Reply to: Beyond microbial carbon use efficiency

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Abstract

In their commentary[1], Xiao et al. cautioned that the conclusions on the critical role of microbial carbon use efficiency (CUE) in global soil organic carbon (SOC) storage in a paper by Tao et al. (2023)[2] might be too simplistic. They claimed that Tao et al.'s study lacked mechanistic consideration of SOC formation and excluded important datasets. Xiao et al. brought up important points, which can be largely reconciled with our findings by understanding the differences in expressing processes in empirical studies and in models.

Main

Mechanistic understanding of complex processes from empirical research is usually translated into mathematical models with some level of simplification. For example, processes involved in SOC stabilization and persistence, as brought up by Xiao et al., were considered by the model and evaluated together with microbial CUE for their relative importance to global SOC storage in Tao et al. (2023). The mechanisms for stabilizing necromass in soils with soil minerals are represented as the non-microbial carbon transfer by various chemical and physical processes (see carbon flows in Extended Data Fig. 3 in Tao et al. (2023)). Parameter $a_{mSOC,MIC}$ represents the fraction of microbial necromass that is stabilized as mineral-associated SOC via organo-mineral interactions (i.e., the *in vivo* pathway of stabilization; see ref[3]); parameter $a_{mSOC,LL}$ indicates the fraction of lignin litter that is directly stabilized as SOC with minerals and without going through microbial processes (i.e., the *ex vivo* pathway of stabilization; see Supplementary Table 6 in Tao et al. 2023). The organic compounds associated with microbial products and necromass that Xiao et al. suggested to be stabilized against decomposition through various chemical and physical processes are expressed in the model by decomposition coefficients, K_i. The inverses of K_i represent the persistence of various organic compounds in soil. Tao et al. (2023) compared the relative importance of non-microbial carbon transfer and decomposition coefficients with microbial CUE. The latter was found to be more important than the formers in determining SOC storage and its distributions at the global scale.

The dominant role of CUE in global SOC storage emerging from Bayesian inference by Tao et al. (2023) does not mean that CUE is the sufficient process. But it is likely a necessary process as soil might have very little organo-mineral interactions without microbial metabolites. Our current understanding of stabilization mechanisms is highly fragmented from empirical research, which makes model representation very challenging. The inferred role of CUE in global SOC storage from our PRODA approach should be further tested by more studies. We expect that not only other processes may be dominant in individual empirical studies, but that the relationship of CUE and SOC may vary among individual laboratory or site case studies.

We agree with Xiao et al. that causal relations between CUE and SOC need to be supported by more mechanistic empirical evidence and modelling studies. Tao et al. (2023) showed both statistical (from the meta-analysis) and process-based (from the microbial model results) evidence that microbial CUE promotes SOC storage at the global scale. First, Tao et al. (2023) applied mixed-effects modeling to ensure the statistical rigor of the meta-analysis. The positive CUE-SOC relationship was robust after considering the influence of various predictors (e.g., temperature, soil depth, etc.) and their potential interactions (Extended Data Table 1 in Tao et al. 2023). Second, Tao et al. (2023) investigated relationships among microbial CUE, microbial biomass, and non-microbial biomass storage (i.e., the remaining amount of organic carbon after excluding microbial biomass; see Supplementary Table 2 in Tao et al. 2023). The results showed that a high CUE accompanied not only high microbial biomass carbon, but also high non-microbial biomass carbon. Third, the above findings in the meta-analysis were further verified by the results of the microbial model after data assimilation (Extended Data Table 2 and Supplementary Tables 3-4 in Tao et al. 2023). While the microbial model can theoretically generate positive, negative, or null relationships between CUE and SOC, as noticed by Xiao et al., Tao et al. (2023) applied Bayesian data assimilation to identify the most probable regulatory pathway of CUE to SOC storage. That is, microbial partitioning of carbon toward microbial growth enhances SOC accumulation via microbial by-products and necromass. We acknowledge that this is inferred and not an iron-clad proof. The relationship of CUE and SOC might have complex interactions with other processes even though the result shown in Tao et al (2023) is an important step forward to mechanistically understand SOC formation at the global scale and identify what needs to be investigated in the future.

We greatly appreciate the point made by Xiao et al. that more data, especially from tropical and arid regions, are needed to avoid biased analysis. We welcome any more field-measured microbial CUE and SOC data to further test the CUE-SOC relationship. We thank Xiao et al. for bringing up the point that soil pH may alter the CUE-SOC relationship as shown in Malik et al. (2018). Including the data from Malik et al. (2018)[4] with considering pH as a fixed effect in the meta-analysis does not influence the overall positive CUE-SOC relationship (Table 1). Moreover, the Fig. 2 in Xiao et al. used a linear regression between CUE and SOC without considering any other factors, such as sampling depth, temperature, and methodological differences across studies. These factors influence the CUE-SOC relationship and thus result in their weak correlation. When discussing the relationship between two variables, accounting for potentially confounding factors is essential in a statistical analysis. Tao et al. (2023) applied the mixed-effects models that accounted for the above factors to explore the relationship between microbial CUE and SOC. As a result, the positive CUE-SOC relationship explains 55% variation in observations. Nonetheless, Tao et al. (2023) discussed caveats of the meta-analysis. The PRODA analysis of 57,267 globally distributed vertical SOC profiles complemented the latter to avoid potential regional biases.

Establishing a globally causal link between CUE and SOC and evaluate the relative importance of soil carbon processes needs leveraging the potentials of empirical studies, process-based models, and big data. We acknowledge that the model we used, as any models, remains a simplified representation of real-world complexities of the soil system. Indeed, navigating sophisticated observations to a reasonable abstraction for useful predictions is part of the essence of modelling. Meanwhile, we agree with Xiao et al. that more sophisticated empirical measurements guarantee better understanding of SOC formation. While models allows us to holistically evaluate soil as a system and the relative importance of their components, data from field measurements potentially provide direct evidence on key relationships in soil carbon cycle. Tao et al. (2023) developed the PRODA approach to effectively incorporate process-based models with big data to gain emerging understanding of global SOC storage. To our knowledge, the relative importance of the seven components of soil carbon dynamics presently cannot be experimentally evaluated in any laboratory and field studies. PRODA provides a common tool for both modellers and experimentalists in reconciling mechanistic understanding in fields and theoretical reasoning in modelling. New findings and relationships revealed by the PRODA approach will further stimulate new experimental studies in laboratory and field, and improvement of models.

Methods

All the data, statistical methods, and the microbial model have been described in Tao et al. (2023) and can be publicly accessed via https://www.nature.com/articles/s41586-023-06042-3.

Competing interests:

The authors declare no competing interests.

Author contributions:

F. T. and Y. L. drafted the reply. All authors contributed to the text and approved the final version.

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Table 1 | Unstandardized coefficients of CUE-SOC relationship in the mixed-effects model including data from Malik et al. (2018). CUE, depth, mean annual temperature (MAT), and pH were set as the fixed effects to logarithmic SOC content. The study source was set as the random effect. We set random intercepts with common slopes to test the CUE-SOC relationship. The total observation size n_{sample} = 295; the random effects size n_{study} = 17.

		Intercept	CUE	Depth	MAT	pH
$log10(SOC) \sim CUE + Depth + MAT + pH + (1\|Study\ Source)$ variance explained by mixed model: 50%						
Fixed Effects	Estimates	1.47	0.76	-0.019	0.012	-0.046
	Std. Error	0.15	0.16	0.0034	0.0053	0.019
	t value	10.02	4.82	-5.70	2.32	-2.50
	P	<0.0001	<0.0001	<0.0001	0.021	0.013
Random Effects	Standard Deviation	0.22	NA	NA	NA	NA