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# Soil-carbon response to warming dependent on microbial physiology

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**Most ecosystem models predict that climate warming will stimulate microbial decomposition of soil carbon, producing a positive feedback to rising global temperatures[1,2]. Although field experiments document an initial increase in the loss of $CO_2$ from soils in response to warming, in line with these predictions, the carbon dioxide loss from soils tends to decline to control levels within a few years[3–5]. This attenuation response could result from changes in microbial physiological properties with increasing temperature, such as a decline in the fraction of assimilated carbon that is allocated to growth, termed carbon-use efficiency[6]. Here we explore these mechanisms using a microbial-enzyme model to simulate the responses of soil carbon to warming by 5 °C. We find that declines in microbial biomass and degradative enzymes can explain the observed attenuation of soil-carbon emissions in response to warming. Specifically, reduced carbon-use efficiency limits the biomass of microbial decomposers and mitigates the loss of soil carbon. However, microbial adaptation or a change in microbial communities could lead to an upward adjustment of the efficiency of carbon use, counteracting the decline in microbial biomass and accelerating soil-carbon loss. We conclude that the soil-carbon response to climate warming depends on the efficiency of soil microbes in using carbon.**

Most existing models of soil-carbon (C) response to warming are based on first-order decay of soil organic C (SOC) with the role of microbes as decomposers implicit in the decay constants[7–9]. However, new models are emerging that couple soil C turnover directly to microbial biomass and physiology[10,11]. In these models, microbial biomass and extracellular enzymes catalyse the conversion of polymeric SOC to dissolved organic carbon (DOC), which is presumed to be the rate-limiting step in SOC decomposition. Microbial-enzyme models could prove powerful tools for investigating feedbacks between warming and SOC, because temperature directly affects enzyme activity and microbial physiology[6,12–14].

We incorporated temperature sensitivity into a microbial-enzyme model (Fig. 1a) to explore mechanisms underlying the ephemeral increase in soil respiration with sustained warming. These mechanisms include depletion of SOC (refs 4,7–9), thermal acclimation of microbial physiology[3,14] and altered plant C inputs[15]. On the basis of positive empirical relationships between enzyme activities and microbial biomass[16], we assume that enzyme production is directly proportional to microbial biomass in our model. We represent the temperature sensitivity of enzyme activity according to the Arrhenius relationship and established biochemical theory[12]. Our model also incorporates temperature sensitivity of microbial carbon-use efficiency (CUE). CUE may decline with temperature if respiration responds more positively to temperature than biomass production, thereby reducing allocation of assimilated C to growth[17]. Empirical studies in soils suggest that microbial CUE declines by at least 0.009 °C$^{-1}$ (ref. 6), but in aquatic systems the magnitude of the decline is uncertain[17] (see Supplementary Information for a literature review). Therefore, we conducted model runs with and without temperature-sensitive CUE.

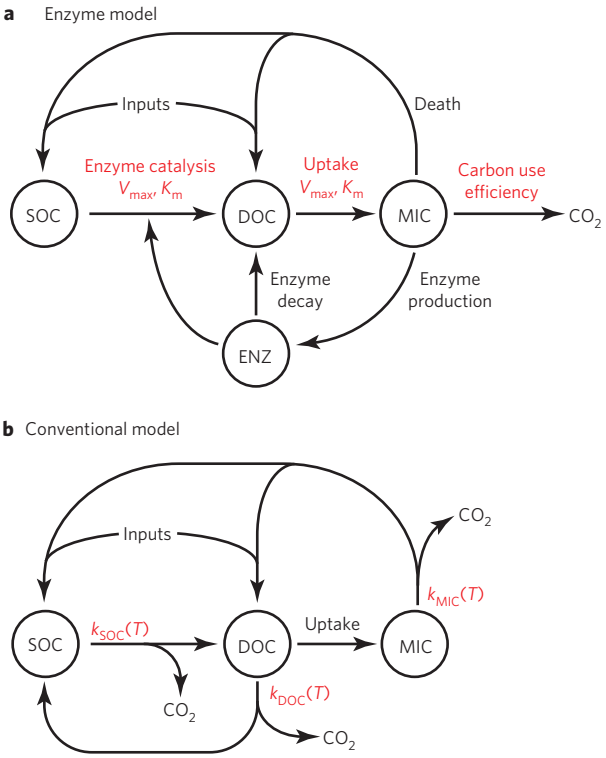


**Figure 1 | Diagram of soil C models.** Structure of the microbial-enzyme (**a**) and conventional (**b**) models of soil C decomposition under warming. Temperature-sensitive parameters are shown in red. The distinguishing feature of the enzyme model is that microbial biomass (MIC) affects the conversion of SOC to DOC through the production of extracellular enzymes (ENZ). In the conventional model, microbial processes are not explicitly coupled to soil C turnover, so changes in microbial biomass and enzyme production cannot feed back on decomposition.

Soil-warming models should not only reproduce the ephemeral increase in soil respiration, but also generate plausible changes in SOC, microbial biomass and enzyme pools. For example, empirical studies suggest that microbial biomass and enzyme activity may decline with warming[14,18,19]. The SOC response is less clear, but dramatic changes in SOC pools have not yet been reported, except in

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arctic systems[20]. We therefore focused on parameter combinations that could generate these patterns. We also conducted preliminary runs to verify that model behaviours were consistent with theory and other empirical observations (Supplementary Discussion). For example, our model predicts that the temperature sensitivity ($Q_{10}$) of respiration declines at higher temperatures and at lower substrate availabilities[12].

Our initial simulations enabled CUE to decline with temperature and examined the effects of 5 °C warming on soil respiration, SOC, DOC, microbial biomass and enzymes. The model predicted an initial increase in soil respiration due to the temperature sensitivity of enzyme activity (Fig. 2a: blue dotted lines). However, warming reduced CUE from 0.31 to 0.23, which reduced the amount of assimilated C that was allocated to microbial growth. Consequently, microbial biomass declined and soil respiration returned to control levels within a few years as the model approached steady state. As enzyme production is linked to biomass, the decline in CUE ultimately limited the enzyme catalyst for SOC decomposition. At this level of temperature sensitivity for CUE, the SOC pool increased slightly after 30 yr of warming (Table 1; Fig. 2a: blue dotted lines). This increase contrasts with the depletion of SOC substrates predicted by models lacking an explicit coupling of microbial processes and SOC turnover[7–9].

As some studies find that CUE is invariant with temperature[17], we also investigated warming effects with CUE held constant at 0.31. As with the temperature-sensitive CUE scenario, warming increased enzyme activity, but the $CO_2$ pulse and SOC losses were much greater (Fig. 2a: red dashed lines). Because inputs must equal outputs at steady state, soil respiration ultimately returned to control values, but only after the SOC pool declined by more than 30%. These patterns were observed because enzymatic conversion of SOC to DOC initially stimulated microbial growth. Increased biomass led to more enzyme production, which fed back positively to SOC decomposition and respiration. With CUE held constant, SOC depletion ultimately constrained respiration because enzymes ran short of substrate. Notably, microbial biomass under warming consistently exceeded control values, which contradicts evidence from field and laboratory experiments[14,18,21].

Thermal acclimation has also been proposed to explain the ephemeral increase in soil respiration with warming[3,14]. We therefore examined the impact of acclimation on carbon cycling responses to warming to see if they were consistent with empirical observations. We define acclimation broadly to include evolutionary adaptation, community shifts and physiological changes. We first simulated acclimation by reducing the temperature sensitivity of CUE. Relative to the variable-CUE scenario, microbial biomass and enzyme pools increased (owing to greater allocation of assimilated C to production), thereby stimulating SOC decomposition and $CO_2$ release (Fig. 2a: green dot–dashed lines).

Ecological and evolutionary processes in the microbial community could also reduce the temperature sensitivity of enzymes through reductions in maximal activity ($V_{max}$; ref. 13) and increases in the half-saturation constant ($K_m$), consistent with thermal adaptation of respiratory enzymes[22]. Therefore, we invoked acclimation through a 50% reduction in the temperature sensitivity of $V_{max}$ and a 50% increase for $K_m$. Enzyme acclimation reduced $CO_2$ losses, regardless of the CUE–temperature relationship, with peak soil respiration declining by 14–21% (Fig. 2b). SOC conversion to DOC was slower under these conditions, which constrained microbial biomass and resulted in SOC pools that were 20–23% greater after 30 yr relative to the no enzyme acclimation scenario. Notably, the enzyme-acclimation scenario with acclimated CUE (Fig. 2b: green dot–dashed lines) was consistent with empirical patterns, showing an ephemeral increase in soil respiration[3–5] and a decline in microbial biomass[14,18,21].

Some studies suggest that climate warming may alter plant C inputs[15,23], so we asked whether this mechanism could contribute to an ephemeral response of soil respiration. In these simulations, microbial CUE was temperature sensitive, and we varied SOC and DOC inputs by ±20%. Altering total SOC + DOC inputs changed the equilibrium $CO_2$ efflux proportionately, but had relatively little effect on SOC pool size (Fig. 2c: pink hatched and brown dotted lines). However, holding total input constant while decreasing the DOC:SOC ratio decreased the availability of labile C, which caused a reduction in microbial biomass and an accumulation of SOC (Fig. 2c: purple dot–dashed lines; compare to base model in Fig. 2a: blue dotted lines). Increasing DOC relative to SOC inputs had the opposite effect—microbial growth and enzyme production increased relative to the base model, resulting in a more than 15% decline in the SOC pool (Fig. 2c: yellow dashed lines). The DOC addition partly offset the decline in microbial biomass derived from reduced CUE under warming. This simulation is consistent with an ephemeral increase in soil respiration[3–5] and a reduction in microbial biomass[14,18,21] under warming, although the SOC losses are greater than in the base model scenario, where inputs are constant.

Several of our simulations show an attenuation of the soil-respiration response to warming (Fig. 2), which is expected because $CO_2$ losses must ultimately equal C inputs in a steady-state model. However, the defining feature of our enzyme model is that microbial processes affect the integral under the soil-respiration curve, resulting in a range of predictions for soil C storage (Table 1). For instance, enabling CUE to decline with temperature while increasing the DOC:SOC input ratio releases more than 15% of SOC. If we assume no change in C inputs but a lower (acclimated) temperature sensitivity for CUE, we observe a similar SOC loss (Fig. 2a). In contrast, higher temperature sensitivities for CUE cause little change in the SOC pool (Fig. 2a). For the scenarios predicting large SOC losses with warming, the soil-respiration curves imply large and sustained $CO_2$ losses and a slow return to control respiration values, which would be inconsistent with empirical data[3–5]. However, we need additional studies of microbial biomass, enzyme activity and CUE responses to warming to test our model scenarios and accurately predict the timescale and magnitude of SOC change.

Last, we tested whether conventional soil C models[7–9,24] could reproduce the observed ephemeral increase in respiration[3–5] with a decline in microbial biomass[14,18,21]. As conventional model structures vary and do not always include a microbial biomass pool, we constructed a second model with a biomass pool and a structure representative of many conventional models (Fig. 1b). Even though microbial processes were not explicitly coupled with soil C turnover, our conventional model predicted an ephemeral increase in respiration under warming accompanied by decreases in microbial biomass and DOC, whether we simulated a fixed or declining CUE (Fig. 3, Supplementary Discussion). Yet, in contrast to our enzyme model with temperature-sensitive CUE, warming caused a large net loss of SOC over 30 yr. Therefore, conventional models without direct coupling between microbes and soil C turnover cannot simulate negative feedbacks on decomposition caused by reductions in microbial biomass and enzyme production.

Our enzyme-model simulations demonstrate that soil microbial biomass and enzyme activities may control feedbacks between climate warming and SOC loss. In our model, increases in microbial biomass stimulate SOC release. We hypothesize that studies detecting large losses of SOC in response to environmental drivers should also find increased decomposer biomass. For example, permafrost melting alleviates diffusion constraints on enzyme activity and probably enables microbial biomass to increase, generating large SOC losses[20]. Similarly, relieving nutrient

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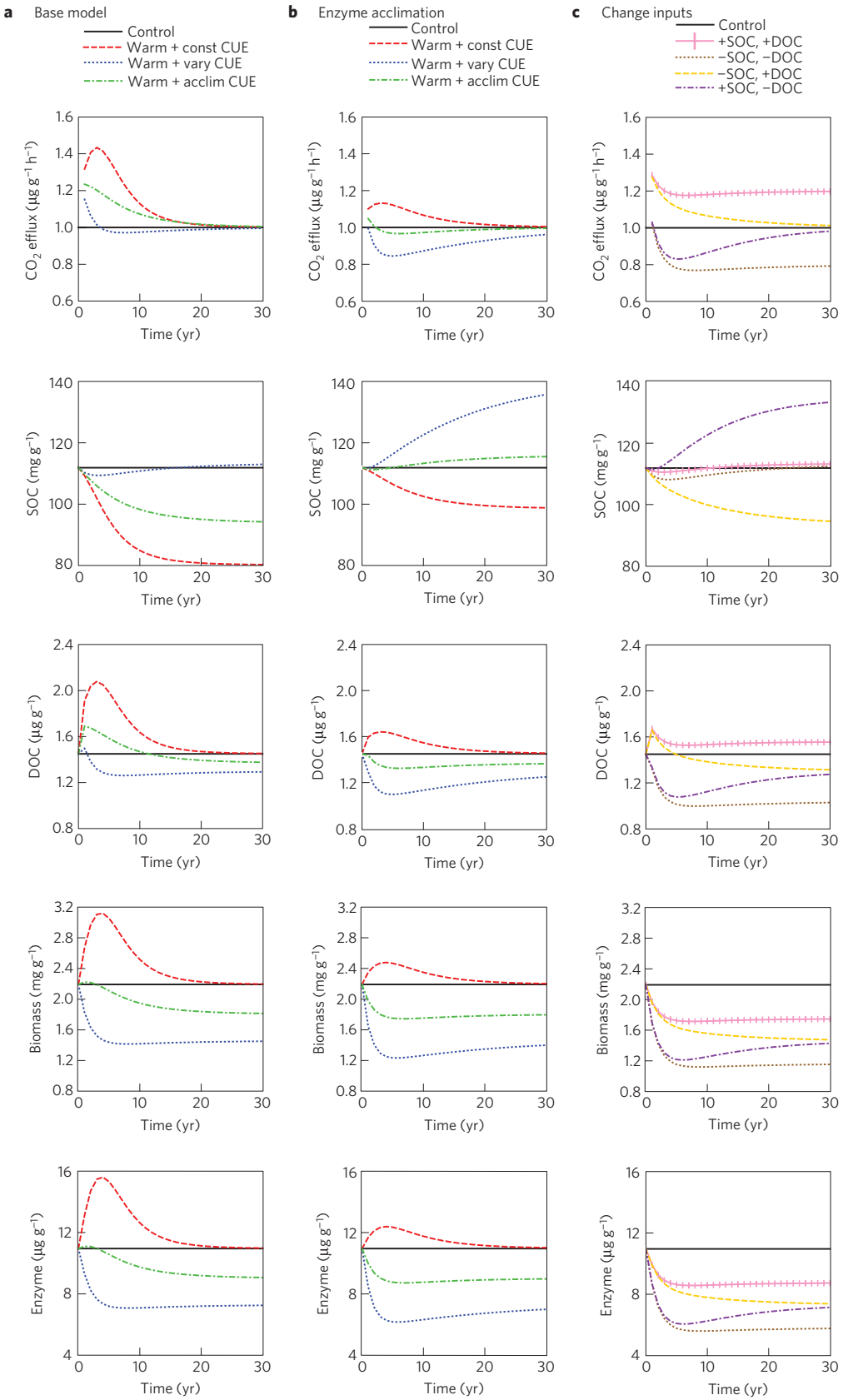


**Figure 2 | Modelled soil $CO_2$ and carbon-pool responses to 5 °C warming in the enzyme-driven model. a**, CUE was held constant, varied or acclimated to vary with a 50% reduction in temperature sensitivity. **b**, The same as **a** but with acclimation of enzyme and kinetic parameters simulated as a 50% increase in the temperature sensitivity of $K_m$ and a 50% decline in the sensitivity of $V_{max}$. **c**, C inputs altered by ±20% with CUE varying. Panels show predicted $CO_2$ efflux rates from the soil surface and pool sizes of SOC, DOC, microbial biomass and extracellular enzyme concentration.

**Table 1 | Modelled changes in SOC pool size.**

| Scenario* | 30 yr change in SOC pool size (%) |
|---|---|
| Control | 0 |
| CUE varies | +1 |
| CUE acclimates | −16 |
| CUE acclimates + enzyme acclimation | +3 |
| Low SOC, high DOC inputs + CUE varies | −15 |
| LH inputs + CUE varies + enzyme acclimation | +2 |
| LH inputs + CUE acclimates | −29 |
| LH inputs + CUE acclimates + enzyme acclimation | −13 |

*Control run and model scenarios predicting an ephemeral rise in soil respiration and reduced microbial biomass in response to 5 °C warming, consistent with empirical observations[3–5,14]. LH inputs = Low SOC, high DOC inputs.

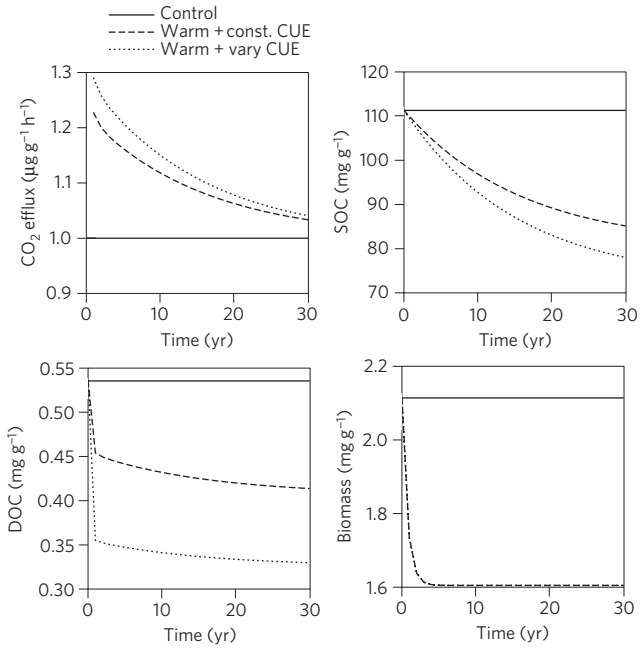


**Figure 3 | Modelled soil $CO_2$ and carbon-pool responses to 5 °C warming in the conventional model.** A reduction in CUE was represented by a 50% reduction in transfer efficiency between carbon pools shown in Fig. 1b. Panels show predicted $CO_2$ efflux rates from the soil surface and pool sizes of SOC, DOC and microbial biomass. Lines overlap in the bottom right panel owing to identical microbial biomass values.

constraints on microbes may result in greater biomass, enzyme production and SOC loss[10,25]. Conversely, in ecosystems where low temperature does not strongly constrain microbial biomass, C feedbacks may be weak or negative. For example, in ecosystems without permafrost, reductions in microbial CUE and soil moisture resulting from warming can reduce microbial biomass and generate a negative feedback to soil C losses[19,26]. Overall, our model simulations and sensitivity analyses (Supplementary Table S1) suggest that empirical studies could advance understanding of carbon–climate feedbacks by focusing on the temperature sensitivity of microbial CUE and extracellular enzyme activity.

Our enzyme model provides a simple framework for representing interactions between microbial processes and environmental change. However, different model structures could reveal other mechanisms consistent with empirical studies. CUE and enzyme activities need not be the only factors that control soil C responses to warming, though we note that researchers can readily measure the importance of these parameters. Furthermore, our framework could be extended to incorporate other factors that influence environmental feedbacks through microbial communities. For example, the original model that we adapted from ref. 10 couples C cycling to N, a linkage that may alter the magnitude and direction of carbon–climate feedbacks in global models[27]. Accounting for C quality might also refine our model predictions, because the temperature sensitivity of enzymatic degradation may increase as substrate quality declines[9,12,28]. This relationship could be important over decades to centuries if microbial decomposition drives large SOC losses, because residual C may be lower in quality. Warming-induced changes in microbial community composition could also influence substrate quality through microbial turnover and SOC formation[29]. Furthermore, our model parameters represent community composition only implicitly, yet community shifts could affect biomass and enzyme production directly. A new generation of coupled models that account for these microbial properties should improve estimates of soil C change and the magnitude of feedbacks in the carbon–climate system.

## Methods

Initial pool sizes were derived from a spin-up model run at 20 °C (Supplementary Tables S2, S3). Inputs of SOC and DOC each represent an annual flux of ~44 g C $m^{-2}$ to the top 1 cm of soil surface. Other rate parameters were selected to produce reasonable pool sizes at equilibrium. We chose a microbial turnover rate of 0.0002 $h^{-1}$, corresponding to a biomass mean residence time of ~200 d. Half of the dead biomass enters the DOC pool whereas the remainder becomes SOC. Enzyme-loss rates corresponded to a mean residence time of ~42 d. Microbes were assumed to allocate 0.012% of their biomass to enzyme production per day. We assumed that microbial CUE declined linearly (CUE = 0.63–0.016 $T$) with increasing temperature between 0 and 25 °C (Supplementary Methods).

For enzyme kinetic parameters, we made the simplifying assumption that one enzyme degrades the entire SOC pool. We also assumed that SOC substrate would not saturate enzyme reactions, and therefore chose a $K_m$ value of 600 mg $cm^{-3}$, which is larger than our target SOC pool size of ~112 mg $cm^{-3}$. Our temperature sensitivity function is linear and positive for $K_m$. We selected the pre-exponential term in the Arrhenius relationship to produce $V_{max}$ values that generated stable biomass and SOC at 20 °C. We followed a similar procedure for uptake kinetic parameters, but the pools were insensitive to these parameter choices because enzymatic decomposition is the rate-limiting step in our model. Activation energy for SOC decomposition was set at 47 kJ $mol^{-1}$, similar to values found empirically for the degradation of complex organic material[30].

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## Author contributions

M.A.B. and M.D.W. conceived the project, and S.D.A. built the model. S.D.A. and M.A.B. conducted model runs. All authors contributed to writing the paper.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at http://npg.nature.com/reprintsandpermissions. Correspondence and requests for materials should be addressed to S.D.A.

# Soil carbon response to warming is dependent on microbial physiology

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## Supplementary Methods

### Enzyme-driven model: structure, initialisation, and simulations

*Model structure*

Our enzyme model is based on the conceptual framework developed by Schimel and Weintraub[1]. To this framework (Fig. 1a) we added temperature sensitivity of degradation processes, following established theory relating to soil respiration and biochemical responses to warming[2,3]. The model starts by setting the soil organic carbon (SOC), dissolved organic carbon (DOC), microbial biomass, and enzyme pools to their initial values. Microbial biomass changes by the amount of DOC assimilated, times the carbon use (or microbial growth) efficiency, minus biomass death and enzyme production:

$$\frac{dMIC}{dt} = ASSIM * CUE - DEATH - EPROD \quad (1)$$

where assimilation is a Michaelis-Menten function scaled to the size of the microbial biomass pool:

$$ASSIM = Vmax_{uptake} * MIC * \frac{DOC}{Km_{uptake} + DOC} \quad (2)$$

We assume that the cell surface area available for uptake will be directly proportional to the number of cells. Microbes may not assimilate more DOC than is available in the DOC pool. Microbial biomass death is modeled as a first-order process with a rate constant $r_{death}$:

$$DEATH = r_{death} * MIC \quad (3)$$

Enzyme production is modelled as a constant fraction ($r_{EnzProd}$) of microbial biomass:

$$EPROD = r_{EnzProd} * MIC \quad (4)$$

During uptake, the $Vmax$, $Km$, and carbon use efficiency (CUE) parameters are temperature sensitive. The model calculates a temperature-specific $Vmax$ using the Arrhenius equation, where $Vmax_{uptake_0}$ is the pre-exponential coefficient, $gas_{const}$ is the ideal gas constant, and $Ea$ is the activation energy, or the amount of energy required to convert substrate into product:

$$Vmax_{uptake} = Vmax_{uptake_0} * \exp\left(-\frac{Ea_{uptake}}{gas_{const} * (temp + 273)}\right) \quad (5)$$

SOC with higher $Ea$ reacts more slowly, but the temperature sensitivity of the reaction is greater[2]. $Km$ values are calculated as a linear function of temperature between 0 and 50ºC:

$$Km_{uptake} = Km_{uptake_{slope}} * temp + Km_{uptake_0} \quad (6)$$

The CUE is also a linear function of temperature:

$$CUE = CUE_{slope} * temp + CUE_0 \quad (7)$$

$CO_2$ production is the fraction of DOC assimilated by microbes that is not allocated to biomass production:

$$CO_2 = ASSIM * (1 - CUE) \quad (8)$$

The enzyme pool increases with enzyme production and decreases with enzyme turnover:

$$\frac{dEnz}{dt} = EPROD - ELOSS \quad (9)$$

where enzyme turnover is modelled as a first-order process with a rate constant $r_{EnzLoss}$:

$$ELOSS = r_{EnzLoss} * Enz \quad (10)$$

The SOC pool increases with external inputs and a fraction of dead microbial biomass ($MICtoSOC$) and decreases due to decomposition losses:

$$\frac{dSOC}{dt} = inputSOC + DEATH * MICtoSOC - DECOMP \quad (11)$$

where decomposition of SOC is catalysed according to Michaelis-Menten kinetics by the enzyme pool:

$$DECOMP = Vmax * Enz * \frac{SOC}{Km + SOC} \quad (12)$$

The amount of SOC decomposed may not exceed the total SOC pool. The temperature sensitivity of decomposition is modelled in the same way as uptake, with temperature dependency built into the extracellular enzyme parameters $Vmax$ and $Km$:

$$Vmax = Vmax_0 * \exp\left(-\frac{Ea}{gas_{const} * (temp + 273)}\right) \quad (13)$$

$$Km = Km_{slope} * temp + Km_0 \quad (14)$$

The DOC pool receives external inputs, the remaining fraction of dead microbial biomass, the decomposition flux, and dead enzymes, while assimilation of DOC by microbial biomass is subtracted:

$$\frac{dDOC}{dt} = inputDOC + DEATH * (1 - MICtoSOC) + DECOMP + ELOSS - ASSIM \quad (15)$$

*Model initialisation*

After running the model with the spin-up parameters in Supplementary Table 2, pool sizes of SOC, DOC, microbial biomass, and extracellular enzymes equilibrated at reasonable proportions. For example, microbial biomass represented approximately 2% of SOC, consistent with empirical studies[4]. These equilibrium pool sizes were used as default initial values (Supplementary Table 2) in subsequent model simulations.

*Model simulations and parameter justification*

We simulated warming by increasing temperature from 20ºC to 25ºC and varied the temperature sensitivity of CUE in our analyses between zero and –0.016 $^{o}C^{-1}$. We also conducted runs with constant CUE by fixing this parameter at 0.31, its value at 20ºC. These values are reasonable given that microbial CUE varies widely across ecosystems, from 0.01 to 0.85[5]. Physiological studies with bacteria suggest that CUE (a.k.a. growth efficiency or growth yield) should decline with increasing temperature because maintenance respiration increases more steeply than biomass production[6-8]. The increase in respiration is thought to be driven by more rapid protein turnover and increased energy requirements to maintain ion gradients across the cell membrane at higher temperatures[6-8]. However, the direct influence of temperature on CUE in more complex communities remains uncertain.

In soil systems, there are relatively few measurements of CUE temperature response, but all show a consistent pattern of declining CUE with increased temperature. Following addition of rice straw to soil microcosms, Devêvre and Horwath[9] found a decline in CUE of ~0.012 $^{o}C^{-1}$ across a temperature range of 5ºC to 25ºC. Van Ginkel et al.[10] observed a decline in CUE of $^{14}C$-labeled grass roots from 0.444 to 0.347 when the incubation temperature increased from 14ºC to 16ºC. This corresponds to a CUE temperature dependence of -0.049 $^{o}C^{-1}$, although the measurement was replicated only once. Although they did not calculate CUE, Pietikäinen et al.[11] found that soil bacterial and fungal respiration increased exponentially up to 45ºC while growth increased linearly and then declined above 25ºC, suggesting a sharp decline in CUE at higher temperatures. Finally, Steinweg et al.[12] measured a CUE temperature dependence of -0.009 $^{o}C^{-1}$ across a temperature range of 15ºC to 25ºC using cellobiose as a substrate.

Bacterial growth efficiency (equivalent to CUE) has been measured much more frequently in marine and freshwater systems, but there has been substantial controversy over its temperature response. A 1998 literature review by del Giorgio et al.[13] did not find a temperature response, but in another global analysis of ocean systems, Rivkin and Legendre[14] found a negative relationship of the form $0.374 - 0.0104 \cdot T$. López-Urrutia and Morán[15] later argued that the negative relationship was due to a confounding effect of resource availability rather than temperature; at low latitudes in the ocean, nutrient availabilities are often low and may constrain bacterial growth efficiency. However, a recent study in estuarine systems found that bacterial growth efficiency declined by 0.014 $^{o}C^{-1}$, and argued that both temperature and nutrient availability controlled the relationship[16].

One difference between the research in aquatic versus soil systems is that the former has focused on bacterial CUE and the latter on microbial (i.e. bacteria + fungal) CUE. We do not know whether fungal CUE might respond differently to temperature than bacterial CUE, and

hence explain why the relationship between temperature and CUE is consistently negative in soils but more uncertain in aquatic systems. Yet given the few measures of microbial CUE in soils, and the debate about temperature sensitivity of bacterial CUE in aquatic systems, we felt it important to model both declining and constant CUE with increasing temperature.

We simulated microbial acclimation and altered C inputs in several ways. To represent acclimation of CUE, we reduced its temperature sensitivity by 50% under warming (resulting in a value of 0.27 instead of 0.23). Acclimation of extracellular and uptake enzyme kinetics was accomplished by making $Vmax$ half as sensitive and $Km$ 50% more sensitive to a 5ºC increase in temperature[3]. This representation of acclimation reduces the sensitivity of total enzymatic activity to a change in temperature, as assumed in literature definitions and following expected biochemical trade-offs[17,18]. Runs with altered C inputs involved 20% reductions or increases in both the DOC and SOC inputs. Since very few (if any) studies have directly measured the temperature sensitivities of plant inputs or enzyme kinetic parameters in soil, our parameter manipulations are necessarily arbitrary. However, varying these parameters is useful for identifying potentially important biological controls on SOC turnover and stimulating future empirical work to fill gaps in knowledge. These parameter manipulations were ultimately chosen because they represent alternate explanations for the ephemeral increase of soil respiration with elevated temperature[17,19-24].

**Enzyme-driven model: sensitivity analysis**

We conducted a model sensitivity analysis by varying parameters over two orders of magnitude, or a broad range of their possible values. We used the latter approach for the slope and intercept of the CUE temperature function because these parameters are unlikely to vary over orders of magnitude. We assessed the sensitivities of the model pool sizes and $CO_2$ fluxes in the analysis. Sensitivity is expressed as:

$$\frac{|\log_{10}|High\ output| - \log_{10}|Low\ output||}{|\log_{10}|High\ parameter| - \log_{10}|Low\ parameter||} \quad (16)$$

Order of magnitude changes in several of the parameters resulted in disproportionate changes in some of the output variables (Supplementary Table 1). SOC pools were most sensitive to changes in the $Ea$ for SOC degradation. This sensitivity is logical because $Ea$ appears in the exponent of the Arrhenius relationship that determines SOC decay rates. SOC, microbial biomass, and enzyme pools were all highly sensitive to the intercept of the microbial CUE function. They were also sensitive to the slope, but to a lesser extent. SOC was also moderately sensitive to enzyme and microbial biomass turnover rates, as well as enzyme production rates. Sensitivities for most other parameter-response combinations were <1, meaning that an order of magnitude change in the parameter resulted in less than an order of magnitude change in the response variable.

## Supplementary Discussion

### Enzyme-driven model: behaviours

Following established biochemical theory[2,3], predictions from models based on empirical responses of soil respiration and SOC to warming[20,21], and empirical observations[17,25], we would expect our model to exhibit a number of different behaviours. We first established that 'apparent' temperature sensitivity ($Q_{10}$) of respiration declined with increasing temperature and increased if we increased the availability of DOC substrate[2]. We also verified that the model recreates the positive, short-term response of soil respiration to warming due to the temperature sensitivity of enzymatic and uptake processes. Next, we determined that soil microbes are C-limited[1] under control scenarios by demonstrating that higher input rates of DOC increased respiration in the short-term (to an asymptote). Next, for the seven scenarios that qualitatively recreated observed patterns of soil respiration and microbial biomass in response to experimental warming in the field[17,19,25] (Table 1), we established that the following behaviours were realised. First, cessation of warming (i.e. return to the control temperature of 20ºC) resulted in an immediate drop in respiration values below the control scenario[17,21]. Second, addition of unlimited substrate (i.e. DOC) did not obscure this observation (due to the lower microbial biomass)[17]. Third, if respiration rates for the test of the second behaviour are divided by the microbial biomass, the calculated mass specific respiration rates are markedly lower than control values only for scenarios where $Vmax$ and $Km$ have been 'acclimated'[3,17]. Overall then we were able to demonstrate that the model structure elicited behaviours consistent with current biochemical and soil biogeochemical theory[1-3,20,21], and that at least seven scenarios (see Table 1) generated predictions qualitatively consistent with empirical observations under field warming[17,19,25] but with markedly different implications for the magnitude of soil C loss.

### Conventional model: structure and predictions

We constructed a second model with a structure representative of conventional box models of SOC dynamics[20,26]. This model (Fig. 1b) included SOC, DOC, and microbial biomass C pools as well as temperature sensitivity of decomposition, but omitted the extracellular enzyme pool. The decomposition rate of each pool was represented as a first-order process with the decay constant $k$ increasing exponentially with temperature according to the Arrhenius relationship:

$$kDOC = kDOC_0 * \exp\left(-\frac{Ea_{DOC}}{gas_{const} * (temp + 273)}\right) \quad (17)$$

$$kSOC = kSOC_0 * \exp\left(-\frac{Ea_{SOC}}{gas_{const} * (temp + 273)}\right) \quad (18)$$

$$kMIC = kMIC_0 * \exp\left(-\frac{Ea_{MIC}}{gas_{const} * (temp + 273)}\right) \quad (19)$$

where $k_0$ is the pre-exponential coefficient and $Ea$ is the activation energy. DOC, SOC, and MIC refer to the different C pools. Decomposition of each pool was represented as:

$$SOC_{DECOMP} = kSOC * SOC \quad (20)$$

$$DOC_{DECOMP} = kDOC * DOC \quad (21)$$

$$DEATH = kMIC * MIC \quad (22)$$

The change in the SOC pool is proportional to external inputs, transfers from the other pools, and losses due to first-order decomposition:

$$\frac{dSOC}{dt} = inputSOC + DOCtoSOC * DOC_{DECOMP} + MICtoOC * MICtoSOC * DEATH - SOC_{DECOMP} \quad (23)$$

where $DOCtoSOC$ is the transfer coefficient from the DOC to the SOC pool, $MICtoOC$ is the transfer coefficient from the MIC to the DOC and SOC pools, and $MICtoSOC$ is the partition coefficient for dead microbial biomass between the SOC and DOC pools. Transfer coefficients can range from 0.0 to 1.0, with lower values indicating a larger fraction of C respired as $CO_2$. The change in the DOC pool is represented similarly, but includes a loss due to microbial uptake:

$$\frac{dDOC}{dt} = inputDOC + SOCtoDOC * SOC_{DECOMP} + MICtoOC * (1 - MICtoSOC) * DEATH - f_{uptake} * DOC - DOC_{DECOMP} \quad (24)$$

The change in the microbial biomass pool is simply the difference between uptake and turnover, where $f_{uptake}$ represents the fraction $h^{-1}$ of the DOC pool taken up by microbial biomass:

$$\frac{dMIC}{dt} = f_{uptake} * DOC - DEATH \quad (25)$$

Thus we assume that the availability of DOC controls microbial growth rates.

We ran the model with the spinup and default parameters listed in Supplementary Table 3. These parameters were chosen to generate conditions similar to the enzyme-based model. We set the $Ea$ for SOC to the same value of 47 kJ $mol^{-1}$ and assigned lower values of 40 kJ $mol^{-1}$ to the DOC and microbial biomass pools. We then adjusted the pre-exponential coefficients so that equilibrium pool sizes were similar to our other model. We assumed that all transfers between pools were 20% efficient, but reduced this value to 10% to simulate changes in microbial CUE.

After running the conventional model to equilibrium, warming by 5ºC resulted in large losses of SOC (Fig. 3). There were also comparable declines in DOC and microbial biomass pools, indicative of substrate depletion. In contrast to the enzyme-based model, reductions in microbial CUE further increased C losses under warming (Fig. 3). Although microbial biomass declined to a similar extent in the conventional model, there was no direct impact on the SOC pool. All loss rates were controlled solely by the first order decay constants, which increased exponentially with warming. Our comparison demonstrates that microbial biomass and enzymes must directly catalyse SOC decomposition to account for warming effects on microbial physiology. Without this model structure, there is no mechanism by which changes in microbial CUE or acclimation within the microbial community can affect SOC pools.

## Supplementary Tables

**Supplementary Table 1. Sensitivity values for enzyme model parameters.**

| Parameter | Sensitivity | | | | |
|---|---|---|---|---|---|
| | SOC | DOC | Biomass | Enzyme | $CO_2$ |
| $inputSOC$ | 0.33 | 0.50 | 0.50 | 0.50 | 0.50 |
| $inputDOC$ | 0.33 | 0.50 | 0.50 | 0.50 | 0.50 |
| $r_{death}$ | 1.47 | 0.24 | 1.05 | 1.05 | 0.10 |
| $r_{EnzProd}$ | 1.47 | 0.10 | 0.05 | 1.05 | 0.10 |
| $r_{EnzLoss}$ | 1.50 | 0.10 | 0.10 | 1.10 | 0.10 |
| $MICtoSOC$ | 0.33 | 0 | 0 | 0 | 0 |
| $CUE_0$ | 5.18 | 1.66 | 5.44 | 5.44 | 0.58 |
| $CUE_{slope}$ | 1.25 | 0.46 | 1.49 | 1.49 | 0 |
| $Vmax_0$ | 1.50 | 0.10 | 0.10 | 0.10 | 0.10 |
| $Vmax_{uptake_0}$ | 0 | 0.26 | 0 | 0 | 0 |
| $Km_0$ | 0.77 | 0 | 0 | 0 | 0 |
| $Km_{uptake_0}$ | 0 | 0.04 | 0 | 0 | 0 |
| $Km_{slope}$ | 0.23 | 0 | 0 | 0 | 0 |
| $Km_{uptake_{slope}}$ | 0 | 0.17 | 0 | 0 | 0 |
| $Ea$ | 23.63 | 0 | 0 | 0 | 0 |
| $Ea_{uptake}$ | 0 | 0 | 0 | 0 | 0 |

**Supplementary Table 2. Spinup and default parameter values for enzyme model runs.**

| Parameter | Units | Spinup | Defaults |
|---|---|---|---|
| $endTime$ | h | 24000000 | 262800 |
| $interval$ | h | 240000 | 8760 |
| $temp$ | 0 to 50 ºC | 20 | 20 |
| $initSOC$ | mg $cm^{-3}$ | 100 | 111.876 |
| $initDOC$ | mg $cm^{-3}$ | 0.5 | 0.00144928 |
| $initMIC$ | mg $cm^{-3}$ | 0.5 | 2.19159 |
| $initEnz$ | mg $cm^{-3}$ | 0.01 | 0.0109579 |
| $inputSOC$ | mg $cm^{-3}$ $h^{-1}$ | 0.0005 | 0.0005 |
| $inputDOC$ | mg $cm^{-3}$ $h^{-1}$ | 0.0005 | 0.0005 |
| $r_{death}$ | $h^{-1}$ | 0.0002 | 0.0002 |
| $r_{EnzProd}$ | $h^{-1}$ | 0.000005 | 0.000005 |
| $r_{EnzLoss}$ | $h^{-1}$ | 0.001 | 0.001 |
| $MICtoSOC$ | mg $mg^{-1}$ | 0.5 | 0.5 |
| $CUE_0$ | mg $mg^{-1}$ | 0.63 | 0.63 |
| $CUE_{slope}$ | $degree^{-1}$ | -0.016 | -0.016 |
| $Vmax_0$ | mg SOM $cm^{-3}$ (mg Enz $cm^{-3})^{-1}$ $h^{-1}$ | 100000000 | 100000000 |
| $Vmax_{uptake_0}$ | mg DOC $cm^{-3}$ (mg biomass $cm^{-3})^{-1}$ $h^{-1}$ | 100000000 | 100000000 |
| $Km_0$ | mg $cm^{-3}$ | 500 | 500 |
| $Km_{uptake_0}$ | mg $cm^{-3}$ | 0.1 | 0.1 |
| $Km_{slope}$ | mg $cm^{-3}$ $degree^{-1}$ | 5 | 5 |
| $Km_{uptake_{slope}}$ | mg $cm^{-3}$ $degree^{-1}$ | 0.01 | 0.01 |
| $Ea$ | kJ $mol^{-1}$ | 47 | 47 |
| $Ea_{uptake}$ | kJ $mol^{-1}$ | 47 | 47 |
| $gas_{const}$ | kJ $mol^{-1}$ $degree^{-1}$ | 0.008314 | 0.008314 |

**Supplementary Table 3. Spinup and default parameter values for conventional model runs.**

| Parameter | Units | Spinup | Defaults |
|---|---|---|---|
| $endTime$ | h | 10000000 | 262800 |
| $interval$ | h | 100000 | 8760 |
| $temp$ | 0 to 50 ºC | 20 | 20 |
| $initSOC$ | mg $cm^{-3}$ | 100 | 111.121 |
| $initDOC$ | mg $cm^{-3}$ | 0.5 | 0.521927 |
| $initMIC$ | mg $cm^{-3}$ | 0.5 | 2.20661 |
| $inputSOC$ | mg $cm^{-3}$ $h^{-1}$ | 0.0005 | 0.0005 |
| $inputDOC$ | mg $cm^{-3}$ $h^{-1}$ | 0.0005 | 0.0005 |
| $f_{uptake}$ | $h^{-1}$ | 0.0005 | 0.0005 |
| $gas_{const}$ | kJ $mol^{-1}$ $K^{-1}$ | 0.008314 | 0.008314 |
| $kDOC_0$ | $h^{-1}$ | 10000 | 10000 |
| $KSOC_0$ | $h^{-1}$ | 1300 | 1300 |
| $kMIC_0$ | $h^{-1}$ | 1600 | 1600 |
| $Ea_{DOC}$ | kJ $mol^{-1}$ | 40 | 40 |
| $Ea_{SOC}$ | kJ $mol^{-1}$ | 47 | 47 |
| $Ea_{MIC}$ | kJ $mol^{-1}$ | 40 | 40 |
| $DOCtoSOC$ | mg $mg^{-1}$ | 0.2 | 0.2 |
| $SOCtoDOC$ | mg $mg^{-1}$ | 0.2 | 0.2 |
| $MICtoOC$ | mg $mg^{-1}$ | 0.2 | 0.2 |
| $MICtoSOC$ | mg $mg^{-1}$ | 0.5 | 0.5 |

**Supplementary Notes**


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