empirical findings.

<table>
<thead>
<tr>
<th>ID</th>
<th>Model prediction</th>
<th>Example empirical studies</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Total SOM stock increases with mineral surface protection capacity (Figure S12b)</td>
<td>Torn et al.\textsuperscript{30}, Sollins et al.\textsuperscript{31}</td>
</tr>
<tr>
<td>2</td>
<td>Total SOM stock increases with carbon input rate (Figure S12a)</td>
<td>Liao et al.\textsuperscript{32}, Hungate et al.\textsuperscript{33}</td>
</tr>
<tr>
<td>3</td>
<td>Decomposition rate per unit total SOM mass decreases with mineral surface protection capacity (Figure 1)</td>
<td>Jenkinson and Coleman\textsuperscript{34}</td>
</tr>
<tr>
<td>4</td>
<td>CUE is highly variable (Figures 2)</td>
<td>Lopez-Urrutia and Moran\textsuperscript{35}, Sinsabaugh et al.\textsuperscript{36}</td>
</tr>
<tr>
<td>5</td>
<td>Decomposition temperature sensitivity has seasonal variability (Figures 1 and S4)</td>
<td>Janssens and Pilegaard\textsuperscript{37}</td>
</tr>
<tr>
<td>6</td>
<td>There is an optimal temperature for decomposition (Figures 1, S6 and S11)</td>
<td>Balser and Wixon\textsuperscript{38}</td>
</tr>
<tr>
<td>7</td>
<td>Respiration temperature response is asymmetric (Figures 1, S4, S6 and S11)</td>
<td>Balser and Wixon\textsuperscript{38}</td>
</tr>
<tr>
<td>8</td>
<td>Decomposition temperature sensitivity is higher at lower temperature (Figure S4)</td>
<td>Hamdi et al.\textsuperscript{39}</td>
</tr>
<tr>
<td>9</td>
<td>“Labile” carbon can be preserved for long periods (Figure S13)</td>
<td>Klebber et al.\textsuperscript{40}</td>
</tr>
<tr>
<td>10</td>
<td>“Recalcitrant” carbon decomposition is more temperature sensitive (Figures S6)</td>
<td>Conant et al.\textsuperscript{27}</td>
</tr>
<tr>
<td>11</td>
<td>Under otherwise equivalent conditions, decomposition temperature sensitivity increases with higher substrate activation energy (Figure S4)</td>
<td>Conant et al.\textsuperscript{27}</td>
</tr>
<tr>
<td>12</td>
<td>Temporal average could underestimate decomposition temperature sensitivity (Figure S4)</td>
<td>Janssens and Pilegaard\textsuperscript{37}</td>
</tr>
</tbody>
</table>
Decomposition response to warming is regulated by both microbial thermal acclimation and community structure change (Figures 3 and S11).

Metabolic reserve enhances microbial plasticity (Figures S5 and S11).
Figure S1. Schematic of the mineral-microbe-enzyme-carbon decomposition model.
Figure S2. Schematic of the temperature response functions for the three categories of processes. Because of numerical approximation (resolution is 1 K), the reference point is slightly off the peak of the enzyme activity curve.
Figure S3: Comparison between the numerical and exact solutions using model parameters in Table S1.
Figure S4. A comparison of temperature sensitivity in terms of transient Q_{10} for the different simulations reported in Figure 1 of the main text. Because of temporal hysteresis caused by microbial population dynamics and the asymmetric Erying's transition state function, the daily average resulted in different total SOM weighted respiration rates even for quantitatively close temperature values near both 280 K and 300 K. This mechanism also led to very large daily Q_{10} values (> 1000).
Figure S5. Effect of mineral surface site density on the predicted emergent Q\textsubscript{10}. The reference Q\textsubscript{10} curve is computed for models with zero mineral surface sites. The upper and lower panels show results over different temperature ranges. We derived the Q\textsubscript{10} curves by first binning the data in Figure S4 with a temperature resolution of 1 K and then taking the mean of each bin as the Q\textsubscript{10} value for the mean temperature over that bin.
Figure S6. Numerical incubation experiments (see Methods in main text) for the single microbe model. Panel a shows the initial condition sampling scheme. Panel b compares the intrinsic decomposition rates for different incubation setups. Panels c and d show temperature response functions for a rigid microbe. Results for plastic microbe are shown in Figure 2.
Figure S7. Trajectories of total soil organic matter stocks for the spinup simulations that provide initial conditions to the temperature perturbation experiment presented in Figure 3 in the main text. Only the first 40 years data are shown for better visualization.
Figure S8. Predicted relative changes in total soil organic matter (TOTSOM) stocks subject to 50-year 4 K temperature perturbations as affected by the static vs. prognostic CUE parameterizations and different mineral surface area. The yearly, daily, and hourly constant T refer to temperature forcing without temporal variability, only with seasonal cycle, and with both seasonal and diurnal cycle respectively. The corresponding equilibrium carbon stocks are in Figure S7.

Compared to the plastic model (Figure 3), the rigid microbial model predicted smaller magnitude of relative soil carbon stocks change. However, the contrast between predictions by CUE-static model and CUE-dynamic model for the plastic model (Figure 3) remains for the rigid model. The effect of increasing mineral surface area is also similar as for the plastic model in Figure 3. Only the first 20-year data are shown for better visualization.
Figure S9. Predicted changes in total soil organic matter stocks subject to 50-year 4 K temperature perturbations as affected by the static vs. prognostic CUE parameterizations and different mineral surface area. These figure panels are corresponding to the relative changes of the plastic microbial model presented in Figure 3 in main text. Only the first 20-year data are shown for better visualization.
Figure S10. Similar as Figure S9, but the results are for the rigid microbial model. The corresponding relative change is in Figure S8.
Figure S11. Effect of microbial community structure on the respiration vs. temperature relationship in response to a 100-year 4 K warming for models driven by hourly temperature forcing. The y=x line is in solid black. When two respiration datasets fall on the y=x line, the two datasets are said to be predicted by two almost identical microbial communities and vice versa. The contrast (panels b and e) that the respiration rates for 1-mic and 3-mic after warming do not overlap on the y=x line for rigid microbes, while they do for plastic microbes, suggests that the reserve pool enhances microbial plasticity.
Figure S12. Steady-state model predicted total SOM as a function of carbon input rate and mineral surface area. Other processes (e.g., abiotic decomposition) present in real soils would lead to a depletion of SOM under zero carbon input scenarios (e.g., deserts).
Figure S13. Example decomposition experiment with zero carbon input. After about five years, the microbial population becomes too small to consume DOM (dissolved organic matter).
Figure S14. Trajectories of total soil organic matter stocks for the spinup simulations that provide initial conditions to the temperature perturbation experiment to evaluate the effect of static-$Q_{10}$. Only the first 40 years data (out of the 100-year spinup) are shown for better visualization. The simulations were conducted with the plastic microbial model.
Figure S15. Predicted relative and absolute changes in total soil organic matter (TOTSOM) stocks subject to 50-year 4 K temperature perturbations as affected by the static $Q_{10}$ vs. prognostic CUE (i.e., full plastic DEB model) parameterizations. The yearly, daily, and hourly constant $T$ refer to temperature forcing without temporal variability, only with seasonal cycle, and with both seasonal and diurnal cycle, respectively. The corresponding equilibrium carbon stocks are in Figure S14. Only the first 20-year data are shown for better visualization.