Matters arising

Model uncertainty obscures major driver of soil carbon

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Understanding the formation and stabilization mechanisms of soil organic carbon (SOC) is important for managing land carbon (C) and mitigating climate change. Tao et al.[1] reported that microbial C use efficiency (CUE) is the primary determinant of global SOC storage and that the relative impact of plant C inputs on SOC is minor. Although soil microbes undoubtedly play an important role in SOC cycling, we are concerned about the robustness of the approach taken by Tao et al.[1]. The potential biases in their analyses may lead to misleading, model-dependent results.

An important piece of evidence in support of an empirical relationship between CUE and SOC stems from a meta-analysis based on 132 paired CUE and SOC measurements. Tao et al.[1] applied a linear mixed-effects model to this dataset that included CUE, mean annual temperature (MAT), soil depth and random effects and explained 55% of the variation in the log-transformed SOC (Fig. 2a and Extended Data Table 1 in Tao et al.[1]). In their linear mixed-effects model, C inputs to soil were not included despite the authors acknowledging past empirical and theoretical evidence for a major role. To demonstrate that C inputs can also drive SOC variation in their dataset, we extracted net primary production (NPP) from the globally gridded MODIS[2] for each soil-sampling location and used it as a first-order proxy for soil C inputs following ref. 1. By replacing CUE with NPP in the authors' linear mixed-effects model, we explained a larger proportion of the variation in SOC, namely, 71% with NPP compared with 55% with CUE (Table 1). This finding suggests that the empirical results of Tao et al.[1] may not be robust to the inclusion of other variables and raises questions about the importance of CUE in explaining SOC variations.

Tao et al.[1] further present results from a parameter sensitivity analysis of a process-oriented model, which showcase a causal and dominant relationship between CUE and SOC (Fig. 4 in Tao et al.[1]). To address uncertainties in model structure and parameters that impede robust model predictions, the authors used a comprehensive model-data-assimilation approach to calibrate a selection of 23 parameters of a SOC model based on a global dataset of SOC measurements. The calibrated SOC model was then used to quantify the sensitivity of SOC predictions to a selection of potential drivers of SOC, that is, by varying their values around the optimal or prescribed values one by one. We argue that the omission of C inputs and a microbial parameter shown to critically affect the sensitivity of SOC to changes in C inputs in microbial-explicit SOC models in the set of optimized parameters raises doubts about the robustness of the findings of the sensitivity analysis.

First, Tao et al.[1] assumed a model structure that may inherently predispose their analyses to suggest a low importance of C inputs on steady-state SOC. In particular, the chosen model represents the rate of microbial turnover as a linear function of microbial biomass (that is, 'density-independent', with exponent $\beta = 1$; unless otherwise specified, β refers to the exponent of microbial turnover rate in this study), as opposed to a potential super-linear function (that is, 'density-dependent', with $\beta > 1$), as suggested in past studies[3–5]. Without this density-dependent microbial turnover, a given change in C inputs may result in a proportional change in the microbial biomass pool and a consequent insensitivity of the SOC pool. This type of model is inconsistent with several empirical and theoretical results showing that steady-state SOC pools are sensitive to changes in C inputs, and that this can be better simulated using SOC models with density-dependent microbial turnover[3]. Figure 1 shows that a switch from density-independent ($\beta = 1$) to density-dependent ($\beta > 1$) microbial turnover greatly increases the impact of C input to SOC in the MIcrobial-MIneral Carbon Stabilization (MIMICS) model[6] (Fig. 1a–c) and in the Millennial model[4] (Fig. 1d–f).

Table 1 | NPP may explain more variation in SOC storage than microbial CUE

Predictors	$\log_{10}$(SOC)		
	Estimates	CI	P
(Intercept)	1.37	1.24–1.50	<0.001
NPP	0.25	0.19–0.32	<0.001
MAT	−0.10	−0.16 to −0.04	0.002
Depth	−0.14	−0.19 to −0.09	<0.001
Random effects			
σ^2	0.05		
$\tau_{00\ \text{Source}}$	0.05		
ICC	0.50		
N_{Source}	15		
Observations	121		
Marginal R^2/conditional R^2	0.417/0.709		

We performed the same mixed-model regression analyses as in Tao et al.[1] but also explored the importance of NPP (g C m^{-2} year^{-1}) as a first-order proxy for C inputs to the soil. In both this study and in Tao et al.[1], the linear mixed-effects model also includes MAT (°C) and soil depth (cm), and the study sources were added as the random effects. To ensure the comparability of coefficients across all three explanatory variables (that is, NPP, MAT and depth) in the results, we applied standardization using the Z-score method, which maintains the explanatory power of the model. CI and P indicate 95% confidence interval and statistical significance, respectively, and ICC is the intraclass correlation coefficient.

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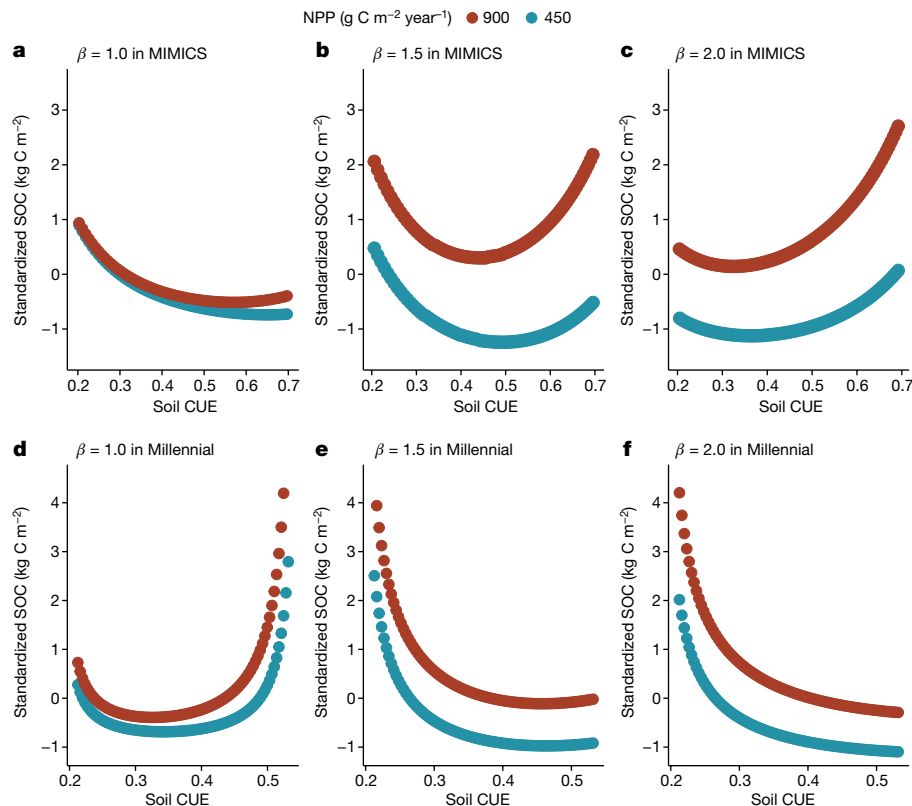NPP (g C m⁻² year⁻¹) ● 900 ● 450

Fig. 1 | Sensitivity of the CUE–SOC relationship to the inclusion of density-dependent microbial turnover in process-based soil models. a–f, Predicted SOC stocks at steady state from the MIMICS (**a–c**) and Millennial (**d–f**) microbial-explicit SOC models using a range of density-dependent microbial turnover exponent (β) values, NPP and microbial CUE. Simulations for a mean annual temperature of 20 °C, soil clay content of 20% and litter lignin-to-nitrogen ratio of 10. The SOC values in each plot were standardized using the Z-score method to ensure comparability.

Although Tao et al.[1] explored the potential need for a sub-linear exponent on the rate of enzyme production—that is, enzyme production ≈ (microbial biomass)$^{\beta_{enz}}$, in which $0 < \beta_{enz} < 1$—in their SOC model (here 'β_{enz}' is used to distinguish it from the exponent β), this modification is functionally and theoretically distinct from the density-dependent microbial turnover with $\beta > 1$ proposed in earlier work[3]. We conducted a sensitivity analysis[7] to determine whether SOC behaved the same if an exponent was assigned to enzyme production ($0 < \beta_{enz} < 1$, as in ref. 1) versus microbial turnover ($1 < \beta < 2$, as in ref. 3). We found that the sensitivity of SOC to a variation of +/−10% of CUE is equal to 1.3 when β and β_{enz} are both equal to 1 but is much less when the exponents are not equal to 1: 0.48 and 0.73 for a 50% change in β_{enz} and β on turnover, respectively. On the other hand, the sensitivity of SOC to a variation of +/−10% of C input is equal to 0 when β and $\beta_{enz} = 1$, 0.52 when β_{enz} is modified by 50% and 0.34 when β on turnover is modified by 50%. This indicates that the results of Tao et al.[1] are very contingent on the assumed model structure. If β associated with turnover is not found with observations to be mostly 1 (as for enzyme production), then a lower sensitivity of SOC to CUE and a greater sensitivity of SOC to C input may have been observed. Besides, the exploration of the exponent β_{enz} by Tao et al.[1] is only in the reply to the reviewers and there is not a sufficient description of how the results were obtained.

Second, Tao et al.[1] approximated C inputs to the soil using NPP from predictions of a land surface model. NPP is a notoriously uncertain C flux and it is not clear to what extent NPP from land surface models actually reflects C inputs to soil and its spatial variations[8]. The use of the interannual variation in NPP from a single land surface model to characterize uncertainty in C inputs, as done in the optimization in this study, falls arguably short to characterize the true uncertainty. Its

implications for the outcome of the study remain elusive, representing a source of uncertainty. The inclusion of C input[9] as a parameter for optimization at the site scale rather than the inclusion of NPP as an environmental driver for the global extrapolation[1] of site-specific optimized parameters could be a way forward.

In summary, we highlight several statistical and process-based model assumptions that may have biased the overarching conclusion that CUE is the dominant control on spatial variation of SOC. We argue that changes in soil microbial CUE itself are influenced by environmental factors, including C inputs as well as the quality of litter[10,11]. The findings of Tao et al.[1] contradict numerous empirical studies that report that changes in plant inputs substantially alter SOC (for example, refs. 12–14). We believe that further examination of statistical and process-based model structures is needed to demonstrate the robustness of the conclusions presented. Moreover, future research efforts should be allocated towards investigating several mechanisms of SOC stabilization and loss, rather than solely focusing on CUE.

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