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Global Biogeochemical Cycles

RESEARCH ARTICLE

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Key Points:

- Spatial climate gradients are insufficient for inferring transient temperature response of soil carbon decomposition and stocks
- The temperature sensitivity of both microbial activity and mineral sorption has large effects on SOC response
- More comprehensive data, including SOC in mineral fractions, from long-term warming experiments may help distinguish between model assumptions

Supporting Information:

- Supporting Information S1

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Soil Organic Matter Temperature Sensitivity Cannot be Directly Inferred From Spatial Gradients

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Abstract Developing and testing decadal-scale predictions of soil response to climate change is difficult because there are few long-term warming experiments or other direct observations of temperature response. As a result, spatial variation in temperature is often used to characterize the influence of temperature on soil organic carbon (SOC) stocks under current and warmer temperatures. This approach assumes that the decadal-scale response of SOC to warming is similar to the relationship between temperature and SOC stocks across sites that are at quasi steady state; however, this assumption is poorly tested. We developed four variants of a Reaction-network-based model of soil organic matter and microbes using measured SOC stocks from a 4,000-km latitudinal transect. Each variant reflects different assumptions about the temperature sensitivities of microbial activity and mineral sorption. All four model variants predicted the same response of SOC to temperature at steady state, but different projections of transient warming responses. The relative importance of Q_{\max} , mean annual temperature, and net primary production, assessed using a machine-learning algorithm, changed depending on warming duration. When mineral sorption was temperature sensitive, the predicted average change in SOC after 100 years of 5 °C warming was –18% if warming decreased sorption or +9% if warming increased sorption. When microbial activity was temperature sensitive but mineral sorption was not, average site-level SOC loss was 5%. We conclude that spatial climate gradients of SOC stocks are insufficient to constrain the transient response; measurements that distinguish process controls and/or observations from long-term warming experiments, especially mineral fractions, are needed.

1. Introduction

Soils store more than 2,500 Pg carbon (C) despite the ubiquity of microorganisms that decompose organic matter (Ciais et al., 2014). Changes in soil organic matter stock over time depend on climate, plant inputs, and soil properties such as mineral surface area (Belay-Tedla et al., 2009; Giardina et al., 2014). Under the 2014 Intergovernmental Panel on Climate Change highest emissions scenario (Representative Concentration Pathway 8.5), global-average soil temperatures are projected to rise 2.6 to 4.8 °C by 2100 (Friedlingstein et al., 2014). Different Earth system models (ESMs) project widely different soil organic carbon (SOC) stock responses to this warming (Knutti & Sedláček, 2012). Experimental warming studies have measured changes in SOC stock over timescales of 1–25 years, with most warming experiments spanning <5 years (Crowther et al., 2016; van Gestel et al., 2018). Moreover, many experiments do not manipulate both plants and soil at the same time. As a result, some studies use climate gradients to infer the long-term influence of temperature on soils (Anderson-Teixeira et al., 2011; Dunne et al., 2004; Giardina & Ryan, 2000; Post et al., 1982; Raich & Schlesinger, 1992; Sinsabaugh et al., 2017; Townsend et al., 1995; Zimmermann & Bird, 2012). This space-for-time substitution approach is a specific case of the state factor approach (Jenny & Amundson, 1941) that uses state factor gradients to understand the influence of a factor on soil properties.

The space-for-time approach assumes that the state factor of interest can be empirically or statistically isolated and that there is no significant transient effect, that is, decadal-scale responses to a change in some factor are similar to steady state differences among sites differing in that factor (Pickett, 1989). For example, if decomposition is primarily limited by temperature, then we would expect a cold site to have a larger steady state carbon stock than an otherwise equivalent warm site. Under these assumptions, warming the cold site would result in SOC loss, effectively shifting the cold site to have the properties of the warm site. Models that

parameterize or validate their temperature response using spatial gradients (e.g., Bugmann, 2010; Schimel et al., 1994; Wieder et al., 2013) implicitly make a space-for-time assumption. This assumption has not been explicitly tested for soil carbon models, though studies have explored more general challenges of modeling steady state versus transient effects (Carvalhais et al., 2008; Ryan et al., 2018; Sierra & Muller, 2015). We recognize that spatial gradients can be important tools to benchmark model responses, but they are not necessarily sufficient to constrain future predictions (Collier et al., 2018; Koven et al., 2017; Torn et al., 2015). We tested whether fitting an SOC model to sites that span a wide range of temperature and other environmental conditions would constrain model projections of future warming responses. We hypothesized that models with different representations of soil processes can make identical predictions across space (where SOC stocks are assumed to be at quasi steady state) yet very different predictions of transient dynamics due to warming. We test this hypothesis using a Reaction-network-based model of Soil Organic Matter and microbes (ReSOM).


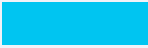


Empirical warming studies ascribe changes in SOC stocks to changes in net primary production (NPP; Saleska et al., 2002; Harte et al., 2015) or microbial decomposition rates (Melillo et al., 2011; Schindlbacher et al., 2011; Zhou et al., 2012; Zogg et al., 1997). Soil microbes respond to increased temperature in various ways, including altered carbon use efficiency, increased mortality rates, faster enzyme activity rates, and greater instability of enzyme binding sites (Alster et al., 2016; Ratkowsky et al., 2005). Studies measuring the instantaneous or short-term (order of days) microbial functional response to changes in temperature have consistently observed increases in extracellular enzyme activity, biomass growth, turnover, and respiration (Bárcenas-Moreno et al., 2009; Hagerty et al., 2014; Schindlbacher et al., 2015). In situ and over longer time periods, observed responses of microbial activity are less consistent. Indeed, studies over annual-to-decadal scales have reported an increase, a decrease, and no change in microbial activity (Frey et al., 2008; Rousk et al., 2012; Schindlbacher et al., 2011; Zhang et al., 2005). This range of responses suggests that the length of the warming treatment and initial site conditions affect the microbial response to warming.

Mineral protection is considered a major control of SOC stocks generally (Giardina et al., 2014; Jagadamma et al., 2014; Mathieu et al., 2015; Tian et al., 2016; Torn et al., 1997), but the temperature response of mineral-associated SOC is not well understood. Soil organic matter, derived from degraded plant C, dead microbial biomass, and microbial secretions, can be protected from decomposition through complexation with minerals or physical isolation in aggregates (Chenu & Plante, 2006; Mikutta et al., 2011; Rumpel & Kögel-Knabner, 2011; Six et al., 2000; Torn et al., 1997). However, the integrated temperature sensitivity of these mechanisms depends on the bond types and chemical species involved (Conant et al., 2011). Though thermal indices of mineral associations can be measured with calorimetric methods (Kleber et al., 2011; Plante et al., 2011), many models that include mineral associations do not represent their temperature sensitivity (Ahrens et al., 2015; Wang et al., 2013).

Current global-scale SOC decomposition models simulate mineral protection of SOC implicitly by modifying the SOC decomposition rate with an empirical factor based on soil clay fraction (Coleman & Jenkinson, 1996; Hararuk et al., 2015; Parton et al., 1987; Sulman et al., 2014; Wieder et al., 2013). Some site-level models explicitly estimate the fraction of SOC sorbed to minerals, using adsorption and desorption rates derived from laboratory sorption experiments (Dwivedi et al., 2017; Grant et al., 1993; Riley et al., 2014; Tang & Riley, 2015; Wang et al., 2013). Sorption can be calculated by imposing rates of the forward and reverse reactions or by using the Equilibrium Chemistry Approximation (ECA; Tang & Riley, 2013; Zhu et al., 2017). The ECA method accounts for the substrate concentration in solution and the total mineral surface area expressed as a sorption capacity. The advantage of this approach is that it can estimate the saturation state and temperature effects in a dynamic and chemically explicit way (Kalbitz et al., 2000; Pignatello, 1999). Even among models that use explicit sorption equations, however, the formulations and parameters for mineral sorption vary, which results in differing temperature responses associated with mineral sorption (Sulman et al., 2018).

To explore how warming could affect future SOC stocks, we developed four model variants of ReSOM (abbreviated NN, TN, TD, and TI) to test how different assumptions about the temperature sensitivity of microbial activity and mineral association affect the response of SOC stocks to warming (Table 1). The NN model assumes that neither microbial activity nor mineral sorption is temperature sensitive. The TN

Table 1
Description of Model Variants

Variant no. abbreviation	Microbial activity assumption	Mineral sorption assumption	Plot color
1: NN	Not temperature sensitive	Not temperature sensitive	
2: TN	Temperature sensitive	Not temperature sensitive	
3: TD	Temperature sensitive	Temperature sensitive: adsorption decreases with warming	
4: TI	Temperature sensitive	Temperature sensitive: adsorption increases with warming	

model assumes that microbial activity is temperature sensitive but mineral sorption is not. In reality, the temperature sensitivity of microbial activity is likely in between these two extremes, with incomplete microbial acclimation lowering the apparent temperature sensitivity to rapid warming. The TD and TI models both assume that microbial activity and mineral sorption are temperature sensitive but differ in the temperature sensitivity of mineral sorption as follows. The TD model assumes that adsorption to minerals decreases with warming, and the TI model assumes that adsorption to minerals increases with warming. These two variants reflect assumptions about the dominant type of mineral-association and their hypothesized temperature sensitivity (i.e., primarily exothermic [TD] and endothermic [TI] reactions; Conant et al., 2011), where the TN model represents the null hypothesis that mineral-association is not temperature sensitive (Nguyen et al., 2019). We used a large data set to parameterize ReSOM, to ensure that it could match observations spanning a wide range of climate and edaphic conditions. We predicted SOC stock at 24 sites along a 4,000-km spatial gradient in South America, spanning 11 soil orders, a 20 °C range in mean annual temperature, and a 2,200-mm range in annual precipitation (Doetterl et al., 2015). We then ran the four model variants for 100 years under a sustained 5 °C warming to compare the warming responses between model variants.

2. Methods

2.1. Data Set

We used previously published measurements of near-surface SOC stocks at 24 sites along a 4,000 km South American transect (Doetterl et al., 2015). This data set represents a wide range of relevant state factors: climate, mineralogy, and NPP. Hereafter, we refer to this data set as *D2015* and use SOC and SOC stock interchangeably, unless otherwise stated. The *D2015* data set contains measurements of mean annual temperature (MAT), mean annual precipitation (MAP), annual plant biomass increment, elevation, SOC, and a variety of soil chemistry and texture information (Table S1 in the supporting information). We derived the model forcing (MAT, NPP, and maximum mineral sorption capacity [Q_{\max}]) from this data set. We used mean annual plant biomass increment ($\text{kg ha}^{-1} \text{yr}^{-1}$) as a proxy for annual NPP at each site and assumed that dry plant biomass is 44% carbon (Harmon, 2013). We performed a sensitivity analysis to estimate the effect of this assumption on predicted SOC (Text S1 and Figure S1). We estimated Q_{\max} (g C eqv/m^{-2}) for each site from observed carbon (g C/m^{-2}) in the mineral fraction, measured using density fractionation, and the fraction of the mineral surface occupied by SOC, or saturation fraction. Because saturation data were not available, we fitted the saturation fraction as a parameter during the multiparameter optimization described in section 2.3. It would be ideal to estimate Q_{\max} from relationships with variables that are not affected by organic matter stocks, such as geochemical variables. But these types of relationships have not yet been developed, and the data that could be used to build them are sparse across soil types (Jagadamma et al., 2012, 2014; Mayes et al., 2012). The model does not take MAP as a direct input, but mean annual plant increment and MAP are positively correlated with an R^2 of 0.89 (Figure S2).

Table 2

Equations Governing the Change in Each Carbon Pool Over Time in the ReSOM Model. All pools are in units of carbon mass per soil volume (g C m^{-3}).

Pool	Description	Differential equation
S	polymeric organic carbon	$\frac{dS}{dt} = I_S - F_S + \gamma_{B1}B + f_E\gamma_E E$ (1)
D	monomeric organic carbon	$\frac{dD}{dt} = I_D + F_S - F_D + \gamma_{B1}X + (1 - f_E)\gamma_E$ (2)
X	reserve microbial biomass	$\frac{dX}{dt} = Y_X F_D - (\kappa - g + \gamma_{B1})X$ (3)
B	structural microbial biomass	$\frac{dB}{dt} = (g - \gamma_{B1})B$ (4)
E	extracellular enzymes	$\frac{dE}{dt} = p_E B - \gamma_E$ (5)
where		
I_S	polymeric input flux ($\text{g C m}^{-3} \text{ day}^{-1}$)	
I_D	monomeric input flux ($\text{g C m}^{-3} \text{ day}^{-1}$)	
F_S	polymeric depolymerization flux ($\text{g C m}^{-3} \text{ day}^{-1}$)	
F_D	monomeric uptake flux ($\text{g C m}^{-3} \text{ day}^{-1}$)	
Y_X	yield coefficient for reserve biomass (unitless)	
f_E	fraction of decayed extracellular enzymes contributing to the polymer pool (unitless)	
γ_{B1}	microbial mortality rate (day^{-1})	
γ_E	enzyme turnover rate (day^{-1})	
κ	metabolic turnover rate (day^{-1})	
g	growth rate (day^{-1})	
p_E	enzyme production rate (day^{-1})	

2.2. Model Description

The ReSOM model was originally developed in Tang and Riley (2015). We here developed four new variants of the ReSOM model with different process-level assumptions about microbial and mineral sorption temperature sensitivity. Throughout the text, we will refer to the model variants using their two-letter abbreviations (Table 1). The ReSOM model represents microbial activity and mineral sorption as potential controls of the emergent decomposition rates and thus SOC stocks. The model represents five carbon pools: polymers, monomers, microbial structural biomass, microbial reserve biomass, and extracellular enzymes (Table 2). Pool, flux, and parameter values are defined in Tables 2 and S2. All units are given in Table S2. For full equations, additional parameters, and model development, see Tang and Riley (2015).

The ReSOM model computes depolymerization of polymers, sorption of monomers and enzymes, and uptake of monomers (i.e., microbial assimilation) using equilibrium chemistry approximation (ECA) kinetics, a generalization of Michaelis-Menten (MM) kinetics (Tang & Riley, 2013). ECA is more accurate than MM kinetics in approximating the law of mass action kinetics, which underlies both approaches (Michaelis & Menten, 1913; Tang, 2015; Tang & Riley, 2013). ECA kinetics represents decomposition and substrate uptake as a competition between minerals and SOC for enzymes, and minerals and microbes for low molecular weight C, respectively. Two advantages of the ECA approach are the ability to (i) include distinct temperature-dependent effects on mineral sorption and microbial processes (i.e., decomposition, uptake, and maintenance) based on well-established kinetic theory and (ii) represent the multi-consumer, multi-substrate competitive environment in a computationally efficient manner. Thus, depolymerization (F_S) and uptake (F_D) are defined as

$$F_S = \frac{ESV_{E, \max}}{k_{ES} \left(1 + \frac{S}{k_{ES}} + \frac{E}{k_{ES}} + \frac{M}{k_{ME}} \right)} \quad (6)$$

$$F_D = \frac{zBDV_{B, \max}}{k_{BD} \left(1 + \frac{D}{k_{BD}} + \frac{zB}{k_{BD}} + \frac{M}{k_{MD}} \right)} \quad (7)$$

where E is the extracellular enzyme pool, S is the polymeric organic carbon pool, B is the structural

microbial biomass pool, D is the monomeric organic carbon pool, and M is the mineral sorption capacity (i.e., Q_{\max}), V_{\max} is the maximum rate of each process, z is a scaling parameter for transporter density, and k is the affinity parameter for decomposition (k_{ES}), uptake (k_{BD}), sorption to enzymes (k_{ME}), and sorption to monomers (k_{MD}).

Plant inputs estimated from site-level NPP are partitioned (Tang & Riley, 2015) into polymer and monomer pools, respectively, where the polymer pool represents polymeric compounds in litter (e.g., cellulose, hemicellulose, and lignin) and the monomer pool represents intracellular material, easily leached monomeric compounds in litter, and root exudates.

2.2.1. Variant 1: NN

To test the case where neither microbial activity nor mineral sorption is temperature sensitive, we created a model variant by assuming that no soil processes are temperature sensitive. This variant implicitly assumes that microbes are capable of either upregulating the production of temperature-optimal proteins or shifting the activity and/or dormancy state within the community to organisms that are adapted to the current thermal regime (Bradford et al., 2010; Lennon & Jones, 2011). Some empirical evidence suggests that decomposition is insensitive to temperature over wide spatial gradients (Giardina & Ryan, 2000), although these studies are the exceptions. This variant also simulates a condition where acclimation to temperature change is perfect and instantaneous.

2.2.2. Variant 2: TN

To test the case where microbial activity is temperature-sensitive but mineral sorption is not, we created a model variant where the temperature sensitivity of microbial activity is defined using thermodynamic equations governing enzyme and microbial reactions. Overall microbial activity has a temperature optimum that emerges from a trade-off between temperature limitation on maximum reaction rates (often approximated with the Arrhenius relationship) and the denaturation of enzymes at high temperatures (Conant et al., 2011; Murphy et al., 1990; Ratkowsky et al., 2005; Schipper et al., 2014). Considering the positive and negative effects of warming on microbial activity leads to a temperature response curve with the highest rates of activity centered on an optimum temperature. If this response curve does not shift or flatten (i.e., acclimate) under warming, then at any particular time, microbes in a given biome would respond differently to warming based on their initial acclimated temperature.

The temperature-dependent processes in the TN model variant are grouped into three categories: (i) equilibrium reactions, (ii) nonequilibrium reactions, and (iii) enzyme-mediated reactions. Some processes such as depolymerization and uptake may have equilibrium, nonequilibrium, and enzyme-mediated components affecting different parameters (e.g., binding affinity, maximum rate, and fraction of active enzymes, respectively). Equilibrium reactions include reversible binding (enzyme-polymer, microbe-monomer, enzyme-mineral, and monomer-mineral) and microbial maintenance.

The temperature dependence of these reactions is based on Eyring's transition state theory (Eyring, 1935; Tang & Riley, 2013),

$$K_{EQ}(T) = K(T_0) \exp \left[-\frac{\Delta G_{EQ}}{R} \left(\frac{1}{T} - \frac{1}{T_0} \right) \right] \quad (8)$$

where T_0 is the reference temperature, set to the mean annual temperature, $K(T_0)$ is the reference affinity, ΔG_{EQ} is the Gibbs free energy change of the equilibrium reaction, R is the gas constant, and T is the current temperature. Maximum reaction rates for depolymerization and monomer uptake are classified as nonequilibrium or forward reactions. The temperature dependence of the forward reaction is

$$V_{NEQ}(T) = V(T_0) \frac{T}{T_0} \exp \left[-\frac{\Delta G_{NEQ}}{R} \left(\frac{1}{T} - \frac{1}{T_0} \right) \right] \quad (9)$$

where $V(T_0)$ is the reference maximum rate for the forward reaction and ΔG_{NEQ} is the Gibbs free energy change of the nonequilibrium reaction. Enzyme-mediated processes considered in this model include depolymerization of polymers by extracellular enzymes and uptake of monomers by transporter proteins. Enzyme-mediated processes are governed by a temperature-dependent optimum, which affects the fraction of enzymes that are active (i.e., conformationally able to bind to substrates), defined by

$$f_{\text{act}} = \frac{1}{1 + \exp\left(-\frac{n\Delta G_E}{RT}\right)} \quad (10)$$

$$\Delta G_E = \Delta H^* - T\Delta S^* + \Delta C_P \left[(T - T_H^*) - T \ln\left(\frac{T}{T_S^*}\right) \right] \quad (11)$$

$$\Delta C_P = -46 + 30(1 - 1.54n^{-0.268})N_{\text{CH}} \quad (12)$$

where f_{act} is the fraction of enzymes that are active at a given temperature and varies between 0 and 1 (Figure S3), ΔG_E is the Gibbs free energy change of the enzyme reaction, ΔH^* is the enthalpy change at the convergence temperature for enthalpy (T_H^*), ΔS^* is the entropy change at the convergence temperature for entropy (T_S^*), ΔC_P is the change in heat capacity, n is the average number of amino acid residues in an enzyme, and N_{CH} is the average number of nonpolar hydrogen atoms per amino acid residue. From Murphy et al. (1990), Ratkowsky et al. (2005), and Schipper et al. (2014), we defined parameters for amino acid traits (n , N_{CH} , ΔH^*) that result in a thermal optimum at 290 K.

This model variant (TN) assumes that mineral sorption is not temperature sensitive. The temperature dependence of mineral sorption is applied to the binding-affinity parameters following equation (8). We set the expression $\left(\frac{1}{T} - \frac{1}{T_0}\right)$ equal to 0, so that the binding-affinity parameter is equal to the reference binding affinity at any temperature.

2.2.3. Variant 3: TD

To test the case where microbial activity and mineral sorption are temperature sensitive, we created a model variant with microbial temperature sensitivity as described in section 2.2.2. Conant et al. (2011) described several hypotheses for how the temperature sensitivity of mineral sorption could depend on the thermodynamics of the binding compounds. For example, if a forward reaction (e.g., adsorption) is exothermic, increasing temperatures would shift the equilibrium toward the reactants or unbound (desorbed) state. Conversely, an endothermic reaction would shift toward the bound (adsorbed) state with warming. Organic matter associates with a wide variety of mineral surfaces and metal complexes (e.g., Fe and Al oxides, phyllosilicates, metal ions) that all have different enthalpies of reaction. This model variant assumes that adsorption will decrease with warming (i.e., is an exothermic reaction). Many adsorption reactions can be exothermic, such as adsorption of organic matter to iron oxides and to expandable clays such as montmorillonite (Arnarson & Keil, 2000; Gu et al., 2008). We represent exothermic sorption reactions using equation (8) to modify the binding-affinity parameter of sorption (k_{ME} and k_{MD} in equations (6) and (7); Table 2). We chose a value for ΔG_{EQ} (20 kJ/mol^{-1}) that is less temperature sensitive, and therefore conservative, relative to the empirically equivalent activation energy parameter of chemically resistant pool decomposition in other models (e.g., 54 kJ/mol in Sulman et al., 2014) and measurements (e.g., 32 kJ/mol for phenol oxidase activity in Davidson et al., 2012).

2.2.4. Variant 4: TI

To test an alternative theory of mineral sorption temperature sensitivity, we created a model variant that assumes microbial activity is temperature sensitive as described in section 2.2.2 and that mineral sorption is also temperature sensitive. The temperature sensitivity of mineral sorption in Variant 4 differs from Variant 3 in that it assumes that increasing temperatures favor adsorption relative to desorption (i.e., is an endothermic reaction). Endothermic adsorption reactions in soils include sorption of soils to lead (Adhikari & Singh, 2003; Tan et al., 2008). In two calorimetry experiments with phosphorus on Al and Fe minerals and kaolinite, Penn and colleagues found that reactions could be endothermic or exothermic depending on the pH of the soil and the type of reaction that occurred (Penn, 2010; Penn & Warren, 2009). Indeed, the thermal properties of different adsorption reactions may vary widely depending on the organic and mineral substrates and the soil environment. To represent endothermic adsorption, we modified equation (9) so that the Gibbs free energy change of the monomer-mineral or enzyme-mineral binding affinity has the opposite sign compared to the TD variant. For the TD variant, equation (8) defines ΔG_{EQ} as a negative value, describing an exothermic forward reaction where higher temperatures shift the equilibrium toward the unbound state, assuming that entropy change is negligible. In this model variant (TI), ΔG_{EQ} is given the equivalent positive value (i.e., endothermic forward reaction), such that higher temperatures shift the equilibrium toward the bound state.

$$K_{\text{EQ}}(T) = K(T_0) \exp \left[\frac{\Delta G_{\text{EQ}}}{R} \left(\frac{1}{T} - \frac{1}{T_0} \right) \right] \quad (13)$$

2.3. Parameterization and Model Runs

We fit the model to the SOC stocks measured in D2015 by minimizing the sum of squared residuals between modeled and measured SOC stocks. We used interior-point optimization with upper and lower bounds set at +50% and –50% of the default parameters reported in Tang et al. (2015; `fmincon`; MATLAB, 2018; MATLAB Optimization Toolbox, 2018). We fit 27 parameters related to microbial, enzyme, substrate, and mineral interactions (marked with an asterisk in Table S2). We did not fit certain parameters that we considered to be constants, such as the gas constant, convergence temperature for entropy, and the number of amino acids per average enzyme. Given the bounds on each parameter, the large number of parameters, and model complexity, it is possible that other minima exist. However, the aim of this paper is to examine the temperature sensitivity of a model that fits site-level data well, and not to identify the most realistic or general parameters for use in future studies.

We ran ReSOM at each of the 24 sites in D2015 assuming 10-cm soil depth to match observations. We spun up each site for 1,000 years using Q_{max} , MAT, and NPP as model forcing (Table S3). We imposed the MAT with a constant temperature forcing. We verified that the system had reached steady state by confirming that the first derivative of each carbon pool over the last 100 years of the model run was statistically indistinguishable from zero using a one-sample t test.

To test the effects of warming on model predictions, we projected SOC stock for 100 years with a sustained +5 °C step change in temperature. For subsequent analyses of site-level SOC under ambient conditions and after warming, we used the mean SOC stock during the last year of the model run.

2.4. Statistical Analysis

Linear regression and generalized least squares regression relationships between model-predicted SOC and explanatory factors of interest (i.e., Q_{max} , MAT, and NPP) did not satisfy assumptions of normality. Specifically, all linear regression models tested in this study showed significant curvature and heteroskedasticity of residuals, both by visual inspection and by formal testing following Peña and Slate (2017). Similarly, in the D2015 data set, we identified significant curvature in the relationship between SOC and MAT. As a result, we used the Random Forest nonparametric machine-learning algorithm to identify the predictor variables that had the greatest influence on predicted SOC stock at different timescales. Random Forest identifies important predictor variables using an ensemble of regression trees grown by subsampling from the data set (Liaw & Wiener, 2002). Trees produced using the bootstrapped subsample and the remaining “Out-of-Bag” data are compared and aggregated across trees to estimate the mean square error and the percentage of variance explained by the model. Variable importance is reported as the mean decrease in prediction accuracy when the variable is excluded from the model (Breiman, 2001). Importance values are comparable for predictors within a model for the purpose of ranking. However, because these values are aggregated estimates of prediction accuracy that do not relate to classical statistical measurements, the values themselves cannot be compared across models.

We applied the Random Forest algorithm to all model variants' SOC stock predictions at steady state and to changes in SOC stock after 100 years of +5 °C warming. To reanalyze the D2015 transect data in a consistent manner, we also applied the Random Forest algorithm to all of the soil and environmental properties provided in that data set. All analyses were performed in the R Statistical Language (packages “`lm`,” “`glm`,” and “`randomForest`”; Version 3.5.1; R Core Team, 2018).

3. Results

3.1. Predicted SOC at Steady State and Measured SOC Across a Spatial Gradient

We predicted steady state SOC stock with ReSOM at the 24 D2015 sites. To force the model, MAT was taken directly from D2015 and NPP and mineral sorption capacity (Q_{max}) were estimated from D2015 measurements of annual plant biomass increment and mineral-associated SOC stock as described in section 2.1. There was a strong correlation and little bias between modeled and observed SOC stock for all model variants (slope = 1.18, $R^2 = 0.94$, $P < 0.001$; Figures 1 and S4), and all model variants predicted the observed

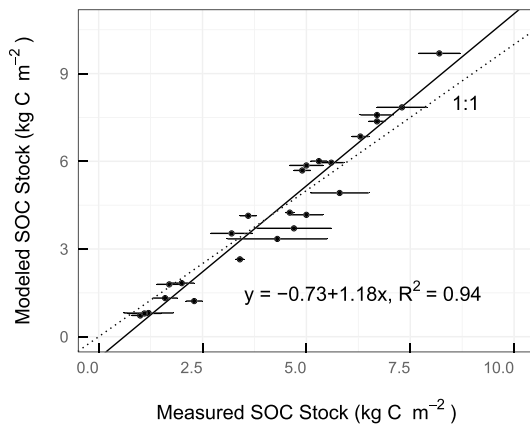


Figure 1. Modeled versus measured soil organic carbon (SOC) at each of the 24 sites in the D2015 data set. All model variants make identical SOC stock predictions at steady state. The black solid line is the regression fit, and the gray dotted line is the 1:1 line. Error bars are standard error of measured SOC.

base cations, MAT, and other geochemical and texture variables (Figure S5). Notably, clay fraction (fClay) was the least important predictor of observed SOC stock, despite being commonly used as a proxy for mineral sorption capacity in global-scale soil decomposition models (Sulman et al., 2014; Wieder et al., 2013). At some sites, clay fraction has been well correlated with the sorption capacity of dissolved organic carbon (Mayes et al., 2012), but across a global range of soil orders, clay fraction is a poor predictor of mineral-associated carbon (Jagadamma et al., 2014). Some of the predictors of total SOC in Figure S5, such as CEC and bulk density, and to a lesser extent Q_{\max} , are confounded with SOC because organic matter affects these soil properties. However, data on CEC and bulk density are widely available (Hengl et al., 2014; Nachtergaele et al., 2012) and could be used with geochemical variables to create proxies for sorption capacity, especially if sorption is considered to represent not only the monolayer organomineral interaction that is assumed in ECA (Tang & Riley, 2013) but also multilayer sorption and complexation.

3.2. Predicted Changes in SOC After Warming

The four model variants diverged in their predictions of SOC response to a +5 °C step change in temperature (Figure 3). When SOC stock was projected for 100 years under a 5 °C warming scenario, the NN model (no temperature sensitivities) predicted no change in SOC stock at all sites, as expected, regardless of Q_{\max} , initial MAT, and NPP (Figure 3a, dark blue). In contrast, the TN model (microbial activity is temperature sensitive but mineral sorption is not, light blue) predicted an average loss in SOC stock of 0.2 kg C/m² after 100 years of warming across the sites, with a maximum loss of 0.6 kg C/m². This change represents a 5% to 6% decrease from the total initial SOC. The TD model (microbial activity is temperature sensitive and adsorption decreases with warming) predicted an average loss of 0.8 kg C/m² across sites, with a maximum loss of 1.8 kg C/m² and a strong relationship with initial SOC (slope = -0.02, $R^2 = 0.62$; Figure S6). The TI model (microbial activity is temperature sensitive and adsorption increases with warming) predicted no loss in SOC and up to a 0.9 kg C/m² increase in SOC, depending on the site. These absolute changes represented an average SOC stock change of -18% and +9% for the TD and TI models, respectively.

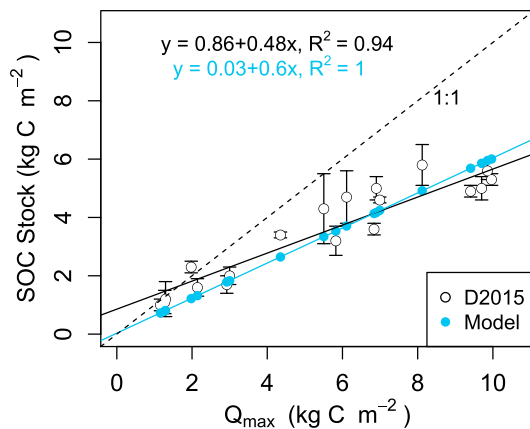


Figure 2. Relationship between estimated Q_{\max} at each site and the soil organic carbon (SOC) stock measured by D2015 (open symbols) and predicted by all model variants (light blue symbols).

spatial data equally well (Figure 1)—across sites spanning a 7.2 kg C/m⁻² range in observed SOC stocks, a 20 °C range in mean annual temperature, and 11 soil orders. The difference among model-variant temperature-response functions did not affect within site predictions at steady state. The microbial temperature response curve assumed microbes were initially acclimated to their site MAT, such that their reference temperature (T_0 ; Table S2) is set equal to the site MAT. The reaction rates were the same at steady state for all model variants at a given site, because reaction rates are calculated based on deviation from the reference temperature (e.g., terms $\frac{T}{T_0}$ and $(\frac{1}{T} - \frac{1}{T_0})$ in equation (9)). Because all model variants made identical steady state predictions, we represent them in Figure 2 using only one symbol (light blue symbols).

Steady state SOC stock predictions (Figure 2, blue symbols) were highly correlated with mineral sorption capacity Q_{\max} . There was also a significant correlation between measured SOC stock and Q_{\max} in the D2015 data set (Figure 2, open symbols). In our Random Forest analysis of all soil and environmental properties in the D2015 data set, Q_{\max} was the highest ranked soil property, followed by CEC, bulk density, NPP, total reserve

carbon, and other geochemical and texture variables (Figure S5). Notably, clay fraction (fClay) was the least important predictor of observed SOC stock, despite being commonly used as a proxy for mineral sorption capacity in global-scale soil decomposition models (Sulman et al., 2014; Wieder et al., 2013). At some sites, clay fraction has been well correlated with the sorption capacity of dissolved organic carbon (Mayes et al., 2012), but across a global range of soil orders, clay fraction is a poor predictor of mineral-associated carbon (Jagadamma et al., 2014). Some of the predictors of total SOC in Figure S5, such as CEC and bulk density, and to a lesser extent Q_{\max} , are confounded with SOC because organic matter affects these soil properties. However, data on CEC and bulk density are widely available (Hengl et al., 2014; Nachtergaele et al., 2012) and could be used with geochemical variables to create proxies for sorption capacity, especially if sorption is considered to represent not only the monolayer organomineral interaction that is assumed in ECA (Tang & Riley, 2013) but also multilayer sorption and complexation.

The range of predicted change in (Δ) SOC stock in the lowest and highest quintiles of site MAT were 2.8 and 1.0 kg C/m², respectively, reflecting assumptions about the change in enzyme activity relative to the initial site MAT. The range of predicted Δ SOC in the lowest and highest quintiles of site Q_{\max} were more similar, 2.9 and 2.2 kg C/m², respectively. This means

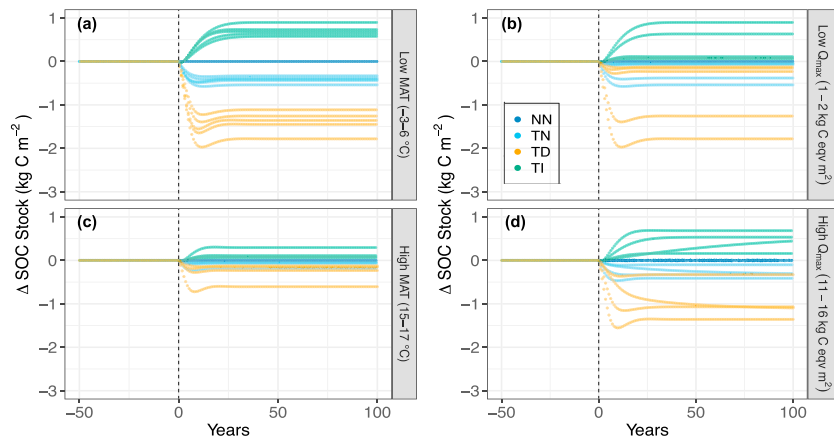


Figure 3. Time series of the change in soil organic carbon (SOC) stock following a +5 °C step change imposed at year 0 for sites with a mean annual temperature (MAT) in the lowest quintile (a), Q_{\max} in the lowest quintile (b), MAT in the highest quintile (c), and Q_{\max} in the highest quintile. Color indicates the model variant (NN, TN, TD, and TI) used for each run. Each colored line represents the predicted change SOC stock at an individual site.

that the effect of warming differed by initial site MAT, with warmer sites losing less SOC than colder sites.

3.3. Controls on SOC Across Timescales

Using the Random Forest algorithm (Table S4), we ranked the importance of Q_{\max} , MAT, and NPP on the data set derived from D2015 observations and on modeled SOC stock at the D2015 sites. Variable importance was calculated as the mean decrease in statistical prediction accuracy when the variable was excluded from the model (Breiman, 2001). Mineral sorption capacity (Q_{\max}) was more important than MAT and NPP in explaining modeled steady state SOC stock and measured SOC stock (Figure 4). The agreement among model variants in the ranking of predictor variable importance suggests that Q_{\max} is the most important factor determining site-level SOC at steady state regardless of microbial or mineral temperature sensitivity.

According to the Random Forest results, the relative importance of the environmental variables explaining SOC stock were different in the steady state case (Figure 4) compared to the decadal-scale warming case (Figure 5). Modeled steady state SOC stock was controlled by Q_{\max} but controls on the SOC warming response varied by timescale. In particular, MAT was the most important predictor of SOC stock change after 1, 5, and 10 years of +5 °C warming, but after 100 years NPP was the most important predictor. This result challenges the assumption that decadal-scale responses to warming are similar to steady state

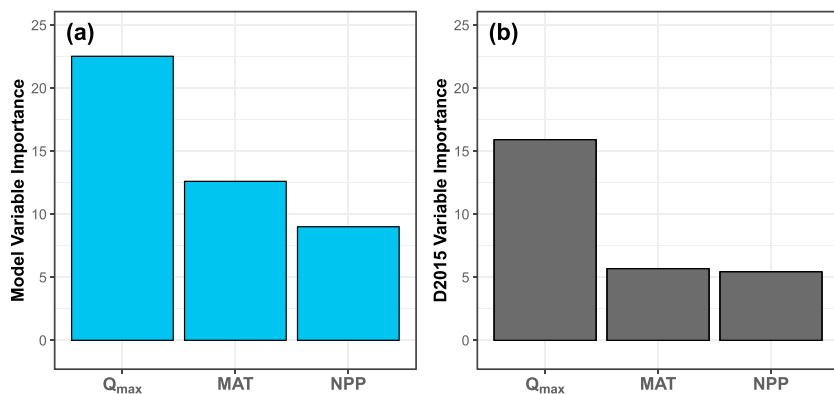


Figure 4. Random Forest variable importance values (y axis) for predicting SOC stock at steady state across D2015 sites using the ReSOM model (a; light blue bars) and SOC stock measured at the D2015 sites (b; gray bars). SOC = soil organic carbon; ReSOM = reaction-network-based model of Soil Organic Matter and microbes; MAT = mean annual temperature; NPP = net primary production.

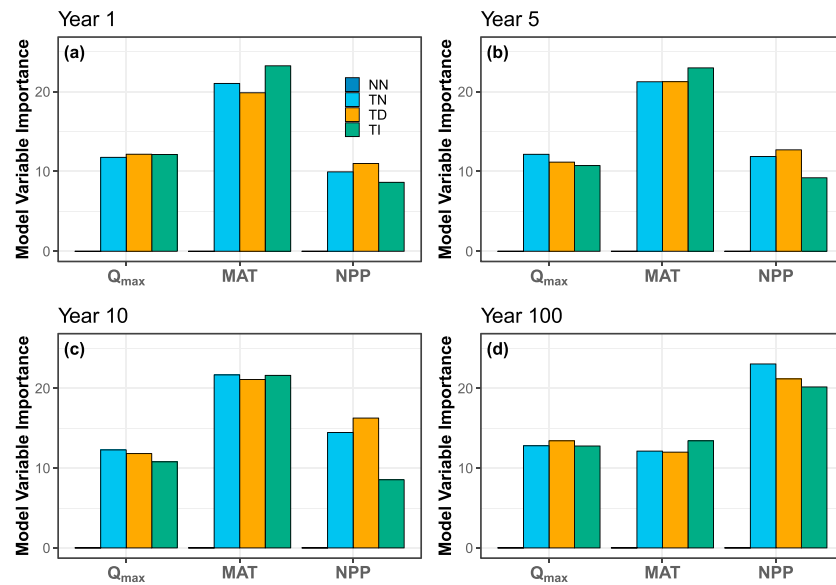


Figure 5. Random Forest variable importance values for predicting the change in soil organic carbon (SOC) stock for 100 years of 5 °C warming using the NN model (dark blue bars), the TN model (light blue bars), the TD model (orange bars), and the TI model (green bars). The three variables considered are Q_{\max} , mean annual temperature (MAT), and net primary production (NPP). Model variable importance values are shown for predicted change in SOC after (a) 1 year of the +5 °C step change; (b) 5 years; (c) 10 years; and (d) 100 years. Model variable importance for the NN model variant cannot be seen because this model variant predicted no change in SOC stock.

differences across a temperature gradient of a similar magnitude in temperature change (i.e., the space-for-time assumption), at least as interpreted by the TN, TD, and TI models. For the NN model, none of the predictor variables were explanatory because there were no SOC changes in response to temperature (Table S4). The TN, TD, and TI models predicted similar importance of variables across timescales, suggesting no interaction effect between the temperature sensitivity of mineral sorption and the relative importance of Q_{\max} , MAT, and NPP.

4. Discussion

We found that measurements from sites in quasi steady state across a spatial gradient in temperature could not help distinguish how model variants with different temperature sensitivities would respond to changes in temperature over time. More generally, differences in model behavior could not be constrained by steady state observations. Thus, a key implication of our simulations is that spatial gradients may be insufficient to infer (or have confidence in model predictions of) future SOC changes under transient warming. While spatial gradients generate useful insights into the influence of various factors on SOC (Clemmensen et al., 2015; Doetterl et al., 2018; Koven et al., 2017; Raymer et al., 2013), the fast timescales of anthropogenic climate change will likely create transient responses that cannot be inferred from variation among sites at or near steady state. Using different process representations of microbial and mineral temperature sensitivity, we showed that models with identical steady state predictions across spatial gradients make different dynamic predictions under future warming scenarios. We also demonstrated that large, warming-induced losses of mineral-associated C are possible with or without direct temperature effects on mineral-associated C, as long as microbial activity is temperature sensitive. The converse was also shown: if mineral sorption is temperature sensitive, then overall SOC stocks will be temperature sensitive as well even if microbial parameters are not temperature sensitive, because sorption coefficients control the transfer of carbon from a mineral-associated state to a more microbially accessible dissolved state (Figure S7 and Text S2).

The ReSOM model agreed well with the observations from the large D2015 transect of SOC stocks and the factors controlling them. For both the models and observations, Q_{\max} was strongly correlated with steady state SOC stocks (Figure 2), suggesting that minerals control the long-term spatial distribution of SOC stocks. Similarly, the Random Forest analysis showed that Q_{\max} was more important than MAT and NPP

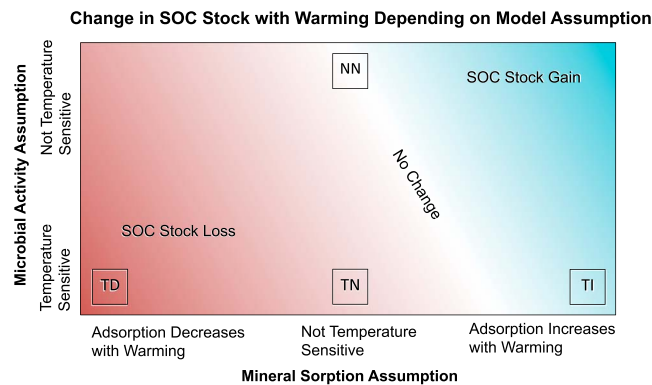


Figure 6. Diagram of the predicted soil organic carbon (SOC) stock loss or gain depending on temperature sensitivity assumptions of microbial activity (y axis) and mineral sorption (x axis). The color shading represents potential changes in SOC stock as a result of a given combination of assumptions, ranging from SOC stock loss (red) to no change (white) to SOC stock gain (blue). The shading of the inset boxes indicates the change in SOC for each of the four models: NN, TN, TD, and TI. The position of each inset box corresponds to the assumptions used to create the model.

in explaining steady state SOC stocks (Figure 4). Although mineral-SOC tends to be old and relatively stable (Trumbore, 2009), mineral control of SOC stocks did not prevent large temperature responses under warming. We predicted -1.8 to $+0.9$ kg C/m² changes in SOC stocks across the model variants (Figure S8). These absolute changes represented a -19% loss to a $+11\%$ gain in SOC stocks, with a mean [1st, 3rd quartiles] of -4% [-9% , $+1.6\%$]. The largest losses were predicted when adsorption decreases with warming (TD), which increases the availability of C accessible to microbes (Figures 3 and S7). Conversely, SOC stocks increased even without changes to NPP in the TI model variant where adsorption increases with warming, decreasing microbially available C. Further, fairly large losses were observed in the TN model where mineral sorption is not temperature sensitive but microbial activity is. Warming increased microbial consumption of monomer and enzyme C, creating increased competition for the remaining C, and ultimately less C sorbed to minerals. Therefore, mineral-associated C that exchanges dynamically with aqueous C is temperature sensitive as long as microbial activity is temperature sensitive. This dependency should be the case for all models that have an explicit sorption model that depends on the concentration of total C, but to our knowledge, it has never been demonstrated with a soil C model before. Thus, a key implication of reversible mineral sorption is that mineral-associated C is vulnerable to warming, regardless of the explicit temperature sensitivity of sorption.

The range in site-level SOC stock changes due to warming was not affected by mineral sorption capacity (Q_{\max} ; Figures 3b and 3d) but was affected by initial site MAT (Figures 3a and 3c). At low initial site MAT, there was a larger range of SOC stock change predictions than at high initial site MAT. At warm sites, microbial enzyme activity was closer to the predicted maximum activity based on the heat capacity of enzymes (Figure S3). As a result, the model variants predicted smaller SOC stock losses with warming because the increased encounter rate between molecules when warmed (Davidson et al., 2012; Rodrigo et al., 1997) was compensated by the decreased ability of proteins (such as enzymes) to bind substrates at high temperatures (Alster et al., 2016; Ratkowsky et al., 2005; Schipper et al., 2014).

The relative importance of the different variables governing soil response to warming are not consistent over time. For some of the model variants, there was a relationship between initial SOC stock and SOC stock change after warming, similar to that observed in Crowther et al. (2016). For example, the TN and TD models have a significant negative relationship between initial SOC and change in SOC stock with warming, implying that sites with large SOC stocks before warming will lose more SOC than sites with small SOC stocks (Figure S6). However, this relationship is not observed in van Gestel et al. (2018), suggesting that controls on SOC stocks with warming cannot be described with the single factor relationships (to initial SOC, MAT, MAP, percent clay, pH) tested in those two studies. The relative influence of controls like mineral sorption, MAT, and NPP may change over time in response to a perturbation, resulting in a phased SOC stock response such as that observed in a 26-year soil warming experiment (Melillo et al., 2017). At seasonal timescales and in response to perturbations, there are also many examples of transient responses whose

controlling factors are not linearly related to climate or site characteristics (Oikawa et al., 2014; Placella et al., 2012). For example, soil respiration responses to pulses of water cannot be explained by instantaneous soil moisture alone and are thought to involve interaction effects between microbial drought responses, buildup of substrates in drying soils, and changes to soil structure (Arnold et al., 2015; Blankinship & Schimel, 2018; Evans & Wallenstein, 2012; Waring & Powers, 2016).

There is a wide range of possible soil responses to warming, and the predicted responses were different between model variants (Figure 3). There was little sensitivity of SOC stock to warming in the variants without microbial or mineral sensitivity (NN) or with opposing sensitivities in which temperature-sensitive microbial activity is offset by increasing mineral adsorption (TI; Figure S6). Because different combinations of process-level assumptions can make similar predictions of SOC stocks (Figure 6), it is not possible to determine the most accurate model variant from measured changes in total SOC such as those reported in Crowther et al. (2016) and van Gestel et al. (2018). However, the factors affecting model predictions differ across the model variants (Figure 5), and the model predicts multiple measurable pools and fluxes, including soil fractions, heterotrophic respiration, and enzyme activity. Therefore, given additional measurements from long-term warming experiments, especially mineral fractions, it may be possible to invalidate some of the temperature assumptions simulated here.

This study is the first application of the ReSOM model to a large, spatially extensive data set. Like other standalone soil decomposition models, ReSOM lacks plant feedbacks and other processes relevant to global change predictions. However, this model is suitable for our analyses investigating the impact of microbial and mineral temperature responses under steady state and transient warming conditions. The evidence presented here is consistent with the emerging perspective that interactions between microbes and their environment (e.g., temperature and mineral surfaces) affect SOC stocks (Sulman et al., 2018; Wieder et al., 2015). These results imply the need to improve soil biogeochemical modules in ESM land models and the observations used to constrain these models, because many reasonable assumptions can lead to a broad set of SOC stock change predictions. For example, ReSOM could be better constrained with targeted measurements of sorption and enzyme kinetic parameters in response to temperature perturbations, plant inputs, and other effects on microbial access to inputs (e.g., soil moisture, pH, and microbial allocation). Experiments that measure microbial responses to temperature over different timescales and consider the enzymatic capabilities of different microbial communities will help determine the shape and flexibility of microbial temperature responses across space and time. Predictions made by ESM-scale land models may benefit from using microbe- and chemical-explicit processes such as sorption and enzyme catalysis to estimate SOC accumulation and decomposition. Most importantly, long-term warming experiments used to validate soil C models, such as those reported in Crowther et al. (2016) and van Gestel et al. (2018), would benefit from ancillary measurements of as many factors (e.g., Q_{max} , MAT, NPP, MAP, pH, and other soil C pools) as possible to enable modelers to distinguish between models that make the same SOC stock predictions for different reasons.

We found that models developed to reproduce observed SOC spatial gradients may be inadequate for predicting transient temperature responses, in part because the effects on SOC stocks of some chemical and biological processes are indistinguishable at steady state. Different combinations of reasonable assumptions about microbial and mineral temperature sensitivity resulted in a wide range of SOC stock changes. Although many soil C models have considered and incorporated explicit assumptions about microbial temperature sensitivity (Abramoff et al., 2017, 2018; Allison et al., 2010; Finzi et al., 2015; German et al., 2012; He et al., 2015; Lawrence et al., 2009; Sistla et al., 2014; Sulman et al., 2014; Wang et al., 2013; Wieder et al., 2013), there are fewer models that consider the temperature sensitivity of mineral sorption (Dwivedi et al., 2017; Huang et al., 2018; Riley et al., 2014; Tang & Riley, 2015). The wide range of SOC stock changes predicted by varying only mineral sorption assumptions implies that the temperature sensitivity of sorption may be just as important as that of microbial activity in determining total C stock changes with warming.

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