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Multiple models and experiments underscore large uncertainty in soil carbon dynamics

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Abstract

Soils contain more carbon than plants or the atmosphere, and sensitivities of soil organic carbon (SOC) stocks to changing climate and plant productivity are a major uncertainty in global carbon cycle projections. Despite a consensus that microbial degradation and mineral stabilization processes control SOC cycling, no systematic synthesis of long-term warming and litter addition experiments has been used to test process-based microbe-mineral SOC models. We explored SOC responses to warming and increased carbon inputs using a synthesis of 147 field manipulation experiments and five SOC models with different representations of microbial and mineral processes. Model projections diverged but encompassed a similar range of variability as the experimental results. Experimental measurements were insufficient to eliminate or validate individual model outcomes. While all models projected that CO_2 efflux would increase and SOC stocks would decline under warming, nearly one-third of experiments observed decreases in CO_2 flux and nearly half of experiments observed increases in SOC stocks under warming. Long-term measurements of C inputs to soil and their changes under warming are needed to reconcile modeled and observed patterns. Measurements separating the responses of mineral-protected and unprotected SOC fractions in manipulation experiments are needed to address key uncertainties in microbial degradation and mineral stabilization mechanisms. Integrating models with experimental design will allow targeting of these uncertainties and help to reconcile divergence among models to produce more confident projections of SOC responses to global changes.

Keywords

Soil organic carbon, Warming, Modeling, Meta-analysis, Litter addition, Decomposition

Introduction

Global changes such as warming and rising atmospheric CO_2 concentrations are altering carbon (C) exchanges between terrestrial ecosystems and the atmosphere (Bond-Lamberty and Thomson 2010; Bond-Lamberty et al. 2018). Warming initially speeds biochemical reactions and accelerates decomposition, leading to a decline in SOC stocks (Li et al. 2016; Melillo et al. 2017). However, long-term impacts of warming are unclear; C loss could slow over time (Bradford et al. 2008; Conant et al. 2011) or move through phases of C equilibrium and loss (Melillo et al. 2017). Higher CO_2 levels

stimulate plant growth and inputs to soil, but long-term impacts on SOC stocks are uncertain. Some litter addition experiments have observed increased SOC accumulation (Lajtha et al. 2014a; Liu et al. 2009), while others suggest only weak SOC responses (Lajtha et al. 2014b; van Groenigen et al. 2016). Overall, the lack of a systematic synthesis of long-term warming and litter addition experiments has made it difficult to draw general conclusions with which to test current SOC models or guide model development.

For decades SOC models represented C cycling and storage using a simplified, linear approach (i.e. first-order kinetics) (Coleman and Jenkinson 1996; Parton et al. 1998) that did not explicitly simulate microbial activity and soil mineral interactions (Schmidt et al. 2011). Similarly, experiments tended to measure bulk SOC or CO_2 efflux responses to warming and changes in litter inputs, largely ignoring microbial-mineral interactions occurring in different SOC pools (e.g. Crowther et al. 2016; Romero-Olivares et al. 2017). Meta-analyses of these experimental data often highlighted considerable variation in SOC responses across space (Carey et al. 2016) and time (Rustad et al. 2001), and have sometimes yielded contradictory results (Crowther et al. 2016; van Gestel et al. 2018). A lack of process-specific information in modeling, experimental, and synthesis approaches has made it difficult to tease apart the mechanisms that drive SOC responses to global changes.

Recently, models and experiments have begun exploring in more detail how microbial and mineral interactions influence SOC cycling (Cotrufo et al. 2013; Kallenbach et al. 2015; Lehmann and Kleber, 2015; Schmidt et al. 2011). A new family of SOC models has emerged incorporating a range of different structures that represent a diverse array of assumptions related to microbial control of decomposition and stabilization of SOC via interactions with mineral particles (Dwivedi et al. 2017; Riley et al. 2014; Salazar et al. 2018; Sulman et al. 2014; Tang and Riley 2015; Wang et al. 2015; Wieder et al. 2014; Wieder et al. 2015). The high structural variation among models reflects knowledge gaps pertaining to soil biogeochemical processes such as enzymatic decomposition, microbial dormancy, sorption of organic matter to minerals, and interactions among these processes, with alternative formulations representing alternative hypotheses that cannot yet be resolved (Fig. 1). Because they allow more alternative choices of model structures, the introduction of nonlinear process representations into models has the potential to produce divergent model projections (Wieder et al. 2018; Bradford et al. 2016). However, examination of the outcomes of alternative structural choices also provides opportunities to identify key process uncertainties and evaluate their potential importance in driving model projections. A wealth of experimental data exists showing SOC responses to long-term warming (Carey et al. 2016; Crowther et al. 2016; Romero-Olivares et al. 2017; Rustad et al. 2001) and C inputs (Bowden et al. 1993;

Nadelhoffer et al. 2006) across a variety of ecosystems, enabling us to systematically explore the assumptions of the new family of SOC models.

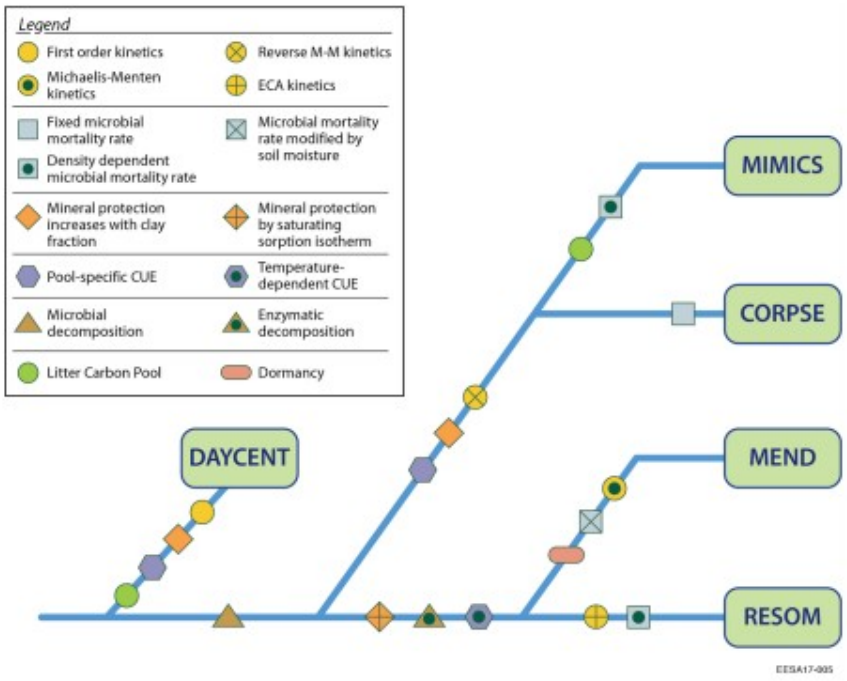

Fig. 1 Models included in the comparison. Models are arranged in a tree based on major differences in explicit process representation. Specific processes are indicated with symbols

Combining modeling, experimental, and synthesis efforts can effectively highlight key uncertainties underpinning SOC cycling. Here, we synthesized, using a meta-analysis approach, SOC increases and losses due to warming (Carey et al. 2016; Crowther et al. 2016) and long-term detritus input and removal treatments (DIRT) (Bowden et al. 1993; Nadelhoffer et al. 2006). We selected these two manipulations because they probe fundamental assumptions within models and are directly related to key ongoing global environmental changes. We simulated the effects of warming and increased litter inputs on SOC stocks and respiration rates in five models that were developed with the intention of projecting C cycle responses to global changes: one first-order model and four models that explicitly represent microbial and mineral interactions. We compared model results to synthesized experimental data to ask: (1) Did the models reproduce experimental responses? and (2) Which mechanisms caused divergence among models and between modeled and experimental responses? Based on these results, we make suggestions to guide the next generation of SOC models and experiments.

Methods

Models and simulations

We conducted a model-experiment comparison using five SOC models (Fig. 1) coupled with a meta-analysis of warming and litter addition experiments. The five models were DAYCENT (Parton et al. 1998), CORPSE (Sulman et al. 2014), MIMICS (Wieder et al. 2014), MEND (Wang et al. 2015),

and RESOM (Tang and Riley 2015). These models were developed independently by different research groups, and were chosen to represent a sample of SOC modeling approaches being actively used or developed for application in Earth system models (ESMs). DAYCENT is a version of the CENTURY model, one of the most widely used SOC models, and employs first-order structural assumptions similar to those of other widely used models such as RothC (Coleman and Jenkinson 1996) as well as all Coupled Model Intercomparison Project Phase 5 (CMIP5) ESMs (Todd-Brown et al. 2011). The other four models diverge from DAYCENT and other models used in current ESMs by explicitly modeling the activity and growth of soil microbial biomass and its effects on decomposition rates, along with physical protection of organic matter from microbial decomposition via occlusion in aggregates or sorption to mineral surfaces (Fig. 1 and described below).

The models differ in their decomposition kinetics and representations of microbial biomass. DAYCENT simulates decomposition as a first-order process without explicit microbial activity. CORPSE simulates decomposition rate as a saturating function of the ratio of microbial biomass to substrate carbon. MEND explicitly simulates enzymatic depolymerization using Michaelis–Menten kinetics (saturating with increasing substrate concentration) as well as active and dormant fractions of microbial biomass. MIMICS uses reverse Michaelis–Menten decomposition kinetics (saturating with increasing microbial biomass) and divides microbes into two functional groups representing copiotrophs and oligotrophs. RESOM calculates depolymerization and microbial monomer uptake rates using equilibrium chemistry approximation (ECA) kinetics.

The models can be further divided based on their representations of SOC protection. Protected pools in CORPSE and MIMICS have linear growth and turnover rates, comparable to DAYCENT's passive pool, which has a very slow turnover rate. MEND and RESOM have non-linear, saturating representations of SOC protection, reflecting the assumption that there is a finite supply of mineral sorption sites in a soil. Protected SOC in MEND can be decomposed, but at a slower rate than unprotected SOC. While the conceptual representations of physical protection differ somewhat among models, we grouped SOC fractions in each model into protected and unprotected categories to compare among models. Despite the broad model groupings (Fig. 1), each model contains a unique set of assumptions, and they collectively represent diverse alternative hypotheses about processes and interactions such as mineral protection and microbial feedbacks to C additions. See SI for a detailed description of model assumptions and key equations.

Using each of the five models, we conducted simulations of simple, idealized experiments that focused on key differences in model behaviors that were comparable with observed results from existing global change manipulations. We conducted simulations for three soil textures (5, 20, and

70% clay) and two litter qualities (low: 0.73% N, 24.4% lignin; high: 1.37% N, 16.6% lignin, but note that models used varying definitions of litter quality).

Each model was spun up to equilibrium under constant temperature (20 °C) and moisture (50% of saturation), with constant C inputs of 500 g C m^{-2} $year^{-1}$, with an equilibration target of less than 0.5% change in total C stock over a 50-year period. Because different clay content and litter quality values yielded different model equilibrium states, model simulations were spun up to equilibrium separately for each combination of clay content and litter quality. Next, we simulated manipulations to determine model responses to sustained warming and increased C inputs. Increased C inputs were applied as a doubling of the continuous C input rate relative to the input rate used in the spin-up and the control simulations, maintaining the same litter composition and quality. We conducted warming manipulations for 2 °C and 5 °C of simulated warming by increasing the temperature relative to the 20 °C used in the spin-up and control simulations, again reflecting many of the experiments captured in our meta-analysis (see below). Manipulations were simulated as instantaneous step changes from the spin-up conditions, and continued for 50 years. Simulations were conducted for each manipulation individually, for each combination of clay content and litter quality.

Experimental meta-analysis

To quantify the observed effects of experimental warming and increasing C inputs on SOC stocks and soil respiration rates, we performed a meta-analysis on data from existing studies. For warming, we used data published in two recent comprehensive reviews of warming experiments (Carey et al. 2016; Crowther et al. 2016). These studies were supplemented with additional published data located using the search terms “warming” AND “soil” AND/OR “respiration” in ISI Web of Science and Google Scholar through August 2016. We narrowed our search to field studies reporting SOC in 0–10 cm mineral soil or soil respiration. Our litter manipulation meta-analysis focused on DIRT (Detritus Input and Removal Treatment) experiments. To locate these, we used the search terms “DIRT” AND “litter”, and we supplemented this search with publications listed on the DIRT website (dirtnet.wordpress.com). In general, we included studies that manipulated warming or litter for at least 6 months to facilitate comparison with our model simulations. We recorded soil clay percent if it was reported, and if texture (e.g., sandy loam) was reported we used the USDA texture classification system to estimate soil clay percent as the center value for the textural class. Experiment locations included North America, Europe, Asia, and Antarctica (Supplementary Fig. S1a). In total, we examined 147 studies from 95 field experiments. We analyzed 111 warming studies, of which 47 reported SOC and 64 reported soil respiration changes (Supplementary Table S1). We analyzed 36 DIRT studies that included data from 12 field experiments. Of these studies, 17 measured SOC and 19 measured soil respiration responses to doubling leaf litter inputs (Supplementary Table S2).

We extracted mean responses from treatment and control groups, their respective standard deviations, and sample sizes. If necessary, we calculated standard deviation using standard error and sample size. To extract data from graphs, we used Data Thief III (Version 1.7, datathief.org). To determine the effect of each treatment relative to control, we calculated the log-response ratio (*LRR*):

$$LRR_{Temperature} = \ln(Y_{warmed}) - \ln(Y_{control}) \quad (1)$$

$$LRR_{Addition} = \ln(Y_{addition}) - \ln(Y_{control}) \quad (2)$$

where *Y* is the mean of a treatment (warmed or addition) or control group. *LRR* is centered around 0 such that positive *LRR* indicates the treatment mean was higher than control, and negative *LRR* indicates the treatment mean was lower than control. For each *LRR*, we calculated the pooled study variance (*V*) as:

$$V = \frac{s_t^2}{n_t} Y_t^2 + \frac{s_c^2}{n_c} Y_C^2, \quad (3)$$

where *s* is standard deviation, *n* is sample size, *Y* is sample mean, and *t* and *c* subscripts denote treatment and control, respectively. To account for non-independence of multiple studies conducted at the same site or using the same control plots, we included site as a random effect in our analyses (Gurevitch and Hedges 1999; Nakagawa and Santos 2012). We synthesized *LRR* across studies using multivariate linear mixed effects models separately for temperature and litter addition manipulations. Standard deviations for all data sets analyzed were known or calculated from standard error and sample size. Therefore, when responses in two categories were compared (e.g., warmed versus control), we used the Z-test, a standard statistical comparison of two means when population standard deviations are known. A high Z-score indicated low overlap between the data distributions and we report statistical significance (*P* value) of the overlap at alpha = 0.05. We used regression analysis to test for relationships between continuous variables, for example temperature and percent clay, and we report the coefficient of determination (R^2) for those relationships. We visually checked for publication bias using a funnel plot, which plots the standardized mean difference in control and treatment groups against the inverse standard error and is used to detect unpublished, often null, results (Duval and Tweedie 2000). We determined the correlation between response effect size (*LRR*) and potential explanatory factors using bivariate correlation tests. The explanatory factors we examined were soil clay percent, temperature difference from ambient, and duration of study. All statistical analyses were performed using the metafor package (version 2.0-0; Viechtbauer 2010) in R (version 3.5.0; R Core Team 2015).

Model and analysis code are available at https://github.com/bsulman/INTERFACE-model-experiment-synthesis.

Model output and meta-analysis data are available on Figshare (https://doi.org/10.6084/m9.figshare.6981842).

Results

Measured and modeled variability in response to warming

The meta-analysis revealed high variation in warming responses of both soil CO_2 flux ($P = 0.26$, $Z = -1.13$, Fig. 2a) and SOC ($P = 0.18$, $Z = -1.35$, Fig. 2b). Experiments with larger increases in temperature had stronger positive respiration responses to warming ($P < 0.01$, $Z = 5.48$, Supplementary Fig. S1c), but observed SOC losses did not vary significantly with temperature ($P = 0.11$, $Z = -1.60$). Observed respiration responses to warming were positively correlated with clay content ($P = 0.04$, $R^2 = 0.11$, Supplementary Fig. S1b). Nearly one-third (19 of 64) of the experiments measured lower CO_2 production following the onset of experimental warming (Fig. 2a). By contrast, all models projected transient increases in CO_2 flux, although some projected brief subsequent oscillations below control levels. Modeled and experimental CO_2 flux responses were not significantly different ($P = 0.16$, $T = 1.42$), and the ranges of LRR (minimum to maximum values within each dataset) largely overlapped (model LRR 0.00 to 1.40; experiment LRR −0.25 to 0.95). Nearly half (22 of 47) of the experiments showed an increase in SOC under warming (potentially connected to changes in plant productivity or soil moisture; see Discussion) while all models projected decreases in SOC (Fig. 2b). Overall, these responses were significantly different (t-test: $P < 0.01$, $T = 3.74$), although the response ranges overlapped (model LRR −0.82 to 0.00; experiment LRR −0.61 to 0.31).

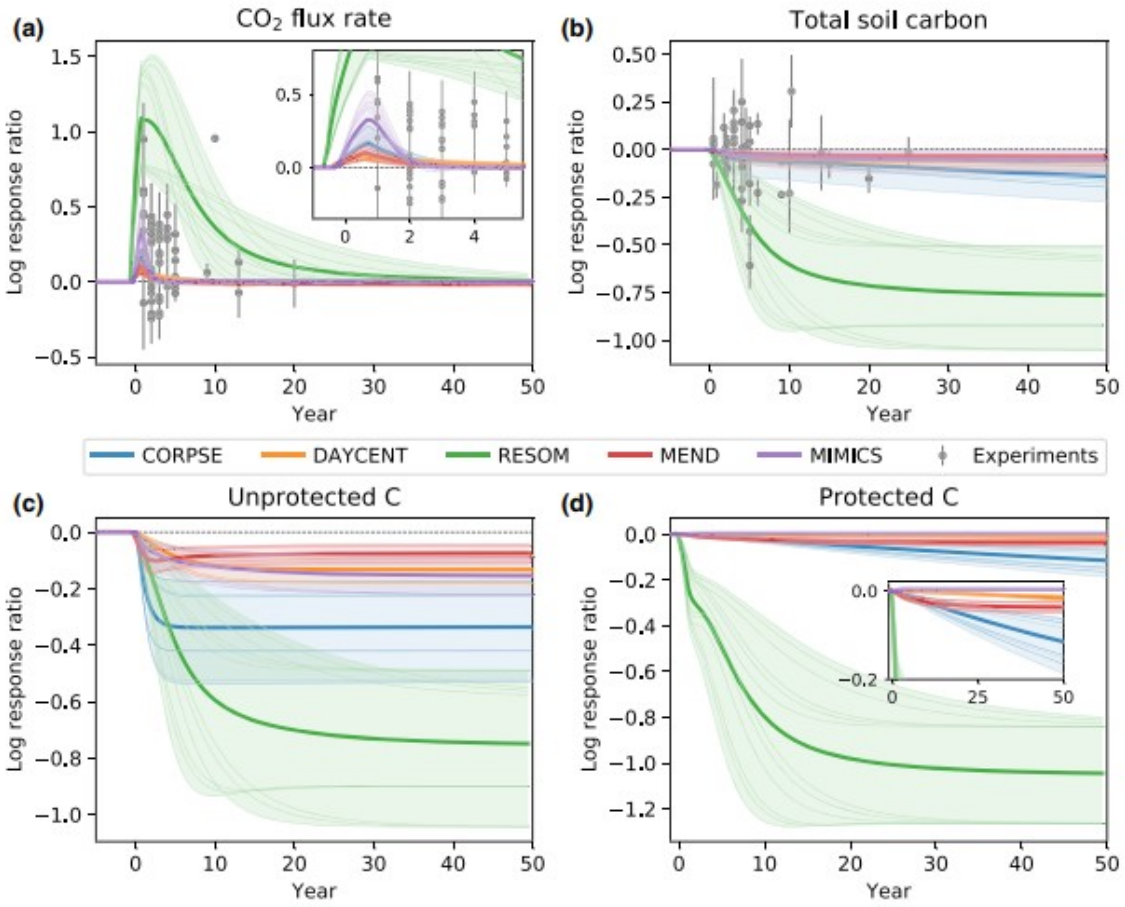

Fig. 2 Responses to warming. All panels show log response ratio of experiment relative to control. Changes in soil CO_2 efflux (**a**), total soil organic C (SOC) (**b**), unprotected SOC (**c**), and protected SOC (**d**). Observations from field studies are shown in gray with error bars representing standard error. Colored lines show model simulations, including all values of clay content, litter quality, and warming (2 or 5 °C). Shading shows range of model simulations with different warming, soil texture, and litter quality; light lines show individual simulations; and dark solid lines show the mean across simulations. Insets magnify key areas of plots

Rates and trajectories of SOC loss varied among models, with some continuing to lose SOC after 50 years and others approaching a new steady state. Model trajectories only diverged significantly after 15–20 years of warming (except for RESOM, which diverged rapidly from the other models), and only three experiments in the meta-analysis dataset lasted longer than 20 years, making it difficult to evaluate long-term model trajectories directly against experiments. Initial simulated losses were generally driven by unprotected C, which rapidly adjusted to new steady states (Fig. 2c). Long-term trajectories were controlled by protected C responses, some of which plateaued or did not respond significantly and some of which continued to decline after 50 years (Fig. 2d). Due to the contrasting responses of SOC components that were protected or unprotected from microbial decomposition, the long-term impacts of warming were sensitive to a combination of the shape of the protected SOC response and the fraction of total SOC that was in the protected pool. This fraction varied widely among models (Supplementary Fig. S3).

Measured and modeled variability in response to C inputs

In addition to warming responses, we examined the responses of soil respiration and SOC stocks to doubling of litter inputs in published studies (simulating global change effects on plant productivity and litterfall). Doubling litter inputs increased observed soil respiration over time resulting in up to 60% higher respiration compared to control treatments ($P = 0.03$, $Z = 2.23$, Fig. 3a). Simulated CO_2 flux rates in most models responded more rapidly than observed fluxes to increases in litter addition. The models also had stronger CO_2 flux responses to litter inputs than the experiments (t-test: $P = 0.01$, $T = 4.33$), but again the ranges overlapped (model LRR 0.03 to 0.71; experiment LRR −0.03 to 0.44). Our meta-analysis showed that, within 7 years, doubling litter inputs increased SOC by a mean of 7% (Standard error ± 3%, $P = 0.02$, $Z = 2.34$, Figs. 3b, S2), although there was significant variability among experiments with some documenting decreases in mineral soil C concentrations. Across models, doubling litter inputs caused increases in SOC that ranged from 5 to 80% by the end of the 50-year simulations (Fig. 3b). Overall, the models reported greater SOC accumulation than experiments in response to litter inputs (t-test: $P < 0.01$, $T = 4.53$) and their ranges overlapped substantially (model LRR 0.00 to 0.56; experiment LRR −0.08 to 0.32). As with warming, short-term responses were dominated by rapid shifts of unprotected C toward new steady state values or, for MEND, a return to the control steady state value (Fig. 3c). By contrast, long-term trajectories were driven by slower shifts in protected C that varied among models (Fig. 3d).

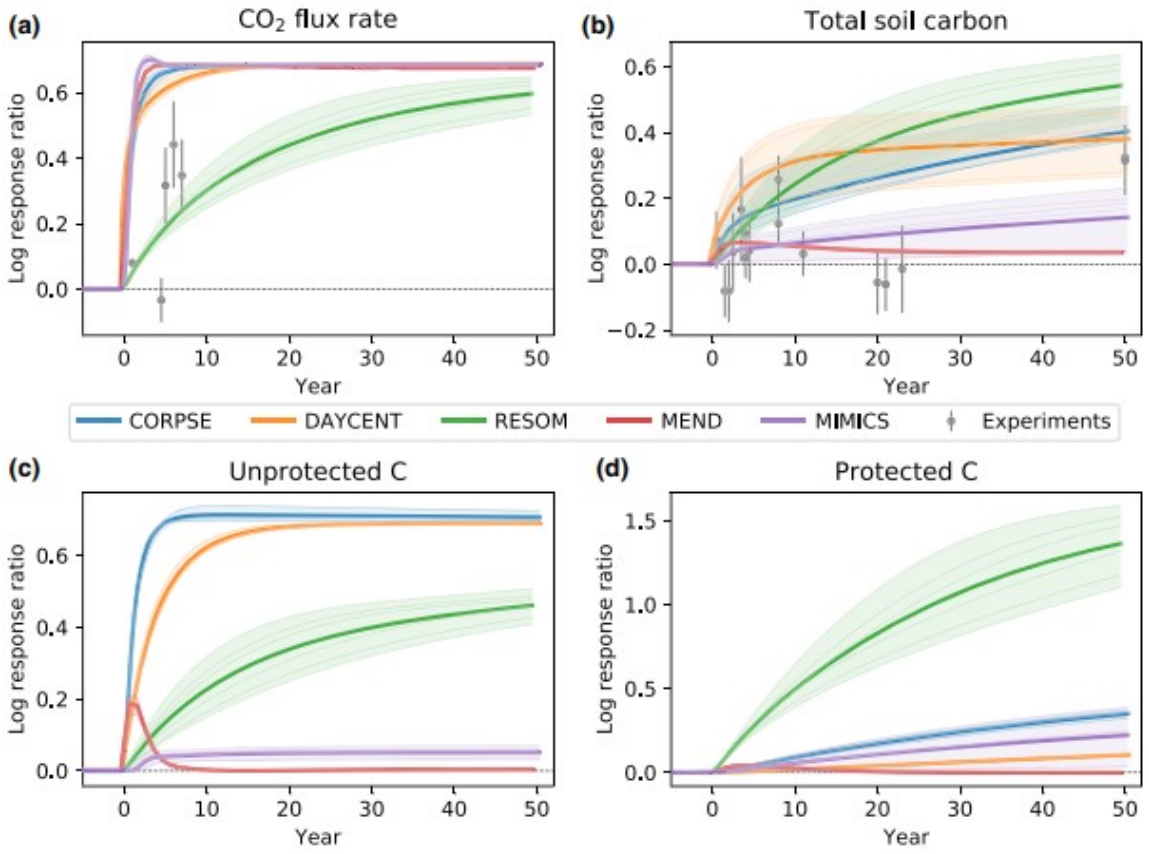

Fig. 3 Responses to litter addition. Panels are the same as Fig. 2. Models simulated doubling of litter addition, and observations were based on double leaf litter DIRT experiments

Modeled SOC responses to litter addition were more divergent than modeled responses to warming. Variations in responses over the first ten years of enhanced litter addition were driven by differences in the representation of unprotected SOC dynamics among models. These were primarily determined by key differences in model assumptions governing microbial growth and SOC decomposition (Table 1). Unprotected SOC in models with weak or nonexistent microbial growth responses to increasing substrate concentrations (CORPSE, DAYCENT) rapidly approached new, higher equilibrium values close to a 100% increase relative to control. By contrast, models with strong microbial growth responses (due to Michaelis–Menten or ECA kinetics) either returned to initial unprotected SOC stocks after a transient increase (MEND), approached a new equilibrium unprotected SOC stock only moderately higher than the control simulation (MIMICS), or increased slowly toward a new equilibrium unprotected SOC lower than a 100% increase (RESOM).

Table 1 Summary of key uncertainties in processes and parameters identified in the model inter-comparison

Key uncertainty	Model representation	Symbols Used in Fig. 1	Guiding questions for future experiments	Example studies
Microbial feedbacks to decomposition	Microbial enzymatic decomposition functions		SOC decomposition best fits which kinetics function? At what scale are these functions most appropriate?	(Blagodatskaya and Kuzyakov 2008; Kuzyakov and Blagodatskaya 2015; Tang and Riley 2013)
	Strength of microbial biomass response to C inputs		How does microbial biomass change under long-term addition of C inputs?	(Kallenbach and Grandy 2011; Sanaullah et al. 2016)
	Fixed versus dynamic CUE		How temporally variable is CUE? How does CUE vary with microbial biomass?	(Blagodatskaya et al. 2014; Frey et al. 2013; Devevre and Horwath 2000; Kallenbach et al. 2015)
	Microbial dormancy		What is the rate at which microbial populations shift from active to dormant? How do environmental conditions modify this rate?	(Lennon and Jones 2011; Salazar et al. 2018; Placella et al., 2012)
Protected and unprotected fractions of SOC	Temperature sensitivity of protected SOC formation and deformation		How do physically fractionated pools of C vary through time under long-term warming?	(Poeplau et al. 2017; Schnecker et al. 2016; Pold et al. 2017; Kleber et al. 2011)
	Capacity of microbes to decompose protected SOC		Using isotope tracers in different C pools, how does microbial uptake of C vary?	(Verchot et al. 2011)
	Ratio of protected:unprotected SOC at equilibrium		Using a data synthesis approach, how does protected:unprotected SOC vary across studies?	(Lajtha et al. 2014a; Grandy et al. 2007; Doetterl et al. 2015)
	Maximum protected SOC stock		Is there a saturating amount of protected SOC, or does it increase linearly with inputs?	(West and Six 2006; Gulde et al. 2008; Stewart et al. 2008; Castellano et al. 2015)
	Effect of soil mineralogy on protected SOC formation and deformation		How does the rate of protected SOC accumulation vary with mineralogy?	(Han et al. 2016; Rasmussen et al. 2018; Doetterl et al., 2015)
Context dependency	Various parameter settings for soil texture, temperature, moisture, and litter chemistry		At what spatial scale do these factors contribute to variation in SOC responses across time?	(West and Six 2006; Torn et al. 1997)
	Microbial mortality		How do soil properties influence microbial mortality?	(Schmidt et al. 2007; Burke et al. 1989; Xu et al. 2017)

Protected SOC responses were contingent on each model's assumptions about the accessibility of protected SOC to decomposers. Models with protected pools that were highly (MIMICS, CORPSE) or relatively (RESOM) inaccessible to microbes could accumulate more protected SOC over time, while MEND, in which protected SOC was more susceptible to microbial action, predicted a limited and transient response. Importantly, we were unable to directly compare modeled protected and unprotected SOC responses with experimental results, because only two of the manipulative experiments in our meta-analysis reported density fractionation

measurements (Crow et al. 2009; Lajtha et al. 2014a). Both those studies observed increases in light fraction SOC under litter addition.

Influence of soil texture and litter quality

Model responses to both warming and doubled litter addition were sensitive to clay content and litter quality, resulting in relatively wide ranges in simulated total SOC responses from each model (Figs. 2, 3). SOC in all models was less sensitive to both warming (losing less SOC) and litter addition (gaining less SOC) with higher clay content (Supplementary Fig. S4), primarily because simulations with higher clay content had larger fractions of SOC in protected pools that were less sensitive to manipulations (Supplementary Fig. S3). These model results contrasted with the meta-analysis, which found that SOC was more sensitive to both warming and litter addition when clay content was higher (see Supplement). Litter quality effects differed by model for both manipulations, with higher litter quality associated with higher sensitivity in some models and lower sensitivity in others. Variability among experiments in the meta-analysis was on the same order as variability among different models, which was generally larger than the range in simulation results driven by differences in clay content, litter quality, and warming intensity from any individual model.

Discussion

How much C will be lost from or sequestered in soils as the Earth's climate and biogeochemistry continue to change remains a pressing question that requires insights from both experiments and models. Using a diverse ensemble of state-of-the-art SOC models (Fig. 1) and a multi-continent set of experimental manipulations (Supplementary Fig. S1a), we demonstrated that variability in SOC responses to warming and litter addition observed across experiments is similar in magnitude to variability among model projections of SOC. However, no models reproduced increases in SOC or decreases in CO_2 efflux observed in a significant fraction of warming experiments. Individual models differed in their assumptions regarding the mechanisms for SOC turnover. However, neither the individual assumptions nor the overall model responses to warming and litter addition could be confirmed or ruled out using the set of experimental results—the experimental results were too variable and their reported measurements were incongruent with model representations of protected and unprotected SOC fractions.

Models qualitatively diverged in their responses to warming (Fig. 2) and litter addition (Fig. 3). Given these disagreements among models, we highlight fundamental uncertainties in the key mechanisms that drive SOC cycling that we identified based on this analysis, suggest key questions to guide future experiments, and provide examples of studies targeting those questions (Table 1). These uncertainties in microbial and mineral mechanisms could contribute to substantial uncertainties in the magnitude of terrestrial C cycle feedbacks to climatic changes when they are integrated over broad spatiotemporal scales in global models.

All models projected SOC losses in response to warming while experiments found both increases and losses. Observed increases in SOC under warming could be due to effects not included in the simulations, such as increased plant growth and inputs to soil, changing soil moisture, microbial community shifts, or changes in microbial carbon use efficiency (CUE) (Allison et al. 2010; DeAngelis et al. 2015; Frey et al. 2008, 2013; Melillo et al. 2017; Wang et al. 2013; Wieder et al. 2013). Bradford et al. (2017) recently found that site-specific variations in microbial biomass can explain high variability in decomposition responses to temperature. The wide spread among both models and experiments reflected complex processes underlying SOC decomposition and stabilization, and the models included a range of representations of these complex processes. For example, RESOM, MEND, and MIMICS included microbial CUE responses to warming. However, our results suggest that key dynamics that drive divergent SOC responses to warming were either beyond the current capabilities of the models (e.g., microbial community shifts) or were not included in forcing information for the warming simulations (e.g., increases in plant inputs or decreases in soil moisture).

Model-empirical comparison of protected and unprotected fractions

The generally slow response of protected relative to unprotected SOC stocks was consistent with several warming experiments that measured mineral-associated SOC and found that most SOC losses were concentrated in the free light fraction, which is typically assumed to be unprotected (Lajtha et al. 2014a; Phillips et al. 2016; Pries et al. 2017; Schnecker et al. 2016). However, Pold et al. (2017) found that mineral-associated SOC declined under warming while particulate SOC did not. Temperature sensitivity of protected SOC was an important source of uncertainty in simulations (Table 1). Models that represented protected C fluxes as temperature-sensitive processes (DAYCENT, MEND, RESOM, CORPSE) lost protected SOC under warming, while MIMICS, in which protected SOC turnover did not accelerate with warming, did not lose protected SOC. Short-term responses to litter addition were also dominated by changes in unprotected SOC fractions (Fig. 3c). This was consistent with observations from a 50-year litter addition experiment showing that the largest SOC increases under litter additions were in the light fraction and detecting no differences in protected SOC fractions (Lajtha et al. 2014a). Note that minimal changes in protected SOC stocks do not necessarily imply that those stocks are inactive—balancing increases or decreases in production and loss rates of protected SOC could also explain steady C stocks even in an actively cycling pool. The differences in model structures and resulting behaviors represent mechanistic uncertainties in projections of SOC cycling.

The suite of models investigated here varied in their representation of physicochemical SOC protection and how microbes respond to substrate availability, processes which drive decomposition and stabilization of SOC. Our simulation results suggest that more widespread use of size and/or

density fractionation measurements (e.g., Christensen 2001)—which partition mineral-associated, occluded, and free light SOC fractions and are useful proxies for SOC pools with varying stabilities (Bailey et al. 2018)—could improve testing of alternative model structures and parameterizations, especially if they were repeated over the course of manipulation experiments. While these fractions have been widely used in studies related to land use change and agricultural conversion (e.g., Del Galdo et al. 2003; John et al. 2005; Tan et al. 2007), they have been less commonly measured in warming and litter addition experiments (but see Crow et al. 2009; Lajtha et al. 2014a; Phillips et al. 2016; Pries et al. 2017; Schnecker et al. 2016; Pold et al. 2017). Combining fractionation measurements with techniques that estimate soil C age and attribute CO_2 production to different fractions (e.g., Lajtha et al. 2014a; Pries et al. 2017) could be especially useful. However, comparisons of soil fractionation measurements with models do require caution. Measured fractions may integrate a spectrum of substrates with different residence times (Chenu and Plante 2006; Kögel-Knabner et al. 2008; von Lützow et al. 2007), and definitions of protected pools differ among models. We recommend further examination by the global change community of how different models define these pools and represent their dynamics, and how these representations relate to measurable quantities. We also recommend that global change experiments measure and report soil mineralogical factors that are known to be proxies for physico-chemical protection capacity, such as soil texture, cation exchange capacity (CEC), iron and aluminum oxides, and clay mineralogy (Doetterl et al. 2015; Kallenbach et al. 2016; Rasmussen et al. 2018; Xu et al. 2016). Clay content serves as a proxy for other soil factors that affect cycling of both unprotected and protected SOC fractions (Bailey et al. 2018), despite the assumption in most models that soil texture primarily affects protected SOC formation and persistence. This assumption could explain why models were unable to reproduce the observed increase in sensitivity of SOC stocks to warming and litter addition in soils with higher clay content.

Coupling of biogeochemical models with soil genesis and soil physics models (e.g., Finke and Hutson 2008), or comparison with measurements along gradients of weathering (e.g., Doetterl et al. 2018), could also help to address uncertainties in mineralogy-SOC coupling. In addition, existing experiments included in our meta-analysis were heavily biased toward temperate climatic zones in North America, Europe, and China. Experiments in other regions of the world are necessary to develop better constraints on SOC cycling across gradients of climate, ecosystems, and soil types. Finally, the long time-scale associated with divergence among models underscores the need for multi-decadal experimental manipulations to develop effective model constraints.

Harnessing uncertainty: the way forward

While our comparison of multiple model structures produced a wide range of qualitatively and quantitatively different SOC projections, we found that

existing experimental measurements of CO_2 fluxes and total SOC were not sufficient to either eliminate or validate any of the individual model outcomes. This result highlights real uncertainties related to the multiple ways microbes and minerals interact to produce contrasting responses under global change (Table 1). Often, adding more detailed process representation is expected to improve model predictions (Todd-Brown et al. 2011; Wieder et al. 2013). However, our results suggest that the increasingly diverse mechanistic representations of microbial and mineral processes among recently developed soil C models increase the spread among model projections, because these changes introduce more choices of how to represent processes (Wieder et al. 2018; Bradford et al. 2016). First-order models can already generate divergent projections due to parameter uncertainties (Luo et al. 2015, 2017), and the structural diversity explored in our model comparison adds to those already wide uncertainty ranges. We contend that the widening spread among models due to structural diversity represents not a degradation of predictive ability but a more accurate estimation of predictive uncertainty (Bradford et al. 2016; Lovenduski and Bonan 2017).

High variability in measured SOC responses to experimental manipulations currently limits the ability to constrain these models using comparisons to manipulative field experiments, but also exemplifies the value of targeting experiments and measurements to address the greatest sources of uncertainty. Testing the fundamental assumptions underlying transfers of carbon among pools within decay models rather than comparing model projections of CO_2 flux and total SOC to field experiments may help clarify differences among models and their projections. Using this integrated model-experiment approach will advance basic understanding of SOC cycling and ultimately produce more confident projections of soil C responses to global changes.

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