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

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The large uncertainty in soil carbon–climate feedback predictions has been attributed to the incorrect parameterization of decomposition temperature sensitivity (Q_{10}; ref. 1) and microbial carbon use efficiency[2]. Empirical experiments have found that these parameters vary spatiotemporally[3–6], but such variability is not included in current ecosystem models[7–13]. Here we use a thermodynamically based decomposition model to test the hypothesis that this observed variability arises from interactions between temperature, microbial biogeochemistry, and mineral surface sorptive reactions. We show that because mineral surfaces interact with substrates, enzymes and microbes, both Q_{10} and microbial carbon use efficiency are hysteretic (so that neither can be represented by a single static function) and the conventional labile and recalcitrant substrate characterization with static temperature sensitivity is flawed. In a 4-K temperature perturbation experiment, our fully dynamic model predicted more variable but weaker soil carbon–climate feedbacks than did the static Q_{10} and static carbon use efficiency model when forced with yearly, daily and hourly variable temperatures. These results imply that current Earth system models probably overestimate the response of soil carbon stocks to global warming. Future ecosystem models should therefore consider the dynamic interactions between sorptive mineral surfaces, substrates and microbial processes.

Most ecosystem models used for soil carbon–climate feedback predictions use the turnover pool based structure and static Q_{10} for soil carbon dynamics[7,8], but these models underestimate soil carbon variability[14] and predict very uncertain soil carbon stocks[15]. Some recent microbe-explicit models, aiming to improve soil carbon modelling, explicitly consider microbe–mineral–surface interactions[9–13]. These models have shown that microbial carbon use efficiency (CUE) is an important controller of carbon decomposition in response to temperature change[11,12], but dynamic interaction of CUE with temperature-dependent adsorption is rarely investigated (except see ref. 9). Further, in representing respiration and its response to temperature change, many of these microbe-explicit models impose static CUE (refs 9–12), and some even characterize carbon substrates using the conventional 'labile' and 'recalcitrant' paradigm[13], but empirical experiments[5,6,16] and our results described below challenge each of these concepts.

In addition to binding to polymeric soil organic matter (SOM), extracellular enzymes can adsorb to mineral surfaces and temporarily lose their capacity to degrade SOM (ref. 17). Our model (Supplementary Fig. 1) therefore allows SOM and mineral surfaces to compete for extracellular enzyme binding, such that increasing mineral surface area inhibits SOM degradation into dissolvable organic matter (DOM), all else equal. Simultaneously, DOM competes with extracellular enzymes for mineral surface adsorption and mineral surface adsorption competes with microbes for DOM. The model forms a network of SOM, DOM, microbes, extracellular enzymes and mineral surfaces, and models their competitive interactions using equilibrium chemistry approximation kinetics[18].

We predicted CUE using the dynamic energy budget (DEB) theory[19], which allows for a thermodynamically consistent treatment of the balance between structural maintenance, structural growth and extracellular enzyme production in microbial metabolism. Our DEB model includes an internal reserve pool, which buffers between environmental substrate uptake and microbial cell metabolism. A reserve pool could increase microbes' plasticity under environmental stress[20]. We illustrate the role of microbial plasticity by analysing a second model, identical except that it has no reserve pool (called a 'rigid' microbe).

To resolve the variability of the soil carbon decomposition temperature sensitivity, in contrast to using a static Q_{10} (or Arrhenius activation energy) and CUE, we explicitly modelled the temperature dependencies (Methods) of enzymatic SOM degradation, microbial DOM uptake, microbial reserve pool turnover, mineral surface sorption and microbial maintenance, and implicitly for microbial cell growth and enzyme production (see Supplementary Methods). We calibrated (Methods) and evaluated the model (Supplementary Table 1) to be qualitatively consistent with 14 emergent empirical metrics (Supplementary Table 2) and addressed parameterization uncertainty through perturbation simulations.

We identified three salient emergent responses from our transient simulations (Fig. 1). First, higher mineral surface adsorption capacity leads to lower respiration per total soil carbon mass (see contrast between Fig. 1a–c). Second, temperature sensitivity has large variability, depending, to various degrees, on many properties of the system. Third, the daily averaged respiration (red and green solid lines in Fig. 1) has lower temperature sensitivity and smaller range than does the original hourly respiration (blue and grey dots in Fig. 1), implying that models derived from coarse temporal resolution (daily) data will lead to error when applied at fine temporal resolution (hourly scales).

In natural soils, the ratio of carbon input rate to available mineral surface adsorption sites generally decreases with depth. Therefore, the first response implies lower decomposition rates at depth, a feature that has proved critical for the turnover pool based models to represent observed vertical radiocarbon profiles[14,21]. The second and third responses are well supported by field measurements[3,4,22], that is, that the inferred Q_{10} varies spatiotemporally and that temporal data averaging can reduce temperature sensitivity and variability. Although empirical measurements have often found that Q_{10} varies from small positive (<1) to large (>100) values[23], turnover pool based models have exclusively used static values in the range [1, 10]

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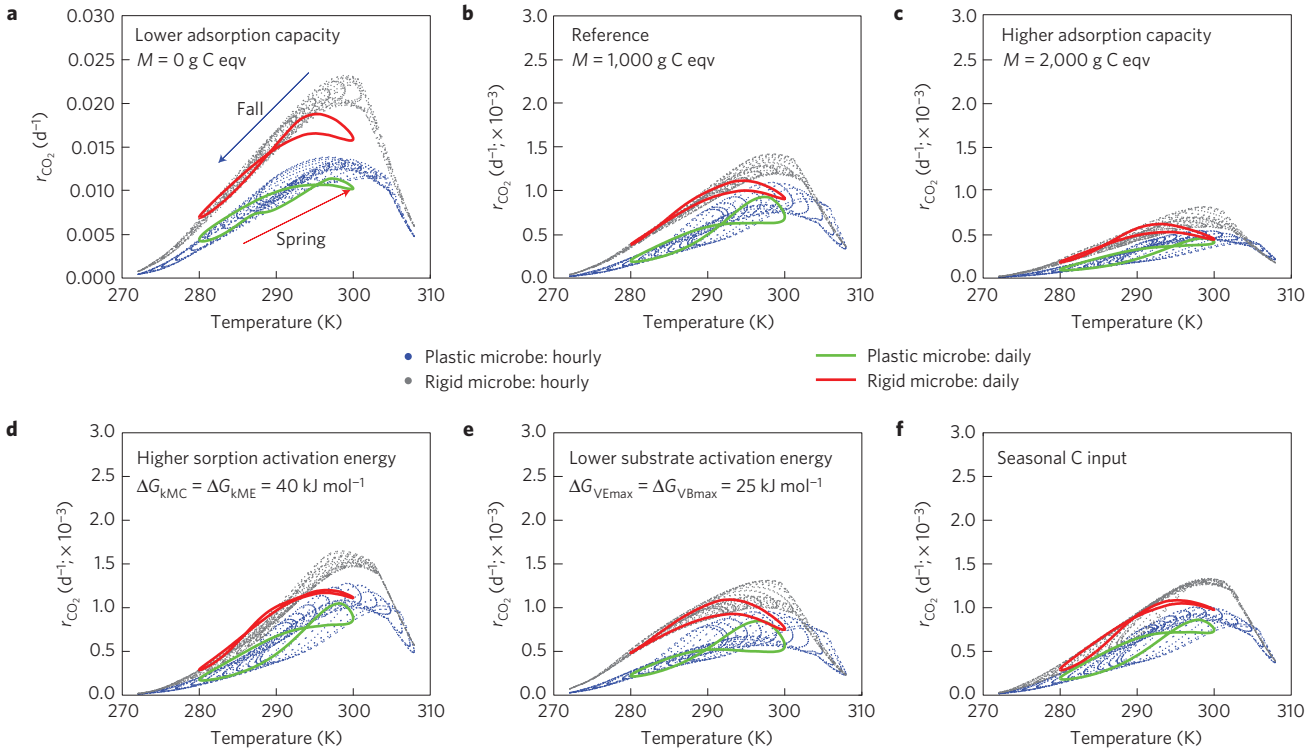

Figure 1 | Relationships between total-SOM-weighted respiration (r_{CO_2}) and temperature under parameter perturbations. a, Simulation with lower adsorption capacity. **b**, Reference simulation. **c**, Simulation with higher adsorption capacity. **d**, Simulation with higher sorption activation energy. **e**, Simulation with lower substrate activation energy. **f**, Simulation with seasonal carbon input. Parameters for the reference simulation are in Supplementary Table 1. The daily data are averages from the corresponding hourly data. All outputs are from the last year of the 100-year simulations. The red arrow in **a** indicates the transition from winter through spring to summer; the blue arrow indicates the transition from summer through autumn to winter. r_{CO_2}, total SOM stock weighted respiration; M, mineral surface sites; C_{eqv}, carbon equivalent; G, Gibbs energy; kMC, affinity parameter for mineral surface adsorption of DOM; kME, affinity parameter for mineral surface adsorption of enzymes; V_{Emax}, maximum processing rate of enzymatic SOM degradation; V_{Bmax}, maximum processing rate of DOM assimilation.

(refs 7,14,21). By including the temperature dependence of enzyme activation, our model predicted this large observed Q_{10} variability (Supplementary Fig. 4). In addition, our model predicted higher temperature sensitivity in winter than in summer (Supplementary Fig. 4), consistent with empirical measurements[3,23].

With perturbation experiments, we found that increasing the activation energies of mineral adsorption (Fig. 1d versus b and Supplementary Fig. 4d versus b) and enzyme catalysis of SOM degradation and DOM assimilation (Fig. 1e versus b and Supplementary Fig. 4e versus b) all independently increased respiration temperature sensitivities, particularly in winter. Increasing mineral surface sites from 0 to 1,000 g C eqv generally increased temperature sensitivity (more persistently for the rigid microbe, see Fig. 1a versus b and Supplementary Fig. 5), but additional increases had smaller impacts (Supplementary Fig. 5). Applying a seasonally varying carbon input changed the temporal relationship between respiration and temperature slightly (Fig. 1f).

Analyses using conventional Q_{10} or Arrhenius-equation-based theory have argued that higher respiration temperature sensitivity is due to higher substrate activation energy[24]. Our results partly support this argument, but also demonstrate that this effect manifests most strongly at low respiration rates (Supplementary Fig. 4), which could occur in winter when decomposition is both kinetically and physiologically stressed (because lower temperature induces stronger enzyme deactivation and lower catalysis rate), or in peak summer when decomposition is physiologically stressed (because higher temperature induces stronger enzyme deactivation, although catalysis rate is higher).

In addition to rejecting a static Q_{10} parameterization, our model also predicts a highly variable and hysteretic CUE under realistic temperature variability (Fig. 2b,c), indicating that neither a constant CUE nor a CUE that decreases linearly with temperature[12] (Fig. 2a) is sufficient for model applications. In particular, in simulations with realistic diurnal temperature variability (Fig. 2c), CUE could increase with temperature, be insensitive to temperature, decrease with temperature, or even be negative. These highly variable emergent CUE responses explain why empirical experiments often find highly variable CUE (refs 5,6,25).

Further, our model indicates that the temporal variability of temperature forcing leads to different total soil carbon stock predictions through impacts on the emergent CUE (Fig. 2d). In our experiments, the simulation forced with diurnal and seasonal temperature cycles predicted a total carbon stock 34% and 97% higher than when the diurnal cycle is removed and temperature is held constant, respectively (mean annual temperatures = 290 K and identical carbon input for all three simulations).

This dependence of SOM dynamics on temperature variability also leads to different inferred respiration temperature sensitivities between transient simulations and simulations mimicking incubations. We applied the 'equal-carbon' method (to be argued faulty) to disaggregate our simulations, as is often done with laboratory incubation data[26]. Our results indicate asymmetric respiration temperature sensitivities (Fig. 2e,f and Supplementary Fig. 6c,d) and that what would be interpreted as 'recalcitrant' carbon (Fig. 2f) has higher temperature sensitivity than 'labile' carbon[26] (Fig. 2e). As our prognostic CUE model includes only one polymeric (SOM) and one dissolved (DOM) compound

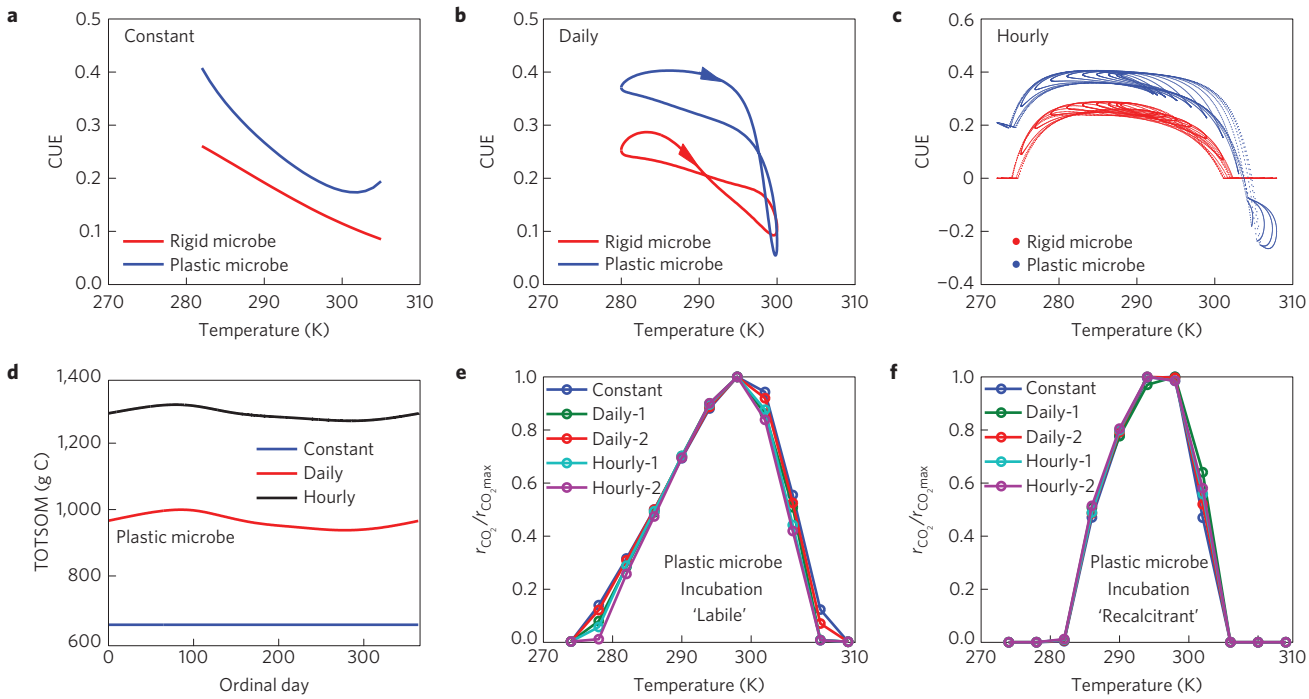

Figure 2 | Predicted emergent responses as a function of temperature forcing of different temporal variability. a, Steady-state models forced with constant temperature. **b**, Transient models forced with seasonally varying, but daily constant, temperature. **c**, Transient models forced with seasonally varying, but hourly constant, temperature. **d**, Total SOM (TOTSOM) stock predictions from simulations forced with different temperature temporal variability. **e**,**f**, 'Labile' (**e**) and 'recalcitrant' (**f**) carbon decomposition versus temperature derived using the equal-carbon method[26] from numerical incubation experiments (Methods); their intrinsic decomposition rates, including those for rigid microbe, are compared in Supplementary Fig. 6.

(with the same activation energy; Supplementary Table 1), the dependence of temperature sensitivity on decomposition stage does not indicate a change in substrate but an emergent manifestation of mineral surfaces, enzymes, substrates and microbial interactions. The asymmetric temperature sensitivity has been observed in laboratory incubations[27] and is parameterized in the CENTURY model[8]. Taken together with the highly variable inferred intrinsic decomposition rates of 'labile' and 'recalcitrant' substrates (Supplementary Fig. 6b), we conclude that models using this type of parameterization are unlikely to accurately predict decomposition temperature sensitivity.

Finally we investigate the effect of imposing a static CUE function (Methods) on simulated soil carbon–climate feedbacks (Fig. 3). Under constant temperature forcing, the CUE-prognostic model (that is, the nonlinear DEB model) predicted almost identical relative changes in carbon stocks compared to the CUE-static model (Fig. 3a,d). When the seasonal cycle is included in the temperature forcing (Fig. 3b,e), the CUE-prognostic model predicted increased soil carbon stocks under the 4-K warming (red lines), opposite to that predicted by the CUE-static model (blue lines). Although both models predicted increased carbon stocks under the 4-K cooling, the CUE-static model predicted much higher temperature sensitivity (black lines versus purple lines). When the diurnal cycle was included in the temperature forcing (Fig. 3c,f), the two models predicted relatively similar reduction in total soil carbon stocks under the 4-K warming, but the CUE-static model again predicted larger increase in carbon stocks under the 4-K cooling. Interestingly, we found that including the diurnal temperature cycle reduced the relative change in carbon storage in response to a temperature perturbation. We found, by doubling the mineral surface area (Fig. 3d–f) compared with the reference simulations (Fig. 3a–c), that the amplitude of the temperature sensitivity was reduced, and the peak changes in soil carbon stocks due to temperature perturbations were delayed at all temperature forcings. Overall, the temperature perturbation experiments indicate that the CUE-static model (and the static-Q_{10} model, Supplementary Discussion) will over-predict the magnitude of soil carbon–climate feedback but underestimate its temporal variability.

Our results indicate that many statically used concepts in current soil carbon models, such as Q_{10} and CUE, and the empirically defined 'labile' and 'recalcitrant' carbon pools, are dynamic system responses emerging from interactions between abiotic factors, microbial metabolism and enzymes. Therefore, soil carbon models that have statically parameterized these emergent responses on the basis of laboratory incubations or temporally averaged field data are mechanistically incorrect and probably inaccurately predicting long-term SOM dynamics. For instance, static Q_{10} models calibrated with daily respiration data cannot resolve the higher temperature sensitivity (at low temperature) present in the original hourly respiration data (Supplementary Fig. 4), nor can they account for respiratory thermal acclimation. In addition, our results indicate that incubation experimental protocol strongly impacts inferred temperature response functions and intrinsic decomposition rates for 'labile' and 'recalcitrant' carbon (Fig. 2e,f and Supplementary Fig. 6). Further, even the method to quantify 'labile' and 'recalcitrant' carbon pools is ambiguous and probably flawed (Supplementary Fig. 6b). These problems imply substantial uncertainty in the associated predicted soil carbon–climate feedbacks.

Most existing ecosystem models are not dynamically resolving the many complexities involved in soil carbon decomposition and are therefore probably propagating large uncertainties into coupled soil carbon–climate predictions. Although it is simple, our new model structure is an important step towards ameliorating this problem. Our model predicted emergent temperature responses that are consistent with many empirical studies (Supplementary Table 2), avoiding static parameterizations that most existing models have used. Adding even more mechanistic realism, such

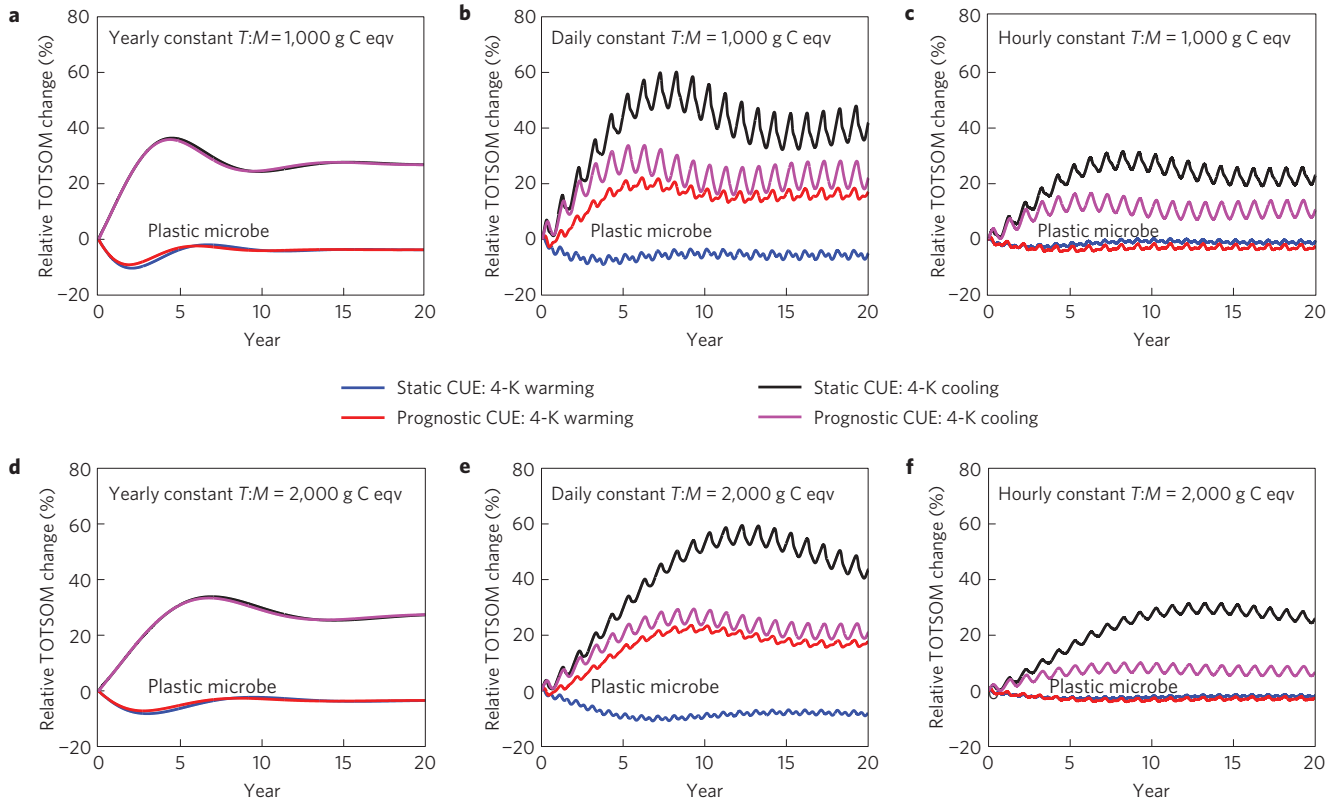

Figure 3 | Predicted relative changes in TOTSOM stocks subject to 50-year 4-K temperature perturbations as affected by the static versus prognostic CUE parameterizations and different mineral surface areas. a,**d**, Simulations driven by yearly constant temperature. **b**,**e**, Simulations driven by daily constant temperature. **c**,**f**, Simulations driven by hourly constant temperature. Only the first 20-year data are shown for better visualization.

as substrate diversity, stoichiometric constraint, moisture effects and even trophic dynamics, would enable our model to predict carbon decomposition at hierarchically different levels of model complexities. Although calibrating such a model will be challenging, such a process-rich approach will predict state variables and fluxes that are more relevant to empirical measurements and provide more specific guidance towards designing new empirical studies, which in turn will improve models and thereby future soil carbon–climate feedback predictions.

Methods

We explicitly modelled the different temperature-dependent processes by grouping them into three categories: equilibrium processes, non-equilibrium forward reactions, and enzyme activation, which are, respectively, represented by the Arrhenius equation[1], Eyring's transition state theory[28], and the equation in ref. 29. We described their relevant equations in Supplementary Methods.

Our analyses in this paper focused solely on carbon, although we are designing a model to resolve soil carbon dynamics with multiple chemical elements and a range of different substrates. As in other studies, we excluded trophic dynamics, and we discuss the implication of this decision in Supplementary Methods. As we were not able to identify a single observational data set to constrain every aspect of our model, we calibrated the parameter qualitatively (Supplementary Table 2). Specifically, we collected or inferred model parameters from existing literature whenever possible. Some parameters, such as maximum production rate, enzyme decay rate and cell mortality, were numerically inferred to ensure the steady-state solutions predict microbial biomass to carbon storage ratios within the range derived by empirical studies (see Supplementary Methods). The maximum cell growth rate was inverted from the steady-state solution, with all other parameters assigned.

Initial conditions for the transient spinup simulations were taken from the corresponding steady-state constant forcing analytical solution. The numerical solutions were obtained using adaptive time step integration and were verified with steady-state solutions (Supplementary Fig. 3).

The temperature forcing used for transient simulations is

$$T = 290 - \delta_1 10\cos\left(\frac{2\pi}{365}t\right) + \delta_1 8\sin(2\pi t)$$

where T is temperature (K), t is time (day), and δ_1 and δ_2 are indices for seasonal and diurnal cycles, respectively. To remove the diurnal cycle, δ_2 is set to 0, and to remove the seasonal cycle, δ_1 is set to 0.

Numerical incubation experiments were conducted by first running the model to equilibrium, then setting the carbon input rate to zero, and then continuing the simulation for three years at 11 different temperatures (274–314 K with increments of 4 K). Initial conditions for different incubation experiments were sampled from the equilibrium period when the transient temperature was at 290 K, that is, the reference temperature where the enzymes and microbes have their peak activity. This approach produces two different initial conditions for each transient simulation with seasonally varying temperature forcing, one from the first half-year (that is daily-1 and hourly-1 in Fig. 2e,f) and the other from the second half-year (that is daily-2 and hourly-2 in Fig. 2e,f; also see Supplementary Fig. 6a for further information). As such, each of the plastic and rigid microbial models has five simulations with different initial conditions for the incubation experiments (Fig. 2e,f and Supplementary Fig. 6b).

We described the methods to determine the emergent temperature sensitivity in Supplementary Methods. We reported all temperature sensitivities in terms of relative sensitivity of decomposition rates and respiration rates, such that in the conventional Q_{10} or Arrhenius-equation-based theory, higher substrate activation energy corresponds to higher temperature sensitivity[24].

We described the CUE-static model in the Supplementary Methods. Essentially, it replaces the dynamic CUE using the CUE predicted from the model's steady-state solution (Fig. 2a), all else equal. The CUE-static model predicts identical equilibrium carbon stocks to that by the CUE-prognostic model under constant temperature forcing (Fig. 3a,d and Supplementary Fig. 7). A discussion on the static-Q_{10} model is also provided in the Supplementary Methods.

To analyse the change in total soil carbon stocks in response to temperature perturbations, we ran the models for 100 years to equilibrium and then abruptly changed the temperature by ±4 K and continued the simulations for another 50 years to new equilibrium. However, in all simulations, the first equilibrium was

reached approximately in 40 years and the second equilibrium (after perturbation) was reached approximately in 20 years (except the cooling experiment for the CUE-static model at daily constant temperature, which took slightly longer; see Fig. 2e). The simulations were conducted for temperature forcings of three different types of temporal variability, including constant temperature, seasonally varying temperature at daily time steps, and both seasonally and diurnally varying temperature at hourly time steps. We reported the spinup simulations (corresponding to Fig. 3) in the Supplementary Methods (Supplementary Fig. 7).

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Author contributions

J.Y.T. and W.J.R. conceived the project, J.Y.T. developed the model and conducted model runs, and J.Y.T. and W.J.R. analysed the data and wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.Y.T.

Competing financial interests

The authors declare no competing financial interests.