



1 **Modeling the effects of litter stoichiometry and soil mineral N**
2 **availability on soil organic matter formation**

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15 Type: primary research

16



17 **Abstract**

18 Microbial decomposition of plant litter is a crucial process for the land
19 carbon (C) cycle, as it directly controls the partitioning of litter-C between CO₂
20 released to the atmosphere versus the formation of new soil organic matter (SOM).
21 Land surface models used to study the C cycle rarely considered flexibility in the
22 decomposer C use efficiency (CUE_d) defined by the fraction of decomposed litter-C
23 that is retained as SOM (as opposed to be respired). In this study, we adapted a
24 conceptual formulation of CUE_d based on assumption that litter decomposers
25 optimally adjust their CUE_d as a function of litter substrate C to nitrogen (N)
26 stoichiometry to maximize their growth rates. This formulation was incorporated into
27 the widely used CENTURY soil biogeochemical model and evaluated based on data
28 from laboratory litter incubation experiments. Results indicated that the CENTURY
29 model with new CUE_d formulation was able to reproduce differences in respiration
30 rate of litter with contrasting C:N ratios and under different levels of mineral N
31 availability, whereas the default model with fixed CUE_d could not. Using the model
32 with adapted CUE_d formulation, we also illustrated that litter quality affected the
33 long-term SOM formation crucially. Litter with a small C:N ratio tended to form a
34 larger SOM pool than litter with larger C:N ratios, as it could be more efficiently
35 incorporated into SOM by microorganisms. This study provided a simple but effective
36 formulation to quantify the effect of varying litter quality (N content) on SOM
37 formation across temporal scales. Optimality theory appears to be suitable to predict
38 complex processes of litter decomposition into soil C, and to quantify how plant
39 residues and manure can be harnessed to improve soil C sequestration for climate
40 mitigation.

41

42 *Keywords:* microbial carbon use efficiency, litter decomposition, litter stoichiometry,
43 soil organic matter, litter decay model, nitrogen

44



45 **1 Introduction**

46 Plant litter decomposition plays a key role in global carbon (C) cycle, thus
47 needs to be well represented in land surface models. The decomposition and
48 transformation processes of plant litter control the formation of soil organic matter
49 (SOM) (Prescott, 2010; Schmidt *et al.*, 2011; Walela *et al.*, 2014; Cotrufo *et al.*, 2015)
50 and associate immobilization and mineralization of essential plant nutrients
51 (Moorhead and Sinsabaugh, 2006; Parton *et al.*, 2007; Manzoni *et al.*, 2008; Manzoni
52 and Porporato, 2009). Hence a reliable litter decay model is necessary for estimating
53 soil C balance and turnover of ecosystem C (Allison, 2012; Bonan *et al.*, 2013;
54 Wieder *et al.*, 2013; Campbell and Paustian, 2015). In particular, a realistic
55 representation of litter decomposition process in land surface models is also helpful to
56 decrease the uncertainties in predicted effects of climate change and anthropogenic
57 management on ecosystems (Gholz *et al.*, 2000; Campbell and Paustian, 2015; Luo *et al.*,
58 2016). As litter decomposition is a very complex process determined by climate
59 (e.g. temperature and moisture), litter quality (e.g. nitrogen (N) concentration), soil
60 nutrients and the physiological characteristics of microorganisms (Lekkerkerk *et al.*,
61 1990; Prescott, 2010; Manzoni *et al.*, 2012; Frey *et al.*, 2013; Sinsabaugh *et al.*, 2013;
62 Garc ía-Palacios *et al.*, 2016), there remain large uncertainties in existing litter decay
63 models (Zhang *et al.*, 2008; Bonan *et al.*, 2013; Campbell and Paustian, 2015). Many
64 litter decay models, especially those incorporated in global land surface models, have
65 ignored microbial mechanisms related to stoichiometry (Bonan *et al.*, 2013; Cotrufo
66 *et al.*, 2013; Wieder *et al.*, 2013; Wieder *et al.*, 2014).

67 Microbial carbon use efficiency (CUE), defined as the ratio of microbial
68 biomass production to material uptake from substrates (Lekkerkerk *et al.*, 1990;
69 Manzoni *et al.*, 2012), is an important emerging property of litter decay, however it
70 has rarely been represented in land surface models. During litter decomposition, only a
71 part of the decomposed litter-C is being transferred into SOM, while the remaining C is
72 being released as CO₂ to the atmosphere by microbial respiration. While CUE is a
73 physiological property of each decomposer community, it also determines the



74 ecosystem-level efficiency at which litter C is transferred into SOM a step further from
75 simple microbial incorporation. We denote this efficiency as carbon use efficiency of
76 litter decomposition (CUE_d). With higher CUE_d , more plant-produced litter is
77 transformed biologically into SOM, and soil C storage can reach higher values (Six *et al.*,
78 2006; Sinsabaugh *et al.*, 2013). In most existing soil biogeochemical models,
79 CUE_d of decomposition is assumed to be same to microbial CUE and considered as a
80 fixed parameter. The Verberne model (Verberne *et al.*, 1990) assumes for instance
81 $CUE_d \approx 0.25$. In the Yasso model (Liski *et al.*, 2005), the CUE_d is set to 0.2. The
82 CENTURY model (Parton *et al.*, 1988) sets the CUE_d for decomposition of surface
83 and belowground metabolic litter to 0.55 and 0.45, respectively. In Daisy (Hansen *et al.*,
84 1991), NCSOIL (Molina *et al.*, 1983) and ICBM (Kätterer and Andr n, 2001),
85 $CUE_d = 0.6$ for the labile litter pools and takes a lower value for recalcitrant substrates.
86 Only a few models account for variable CUE_d , letting it vary in response to substrate
87 stoichiometry (Schimel and Weintraub, 2003) or temperature (Allison *et al.*, 2010).

88 The increasing evidence for a variable microbial CUE leads to a conceptual
89 CUE model which can explain trends in CUE of microorganisms along stoichiometric
90 gradients (Manzoni *et al.*, 2017). The values of CUE_d used in existing litter decay
91 models are mostly derived from laboratory study on microbial physiology or limited
92 observations at some certain ecosystems, thus show large variations (Parton *et al.*,
93 1988; Verberne *et al.*, 1990; Hansen *et al.*, 1991; Liski *et al.*, 2005; Manzoni *et al.*,
94 2012). Recent studies (Manzoni *et al.*, 2008, 2012) suggested that the microbial CUE
95 of terrestrial ecosystems ranges from less than 0.1 for wood decomposers to about 0.5
96 for decomposition of N-rich and high-quality litter. To explain those differences,
97 Manzoni *et al.* (2017) proposed a conceptual model of microbial CUE based on the
98 assumption that decomposers seek to reach an optimum (maximum) growth rate. This
99 model based on optimality theory links CUE to substrate and decomposers
100 stoichiometry, where the optimal CUE decreases with increasing substrate
101 C-to-nutrient ratio, and increases with soil nutrient availability. The predictions of this
102 theoretical model have been verified by empirical evidence from CUE estimates for
103 different microorganisms in both aquatic and terrestrial ecosystems (Manzoni *et al.*,



104 2017).

105 Besides variable CUE_d, many previous studies have also indicated the
106 necessity for litter decomposition models to consider soil mineral N availability as a
107 driver of litter decomposition rates, in particular under low N availability (Wieder *et*
108 *al.*, 2015; Luo *et al.*, 2016; Averill and Waring, 2018). Biomass of microbes is
109 stoichiometrically constrained (Cleveland and Liptzin, 2007; Franklin *et al.*, 2011;
110 Allison, 2012). When the supply of N from substrates is lower than the demand of
111 microbes to fulfill their specific stoichiometric C:N ratio, microbes will utilize the
112 mineral N (immobilization) (Manzoni *et al.*, 2012). Thus low availability of mineral
113 N can limit microbial activity, and in turn litter decay rate (Manzoni and Porporato
114 2009; Fujita *et al.*, 2014). Although there are fertilization experiments which reported
115 insignificant or even negative impacts of added N on litter decay rate (Fog, 1988;
116 Hobbie and Vitousek, 2000; Finn *et al.*, 2015), many incubation experiments showed
117 a significant decrease of litter decomposition rate with declining mineral N
118 availability (Recous *et al.*, 1995; Hobbie and Vitousek, 2000; Guenet *et al.*, 2010).
119 Moreover, recent modeling studies have indicated that the soil biogeochemical model
120 and Community Land Model could better replicate observed C and N flux when they
121 included the limiting effect of low mineral N (Bonan *et al.*, 2013; Fujita *et al.*, 2014).
122 It seems that soil mineral N can alter litter C flux though affecting both the litter
123 decay rate and the partition of decayed litter-C.

124 Some detailed microbial decomposition models actually have included
125 variable microbial CUE and the limitation of low mineral N availability on litter decay
126 rate (Ingwersen *et al.*, 2008; Pagel *et al.*, 2013; Campbell *et al.*, 2016; Huang *et al.*,
127 2018), however the parameterization and the evaluating of these models pose
128 significant challenges due to their complexity and limited verification data (Wieder *et*
129 *al.*, 2014; Campbell and Paustian, 2015). There is still scope for implementing the
130 effects of litter stoichiometry and soil mineral N availability on litter decomposition in
131 litter decay models with more generalizable structure. In particular, it is important to
132 test the role of these effects in models that have been extensively incorporated into
133 land surface model for long-term and large-scale application (e.g. CENTURY, Parton



134 *et al.*, 1988). In this study, we incorporated flexible CUE_d based on substrate C:N ratios
135 and mineral N limitations into a soil biogeochemical model based on the CENTURY
136 equations to simulate the decomposition and transfer processes of litter-C. The study
137 was organized as follows. First, the new model was calibrated and tested against data
138 from laboratory litter incubation experiments for its ability to capture the effect of
139 variable litter quality and soil mineral N on litter respiration rates (short-term
140 simulations). Second, the model parameterized assuming flexible CUE_d and mineral
141 N limitations was used to explore the consequences of such stoichiometric constraints
142 on the production of soil organic carbon (SOC) (long-term simulations). With these
143 two modeling analyses, we aimed at linking stoichiometric constraints acting on
144 short-term (months to years) decomposition dynamics to their consequences on SOC
145 accumulation occurring at decadal to centennial time scales.

146

147 **2 Materials and methods**

148 2.1 The CENTURY decomposition model

149 The basis of the litter decay model used in this study is the CENTURY model
150 (Fig. 1), a first-order decay model that describes decomposition as a function of
151 substrate availability and quality, clay content, soil moisture and soil temperature
152 (Parton *et al.*, 1988). Most land surface models (e.g. Kucharik *et al.*, 2000; Sitch *et al.*
153 *et al.*, 2003; Krinner *et al.*, 2005) adopted a similar structure to simulate the litter and
154 soil biogeochemical processes. Dead organic matter in CENTURY is separated into
155 structural and metabolic litter and three SOM pools (active, slow, passive) with
156 different turnover times. There is no explicit representation of microbial biomass in
157 CENTURY, instead the biomass of microbes is assumed to be in equilibrium with
158 active SOM and thus implicitly included in the active SOM pool. When C is being
159 transferred between pools, a fraction of it is respired to the atmosphere and the
160 remaining fraction (CUE_d conceptually equal to microbial CUE) enters the acceptor
161 pool. Three of such fractions are defined to characterize the transfer of C from the
162 metabolic litter to the active SOM pool (CUE_{ma}), and from the structural litter to



163 active and slow SOM pool (CUE_{sa} and CUE_{ss} , respectively, Fig. 1). These fractions
 164 are set to be time invariant in the original version of CENTURY, so that a fixed
 165 fraction of decomposed C is retained in the acceptor pool regardless of environmental
 166 conditions and changes in the quality of the donor pool. The N flows in CENTURY
 167 follow the C flows and are equal to the product of C flow by the N:C ratio of the
 168 acceptor SOM pool. N mineralization is defined as the difference between N obtained
 169 from the donor pools and N stoichiometric demand of the acceptor pool (Parton et al.,
 170 1988; Metherell et al., 1993). In this way, net N mineralization occurs when the donor
 171 pool has low C:N ratio, but N is immobilized (taken up by microbes) when the donor
 172 pool has high C:N ratio.

173

174 2.2 Optimal CUE

175 To quantify how microbial CUE varies along gradients of nutrient
 176 availability, it can be hypothesized that microorganisms maximize their growth rate,
 177 and hence their ecological competitiveness, by adapting resource (C and nutrients) use
 178 efficiencies. This follows the growth maximization hypothesis (Mooshammer *et al.*,
 179 2014; Manzoni *et al.*, 2017). Based on this hypothesis, Manzoni *et al.* (2017)
 180 formulated a theoretical model expressing microbial CUE as a function of the
 181 stoichiometric difference between decomposers and their substrate. The CUE for
 182 which growth rate is maximized is the optimal CUE (CUE_{opt}) given by:

$$183 \quad CUE_{opt} = CUE_{max} \times \min \left\{ 1, \frac{CN_D}{CUE_{max}} \times \left[\frac{1}{CN_S} + \frac{I_N}{U_0} \right] \right\} \quad (1)$$

184 where CUE_{max} is the maximum microbial CUE (dimensionless) when growth is
 185 limited by C from the organic substrate. CN_D and CN_S are the C:N ratio (in mass,
 186 dimensionless) of decomposer and their substrate, respectively. Although Manzoni *et al.*
 187 *et al.* (2017) indicated that mineral phosphorus (P) could also affect optimal CUE we
 188 only considered N as a limiting nutrient. I_N (g N kg⁻¹ soil) is the maximum rate at
 189 which mineral N can be taken up by microbes, and U_0 (g C kg⁻¹ soil) is the C-limited
 190 uptake rate (corresponding to the decomposition rate at optimal mineral N
 191 concentration). When litter C:N is low or soil mineral N is in excess, the second term



192 in the minimum function (Eq. (1)) is higher than one, and $CUE_{opt} = CUE_{max}$ (C limited
 193 conditions, as in nutrient-rich litter). In contrast, when mineral N is scarce, CUE_{opt}
 194 decreases with increasing substrate C:N ratio (N limited conditions, N-poor litter).
 195 Lack of N in the organic substrates can be compensated by mineral N being
 196 immobilized by microorganisms from the soil solution. Immobilization meets the
 197 nutrient demands as long as it is lower than the maximum supply rate I_E , at which
 198 point microbial CUE starts being down regulated. Thus, for any given C:N ratio in the
 199 substrate, CUE_{opt} increases with inorganic N concentration in the soil solution until
 200 CUE_{max} is reached. It should also be noted that Eq. (1) is interpreted at the microbial
 201 community scale, not for individual organism.

202

203 2.3 Adaption of the optimal CUE model in the CENTURY model

204 CUE of decomposition (CUE_d) is also assumed to be equivalent to microbial
 205 CUE in this study. Then we followed the theory from Manzoni *et al.* (2017) (Eq. (1))
 206 to parameterize CUE_d during litter decomposition into CENTURY (Fig. 1). Due to the
 207 implicit representation of microbial growth in CENTURY, we replaced the original
 208 optimality CUE model (Eq. (1)) by a simpler equation that involves the C:N ratios of
 209 the donor and acceptor pools, rather than microbial C:N ratios:

$$210 \quad CUE_{opt} = CUE_{max} \times \min\left(1, \left(\frac{CN_{lit}}{CN_{SOM}}\right)^a\right) \quad (2)$$

211 Where CN_{lit} and CN_{SOM} are the C:N ratio (dimensionless) of litter (metabolic or
 212 structural) and SOM pools (active, slow or passive), respectively. The The C:N ratio
 213 of SOM (around 9:1 on a mass basis in CENTURY) is representative of the
 214 decomposer biomass, its value being between the C:N ratios of the two major group
 215 decomposers, soil microbes (7.4:1) (Cleveland and Liptzin, 2007) and soil fungi
 216 (13.4:1, Zhang *and* Elser, 2017). $CUE_{max} = 0.8$ (dimensionless) is the maximum CUE_d
 217 achieved when nutrients are not limiting (Manzoni *et al.*, 2012; Sinsabaugh *et al.*,
 218 2013) and a (g N kg^{-1} soil) is an exponent capturing the effect of mineral N uptake by
 219 microbes on CUE_d . CUE_d being expected to increase with mineral N availability (Eq.
 220 (1)), a is assumed to be a linear function of the mineral N concentration (N_{min} , g N kg^{-1}



221 soil):

$$222 \quad a = m_1 \times (N_{min} - n_1) \quad (3)$$

223 m_1 ($\text{kg g}^{-1} \text{N}$) and n_1 ($\text{g N kg}^{-1} \text{soil}$) are two coefficients that need to be calibrated. Eqs.

224 (2) and (3) modulate the decrease in CUE_d with decreasing litter quality when mineral

225 N availability changes – the exponent a increases with increasing mineral N

226 availability, causing an increase in CUE_d at any given litter C:N ratio. Hence,

227 increasing a value mimics an increase in I_N in Equation 1. Fig. 2a illustrates how CUE_d

228 from Eq. (2) varies as a function of mineral N concentration, for different values of

229 litter C:N.

230 Eqs. (2) and (3) were implemented in CENTURY to modify the originally

231 fixed CUE_d (Fig. 1). With this change, the fractions of C from litter that remain in

232 SOM are all mediated by stoichiometric constraints and mineral N availability, at the

233 expense of additional parameters to fit.

234

235 2.4 Constraint of soil nutrient availability on litter decomposition rate

236 CENTURY is a first-order decay model in which decomposition rates of

237 metabolic and structural litter are modulated by scaling factors of soil temperature

238 ($f(\text{tem})$) and moisture ($f(\text{water})$) (Parton *et al.*, 1988). Here, we introduced an

239 additional mineral N scaling factor ($f(N_{min})$, 0–1, dimensionless) to account for the

240 limitation of very low mineral N availability on litter decay rate ($D(C_{lit})$).

$$241 \quad D(C_{lit}) = C_{lit} \times k \times f(\text{tem}) \times f(\text{water}) \times f(N_{min}) \quad (4)$$

242 where C_{lit} is the C ($\text{g C kg}^{-1} \text{soil}$) in litter pool (metabolic or structural). k is the

243 potential maximum turnover rate (day^{-1}) at optimal soil temperature, moisture and

244 nutrient conditions. We assumed that the scaling factor of mineral N increases linearly

245 with increasing soil mineral N concentration (N_{min} , Eq. (5)) below a threshold value of

246 $1/m_2 \text{ g N kg}^{-1} \text{soil}$, where m_2 is a positive coefficient which needs to be calibrated (Fig.

247 2b). The inhibition effect of mineral N only occurs in case of immobilization ($1/CN_{lit}$

248 $< CUE_{opt}/CN_{SOM}$). The specific function $f(N_{min})$ can be expressed as:



$$f(N_{min}) = \begin{cases} \min(1, m_2 \times N_{min}), & \frac{cue_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} > 0 \\ 1, & \frac{cue_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} \leq 0 \end{cases} \quad (5)$$

250

251 2.5 Model parameterization and validation

252 To determine the respective impacts of including flexible CUE_d and N
 253 availability constraining decay rates, we built four conceptual litter decay models
 254 (Table 1). Model M0 corresponds to the default CENTURY parameterization of a
 255 fixed CUE_d and no constraints of N availability on litter decay rates ($f(N_{min}) = 1$).
 256 Model M1 accounts for flexibility in CUE from Eq. (2) and N constraints on decay
 257 rates by Eq. (5). Model M2 has flexible CUE_d but no N constraints on decay rates
 258 ($f(N_{min}) = 1$). Model M3 has N constraints on decay rates but a fixed CUE_d (Table 1).
 259 All of these four models are run at a daily time step. This range of models allows
 260 identifying which mechanisms are at play during decomposition – flexible CUE_d only
 261 (M3), mineral N limitation only (M2), both mechanisms (M1), or none (M0).

262 For calibrating model parameters and evaluation of their results, we collected
 263 data of laboratory litter incubation experiments from Recous *et al.* (1995) (5
 264 experiments) and Guenet *et al.* (2010) (9 experiments, Table A2). The incubation
 265 experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) continued 80 and 124
 266 days, respectively. Recous *et al.* (1995) used corn residues (C:N = 130) and Guenet *et al.*
 267 *et al.* (2010) used wheat straw (C:N = 44) in their incubation experiments. The C:N
 268 ratios of those corn residue and wheat straw span the range of litter C:N ratios among
 269 different ecosystems (Manzoni *et al.*, 2012;
 270 <https://www.planetnatural.com/composting-101/making/c-n-ratio/>). In the incubation
 271 experiments, plant litter was firstly cut into fine fragments before it was mixed with
 272 mineral soil. Soil temperature and moisture condition were kept constant during the
 273 experiment. Respired C from the incubated litter and SOC, as well as the soil mineral
 274 N concentrations were measured continuously across the incubation period. More
 275 detailed information about the incubation experiments of Recous *et al.* (1995) and
 276 Guenet *et al.* (2010) can be found in Table A2.

277 The initial C storage and C:N ratios of litter and SOM pool, as well as soil



278 temperature and moisture condition for decomposition in all of the four version
 279 models (M0-M3) were set based on observations (Table A2). In M1 and M4 model,
 280 the observed mineral N concentrations across the incubation period were used to
 281 calculate daily N inhibition effect (Eq. (5)). The observed cumulative respired litter-C
 282 (g C kg^{-1} soil) measured in the incubation experiments was used to calibrate the model
 283 parameter values. Parameter calibration was performed for each model with the
 284 shuffled complex evolution (SCE) algorithm developed by Duan *et al.*, (1993). The
 285 SCE algorithm relies on a synthesis of four concepts that have proved successful for
 286 global optimization: combination of probabilistic and deterministic approaches;
 287 clustering; systematic evolution of a complex of points spanning the space in the
 288 direction of global improvement and competitive evolution (Duan *et al.*, 1993). More
 289 detailed description of this SCE optimization method can be found in Duan *et al.*
 290 (1993, 1994). In this study, the RMSE (root mean square error, Eq. (6)) between
 291 simulated and measured cumulative respired litter-C (%) on all observation days
 292 (Table A2) of each incubation experiment was used as the objective function, and the
 293 parameters minimizing RMSE between simulated and observed cumulative respired
 294 litter-C were regarded as optimal parameter values.

$$295 \quad RMSE = \sqrt{\left(\frac{\sum_{i=1}^n (Sim_i - Obs_i)^2}{n}\right)} \quad (6)$$

296 where n is the number of observation days, Sim_i and Obs_i (%) are the simulated
 297 and observed percent of cumulative litter-C flux on day i , respectively.

298 We used leave-one-out cross-validation (Kearns and Ron, 1997; Tramontana
 299 *et al.*, 2016) to evaluate each of the four models (i.e. M0-M3), a cross validation
 300 method used when data is scarce. The number of cross-validations corresponds to the
 301 number of incubation experiments (14). Each time, one of the 14 incubation
 302 experiments was left out as the validation sample, and the remaining 13 experiments
 303 were used to train model parameters. In addition to RMSE, we also adopted the
 304 Akaike Information Criterion (AIC, Bozdogan, 1987, Eq. (7)) to determine the
 305 relative quality of the four version models on estimating cumulative respired litter-C.

$$306 \quad AIC = n \times \ln\left(\frac{\sum_{i=1}^n (Sim_i - Obs_i)^2}{n}\right) + 2n_p \quad (7)$$



307 where n_p is the number of model parameters. The evaluation of AIC is important here
308 because depending on the model M1, M2, or M3 parameters have to be determined
309 (Table 1), requiring us to weigh both model accuracy and robustness.

310

311 2.6 Impacts of litter stoichiometry and mineral N availability on SOM accumulation

312 We used the model M1, with flexible CUE_d and decomposition rate function
313 of available N to study the impacts of litter stoichiometry (C:N ratio) and soil mineral
314 N availability on the formation and accumulation of SOM. Totally, 24 idealized
315 simulation experiments with different values of litter C:N ratios and soil mineral N
316 availabilities were conducted (Table A3). The assumed litter C:N ratios (CN_{lit}) of 10,
317 15, 30, 60, 120 and 200 span the variation among most natural substrates and soil
318 amendments from organic matter input in agriculture (Manzoni *et al.*, 2012;
319 <https://www.planetnatural.com/composting-101/making/c-n-ratio/>). The assumed
320 range of mineral N availability (N_{min}) of 0.001, 0.005, 0.01 and 0.05 g N kg⁻¹ soil span
321 the observed concentrations of soil mineral N in major terrestrial ecosystems
322 (Metherall *et al.*, 1993).

323 In each simulation experiment, M1 was run for 5000 years to bring the litter
324 and SOM pools in equilibrium with the prescribed litter input flux. The daily input rate
325 of plant litter was set to 0.006 g C kg⁻¹ soil day⁻¹, and the initial C stock of litter and
326 SOM pools were all set to be 0 g C kg⁻¹ soil. During the simulation, soil temperature
327 and soil water content were assumed to be 25 °C and 60% of water holding capacity,
328 respectively. We emphasized that our goal with this simplified scenario was to single
329 out the effects of stoichiometric constraints, not to simulate the effects of a realistic
330 climatic regime. Parameter values for M1 (with $m_1 = 0.54$, $n_1 = 0.50$ and $m_2 = 296.8$)
331 used here were optimized based on all of the 14 incubation experiments from Recous
332 *et al.* (1995) and Guenet *et al.* (2010) (see above). More detailed information about
333 the specific settings of our simulation experiments can be found in Table A3.

334

335 3 Results



336 3.1 Evaluation of different models

337 Results of leave-one-out cross-validation suggest that model M1 provides
338 more accurate prediction of cumulative respired litter-C than other models (Fig. 3).
339 The differences between simulated and observed cumulative respired litter-C from
340 M1 are mostly (over 93% of the data) less than 6% (Fig. S1b in supplementary
341 materials). The average RMSE of predicted cumulative respired litter-C from M1
342 (3.0%) is lower than that of model M0 (4.1%). Models M2 and M3 have slightly
343 lower RMSE values than M0 (3.7% and 3.8%, respectively) but perform worse than
344 M1 (Fig. 4). However, the average AIC of all the models are comparable, suggesting
345 that models with more fitted parameters do not over-fit the observations (Fig. 4).

346 Model M1 captures the differences in respiration rates due to different C:N
347 ratios of substrate and varying levels of mineral N availability across the 14
348 incubation experiments (Fig. 5). While model M3 can reproduce the observed effect
349 of soil mineral N availability on litter respirations rates (Fig. 5d), it underestimate the
350 cumulative respired CO₂ from low quality litter ($CN_{li} = 130$) at high mineral N
351 concentrations ($> 0.04 \text{ g N kg}^{-1}$ soil). Models M0 and M2 cannot represent the effects
352 of soil mineral N on litter respiration rate (Figs. 5a, c), and their predictions are more
353 biased from the observed values compared to M1. In addition, model M1 can also
354 capture the temporal evolution of cumulative respired litter-C in different incubation
355 experiments (Fig. 5b).

356 The predicted CUE_d of decomposed litter and the limitation effects of soil
357 mineral N availability on litter decay rate from the $f(N_{min})$ function (Eq. (5)) are
358 different among the four tested models (Fig. A2). In models M0 and M3, which used a
359 fixed CUE_d , the fitted values of CUE_d calculated with optimized parameters during
360 the incubation period are about 0.57 and 0.54, respectively (Figs. A2a, d). In models
361 M1 and M2, the CUE_d varies with the C:N ratios of plant litter, and is only slightly
362 affected by soil mineral N concentrations (Figs. A2b, c). For very low quality litter
363 with a C:N ratio of 130, the CUE_d in models M1 and M2 are 0.55 and 0.56,
364 respectively, which are higher than for better quality litter with C:N ratio of 44
365 (approximately 0.40 and 0.44 in M1 and M2, respectively). CUE_d from Eq. (2)



366 calibrated with the data of the two incubation experiments, decreases with increasing
367 CN_{lit}/CN_{SOM} (Fig. 6). The average CUE_d value is larger than the average of data
368 compiled for microbial CUE of litter decomposition in terrestrial ecosystems by
369 Manzoni *et al.* (2017). This is shown by the gray circles in Fig. 6. Our optimized
370 values of CUE_d for a given C:N ratio are more comparable with microbial CUE
371 observed in incubations of soil mixed with litter (Gilmour and Gilmour, 1985;
372 Devêre and Horváth, 2000; Thiet *et al.*, 2006), shown as black squares in Fig. 6.
373 Models M0 and M2 do not include the N inhibition effects on litter decay rate, thus
374 the $f(N_{min})$ in these two models is always 1 (Figs. A2e, g). In M1 and M3, the N
375 inhibition effect changes with both the litter C:N ratio and the mineral N availability
376 (Figs. A2f, h).

377

378 3.2 The effect of litter quality vs quantity on equilibrium SOM stocks

379 Model M1 predicts that the size of the SOM pool at equilibrium is mainly
380 determined by litter stoichiometry, with a minor effect of soil mineral N (Fig. 7). The
381 lower C:N ratio of litter is, the higher equilibrium SOC stock. For litter with a specific
382 C:N ratio, high soil mineral N concentration (e.g. above 0.05 g N kg^{-1} soil) generally
383 produces a slightly larger equilibrium SOC stock than a low mineral N concentration
384 (Fig. 7). Further analysis suggests that the SOC at equilibrium increases with
385 decreasing litter C:N because the SOC pool is positively related to the CUE_d ; however
386 the limitation of soil mineral N on litter decomposition rate almost shows no impact
387 on SOC (Fig. A3).

388

389 4 Discussion

390 We hypothesized that stoichiometric constraints (flexible CUE_d or inhibition
391 of decomposition under N limited conditions) played a role in shaping the trajectory
392 of litter decomposition, with potential consequences on predicted SOC stocks. Our
393 results suggest that with flexible CUE_d and the inhibition effects of soil mineral N on
394 litter decay rate, the model M1 developed from CENTURY can be a reliable tool for



395 predicting litter decomposition. Evaluation of the model (M1) using data from
396 incubation experiments indicate that this modified model captures the effect of
397 variable litter quality (stoichiometry) and mineral N availability on respiration rates
398 (Fig. 5), without strongly inflating the complexity of CENTURY (Table 1). As the
399 stoichiometric constraints are implemented in the generalizable and widely used
400 structure of CENTURY and require only three parameters to be calibrated, they can
401 also be easily implemented into land surface models for large spatial scale
402 applications.

403 Accurately representing N control of microbial processes during litter
404 decomposition has been suggested to be important for modeling the connection
405 between the litter inputs, CUE_d , and soil C dynamics (Gerber *et al.*, 2010; Manzoni *et al.*,
406 2012; Cotrufo *et al.*, 2013; Sinsabaugh *et al.*, 2013). In model M1, soil mineral N
407 affects the litter-C flux via two mutually different pathways: (1) mineral N availability
408 affects the litter decay rate and (2) flexible CUE_d determining the partition of
409 decomposed C into SOC products and respired CO_2 (Fig. 1). Therefore, an increase in
410 soil mineral N concentration enhances litter decay rates, which alone will increase the
411 flux of litter-derived CO_2 (Eq. (5) and Fig. A4). However, as higher N concentration
412 also results in a higher CUE_d (Eq. (2)), more C is transferred to SOC and less C is
413 respired. In this way, SOC is predicted to accumulate with increasing mineral N
414 availability when using model M1 (Fig. 7).

415 Moreover, describing N limitations on both the decomposition rate and
416 flexible CUE_d might allow our model to explain the observed diverse responses of
417 litter respiration rate to added mineral N in fertilization experiments (Hobbie and
418 Vitousek, 2000; Guenet *et al.*, 2010; Janssens *et al.*, 2010). In these experiments, the
419 net changes in respiration rate depend on the combined effects of added N on litter
420 decay rate and CUE_d of the decayed litter (Fig. A4).

421 Existing studies have adopted approaches that differ from our definition to
422 explicitly represent the N inhibition effects on microbial processes (Eq. (5)) (Manzoni
423 and Porporato, 2009; Bonan *et al.*, 2013; Fujita *et al.*, 2014; Averill and Waring, 2018).
424 In these previous studies, $f(N_{min})$ was assumed equal to the ratio between immobilized



425 mineral N and the N deficit for keeping the stoichiometric balance (i.e. C:N) of
426 decomposer biomass or other receiver pools. Using the notation of Section 2, this
427 constant can be expressed as:

$$428 \quad f(N_{min}) = \begin{cases} \min\left(1, \frac{m_3 \times N_{min}}{U_0 \times \left(\frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}}\right)}\right), & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} > 0 \\ 1, & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} \leq 0 \end{cases} \quad (8)$$

429 where m_3 is a coefficient that needs to be optimized. U_0 (g C kg⁻¹ soil day⁻¹) is the C
430 uptake rate (equivalent to the litter decomposition rate in absence of leaching) when
431 soil mineral N is fully adequate for litter decay (i.e. $f(N_{min}) = 1$), and can be calculated
432 as:

$$433 \quad U_0 = C_{lit} \times k \times f(tem) \times f(water) \quad (9)$$

434 We have tested this formulation in the CENTURY-based model, in addition to the
435 other formulations (Table 1). The model with Eq. (8) gave a more biased estimation
436 on cumulative respired litter-C than the model using Eq. (5) (Fig. A5). We surmise
437 that although Eq. (8) can better represent the underlying microbial mechanisms of N
438 inhibition effects, it also increases the model complexity and in turn the efforts and
439 uncertainty in model parameterization.

440 The importance of litter quality for SOM formation as found here is in line
441 with recent experiments (Bahri *et al.*, 2008; Rubino *et al.*, 2010; Walela *et al.*, 2014)
442 and modeling studies (Grandy and Neff, 2008; Cotrufo *et al.*, 2013). SOM is mainly
443 formed though the partial decomposition of plant debris by microorganisms (Paul,
444 2007; Knicker, 2011; Cotrufo *et al.*, 2013). The conceptual model developed by
445 Cotrufo *et al.* (2013) suggested that although labile litter was decomposed faster than
446 recalcitrant litter, a higher fraction of this labile litter-C would be incorporated into
447 microbial biomass and subsequently incorporated into SOM pool (corresponding to a
448 higher CUE_d). Therefore, labile litter inputs tend to form a larger SOM pool than the
449 poor-quality (high C:N ratio) litter that is generally used by microbes at lower
450 efficiency. Our simulations of decomposition process of plant litter with different C:N
451 ratios also suggest that litter of good quality (with low C:N ratio) can induce a larger



452 SOM pool than the poor-quality litter (Fig. 7). CUE_d plays a more important role than
453 the inhibition effect of low mineral N concentration in determining the size of the
454 stable SOM pool (Fig. A3).

455 The predictions from Cotrufo *et al.* (2013) and this study contrasts with the
456 conventional hypothesis whereby the poor-quality litter with low decay rate and small
457 CUE_d are preferential to be accumulated in SOM (Berg and Mcclaugherty, 2008;
458 Walela *et al.*, 2014). This view of SOM stabilization, however, seems to apply to
459 N-limited systems with high C:N litter and where microbial remains are recalcitrant to
460 decomposition (e.g., boreal forests) – in these systems SOC does accumulate despite
461 its low quality (Kyaschenko *et al.* 2017). Moreover, one could argue that higher CUE_d
462 implies larger microbial biomass, allowing faster decomposition (Allison *et al.*, 2010).
463 These feedbacks between microbial biomass and decomposition rate were not
464 implemented in the current model, but could offer additional flexibility – again at the
465 expense of more difficult model parameterization.

466 The CUE_d formulation from Eq. (2) with parameters calibrated from the two
467 sets of incubation experiments might underestimate the impacts of litter quality on
468 microbial CUE under natural conditions, in particular in case of SOM decomposition.
469 In both incubation experiments, litter is firstly cut into fine fragments and then fully
470 mixed with mineral soil (Recous *et al.*, 1995; Guenet *et al.*, 2010). Thus, the nutrient
471 accessibility, air permeability and some other environmental factors (e.g. pH) of
472 incubated litter are different from those of decaying litter in more natural,
473 heterogeneous soil conditions. Those different decomposition conditions might be
474 responsible for the differences observed in Fig. 6 between our CUE estimates and
475 previously reported values. We speculate that more heterogeneous conditions reduce
476 nutrient availability and thus might cause lower CUE. Similarly, CUE of surface litter
477 decomposers may be lower than we estimated because litter not mixed with soil is
478 probably subject to strongly nutrient limitation.

479 This study provides some insights on processes leading to increased SOM
480 sequestration. Soil C sequestration plays a crucial role in food security and land CO_2
481 emission (Lal, 2004). The international initiative ‘4 per 1000’ has been proposed to



482 increase global SOM stock by 0.4% per year to compensate for anthropogenic CO₂
483 emissions (Baveye *et al.*, 2018). Transforming more plant litter into stable SOM (e.g.
484 humic substances) has been suggested as an effective strategy to sequester more C in
485 soil (Prescott, 2010). Our model results show a positive linear relationship between
486 equilibrium SOC stock and CUE of decomposed litter (Fig. A3). This result can also
487 be interpreted by calculating the analytical equilibrium SOC storage of a fully linear
488 model including only one litter pool and one SOC pool. In such a model, SOC
489 receives C from the litter at a rate $CUE_d \times D$, where D is the litter decomposition rate,
490 which equals to litterfall at steady state. SOC is lost via first order decay with a decay
491 constant k . At steady state, input to and outputs from the SOC pool are equal and thus,

$$492 \quad CUE_d \times D = k \times SOC \rightarrow SOC = CUE_d \frac{D}{k} \quad (10)$$

493 With a mean residence time of C in the SOC between 10 and 20 years and D
494 approximated by litterfall (Table A3), SOC at equilibrium is predicted to scale linearly
495 with CUE_d , with a slope approximately between 20 and 40, consistent with results in
496 Fig. A3.

497 Therefore, litter quality needs to be controlled to maximize C sequestration
498 in SOM pool (Eq. (2)). In line with previous studies (Prescott, 2010; Smith, 2016),
499 our model predicts that adding N through fertilization and N-fixing plants will not
500 only increase litter decay but also the fraction of litter-C being transformed into SOM
501 and ultimately SOC stocks. However, application of mineral N fertilizer is associated
502 with risk not considered here, like increasing land N₂O emission (Mosier and Kroeze,
503 2000; Kanter *et al.*, 2016; Yi *et al.*, 2017) and causing nitrate leaching which in turn
504 can induce water pollution (Cao *et al.*, 2006; Stokal *et al.*, 2016). Due to the negative
505 environmental impacts of mineral N addition, the use of N-rich litter substrates for
506 increasing SOM is advised.

507 Further validation and development of our model are still necessary to
508 decrease the model uncertainties. Soil mineral N which affects both litter decay rate
509 and CUE of decayed litter is seldom monitored in litter incubation experiments (e.g.
510 Walela *et al.*, 2014; Stewart *et al.*, 2015) and field litter decay experiments (e.g. Gholz



511 *et al.*, 2000; Harmon *et al.*, 2009), with few exceptions (Recous *et al.*, 1995; Guenet *et*
512 *al.*, 2010). An increasing number of land surface models (e.g. ORCHIDEE-CNP, Goll
513 *et al.*, 2017) have representations of the terrestrial N cycle. By incorporating our litter
514 decomposition formulation in these land surface models that simulate the dynamics of
515 soil mineral N concentration, it will be possible to test and validate our developments
516 with more extensive data from laboratory and field experiments. Moreover, similar to
517 N, P has also been suggested as another important factor for litter decomposition and
518 SOM formation (Güsewell and Verhoeven, 2006; Talkner *et al.*, 2009; Manzoni *et al.*,
519 2010; Prescott, 2010), especially in regions with highly weathered soil (Goll *et al.*,
520 2012, 2017; Yang *et al.*, 2014). So it might be necessary to include the effects of P on
521 litter decay rate and CUE_d into our model for further decrease the simulation
522 uncertainties.

523

524 **5 Conclusions**

525 By adapting the hypothesis of optimal microbial CUE proposed by Manzoni
526 *et al.* (2017) for use in a CENTURY-based model and also introducing a N scaling
527 function to represent the limits of mineral N availability on litter decay rate, we
528 developed a simple but effective litter decomposition model that accounts for key
529 stoichiometric constraints during decomposition. Validation using observation data
530 obtained from laboratory incubation experiments indicated that our model could well
531 predict the respiration rates of litter in different qualities at various levels of mineral N
532 availability. Idealized simulations using our model revealed that the quality of litter
533 inputs plays an important role in determining the soil C stock at equilibrium SOM
534 pool. High-quality litter (i.e. with low C:N ratio) tends to form a larger SOM pool as
535 it can be more efficiently utilized by microorganisms than recalcitrant litter (e.g. high
536 C:N ratio). Overall, the developed model captures the microbial mechanisms
537 mediating litter stoichiometry and soil mineral N effects on litter decomposition and
538 SOM formation – representing an improvement over most existing large-scale litter
539 decay models. Due to the simple and generalizable structure of our model, it can be



540 incorporated into existing land surface models for further long-term and large spatial

541 scale applications.

542



543 **Code and data availability**

544 The CENTURY-based model used here is programmed in MATLAB
545 language. The source code is available online
546 (https://github.com/hchzhang/CENYUTY_CUE/tree/v1.0, DOI:
547 10.5281/zenodo.1307384). All the data used in this study can be obtained from
548 published literatures. Specific references of these data can be found in section 2.5.
549

550 **Competing interests**

551 The authors declare that they have no conflict of interest.
552

553 **Acknowledgements**

554 HZ, DSG, PC and YH are funded by the IMBALANCE-P project of the European
555 Research Council (ERC-2013-SyG- 610028). SM acknowledges the support of the
556 Swedish Research Council Vetenskapsrådet (grants 2016-04146 and 2016-06313).
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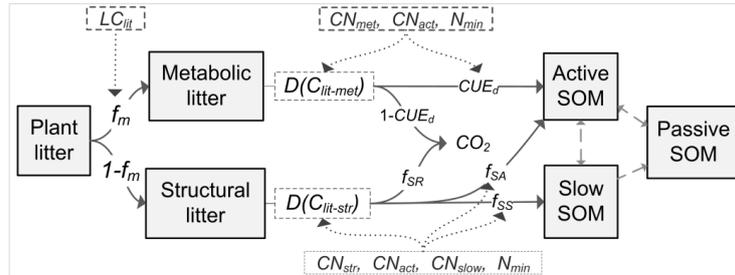
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810 **Table 1** The four version of the litter decomposition model used in this study. cue_{fit} is
 811 optimized value of CUE. m_1 and n_1 are the coefficients in Eq. (3), and m_2 is the
 812 coefficients in Eq. (5).

Model version	CUE	$f(N_{min})$	Parameters
M0	fixed	1	cue_{fit}
M1	Eqs. (2), (3)	Eq. (5)	m_1, n_1, m_2
M2	Eqs. (2), (3)	1	m_1, n_1
M3	fixed	Eq. (5)	cue_{fit}, m_2

813



814

815 **Figure 1** Schematic diagram of the C flows in the litter decay model used in this study.

816 f_m is the fraction of metabolic compounds in plant litter. $D(C_{lit-met})$ and $D(C_{lit-str})$ are
 817 the decomposition rates ($\text{g C kg}^{-1} \text{ day}^{-1}$) of metabolic or structural litter, respectively.

818 LC_{lit} is the lignin:C ratio (on a mass basis) of plant litter; CN_{met} , CN_{str} , CN_{act} , and
 819 CN_{slow} are the C:N ratio of metabolic litter pool, structural litter pool, active SOM

820 pool and slow SOM pool, respectively; N_{min} is the concentration of mineral N in

821 solution ($\text{g N kg}^{-1} \text{ soil}$); CUE_d is C use efficiency of the transformation from litter to

822 soil organic matter (SOM); f_{SA} , f_{SS} and f_{SR} are the fractions of decomposed structural
 823 litter-C that is transferred to active SOM pool, slow SOM pool and released to

824 atmosphere in forms of CO_2 , respectively. As in the algorithms in CENTURY model

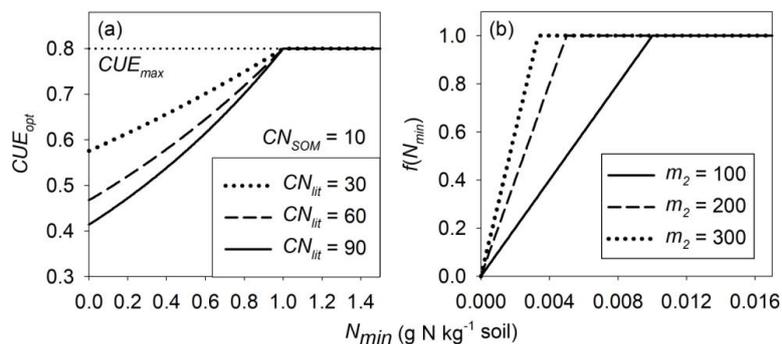
825 (Parton et al., 1988), here $f_{SA} = CUE_{d_SA} \times (1 - f_{lig})$, $f_{SS} = CUE_{d_SS} \times f_{lig}$, $f_{SR} = 1 - (f_{SA} + f_{SS})$,

826 where f_{lig} is the lignin fraction (0–1, dimensionless) in the structural litter pool, and

827 CUE_{d_SA} and CUE_{d_SS} are the CUE of C transformation from structural litter pool to

828 active and slow SOM pool, respectively.

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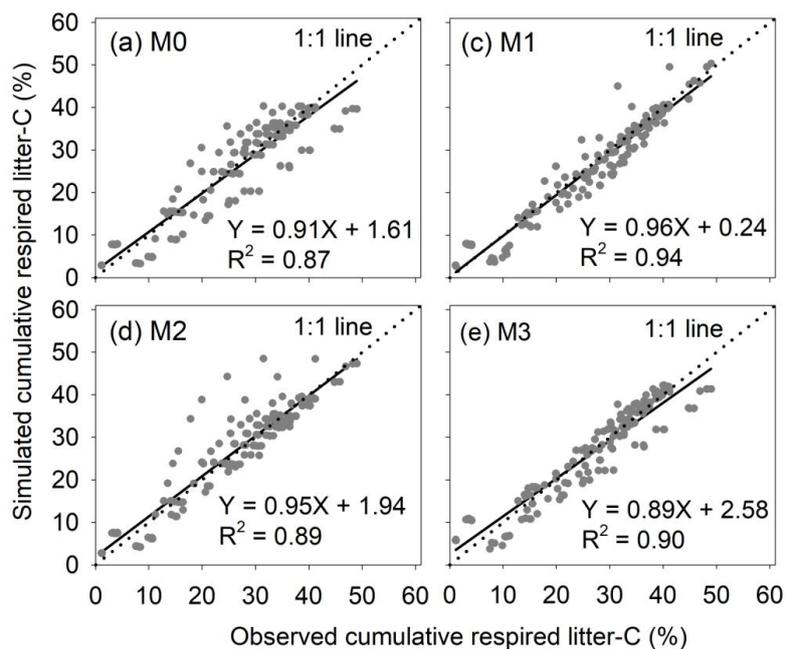
831 **Figure 2.** Schematic plot of (a) the optimal carbon use efficiency (CUE_{opt}) function of
 832 soil mineral nitrogen for different litter C:N ratios (from Eq. (2) in the main text with
 833 $m_l = 0.3$, $n_l = 1.0$) and (b) the N limitation function $f(N_{min})$ applied to litter
 834 decomposition rates (from Eq. (5) in the main text). CN_{lit} and CN_{SOM} are the C:N ratio
 835 of litter pool and SOM pool, respectively. $CUE_{max} = 0.8$ is the maximum CUE under
 836 optimal nutrient condition (C limitation only). m_l and n_l are the parameters of Eq. (3)
 837 and m_2 are the parameter of Eq. (5).

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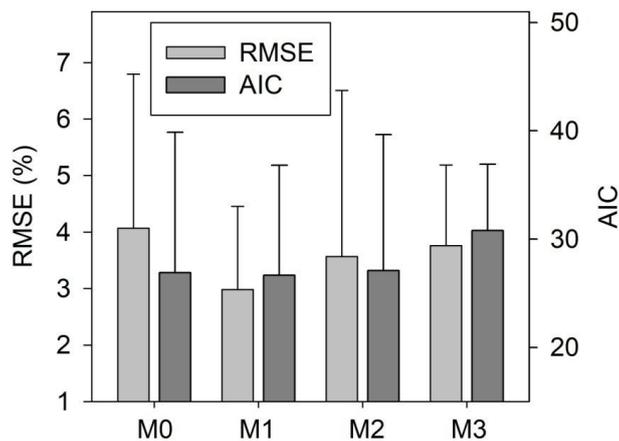
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842 **Figure 3** Comparison of the predicted cumulative respired litter-C to observed values
 843 at different times during litter decomposition process. Each dot denotes an
 844 observation of cumulative respired litter-C at a certain day. Totally, there are 149
 845 points. M0-M3 are the four versions of litter decay model tested in this study (Table
 846 1).

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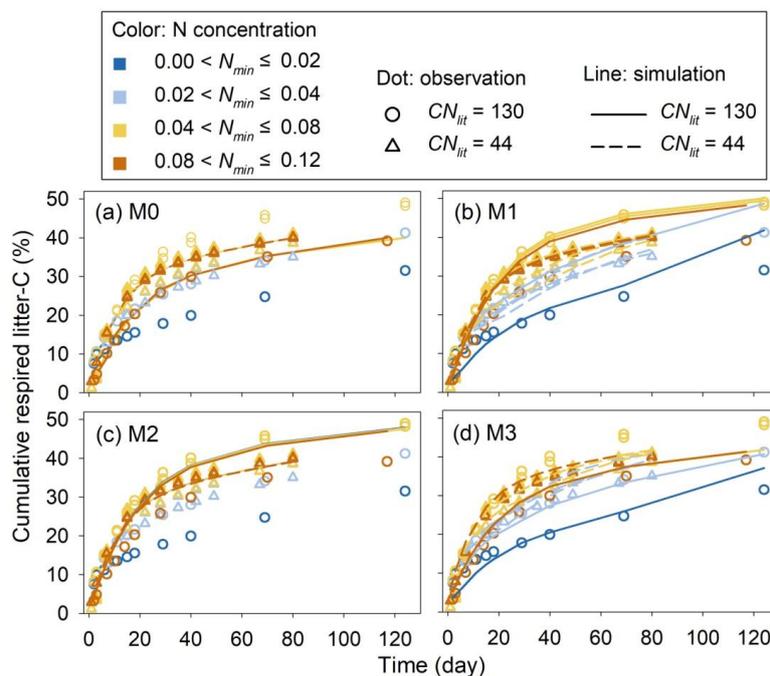


848

849 **Figure 4** The RMSE and AIC of the simulated cumulative respired litter-C from the
850 four versions of litter decay model used in this study. Error bars denote the standard
851 deviation of RMSE or AIC for different incubation experiments. M0 and M1-3 denote
852 the four models tested in this study (Table 1).

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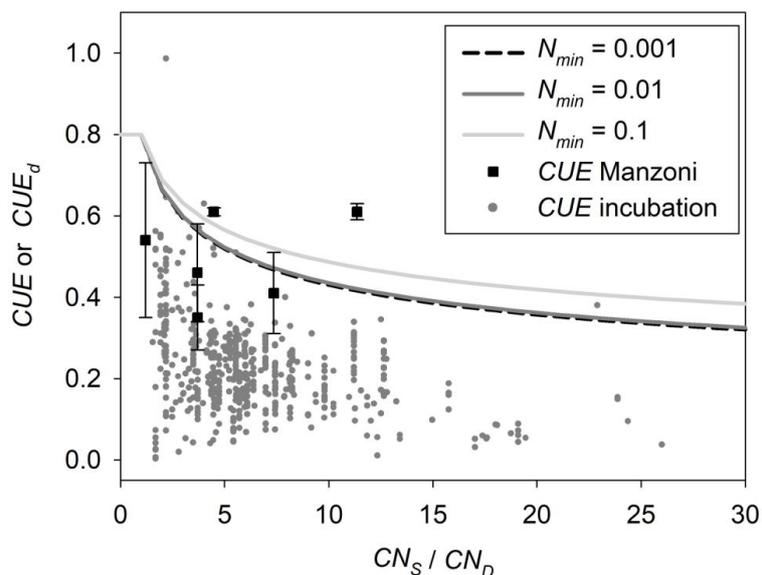
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856 **Figure 5** Time series of the simulated (lines) and observed (dots) cumulative respired
 857 litter-C (% of initial litter-C) at four different levels of soil mineral N availability (N_{min} ,
 858 g N kg^{-1} soil). CN_{lit} is the C:N ratio of plant litter. M0 and M1-3 denote the four
 859 models tested in this study (Table 1). Here the simulation results of each model were
 860 calculated with parameters optimized based on all of the 14 samples of incubation
 861 experiments (Table A2).

862



863

864 **Figure 6** Comparison of CUE_d (lines) predicted by Eq. (2) with parameter values (m_2 865 $= 0.54$, $n_l = 0.50$) calibrated based on the incubation experiments (Table A2) of866 Recous *et al.* (1995) and Guenet *et al.* (2010) to observed CUE of terrestrial867 microorganisms along a gradient of CN_S/CN_D , where CN_D and CN_S are the C:N ratio

868 of decomposers and their substrates, respectively. Gray dots are the estimated

869 microbial CUE of litter decomposition in natural terrestrial ecosystems from Manzoni

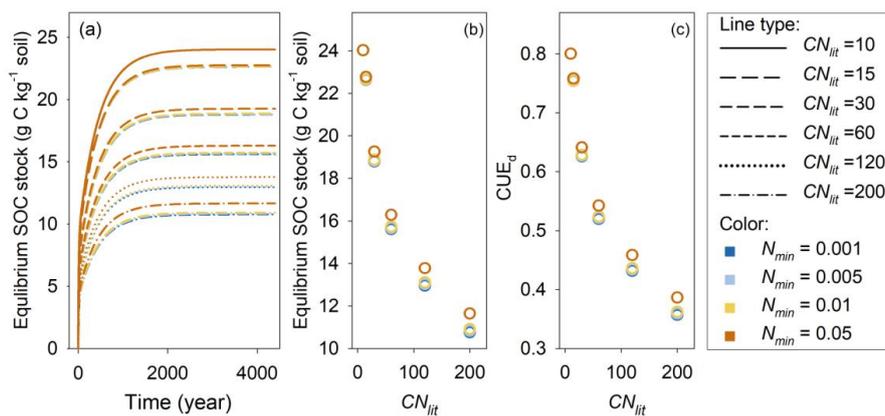
870 *et al.* (2017). Black squares are the microbial CUE measured via laboratory

871 incubation experiments of Gilmour & Gilmour, (1985), Devêre & Horváth (2000)

872 and Thiet *et al.* (2006). Error bars represent the standard deviations. N_{min} (g N kg^{-1} soil)

873 is the concentration of soil mineral N.

874



875

876 **Figure 7** (a) Accumulation of soil organic carbon (SOC) for constant substrates input
 877 (plant litter) with different C:N ratios (CN_{lit}) at different levels of soil mineral N
 878 concentrations (N_{min} , g N kg⁻¹ soil), (b) Change trends of equilibrium SOC stock and
 879 carbon use efficiency of decomposed litter (CUE_d) with increasing litter C:N ratio.
 880

881 **Appendix:**882 **Table A1** List of symbols used in this study

Symbol	Unit	Description
a	g N kg ⁻¹ soil	Exponent in Eq. 2
AIC	dimensionless	The Akaike Information Criterion (Eq. 7)
CN_{act}	dimensionless	C to N ratio of active soil organic matter pool
CN_D	dimensionless	C to N ratio of decomposer (Eq. 1)
CN_{met}	dimensionless	C to N ratio of metabolic litter pool
CN_{slow}	dimensionless	C to N ratio of slow soil organic matter pool
CN_{str}	dimensionless	C to N ratio of structural litter pool
CN_S	dimensionless	C to N ratio of substrate (Eq. 1)
C_{lit}	g C kg ⁻¹ soil	C stock of litter pool (Eq. 4)
CN_{lit}	dimensionless	C to N ratio of litter pool (metabolic or structural, Eq. 2)
CN_{SOM}	dimensionless	C to N ratio of soil organic matter pool
CUE	dimensionless	Microbial carbon use efficiency
CUE_d	dimensionless	Carbon use efficiency of decomposition (C incorporated in SOC over litter C decomposed)
CUE_{fit}	dimensionless	Optimized value of fixed CUE in model M0 and M4
CUE_{max}	dimensionless	Maximum CUE_d (Eqs. 1 and 2)
CUE_{opt}	dimensionless	Optimal CUE_d (Eq. 1)
$CUE_{d,SA}$	dimensionless	CUE of the transformation from structural litter to active SOM pool
$CUE_{d,SS}$	dimensionless	CUE of the transformation from structural litter to slow SOM pool
D	g C kg ⁻¹ soil day ⁻¹	Daily litterfall input rate (Eq. 10)
$D(C_{lit-met})$	g C kg ⁻¹ soil day ⁻¹	Decomposition rate of metabolic litter
$D(C_{lit-str})$	g C kg ⁻¹ soil day ⁻¹	Decomposition rate of structural litter
$f(N_{min})$	dimensionless	Limit factor of soil mineral N on litter decomposition (Eqs. 4 and 5)
$f(tem)$	dimensionless	Limit factor of soil temperature on litter decomposition (Eq. 4)
$f(water)$	dimensionless	Limit factor of soil water content on litter decomposition (Eq. 4)
f_m	dimensionless	Fraction of metabolic plant litter
f_{SA}	dimensionless	Fractions of decomposed structural litter-C that is transferred to active SOM pool
f_{SR}	dimensionless	Fractions of decomposed structural litter-C that is released to atmosphere
f_{SS}	dimensionless	Fractions of decomposed structural litter-C that is transferred to slow SOM pool
I_N	g kg ⁻¹ soil	Maximum mineral N immobilization rate (Eq. 1)
k	day ⁻¹	potential maximum turnover rate (Eq. 10)
LC_{lit}	dimensionless	Lignin to C ratio of litter input
m_1	kg g ⁻¹ N	Coefficients in Eq. 3
n_1	g N kg ⁻¹ soil	Coefficients in Eq. 3
m_2	day ⁻¹	Coefficients in Eq. 5
m_3	kg g ⁻¹ N	Coefficients in Eq. 8
N_{min}	g N kg ⁻¹ soil	Soil mineral N concentration (Eq. 5)



<i>RMSE</i>	%	Root mean square error (Eq. 6)
<i>SOC</i>	g C kg ⁻¹ soil	Soil organic carbon
<i>SOM</i>	g C kg ⁻¹ soil	Soil organic matter
<i>U₀</i>	g C kg ⁻¹ soil day ⁻¹	C uptake rate when soil mineral N is fully adequate for litter decay (Eq. 1)

883



Table A2 Information about the 14 samples of laboratory incubation experiment used in this study. CN_{lit} and LC_{lit} are the C to N ratio and lignin to C ratio of plant litter, respectively. CN_{SOM} is the C to N ratio of SOM pool. N_{min} is the concentration of soil mineral N (NO_3^- -N + NH_4^+ -N). For the incubation experiments of Guenet *et al.* (2010), cumulative respired litter-C was measured on days 1, 3, 7, 15, 22, 28, 35, 42, 49, 67 and 80, and N_{min} was measured on days 3, 7, 17, 28 and 80. For the incubation experiments of Recous *et al.* (1995), both cumulative respired litter-C and N_{min} were mostly measured on days 2, 3, 6, 11, 15, 18, 29, 40, 69 and 124.

Sample	CN_{lit}	LC_{lit}	CN_{SOM}	Initial N_{min} (g N kg ⁻¹ soil)	Duration (day)	Temperature (°C)	Soil moisture (%, in volume)	Litter type	Reference
1	44	0.26	11	0.035	80	20	50	Crop (wheat)	Guenet <i>et al.</i> , 2010
2	44	0.26	11	0.051	80	20	50	Crop (wheat)	
3	44	0.26	11	0.055	80	20	50	Crop (wheat)	
4	44	0.26	11	0.033	80	20	50	Crop (wheat)	
5	44	0.26	11	0.049	80	20	50	Crop (wheat)	
6	44	0.26	11	0.067	80	20	50	Crop (wheat)	
7	44	0.26	11	0.033	80	20	50	Crop (wheat)	
8	44	0.26	11	0.048	80	20	50	Crop (wheat)	
9	44	0.26	11	0.079	80	20	50	Crop (wheat)	
10	130	0.23	9	0.010	124	15	42	Crop (Corn)	Recous <i>et al.</i> , 1995
11	130	0.23	9	0.030	124	15	42	Crop (Corn)	
12	130	0.23	9	0.060	124	15	42	Crop (Corn)	
13	130	0.23	9	0.080	124	15	42	Crop (Corn)	
14	130	0.23	9	0.100	124	15	42	Crop (Corn)	



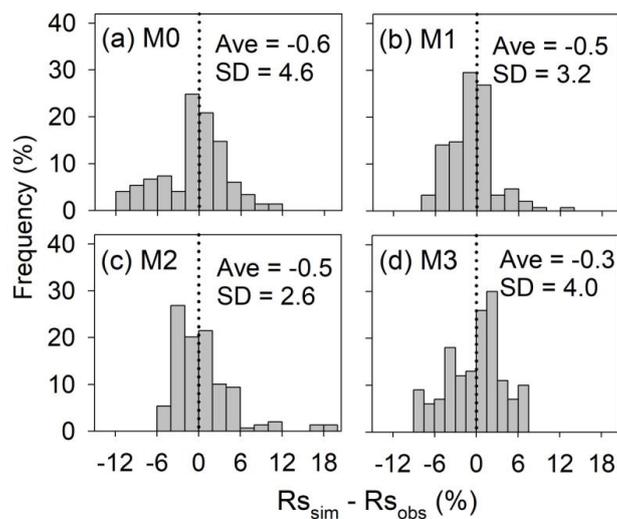
1 **Table A3** Specific setting of litter and SOM properties, and soil conditions in the 16
 2 idealized simulations for exploring the impacts of litter stoichiometry (i.e. C:N ratio)
 3 and soil mineral N on SOC accumulation. CN_{lit} and LC_{lit} are the C to N ratio and
 4 lignin to C ratio of plant litter, respectively. Lit_{inp} (g C kg^{-1} soil day^{-1}) is the daily input
 5 rate of plant litter. CN_{SOM} is the C to N ratio of SOM pool. N_{min} (g N kg^{-1} soil) is the
 6 concentration of soil mineral N (NO_3^- -N + NH_4^+ -N). Tem ($^{\circ}\text{C}$) and SWC (%) are the
 7 temperature and soil water content, respectively.

Experiment	CN_{lit}	LC_{lit}	Lit_{inp}	CN_{SOM}	N_{min}	Tem	SWC
1	15	0.2	0.006	12	0.001	25	60
2	30	0.2	0.006	12	0.005	25	60
3	60	0.2	0.006	12	0.01	25	60
4	120	0.2	0.006	12	0.05	25	60
5	15	0.2	0.006	12	0.001	25	60
6	30	0.2	0.006	12	0.005	25	60
7	60	0.2	0.006	12	0.01	25	60
8	120	0.2	0.006	12	0.05	25	60
9	15	0.2	0.006	12	0.001	25	60
10	30	0.2	0.006	12	0.005	25	60
11	60	0.2	0.006	12	0.01	25	60
12	120	0.2	0.006	12	0.05	25	60
13	15	0.2	0.006	12	0.001	25	60
14	30	0.2	0.006	12	0.005	25	60
15	60	0.2	0.006	12	0.01	25	60
16	120	0.2	0.006	12	0.05	25	60

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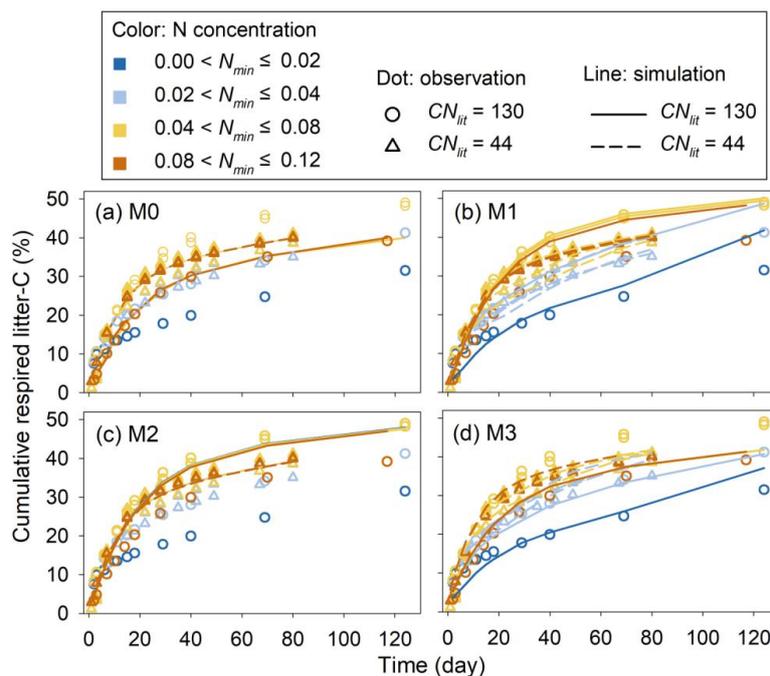
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10

11 **Figure A1** Distribution of the difference between the predicted cumulative respired
 12 litter-C ($R_{s_{sim}}$, %) and the observed values ($R_{s_{obs}}$, %) for all experiments and points in
 13 time. SD is standard deviation of the biases. M0-M3 denote the four models tested in
 14 this study (Table 1).

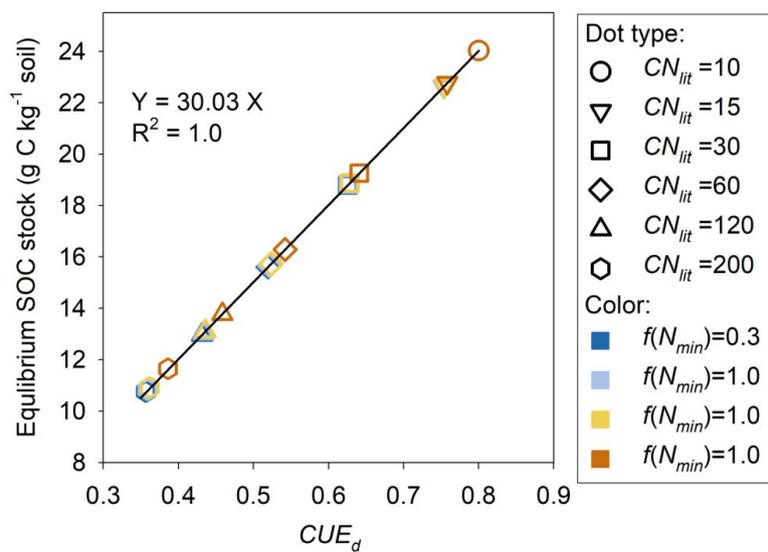
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17 **Figure A2** Dynamic of the simulated carbon use efficiency (CUE) and $f(N_{min})$ during
 18 the incubation experiments (Table S3). CN_{lit} is the C:N ratio of incubated litter, and
 19 N_{min} is the initial soil mineral N concentration (g N kg^{-1} soil). M0-M3 denote the four
 20 models in Table 1. Here the simulation results of each model were calculated with
 21 parameters optimized based on all of the 14 samples of incubation experiments (Table
 22 S2).

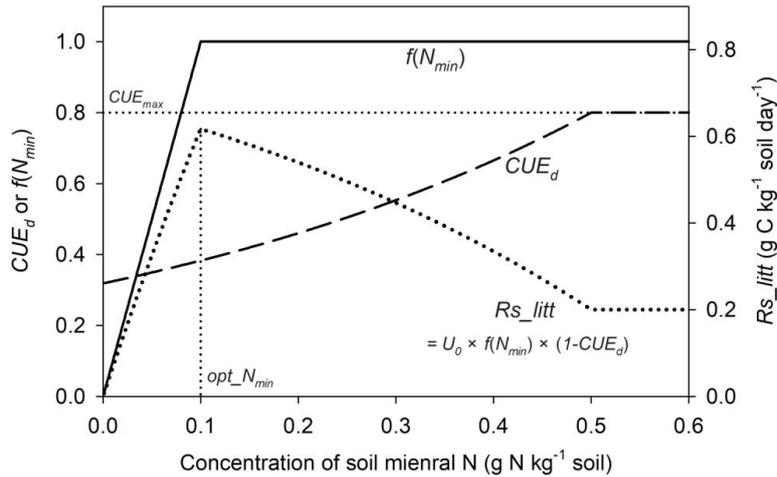
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25 **Figure A3** Relationship between C stock of the potentially equilibrated SOM pool
 26 and the carbon use efficiency of decomposed metabolic litter (CUE_d) at the dynamic
 27 equilibrium stage. $f(N_{min})$ denote the inhibition factor (0–1) of soil mineral N on litter
 28 decomposition.

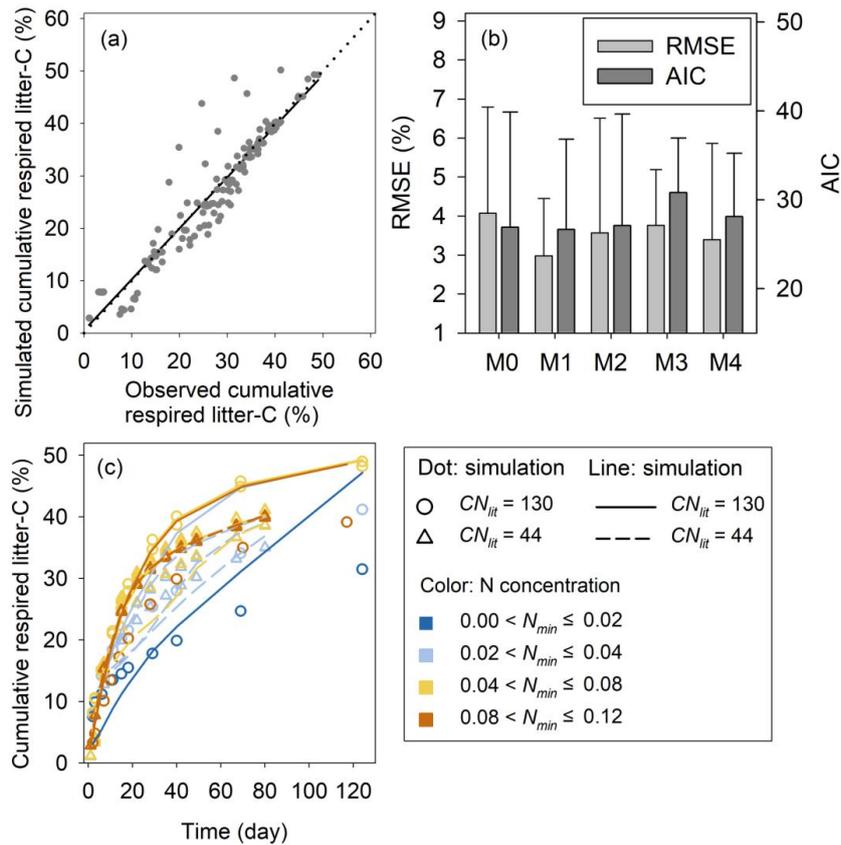
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31 **Figure A4** Schematic plot for change trends of $f(N_{min})$ (inhibition effect of mineral N,
 32 Eq. 6), CUE_d (carbon use efficiency of decomposed litter, Eq. 2,3) and Rs_{litt} (litter
 33 respiration rate) with increasing concentration of soil mineral N. CUE_{max} (= 0.8) is the
 34 maximum CUE set in this study. opt_N_{min} denotes the concentration of soil mineral N
 35 at which litter respiration is maximized. U_0 is the potential decomposition rate when
 36 mineral N is fully adequate for litter decay.

37



38

39 **Figure A5** Comparison between simulated cumulative respired litter-C with $f(N_{min})$
 40 (inhibition effect of soil mineral N on litter decomposition) calculated by Eq. 9 and
 41 the observed results from incubation experiments. In figure (c), M0-M3 denote the
 42 four versions of litter decay model in Table 1. M4 denote the model which used Eq. 2
 43 to calculate the dynamic CUE and used Eq. 9 to calculate $f(N_{min})$.

44