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12 **Microbial dynamics and soil physicochemical properties**  
13 **explain large scale variations in soil organic carbon**

14

15 Running Title: Microbe & soil property explain SOC variation

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## Abstract

42

First-order organic matter decomposition models are used within most Earth

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System Models (ESMs) to project future global carbon cycling; these models have

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been criticized for not accurately representing mechanisms of soil organic carbon

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(SOC) stabilization and SOC response to climate change. New soil biogeochemical

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models have been developed, but their evaluation is limited to observations from

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laboratory incubations or few field experiments. Given the global scope of ESMs, a

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comprehensive evaluation of such models is essential using *in situ* observations of a

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wide range of SOC stocks over large spatial-scales before their introduction to ESMs.

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In this study, we collected a set of *in situ* observations of SOC, litterfall and soil

51

properties from 206 sites covering different forest and soil types in Europe and China.

52

These data were used to calibrate the model MIMICS (The Microbial-Mineral Carbon

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Stabilization model), which we compared to the widely used first-order model

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CENTURY. We show that, compared to CENTURY, MIMICS more accurately

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estimates forest SOC concentrations and the sensitivities of SOC to variation in soil

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temperature, clay content and litter input. The ratios of microbial biomass to total

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SOC predicted by MIMICS agree well with independent observations from

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58 globally-distributed forest sites. By testing different hypotheses regarding (by using  
59 alternative process representations) of the physicochemical constraints on SOC  
60 deprotection and microbial turnover in MIMICS, the errors of simulated SOC  
61 concentrations across sites were further decreased. We show that MIMICS can  
62 resolve the dominant mechanisms of SOC decomposition and stabilization and that it  
63 can be a reliable tool for predictions of terrestrial SOC dynamics under future climate  
64 change. It also allows us to evaluate at large scale the rapidly evolving understanding  
65 of SOC formation and stabilization based on laboratory and limited field observation.

66

## 67 **KEYWORDS**

68 Soil organic carbon, soil biogeochemical model, microbial physiology, soil  
69 physicochemical property, soil carbon stabilization, soil carbon classification, climate  
70 change

## 71 **1 | INTRODUCTION**

72 Soil organic carbon (SOC) is the largest terrestrial carbon (C) pool (Ciais et al.,  
73 2013), and contains more than three times as much C as either the atmosphere or  
74 terrestrial vegetation. Therefore, a small change (< 1 %) in the global SOC pool might  
75 drastically alter the land-atmosphere C balance (Heimann & Reichstein, 2008; Shi et  
76 al., 2018). SOC is also closely related to soil fertility, structure, water holding  
77 capacity and ecosystem biogeochemical cycles (Six et al., 2004; Campbell & Paustian,  
78 2015). Dynamics of SOC have received increasing attention in many research areas  
79 ranging from small-scale projects for preserving or improving soil health, to  
80 large-scale climate change mitigation (e.g. the “4per1000” initiative) (Lal, 2016). Soil  
81 biogeochemical models are the main tools for estimating global land C stock and the  
82 interactions between SOC dynamic and changes in climate and land use.

83 The majority of global soil C models are developed based on first-order kinetics,  
84 in which the decomposition rate of organic matter is proportional to the pool size and  
85 turnover rate, modified by environmental factors (Parton et al., 1987; Manzoni &  
86 Porporato, 2009). These models are mathematically simple and stable, and have been  
87 proven effective for simulating soil organic matter dynamics (e.g. the decreasing trend

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88 of remaining organic matter mass during decomposition experiments, Barré et al.,  
89 2010; Bonan et al., 2013). However, these models are unable to mechanically  
90 represent the transient SOC dynamics in response to increased fresh litter input  
91 (Fontaine et al., 2007; Guenet et al., 2010; Kuzyakov, 2010), likely because they lack  
92 explicit representation of microbial decomposition and SOC stabilization (Schmidt et  
93 al., 2011; Creamer et al., 2015). Earth System Models (ESMs) which use the  
94 first-order soil C models also show poor agreement with global spatial variation of  
95 SOC stock (Todd-Brown et al., 2013; Hararuk & Luo, 2014; Wu et al., 2018).  
96 Moreover, the conceptual SOC pools used in conventional models are largely not  
97 observable (Elliot et al., 1996; Abramoff et al., 2018; Robertson et al., 2019), making  
98 it challenging to validate conventional soil C models using field observations (Six et  
99 al., 2014; Viscarra Rossel et al., 2019).

100 New theories and soil biogeochemical models have been developed to explicitly  
101 represent microbial biomass and physiology (Allison, 2012; Cotrufo et al., 2013;  
102 Wieder et al., 2014b; Campbell et al., 2016; Abramoff et al., 2018, 2019; Huang et al.,  
103 2018; Robertson et al., 2019). These microbial models are valuable for testing specific  
104 responses of SOC at small spatial scales, such as the effect of short-term priming  
105 observed during litter manipulation experiments or the addition of labile organic  
106 matter to the incubated soil samples in the lab. However, they introduce parameters  
107 determined from short term experiments or under laboratory conditions. Thus,  
108 microbial models add uncertainty to large-scale simulations (Stockmann et al., 2013;  
109 Wang et al., 2014; Shi et al., 2018; Robertson et al., 2019), because most of these  
110 models are calibrated against observed litter or SOC decomposition rates obtained  
111 from limited laboratory or field experiments (Wieder et al., 2014b; Campbell et al.,  
112 2016; Georgiou et al., 2017). Robust datasets which can be used to comprehensively  
113 evaluate the simulated quasi-equilibrium SOC pool sizes are still scarce (Wieder et al.,  
114 2014a). Furthermore, it remains difficult to determine whether microbial explicit  
115 models outperform conventional first-order models on predicting large-scale SOC  
116 spatial gradients and temporal dynamics (Campbell & Paustian, 2015; Wieder et al.,  
117 2015, 2018). Microbial models have to be carefully calibrated and evaluated before

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118 they are used to replace conventional first-order models in ESMs (Wieder et al., 2013;  
119 Wang et al., 2014).

120 Several studies have calibrated and validated microbial decomposition models  
121 (Wieder et al., 2013, 2015; Robertson et al., 2019) using globally gridded soil  
122 databases such as the Harmonized World Soils Database (HWSD,  
123 FAO/IIASA/ISRIC/ISSCAS/JRC, 2012) and the Northern Circumpolar Soil Carbon  
124 Database (NCSDC, Tarnocai et al., 2009). However these global databases do not  
125 contain uncertainty estimates (Dai et al., 2018), and previous studies have identified  
126 significant differences between SOC estimates from these databases or between  
127 grid-scale estimates from these databases and point-scale *in situ* observations (Tifafi  
128 et al., 2018; Fig. S1 in supplementary material). In addition, there is still no reliable  
129 globally gridded database of plant litter input. Uncertainties in the boundary  
130 conditions (e.g. litter inputs simulated by ESMs and soil physical and chemical  
131 properties) used as model forcing data further hamper the use of these global  
132 databases for model evaluation. An alternative approach is to calibrate and evaluate  
133 the microbial-explicit SOC models using extensive *in situ* observations of SOC  
134 contents, soil properties, litterfall production and climate conditions. Moreover, to  
135 ensure that the tested microbial model can capture many key processes related to SOC  
136 decomposition and stabilization, rather than only simulate the total SOC contents, it is  
137 necessary to evaluate the simulated composition of different C pools to total SOC, the  
138 turnover time of each C pool, and the sensitivity of SOC content to litter input and  
139 soil properties.

140 In this study we compiled a large set of *in situ* observations of SOC  
141 concentrations for northern forests, as well as related soil property measurements (e.g.  
142 texture, bulk density and pH), annual litter input and climate from 206 forest sites  
143 distributed across different climate zones of Europe and China. Using this database,  
144 we calibrated and evaluated the first-order soil biogeochemical model CENTURY  
145 (Parton et al., 1987) and the microbial trait-based model MIMICS (Microbial-MIneral  
146 Carbon Stabilization, Wieder et al., 2015). To evaluate the simulated SOC  
147 composition, we acquired observations of the ratio of microbial biomass to total SOC,

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148 and the SOC fractions that represent the different SOC pools in the total SOC stock  
149 from sites that are independent from the European and Chinese sites.

150 The aim of this study is to assess the strength and weakness of microbial implicit  
151 and microbial explicit models in simulating the stocks and composition of SOC with  
152 the intent of guiding future experiments and model developments. Specifically, we: 1)  
153 compared CENTURY and MIMICS with observed forest SOC concentrations at the  
154 continental scale, and explored the sources of model biases; 2) quantified the  
155 sensitivity of CENTURY- and MIMICS-simulated sensitivities of SOC concentration  
156 to changing soil conditions and litterfall inputs; 3) evaluated the MIMICS-simulated  
157 SOC compositions including ratios of microbial biomass to total SOC and the  
158 proportions of different SOC pools using observed values globally; 4) explored the  
159 main drivers of the variation in SOC composition. Finally we discussed the  
160 implications of our results for SOC modeling at global scales.

161

## 162 **2 | MATERIALS AND METHODS**

### 163 **2.1 | Observation data on SOC concentration and soil properties**

164 To calibrate and evaluate both soil C models under a wide range of climate  
165 conditions and forest types, we compiled observed SOC concentrations and the  
166 corresponding plant biomass, litterfall, soil properties (e.g. bulk density, soil texture,  
167 pH) and climate conditions (mean annual temperature) from 72 European forest sites  
168 and 134 Chinese forest sites (Fig. S2). The European sites are part of the International  
169 Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on  
170 Forests (ICP Forests, <http://icp-forests.net>) operating under the UNECE Air  
171 Convention and featuring consistent methods and harmonized data across the whole  
172 network (Gleck et al., 2016; Ukonmaanaho et al., 2016). The Chinese forest sites  
173 belong to a reviewable and consistent nationwide inventory system established by the  
174 Chinese Ministry of Forestry (Tang et al., 2018). The forest stand ages at most sites  
175 are older than 40 years. *In situ* observations are mostly conducted during the period  
176 from 2000 to 2015, with durations ranging from one to more than 10 years. The  
177 observation sites cover four forest types (temperate needle-leaved evergreen forest

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178 (TeNE), temperate broad-leaved evergreen forest (TeBE), temperate broad-leaved  
179 summer-green forest (TeBS), boreal needle-leaved evergreen forest (BoNE)) and  
180 more than 15 soil types (based on the FAO-90 soil classification in HWSO v1.2).  
181 Mean annual temperatures of the observation sites span a large range from -10 °C to  
182 higher than 20 °C (Fig. S3a). Values of mean annual total precipitation ranged from  
183 less than 300 mm yr<sup>-1</sup> to more than 2000 mm yr<sup>-1</sup> (Fig. S3b). Annual total litterfall  
184 production was between 100 g C m<sup>-2</sup> yr<sup>-1</sup> and 2000 g C m<sup>-2</sup> yr<sup>-1</sup> (Fig. S3c). Soil  
185 properties at the observation sites vary widely (Figs. S3d-i), with soil pH ranges from  
186 4.5 to 8.5, and clay fraction ranges from 1% to 45%. Moreover, observation data at  
187 European ICP Forest sites provide measurements of SOC concentrations and soil  
188 properties at four different layers (0-10, 10-20, 20-40, 40-80 cm) of the top 80 cm soil,  
189 whereas data at Chinese sites provide the mean condition of the top 1 m soil.

190 At the European ICP Forest sites, leaf litterfall (including twig litterfall for some  
191 sites) was measured *in situ*, but not wood and root litterfall. We estimate the wood  
192 litterfall based on the ratios of wood litterfall to leaf litterfall, and the root litterfall  
193 based on the root turnover rates and the ratios of root biomass to leaf biomass (Table  
194 S1 in supplementary material). At Chinese sites, there are no *in situ* observations of  
195 litterfall. We calculated the leaf, wood and root litterfall from observed standing  
196 biomass (including leaf, wood and root) and the annual leaf and root turnover rates  
197 and the ratios of wood litterfall to leaf litterfall (Table S1). The leaf and root turnover  
198 rate, the ratios of wood and root litterfall to leaf litterfall and the ratios of root  
199 biomass to leaf biomass used in this study were obtained from a statistical analysis of  
200 extensive global observations (Zhang et al., 2014; Holland et al., 2015; Jia et al., 2016,  
201 Fig. S4).

202 C:N ratios of leaf litterfall at both European and Chinese sites were measured *in*  
203 *situ*. C:N ratios of wood and root litterfall, as well as the litterfall lignin:C ratios for  
204 each forest type were obtained from the global Fine-Root Ecology Database (FRED,  
205 Iversen et al., 2017), the TRY database (Kattge et al., 2011) and the Long-Term  
206 Inter-site Decomposition Experiment Team (LIDET, Harmon et al., 2009).

207 The soil base saturation (BS, %), Cation Exchange Capacity (CEC, cmol kg<sup>-1</sup>)

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208 and soil gravel content (% of volume) at each observation site were obtained from the  
209 Global Soil Dataset for Earth System Models (GSDE, Shangguan et al., 2014). Soil  
210 type was determined based on the map from HWSD v1.2. Annual mean soil water  
211 content (%) was extracted from the estimation of land surface model  
212 ORCHIDEE-trunk (r5504, Krinner et al., 2005). LAI and NDVI data were extracted  
213 from the GLASS (resolution: 0.05°, Liang et al., 2013) and GIMMS NDVI products  
214 (resolution: 8-km, Tucker et al., 2005), respectively. Evapotranspiration (ET) and the  
215 potential evapotranspiration (PET) were obtained from Jung et al. (2010) and the  
216 CRUNCEP v7 database (Viovy, 2018), respectively. More details of the datasets used  
217 in this study can be found in Table S1.

218

## 219 **2.2 | Decomposition models**

### 220 **2.2.1 | CENTURY**

221 We selected the CENTURY model (the version presented by Parton et al., 1987)  
222 to represent first-order soil biogeochemical models, because it has been widely  
223 incorporated into ESMs (e.g. Sitch et al., 2003; Krinner et al., 2005; Koven et al.,  
224 2013). In CENTURY, organic matter is separated into metabolic litter (high quality,  
225  $LIT_m$ ) and structural litter (low quality,  $LIT_s$ ) and three SOC pools (active pool  
226 ( $SOC_{act}$ ), slow pool ( $SOC_{slow}$ ), passive pool ( $SOC_{pas}$ )) with different turnover times  
227 (Fig. 1a). Fresh litter inputs are partitioned into metabolic and structural litter pools  
228 based on a linear function ( $f_{met}$ , dimensionless) of litter lignin to nitrogen (N) ratios  
229 ( $LN$ ) (Parton et al., 1987):

$$230 \quad f_{met} = \max(0.0, 0.85 - 0.013 \times LN) \quad (1)$$

231 There is no explicit representation of microbial biomass in CENTURY. The  
232 decomposition of litter and SOC is described by first order kinetics. At each daily  
233 time step, the decomposition of litter or SOC ( $mg\ C\ cm^{-3}\ day^{-1}$ ) is calculated  
234 following:

$$235 \quad \frac{dC_s}{dt} = I_c - k_{max} \times C_s \times f(tem) \times f(swc) \times f(clay) \quad (2)$$

236 where  $C_s$  ( $mg\ C\ cm^{-3}$ ) is an individual litter or SOC pool,  $I_c$  ( $mg\ C\ cm^{-3}\ day^{-1}$ ) is the C



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237 input to the pool considered,  $k_{max}$  is the potential maximum turnover rate of  $C_s$  ( $\text{day}^{-1}$ )  
238 and is equal to the reciprocal of maximum turnover time.  $f(tem)$ ,  $f(swc)$  and  $f(clay)$  are  
239 the soil temperature factor, moisture factor and clay factor modulating decomposition  
240 rate, respectively.

## 241 2.2.2 | MIMICS (default and modified versions)

### 242 *The default version of MIMICS (MIMICS-def)*

243 The Microbial-MIneral Carbon Stabilization model (MIMICS, Wieder et al.,  
244 2014b, 2015) explicitly considers the relationships among litter quality, functional  
245 tradeoffs in microbial physiology, and the physical and physicochemical protection of  
246 microbial byproducts in forming stable soil organic matter. Like CENTURY,  
247 MIMICS also has two types of litter pool: metabolic ( $LIT_m$ ) and structural ( $LIT_s$ ) litter  
248 (Fig. 1b), and the method used to partition fresh litter input into metabolic and  
249 structural pools ( $f_{met}$ , Fig. 1b) is the same as that used in CENTURY (Eq. 1). SOC in  
250 MIMICS is divided into three pools: the physically and physicochemically protected  
251 ( $SOC_p$ ), the chemically recalcitrant ( $SOC_c$ ) and available ( $SOC_a$ ). Two microbial  
252 functional types are represented in MIMICS that roughly correspond to  
253 microorganisms with copiotrophic (r-strategy,  $MIC_r$ ) and oligotrophic (k-strategy,  
254  $MIC_k$ ) growth strategies (Fig. 1b). The  $MIC_r$  is assumed to have higher growth and  
255 turnover rates and prefers to consume more labile litter ( $LIT_m$ ), whereas the  $MIC_k$  has  
256 relatively lower growth and turnover rates and is more competitive when consuming  
257 low-quality litter ( $LIT_s$ ) and chemically recalcitrant SOC ( $SOC_c$ ).

258 C fluxes in MIMICS are simulated at an hourly (h) time step. Decomposition of  
259 litter and SOC pools ( $\text{mg C cm}^{-3} \text{ h}^{-1}$ ) is based on temperature-sensitive  
260 Michaelis–Menten kinetics (Schimel & Weintraub, 2003; Allison et al., 2010) through  
261 the equation:

$$262 \quad \frac{dC_s}{dt} = I_c - MIC \times \frac{V_{max} \times C_s}{K_m + C_s} \quad (3)$$

263 where  $C_s$  ( $\text{mg C cm}^{-3}$ ) is a substrate pool ( $LIT$  or  $SOC$ ) and  $MIC$  ( $\text{mg C cm}^{-3}$ )  
264 corresponds to the biomass of each microbial pool ( $MIC_r$  or  $MIC_k$ ).  $I_c$  is the C input  
265 to the pool considered ( $\text{mg C cm}^{-3} \text{ h}^{-1}$ ).  $V_{max}$  and  $K_m$  are the microbial maximum

266 reaction velocity ( $\text{mg C (mg MIC)}^{-1} \text{ h}^{-1}$ ) and half-saturation constant ( $\text{mg C cm}^{-3}$ ),  
 267 respectively. They are calculated as:

$$268 \quad V_{max} = e^{V_{slope} \times T + V_{int}} \times av \times V_{mod} \quad (4)$$

$$269 \quad K_m = e^{K_{slope} \times T + K_{int}} \times ak \times K_{mod} \quad (5)$$

270 where  $T$  is soil temperature ( $^{\circ}\text{C}$ ),  $V_{mod}$  and  $K_{mod}$  represent the modifications of  $V_{max}$   
 271 and  $K_m$  based on assumptions regarding to microbial functional types, litter chemical  
 272 quality and soil texture effects,  $av$  and  $ak$  are the tuning coefficient of  $V_{max}$  and  $K_m$ ,  
 273 respectively.  $V_{slope}$  and  $K_{slope}$  are two regression coefficients.  $V_{int}$  and  $K_{int}$  are the  
 274 regression intercepts.

275 Decomposition rate of substrates and the microbial growth efficiency (MGE, Fig.  
 276 1b) determine the growth rate of microbes. The turnover of  $\text{MIC}_r$  and  $\text{MIC}_k$  ( $\text{MIC}_r$ ,  
 277  $\text{mg C cm}^{-3} \text{ h}^{-1}$ ) at each time step is calculated based on their specific turnover rate  
 278 ( $k_{mic}$ ,  $\text{h}^{-1}$ ), annual total litterfall input ( $\text{LIT}_{tot}$ ,  $\text{g C m}^{-2} \text{ yr}^{-1}$ ) and  $f_{met}$  by following:

$$279 \quad \text{MIC}_r = a_r \times k_{mic} \times e^{c \times f_{met}} \times \max(\min(\sqrt{\text{LIT}_{tot}}, 1.2), 0.8) \times \text{MIC} \quad (6)$$

280 where  $a_r$  ( $=1.0$ , dimensionless) is a tuning coefficient of  $k_{mic}$ .  $c$  is the regression  
 281 coefficients, and its value is 0.3 for  $\text{MIC}_r$  and 0.1 for  $\text{MIC}_k$ . Turnover of microbial  
 282 biomass provides C inputs to SOC pools (Fig. 1b). The fractions of microbial residues  
 283 to different SOC pools are determined by soil clay content ( $f_{clay}$ ) and the quality of  
 284 litter inputs (lignin:N), and can be specifically calculated by following:

$$285 \quad f_{rp} = \min(1.0, a_1 \times e^{1.3 \times f_{clay}}) \quad (7)$$

$$286 \quad f_{kp} = \min(1.0, a_2 \times e^{0.8 \times f_{clay}}) \quad (8)$$

$$287 \quad f_{rc} = \min(1.0 - f_{rp}, a_4 \times e^{a_3 \times f_{met}}) \quad (9)$$

$$288 \quad f_{kc} = \min(1.0 - f_{kp}, a_5 \times e^{a_3 \times f_{met}}) \quad (10)$$

$$289 \quad f_{ra} = 1.0 - f_{rp} - f_{rc} \quad (11)$$

$$290 \quad f_{ka} = 1.0 - f_{kp} - f_{kc} \quad (12)$$

291 where  $f_{rp}$ ,  $f_{kp}$ ,  $f_{rc}$ ,  $f_{kc}$ ,  $f_{ra}$  and  $f_{ka}$  represent the fractions of  $\text{MIC}_r$  and  $\text{MIC}_k$  residues to  
 292  $\text{SOC}_p$ ,  $\text{SOC}_c$  and  $\text{SOC}_a$ s, respectively.  $LN$  is the lignin:N ratio.  $a_{1-5}$  are coefficients and

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293 their values in default MIMICS can be found in Table S1 in supplementary materials.  
294 In addition to microbial residues, a fraction of inputs ( $f_{i,met}$  and  $f_{i,stru}$ ) which bypasses  
295 litter and microbial biomass pools is transferred directly to corresponding SOC pools  
296 (Fig. 1b).

297 The transfer of  $SOC_p$  to  $SOC_a$  ( $D$ ,  $mg\ C\ cm^{-3}\ h^{-1}$ ), which is intended to represent  
298 the deprotection of SOC, i.e. desorption of physico-chemically protected SOC from  
299 mineral surfaces and/or the breakdown of aggregates de-protecting physically  
300 protected SOC, is calculated as a function of soil clay content ( $f_{clay}$ ) by following:

$$301 \quad D = 1.5 \times 10^{-5} \times k_d \times e^{-1.5 \times f_{clay}} \quad (13)$$

302 where  $k_d$  ( $=1.0$ , dimensionless) is a tuning coefficient of the deprotection rate. Some  
303 parameter values of the default MIMICS are provided in Table S1 in supplementary  
304 materials. Please see Wieder *et al.* (2014b, 2015) for more details of the structure,  
305 algorithms, parameters and underlying assumptions of MIMICS.

306

#### 307 *MIMICS with revised SOC deprotection rate (MIMICS-D)*

308 In addition to the default version of MIMICS (MIMICS-def), we also developed  
309 and tested a new version of MIMICS (MIMICS-D) that considers the saturation of  
310 SOC protected by the mineral matrix ( $SOC_p$ ). In the MIMICS-def, the deprotection  
311 rate of  $SOC_p$  in a specific soil was a fixed value determined by the abundance of the  
312 soil clay fraction (Eq. 13). However, field and laboratory research suggests that there  
313 might be an upper limit, or ‘saturation level’, in the amount of physicochemically and  
314 physically protected SOC that can be held in soil (Six *et al.*, 2002; Stewart *et al.*, 2007;  
315 Robertson *et al.*, 2019). Deprotection rate of the SOC protected by the mineral matrix  
316 is closely related to this saturation degree (defined as the ratio of existing  $SOC_p$  to the  
317 soil maximum adsorption capacity; Kothawala *et al.*, 2008; Wang *et al.*, 2013). In this  
318 study, we did not calculate the maximum adsorption capacity directly, as it is  
319 determined by soil physical and chemical characteristics, and there is still no widely  
320 recognized method to calculate it (Lützow *et al.*, 2006; Campbell & Paustian, 2015;  
321 Huang *et al.*, 2018), The upper-limit of  $SOC_p$  was represented by assuming that the

322 deprotection rate increases exponentially with the pool size of SOC<sub>p</sub>:

$$323 \quad D = 1.5 \times 10^{-5} \times k_d \times e^{-1.5 \times f_{clay}} \times e^{k_{dp} \times SOC_p} \quad (14)$$

324 where  $k_{dp}$  is a coefficient for tuning the relationship between the deprotection rate ( $D$ )  
325 and the pool size of SOC<sub>p</sub>.

326

327 *MIMICS considering the impact of base saturation (BS) on deprotection rate*  
328 *(MIMICS-DB)*

329 We tested several new modifications of MIMICS to see if the inclusion of soil  
330 chemical properties (BS and pH) could further decrease the uncertainties in simulated  
331 SOC concentrations. We modified the microbial maximum reaction velocity ( $V_{max}$ , Eq.  
332 4), the C input rates to SOC<sub>p</sub> ( $f_p$  and  $f_{i,met}$  in Fig. 1b) and the deprotection rate of SOC<sub>p</sub>  
333 with some simple linear or exponential functions of soil BS and pH, separately. In this  
334 study, we only present the results from the modification called MIMICS-DB, where  
335 the modified deprotection rate of SOC<sub>p</sub> is calculated as:

$$336 \quad D = 1.5 \times 10^{-5} \times k_d \times e^{-1.5 \times f_{clay}} \times e^{k_{dp} \times SOC_p} \times e^{k_{bs} \times BS} \quad (15)$$

337 where  $k_{bs}$  is a coefficient modifying the impacts of BS on the deprotection rate.

338

339 *MIMICS considering density-dependent microbial turnover rate (MIMICS-DBT)*

340 Following the method of Georgiou et al. (2017), we also incorporated a  
341 density-dependent microbial turnover rate into MIMICS. In this version  
342 (MIMICS-DBT), microbial turnover rate increases with growing microbial biomass  
343 density (MIC, mg C cm<sup>-3</sup>) by modifying Eq. 6:

$$344 \quad MIC_\tau = a_\tau \times k_{mic} \times e^{c \times f_{met}} \times \max(\min(\sqrt{LIT_{tot}}, 1.2), 0.8) \times (MIC)^\beta$$

345 (16)

346 where  $\beta$  is the density-dependence exponent.

347

### 348 **2.3 | Model parameterization and validation against SOC concentrations**

349 We assumed that all the forest sites included in this study are at steady state (i.e.  
350 no interannual variation of SOC, litterfall and stand biomass). CENTURY and the

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351 four versions of MIMICS introduced above (Table 1) were then calibrated and  
352 evaluated against the ‘equilibrium’ SOC concentrations using observation data of soil  
353 texture, annual total litterfall and mean annual temperature. We also ignored the  
354 interannual and seasonal dynamics of climate and vegetation. Historical climate,  
355 litterfall input and soil properties were all assumed to be similar to the average  
356 condition during the observation period. Vertical discretization in SOC and soil  
357 properties is not considered in CENTURY and MIMICS. We focus only on the spatial  
358 variation of average SOC concentrations in the upper soil horizons (0-80 cm for  
359 European sites and 0-1 m for Chinese sites). The semi-analytic approach was used to  
360 calculate the steady state microbial and soil C pool sizes (Xia et al., 2012) based on  
361 annual total litterfall production (evenly distributed to each time step of simulation),  
362 annual mean soil temperature and moisture conditions and observed soil properties at  
363 each forest site.

364 Parameters of CENTURY and MIMICS were optimized against the observed  
365 SOC concentrations (Table 1). Although many parameters (e.g. carbon use efficiency  
366 and parameters related to the constraints of temperature and soil clay on C  
367 decomposition rate) of CENTURY and MIMICS can impact the simulated SOC  
368 concentrations, we only optimized the parameters which directly control the organic  
369 matter decomposition rates. Because these parameters generally contain large  
370 uncertainties and the simulated SOC stocks are generally more sensitive to these  
371 parameters than to other model parameters (Wieder et al., 2014b, 2015; Shi et al.,  
372 2018). Specifically, we added two scaling parameters  $k_{litt}$  and  $k_{soc}$  (dimensionless) in  
373 CENTURY to tune the turnover rates of litter and SOC pools, respectively.

$$374 \quad k_{max\_litt\_opt} = k_{litt} \times k_{max\_litt} \quad (17)$$

$$375 \quad k_{max\_soc\_opt} = k_{soc} \times k_{max\_soc} \quad (18)$$

376 where  $k_{max\_litt}$  and  $k_{max\_litt\_opt}$  are the default and optimized litter turnover rates,  
377 respectively.  $k_{max\_soc}$  and  $k_{max\_soc\_opt}$  are the default and optimized SOC turnover rates,  
378 respectively. The default litter and SOC turnover rates (see Table S2) were obtained  
379 from Parton et al. (1987). Optimization of only  $k_{litt}$  and  $k_{soc}$  may be not enough to  
380 minimize the uncertainties in the turnover rates of litter and SOC pools and the

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381 simulated SOC concentrations. We therefore also tested the effectiveness of  
382 CENTURY on capturing observed SOC concentrations when five free parameters  
383 were introduced to tune the turnover rates of metabolic litter, structural litter, active  
384 SOC, slow SOC and passive SOC, respectively (Fig. S5).

385 For the MIMICS models, we optimized the scaling parameters ( $av$ ,  $ak$  and  $k_d$ ) of  
386 the microbial maximum reaction velocity ( $V_{max}$ , Eq.4), half-saturation constant ( $K_m$ ,  
387 Eq. 5) and of the deprotection rate of  $SOC_p$  (Eqs. 13-15), as they are all closely  
388 related to the decomposition and the physical stabilization of organic matter (Wieder  
389 *et al.*, 2014b, 2015). Parameters in the newly introduced equations (Eqs. 14-16) for  
390 modifying deprotection rates and microbial turnover rate were also optimized (Table  
391 1).

392 Parameter optimization was performed using the shuffled complex evolution  
393 (SCE) algorithm developed by Duan *et al.* (1993, 1994), which has proven to be  
394 effective for global optimization by many previous studies (e.g. Muttil &  
395 Jayawardena, 2008; Franchini *et al.*, 2009). Prior value and the range of each  
396 parameter used for the SCE algorithm are listed in Table S3. Root mean square error  
397 (RMSE, Eq. 19) between simulated ( $SOC_{sim_i}$ ) and observed ( $SOC_{obs_i}$ ) SOC  
398 concentrations (g C kg<sup>-1</sup> soil) was used as the objective function, and parameters that  
399 minimized the RMSE were regarded as optimal.

$$400 \quad RMSE = \sqrt{\left(\frac{\sum_{i=1}^n (SOC_{obs,i} - SOC_{sim,i})^2}{n}\right)} \quad (19)$$

401 where  $n$  is the number of observation sites. In addition to RMSE, the Akaike  
402 information criterion (AIC, Eq. 20), which considers both the goodness of fit and  
403 the number of free model parameters ( $n_{param}$ ) were also used to evaluate the  
404 optimized models (Table 1).

$$405 \quad AIC = n \times \ln\left(\frac{\sum_{i=1}^n (SOC_{obs,i} - SOC_{sim,i})^2}{n}\right) + 2n_{param} \quad (20)$$

406 Our preliminary-analyses indicated that parameter optimizations of MIMICS  
407 based solely on observed SOC concentration might result in unrealistic estimates of  
408 SOC composition (e.g. the  $SOC_p$  pool approaching to zero at all sites) and of turnover

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409 rates (e.g. the  $\text{SOC}_p$  turnover rates being significantly larger than  $\text{SOC}_a$ ), although the  
410 simulated concentrations of total SOC agreed well with the observations. To mitigate  
411 this problem, some additional constraints on simulated SOC composition and turnover  
412 rates were incorporated into our optimization scheme (see below). Parameter sets that  
413 did not meet the imposed constraints on SOC composition and turnover rates were  
414 excluded. Note that the simulated turnover rates of different SOC pools from  
415 CENTURY are always consistent with the definition of SOC pools (i.e. the active  
416 pool has the largest turnover rate, followed by the slow pool, and the passive pool has  
417 the lowest turnover rate), and the simulated SOC composition (mainly determined by  
418 the turnover rate of each pool, see section 3.2) did not show any ‘abnormalities’ (i.e.  
419 no simulated SOC pool declined to very small values approaching zero), so we did  
420 not incorporate additional constraints when optimizing the parameters of CENTURY.

421 Previous studies suggest that the organic C associated with soil minerals or stored  
422 within soil aggregates, corresponding to the  $\text{SOC}_p$  pool of MIMICS, is the most stable  
423 fraction of SOC with turnover times approaching hundreds to thousands of years.  
424 Further, the recalcitrant SOC fractions composed by structurally complex compounds  
425 corresponding to the  $\text{SOC}_c$  pool of MIMICS generally have longer turnover time than  
426 the labile SOC fraction (Benbi *et al.*, 2014; Robertson *et al.*, 2019; Sokol *et al.*, 2019).  
427 Therefore, we set a constraint that the simulated mean  $\text{SOC}_p$  turnover time for all of  
428 the 206 observation sites must be longer than that of  $\text{SOC}_c$ , and that the mean  $\text{SOC}_c$   
429 turnover time must be longer than  $\text{SOC}_a$ .

430 Observations found that a large fraction (e.g. 10-50%) of SOC is in stable pool  
431 (Lützow *et al.*, 2007; Barré *et al.*, 2010; Benbi *et al.*, 2014; Viscarra Rossel *et al.*,  
432 2019). To avoid the optimized parameters giving a very low (approaching to zero)  
433 estimate of the fraction of  $\text{SOC}_p$ , we also added as a constraint of model results with  
434 optimized parameters that the simulated average proportion of  $\text{SOC}_p$  at the 206  
435 observation sites (not for every individual site) must be larger than 5%, that average  
436 proportion of  $\text{SOC}_c$  cannot exceed 70%, and that the total amount of  $\text{SOC}_p$  and  $\text{SOC}_c$   
437 should be higher than  $\text{SOC}_a$ .

438 Note that the parameters ( $a_{1-5}$  in Eqs. 7-10) controlling the partition of microbial

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439 residues to different SOC pools were modified before the parameters listed in Table 1  
440 are optimized, because MIMICS did not give reasonable estimates of the SOC  
441 concentrations, compositions and the turnover rates simultaneously when only the  
442 parameters listed in Table 1 were calibrated. The modified values of  $a_{1-5}$  are provided  
443 in Table S2.

444 To explore the sources of simulation errors (i.e. the difference between simulated  
445 and observed SOC concentrations), we first calculated the partial correlation  
446 coefficient between the errors of the simulated SOC concentration and different soil  
447 (e.g. texture, pH, BS and CEC), plant (NDVI and LAI) and climate (temperature,  
448 precipitation, ET) variables (see section 2.1 and Table S1 for the source of each  
449 variable). Then we fitted a linear mixed-effects (LME) model to quantify the  
450 combined contribution of the fixed-effects (soil, plant and climate variables listed  
451 above) and site-specific random-effects (e.g. soil type, forest type, stand age and  
452 micro-topography) on explaining the simulation errors. All the important variables  
453 that might potentially affect SOC dynamics, for example soil texture, temperature, pH,  
454 moisture, BS, CEC, bulk density, litterfall inputs, precipitation and ET, were included  
455 as fixed-effects in the LME. Observation site was used as a random-effect. We also  
456 fitted a multiple linear regression (MLR) with all of the fixed-effects of the LME as  
457 the predictor variables to quantify the relative contributions of fixed- and  
458 random-effects to the simulation errors. Then the relative contributions of fixed- and  
459 random-effects were quantified based on the coefficient of determination of the LME  
460 ( $R^2_{LME}$ ) and MLR ( $R^2_{MLR}$ ). The contributions of model choice ( $f_{model}$ ), fixed-effects  
461 ( $f_{fixed}$ ) and random-effects ( $f_{random}$ ) to explaining the variation of SOC concentrations  
462 can be quantified by:

$$463 \quad f_{model} = R^2_{model} \quad (21)$$

$$464 \quad f_{fixed} = R^2_{MLR} \times (1 - R^2_{model}) \quad (22)$$

$$466 \quad f_{model} = (R^2_{LME} - R^2_{MLR}) \times (1 - R^2_{model}) \quad (23)$$

467 where  $R^2_{model}$  is the determining coefficient of the regression equation between



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468 simulated and observed SOC concentrations.

#### 469 **2.4 | Model evaluation against sensitivities of SOC concentrations to key model** 470 **drivers**

471 To assess whether each model simulated the variations of SOC concentrations for  
472 the right reasons, we first identified the key drivers of the spatial variations of SOC  
473 concentration, and then compared modeled sensitivities of SOC concentration to these  
474 drivers to the values derived from the observations. The potential key drivers we  
475 evaluated include soil temperature, moisture, clay content, litterfall input, the mean  
476 C:N ratio and the lignin:C ratio of litterfall. The sensitivities of organic matter  
477 decomposition rate to manipulated soil temperature, moisture and litter inputs have  
478 been widely investigated via laboratory and field experiments (Parton et al., 2007;  
479 Bonan et al., 2013; Sierra et al., 2015). However, no experiments have measured the  
480 sensitivity of equilibrium SOC stock to changing soil properties and litter inputs, as it  
481 would take decades to hundreds of years for the SOC pool to reach equilibrium after  
482 manipulating litter. Here we estimated the sensitivities by making use of observed  
483 spatial variation of SOC with different drivers, including soil temperature, water  
484 content, clay fraction, annual total litter input and the C:N ratio and lignin:C ratio of  
485 litter input. We assumed the soil-litter system is in steady-state, and the sensitivities of  
486 equilibrium SOC to different drivers were quantified by multiple linear regression.  
487 The regression coefficient of each driver was regarded as the observed sensitivity.

488 The sensitivities of simulated SOC concentration to soil and litter properties from  
489 optimized CENTURY and MIMICS were obtained using Monte Carlo simulations.  
490 We sampled 1000 sets of unique soil and litter input condition within the observed  
491 space of each variable using Latin Hypercube technique (Tang & Zhuang, 2009). All  
492 soil and litter variables were assumed to be uniformly distributed and the range of  
493 each variable was set based on the maximum and minimum observed values at the  
494 European and Chinese sites. For each combination of soil and litter input condition,  
495 the sensitivity ( $S_i$ ) of SOC concentration to each variable ( $d_i$ ) was calculated as

$$496 \quad S_i = \frac{f(d_1, d_2, \dots, d_i + \delta, \dots, d_n) - f(d_1, d_2, \dots, d_i, \dots, d_n)}{\delta}$$

497

498 where  $\delta$  is the step size of a change in variable  $d_i$  assumed to be one percent of the  
499 difference between maximum and minimum  $d_i$  (i.e.  $\delta = (d_{i\_max} - d_{i\_min})/100$ ).

500

## 501 **2.5 | Model evaluation against SOC composition**

502 We evaluated the simulated proportions of the different SOC pools using  
503 observations from sites that are independent of the European and Chinese forest sites,  
504 for which the model parameters were calibrated. The simulated ratios of microbial  
505 biomass to total SOC were validated against 655 observations from forest sites around  
506 the world (Xu et al., 2013). The simulated SOC composition from CENTURY and  
507 MIMICS was compared to measurements of SOC composition from 505 sites under  
508 native forests and grasslands in Australia (Viscarra Rossel & Hicks, 2015; Viscarra  
509 Rossel et al. 2019). These data were partitioned into three fractions, the particulate  
510 organic C (POC), humic organic C (HOC) and resistant organic C (ROC, which is the  
511 mineral-associated organic carbon) based on the particle size and chemical  
512 compositions of organic matter. We acknowledge the fact that the observed pools are  
513 not modeled conceptual pools and we propose a correspondence between both in  
514 Table S4. We compared the simulated SOC pools to the observed SOC fractions to  
515 assess their correspondence in terms of their expected/assumed turnover rates.

## 516 **2.6 | Model evaluation against the key drivers of variations in SOC composition**

517 To determine whether the key drivers of variations in SOC composition in  
518 MIMICS and CENTURY models are consistent with the observations, we calculated  
519 the partial correlation coefficient between fraction of each SOC pool and different  
520 model drivers using the simulated proportions of different SOC pools by optimized  
521 MIMICS and CENTURY models at all of the 206 forest sites in Europe and China  
522 (Fig. S2), and using the observed proportions of different SOC pools at the 505  
523 Australia sites (Viscarra Rossel et al. 2019). The key drivers we considered in this  
524 analysis include soil temperature, moisture, clay fraction, BS, annual litterfall input,  
525 litter C:N and lignin:C ratios and the total SOC pool size). For each model driver, all  
526 of the other drivers described above were used as the controlling factor for calculating

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527 the partial correlation coefficient.

528

### 529 **3 | RESULTS**

#### 530 **3.1 | Evaluation of simulated SOC concentrations**

531 Our evaluation indicates that MIMICS can better capture the observed spatial  
532 variation of SOC concentrations than CENTURY across European and Chinese forest  
533 sites. The default version MIMICS-def explains 48% observed SOC spatial variation,  
534 as compared to only 10% by CENTURY model (Fig. 2). MIMICS-D, MIMICS-DB  
535 and MIMICS-DBT explain 52%, 57% and 59% SOC spatial variation, respectively  
536 (Fig. 2). The RMSE and Akaike information criterion (AIC) indicate that all MIMICS  
537 versions estimate the spatial variation of SOC concentration more accurately than  
538 CENTURY, with MIMICS-DBT having the best performance overall (Fig. 2f). We  
539 also note that the CENTURY model with 5 free parameters for tuning turnover rates  
540 of litter and SOC pools (Fig. S5a) does not estimate SOC concentrations more  
541 accurately than the CENTURY with 2 free parameters (Table 1). CENTURY with 5  
542 free parameters has a slightly smaller RMSE (16.89) but a higher AIC (1174.7) than  
543 the RMSE (16.97) and AIC (1170.5) respectively from CENTURY with 2 parameters  
544 (Fig. S5a).

545 There are systematic biases in the simulated SOC concentrations along the  
546 gradients of SOC pool size, soil properties, and climate and plant variables (Figs. 3  
547 and S6). Both CENTURY and MIMICS overestimate the low SOC concentrations but  
548 underestimate the high concentrations (Figs. 2 and S6). The simulation biases of  
549 CENTURY are significantly correlated with soil (e.g. moisture, BS, pH, and bulk  
550 density), plant (e.g. litterfall, LAI) and climate (e.g. mean annual temperature and  
551 annual total precipitation) variables (Fig. 3), suggesting that CENTURY has structural  
552 biases in the processes depending upon those factors. Similar to CENTURY, the  
553 simulation bias of MIMICS is also significantly correlated with some soil and  
554 litterfall-related variables. By including the effect of BS on deprotection rate into  
555 MIMICS (MIMICS-DB), the significant relationships between simulation biases and  
556 soil, plant and climate variables are largely eliminated, but a significant negative

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557 relationship between simulation biases and soil CEC appears. The significant  
558 relationship between simulation biases and annual litterfall input can be eliminated  
559 only when the density dependence of microbial turnover rate in MIMICS-DBT is  
560 represented. Moreover, the simulation biases of all models are positively related to  
561 soil bulk density (Fig. 3).

562 Soil properties, litter input rate and the plant and climate conditions together can  
563 only explain a small portion of the simulation biases in SOC concentrations,  
564 especially for MIMICS (Figs. S7, S8). The linear mixed-effects (LME) models which  
565 consider both fixed factors (i.e. the soil, litter and climate variables) and site-specific  
566 random factor (e.g. soil type, forest type, stand age and micro-topography) explain  
567 most of the variations in the simulation biases (Fig. S7). Further statistics indicated  
568 that the SOC variation explained by CENTURY, fixed factors and random factors are  
569 10%, 27% and 54%, respectively (Fig. S8). But for MIMICS, the model itself  
570 explained the largest part (48-59%) of SOC variation, followed by the random factor  
571 (24-32%), with fixed factors explaining 5-9% of SOC variation (Fig. S8). Our further  
572 analysis on the potential contributors to random factors indicated that CENTURY  
573 estimations of SOC are consistently biased regardless of soil type, plant type and  
574 stand age (Fig. S9). But the estimations of SOC made by MIMICS are, with few  
575 exceptions, unbiased across sites with different soil types, plant types and stand ages.  
576 Overall, the constraints of soil, litter and climate factors on SOC stocks are  
577 significantly better represented in MIMICS than in CENTURY.

### 578 **3.2 | Evaluation of simulated sensitivities of SOC concentration to key model** 579 **drivers**

580 Based on observations, SOC concentrations are sensitive to local soil temperature  
581 and soil clay content (Figs. 4a, c), but are not sensitive to local soil moisture or litter  
582 quantity and quality (Figs. 4b, d, e, f). On average, SOC concentration declines by  
583 0.53 g C kg<sup>-1</sup> soil with a 1 °C increase in soil temperature, and increases by 0.37 g C  
584 kg<sup>-1</sup> soil with a 1 percent increase in soil clay fraction.

585 MIMICS models provide more accurate estimates of the observation-based partial  
586 sensitivity of SOC concentration to changes in soil temperature, compared to

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587 CENTURY (Fig. 4a). With a 1 °C increase in soil temperature, the simulated SOC  
588 concentration declines by 0.4-0.55 g C kg<sup>-1</sup> soil (median value) depending on the  
589 version of MIMICS. The sensitivity is comparable to the value calculated based on  
590 observation data, but significantly lower than the value simulated by CENTURY  
591 (-0.92±4.1 g C kg<sup>-1</sup> soil °C<sup>-1</sup>). Both CENTURY and MIMICS underestimate the  
592 observed sensitivity of SOC to soil clay fraction. Despite this, the sensitivities  
593 estimated by MIMICS (0.17 – 0.26 g C kg<sup>-1</sup> soil (clay%)<sup>-1</sup>) are closer to the observed  
594 value than CENTURY (0.02 g C kg<sup>-1</sup> soil (clay%)<sup>-1</sup>, Fig. 4c). In CENTURY or  
595 MIMICS, the sensitivities of SOC concentration to these variables generally show  
596 large variations. Overall, SOC simulated by CENTURY is more sensitive to the  
597 changes in soil condition and litter input than MIMICS.

### 598 3.3 | Evaluation of simulated SOC composition

599 The simulated ratios of microbial biomass (MIC) to total SOC stock (MIC/SOC)  
600 from the MIMICS models is broadly consistent with the observations collected from  
601 global forest sites (Xu *et al.*, 2013), both in terms of mean (or median) value and the  
602 range of variation (Fig. 5). Overall, both observed and simulated MIC/SOC ranged  
603 from 0.005 to approximately 0.05, with a mean value of approximately 0.017  
604 (0.015-0.019) and a median value of 0.013 (0.012-0.014).

605 MIMICS simulated fractions of SOC pools that are consistent with measurements  
606 of the Australian soil samples based on the particle size and chemical compositions of  
607 organic matter (Table S4), but CENTURY did not (Fig. 6). Observations at 505  
608 Australian sites indicate that HOC (46-60%) accounts for the largest proportion of  
609 SOC, followed by the most stable pool ROC (25-33%). The labile pool POC makes  
610 up a small fraction (12-23%) of total SOC (Fig. 6a). MIMICS predicts a similar  
611 composition of SOC pools. The moderately stable pool (SOC<sub>c</sub>) accounts for the  
612 largest proportion of total SOC, followed by the most stable pool protected by the  
613 mineral matrix (SOC<sub>p</sub>), and the available pool (SOC<sub>a</sub>, Fig. 6c). SOC composition  
614 simulated by CENTURY can be very different depending on the optimized turnover  
615 rates of the active, slow and passive SOC pools (Figs. 6b and S5b). Increasing  
616 turnover rate of a specific SOC pool generally results in a smaller proportion of this

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617 pool compared to the total SOC (if the turnover rates of other SOC pools are assumed  
618 to be fixed).

### 619 **3.4 | Key drivers of the variation in SOC composition**

620 The key factors controlling the simulated SOC composition in CENTURY and  
621 MIMICS are different from the observations (Fig. 7). Based on observation data, soil  
622 moisture, clay fraction, BS and litter input show significant empirical correlations  
623 with SOC composition, whereas soil temperature shows no significant correlation. In  
624 both CENTURY and MIMICS, soil temperature strongly affects SOC composition.  
625 Higher temperature however decreases the ‘stable’ SOC fraction ( $\text{SOC}_{\text{pas}}$ ) in  
626 CENTURY, but increases the stable fraction ( $\text{SOC}_{\text{p}}$ ) in MIMICS. MIMICS can  
627 represent the impacts of litter input on SOC composition, but CENTURY does not.  
628 Similar to the observations, higher litter input rate increases the proportion of the  
629 stable SOC pools (ROC and  $\text{SOC}_{\text{p}}$ ) but decreases the proportion of moderately stable  
630 pools (HOC and  $\text{SOC}_{\text{c}}$ ). The simulated decreasing trend of labile SOC ( $\text{SOC}_{\text{a}}$ ) with  
631 increasing litter input is contrary to the observation (POC). In MIMICS-DB and  
632 MIMICS-DBT, soil chemical properties represented by BS also show strong impact  
633 on SOC composition. Moreover, SOC composition also changes with the pool size of  
634 total SOC. It is necessary to note that the partial correlation coefficients might not be  
635 able to fully represent the relationships between SOC composition and soil and litter  
636 variables (Fig. 7), as SOC composition might not be linearly related to these variables  
637 (Fig. S10).

## 638 **4 | DISCUSSION**

639 Using *in situ* observations of SOC, litterfall and soil properties from 206 forest  
640 sites in Europe and China, we compared the performance of a first-order soil  
641 biogeochemical model (CENTURY) and four different versions of the microbial  
642 trait-based model (MIMICS) for simulating the large-scale spatial variation of SOC  
643 concentrations, the sensitivity of SOC concentration to key model drivers and the  
644 SOC composition. Our evaluation provides strong evidence that soil biogeochemical  
645 models with explicit microbial processes can be applied to simulate the large-scale  
646 SOC dynamics across different soil, vegetation and climate conditions. Below we

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647 discuss in detail the implications of these results, uncertainties associated with the  
648 analysis, and an outlook for future data and model needs.

#### 649 **4.1 | Implications of simulation results**

##### 650 **4.1.1 | Decomposition model should be calibrated and evaluated comprehensively**

651 This study reveals the necessity to calibrate and evaluate MIMICS  
652 comprehensively. Preliminary parameter estimates for this study showed that although  
653 parameters optimized based solely on observed SOC concentrations can accurately  
654 estimate total SOC stocks; they may not be able to estimate SOC composition and  
655 turnover time. In order to avoid unreasonable estimates of SOC composition (e.g.  
656 SOC<sub>p</sub> of MIMICS calibrated only against the SOC concentrations at European and  
657 China forest sites always approaches to zero) and C turnover times, we imposed  
658 additional constraints to restrict the ranges of proportions and turnover times of  
659 MIMICS SOC pools (see section 2.3). Our results highlight the need for comparing  
660 model results with total SOC and microbial biomass, SOC composition and turnover  
661 time, as well as the response of SOC to changed climate, litter input and soil  
662 properties with a wide range of observations. Moreover, the optimized parameter  
663 values of both CENTURY and MIMICS in this study (Table S3) are different from  
664 the default values calibrated against manipulated decomposition experiments (Parton  
665 et al., 1987; Wieder et al., 2015), suggesting that model parameters obtained based on  
666 local decomposition experiments might not work well at large spatial scales.

##### 667 **4.1.2 | Importance of explicitly representing microbial dynamics in** 668 **decomposition model**

669 Explicit representation of microbial biomass and substrate-limited growth rates is  
670 important for soil biogeochemical models to accurately capture the observed SOC  
671 concentration variations and the responses of SOC to climate changes (Wieder et al.,  
672 2014b; Campbell & Paustian, 2015). In our research, simulations of SOC  
673 concentration at forest sites using MIMICS were more accurate and parsimonious  
674 compared to using CENTURY (Fig. 2), and MIMICS better capture the observed  
675 sensitivities of SOC concentrations to temperature and soil clay than CENTURY.  
676 Conventional first-order models do not explicitly simulate microbial activity, but

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677 instead strongly emphasizes the relationship between litter chemical recalcitrance and  
678 soil C stock (Jenkinson & Rayner, 1977; Parton et al., 1987; Wieder et al., 2014b).  
679 Recent analytical and experimental advances have demonstrated that molecular  
680 structure alone does not control SOC stability. Rather, microbial products of  
681 decomposition are the main precursors of stable SOC (Cotrufo et al., 2013;  
682 Kallenbach et al., 2016), suggesting that, in fact, environmental and biological  
683 controls predominate (Lützow et al., 2006; Schmidt et al., 2011; Lehmann & Kleber,  
684 2015).

#### 685 **4.1.3 | Impacts of soil physiochemical properties on SOC decomposition and** 686 **stabilization**

687 Besides microbial dynamics, it is also necessary to accurately represent the effects  
688 of soil physiochemical properties on SOC dynamics in soil biogeochemical models,  
689 especially for the formation and release of SOC protected by the mineral matrix. It  
690 has been widely recognized that soil clay fractions can influence SOC stock and  
691 stabilization by promoting the sorption of organic C to mineral surfaces and  
692 entrapment into micropores (Schimel et al., 1994; Wagner et al., 2007). CENTURY  
693 uses the soil clay fraction to modify the decomposition rate of the active SOC pool  
694 and the C transfer from active to slow pool (Parton et al., 1987). As the active pool  
695 generally accounts for only a small fraction (c.a. 3.5%) of total SOC (Fig. 6b), this  
696 might explain why the sensitivity of SOC concentration to soil clay content in  
697 CENTURY is drastically underestimated compared to the observation-based  
698 sensitivity (Fig. 4c). In MIMICS, soil clay influences both the decomposition rate of  
699 available SOC pool and the deprotection rate of protected by the mineral matrix.

700 MIMICS thus better represents current understanding of SOC stabilization processes  
701 and appears to more accurately estimate the sensitivity of SOC to soil clay fraction  
702 than CENTURY (Fig. 4c).

703 Numerous experimental studies also reported the significant impacts of soil  
704 chemical properties such as pH, exchangeable cations (e.g. Ca<sup>2+</sup>) and extractable  
705 metals (e.g. iron- and aluminum-oxyhydroxides) on SOC dynamics (Six et al., 2004;  
706 Doetterl et al., 2015; Rasmussen et al., 2018; ViscarraRossel et al., 2019), and the



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707 relative importance of these factors likely varies across scales and ecosystems  
708 (Jobbágy & Jackson, 2000; Schmidt et al., 2011; ViscarraRossel et al., 2019). Indeed,  
709 representing the diversity of mechanisms by which the soil physicochemical  
710 environment influences the persistence of soil organic matter in numerically tractable  
711 ways remains an outstanding challenge in models (Bailey et al. 2018). Our work  
712 suggests one opportunity to use base saturation (BS) as a proxy variable that can  
713 modify C deprotection rates from the SOC<sub>p</sub> pool in MIMICS (MIMICS-DB). This  
714 modification significantly decreased the biases in simulated SOC concentrations (Fig.  
715 2) and eliminated the systematic estimation biases along gradients of soil pH, clay  
716 content and annual precipitation at the observation sites (Fig. 3). Moreover, our  
717 analysis on the relative contributions of model choice, fixed effects and site-specific  
718 random effects to explaining the SOC variation (Fig. S8) reveals that the constraints  
719 of soil physical (e.g. temperature and clay content) and chemical (e.g. BS) properties  
720 on SOC dynamics has been better represented in MIMICS than in CENTURY, as the  
721 fixed effects including all potentially important soil variables can only explain a small  
722 part of the simulation errors of MIMICS, but a considerable part (~ 30%) of the  
723 simulation errors of CENTURY (Fig. S7, S8).

#### 724 **4.1.4| Impacts of litter inputs on SOC decomposition and stabilization**

725 First order models like CENTURY assume a linear relationship with productivity  
726 and soil C stocks (Todd-Brown et al. 2013), and the same is true for default  
727 parameterizations of MIMICS. Our analysis shows that the simulated SOC  
728 concentrations from CENTURY and MIMICS models are systematically biased from  
729 observations along the gradients of local litterfall production, except for the  
730 MIMICS-DBT which considers the density-dependent turnover of microbes (Fig. 3).  
731 This suggests that at the community level, regulatory mechanisms like competition,  
732 space constraints and other controls that depend on the density of individuals (such as  
733 disease and production of toxins) may limit microbial population sizes (Hibbing et al.,  
734 2010; Kaiser et al., 2014; Kaiser et al., 2015) Indeed, a recent study from Georgiou et  
735 al. (2017) indicated that the density-dependent microbial processes can play an  
736 essential, but often overlooked role in regulating SOC dynamics. We recognize that

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737 the parameterization of density dependent turnover implemented in MIMCS-DBT  
738 simplifies the complex community interactions that occur in soils, but they represent a  
739 tractable means for capturing the emergent dynamics in models that are intended for  
740 global-scale application and projections.

741 Litter input is not as important as soil physicochemical properties for predicting  
742 total SOC stock (Fig. 4d), but it nevertheless strongly affects SOC composition (Fig.  
743 7), which determines the vulnerability of SOC (i.e. risk of C loss) to perturbations  
744 such as climate change and human disturbances. Litter quality can impact microbial C  
745 use efficiency and short-term SOC dynamics (Manzoni et al., 2017; Zhang et al.,  
746 2018), but evidence is inclusive on the significant role of litter quality in long-term  
747 SOC dynamics (Helfrich et al., 2008; Gentile et al., 2011). The effect of litter quality  
748 on SOC stabilization is mostly modulated by the extent of soil C saturation, and it  
749 may alter SOC stocks only when there is a saturation deficit (Castellano et al., 2015).  
750 Consistent with our results (Fig 7), previous studies also reported that litter quantity  
751 rather than quality is one of the main determinants of SOC stability (Carrington et al.,  
752 2012; Dungait et al., 2012). Experiments by Wang et al. (2016) suggested that the  
753 ratio between different SOC fractions is related to microbial biomass and community  
754 composition (which depends on the amounts of litter inputs), but not to litter chemical  
755 composition.

756

## 757 **4.2 | Uncertainties in this study**

758 Some uncertainties in our simulation results may be caused by biases of forcing  
759 and validation data. In this study, we assumed the forest and soil C at all observation  
760 sites are at equilibrium. However, even though most observation sites have a stand  
761 age older than 40 years and have not been strongly disturbed by fire or human  
762 activities (e.g. reforestation and deforestation can induce a 30% change in soil C stock,  
763 Don et al., 2011), the forest systems at some sites may not be at equilibrium,  
764 especially under the background of global climate change. Some uncertainties also  
765 arise due to lack of observations. Specifically, the wood and root litterfall at European  
766 sites have not been measured and Chinese observation data only provides

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767 measurements of plant biomass but not litterfall, so we have adopted the leaf turnover  
768 rates and ratios of wood litter and root litter to leaf litter from databases of plant traits  
769 and litterfall production to calculate the total litterfall production at each observation  
770 site (see section 2.1). Moreover, most of the litter C:N ratios and the lignin:C ratios  
771 were obtained from previously compiled litterfall databases and publications and not  
772 from site level observations, Thus, biases and uncertainties that exist in the litter input  
773 data are poorly quantified.

774 Additional uncertainties are related to model structural assumptions and  
775 parameterizations. Specifically, soil moisture has been widely regarded as one of the  
776 primary physical factors that control microbial activity (Arnold et al., 2015; Manzoni  
777 et al., 2016; Ghezzehei et al., 2019); however the soil moisture control over microbial  
778 dynamics is not used in the current parameterization of MIMICS. Soil structure  
779 (characterized by porosity or bulk density) determines soil O<sub>2</sub> availability and the  
780 accessibility of C particles to microbes (Lützow et al., 2006; Davidson et al., 2012).  
781 Soil nutrient availability (e.g. mineral nitrogen and phosphorus) strongly affects  
782 microbial C use efficiency and growth rate (Manzoni *et al.*, 2017). Again, soil  
783 moisture, structure and nutrient availability have not been considered in this  
784 implement MIMICS. Finally, neither of the models considered here implement  
785 vertically resolved soil biogeochemistry, which are clearly important to capture soils  
786 with strong vertical profiles or vertical perturbations such as in permafrost C (Kovenet  
787 al. 2015; McGuire et al. 2018). The insufficient representation of interactions between  
788 soil physicochemical properties, nutrient availability, microbial dynamics and SOC  
789 stabilization therefore may induce additional uncertainties in our results. We  
790 appreciate that these additional complexities in model form also generates greater data  
791 demands to appropriately parameterize and evaluate models, but may be necessary to  
792 build confidence in soil carbon projections (Bradford *et al.* 2016).

### 793 **4.3 | Outlooks and challenges**

794 A study by Wieder et al. (2014) demonstrated that MIMICS could capture the  
795 observed temporal decreasing trends of litter and SOC stocks in field decomposition  
796 experiments. Our evaluation further demonstrates that MIMICS can simulate SOC

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797 stock and composition across ecosystems with different climate, and soil and forest  
798 types. MIMICS also represents the SOC decomposition and stabilization processes  
799 more realistically (e.g. explicitly represents microbial dynamics) than conventional  
800 first-order models. Therefore MIMICS can be used to replace the conventional  
801 decomposition models used in existing ESMs.

802 The parameters, structure and algorithms of MIMICS can still be improved. We  
803 encourage future studies to assess the global applicability of MIMICS or similar  
804 models based on more integrated *in situ* observations on plant biomass, litterfall (both  
805 aboveground and belowground), SOC stock and composition, soil physicochemical  
806 properties and local climate from more ecosystems, in particular observations from  
807 grasslands and tropical forests. We also encourage more studies to quantify the  
808 interactions between soil physicochemical properties, microbial dynamics and the  
809 stabilization of SOC. In this study, the MIMICS model considering the  
810 physicochemical constraints of soil properties on SOC deprotection rate and microbe  
811 turnover more accurately estimated SOC concentration than the default model (Fig. 2).  
812 But the empirical functions (Eqs. 13, 14) used to represent physicochemical  
813 constraints were built empirically based on analysis of the biases of simulated SOC  
814 concentration from the default version of MIMICS (Fig. 3). More experiments  
815 investigating influences of soil physicochemical properties on microbial activity and  
816 the C adsorption/desorption rate of mineral soil are needed to improve these empirical  
817 functions. Furthermore, many soil properties are significantly correlated (e.g. Fig. S12)  
818 and the changes in litter inputs and SOC contents can in return dramatically alter soil  
819 physical, chemical, and biological properties (Schmidt et al., 2011; Murphy et al.,  
820 2015). Thus, research focusing on the interactions between litter, SOC and different  
821 soil properties is also essential.

822

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837

838 **Data accessibility:** The European ICP forest data can always be requested from the  
839 Programme Co-ordinating Centre (PCC, <http://icp-forests.net/page/data-requests>) of  
840 ICP Forests in Eberswalde, Germany. The Chinese forest data can be obtained by  
841 contacting the Prof. Tang X ([xltang@scib.ac.cn](mailto:xltang@scib.ac.cn)) in South China Botanical Garden,  
842 Chinese Academy of Sciences, Guangzhou, China. All of the other databases of soil,  
843 climate, litterfall and vegetation are publicly accessible, and the specific references  
844 and links to these databases are provided in section 2.1.

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## 846 REFERENCES

- 847 Abramoff, R., Xu, X., Hartman, M., O'Brien, S., Feng, W., Davidson, E., Finzi, A., Moorhead, D., Schimel, J.,  
848 Torn, M. & Mayes, M.A. (2018). The Millennial model: in search of measurable pools and  
849 transformations for modeling soil carbon in the new century. *Biogeochemistry*, 137, 51-71.
- 850 Abramoff, R. Z., Torn, M. S., Georgiou, K., Tang, J. & Riley, W. J. (2019). Soil organic matter temperature  
851 sensitivity cannot be directly inferred from spatial gradients. *Global Biogeochemical Cycles*.  
852 doi:10.1029/2018gb006001
- 853 Akaike, H. (1974). A new look at the statistical model identification, *IEEE T. on Automat. Cont.*, 19, 716–723.
- 854 Allison, S. D. (2012). A trait-based approach for modelling microbial litter decomposition. *Ecology Letters*, 15,  
855 1058-1070.
- 856 Allison, S. D., Wallenstein, M. D. & Bradford, M. A. (2010). Soil-carbon response to warming dependent on

---

857 microbial physiology. *Nature Geoscience*, 3, 336-340.

858 Arnold, C., Ghezzehei, T. A. & Berhe, A. A. (2015). Decomposition of distinct organic matter pools is regulated  
859 by moisture status in structured wetland soils. *Soil Biology and Biochemistry*, 81, 28-37.

860 Bailey, V. L., Bond-Lamberty, B., De Angelis, K., Grandy, A. S., Hawkes, C. V., Heckman, K., . . . Wallenstein,  
861 M. D. (2018). Soil carbon cycling proxies: Understanding their critical role in predicting climate change  
862 feedbacks. *Global Chang Biology*, 24, 895-905.

863 Barré, P., Eglin, T., Christensen, B. T., Ciais, P., Houot, S., Kätterer, T., van Oort, F., Peylin, P., Poulton, P. R.,  
864 Romanenkov, V. & Chenu, C. (2010). Quantifying and isolating stable soil organic carbon using  
865 long-term bare fallow experiments. *Biogeosciences*, 7, 3839-3850.

866 Benbi, D. K., Boparai, A. K. & Brar, K. (2014). Decomposition of particulate organic matter is more sensitive to  
867 temperature than the mineral associated organic matter. *Soil Biology and Biochemistry*, 70, 183-192.

868 Bonan, G. B., Hartman, M. D., Parton, W. J. & Wieder, W. R. (2013). Evaluating litter decomposition in earth  
869 system models with long-term litterbag experiments: an example using the Community Land Model  
870 version 4 (CLM4). *Global Chang Biology*, 19, 957-974.

871 Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., & Crowther, T. W. (2016). Managing  
872 uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change*, 6, 751-758.

873 Campbell, E. E. & Paustian, K. (2015). Current developments in soil organic matter modeling and the expansion of  
874 model applications: a review. *Environmental Research Letters*, 10, 123004.

875 Campbell, E. E., Parton, W. J., Soong, J. L., Paustian, K., Hobbs, N. T. & Cotrufo, M. F. (2016). Using litter  
876 chemistry controls on microbial processes to partition litter carbon fluxes with the Litter Decomposition  
877 and Leaching (LIDEL) model. *Soil Biology and Biochemistry*, 100, 160-174.

878 Carrington, E. M., Hernes, P. J., Dyda, R. Y., Plante, A. F. & Six, J. (2012). Biochemical changes across a carbon  
879 saturation gradient: Lignin, cutin, and suberin decomposition and stabilization in fractionated carbon  
880 pools. *Soil Biology and Biochemistry*, 47, 179-190.

881 Castellano, M. J., Mueller, K. E., Olk, D. C., Sawyer, J. E. & Six, J. (2015) Integrating plant litter quality, soil  
882 organic matter stabilization, and the carbon saturation concept. *Global Chang Biology*, 21, 3200-3209.

883 Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J.,  
884 Heimann, M., Jones, C., Le Quéré, C., Myneni, R. B., Piao, S. L. & Thornton, P. (2013). Carbon and  
885 Other Biogeochemical Cycles. In: *Climate Change 2013: The Physical Science Basis. Contribution of*  
886 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* eds.

---

887 T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex  
888 and M. P.M.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

889 Cools, N. & De Vos, B. (2016). Part X: Sampling and Analysis of Soil. In: UNECE ICP Forests Programme  
890 Coordinating Centre (ed.): Manual on methods and criteria for harmonized sampling, assessment,  
891 monitoring and analysis of the effects of air pollution on forests. In, Thünen Institute of Forest  
892 Ecosystems, Eberswalde, Germany.

893 Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Deneff, K. & Paul, E. (2013). The Microbial Efficiency-Matrix  
894 Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter  
895 stabilization: do labile plant inputs form stable soil organic matter? *Glob Chang Biol*, 19, 988-995.

896 Creamer, C. A., de Menezes, A. B., Krull, E. S., Sanderman, J., Newton-Walters, R. & Farrell, M. (2015).  
897 Microbial community structure mediates response of soil C decomposition to litter addition and warming.  
898 *Soil Biology and Biochemistry*, 80, 175-188.

899 Dai, Y., Shangguan, W., Wang, D., Wei, N., Xin, Q., Yuan, H., Zhang, S., Liu, S. & Yan, F. (2018) A review on  
900 the global soil datasets for earth system modeling. *SOIL Discussions*, 1-30.

901 Davidson, E. A., Samanta, S., Caramori, S. S. & Savage, K. (2012). The Dual Arrhenius and Michaelis-Menten  
902 kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change  
903 Biology*, 18, 371-384.

904 Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C.,  
905 Boudin, M., Venegas, E. & Boeckx, P. (2015). Soil carbon storage controlled by interactions between  
906 geochemistry and climate. *Nature Geoscience*, 8, 780-783.

907 Don, A., Schumacher, J. & Freibauer, A. (2011). Impact of tropical land-use change on soil organic carbon stocks  
908 – a meta-analysis. *Global Change Biology*, 17, 1658-1670.

909 Duan, Q., Gupta, V. & Sorooshian, S. (1993). Shuffled complex evolution approach for effective and efficient  
910 global minimization. *Journal of Optimization Theory and Its Applications*, 76, 501-521.

911 Duan, Q., Sorooshian, S. & Gupta, V. K. (1994). Optimal use of the SCE-UA global optimization method for  
912 calibrating watershed models. *Journal of Hydrology*, 158, 265-284.

913 Dungait, J. A. J., Hopkins, D. W., Gregory, A. S. & Whitmore, A.P. (2012). Soil organic matter turnover is  
914 governed by accessibility not recalcitrance. *Global Change Biology*, 18, 1781-1796.

915 Elliott, E. T., Paustian, K. & Frey, S. D. (1996). Modeling the Measurable or Measuring the Modelable: A  
916 Hierarchical Approach to Isolating Meaningful Soil Organic Matter Fractionations. In: Powlson D. S.,

- 
- 917 Smith P., Smith J. U. (eds) *Evaluation of Soil Organic Matter Models. NATO ASI Series (Series I:*  
918 *Global Environmental Change)*, vol 38. Springer, Berlin, Heidelberg.
- 919 FAO/IIASA/ISRIC/ISSCAS/JRC (2012). Harmonized World Soil Database (version 1.2). In, FAO, Rome, Italy  
920 and IIASA, Laxenburg, Austria.
- 921 Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B. & Rumpel, C. (2007). Stability of organic carbon in deep  
922 soil layers controlled by fresh carbon supply. *Nature*, 450, 277-280.
- 923 Frankenberg, C., Fisher, J. B., Worden, J., Badgley, G., Saatchi, S.S., Lee, J. E., Toon, G. C., Butz, A., Jung, M. &  
924 Kuze, A. (2011). New global observations of the terrestrial carbon cycle from GOSAT: Patterns of plant  
925 fluorescence with gross primary productivity. *Geophysical Research Letters*, 38, 351-365.
- 926 Gentile, R., Vanlauwe, B. & Six, J. (2011). Litter quality impacts short- but not long-term soil carbon dynamics in  
927 soil aggregate fractions. *Ecological Applications*, 21, 695-703.
- 928 Georgiou, K., Abramoff, R. Z., Harte, J., Riley, W. J. & Torn, M. S. (2017). Microbial community-level regulation  
929 explains soil carbon responses to long-term litter manipulations. *Nature Communications*, 8, 1223.
- 930 Ghezzehei, T. A., Sulman, B., Arnold, C. L., Bogie, N. A. & Berhe, A. A. (2019). On the role of soil water  
931 retention characteristic on aerobic microbial respiration. *Biogeosciences*, 16, 1187-1209.
- 932 Hararuk, O. & Luo, Y. (2014). Improvement of global litter turnover rate predictions using a Bayesian MCMC  
933 approach. *Ecosphere*, 5, art163.
- 934 Harmon, M. E., Silver, W. L., Fasth, B., Chen, H. U. A., Burke, I. C., Parton, W. J., Hart, S. C. & Currie, W. S.  
935 (2009). Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite  
936 comparison. *Global Change Biology*, 15, 1320-1338.
- 937 Hartono, A., Funakawa, S. & Kosaki, T. (2005). Phosphorus Sorption-Desorption Characteristics of Selected Acid  
938 Upland Soils in Indonesia. *Soil Science and Plant Nutrition*, 51, 787-799.
- 939 Heimann, M. & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451,  
940 289-292.
- 941 Helfrich, M., Ludwig, B., Potthoff, M. & Flessa, H. (2008). Effect of litter quality and soil fungi on  
942 macroaggregate dynamics and associated partitioning of litter carbon and nitrogen. *Soil Biology and*  
943 *Biochemistry*, 40, 1823-1835.
- 944 Hibbing, M. E., Fuqua, C., Parsek, M. R. & Peterson, S. B. (2010) Bacterial competition: surviving and thriving in  
945 the microbial jungle. *Nature Reviews Microbiology*, 8, 15-25.
- 946 Holland, E. A., Post, W. M., Matthews, E., Sulzman, J., Staufer, R. & Krankina, O. (2015). A Global Database of



---

947 Litterfall Mass and Litter Pool Carbon and Nutrients. Data set. Available on-line [<http://daac.ornl.gov>]  
948 from Oak Ridge National Laboratory Distributed Active Archive Center. In, Oak Ridge, Tennessee,  
949 USA.

950 Huang, Y., Guenet, B., Ciais, P., Janssens, I.A., Soong, J. L., Wang, Y., Goll, D., Blagodatskaya, E. & Huang, Y.  
951 (2018). ORCHIMIC (v1.0), A microbe-driven model for soil organic matter decomposition designed for  
952 large-scale applications. *Geoscientific Model Development*, 11, 2111-2138.

953 Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C.,  
954 Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M. & Violle, C. (2017).  
955 A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New*  
956 *Phytologist*, 215, 15-26.

957 Jenkinson, D. & Rayner, J. (1977). The turnover of soil organic matter in some of the Rothamsted classical  
958 experiments. *Soil Science*, 123, 298-305.

959 Jia, B., Zhou, G. & Xu, Z. (2016). Forest litterfall and its composition: a new data set of observational data from  
960 China. *Ecology*, 97, 1365.

961 Jobbágy, E. G. & Jackson, R. B. (2000). The Vertical Distribution of Soil Organic Carbon and Its Relation to  
962 Climate and Vegetation. *Ecological Applications*, 10, 423-436.

963 Jung, M., Reichstein, M., Ciais, P., Seneviratne, S.I., Sheffield, J., Goulden, M. L., Bonan, G., Cescatti, A., Chen,  
964 J., de Jeu, R., Dolman, A. J., Eugster, W., Gerten, D., Gianelle, D., Gobron, N., Heinke, J., Kimball, J.,  
965 Law, B. E., Montagnani, L., Mu, Q., Mueller, B., Oleson, K., Papale, D., Richardson, A. D., Rouspard,  
966 O., Running, S., Tomelleri, E., Viovy, N., Weber, U., Williams, C., Wood, E., Zaehle, S. & Zhang, K.  
967 (2010). Recent decline in the global land evapotranspiration trend due to limited moisture supply. *Nature*,  
968 467, 951-954.

969 Kaiser, C., Franklin, O., Dieckmann, U. & Richter, A. (2014). Microbial community dynamics alleviate  
970 stoichiometric constraints during litter decay. *Ecology Letters*, 17, 680-690.

971 Kaiser, C., Franklin, O., Richter, A. & Dieckmann, U. (2015). Social dynamics within decomposer communities  
972 lead to nitrogen retention and organic matter build-up in soils. *Nat Commun*, 6, 8960.

973 Kallenbach, C., Frey, S. & Grandy, S. (2016). Direct evidence for microbial-derived soil organic matter formation  
974 and its ecophysiological controls. *Nature Communications*, 7, 13630.

975 Kattge, J., *et al.* (2011). TRY - a global database of plant traits. *Global Change Biology*, 17, 2905-2935.

976 Kothawala, D. N., Moore, T. R. & Hendershot, W. H. (2008). Adsorption of dissolved organic carbon to mineral

- 
- 977 soils: A comparison of four isotherm approaches. *Geoderma*, 148, 43-50.
- 978 Koven, C. D., Lawrence, D. M., & Riley, W. J. (2015). Permafrost carbon–climate feedback is sensitive to deep  
979 soil carbon decomposability but not deep soil nitrogen dynamics. *Proceedings of the National Academy  
980 of Sciences*, 112, 3752-3757.
- 981 Koven, C. D., Riley, W. J., Subin, Z. M., Tang, J. Y., Torn, M. S. Collins, W. D., Bonan, G. B., Lawrence, D. M.  
982 & Swenson, S. C. (2013). The effect of vertically resolved soil biogeochemistry and alternate soil C and  
983 N models on C dynamics of CLM4. *Biogeosciences*, 10, 7109-7131.
- 984 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S. &  
985 Prentice, I.C. (2005). A dynamic global vegetation model for studies of the coupled  
986 atmosphere-biosphere system. *Global Biogeochemical Cycles*, 19
- 987 Kuzyakov, Y. (2010). Priming effects: Interactions between living and dead organic matter. *Soil Biology and  
988 Biochemistry*, 42, 1363-1371.
- 989 Lützw, M. v., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E. & Marschner, B.  
990 (2007). SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. *Soil  
991 Biology and Biochemistry*, 39, 2183-2207.
- 992 Lützw, M. v., Kogel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B. & Flessa, H.  
993 (2006). Stabilization of organic matter in temperate soils: mechanisms and their relevance under  
994 different soil conditions - a review. *European Journal of Soil Science*, 57, 426-445.
- 995 Lal, R. (2016). Beyond COP 21: Potential and challenges of the "4 per Thousand" initiative. *Journal of Soil and  
996 Water Conservation*, 71, 20A-25A.
- 997 Lehmann, J. & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, 528, 60-68.
- 998 Liang, S., Zhao, X., Liu, S., Yuan, W., Cheng, X., Xiao, Z., Zhang, X., Liu, Q., Cheng, J., Tang, H., Qu, Y., Bo, Y.,  
999 Qu, Y., Ren, H., Yu, K. & Townshend, J. (2013). A long-term Global LAnd Surface Satellite (GLASS)  
1000 data-set for environmental studies. *International Journal of Digital Earth*, 6, 5-33.
- 1001 Manzoni, S. & Porporato, A. (2009). Soil carbon and nitrogen mineralization: Theory and models across scales.  
1002 *Soil Biology and Biochemistry*, 41, 1355-1379.
- 1003 Manzoni, S., Moyano, F., Kätterer, T. & Schimel, J. (2016). Modeling coupled enzymatic and solute transport  
1004 controls on decomposition in drying soils. *Soil Biology and Biochemistry*, 95, 275-287.
- 1005 Manzoni, S., Taylor, P., Richter, A., Porporato, A. & Agren, G. I. (2012). Environmental and stoichiometric  
1006 controls on microbial carbon-use efficiency in soils. *New Phytologist*, 196, 79-91.

- 
- 1007 Manzoni, S., Capek, P., Mooshammer, M., Lindahl, B. D., Richter, A. & Santruckova, H. (2017). Optimal  
1008 metabolic regulation along resource stoichiometry gradients. *Ecol Lett*, 20, 1182-1191.
- 1009 McGuire, A. D., Lawrence, D. M., Koven, C., Clein, J. S., Burke, E., Chen, G. & Zhuang, Q. (2018). Dependence  
1010 of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate  
1011 change. *Proceedings of the National Academy of Sciences*. 115, 3882-3887.
- 1012 Muttil, N. & Jayawardena, A. W. (2008). Shuffled Complex Evolution model calibrating algorithm: enhancing its  
1013 robustness and efficiency. *Hydrological Processes*, 22, 4628-4638.
- 1014 Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., King, J. Y., Adair, E. C.,  
1015 Brandt, L.A., Hart, S. C. & Fasth, B. (2007). Global-scale similarities in nitrogen release patterns during  
1016 long-term decomposition. *Science*, 315, 361-364.
- 1017 Parton, W. J., Schimel, D. S., Cole, C. V. & Ojima, D. S. (1987). Analysis of Factors Controlling Soil Organic  
1018 Matter Levels in Great Plains Grasslands I. *Soil Science Society of America Journal*, 51, 1173-1179.
- 1019 Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C.,  
1020 Crow, S. E., Druhan, J. L., Hicks Pries, C. E., Marin-Spiotta, E., Plante, A.F., Schädel, C., Schimel, J. P.,  
1021 Sierra, C. A., Thompson, A. & Wagai, R. (2018). Beyond clay: towards an improved set of variables for  
1022 predicting soil organic matter content. *Biogeochemistry*, 137, 297-306.
- 1023 Robertson, A. D., Paustian, K., Ogle, S., Wallenstein, M. D., Lugato, E. & Cotrufo, M. F. (2019). Unifying soil  
1024 organic matter formation and persistence frameworks: the MEMS model. *Biogeosciences*, 16,  
1025 1225-1248.
- 1026 Schimel, D. S., Braswell, B. H., Holland, E. A., McKeown, R., Ojima, D. S., Painter, T. H., Parton, W. J. &  
1027 Townsend, A. R. (1994). Climatic, edaphic, and biotic controls over storage and turnover of carbon in  
1028 soils. *Global Biogeochemical Cycles*, 8, 279-293.
- 1029 Schimel, J. P. & Weintraub, M. N. (2003). The implications of exoenzyme activity on microbial carbon and  
1030 nitrogen limitation in soil: a theoretical model. *Soil Biology and Biochemistry*, 35, 549-563.
- 1031 Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M.,  
1032 Kogel-Knabner, I., Lehmann, J., Manning, D. A., Nannipieri, P., Rasse, D. P., Weiner, S. & Trumbore,  
1033 S.E. (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, 478, 49-56.
- 1034 Shangguan, W., Dai, Y., Duan, Q., Liu, B. & Yuan, H. (2014). A global soil data set for earth system modeling.  
1035 *Journal of Advances in Modeling Earth Systems*, 6, 249-263.
- 1036 Shi, Z., Crowell, S., Luo, Y. & Moore, B., III. (2018). Model structures amplify uncertainty in predicted soil

- 
- 1037 carbon responses to climate change. *Nature Communications*, 9, 2171.
- 1038 Sierra, C. A., Trumbore, S. E., Davidson, E. A., Vicca, S. & Janssens, I. (2015). Sensitivity of decomposition rates  
1039 of soil organic matter with respect to simultaneous changes in temperature and moisture. *Journal of*  
1040 *Advances in Modeling Earth Systems*, 7, 335-356.
- 1041 Six, J., Bossuyt, H., Degryze, S. & Denef, K. (2004). A history of research on the link between (micro)aggregates,  
1042 soil biota, and soil organic matter dynamics. *Soil and Tillage Research*, 79, 7-31.
- 1043 Six, J., Feller, C., Denef, K., Ogle, S.M., de Moraes, J.C. & Albrecht, A. (2002). Soil organic matter, biota and  
1044 aggregation in temperate and tropical soils - Effects of no-tillage. *Agronomie*, 22, 755-775.
- 1045 Six, J. & Paustian, K. (2014) Aggregate-associated soil organic matter as an ecosystem property and a  
1046 measurement tool. *Soil Biology & Biochemistry*, 68, A4-A9.
- 1047 Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W.,  
1048 Sykes, M. T., Thonicke, K., & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography  
1049 and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9,  
1050 161–185.
- 1051 Sokol, N. W., Sanderman, J. & Bradford, M. A. (2019). Pathways of mineral-associated soil organic matter  
1052 formation: Integrating the role of plant carbon source, chemistry, and point of entry. *Global Change*  
1053 *Biology*, 25, 12-24.
- 1054 Stewart, C. E., Paustian, K., Conant, R. T., Plante, A. F. & Six, J. (2007). Soil carbon saturation: concept, evidence  
1055 and evaluation. *Biogeochemistry*, 86, 19-31.
- 1056 Stewart, C. E., Plante, A. F., Paustian, K., Conant, R. T. & Six, J. (2008). Soil Carbon Saturation: Linking Concept  
1057 and Measurable Carbon Pools. *Soil Science Society of America Journal*, 72, 379.
- 1058 Stockmann, U., Adams, M. A., Crawford, J. W., Field, D. J., Henakaarchchi, N., Jenkins, M., Minasny, B.,  
1059 McBratney, A. B., Courcelles, V. d. R. d., Singh, K., Wheeler, I., Abbott, L., Angers, D. A., Baldock, J.,  
1060 Bird, M., Brookes, P. C., Chenu, C., Jastrow, J. D., Lal, R., Lehmann, J., O'Donnell, A. G., Parton, W. J.,  
1061 Whitehead, D. & Zimmermann, M. (2013). The knowns, known unknowns and unknowns of  
1062 sequestration of soil organic carbon. *Agriculture, Ecosystems & Environment*, 164, 80-99.
- 1063 Tang, J. & Zhuang, Q. (2013). A global sensitivity analysis and Bayesian inference framework for improving the  
1064 parameter estimation and prediction of a process-based Terrestrial Ecosystem Mode. *Journal of*  
1065 *Geophysical Research: Atmospheres*, D15303. doi:10.1029/2009JD011724
- 1066 Tang, X., Zhao, X., Bai, Y., Tang, Z., Wang, W., Zhao, Y., Wan, H., Xie, Z., Shi, X., Wu, B., Wang, G., Yan, J.,

- 
- 1067 Ma, K., Du, S., Li, S., Han, S., Ma, Y., Hu, H., He, N., Yang, Y., Han, W., He, H., Yu, G., Fang, J. &  
1068 Zhou, G. (2018). Carbon pools in China's terrestrial ecosystems: New estimates based on an intensive  
1069 field survey. *Proc Natl Acad Sci U S A*, 115, 4021-4026.
- 1070 Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G. & Zimov, S. (2009). Soil organic carbon  
1071 pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23, GB2023,  
1072 doi:10.1029/2008GB003327
- 1073 Thornton, P. E. & Rosenbloom, N. A. (2005). Ecosystem model spin-up: Estimating steady state conditions in a  
1074 coupled terrestrial carbon and nitrogen cycle model. *Ecological Modelling*, 189, 25-48.
- 1075 Tifafi, M., Guenet, B. & Hatté C. (2018). Large Differences in Global and Regional Total Soil Carbon Stock  
1076 Estimates Based on SoilGrids, HWSD, and NCSCD: Intercomparison and Evaluation Based on Field  
1077 Data From USA, England, Wales, and France. *Global Biogeochemical Cycles*, 32, 42-56.
- 1078 Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. A. G. & Allison, S.  
1079 D. (2013). Causes of variation in soil carbon simulations from CMIP5 Earth system models and  
1080 comparison with observations. *Biogeosciences*, 10, 1717-1736.
- 1081 Tucker, C. J., Pinzon, J. E., Brown, M. E., Slayback, D. A., Pak, E. W., Mahoney, R., Vermote, E. F. & El Saleous,  
1082 N. (2005). An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation  
1083 NDVI data. *International Journal of Remote Sensing*, 26, 4485-4498.
- 1084 Ukonmaanaho, L., Pitman, R., Bastrup-Birk, A., Breda, N. & Rautio, P. (2016). Part XIII: Sampling and Analysis  
1085 of Litterfall. In: UNECE ICP Forests Programme Co-ordinating Centre (ed.): Manual on methods and  
1086 criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on  
1087 forests. In, Thünen Institute for Forests Ecosystems, Eberswalde, Germany.
- 1088 Viovy, N. (2018). CRUNCEP Version 7 - Atmospheric Forcing Data for the Community Land Model. Research  
1089 Data Archive at the National Center for Atmospheric Research,. In, Computational and Information  
1090 Systems Laboratory. <http://rda.ucar.edu/datasets/ds314.3/>.
- 1091 Viscarra Rossel, R. A. & Hicks, W. S. (2015). Soil organic carbon and its fractions estimated by visible-near  
1092 infrared transfer functions. *European Journal of Soil Science*, 66, 438-450.
- 1093 Viscarra Rossel, R. A., Lee, J., Berhrens, T., Luo, Z., Baldock, J. & Richards, A. (2019). Continental-scale soil  
1094 carbon composition and vulnerability modulated by regional environmental controls. *Nature Geoscience*,  
1095 12, 547-552.
- 1096 Wagner, S., Cattle, S. R. & Scholten, T. (2007). Soil-aggregate formation as influenced by clay content and

- 
- 1097 organic-matter amendment. *Journal of Plant Nutrition and Soil Science*, 170, 173-180.
- 1098 Wang, G., Post, W. M. & Mayes, M. A. (2013). Development of microbial-enzyme-mediated decomposition  
1099 model parameters through steady-state and dynamic analyses. *Ecological Applications*, 23, 255-272.
- 1100 Wang, Q., He, T. & Liu, J. (2016). Litter input decreased the response of soil organic matter decomposition to  
1101 warming in two subtropical forest soils. *Scientific Reports*, 6, 33814.
- 1102 Wang, Y. P., Chen, B.C., Wieder, W. R., Leite, M., Medlyn, B. E., Rasmussen, M., Smith, M. J., Agosto, F. B.,  
1103 Hoffman, F. & Luo, Y. Q. (2014). Oscillatory behavior of two nonlinear microbial models of soil carbon  
1104 decomposition. *Biogeosciences*, 11, 1817-1831.
- 1105 Wieder, W. R., Bonan, G. B. & Allison, S.D. (2013). Global soil carbon projections are improved by modelling  
1106 microbial processes. *Nature Climate Change*, 3, 909-912.
- 1107 Wieder, W. R., Boehner, J. & Bonan, G. B. (2014a). Evaluating soil biogeochemistry parameterizations in Earth  
1108 system models with observations. *Global Biogeochemical Cycles*, 28, 211-222.
- 1109 Wieder, W. R., Grandy, A. S., Kallenbach, C. M. & Bonan, G. B. (2014b). Integrating microbial physiology and  
1110 physio-chemical principles in soils with the Microbial-MIneral Carbon Stabilization (MIMICS) model.  
1111 *Biogeosciences*, 11, 3899-3917.
- 1112 Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G. & Bonan, G. B. (2015). Representing life in the  
1113 Earth system with soil microbial functional traits in the MIMICS model. *Geoscientific Model  
1114 Development*, 8, 1789-1808.
- 1115 Wieder, W. R., Hartman, M. D., Sulman, B. N., Wang, Y-P, Koven, C. D. & Bonan, G. B. (2018). Carbon cycle  
1116 confidence and uncertainty: Exploring variation among soil biogeochemical models. *Global Change  
1117 Biology*, 24, 1563-1579.
- 1118 Wu, D., Piao, S., Liu, Y., Ciais, P. & Yao, Y. (2018). Evaluation of CMIP5 Earth System Models for the Spatial  
1119 Patterns of Biomass and Soil Carbon Turnover Times and Their Linkage with Climate. *Journal of  
1120 Climate*, 31, 5947-5960.
- 1121 Xia, J. Y., Luo, Y. Q., Wang, Y. P., Weng, E. S. & Hararuk, O. (2012). A semi-analytical solution to accelerate  
1122 spin-up of a coupled carbon and nitrogen land model to steady state. *Geoscientific Model Development*,  
1123 5, 1259-1271.
- 1124 Xu, X., Thornton, P. E. & Post, W. M. (2013). A global analysis of soil microbial biomass carbon, nitrogen and  
1125 phosphorus in terrestrial ecosystems. *Global Ecology and Biogeography*, 22, 737-749.
- 1126 Zhang, H., Yuan, W., Dong, W. & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide.

1127 *Ecological Complexity*, 20, 240-247.

1128 Zhang, H., Goll, D. S., Manzoni, S., Ciais, P., Guenet, B. & Huang, Y. (2018). Modeling the effects of litter  
1129 stoichiometry and soil mineral N availability on soil organic matter formation using CENTURY-CUE  
1130 (v1.0). *Geoscientific Model Development*, 11, 4779-4796.

1131

1132 **Table**

1133

1134 **Table 1** Tested models in this study and parameters subject to optimization of each  
1135 model.  $k_{litt}$  and  $k_{soc}$  tune the turnover rate of litter and SOC pools in CENTURY,  
1136 respectively.  $a_v$  and  $a_k$  are parameters tune microbial maximum reaction velocity (Eq.  
1137 4) and half-saturation constant (Eq. 5).  $k_d$ ,  $k_{dp}$  and  $k_{bs}$  tune the deprotection rate of  
1138 SOC<sub>p</sub> (Eqs. 13-15).  $\beta$  tunes the density-dependent microbial turnover rate (Eq. 16).

Model	Optimized parameters
CENTURY	$k_{litt}, k_{soc}$
MIMICS-def	$a_v, a_k, k_d$
MIMICS-D	$a_v, a_k, k_d, k_{dp}$
MIMICS-DB	$a_v, a_k, k_d, k_{dp}, k_{bs}$
MIMICS-DBT	$a_v, a_k, k_d, k_{dp}, k_{bs}, \beta$

1139

1140

1141 **Figure**

1142 **Figure 1** Soil C pools and fluxes represented in CENTURY (a) and MIMICS (b). In  
1143 both models, litter inputs ( $Lit_{inp}$ ) are partitioned into metabolic and structural litter  
1144 pools ( $LIT_m$  and  $LIT_s$ ) based on litter quality ( $f_{met}$ ). The soil organic carbon (SOC) in  
1145 CENTURY are divided into active ( $SOC_{act}$ ), slow ( $SOC_{slow}$ ) and passive ( $SOC_{pas}$ )  
1146 pools. CUE is the carbon use efficiency of decomposed litter or SOC. In MIMICS,  
1147 decomposition of litter and available SOM pools ( $SOC_a$ ) are governed by temperature  
1148 sensitive Michaelis–Menten kinetics ( $V_{max}$  and  $K_m$ ). Microbial growth efficiency  
1149 (MGE) determines the partitioning of C fluxes entering microbial biomass pools vs.

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1150 heterotrophic respiration. Turnover of the microbial biomass ( $\tau$ ) depends on microbial  
1151 functional type ( $MIC_r$  and  $MIC_k$ ), and is partitioned into available, physically and  
1152 physicochemically protected, and chemically recalcitrant SOC pools ( $SOC_a$ ,  $SOC_p$ ,  
1153 and  $SOC_c$ , respectively).  $f_{i,met}$  and  $f_{i,STRU}$  denote the fraction of decomposed metabolic  
1154 litter to  $SOC_p$  and the fraction of decomposed structural litter to  $SOC_c$ , respectively.  $f_p$   
1155 and  $f_c$  denote the fraction of  $\tau$  partitioned to  $SOC_p$  and the fraction of  $\tau$  partitioned to  
1156  $SOC_c$ , respectively.

1157

1158 **Figure 2** Comparison of CENTURY (a) and MIMICS (b-e) for simulating large-scale  
1159 variation of SOC concentrations across the 206 forest sites in Europe and China.

1160 RMSE is the root mean square error, and AIC is the Akaike information criterion.

1161 MIMICS versions include the default model (MIMICS-def), revised SOC

1162 deprotection rate (MIMICS-D), using base saturation to modify deprotection rates

1163 (MIMICS-DB); and density-dependent microbial turnover rate (MIMICS-DBT; see

1164 section 2.2.2).

1165

1166 **Figure 3** Partial correlation coefficients between the biases of simulated SOC

1167 concentrations and the climate condition, amount and quality of litter input, and soil

1168 physical and chemical properties. MAT: mean annual temperature ( $^{\circ}C$ ), MAP: mean

1169 annual total precipitation (mm), MAP-PET: the difference between annual total

1170 precipitation and potential evapotranspiration (mm), ET: evapotranspiration (mm),

1171  $LAI_{max}$ : mean of the annual maximum leaf area index at the observation site during

1172 the period from 1982 to 2000,  $LAI_{trend}$ : change trend of the  $LAI_{max}$  during the period

1173 from 1982 to 2000 ( $yr^{-1}$ ),  $NDVI_{max}$ : mean of the annual maximum normalized

1174 difference vegetation index at the observation site during the period from 1982 to

1175 2000,  $NDVI_{trend}$ : change trend of the  $NDVI_{max}$  during the period from 1982 to 2000

1176 ( $yr^{-1}$ ),  $litter_{ab}$ : aboveground litter-C stock ( $g\ C\ m^{-2}$ ), SWC: soil water content, BD:

1177 bulk density ( $g\ cm^{-3}$ ), BS: base saturation (0-1, dimensionless), CEC: Cation of

1178 exchange capacity ( $cmol\ kg^{-1}$ ). Partial correlation coefficients between -0.14 and 0.14

1179 were not significant ( $p > 0.05$ ).



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1180

1181 **Figure 4** Sensitivity of simulated SOC concentration to mean annual temperature  
1182 ( $S_{MAT}$ , a), soil water content ( $S_{SWC}$ , b), soil clay fraction ( $S_{clay}$ , c), annual litterfall  
1183 input ( $S_{litterfall}$ , d), the C:N ratio of litterfall ( $S_{C:N}$ , e) and the lignin:C ratio of litterfall  
1184 ( $S_{lignin:C}$ , f). The blue and red dashed lines denote insignificant and significant ( $p < 0.05$ )  
1185 sensitivity calculated based on observation data, respectively. The solid line in each  
1186 box denotes the median value. Box boundaries show the 25<sup>th</sup> and 75<sup>th</sup> percentiles,  
1187 whiskers denote the 10<sup>th</sup> and 90<sup>th</sup> percentiles, and the black dots denote the 5<sup>th</sup> and  
1188 95<sup>th</sup> percentiles.

1189

1190 **Figure 5** Comparison between the simulated ratio of microbial C (MIC) to total SOC  
1191 from different versions of MIMICS and the observed values at globally-distributed  
1192 forest sites. The dashed and solid lines in each box are the mean and median value,  
1193 respectively. Box boundaries show the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers denote the  
1194 10<sup>th</sup> and 90<sup>th</sup> percentiles, the dots below and above each box denote the 5<sup>th</sup> and 95<sup>th</sup>  
1195 percentiles, respectively. The 655 samples of observed MIC/SOC at  
1196 globally-distributed forest sites are collected by Xu et al., 2013.

1197

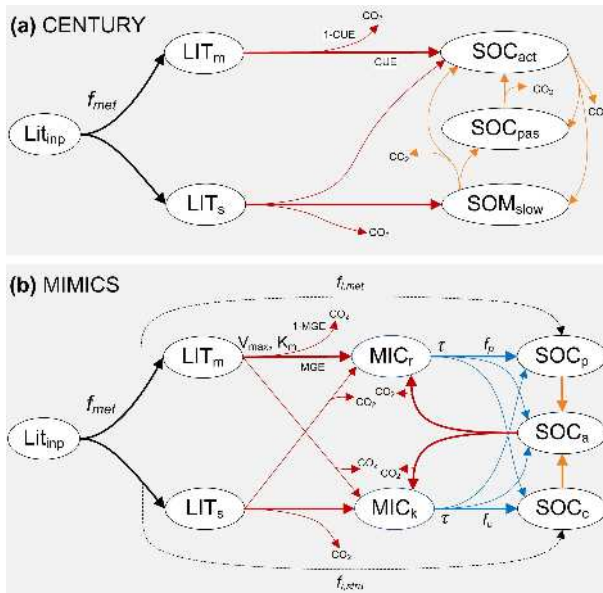
1198 **Figure 6** Comparison between the simulated SOC compositions from optimized  
1199 MIMICS (a) and CENTURY (b) model and the observed SOC compositions at 505  
1200 sites in Australia (c). The observation data in Australia are obtained from  
1201 Viscarra-Rossel et al. (2019). Viscarra-Rossel et al. partitioned total SOC into three  
1202 fractions with different particle-sizes: the particulate organic carbon (POC), the humic  
1203 organic carbon (HOC) and the resistant organic carbon (ROC, which is the  
1204 mineral-associated organic carbon). The line in each box denotes median value. Box  
1205 boundaries show the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers denote the 10<sup>th</sup> and 90<sup>th</sup>  
1206 percentiles, and the dots below and above each box denote the 5<sup>th</sup> and 95<sup>th</sup> percentiles.

1207

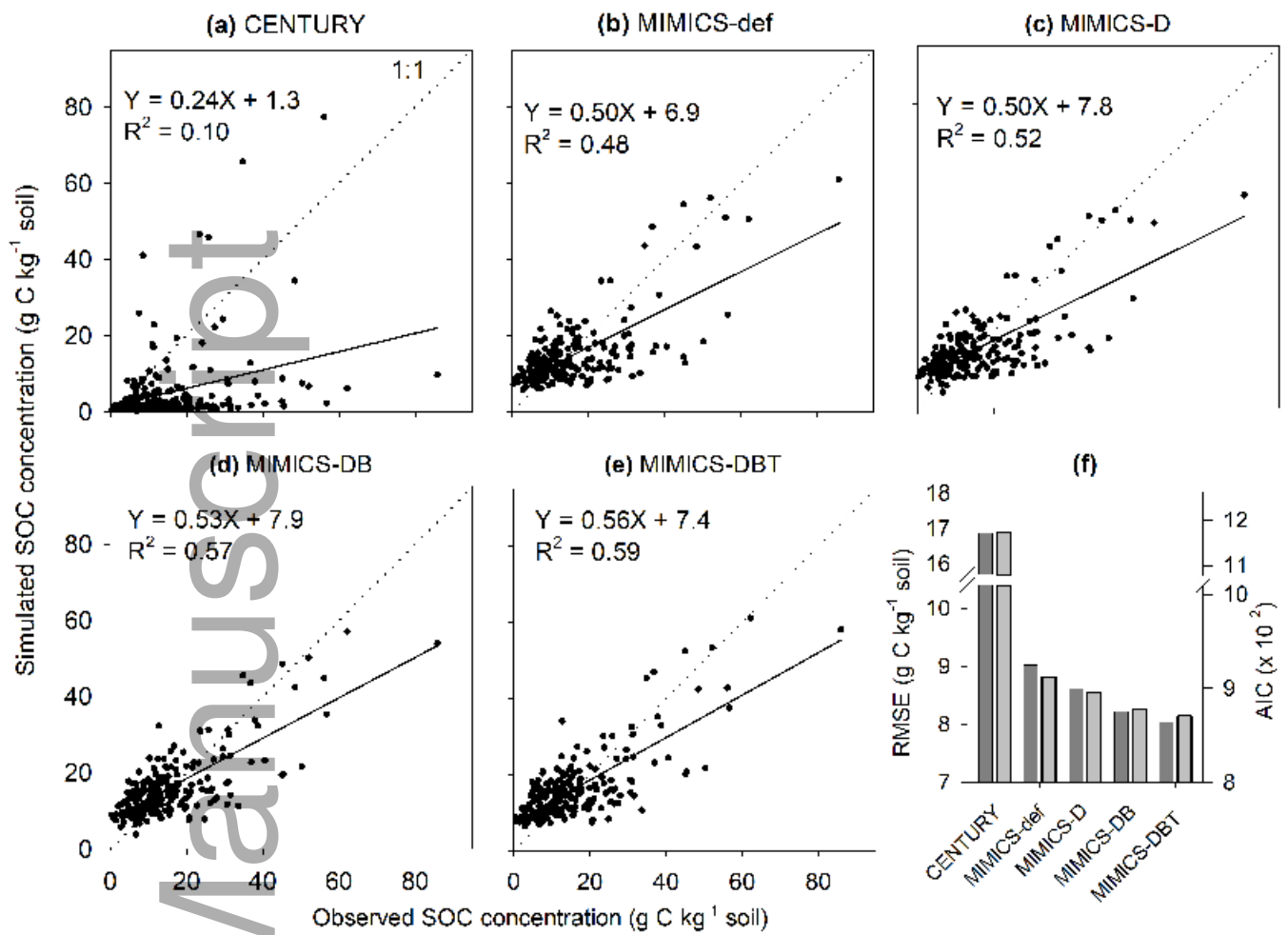
1208 **Figure 7** Partial correlation coefficients between fraction of each SOC pool and  
1209 model drivers, including mean annual temperature (MAT, °C), soil water content

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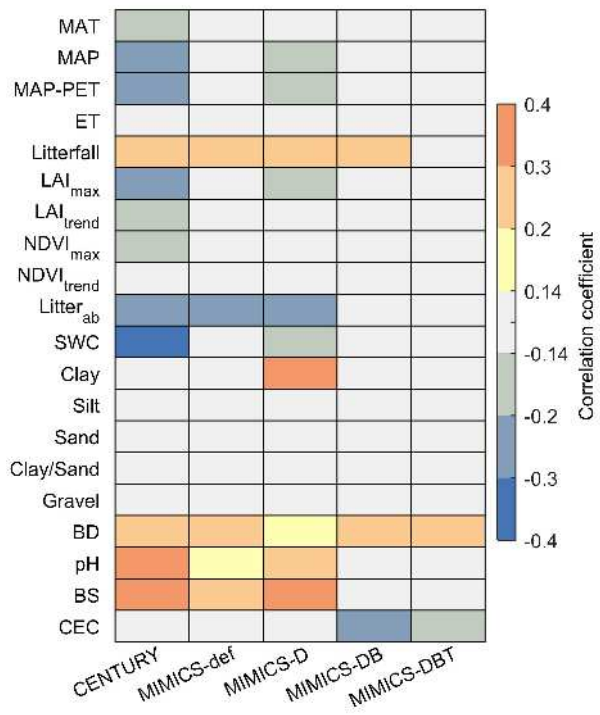
1210 (SWC, dimensionless), soil clay content (clay, dimensionless), annual total litterfall  
1211 production (Litterfall,  $\text{g C m}^{-2} \text{ yr}^{-1}$ ), litter C:N ratio (C:N), litter lignin:C ratio  
1212 (Lignin:C), base saturation (BS, 0-1, dimensionless) and total SOC concentration  
1213 (SOC), Figure (a) Obs show the results based on observation data from Australia.  
1214 Figure (b)-(f) showed the results based on optimized CENTURY and MIMICS  
1215 models. Partial correlation coefficients between -0.14 and 0.14 were not significant  
1216 ( $p > 0.05$ ).



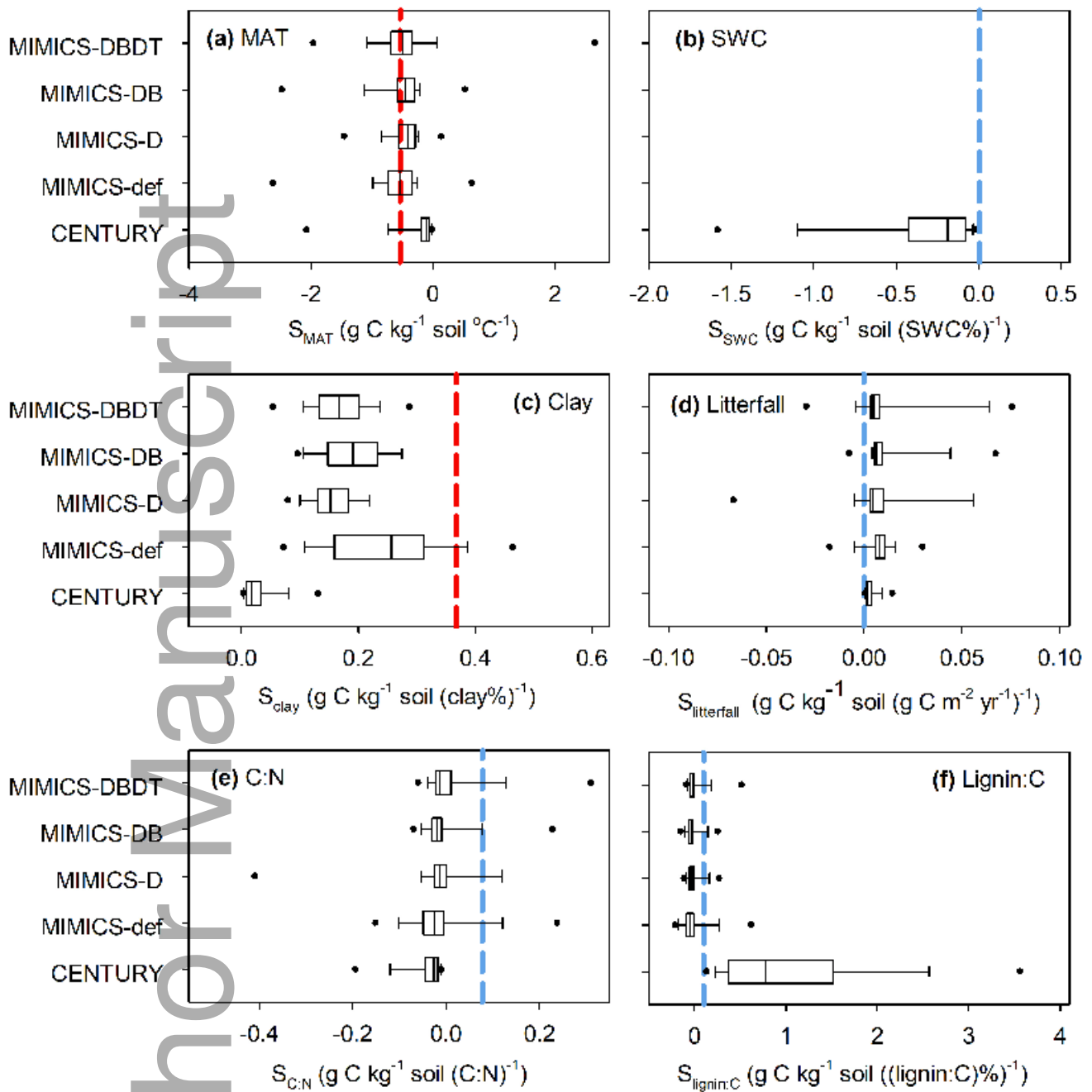
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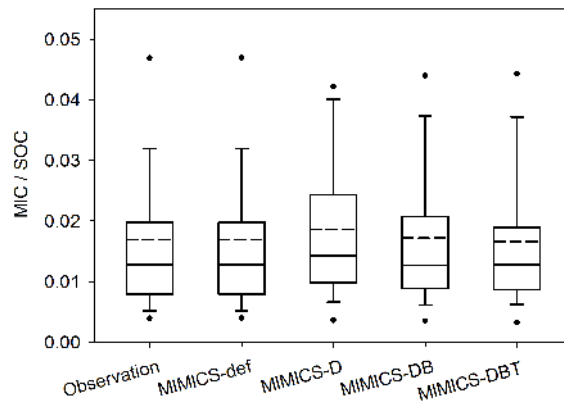
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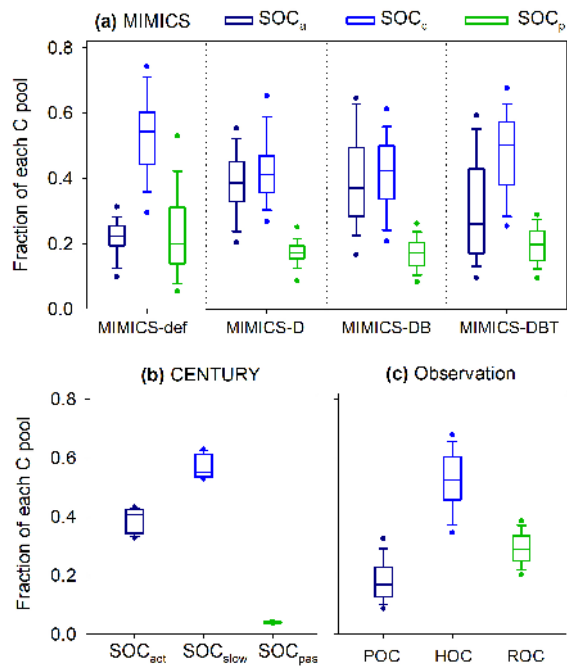
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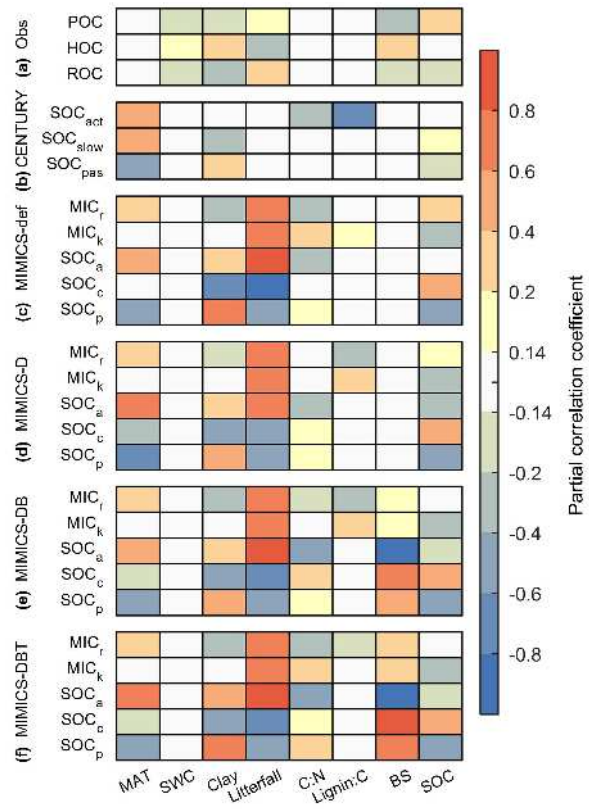


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