1	Beyond microbial carbon use efficiency
2	Ke-Qing Xiao ^{1, *} , Chao Liang ² , Zimeng Wang ³ , Jingjing Peng ⁴ , Yao Zhao ⁵ ,
3	Ming Zhang ⁶ , Mingyu Zhao ⁷ , Yong-Guan Zhu ^{1,*} , Caroline L. Peacock ⁸
4	¹ State Key Lab of Urban and Regional Ecology, Research Center for Eco-
5	Environmental Sciences, Chinese Academy of Sciences, Beijing, China
6	² Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang, China
7	³ Department of Environmental Science and Engineering, Fudan University, Shanghai
8	200438 China
9	⁴ College of Resources and Environmental Sciences, China Agricultural University,
10	Beijing, 100193, China
11	⁵ State Key Laboratory of Environmental Criteria and Risk Assessment,
12	Chinese Research Academy of Environmental Sciences, Beijing, China
13	⁶ State Key Laboratory of Agricultural Microbiology, College of Resources and
14	Environment, Huazhong Agricultural University, Wuhan 430070, China
15	⁷ Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and
16	Geophysics, Chinese Academy of Sciences, Beijing, China
17	⁸ School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK
18	
19	*corresponding: <u>kqxiao@rcees.ac.cn, ygzhu@rcees.ac.cn</u> ,
20	
21	This paper is a non-peer reviewed preprint submitted to EarthArXiv, and it has been

submitted to Nature for peer review.

Microbial carbon use efficiency (CUE) is defined as the proportion of microbial 23 biomass growth C versus substrate C uptake, and thus provides a useful measure of 24 microbially driven accumulation and loss of soil organic carbon (SOC)¹. In a recent 25 study published in Nature², the authors use a data-driven machine learning 26 approach to conclude that CUE promotes global SOC storage based on a positive 27 correlation between CUE and SOC content and that based on sensitivity analysis 28 CUE is at least four times as important as six other evaluated factors, namely plant C 29 inputs, C input allocation, non-microbial C transfer, substrate decomposability, 30 31 environmental modifications and vertical transport. We agree with the authors that there is no consensus in the scientific community about the relationship between 32 CUE and SOC, and that increasingly used big data methods offer an opportunity to 33 synthesize and potentially generate new insights from multiple data aggregation. We 34 argue however, that their study excludes important data sets and lacks mechanistic 35 consideration of the complexities of SOC formation, such that their conclusions need 36 to be clarified. 37

We posit that stabilization matters more than production (CUE) for SOC 38 formation. The accumulation and persistence of SOC is affected by multiple factors 39 including biological, chemical and physical processes ³⁻⁵. Microbial use of carbon 40 input represents the very primary stage of SOC formation (Fig. 1). Microbial 41 42 necromass may possess enhanced stability against decomposition (the microbial carbon pump)⁶, but research also increasingly suggests that the production of 43 microbial biomass and consequently necromass leads to a set of organic 44 compounds that are themselves stabilized against decomposition through a variety 45 of chemical and physical processes (e.g., high activation energies for further 46 decomposition and/or physico-chemical protection with mineral matrices) ^{3,4,7,8} (Fig. 47

1). For example, it is found that necromass accumulation is not solely dependent on 48 CUE but is strongly dependent on mechanisms preserving C components, most 49 notably soil mineral content, with necromass accumulation occurring in soils with 50 high clay-sized fraction ⁹. In other work, CUE is found to be negatively correlated 51 with persistent mineral-associated SOC, suggesting that necromass production is 52 not the primary driver of SOC persistence ⁷. In this work stimulation of microbial 53 growth by high-quality litter enhances SOC decomposition, offsetting the positive 54 effect of litter quality on SOC stabilization ⁷. As such, CUE and SOC are decoupled 55 rather than coupled in some environments ^{9,10}. This decoupling is also reflected in 56 Extended Data Fig. 5c from Tao et al.², where there is no significant correlation 57 between CUE and SOC in soil > 100 cm. 58



59

Figure 1. Conceptual diagram of microbial carbon use efficiency (CUE) and the
 stabilization mechanisms of soil organic carbon (SOC). MCP, microbial carbon
 pump; MnCP, mineral carbon pump; MAOC, mineral associated organic carbon;

63 POC, particulate organic carbon.

It should be cautioned that correlation does not equal causation. In Tao et al.², 64 model-derived CUE is an emergent property of the whole system from SOC profiles, 65 and it is therefore not surprising that the calculated CUE is correlated with SOC (as 66 in their Fig. 2b). Some important factors like temperature have not been 67 parameterized properly in the model, then the conclusion that temperature does not 68 have a big impact on SOC through the sensitivity analysis of this model becomes 69 doubtful. A microbial model was used by the authors to examine the CUE-SOC 70 relationship, yet the results (their Extended Data Fig. 4) clearly show that CUE-SOC 71 72 correlation depends on the parameter chosen and can be either positively or negatively related. Even though a positive relationship between CUE and SOC may 73 exist, we urge that more sophisticated empirical measurements should be done 74 before a globally causal link between CUE and SOC can be established. 75



Figure 2 The correlation between CUE and SOC for the data of 132 measurements:
(a) correlation between CUE and SOC, (b) correlation between CUE and log (SOC).
Public raw data from Supplementary Table 1 of Tao et al., 2023.

80

We also point out that data selection is critical for correlation results. We 81 argue that their meta-analysis needs more data in tropical and arid regions as well 82 as clay soils (their Supplementary Fig. 4), while we posit that results based on 132 83 measurements are somewhat premature for a global assessment. Actually the 84 correlation between CUE and SOC for the data of 132 measurements is very weak 85 $(R^2=0.11)$, and the correlation between CUE and log (SOC) is even weaker 86 87 $(R^2=0.07)$ (Fig. 2). This strongly suggests that while CUE and SOC may be related, CUE does not play a major role in determining SOC. Moreover, the authors state 88 89 that their results agree with findings from a landscape-scale pattern across the United Kingdom¹¹. Whilst the data from that study (168 measurements) are not 90 included in the 132 measurements for meta-analysis by Tao et al.² in their Fig. 2a, 91 that study clearly states that soil pH is an important factor and the "CUE-SOC 92 relationship broke down below the threshold pH (6.2)" (Fig. 2a from Malik et al., 93 2018) ¹¹. 94

Overall, we argue that while this study makes an important contribution 95 towards our understanding of the links between CUE, microbial necromass and SOC 96 persistence, it is premature to establish a globally robust causal relationship between 97 CUE and SOC. We caution inferring mechanisms or causality from large datasets 98 99 ^{12,13}. We posit that the analysis and conclusion would benefit from more 100 consideration of mechanistic processes in SOC formation and caution when dealing with big data. While the strides made in data science have undoubtedly propelled our 101 understanding in many fields, including soil science, we must exercise caution not to 102 oversimplify intricate systems. Just as we still respect and apply Newton's laws when 103 studying the movements of celestial bodies, we must acknowledge and understand 104 the fundamental and intricately linked biological, chemical and physical mechanisms 105

that drive soil carbon dynamics. To lean too heavily on data-driven correlations

107 without a comprehensive understanding of causation is akin to ignoring the

108 foundational intricacies that govern the system. As Leonardo da Vinci wisely

remarked, 'We know more about the movement of celestial bodies than about the

soil underfoot.' We urge to not forget the inherent complexities of the soil system,

even as we apply advanced methodologies to unravel its secrets.

112

113 Data availability

114 All data are public.

115

116 **Contributions**

117 The original idea was formulated by K.-Q. X., C. L., Z. W. and Y-G. Z. K-Q.X. wrote

the manuscript, with contributions from all other authors. All authors reviewed and

approved submission of the final manuscript.

120

121 Competing interests

122 The authors declare no competing interests.

123

124 Acknowledgements

125 KQX is funded by the Hundred Talents Program of the Chinese Academy of

126 Sciences. CLP acknowledges support from the European Research Council (ERC)

under the European Union's Horizon 2020 research and innovation programme

128 (Grant agreement No. 725613 MinOrg,) and Royal Society Wolfson Research Merit

129 Award (WRM/FT/170005).

130

131 **References**

132	1. Allison, S. D., Wallenstein, M. D. & Bradford, M. A. Soil-carbon response to
133	warming dependent on microbial physiology. Nat. Geosci. 3, 336-340,
134	doi:10.1038/ngeo846 (2010).
135	2. Tao, F. et al. Microbial carbon use efficiency promotes global soil carbon storage.
136	Nature 618 , 981-985, doi:10.1038/s41586-023-06042-3 (2023).
137	3. Liang, C., Schimel, J. P. & Jastrow, J. D. The importance of anabolism in microbial
138	control over soil carbon storage. Nat. Microbiol. 2, 17105,
139	doi:10.1038/nmicrobiol.2017.105 (2017).
140	4. Xiao, K. Q. et al. Introducing the soil mineral carbon pump. Nat. Rev. Earth
141	<i>Environ.</i> 4 , 135-136, doi:10.1038/s43017-023-00396-y (2023).
142	5. Ma, T. et al. Divergent accumulation of microbial necromass and plant lignin
143	components in grassland soils. Nat. Commun. 9, 3480, doi:10.1038/s41467-
144	018-05891-1 (2018).
145	6. Liang, C. & Balser, T. C. Microbial production of recalcitrant organic matter in
146	global soils: implications for productivity and climate policy. Nat. Rev.

147 *Microbiol.* **9**, 75-75, doi:10.1038/nrmicro2386-c1 (2011).

148 7. Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K. & Paul, E. The Microbial

149 Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter

decomposition with soil organic matter stabilization: do labile plant inputs form

151 stable soil organic matter? *Glob Chang Biol* **19**, 988-995,

152 doi:10.1111/gcb.12113 (2013).

153 8. Chen, Y. *et al.* Formation of soil organic carbon pool is regulated by the structure

of dissolved organic matter and microbial carbon pump efficacy: A decadal

- study comparing different carbon management strategies. *Glob Chang Biol*,
 doi:10.1111/gcb.16865 (2023).
- 9. Cai, Y. *et al.* Assessing the accumulation efficiency of various microbial carbon
 components in soils of different minerals. *Geoderma* 407, 115562,
- doi:10.1016/j.geoderma.2021.115562 (2022).
- 160 10. Craig, M. E. *et al.* Fast-decaying plant litter enhances soil carbon in temperate
- forests but not through microbial physiological traits. *Nat. Commun.* 13, 1229,
 doi:10.1038/s41467-022-28715-9 (2022).
- 163 11. Malik, A. A. *et al.* Land use driven change in soil pH affects microbial carbon
- 164 cycling processes. *Nat. Commun.* 9, 3591, doi:10.1038/s41467-018-05980-1
 165 (2018).
- 166 12. Derrien, D. *et al.* Current controversies on mechanisms controlling soil carbon
 167 storage: implications for interactions with practitioners and policy-makers. A
- review. Agron Sustain Dev **43**, 21, doi:10.1007/s13593-023-00876-x (2023).
- 169 13. Wadoux, A. M. J. C., Samuel-Rosa, A., Poggio, L. & Mulder, V. L. A note on
- knowledge discovery and machine learning in digital soil mapping. *Eur J Soil*
- 171 *Sci* **71**, 133-136, doi:10.1111/ejss.12909 (2020).

172