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Global soil carbon projections are improved by modelling microbial processes

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Society relies on Earth system models (ESMs) to project future climate and carbon (C) cycle feedbacks. However, the soil C response to climate change is highly uncertain in these models[1,2] and they omit key biogeochemical mechanisms[3–5]. Specifically, the traditional approach in ESMs lacks direct microbial control over soil C dynamics[6–8]. Thus, we tested a new model that explicitly represents microbial mechanisms of soil C cycling on the global scale. Compared with traditional models, the microbial model simulates soil C pools that more closely match contemporary observations. It also projects a much wider range of soil C responses to climate change over the twenty-first century. Global soils accumulate C if microbial growth efficiency declines with warming in the microbial model. If growth efficiency adapts to warming, the microbial model projects large soil C losses. By comparison, traditional models project modest soil C losses with global warming. Microbes also change the soil response to increased C inputs, as might occur with CO_2 or nutrient fertilization. In the microbial model, microbes consume these additional inputs; whereas in traditional models, additional inputs lead to C storage. Our results indicate that ESMs should simulate microbial physiology to more accurately project climate change feedbacks.

Contemporary ESMs use traditional soil C models, which implicitly simulate microbial decomposition through first-order kinetics that determine turnover rates of soil C pools[1,2]. Although such models can replicate extant soil C pools on various scales[9,10], their ability to project soil C response in a changing environment remains unresolved[11,12]. In the past 30 years, researchers have identified key processes and feedbacks that could be important for accurately simulating future C-cycle–climate feedbacks. For example, traditional models neglect microbial physiological processes that transform and stabilize soil C inputs[3–5]. In contrast, recent microbial models explicitly simulate microbial biomass pools that catalyse soil C mineralization[6,8] and produce notably different results in transient simulations[6]. By representing microbial physiological responses, such models may provide a better fit to observations, especially in a changing environment[13,14]. Yet so far, no modelling studies have tested the relevance of microbial mechanisms for soil C responses to climate change on the global scale.

We created a new soil biogeochemistry module for use in the Community Land Model that explicitly simulates microbial biomass pools (CLM microbial model; Fig. 1; modified from ref. 6). The CLM microbial model represents above-ground and below-ground processes and separates below-ground pools into surface (0–30 cm) and subsurface (30–100 cm) horizons. Microbes in this model directly catalyse the mineralization of litter and soil C pools according to Michaelis–Menten kinetics. In this formulation, decomposition losses can be limited by both substrate availability (the organic C pools) and microbial biomass, which is assumed to be the source of enzymatic activity. This structure differs from traditional models in which decomposition losses depend only on first-order decay of substrate (soil C) pools[6].

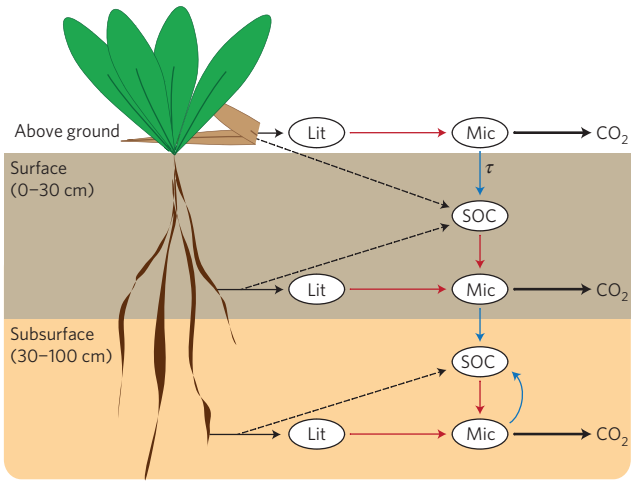

Figure 1 | Diagram of the CLM microbial model. The model explicitly simulates microbial driven soil C cycling in above-ground, surface (0–30 cm) and subsurface (30–100 cm) soil horizons. Ovals represent pools for litter (Lit), microbial biomass (Mic) and SOC. Fluxes between pools are shown with arrows. Plant inputs enter leaf and root litter pools (solid black arrows). A small fraction of litter flux (F_i) enters SOC pools without passing through microbial biomass (dashed black arrows). Otherwise, litter and SOC pools pass through microbial biomass, with rates determined by the size of the microbial biomass pool and temperature-sensitive Michaelis–Menten kinetic parameters (red arrows), based on observations[15] (Supplementary Table S1). Microbial respiration is also assumed to be temperature sensitive and proportional to 1–MGE (bold black arrows). At present, MGE declines linearly with soil temperature, but parameters for this relationship are not well constrained by observations (see also ref. 15). Microbial turnover (that is, mortality, τ) converts microbial biomass to SOC pools (blue arrows). In the present parameterization, $\tau = 0.0005\ h^{-1}$ and $F_i = 0.02\ h^{-1}$ (Supplementary Table S1).

Temperature affects three key microbial parameters in our model. The Michaelis–Menten relationship requires two parameters: K_m, the substrate half-saturation constant and V_{max}, the maximal reaction velocity (Fig. 1). We used observational data to constrain these parameters and their temperature sensitivities,

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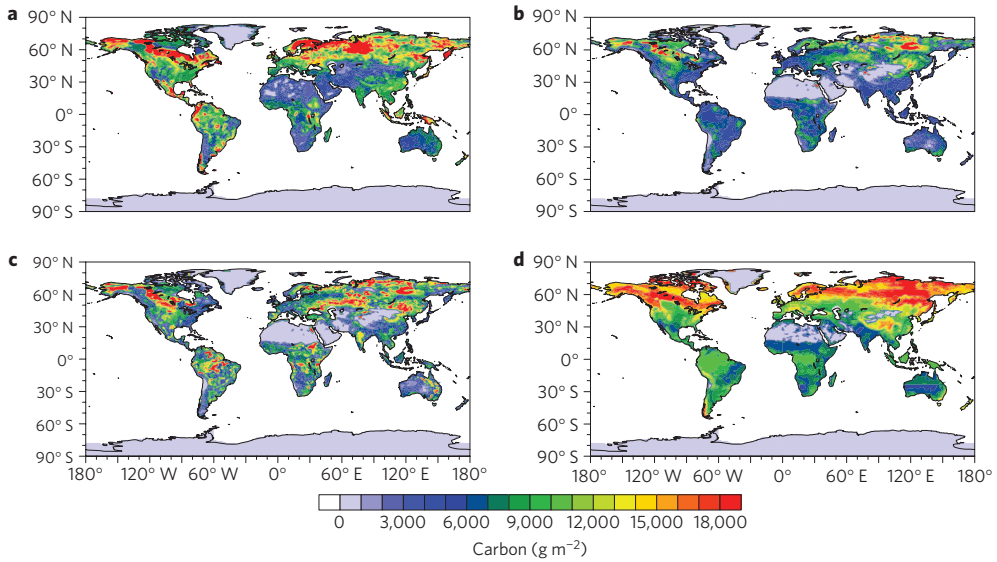

Figure 2 | Global distribution of soil C pools (0–100 cm) from observations[19] and models. a, Observations, global total = 1,259 Pg C. **b**, CLM4cn, global total = 691 Pg C (spatial correlation with observations (r) = 0.55, model-weighted root mean square error (r.m.s.e) = 7.1 kg C m^{-2}). **c**, DAYCENT, global total = 939 Pg C (r = 0.53, r.m.s.e = 7.6). **d**, The CLM microbial model, global total = 1,310 Pg C (r = 0.71, r.m.s.e = 5.3).

which generally follow an exponential form[15]. The third key parameter is microbial growth efficiency (MGE), which determines how much microbial biomass is produced per unit of substrate consumed[16]. MGE probably declines with increasing temperature, although the magnitude of the response is uncertain[17]. Consequently, C decomposition depends on temperature, substrate availability and the size of the microbial biomass pool.

After running to steady state, we compared soil C pools from the CLM microbial model with soil C pools from two traditional models (illustrated with model parameterizations from the Community Land Model version 4 with active carbon–nitrogen biogeochemistry (CLM4cn; ref. 18) and the Daily Century Model (DAYCENT; ref. 10)). We also compared model outputs to observations from the globally gridded Harmonized World Soils Database[19]. Global simulations were forced with observationally derived litter inputs (see Methods) and with soil temperature and moisture from a twentieth-century simulation[18]. Overall, the CLM microbial model explained 50% of the spatial variation in the soil C observations, whereas the traditional models explained 28–30% of the variation and showed greater average deviations from soil C observations (Fig. 2).

Other traditional models perform even worse than the two reported here. For example, a previous version of CLM4cn, using modelled litter inputs, explained only ~2% of the spatial variation in observed soil C stocks at the 1° grid scale, and no other ESM explained more than 16% of the variation[2]. Some of this poor performance may be owing to ESM errors in simulating litter inputs. We avoided these errors by using litterfall observations for our present analysis. Still, the CLM microbial model explained 20% more soil C variation than traditional CLM4cn with observed litterfall, an improvement rivalling the entire explanatory power of previous models. Moreover, the CLM microbial model accurately simulates observed soil C pools in both surface soil layers (0–30 cm) and total soil profiles (0–100 cm; r = 0.75 and 0.71, respectively; Supplementary Fig. S1).

A closer examination of regional patterns illustrates specific gaps in our representation of processes driving soil C cycling (Fig. 2). Some regions, especially in the tropics, have low projected soil C densities compared with soil C observations. These low biases suggest systematic problems with modelling the physiochemical soil environment. Specifically, the CLM microbial model does not simulate the physical protection of soil C or pH effects on soil microbial activity. These mechanisms should be a focus for future model development, especially in tropical soils. Additionally, simulating processes that build and maintain organic soils remains a challenge in ESMs (ref. 20). In the Arctic, the CLM microbial model generates higher soil C densities than traditional modelling approaches (Fig. 2). However, there are poor spatial correlations between our modelled soil C pools and observational data sets (Supplementary Fig. S2). Also, all of the Arctic data sets show a high degree of spatial heterogeneity in soil C, a feature clearly absent from our model simulations (Supplementary Fig. S2). Improved hydrologic and moisture controls over soil C turnover will probably be needed to simulate this heterogeneity in the Arctic. As well as model improvements, measurement efforts should address the wide discrepancies in empirical estimates of Arctic soil C (Supplementary Fig. S2).

Accurate simulation of present soil C stocks is essential, but the main goal of ESMs is to project C–climate feedbacks in the future. When the environment changes, the CLM microbial model makes projections that differ from traditional soil biogeochemistry models (Fig. 3). For example, perturbations such as increased CO_2 or N deposition may increase plant productivity and C inputs to soils. In the CLM microbial model, increasing global litter inputs by 20% results in an ephemeral accumulation of soil C, which concurrently increases microbial biomass. Larger microbial biomass pools then accelerate rates of soil C turnover and increase rates of heterotrophic respiration. The net effect is no change in soil C pools after 30 years. In contrast, increasing litterfall inputs to traditional models causes soil C accumulation. The difference is owing to the joint dependence of soil C loss on substrate pool size and microbial biomass in the microbial model (Fig. 3a).

On balance, projections from the CLM microbial model show better agreement with observations from leaf litter manipulations[21,22] and CO_2 enrichment studies[23]. Increasing litter inputs generally increases rates of soil respiration, but elicits no change in soil C storage (but see ref. 24). Although the mechanisms underlying these observations are not well understood, several studies emphasize the importance of the priming effect. Priming occurs when increased inputs of fresh organic substrates accelerate microbial decomposition of existing soil C (ref. 25). Typically, priming is driven by increased microbial demand for nutrients from soil organic matter, or increased microbial growth and enzyme

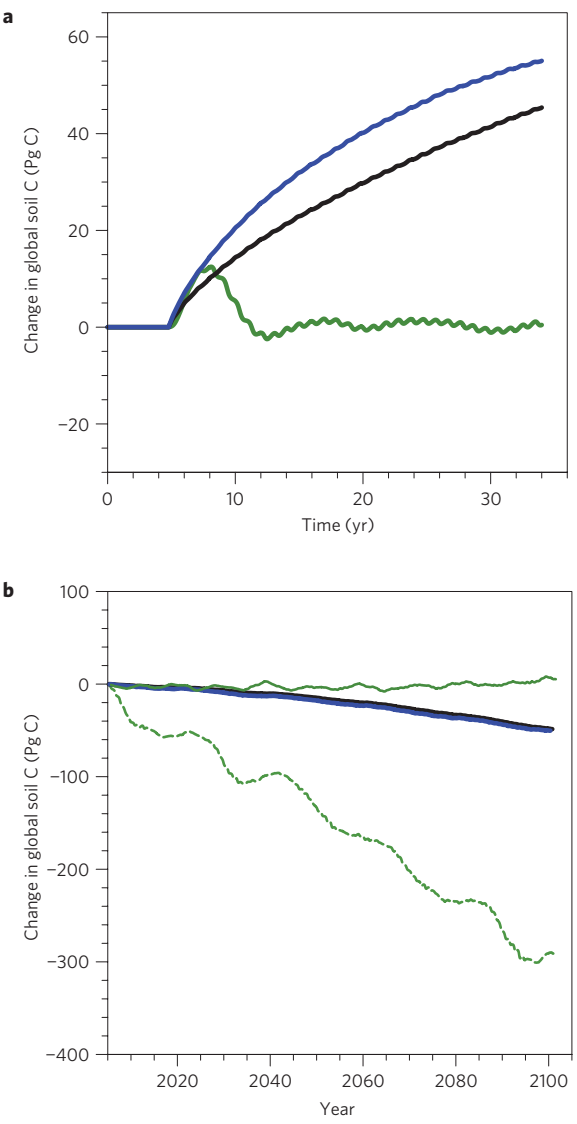

Figure 3 | Divergent model responses of global soil C pools in global change simulations. a, Response of steady-state soil C pools for conventional soil biogeochemistry models (CLM4cn, black; DAYCENT, blue) and the CLM microbial model (green) to a 20% global increase in litterfall beginning in year five. **b**, Response to a 4.8 C increase in mean global temperature by 2100, projected by ensemble member one of CESM simulations for RCP 8.5 used in CMIP5 experiments from 2006 to 2100. For the microbial model, either MGE changes with temperature (solid green line) or microbial communities adapt to increasing temperatures without changing MGE (dashed green line).

production in response to substrate addition. Only the latter mechanism operated in our simulations because the CLM microbial model does not include C–N interactions.

We used both microbial and traditional models to simulate soil C responses to global warming (Fig. 3b). In the microbial model, increased temperatures accelerate enzyme kinetics, which generally leads to soil C loss. However, this effect can be completely offset if MGE declines with warming and reduces the microbial biomass that controls decomposition. If MGE does not change with warming, then enzyme kinetics dominate and soils lose up to 300 Pg C. Consequently, global soil C losses over the twenty-first century could be negligible, or massive, depending on the thermal response of MGE. Empirical studies suggest that MGE declines with increasing temperature, at least in the short term[16,17]. Still, the MGE response to temperature is poorly constrained and adaptive processes in microbial communities could stabilize MGE in a warming world. In traditional models, MGE is a fixed constant. Accordingly, warming temperatures affect only kinetic constants in traditional models, which project modest and similar soil C losses in the warming scenario (Fig. 3b). Thus, traditional ESMs miss an important element of global climate sensitivity driven by microbial control over soil C cycling.

Despite better agreement with soil C observations, nearly 50% of the spatial variation in global soil C pools remains to be explained. Our work is just the first step towards a new generation of models that include key biological and physical mechanisms in the soil C cycle. For example, shifts in microbial community structure could alter the temperature sensitivity of heterotrophic respiration[26], such that soils respire less CO_2 than expected for a given amount of warming. Enzyme K_m and enzyme V_{max} could also adapt to climate warming, such that enzyme catalytic rates increase more than expected at warmer temperatures[14,15]. Some of these parameters may also shift with changes in N availability, possibly as a result of shifts in microbial community structure[27]. Accounting for these mechanisms not only holds promise for improved simulation of present soil C distributions, but should also increase confidence in the projection of soil C responses to future climate change. However, the magnitude of microbial adaptation to climate change remains controversial[28] and more empirical studies are needed to determine the mechanisms underlying adaptation, including physiological acclimation, microbial community shifts and evolutionary processes. Nonetheless our analysis suggests that soil C projections from present ESMs will remain questionable until they can account for critical microbial mechanisms that affect soil C dynamics.

Another key shortcoming in the CLM microbial model is the lack of soil mineral interactions. In particular, there is no physio-chemical protection of soil organic matter on mineral surfaces or within aggregates, yet physical protection is known to affect soil C storage[4,7,29]. This omission is also relevant because minerals and aggregates are involved in soil C responses to perturbations[3,7,29]. For example, soil mineralogy may influence the stabilization of microbial byproducts and the temperature sensitivity of organic matter sorption and desorption. These mechanisms should be high priorities for future model development.

Our results have broad implications because society relies on ESMs to project future atmospheric CO_2 levels and climate. Our model comparison shows that traditional ESMs omit key microbial mechanisms that determine soil C responses to global climate change. Clearly additional mechanisms should be included, but our model is a crucial first step toward a new generation of global models that integrate microbial physiology. Soil biogeochemistry models in ESMs deserve further investigation, development and more rigorous benchmarking with data, but we contend that an explicitly microbial approach, such as the one presented here, has several advantages. Simple microbial models should help bring ESMs into better alignment with our theoretical understanding of processes controlling turnover and stabilization of soil C, without adding undue computational expense. Additionally, key parameters in the CLM microbial model can be measured, a feature that should facilitate future model development, evaluation and validation. Finally, this approach represents biological mechanisms responsible for C turnover in soils and will probably generate more accurate projections of soil C feedbacks on climate change.

Methods

Equilibrium soil C pools were calculated for CLM4cn and DAYCENT models using an analytical solution[30] with globally gridded input data sets for mean annual soil moisture and temperature[18], soil texture and pH (ref. 19), litter chemistry[31] and litterfall inputs derived from observations[32] (described in ref. 33). We forced

the model with these litterfall data to reduce error and biases associated with ESM projections of net primary productivity, plant C allocation and associated litter fluxes. This modification substantially improves soil C estimates in conventional soil biogeochemistry models[33]. Additionally, DAYCENT parameterizations were modified to simulate deeper soil horizons and minimize error between modelled and observed soil C pools[33]. In its present configuration, the CLM microbial model has no structure allowing for the decomposition of coarse woody debris. Accordingly, coarse woody debris inputs were omitted from the litterfall inputs used to force all three models evaluated here. For conventional models, soil C pools reported here are the sums of all pools (Fig. 2b,c).

Using the same soil temperature and litterfall inputs, we calculated equilibrium soil C pools for the CLM microbial model using a traditional spin-up (~1,500 yr run at hourly time steps). For vertically resolved soils in the CLM microbial model, we allocated 65% of root litter inputs to surface soils (0–30 cm) and the remaining 35% to subsurface horizons (30–100 cm). Soil C pools reported for the CLM microbial model represent the sum of soil organic C (SOC) and microbial biomass, although at equilibrium, microbial biomass pools are only ~1% of total soil C pools. We compared modelled soil C pools with observations from the Harmonized World Soils Database[19] using sample cross-correlation and area-weighted r.m.s.e.

We assumed Michaelis–Menten kinetics parameters (V_{max} and K_m) and MGE were temperature sensitive, using parameter values reported in refs 6,15. Median values used to calculate the relationship between temperature and enzyme kinetics produced plausible global soil C pools (Supplementary Fig. S3), although high RMSE, large litter pools and large soil C pools suggested that C turnover was too slow, especially at high latitudes. Therefore we used the upper and lower bounds for the temperature sensitivity of V_{max} and K_m, respectively, in the CLM microbial model to simulate equilibrium soil C pools that minimized RMSE with observations (Fig. 2d and Supplementary Fig. S1).

To examine model behaviours in response to future global change, we took steady-state soil C estimates generated for each model and perturbed litter inputs or soil temperature. In both perturbation experiments, control simulations were forced with observationally derived litter inputs evenly distributed throughout the year and mean monthly soil temperature and soil moisture data from 1985 to 2005 from a single community ESM (CESM) ensemble member from archived Coupled Model Intercomparison Project Phase 5 (CMIP5) experiments (publically available online at http://www.earthsystemgrid.org). In year five of the litter manipulation experiment, we increased global litter fluxes 20% for 30 years, calculating the difference in global soil C pools between control and increased litter simulations (Fig. 3a). Using CESM soil temperature projections from an archived CMIP5 experiment for the Representative Concentration Pathway 8.5 (RCP 8.5) from 2006 to 2100, we calculated the change in soil C pools projected by 4.8 °C warming by the end of this century for each model (Fig. 3b). The CLM microbial model has temperature-sensitive MGE. We explored the implications of assumptions made about changes in MGE with increasing soil temperatures, allowing: instantaneous decreases in MGE with warming soil temperatures (Fig. 3b, solid green line); or instantaneous adaptation of microbial community MGE, so that MGE does not decrease with warming (dashed green line). Data presented in Fig. 3b are a subset of results from these warming experiments showing the range of possible outcomes with different parameters and initial soil C pools. More information is available in Supplementary Fig. S4.

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Author contributions

W.R.W. and S.D.A. conceived the project and built the model. W.R.W. and G.B.B. assembled input and model evaluation data sets. W.R.W. conducted model runs. All authors contributed to writing the paper.

Additional information

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Competing financial interests

The authors declare no competing financial interests.