

1 **Global variation of soil microbial carbon-use efficiency in relation to growth temperature**
2 **and substrate supply**

3 Yang Qiao¹, Jing Wang¹, Guopeng Liang², Zhenggang Du¹, Jian Zhou¹, Chen Zhu¹, Kun
4 Huang¹, Xuhui Zhou¹, Yiqi Luo², Liming Yan^{1,*}, Jianyang Xia^{1,*}

5 ¹Tiantong National Field Observation Station for Forest Ecosystem & Center for Global Change
6 and Ecological Forecasting, School of Ecological and Environmental Sciences, East China Normal
7 University, Shanghai 200062, China

8 ²Center for Ecosystem Science and Society, Northern Arizona University, Arizona, Flagstaff, AZ
9 86011, USA

10 **Correspondence to:** Liming Yan

11 Mailing address: School of Ecological and Environmental Sciences, East China Normal University,
12 500 Dongchuan Road, Shanghai 200062, China

13 Email: lmyan@des.ecnu.edu.cn

14

15 **Supplemental Materials**

16 **Table S1.** Papers from which the dataset was extracted.

- 17 1. Ågren, G.I., Bosatta, E., Magill, A.H., (2001) Combining theory and experiment to understand
18 effects of inorganic nitrogen on litter decomposition. *Oecologia* **128**, 94-98.
- 19 2. Anderson, T.-H., Domsch, K.H., (1986) Carbon assimilation and microbial activity in soil.
20 *Zeitschrift für Pflanzenernährung und Bodenkunde* **149**, 457-468.
- 21 3. Andreasson F, Bergkvist B, Baath E (2009) Bioavailability of DOC in leachates, soil matrix
22 solutions and soil water extracts from beech forest floors. *Soil Biology & Biochemistry*, **41**,
23 1652-1658.
- 24 4. Behera B, Wagner GH (1974) Microbial Growth Rate in Glucose-Amended Soil1. *Soil Science*
25 *Society of America Journal*, **38**, 591-594.
- 26 5. Blagodatskaya, E., Blagodatsky, S., Anderson, T.-H., Kuzyakov, Y., (2014) Microbial growth
27 and carbon use efficiency in the rhizosphere and root-free soil, *PloS one*, p. e93282.
- 28 6. Brant JB, Sulzman EW, Myrold DD (2006) Microbial community utilization of added carbon
29 substrates in response to long-term carbon input manipulation. *Soil Biology & Biochemistry*,
30 **38**, 2219-2232.
- 31 7. Bremer EG, Kuikman PJ (1994) Microbial utilization of ¹⁴C[U]glucose in soil is affected by
32 the amount and timing of glucose additions. *Soil Biology & Biochemistry*, **26**, 511-517.
- 33 8. Chotte, J.L., Ladd, J.N., Amato, M., (1998) Sites of microbial assimilation, and turnover of
34 soluble and particulate ¹⁴C-labelled substrates decomposing in a clay soil. *Soil Biology and*
35 *Biochemistry* **30**, 205-218.

- 36 9. Dahlin AS, Witter E (1998) Can the low microbial biomass C-to-organic C ratio in an acid and
37 a metal contaminated soil be explained by differences in the substrate utilization efficiency and
38 maintenance requirements? *Soil Biology & Biochemistry*, **30**, 633-641.
- 39 10. Devevre OC, Horwath WR (2000) Decomposition of rice straw and microbial carbon use
40 efficiency under different soil temperatures and moistures. *Soil Biology & Biochemistry*, **32**,
41 1773-1785.
- 42 11. Dijkstra P, Dalder JJ, Selmants PC, Hart SC, Koch GW, Schwartz E, Hungate BA (2011a)
43 Modeling soil metabolic processes using isotopologue pairs of position-specific ¹³C-labeled
44 glucose and pyruvate. *Soil Biology & Biochemistry*, **43**, 1848-1857.
- 45 12. Dijkstra P, Salpas E, Fairbanks D *et al.* (2015) High carbon use efficiency in soil microbial
46 communities is related to balanced growth, not storage compound synthesis. *Soil Biology &*
47 *Biochemistry*, **89**, 35-43.
- 48 13. Dijkstra P, Thomas SC, Heinrich PL, Koch GW, Schwartz E, Hungate BA (2011b) Effect of
49 temperature on metabolic activity of intact microbial communities: Evidence for altered
50 metabolic pathway activity but not for increased maintenance respiration and reduced carbon
51 use efficiency. *Soil Biology & Biochemistry*, **43**, 2023-2031.
- 52 14. Elliott ET, Cole CV, Fairbanks BC, Woods LE, Bryant RJ, Coleman DC (1983) Short-term
53 bacterial growth, nutrient uptake, and ATP turnover in sterilized, inoculated and C-amended
54 soil: The influence of N availability. *Soil Biology & Biochemistry*, **15**, 85-91.
- 55 15. Farrell M, Hill PW, Wanniarachchi SD, Farrar JF, Bardgett RD, Jones DL (2011) Rapid
56 peptide metabolism: A major component of soil nitrogen cycling? *Global Biogeochemical*
57 *Cycles*, **25**.

- 58 16. Farrell, M., Macdonald, L.M., Baldock, J.A., (2015) Biochar differentially affects the cycling
59 and partitioning of low molecular weight carbon in contrasting soils. *Soil Biology and*
60 *Biochemistry* **80**, 79-88.
- 61 17. Fierer, N., Schimel, J.P., (2002) Effects of drying–rewetting frequency on soil carbon and
62 nitrogen transformations. *Soil Biology and Biochemistry* **34**, 777-787.
- 63 18. Fisk MC, Fahey TJ (2001) Microbial biomass and nitrogen cycling responses to fertilization
64 and litter removal in young northern hardwood forests. *Biogeochemistry*, **53**, 201-223.
- 65 19. Frey SD, Gupta VVSR, Elliott ET, Paustian K (2001) Protozoan grazing affects estimates of
66 carbon utilization efficiency of the soil microbial community. *Soil Biology & Biochemistry*, **33**,
67 1759-1768.
- 68 20. Frey SD, Lee J, Melillo JM, Six J (2013) The temperature response of soil microbial efficiency
69 and its feedback to climate. *Nature Climate Change*, **3**, 395.
- 70 21. Gilmour CM, Gilmour JT (1985) Assimilation of carbon by the soil biomass. *Plant and Soil*,
71 **86**, 101-112.
- 72 22. Guitong Li, Baogui Zhang, Baoguo Li (2003) Effect of straw pretreatment on soil microbial
73 biomass and respiration activity. *Chi . J. App l. Ecol.* 2003, 14(**12**) : 2225- 2228.
- 74 23. Hagerty SB, Van Groenigen KJ, Allison SD et al. (2014) Accelerated microbial turnover but
75 constant growth efficiency with warming in soil. *Nature Climate Change*, **4**, 903.
- 76 24. Haiyan Zhu, Yuanjin Bo, Xiangui Lin, Jianguo Zhu, Zubin Xie, Zhihong Cao, Huayong Zhang
77 (2003) Effects of exogenous lanthanum on carbon utilization of soil microorganisms. *Rural*
78 *Eco-Environment* 19(**1**) : 47- 49
- 79 25. Hart SC, Nason GE, Myrold DD, Perry DA (1994) Dynamics of gross nitrogen transformation
80 in an old-growth forest: the carbon connection. *Ecology*, **75**, 880-891.

- 81 26. Herron PM, Stark JM, Holt C, Hooker TD, Cardon ZG (2009) Microbial growth efficiencies
82 across a soil moisture gradient assessed using ^{13}C -acetic acid vapor and ^{15}N -ammonia gas.
83 *Soil Biology & Biochemistry*, **41**, 1262-1269.
- 84 27. Jiang, X., Deneff, K., Stewart, C.E., Cotrufo, M.F., (2016) Controls and dynamics of biochar
85 decomposition and soil microbial abundance, composition, and carbon use efficiency during
86 long-term biochar-amended soil incubations. *Biology and Fertility of Soils* **52**, 1-14.
- 87 28. Jones DL, Kielland K, Sinclair FL, Dahlgren RA, Newsham KK, Farrar JF, Murphy DV (2009)
88 Soil organic nitrogen mineralization across a global latitudinal gradient. *Global*
89 *Biogeochemical Cycles*, **23**.
- 90 29. Kallenbach, C.M., Grandy, A.S., Frey, S.D., Diefendorf, A.F., (2015) Microbial physiology
91 and necromass regulate agricultural soil carbon accumulation. *Soil Biology and Biochemistry*
92 **91**, 279-290.
- 93 30. Keiblinger, K.M., Hall, E.K., Wanek, W., Szukics, U., Hämmerle, I., Ellersdorfer, G., Böck,
94 S., Strauss, J., Sterflinger, K., Richter, A., Zechmeister-Boltenstern, S., (2010) The effect of
95 resource quantity and resource stoichiometry on microbial carbon-use-efficiency. *FEMS*
96 *Microbiology Ecology* **73**, 430-440.
- 97 31. Koranda, M., Kaiser, C., Fuchslueger, L., Kitzler, B., Sessitsch, A., Zechmeister-Boltenstern,
98 S., Richter, A., (2013) Seasonal variation in functional properties of microbial communities in
99 beech forest soil. *Soil Biology and Biochemistry* **60**, 95-104.
- 100 32. Ladd JN, Jocteurmonrozier L, Amato M (1992) Carbon turnover and nitrogen transformations
101 in an alfisol and vertisol amended with [^{14}C] glucose and [^{15}N] ammonium sulfate. *Soil*
102 *Biology & Biochemistry*, **24**, 359-371.

- 103 33. Lee, Z.M., Schmidt, T.M., (2014) Bacterial growth efficiency varies in soils under different
104 land management practices. *Soil Biology and Biochemistry* **69**, 282-290.
- 105 34. Lipson, D.A., Monson, R.K., Schmidt, S.K., Weintraub, M.N., (2009) The trade-off between
106 growth rate and yield in microbial communities and the consequences for under-snow soil
107 respiration in a high elevation coniferous forest. *Biogeochemistry* **95**, 23-35.
- 108 35. Liu, Y., Tay, J.-H., (2000) Interaction between catabolism and anabolism in the oxidative
109 assimilation of dissolved organic carbon. *Biotechnology Letters* **22**, 1521-1525.
- 110 36. Lundberg, P., Ekblad, A., Nilsson, M., (2001) ¹³C NMR spectroscopy studies of forest soil
111 microbial activity: glucose uptake and fatty acid biosynthesis. *Soil Biology and Biochemistry*
112 **33**, 621-632.
- 113 37. Nguyen C, Guckert A (2001) Short-term utilisation of ¹⁴C-[U]glucose by soil microorganisms
114 in relation to carbon availability. *Soil Biology & Biochemistry*, **33**, 53-60.
- 115 38. Parsons LL, Smith MS (1989) Microbial Utilization of Carbon-14-Glucose in Aerobic vs.
116 Anaerobic Denitrifying Soils. *Soil Science Society of America Journal*, **53**, 1082-1085.
- 117 39. Roberts, P., Jones, D.L., (2012) Microbial and plant uptake of free amino sugars in grassland
118 soils. *Soil Biology and Biochemistry* **49**, 139-149.
- 119 40. Santrůckova H, Pícek T, Tykva R, Simek M, Pavlů B (2004) Short-term partitioning of ¹⁴C-
120 [U]-glucose in the soil microbial pool under varied aeration status. *Biology and Fertility of*
121 *Soils*, **40**, 386-392.
- 122 41. Schimel DS (1988) Calculation of microbial growth efficiency from ¹⁵N immobilization.
123 *Biogeochemistry*, **6**, 239-243.

- 124 42. Schneckenberger, K., Demin, D., Stahr, K., Kuzyakov, Y., (2008) Microbial utilization and
125 mineralization of [14C]glucose added in six orders of concentration to soil. *Soil Biology and*
126 *Biochemistry* **40**, 1981-1988.
- 127 43. Sharifi, M., Zebarth, B.J., Burton, D.L., Drury, C.F., Grant, C.A., (2013) Mineralization of
128 Carbon-14-Labeled Plant Residues in Conventional Tillage and No-Till Systems. *Soil Science*
129 *Society of America Journal* **77**, 123-132.
- 130 44. Shen, J., Bartha, R., (1996) Metabolic efficiency and turnover of soil microbial communities
131 in biodegradation tests. *Applied and Environmental Microbiology* **62**, 2411-2415.
- 132 45. Shields JA, Paul EA, Lowe WE, Parkinson D (1973) Turnover of microbial tissue in soil under
133 field conditions. *Soil Biology & Biochemistry*, **5**, 753-764.
- 134 46. Spohn, M., Klaus, K., Wanek, W., Richter, A., (2016a) Microbial carbon use efficiency and
135 biomass turnover times depending on soil depth – Implications for carbon cycling. *Soil Biology*
136 *and Biochemistry* **96**, 74-81.
- 137 47. Spohn, M., Pötsch, E.M., Eichorst, S.A., Wobken, D., Wanek, W., Richter, A., (2016b) Soil
138 microbial carbon use efficiency and biomass turnover in a long-term fertilization experiment
139 in a temperate grassland. *Soil Biology and Biochemistry* **97**, 168-175.
- 140 48. Steinweg JM, Plante AF, Conant RT, Paul EA, Tanaka DL (2008) Patterns of substrate
141 utilization during long-term incubations at different temperatures. *Soil Biology & Biochemistry*,
142 **40**, 2722-2728.
- 143 49. Sugai SF, Schimel JP (1993) Decomposition and biomass incorporation of 14C-labeled
144 glucose and phenolics in Taiga forest floor : effect of substrate quality, successional state, and
145 season. *Soil Biology & Biochemistry*, **25**, 1379-1389.

- 146 50. Tianyu Li, Fengfeng Kang, Hairong Han (2015a) Responses of soil microbial carbon
147 metabolism to the leaf litter composition in Liaohe River Nature Reserve of northern Hebei
148 Province, China. *Chin. J. Appl. Ecol.* 2015, 26(3): 715–722.
- 149 51. Tianyu Li, Fengfeng Kang, Hairong Han, Jing Gao, Xiaoshuai (2015b) Song Characteristics
150 of Microbial Carbolic Metabolism in Soils of *Pinus Tabulaeformis* in Liaohe River of Northern
151 Hebei. *Soil* 2015, 47(3): 550–557
- 152 52. Thiet RK, Frey SD, Six J (2006) Do growth yield efficiencies differ between soil microbial
153 communities differing in fungal:bacterial ratios? Reality check and methodological issues. *Soil*
154 *Biology & Biochemistry*, **38**, 837-844.
- 155 53. Tucker C, Bell J, Pendall E, Ogle K (2013) Does declining carbon - use efficiency explain
156 thermal acclimation of soil respiration with warming? *Global Change Biology*, **19**, 252-263.
- 157 54. Van Ginkel JH, Gorissen A, Polci D (2000) Elevated atmospheric carbon dioxide
158 concentration: effects of increased carbon input in a *Lolium perenne* soil on microorganisms
159 and decomposition. *Soil Biology & Biochemistry*, **32**, 449-456.
- 160 55. Van Groenigen KJ, Forristal D, Jones MB, Smyth N, Schwartz E, Hungate BA, Dijkstra P
161 (2013) Using metabolic tracer techniques to assess the impact of tillage and straw management
162 on microbial carbon use efficiency in soil. *Soil Biology & Biochemistry*, **66**, 139-145.
- 163 56. Van Hees PaW, Johansson EMV, Jones DL (2008) Dynamics of simple carbon compounds in
164 two forest soils as revealed by soil solution concentrations and biodegradation kinetics. *Plant*
165 *and Soil*, **310**, 11-23.

166

167 **Table S2.** List of data source experiments.

No.	Incubation temperature (°C)	Substrate addition	Incubation time (d)	Calculate method	Data location	Mean CUE \pm SD	Reference number
1	not mention	litter	>30	Directly extracted	Table1	0.22 ± 0.03	1
2	22	glucose	1-7	Directly extracted	Table2	0.47 ± 0.07	2
3	20	soil leachate	not mention	Directly extracted	Fig. 2	0.41 ± 0.17	3
4	25	glucose	not mention	Directly extracted	article	0.39	4
5	22	glucose	1-7	Directly extracted	Table3	0.30 ± 0.10	5
6	22	glucose, glutamate, oxalate, phenol	1-7	Directly extracted	Table2	0.38 ± 0.28	6
7	21	glucose	>30	Eq. 4	Fig.1, Fig.2	0.20 ± 0.10	7
8	25	glucose, starch, legume, wheat	>30	Directly extracted	Table4	0.41 ± 0.19	8
9	28.5	glucose	7-30	Eq. 4	Table3, Table4, Table5	0.18 ± 0.06	9
10	5, 15, 25	rice straw	not mention	Directly extracted	Table3	0.44 ± 0.11	10
11	20	glucose, sodium, pyruvate	not mention	Directly extracted	Table2	0.72 ± 0.01	11
12	21	glycogen, synthesis,	not mention	Directly extracted	Table1	0.71 ± 0.15	12
13	4, 20	glucose, pyruvate	not mention	Directly extracted	Table3	0.74 ± 0.01	13
14	25	glucose, (NH ₄) ₂ SO ₄	1-7	Directly extracted	Table3, Table4	0.48 ± 0.13	14
15	10	alanine, dialanine, trialanine	not mention	Directly extracted	Table5, Fig.3	0.72 ± 0.11	15

16	22	glucose, fructose, sucrose, oxalate, phenylalanine	7	Directly extracted	Fig.5	0.76 ± 0.19	16
17	20	glucose, glutamic	1	Eq. 4	Fig.9	0.49 ± 0.14	17
18	22	not mention	not mention	Directly extracted	Table6	0.28 ± 0.06	18
19	25	glucose	<1d	Directly extracted	Table5	0.52 ± 0.12	19
20	5, 15, 25	glucose, glutamic, phenol, oxalic acid	not mention	Directly extracted	Fig.1, Fig.2	0.29 ± 0.22	20
21	24	glucose, NH ₄ NO ₃ , litter	1-7	Directly extracted	Table2	0.52 ± 0.19	21
22	25	litter, (NH ₄) ₂ SO ₄	>30	Eq. 5	Fig.1, Fig.3	0.15 ± 0.15	22
23	5, 10, 15, 20	glucose, pyruvate	not mention	Directly extracted	Fig.1	0.72 ± 0.01	23
24	25	glucose, LaCl ₃	1-7	Eq. 4	Table2	0.63 ± 0.04	24
25	25	not mention	>30	Directly extracted	Fig.7	0.38 ± 0.19	25
26	not mention	acetic acid, NH ₃	not mention	Directly extracted	Fig.5	0.50 ± 0.11	26
27	25	glucose	<1	Directly extracted	Fig.5	0.58 ± 0.06	27
28	20	not mention	not mention	Directly extracted	Fig.4	0.71 ± 0.05	28
29	25	glutamic acid	<1	Directly extracted	Fig.1	0.33 ± 0.15	29
30	22	glucose	<1	Directly extracted	Fig.3	0.48 ± 0.10	30
31	12	glucose, protein, cellulose, cell walls	1-7	Directly extracted	Fig.3b	0.30 ± 0.10	31

32	25	glucose, (NH ₄) ₂ SO ₄	>30	Directly extracted	Table2	0.62±0.17	32
33	25	leucine	1	Directly extracted	Fig.1, Fig.2, Fig.5	0.38±0.08	33
34	14	glucose	not mention	Directly extracted	Fig.2	0.45±0.04	34
35	not mention	glucose, fructose, sucrose, lactose, xylose, glycine, alanine, glutamic acid, phenylalanine, acetic acid, propionic acid, butyric acid, butanol, benzoic acid	not mention	Directly extracted	Table1	0.63±0.14	35
36	25	glucose	1-7	Directly extracted	Fig.7	0.67±0.10	36
37	22	glucose	1-7	Directly extracted	Table2	0.81±0.13	37
38	not mention	glucose	1-7	Directly extracted	Fig.1	0.57±0.10	38
39	1, 5, 10, 15	glucose, glucosamine	1	Directly extracted	Fig.2	0.94±0.03	39
40	not mention	glucose	1-7	Directly extracted	Table3	0.64±0.13	40
41	25	(NH ₄) ₂ SO ₄	not mention	Directly extracted	Table3	0.41±0.09	41
42	18	glucose	7-30	Eq. 4	Fig.4	0.54±0.18	42
43	25	wheat residues	>30	Directly extracted	Fig.3	0.91±0.01	43
44	27	glucose	7-30	Directly extracted	article	0.57±0.13	44
45	not mention	glucose	>30	Eq. 3	Table1, Table2	0.35±0.25	45
46	15	H ₂ O	1	Directly extracted	Fig.4	0.24±0.08	46

47	15	H ₂ O	1	Directly extracted	Fig.3	0.38 ± 0.06	47
48	15, 25	cellobiose	>30	Directly extracted	Table1	0.70 ± 0.07	48
49	11	glucose, benzoic acid,	1-7	Directly extracted	article	0.55 ± 0.23	49
50	25	litter	>30	Eq. 5	Fig.1, Fig.2	0.18 ± 0.10	50
51	25	not mention	>30	Eq. 5	Fig.1, Fig.2	0.09 ± 0.02	51
52	25	glucose	<1	Directly extracted	Table1	0.67 ± 0.07	52
53	1.5, 10, 22.5	dextrose	1-7	Directly extracted	Fig.8	0.76 ± 0.14	53
54	14, 16	residue	not mention	Eq. 4	Fig.2	0.31 ± 0.11	54
55	20	glucose, pyruvate	not mention	Directly extracted	Fig.5	0.77 ± 0.01	55
56	5	glucose	7-30	Directly extracted	Fig.1	0.63 ± 0.12	56

168

169

170 **Table S3.** Coefficients of variables based on the multiple stepwise regression analysis.

	Unstandardized		Standardized	t	Sig
	Coefficients		Coefficients		
	B	Std. Error	Beta		
Constant	0.319	0.057	-	5.557	0.000
Temperature	-0.025	0.002	-0.551	-13.952	0.000
Glucose	0.172	0.019	0.306	8.845	0.000
Latitude	-0.006	0.001	-0.454	-11.609	0.000
Longitude	-0.001	0.000	-0.327	-9.195	0.000
MAP	0.000	0.000	0.259	7.065	0.000
pH	0.032	0.008	0.138	3.825	0.000
Organic acid	-	-	-	-0.492	0.623
Plant residue	-	-	-	1.929	0.054
Inorganic substrate	-	-	-	-1.731	0.084

171

172

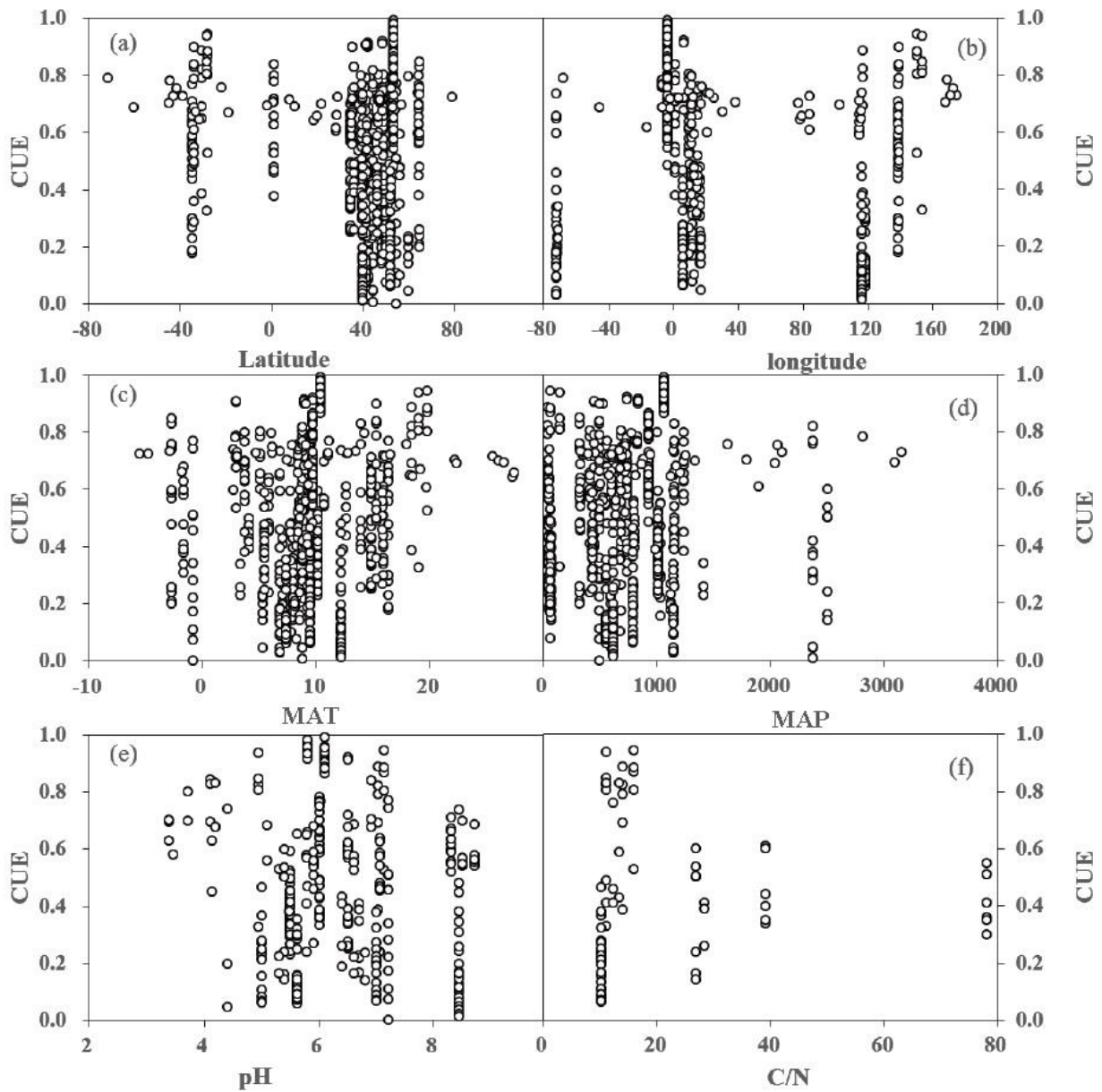
173 **Table S4.** CUE formula including all environmental factors (i.e., Temperature, Latitude, Substrate
 174 type, Longitude, MAP, and pH) based on different substrate type.

Substrate type	CUE formula	R ²
Glucose	$CUE=0.491-0.025\times(T-20)-0.006\times\text{Latitude}-0.001\times\text{Longitude}+0.0002\times\text{MAP}+0.032\times\text{pH}$	0.612
Other	$CUE=0.319-0.025\times(T-20)-0.006\times\text{Latitude}-0.001\times\text{Longitude}+0.0002\times\text{MAP}+0.032\times\text{pH}$	0.612

175

176

177 **Figure S1.** The CUE changes with latitude (a), longitude (b), mean annual temperature (MAT, c),
178 mean annual precipitation (MAP, d), soil pH (e) and the ratio of soil carbon to nitrogen content
179 (soil C/N, f) of the given site.

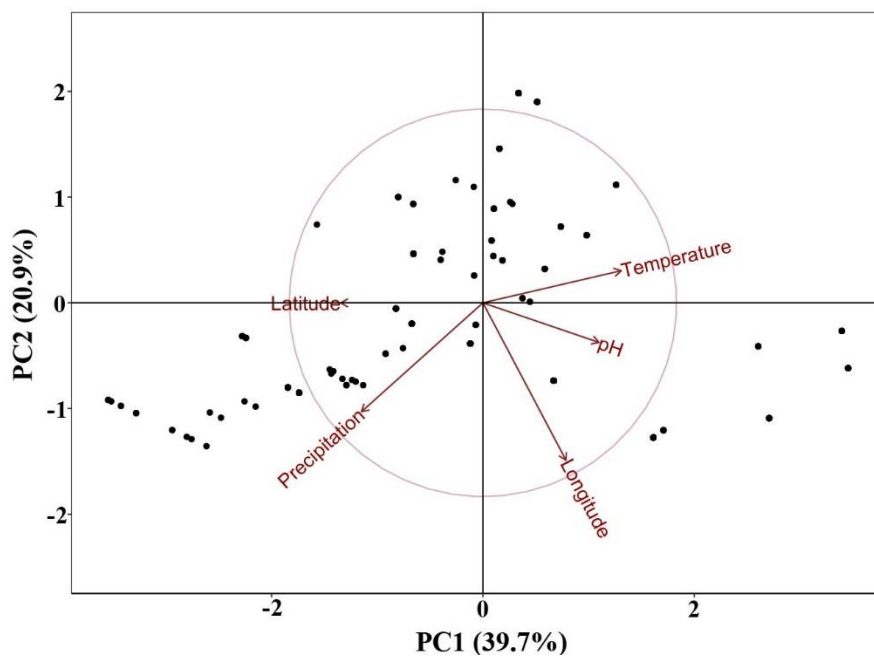


180

181

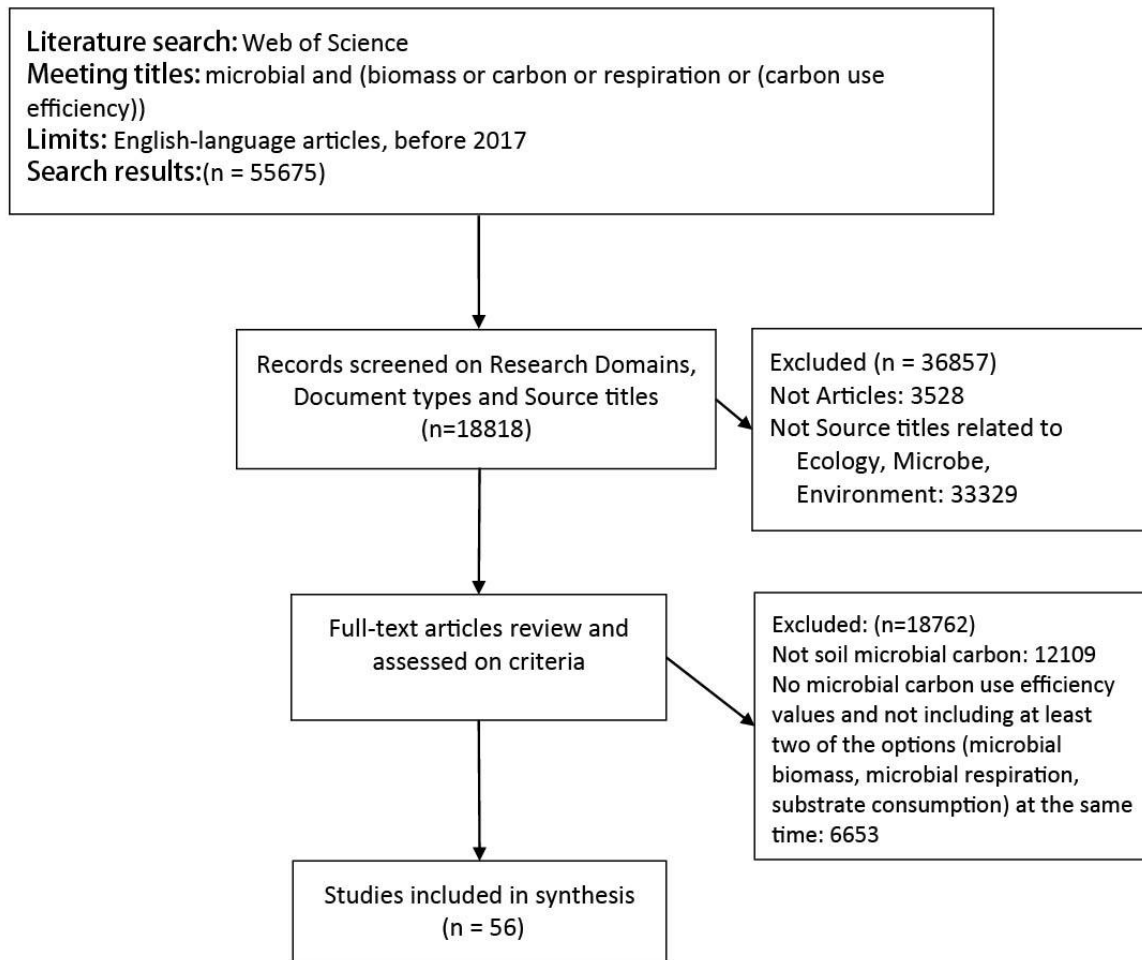
182 **Figure S2.** Principal Component Analysis (PCA) for all the single factor (Latitude, Longitude,
183 Temperature, MAP, pH).

184



185
186

187 **Figure S3.** PRISMA flow-diagram of literature search and study selection.



188
189

```

190 MCMC code for evaluation of  $CUE_0$  and  $m$ .
191
192 clear all;
193 close all;
194 format long e;
195
196 mydata=xlsread('cue2.xlsx');
197 T = mydata(:,1);
198 CUE = mydata(:,2);
199 C = [0.31;-0.016;18];
200 Cmin = [0;-0.1;10];
201 Cmax = [1;0;30];
202
203 Diff = Cmax-Cmin;
204 L_P = length(C);
205 DJ = 2*var(CUE);
206 J_last = 30000;
207 upgraded = 0;
208 nsimu = 1000000;
209
210 for simu = 1:nsimu
211 counter = simu;
212 upgraded = upgraded;
213 while true
214     Cnew = C + (rand(3,1)-0.5).*Diff;
215     Logic = Cnew>Cmin&Cnew<Cmax;
216     if sum(Logic) == L_P
217         break;
218     end
219 end
220
221 CUESimu = Cnew(1) + Cnew(2).*(T-Cnew(3));
222 J = (norm(CUE-CUESimu))^2;
223 J_new = J/DJ;
224 %J_new = J/DJ*200;          %for every year
225 delta_J = J_new-J_last;
226 if min(1,exp(-delta_J)) >rand
227     C_op = Cnew;
228     J_last = J_new;
229     upgraded = upgraded + 1;
230     C_upgraded(:,upgraded) = C_op;
231     J_upgraded(:,upgraded) = J_last;
232 end
233 end
234
235 C_upgraded = C_upgraded';

```