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Authors
Wieder, WR
Bonan, GB
Allison, SD

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Global soil carbon projections are improved by modeling microbial processes

William R. Wieder[1]

Gordon B. Bonan[1]

Steven D. Allison[2]

[1]National Center for Atmospheric Research, Boulder, CO 80307, USA

[2]Department of Ecology and Evolutionary Biology & Department of Earth System Science, University of California, Irvine, CA 92697, USA

Corresponding Author:

William R. Wieder

Phone: 303.497.1352

Fax: 303.497.1348

email: wwieder@ucar.edu

address: TSS, CGD/NCAR

PO Box 3000

Boulder, CO 80307-3000

Society relies on Earth system models (ESMs) to predict 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 lack direct microbial control over soil C dynamics[6-8]. Thus, we tested a new model that explicitly represents microbial mechanisms of soil C cycling at the global scale. Compared to traditional models, the microbial model simulates soil C pools that more closely match contemporary observations. It also predicts 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 predicts large soil C losses. By comparison, traditional models predict 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 in order to more accurately project climate change feedbacks.

Contemporary ESMs use traditional soil C models, which implicitly simulate microbial decomposition via first-order kinetics that determine turnover rates of soil C pools[1,2]. Although such models can replicate extant soil C pools at various scales[9,10], their ability to predict 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 catalyze 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 to date, no modeling studies have tested the relevance of microbial mechanisms for soil C responses to climate change at the global scale.

We created a new soil biogeochemistry module for use in the Community Land Model that explicitly simulates microbial biomass pools (hereafter referred to as the CLM microbial model; Fig. 1; modified from ref.[6]). The CLM microbial model represents aboveground and belowground processes and separates belowground pools into surface (0-30 cm) and subsurface (30-100 cm) horizons. Microbes in this model directly catalyze 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 the 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].

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, 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 to soil C pools from two traditional models (illustrated with model parameterizations from CLM4cn[18] and DAYCENT[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 20th 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 prior version of CLM4cn, using modeled litter inputs, explained only ~2% of the spatial variation in observed soil C stocks at the 1º grid scale, and no other ESM explained more than 16% of the variation[2]. Some of this poor performance may be due to ESM errors in simulating litter inputs. We avoided these errors by using litterfall observations for our current analysis. Still, the CLM microbial model explained 20% more soil C variation than traditional CLM4cn with observed litterfall, an improvement rivaling 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; SI Fig. 1).

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 predicted soil C densities compared to soil C observations. These low biases suggest systematic problems with modeling 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[20]. In the Arctic, the CLM microbial model generates higher soil C densities than traditional modeling approaches (Fig. 2). However, there are poor spatial correlations between our modeled soil C pools and observational datasets (SI Fig. 2). Also, all of the Arctic datasets show a high degree of spatial heterogeneity in soil C, a feature clearly absent from our model simulations (SI Fig. 2). Improved hydrologic and moisture controls over soil C turnover will likely be needed to simulate this heterogeneity in the Arctic. In addition to model improvements, measurement efforts should address the wide discrepancies in empirical estimates of Arctic soil C (SI Fig. 2).

Accurate simulation of current soil C stocks is essential, but the main goal of ESMs is to project carbon – 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 like elevated 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 (Fig. 3a). In contrast, increasing litterfall inputs to traditional models causes soil C accumulation. The difference is due to the joint dependence of soil C loss on substrate pool size and microbial biomass in the microbial model.

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

93 inputs generally increase rates of soil respiration, but elicit no change in soil C storage (but see
94 ref.[24]). Although the mechanisms underlying these observations are not well understood, several
95 studies emphasize the importance of the priming effect. Priming occurs when increased inputs of
96 fresh organic substrates accelerate microbial decomposition of existing soil C[25]. Typically,
97 priming is driven by increased microbial demand for nutrients from soil organic matter, or
98 increased microbial growth and enzyme production in response to substrate addition. Only the
99 latter mechanism operated in our simulations because the CLM microbial model does not include
100 C-N interactions.

101 We use both microbial and traditional models to simulate soil C responses to global
102 warming (Fig. 3b). In the microbial model, elevated temperatures accelerate enzyme kinetics,
103 which generally leads to soil C loss. However, this effect can be completely offset if MGE
104 declines with warming and reduces the microbial biomass that controls decomposition. If MGE
105 does not change with warming, then enzyme kinetics dominate and soils lose up to 300 Pg C.
106 Consequently, global soil C losses over the 21st century could be negligible, or massive,
107 depending on the thermal response of MGE. Empirical studies suggest that MGE declines with
108 increasing temperature, at least in the short term[16,17]. Still, the MGE response to temperature is
109 poorly constrained, and adaptive processes in microbial communities could stabilize MGE in a
110 warming world. In traditional models, MGE is a fixed constant. Accordingly, warming
111 temperatures only affect kinetic constants in traditional models, which predict modest and
112 similar soil C losses in the warming scenario (Fig. 3b). Thus, traditional ESMs miss an important
113 element of global climate sensitivity driven by microbial control over soil C cycling.

114 Despite better agreement with soil C observations, nearly 50% of the spatial variation in
115 global soil C pools remains to be explained. Our work is just the first step toward a new

116 generation of models that includes key biological and physical mechanisms in the soil C cycle.
117 For example, shifts in microbial community structure could alter the temperature sensitivity of
118 heterotrophic respiration[26], such that soils respire less CO_2 than expected for a given amount of
119 warming. Enzyme K_m, and enzyme V_{max} could also adapt to climate warming, such that enzyme
120 catalytic rates increase more than expected at warmer temperatures[14,15]. Some of these
121 parameters may also shift with changes in N availability, possibly as a result of shifts in
122 microbial community structure[27]. Accounting for these mechanisms not only holds promise for
123 improved simulation of current soil C distributions, but should also increase confidence in the
124 prediction of soil C responses to future climate change. However, the magnitude of microbial
125 adaptation to climate change remains controversial[28], and more empirical studies are needed to
126 determine the mechanisms underlying adaptation, including physiological acclimation, microbial
127 community shifts, and evolutionary processes. Nonetheless our analysis suggests that soil C
128 predictions from current ESMs will remain questionable until they can account for critical
129 microbial mechanisms that affect soil carbon dynamics.
130 Another key shortcoming in the CLM microbial model is the lack of soil mineral
131 interactions. In particular, there is no physiochemical protection of soil organic matter on
132 mineral surfaces or within aggregates, yet physical protection is known to affect soil C
133 storage[4,7,29]. This omission is also relevant because minerals and aggregates are involved in soil
134 C responses to perturbations[3,7,29]. For example, soil mineralogy may influence the stabilization
135 of microbial byproducts and the temperature sensitivity of organic matter sorption and
136 desorption. These mechanisms should be high priorities for future model development.
137 Our results have broad implications because society relies on ESMs to predict future
138 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 integrates 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, like 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 carbon turnover in soils and will likely generate more accurate predictions 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 datasets for mean annual soil moisture and temperature[18], soil texture and pH[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 ESMs' predictions 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 modeled and observed soil C pools[33]. In its current 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, 2c).

Using the same soil temperature and litterfall inputs, we calculated equilibrium soil C pools for the CLM microbial model using a traditional spin-up (~1500 y 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 SOC and microbial biomass, although at equilibrium, microbial biomass pools are only ~1% of total soil C pools. We compared modeled soil C pools with observations from the Harmonized World Soils Database[19] using sample cross-correlation and area weighted root-mean-square-error (RMSE).

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 (SI Fig. 3), 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, SI Fig. 1).

To examine model behaviors 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

185 moisture data from 1985-2005 from a single Community Earth System Model (CESM) ensemble
186 member from archived CMIP5 experiments (publically available online at
187 http://www.earthsystemgrid.org). In year 5 of the litter manipulation experiment, we increased
188 global litter fluxes 20% for 30 years, calculating the difference in global soil C pools between
189 control and increased litter simulations (Fig. 3a). Using CESM soil temperature projections from
190 an archived CMIP5 experiment for RCP 8.5 from 2006 to 2100, we calculated the change in soil
191 C pools predicted by 4.8°C warming by the end of this century for each model (Fig. 3b). The
192 CLM microbial model has temperature sensitive MGE. We explored the implications of
193 assumptions made about changes in MGE with increasing soil temperatures, allowing: 1)
194 instantaneous decreases in MGE with warming soil temperatures (Fig. 3b, solid green line); or 2)
195 instantaneous adaptation of microbial community MGE, so that MGE does not decrease with
196 warming (dashed green line). Data presented in Fig. 3b are a subset of results from these
197 warming experiments showing the range of possible outcomes with different parameters and
198 initial soil C pools. More information is available in SI Fig. 4.
199

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205

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

Additional Information The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to W.R.W.

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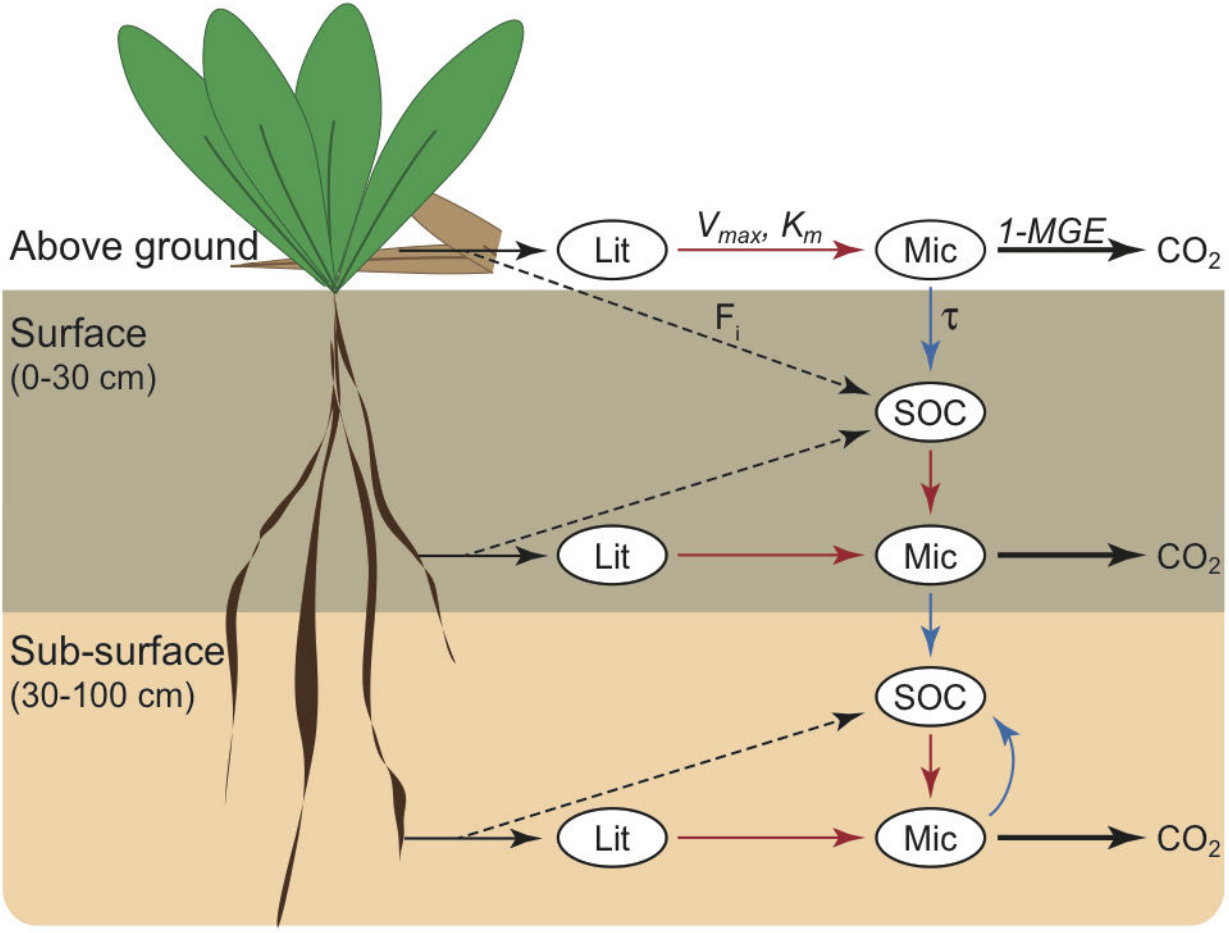
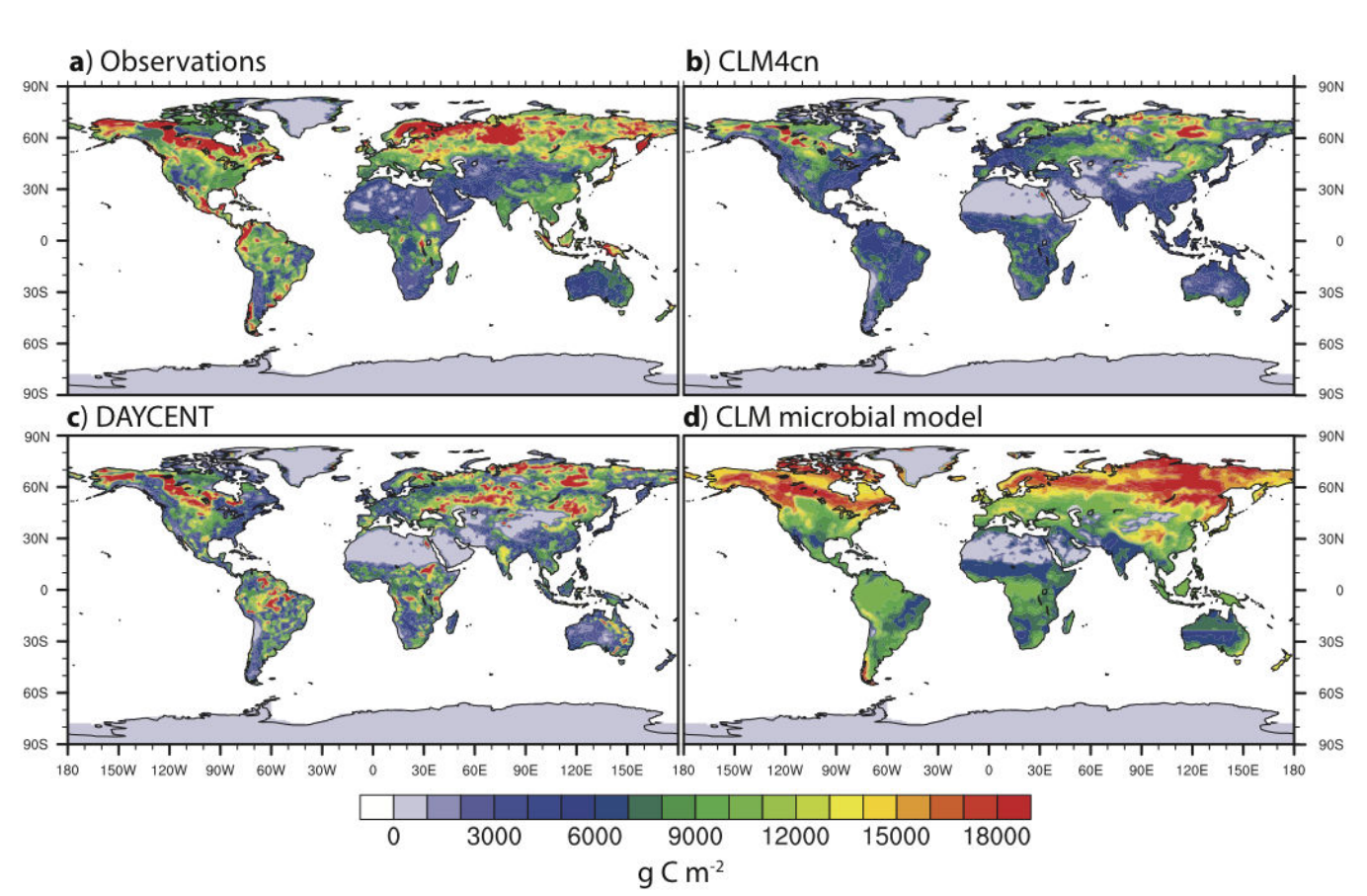
Figure 1 | Diagram of the CLM microbial model. The model explicitly simulates microbial-driven soil C cycling in above ground, surface (0-30 cm) and sub-surface (30-100 cm) soil horizons. Ovals represent pools for litter (Lit), microbial biomass (Mic), and soil organic carbon (SOC). Fluxes between pools 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 (V_{max} and $K_{m,}$ red arrows), based on observations[15] (SI Table 1). Microbial respiration is also assumed to be temperature sensitive, and equal to 1 – MGE (heavy black arrows). Currently, MGE declines linearly with soil temperature, but parameters for this relationship are not well constrained by observations (see also ref[15]). Microbial turnover (i.e., mortality; τ) converts microbial biomass to SOC pools (blue arrows). In the current parameterization, $\tau = 0.0005\ h^{-1}$ and $F_i = 0.02\ h^{-1}$ (SI Table 1).

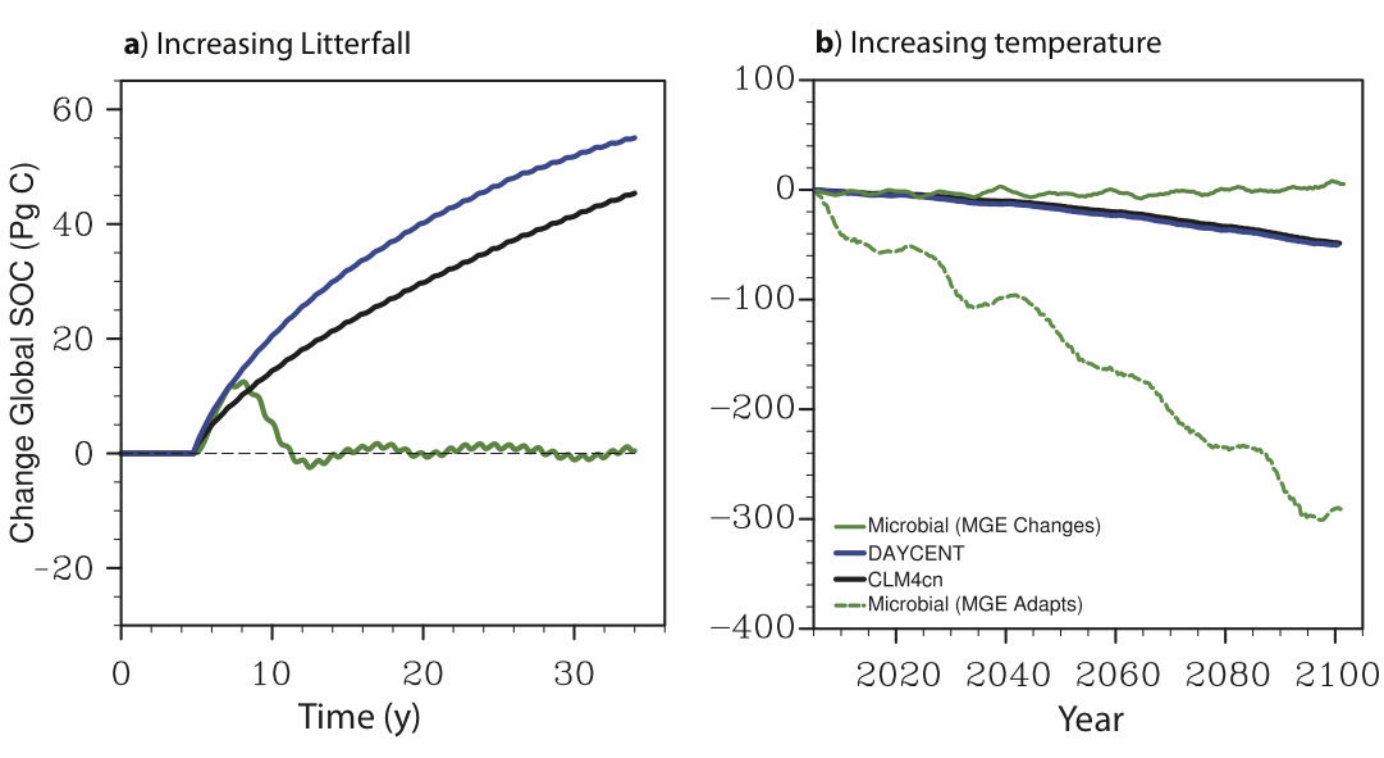
Figure 2 | Global distribution of soil C pools (0-100 cm) from observations[19] and models. **(a)** Observations, global total = 1259 Pg C, **(b)** CLM4cn, global total = 691 Pg C [spatial correlation

with observations (r) = 0.55, model-weighted root mean square error (RMSE) = 7.1 kg C m^{-2}]; **(c)** DAYCENT, global total = 939 Pg C [r = 0.53, RMSE = 7.6]; and **(d)** the CLM microbial model, global total = 1310 Pg C [r = 0.71, RMSE = 5.3].

Figure 3 | Divergent model responses of global soil C pools in global change simulations. Response of steady-state soil C pools for conventional soil biogeochemistry models [CLM4cn (black) and DAYCENT (blue)] and the CLM microbial model (green) to: **(a)** 20% global increase in litterfall beginning in year 5; **(b)** 4.8 ^{o}C mean increase in global temperature by 2100, predicted by ensemble member one of CESM simulations for RCP 8.5 used in CMIP5 experiments from 2006-2100. For the microbial model, MGE changes with temperature (solid line) or microbial communities adapt to increasing temperatures without changing MGE (dashed line).


Above ground
Lit
V_{max}, K_m
Mic
1-MGE
CO_2
F_i
τ
Surface
(0-30 cm)
SOC
Lit
Mic
CO_2
Sub-surface
(30-100 cm)
SOC
Lit
Mic
CO_2


a) Observations
b) CLM4cn
c) DAYCENT
d) CLM microbial model
90N
60N
30N
0
30S
60S
90S
180 150W 120W 90W 60W 30W 0 30E 60E 90E 120E 150E 180
0 3000 6000 9000 12000 15000 18000
g C m-2


a) Increasing Litterfall
Change Global SOC (Pg C)
60
40
20
0
−20
0
10
20
30
Time (y)
b) Increasing temperature
100
0
−100
−200
−300
−400
2020
2040
2060
2080
2100
Year
Microbial (MGE Changes)
DAYCENT
CLM4cn
Microbial (MGE Adapts)