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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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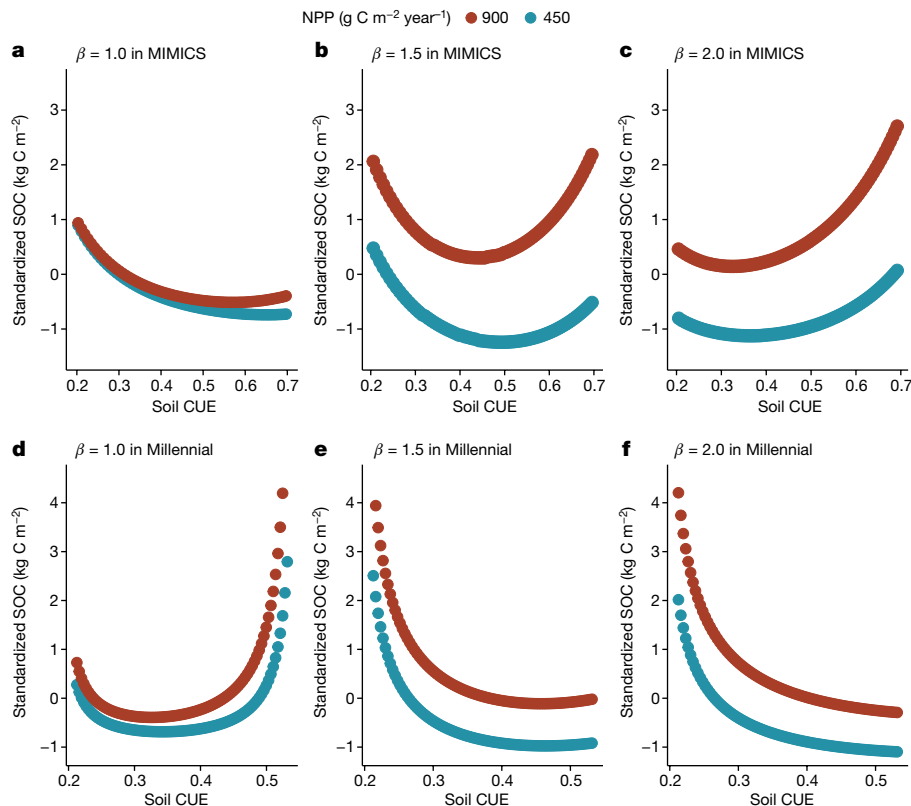
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Fig. 1 | Sensitivity of the CUE–SOC relationship to the inclusion of density-dependent microbial turnover in process-based soil models. a–f, Predicted SOC stocks at steady state from the MIMICS (**a–c**) and Millennial (**d–f**) microbial-explicit 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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Matters arising

Reply to: Model uncertainty obscures major driver of soil carbon

Feng Tao[1,2], Benjamin Z. Houlton[1,3], Serita D. Frey[4], Johannes Lehmann[5], Stefano Manzoni[6], Yuanyuan Huang[7], Lifen Jiang[5], Umakant Mishra[8,9], Bruce A. Hungate[10,11], Michael W. I. Schmidt[12], Markus Reichstein[13], Nuno Carvalhais[13,14], Philippe Ciais[15], Ying-Ping Wang[16], Bernhard Ahrens[13], Gustaf Hugelius[6], Toby D. Hocking[11], Xingjie Lu[17], Zheng Shi[18,19], Kostiantyn Viatkin[5], Ronald Vargas[20], Yusuf Yigini[20], Christian Omuto[20], Ashish A. Malik[21], Guillermo Peralta[20], Rosa Cuevas-Corona[20], Luciano E. Di Paolo[20], Isabel Luotto[20], Cuijuan Liao[2], Yi-Shuang Liang[2], Vinisa S. Saynes[20], Xiaomeng Huang[2✉] & Yiqi Luo[5✉]

REPLYING TO: X. He et al. *Nature* https://doi.org/10.1038/s41586-023-06999-1 (2024).

In the accompanying Comment[1], He et al. argue that Tao et al.[2] overestimated the role of microbial carbon use efficiency (CUE) in global soil organic carbon (SOC) storage because carbon inputs were neglected in our data analysis. They also suggest that our big data analysis could be biased and model-dependent. Their argument is based on a different choice of independent variables in the data analysis and sensitivity analysis of two process-based models without being informed by observations other than that used in our study. We agree that both carbon inputs and outputs (as mediated by microbial processes) matter, and their influences on SOC could vary in models with different structures. By fusing big SOC data with models, the data-assimilation approach used by Tao et al.[2] reconciles inter-model disagreements and reveals converging results in assessing the relative contributions of different processes to global SOC storage. Thus, the claims of He et al. need to be taken as an alternative, unproven hypothesis until empirical data support their specific parameterization. Here we show that another assessment of global data products does not support He et al.'s arguments and further study is essential.

The higher explanatory power of carbon input than microbial CUE for SOC storage envisaged by He et al. does not hold at the global scale when more data are considered (Table 1). He et al. proposed that carbon input is potentially more important than microbial CUE by using the net primary production (NPP) as carbon input to explain the spatial variation of SOC at the 132 datasets used in our meta-analysis. However, the statistical models in Tao et al.[2] were not applied to evaluate the relative importance of either CUE or NPP for SOC but to determine whether microbial CUE is positively or negatively correlated with SOC. This issue raised by He et al. might become relevant if NPP obscures the CUE–SOC relationship to the extent of changing its direction. In Supplementary Table 3, Tao et al.[2] showed that including NPP in a mixed-effects model does not influence the positive CUE–SOC correlation.

Moreover, NPP may have high explanatory power for SOC across these 132 local sites but not at the global scale. We used data products from different sources to test the CUE–SOC and NPP–SOC relationships at the global scale. We extracted global maps of NPP from a MODIS-based product[3] and CUE from PRODA-retrieved results (Fig. 3b of Tao et al.[2]). To avoid potential influence derived from data assimilation that may inherently strengthen the CUE–SOC relationship, we did not use the SOC map retrieved by PRODA but instead five other independent products, namely, SoilGrids250m[4], WISE30sec[5], HWSD[6], NCSCD[7] and FAO-GSOC[8]. Because NCSCD only has the SOC map for permafrost regions, we gap-filled regions outside permafrost for NCSCD with WISE30sec data. We found that CUE explains more spatial variation of SOC (21%) than NPP (4%) at the global scale (Table 1). Indeed, the notion that NPP is a small factor in explaining SOC dynamics and spatial variation at regional and global scales has been well documented in the literature[9–11].

Process-based models can theoretically generate a range of patterns and predictions, as correctly argued by He et al. and well documented in the literature. However, models yield realistic predictions only after they are constrained by observations. He et al. used two models to examine varying sensitivities of SOC storage in response to changes in a parameter (β) that represents the density dependence of microbial mortality[12], arguing that SOC storage could be more sensitive to changes in NPP than microbial CUE under certain parameterizations. Indeed, generating such a pattern does not necessarily require introducing new parameters. The microbial model used by Tao et al.[2] could generate similar sensitivities for SOC storage in response to NPP with assuming that mortality is not density-dependent ($\beta = 1$; Fig. 1). SOC storage could show no response to doubled NPP when the turnover time (τ) of both enzyme (ENZ) and microbial biomass (MIC) is very short (for example, $\tau_{ENZ,decay} = 0.05$ years and $\tau_{MIC} = 0.2$ years; Fig. 1a).

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Table 1 | Microbial CUE explains more spatial variation of SOC storage than NPP at the global scale

		Intercept	CUE or NPP
$\log_{10}(\text{SOC}) \approx \text{CUE} + (1|\text{Data product})$; variance explained by mixed model: 21%			
Fixed effects	Estimates	1.26	0.18
	Standard error	0.044	8.24×10^{-4}
	t-value	28.68	220.93
	P	<0.0001	<0.0001
Random effects	Standard deviation	0.098	–
$\log_{10}(\text{SOC}) \approx \text{NPP} + (1|\text{Data product})$; variance explained by mixed model: 4%			
Fixed effects	Estimates	1.26	0.020
	Standard error	0.044	9.09×10^{-6}
	t-value	28.50	22.06
	P	<0.0001	<0.0001
Random effects	Standard deviation	0.099	–

We included five independent global SOC data products (that is, SoilGrids250m, WISE30sec, HWSD, NCSCD and FAO-GSOC) to assess the CUE–SOC and NPP–SOC relationships. We standardized CUE from the PRODA-retrieved global maps (Fig. 3b in Tao et al.[2]) and NPP from remote-sensing data. Statistics shown in the table are standardized coefficients of CUE–SOC and NPP–SOC relationships in a mixed-effects model. CUE or NPP was set as the fixed effect to predict SOC content. SOC data-product sources were set as the random effect. We assumed random intercepts in all regressions. The total sample size $n_{sample} = 222{,}646$ and the random effect size $n_{data\,product} = 5$.

Alternatively, SOC storage could also dramatically increase with doubled NPP when the turnover time of either of these two pools is higher (for example, $\tau_{ENZ,decay}$ increases from 0.05 years to 0.50 years (Fig. 1a–c) or τ_{MIC} increases from 0.2 years to 1.5 years (Fig. 1d–f)). Nevertheless, after assimilating the SOC data with the microbial model, microbial CUE emerged to be more important than NPP for global SOC storage. It is the Bayesian framework used in our study by means of data assimilation that identified the most probable mechanism among these diverse alternatives. Thus, an analysis in which data assimilation is conducted to estimate the most realistic β value is essential before claiming that such a parameter could overrule the importance of microbial CUE for SOC storage.

Diverging simulations by structurally different models could largely be reconciled by applying data assimilation with the same datasets. In the Peer Review File of Tao et al.[2], results from data assimilation using three structurally different models (one first-order kinetic model, that is, CLM5, and two microbial models) all showed that estimated parameters related to microbial CUE are more important than NPP in determining global SOC. Among these models, the first-order kinetic model (CLM5) simulates the strongest possible sensitivity of SOC to carbon input (that is, a 1% increase in NPP leads to a 1% increase in SOC storage). However, changes in the estimated transfer coefficients, which are conceptually related, at least partially, to microbial CUE, exhibited more predominant effects on SOC simulations than carbon input. Although uncertainties still exist among structurally different models even after data assimilation, our study showed the possibility that using
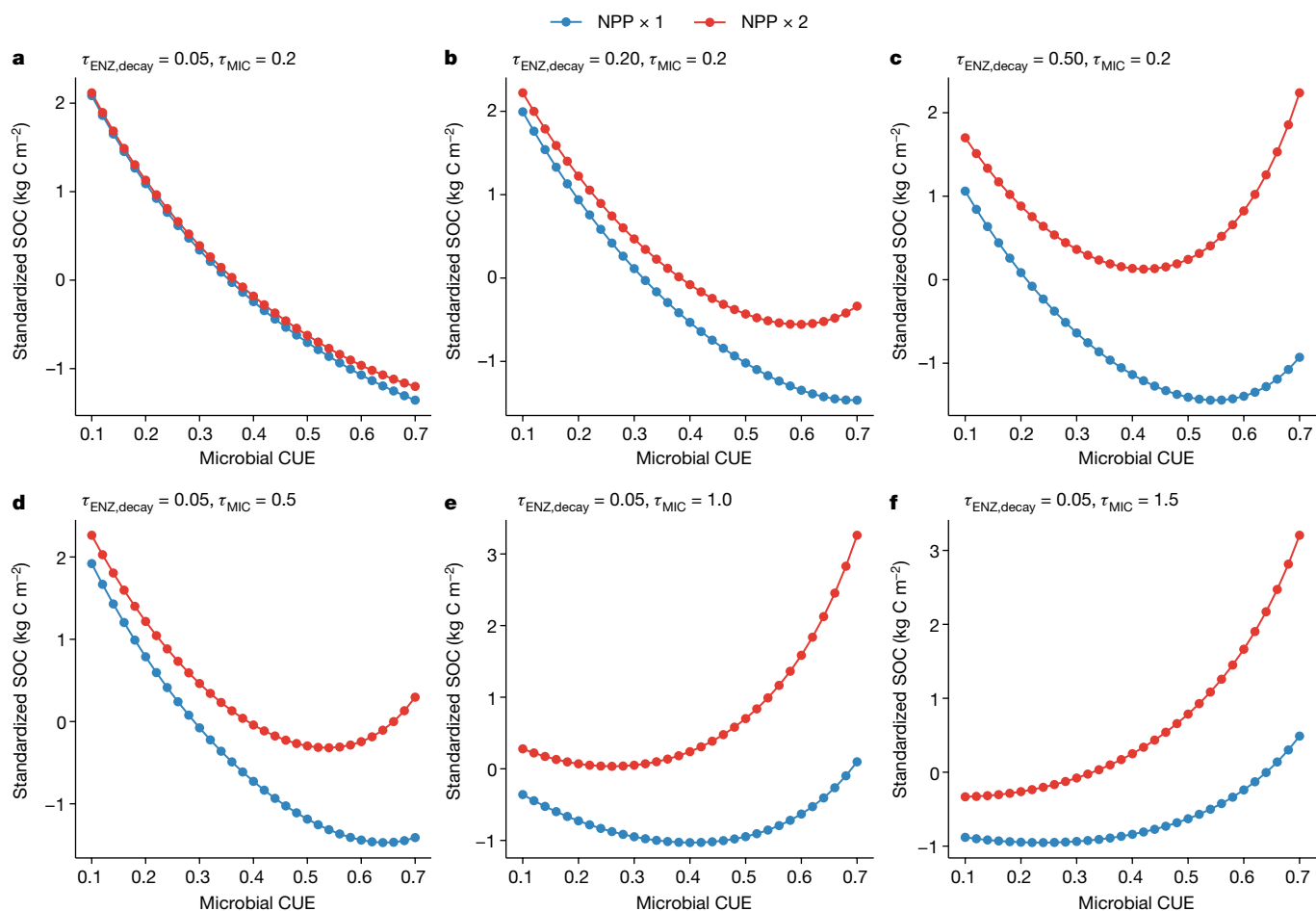

Fig. 1 | Varying sensitivity of SOC storage to doubled NPP under different combinations of parameter values with the microbial model used by Tao et al.[2]. a–f, We chose different values for the turnover time (in years) for enzyme ($\tau_{ENZ,decay}$) and microbial biomass (τ_{MIC}) carbon pools in the microbial model used by Tao et al.[2] at one site and doubled the magnitude of NPP (red curves) in the model simulation for each set of parameterizations. Different panels in this figure present how the relation of CUE and SOC storage changed with increased NPP. The SOC values were standardized using the Z-score method to be comparable with the results shown in He et al.[1].

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big data to inform models can reconcile SOC simulations of different models and gain a converging understanding of the soil carbon cycle.

Estimates of NPP by different process-based models and data products indeed remain uncertain, as pointed out by He et al. Although the uncertainty in NPP might influence CUE–SOC relationships, our analysis showed that variation from −10% to +10% of the NPP values had much less effect on SOC than microbial CUE (Fig. 4b of Tao et al.[2]. Nevertheless, we greatly appreciate the suggestion to include carbon input in data assimilation for parameter optimization. We thus encourage the scientific community to conduct data-assimilation studies to constrain all parameters, including mortality-related and NPP-related ones, that may influence the CUE–SOC relationships. In the future, a better understanding of the global soil carbon cycle will be gained by investigating several processes, such as carbon input, SOC stabilization and loss, as well as microbial processes. Meanwhile, it is critical to test various processes represented by structurally different models against observational data. A tool such as PRODA will help reconcile field observations and theoretical understanding as encoded in models and quantitatively assess the relative importance of various processes across different scales.

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