

Dear editor,

We received the comments from the executive editor and the two referees on our manuscript “Modeling the effects of litter stoichiometry and soil mineral N availability on soil organic matter formation” (gmd-2018-173). We are very grateful for their constructive comments and suggested amendments. We have carefully studied them, and revised our manuscript accordingly. As a consequence, our manuscript has been considerably improved.

The following part is our detailed responses to the comments from the executive editor and referees. Please note that the comments are in **bold** followed by our responses in regular text.

Sincerely,

Haicheng Zhang, on behalf of all coauthors

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## **Response to the Executive editor of GMD**

**1. In my role as Executive editor of GMD, I would like to bring to your attention our Editorial version 1.1:**

**<http://www.geosci-model-dev.net/8/3487/2015/gmd-8-3487-2015.html>. This highlights some requirements of papers published in GMD, which is also available on the GMD website in the 'Manuscript Types' section: [http://www.geoscientific-model-development.net/submission/manuscript\\_types.html](http://www.geoscientific-model-development.net/submission/manuscript_types.html).**

Thank you for this reminder. We have read the requirements of paper published in GMD carefully, and also adapted our manuscript accordingly to ensure it meets all the requirements of GMD. See below for details.

**2. In particular, please note that for your paper, the following requirements have not been met in the Discussions paper: • "The main paper must give the model name and version number (or other unique identifier) in the title." • "If the model development relates to a single model then the model name and the version number must be included in the title of the paper. If the main intention of an article is to make a general (i.e. model independent) statement about the usefulness of a new development, but the usefulness is shown with the help of one specific model, the model name and version number must be stated in the title. The title could have a form such as, "Title outlining amazing generic advance: a case study with Model XXX (version Y)". In order to simplify reference to your developments, please add a model name (and/or its acronym) and a version number in the title of your article in your revised submission to GMD.**

To fulfill these requirements, we have added the model name and version number in the title of our article. The original title has been changed from "Modeling the effects of litter stoichiometry and soil mineral N availability on soil organic matter formation"

to

“Modeling the effects of litter stoichiometry and soil mineral N availability on soil organic matter formation using CENTURY-CUE (v1.0)”. (see lines 1-3)

### **Response to Referee #1**

**1.General Comments: Zhang and coauthors present a numerically tractable way to introduce variable carbon use efficiency (CUE) into a first-order litter decomposition model based on nitrogen availability. The paper is well written, with a very clean introduction that nicely summarizes relevant literature and concludes with a clear organization of the paper. Methods are adequately descriptive, results are clearly presented, and the discussion is on target (but see comment on N enrichment and litter decay below).**

Thank you for your positive comments, and please see our responses to your concerns below.

**2. Specific Comments: The approach outline here is nice, using short term experiments to calibrate the model and subsequently looking at the long-term dynamics. One concern, however, is that by using short term respiration rates from field and lab experiments to calibrate the variable CUE it is not clear if turnover coefficients that control litter mass loss are at all appropriate (more on this below).**

Indeed, the litter turnover times have significant impacts on the fitted values of CUE. In our study, the turnover times for C pools are obtained from the ORCHIDEE-MICT that has good performances in reproducing observed organic carbon pools (v8.4.1, Guimberteau *et al.*, 2018). However, we have calibrated the turnover times of the litter pools to the data of the incubation experiments. This calibration was necessary because the plant residues used in the incubation experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) had been cut into fine fragments before being mixed with soil. It is known that the decomposability of litter is negatively correlated to its physical size (Tuomi *et al.*, 2011). We further argue

that the mixing increases the accessibility of litter for microbes. Therefore, the turnover times of the incubated litter used in the experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) should be shorter than the litter turnover times set in ORCHIDEE-MICT (24 days for metabolic litter and 89 days for structural litter), which are representative of to the turnover times of natural plant residues. In this study, we calibrated the turnover times of litter pools (metabolic and structural) based on the observed cumulative respired litter-C from all of the 14 incubation experiments using the M0 and M1 model (see Table A3 below).

We have added one paragraph to introduce the source of the SOC turnover times used in this study, and how we have calibrated the litter turnover times: “Note that the turnover times of SOM pools (active, slow and passive) used in this study are obtained from the ORCHIDEE-MICT (v8.4.1, Guimberteau *et al.*, 2018). The turnover times of litter pools (metabolic and structural), as well as the coefficient  $m_4$  in Eq. (8) were optimized against the observed cumulative respired litter-C from all of the 14 incubation experiments using the M0 and M1 models (Table A3). A previous study has shown that litter decomposability is negatively correlated to its physical size (for example, Tuomi *et al.*, 2011). Therefore, the turnover times of the fine litter fragments used in the incubation experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) are expected to be shorter than the values set in ORCHIDEE-MICT, which are representative of the turnover times of natural plant residues. In addition, the mixing of soil and litter particle in the incubation experiment likely enhances decomposition as spatial disconnection of decomposer and substrate, which can occur under natural soil conditions (Barnes *et al.*, 2012; Hewins *et al.*, 2013), is prevented. The calibrated turnover times of the metabolic and structural pools and the value of  $m_4$  in Eq. (8) are 3.5 and 30 days and 0.5, respectively.” (lines 465-483)

**Table A3** List of parameters calibrated for two versions of the litter decomposition model (M0, M1):  $k_{lim}$  and  $k_{lis}$  are respectively the turnover rates of metabolic and structural litter pools,  $m_4$  is the coefficient in Eq. (8),  $cue_{fit}$  is the optimized value of

CUE,  $m_1$  and  $n_1$  are the coefficients in Eq. (3), and  $m_2$  is the coefficients in Eq. (5).

Version	CUE	$f(N_{min})$	Parameters
M0	Fixed	1	$cue_{fit}, k_{lim}, k_{lits}, m_4$
M1	Eqs.(2), (3)	Eq. (5)	$m_1, n_1, m_2, k_{lim}, k_{lits}, m_4$

(lines 1532-1536)

**3. In section 2.5 it's a little unclear how the model and observations are disentangling background soil respiration from the litter respiration fluxes that are presumably being fit. Can this be clarified?**

We have added some sentences to explain how the model and observations distinguish the litter- and SOC-derived CO<sub>2</sub>.

For incubation experiments:

“To distinguish the litter- and SOC-derived CO<sub>2</sub> flux, Guenet *et al.* (2010) used straw from wheat grown under <sup>13</sup>C labeled CO<sub>2</sub> and they are therefore able to track the CO<sub>2</sub> coming from litter and the CO<sub>2</sub> coming from soil. In the experiments by Recous *et al.* (1995), litter-derived CO<sub>2</sub> flux is calculated as the difference in CO<sub>2</sub> flux between the incubation samples with both soil and litter, and the control samples without added litter.” (lines 372-377)

For simulations:

“The observed cumulative respired litter-C (g C kg<sup>-1</sup> soil) measured in the incubation experiments was used to calibrate the model parameter values. Moreover, to quantify the simulated CO<sub>2</sub> flux derived from the litter, we also performed a set of control simulations with only SOM (initial litter pools were set to 0 g kg<sup>-1</sup> soil) using the four model versions. The simulated litter-derived CO<sub>2</sub> flux is calculated as the difference in CO<sub>2</sub> flux between the simulation with both litter and SOM inputs and the simulation with only SOM input.” (lines 408-415)

**4. I'm assuming there are no modifications to other CUE terms in CENTURY (between SOM pools), but this should be clarified.**

We have added some sentences to clarify that only CUE for C transfers from litter pools to SOC pools were modified. Please see:

“Eqs. (2) and (3) were implemented in CENTURY to modify the originally fixed  $CUE_d$  (Fig. 1). With this change, the fractions of C from litter that remain in SOM are mediated by stoichiometric constraints and mineral N availability, at the expense of additional parameters to fit. The  $CUE_d$  for C transfers between SOC pools (active, slow and passive) are not modified.” (lines 295-299)

**5. Turnover times used in the model (e.g. tau\_metabolic and tau\_structural and well as the SOM turnover times listed in the github archive) are much larger than the litter turnover times used in CENTURY (Parton et al. 1988). This makes me wonder where the turnover parameterization here comes from? Addressing this concern is important since respiration rates are a product of turnover and CUE (given fixed initial pool sizes). Since the turnover times used here are much lower than in the CENTURY parameterization, the CUE will also have to be lower than if faster turnover times were used in the model. This is all fine, but should be made clearer in the text, which otherwise claims to be using the CENTURY approach.**

The reviewer is correct; please see our response to Comment #2.

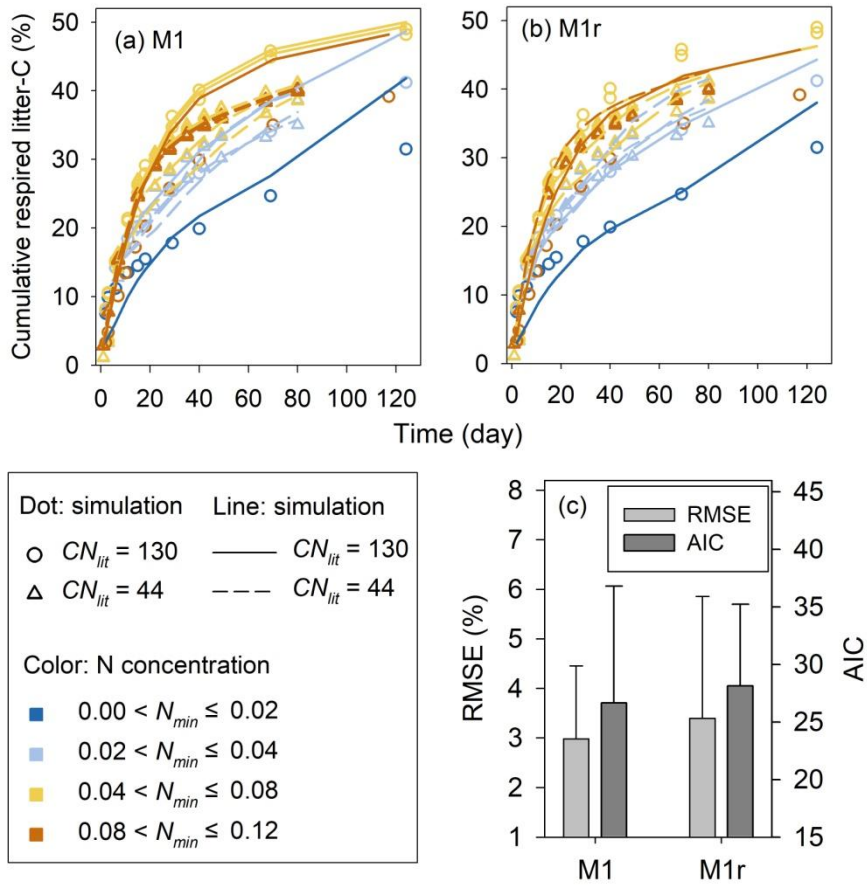
**6. The maximum CUE allowed in the study seems quite high (0.8, Fig. 2). I'm assuming this assumption also causes the apparent high bias in CUE shown in Fig. 6? Is the model able to fit the data as well with a more reasonable upper limit for CUE (say 0.6), or is the high efficiency needed to capture results observed in the experiment?**

We agree that  $CUE=0.8$  is a relatively high value. While the CUEs of soil microbes are mostly concentrated between 0.4 and 0.6 (Manzoni et al., 2012), maximum values for reduced substrates are around 0.8 (Gommers et al., 1988), similar to maximum values also found in soils (Manzoni et al., 2012). Therefore, to allow the calibration procedure to cover a wide range of microbial CUEs, we set the maximum

CUE to 0.8. We have indicated the source reference of the maximum CUE in our manuscript. Please see:

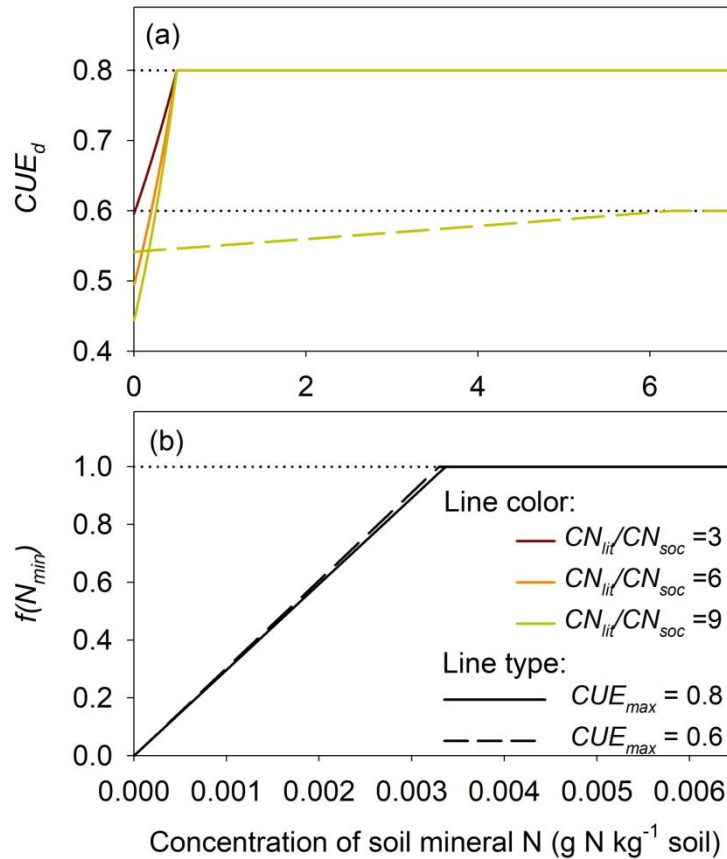
“ $CUE_{max}$  (dimensionless) is the maximum  $CUE_d$  achieved when nutrients are not limiting, and it is set to 0.8 based on a synthesis of observed CUE of soil microbes (Manzoni *et al.*, 2012).” (lines 264-266)

In addition, we also tested the performance of M1 model using a lower  $CUE_{max}$  of 0.6 as the referee suggests to be more reasonable. The result indicates that the optimized M1r is also able to capture the differences in respiration rates due to different C:N ratios of substrate and varying levels of mineral N availability across the 14 incubation experiments (Fig. R1b), although the RMSE (also AIC) of its estimation is slightly higher than that of M1 (Fig. R1c). The optimized function of  $f(N_{min})$  (Eq. 5) with a  $CUE_{max}$  of 0.6 is almost same to that with a  $CUE_{max}$  of 0.8 (Fig. R2b). But the optimized  $CUE_d$  function (Eq. 2) with a  $CUE_{max}$  of 0.6 is very different from that with a  $CUE_{max}$  of 0.8. When the  $CUE_{max}$  is set to 0.6,  $CUE_d$  increases very slowly with increasing soil mineral N concentration (Fig R2a), and shows almost no difference for litter with different qualities.



**Figure R1** Comparison of simulated cumulative respired litter-C between models with CUE upper limit of 0.8 (M1) and 0.6 (M1r), respectively.





**Figure R2.** Change in the relations between carbon use efficiency ( $CUE_d$ , (a)) and N limitation factor ( $f(N_{min})$ , (b)), and mineral N concentration. Here the  $CUE_d$  and  $f(N_{min})$  are calculated based on the optimized parameters when the upper limit of CUE is set to 0.8 (continuous line) and 0.6 (dashed line), respectively.  $CN_{lit}$  and  $CN_{SOM}$  are the C:N ratios of litter and SOM pools, respectively.

**7. The main response of changes in CUE with litter quality seem to be opposite of what's expected. It seems like the authors expected to see a “decrease in CUEd with decreasing litter quality” (line 224), but instead report higher CUEd with the lower quality litter (line 363). Please explain how the parameterization let to this response and seems to contradict findings reported in Fig. 6.**

There was a mistake in the text. We found an increase in  $CUE_d$  with declining litter quality. We revised the text:

“For very low quality litter with a C:N ratio of 130, the  $CUE_d$  in models M1 and M2 are 0.55 and 0.56, respectively, which are higher than for better quality litter with C:N ratio of 44 (approximately 0.40 and 0.44 in M1 and M2, respectively).”

to

“For very low quality litter with a C:N ratio of 130, the  $CUE_d$  in models M1 and M2 are 0.40 and 0.44, respectively, which are lower than for better quality litter with C:N ratio of 44 (approximately 0.55 and 0.56 in M1 and M2, respectively).” (lines 616-640)

**8. Line 400. I agree, it’s nice these parameters can be estimated, but the fit parameter values and their associated uncertainty are never communicated in the text. Can they be given in Table 1, or elsewhere in the manuscript? Similarly, does it make sense to include parameter values in Table A1?**

We have added the parameter values and their associated uncertainties to the Table 1 in our manuscript. Please see:

“**Table 1** Optimized parameter values for the five versions of the litter decomposition model used in this study.  $cue_{fit}$  is the optimized value of CUE,  $m_1$  and  $n_1$  are the coefficients in Eq. (3),  $m_2$  is the coefficient in Eq. (5), and  $m_3$  is the coefficient in Eq. (6). Values in brackets following each parameter are the means ( $\pm$  standard deviations) of the fitted parameter values based on “leave-one-out” cross-validation (see Section 2.5 for more details).

Version	CUE	$f(N_{min})$	Parameters
M0	Fixed	1	$cue_{fit}$ (0.57 $\pm$ 0.004)
M1	Eqs. (2), (3)	Eq. (5)	$m_1$ (0.61 $\pm$ 0.34), $n_1$ (0.53 $\pm$ 0.21), $m_2$ (297.4 $\pm$ 38.0)
M2	Eqs. (2), (3)	1	$m_1$ (0.11 $\pm$ 0.01), $n_1$ (1.96 $\pm$ 0.13)
M3	Fixed	Eq. (5)	$cue_{fit}$ (0.54 $\pm$ 0.01), $m_2$ (396.9 $\pm$ 23.6)
M4	Eqs.(2), (3)	Eq. (6)	$m_1$ (0.13 $\pm$ 0.07), $n_1$ (1.91 $\pm$ 0.37), $m_3$ (0.58 $\pm$ 0.12)

” (lines 1409-1416)

**9. The discussion is largely on target and I was very excited to see the authors try to take on results that generally show lower litter decomposition rates with N enrichment (e.g. Fog 1988, Knorr et al. 2005), line 415. What follows, however,**

**does not really conceptually address the apparent paradox of N additions, litter decay, and CUE. Instead the mathematical approach introduces new simulations and a new set of simulations (eq. 8, 9 & Fig. A5). Introducing new results like this in the discussion seems inappropriate for the journal. Instead it seems like these findings could be: (a) incorporated into the method and results; or (b) dropped from the manuscript. I would encourage the first option, but also ask the authors to more thoughtfully discuss how their results can inform larger questions about litter decay and N enrichment (Nave et al. 2009; Hobbie 2015; see also Wieder et al. 2015).**

Thanks for your suggestion. We have moved the description of the alternative formulation for  $f(N_{min})$  from the discussion section to the method section (see Section 2.4, lines: 326-340).

We added:

“The Model M4, which uses the alternative formulation for N constraints on litter decay (Eq. (6)), reproduces the different respiration rates of substrates with contrasting C:N ratios and at different levels of mineral N availability (Fig. A2), but with a slightly higher average RMSE of cumulative respired litter-C than model M1.” in the Results section (lines 605-609)

We also added:

“In addition, the model M4, which is comparable to model M1 but uses an alternative formulation for N effects on the decomposition rate (Eq. (6)), performed slightly worse than model M1 (Fig. A2). Arguably, Eq. (6) represents the underlying mechanisms of N inhibition effects (Manzoni *et al.*, 2009; Bonan *et al.*, 2013; Fujita *et al.*, 2014; Averill and Waring, 2018) better than Eq. (5) and due to the minor differences in RMSE and AIC (Figure A2b) between these formulations it can serve as an alternative to M1.” in the Discussion section (lines 701-707)

Moreover, we have revised the discussions on the effects of N enrichment on litter respiration rate. The original sentences have been changed from “Moreover, describing N limitations on both the decomposition rate and flexible CUE<sub>d</sub> might allow our model to explain the observed diverse responses of litter respiration rate to

added mineral N in fertilization experiments (Hobbie and Vitousek, 2000; Guenet *et al.*, 2010; Janssens *et al.*, 2010). In these experiments, the net changes in respiration rate depend on the combined effects of added N on litter decay rate and  $CUE_d$  of the decayed litter (Fig. A4)."

to

"Our results indicate that the observed diversity of responses of litter respiration rate to mineral N additions (Hobbie and Vitousek, 2000; Guenet *et al.*, 2010; Janssens *et al.*, 2010) is likely due to the combined effects of changes in litter decay rate and  $CUE_d$  (Fig. A5). Thus, N addition effects can differ among fertilization experiments if litter quality and background N availability vary. In addition to altering litter decay rate and  $CUE_d$ , mineral N addition can induce abiotic formation of compounds that resist microbial attack, inhibit oxidative enzymes involved in lignin degradation, stimulate microbial biomass production early in decomposition, or lead to the accumulation of microbial residues that are resistant to decay (Fog, 1988; Hobbie, 2015). All these effects might decrease litter respiration rate by inhibiting the decomposition process, but have not been considered in our current model." (lines 708-728)

**10. My final concern is somewhat subjective, but I argue that litter decomposition and SOM formation are not the same process. Throughout, however, the text (and especially the discussion) misleadingly conflates these two processes. While it's true that in first order models like CENTURY these processes are intimately linked, a growing body of literature highlights fundamental differences between processes controlling litter decay and SOM formation (see Lehmann and Kleber 2015, Sokol et al. 2018). Results shown in Fig. 7 are fine, but I would caution against linking these processes directly in the text.**

This is also a good point. Indeed, litter decomposition and SOM formation are not the same processes, since SOM formation also involves stabilization processes. However, the first-order decomposition models like CENTURY have represented

these complicated processes in a very simple way, without explicit representation of the continuous transformation processes from decomposed litter to microbial productions and finally to stable SOM. According to your suggestion, we have revised our manuscript and deleted the sentences which might misleadingly conflate the litter decomposition and SOM formation processes. The major revision can be found from our response to your Comment #17 below. Please see lines 729-740 of the revised manuscript.

**11. Technical corrections: Line 215, Don't 'microbes' include fungi and bacteria?**

**Line 215, Cleveland and Liptzin report microbial C:N = 8.6 (molar), so I'm assuming the 7.4 reported here on a mass basis, but this should be clarified in the text?**

We have changed the original sentences from

“The C:N ratio of SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being between the C:N ratios of the two major group decomposers, soil microbes (7.4:1) (Cleveland and Liptzin, 2007) and soil fungi (13.4:1, Zhang *and* Elser, 2017).”

to

“The C:N ratio of SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being between the average C:N ratio of soil microbial communities including fungi and bacteria (7.4:1 in Cleveland and Liptzin, 2007) and the C:N ratio of soil fungi (13.4:1 in Zhang and Elser, 2017), which are probably largely responsible for fresh litter decomposition.”. (lines 259-264)

**12. Methods: It may be helpful to describe how the model handles partitioning of litter into metabolic and structural litter pools, and how the stoichiometry of these LIT pools changes with changes in litter quality (e.g., what are the donor pool C:N ratios if litterfall inputs have a C:N of 40 vs. 130)?**

We have added a few sentences to introduce how the litter input is partitioned into

metabolic and structural pools, as well as how we set the C:N ratio of litter pools.

Please see:

“Plant litter was firstly separated into metabolic and structural litter pools based on its lignin to C ratio ( $LC_{lit}$ , dimensionless). The fraction of metabolic litter-C ( $f_m$ , 0-1, dimensionless) is calculated by:

$$f_m = f_{max} - m_4 \times LC_{lit} \quad (8)$$

where  $m_4$  is a coefficient to be calibrated;  $f_{max}=0.85$  is the maximum fraction of metabolic litter (i.e., the default value in CENTURY; Parton *et al.*, 1988). The fraction of structural litter-C is thus  $1 - f_m$ . The C:N ratios of both metabolic and structural pools are assumed to be equal to the C:N ratio of litter input.” (lines 398-406)

Note that, to avoid a double-consideration of the N content of litter input (that is to say the C:N ratio has been involved in the CUE formula), we just use the lignin content (Lignin:C) to calculate the fraction of metabolic litter. This is different from the algorithm used in the default CENTURY, which separates the litter inputs into metabolic and structural pools based on both lignin and N content.

**13. Line 270 & 319, seems odd to cite a web site for a corporation selling composting material. A better choice may be Brovkin et al. 2012, who report litter quality estimates from the ART-DECO database, or work from the LIDET team (e.g. Harmon et al. 2009).**

Thanks for your suggestion. We have changed the original sentence from “The C:N ratios of those corn residue and wheat straw span the range of litter C:N ratios among different ecosystems (Harmon *et al.*, 2009; <https://www.planetnatural.com/composting-101/making/c-n-ratio/>).”

to

“The C:N ratios of those corn residue and wheat straw span the range of litter C:N ratios among different ecosystems (Harmon *et al.*, 2009; Brovkin *et al.*, 2012; Manzoni *et al.*, 2010).” (lines 365-367)

and from “The assumed litter C:N ratios ( $CN_{lit}$ ) of 10, 15, 30, 60, 120 and 200 span

the variation among most natural substrates and soil amendments from organic matter input in agriculture (Manzoni *et al.*, 2012; <https://www.planetnatural.com/composting-101/making/c-n-ratio/>).

to

“The assumed litter C:N ratios ( $CN_{lit}$ ) of 10, 15, 30, 60, 120 and 200 span the variation among most natural substrates and soil amendments from organic matter input in agriculture (Harmon *et al.*, 2009; [Brovkin \*et al.\*, 2012](#); [Manzoni \*et al.\*, 2010](#)).

**14. Line 355, this statement isn't very obvious from Fig. 5b, in my estimation.**

We have deleted the sentence “In addition, model M1 can also capture the temporal evolution of cumulative respired litter-C in different incubation experiments (Fig. 5b).”

**15. Fig. 6. It's not really clear how the authors plot the C:N ratio of substrates : decomposers for a model that doesn't consider decomposers. I'm assuming this is the C:N ratio of donor (litter) / receiver (SOM pools; eq. 2)? Maybe this can be clarified in the figure caption? This is a fine assumption to make, although Cleveland and Liptzin (2007) found microbial C:N < soil C:N.**

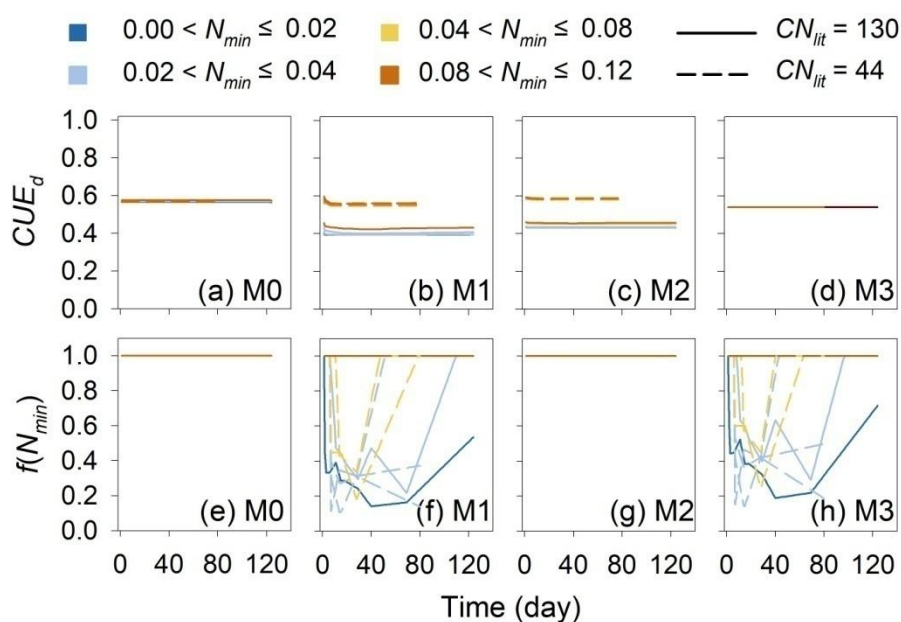
Sorry for the unclear explanation on the x-axis of Fig. 6. We have changed the original figure caption from “**Figure 6** Comparison of  $CUE_d$  (lines) predicted by Eq. (2) with parameter values ( $m_2 = 0.54$ ,  $n_1 = 0.50$ ) calibrated based on the incubation experiments (Table A2) of Recous *et al.* (1995) and Guenet *et al.* (2010) to observed CUE of terrestrial microorganisms along a gradient of  $CN_S/CN_D$ , where  $CN_D$  and  $CN_S$  are the C:N ratio of decomposers and their substrates, respectively. Gray dots are the estimated microbial CUE of litter decomposition in natural terrestrial ecosystems from Manzoni *et al.* (2017). Black squares are the microbial CUE measured via laboratory incubation experiments of Gilmour & Gilmour, (1985), Devêvre & Horváth (2000) and Thiet *et al.* (2006). Error bars represent the standard deviations.  $N_{min}$  ( $g\ N\ kg^{-1}\ soil$ ) is the concentration of soil mineral N.”

to

“**Figure 6** Comparison of  $CUE_d$  (lines) predicted by Eq. (2) with parameter values ( $m_2 = 0.54, n_l = 0.50$ ) calibrated based on the incubation experiments (Table A2) of Recous et al. (1995) and Guenet et al. (2010) to observed  $CUE$  of terrestrial microorganisms along a gradient of  $CN_S/CN_D$ . For observed  $CUE$  (dots),  $CN_D$  and  $CN_S$  are the C:N ratio of decomposers and their substrates, respectively. For simulated  $CUE$  (lines),  $CN_S$  and  $CN_D$  correspond to the C:N ratio of donor (litter pool) and acceptor (the active SOM pool of the CENTURY), respectively. Gray dots are the estimated microbial  $CUE$  of litter decomposition in natural terrestrial ecosystems from Manzoni *et al.* (2017). Black squares are the microbial  $CUE$  measured via laboratory incubation experiments of Gilmour and Gilmour, (1985), Devêvre and Horváth (2000) and Thiet *et al.* (2006). Error bars represent the standard deviations.  $N_{min}$  ( $g\ N\ kg^{-1}$  soil) is the concentration of soil mineral N.” (lines 1494-1506)

**16. How is Fig. A2 different from Fig. 5? Moreover, the caption in A2 doesn't seem to match the display item? (see also lines 374, 376).**

The reviewer is correct: we have inserted a wrong figure as Fig. A2. Now we have corrected the error. Please see:



“



**Figure A3** Dynamic of the simulated carbon use efficiency ( $CUE$ ) and  $f(N_{min})$  during the incubation experiments (Table A4).  $CN_{lit}$  is the C:N ratio of incubated litter, and  $N_{min}$  is the initial soil mineral N concentration ( $\text{g N kg}^{-1}$  soil). M0-M3 are the four models in Table 1. Here the simulation results of each model were calculated with parameters optimized based on all of the 14 samples of incubation experiments (Table A2).” (lines 1571-1577)

**17. From line 480-506 on the discussion wanders well beyond the scope of results presented here. In particular, the emphasis on humic substances and litterfall driving SOM formation seems well out of line with contemporary thinking about factors controlling SOM stabilization (Lehmann and Kleber 2015). Moreover, the positive connection between CUE and steady-state SOM pools in first order models is well established (e.g. Frey et al. 2013). What’s nice with the work presented here is the ability to link ideas about litter quality and SOM formation in ways that are consistent with theory about CUE and substrate quality (MEMs conceptual model, Cortufo et al. 2013) in a first order model. I’d encourage the authors more closely stick to interpreting the results presented with this work.**

Thanks for your suggestion. We have revised the manuscript to make it more closely stick to interpreting the results presented with this work. The original sentences have been changed from “This study provides some insights on processes leading to increased SOM sequestration. Soil C sequestration plays a crucial role in food security and land CO<sub>2</sub> emission (Lal, 2004). The international initiative ‘4 per 1000’ has been proposed to increase global SOM stock by 0.4% per year to compensate for anthropogenic CO<sub>2</sub> emissions (Baveye *et al.*, 2018). Transforming more plant litter into stable SOM (e.g. humic substances) has been suggested as an effective strategy to sequester more C in soil (Prescott, 2010). Our model results show a positive linear relationship between equilibrium SOC stock and CUE of decomposed litter (Fig. A4). This result can also be interpreted by calculating the analytical equilibrium SOC storage of a fully linear model including only one litter

pool and one SOC pool. In such a model, SOC receives C from the litter at a rate  $CUE_d \times D$ , where  $D$  is the litter decomposition rate, which equals to litterfall at steady state. SOC is lost via first order decay with a decay constant  $k$ . At steady state, input to and outputs from the SOC pool are equal and thus,

$$CUE_d \times D = k \times SOC \rightarrow SOC = CUE_d \frac{D}{k} \quad (11)$$

With a mean residence time of C in the SOC between 10 and 20 years and  $D$  approximated by litterfall (Table A4), SOC at equilibrium is predicted to scale linearly with  $CUE_d$ , with a slope approximately between 20 and 40, consistent with results in Fig. A4.

Therefore, litter quality needs to be controlled to maximize C sequestration in SOM pool (Eq. (2)). In line with previous studies (Prescott, 2010; Smith, 2016), our model predicts that adding N through fertilization and N-fixing plants will not only increase litter decay but also the fraction of litter-C being transformed into SOM and ultimately SOC stocks. However, application of mineral N fertilizer is associated with risk not considered here, like increasing land  $N_2O$  emission (Mosier and Kroeze, 2000; Kanter *et al.*, 2016; Yi *et al.*, 2017) and causing nitrate leaching which in turn can induce water pollution (Cao *et al.*, 2006; Stokal *et al.*, 2016). Due to the negative environmental impacts of mineral N addition, the use of N-rich litter substrates for increasing SOM is advised.”

to

“This study provides insight on processes leading to increased SOM sequestration. Enhancing the efficiency at which plant residuals are transformed into stable SOM has been suggested as an effective strategy to sequester C in soil (Prescott, 2010; Cotrufo *et al.*, 2013). Simulation results from our model suggest a positive linear relationship between equilibrium SOC stock and CUE of decomposed litter (Fig. A4), in line with the earlier findings with a similar model (for example Frey *et al.* 2013). In fact, with linear models such as CENTURY it can be shown that the steady state SOC scales linearly with CUE, different from nonlinear models predicting that higher CUE can trigger SOC loss (Allison *et al.*, 2010). Our model goes beyond

earlier attempts (Bonan *et al.*, 2013; Fujita *et al.*, 2014; Averill and Waring, 2018) by adapting the optimal metabolic regulation hypothesis of Manzoni *et al.* (2017) to link CUE, litter quality and SOM formation in a process-oriented way.” (lines 729-740)

**18. Line 512, self-citations are nice, but it may also be worth referencing other modeling groups here?**

We have changed the original sentence from “An increasing number of land surface models (e.g. ORCHIDEE-CNP, Goll *et al.*, 2017) have representations of the terrestrial N cycle.”

to

“An increasing number of land surface models (Wang *et al.*, 2010; Zaehle *et al.*, 2014; Goll *et al.*, 2017) have representations of the terrestrial N cycle.” (lines 1035-1036)

**19. Line 516, didn’t Bonan and others (2013, cited elsewhere in the text) already do this with CLM and CENTURY? Seems worth crediting work that’s already been done along these lines.**

Although the constraint of soil mineral N availability on litter decomposition rate has been represented in some land surface and soil biogeochemical model (Bonan *et al.*, 2013; Fujita *et al.*, 2014; Averill and Waring, 2018), to our knowledge, none of these models have tested the links CUE to litter stoichiometry and soil nutrient availability. However, we acknowledge that other theoretical models have included this link (Schimel and Weintraub, 2003). The original sentence in our manuscript might have not given an accurate statement. We thus changed it from “By incorporating our litter decomposition formulation in these land surface models that simulate the dynamics of soil mineral N concentration, it will be possible to test and validate our developments with more extensive data from laboratory and field experiments.”

to

“By incorporating our newly developed formulations of  $CUE_d$  and  $f(N_{min})$  in these

land surface models that simulate the dynamics of soil mineral N concentration, it will be possible to test and validate our developments with more extensive data from laboratory and field experiments.” (lines 1036-1040)

**20. Line 538, the comparison with ‘most large-scale litter decay models’ was not made in this paper and I would remove this clause from the conclusion.**

Thanks for your suggestion. We have removed this clause. The original sentence is changed from “Overall, the developed model captures the microbial mechanisms mediating litter stoichiometry and soil mineral N effects on litter decomposition and SOM formation – representing an improvement over most existing large-scale litter decay models.”

to

“Overall, the developed model captures the microbial mechanisms mediating litter stoichiometry and soil mineral N effects on litter decomposition and SOM formation.” (lines 1059-1066)

## **Response to Referee #2**

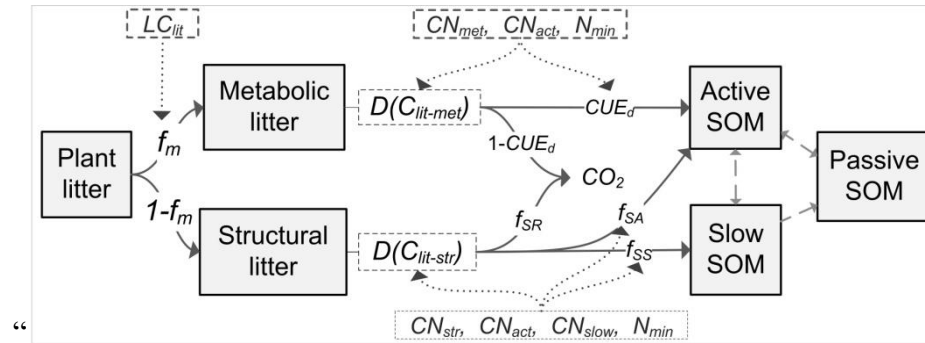
**1. This study adapted a conceptual formulation of CUEd based on assumption that litter decomposers optimally adjust their CUEd as a function of litter substrate C to nitrogen (N) stoichiometry. The new model algorithm was incorporated into CENTURY soil biogeochemical model and evaluated using data from laboratory litter incubation experiments. The results showed that new CUEd formulation with flexible CUE and effect of N availability to decay rate was able to reproduce differences in respiration rate of litter with contrasting C:N ratios and under different levels of mineral N availability. It is well-written, logically organized, and the figures and tables are appropriate.**

Thanks for your positive comments.

**2. Figure 1 seems too simple to include other major processes mentioned in the**

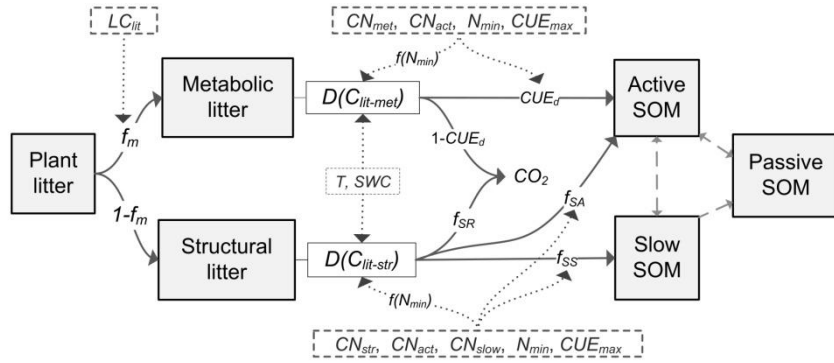
**method section. It should be considered to revise.**

Thanks for your reminding. We have revised the Fig. 1 and checked the Method section to make sure that all important processes have been illustrated in this flowchart. Finally, we added the temperature ( $T$  (°C)) and soil moisture ( $SWC$  (%)) factors for scaling litter decay rate, as well as the inhibition effect of mineral N on litter decay rate ( $f(N_{min})$ ). The original Fig. 1 has been changed from



**Figure 1** Schematic diagram of the C flows in the litter decay model used in this study.  $f_m$  is the fraction of metabolic compounds in plant litter.  $D(C_{lit-met})$  and  $D(C_{lit-str})$  are the decomposition rates ( $g\ C\ kg^{-1}\ day^{-1}$ ) of metabolic or structural litter, respectively.  $LC_{lit}$  is the lignin:C ratio (on a mass basis) of plant litter;  $CN_{met}$ ,  $CN_{str}$ ,  $CN_{act}$ , and  $CN_{slow}$  are the C:N ratio of metabolic litter pool, structural litter pool, active SOM pool and slow SOM pool, respectively;  $N_{min}$  is the concentration of mineral N in solution ( $g\ N\ kg^{-1}\ soil$ );  $CUE_d$  is C use efficiency of the transformation from litter to soil organic matter (SOM);  $f_{SA}$ ,  $f_{SS}$  and  $f_{SR}$  are the fractions of decomposed structural litter-C that is transferred to active SOM pool, slow SOM pool and released to atmosphere in forms of  $CO_2$ , respectively. As in the algorithms in CENTURY model (Parton *et al.*, 1988), here  $f_{SA} = CUE_{d\_SA} \times (1 - f_{lig})$ ,  $f_{SS} = CUE_{d\_SS} \times f_{lig}$ ,  $f_{SR} = 1 - (f_{SA} + f_{SS})$ , where  $f_{lig}$  is the lignin fraction (0–1, dimensionless) in the structural litter pool, and  $CUE_{d\_SA}$  and  $CUE_{d\_SS}$  are the CUE of C transformation from structural litter pool to active and slow SOM pool, respectively.”

to



**Figure 1** Schematic diagram of the C flows in the litter decay model used in this study.  $f_m$  is the fraction of metabolic compounds in plant litter.  $D(C_{lit-met})$  and  $D(C_{lit-str})$  are the decomposition rates ( $g\ C\ kg^{-1}\ day^{-1}$ ) of metabolic or structural litter, respectively.  $LC_{lit}$  is the lignin:C ratio (on a mass basis) of plant litter;  $CN_{met}$ ,  $CN_{str}$ ,  $CN_{act}$ , and  $CN_{slow}$  are the C:N ratio of metabolic litter pool, structural litter pool, active SOM pool and slow SOM pool, respectively;  $N_{min}$  is the concentration of mineral N in solution ( $g\ N\ kg^{-1}\ soil$ );  $f(N_{min})$  is a factor reducing litter decay rate when soil mineral N availability is limiting;  $T$  ( $^{\circ}C$ ) and  $SWC$  (%) are temperature and soil water content, respectively;  $CUE_d$  is C use efficiency of the transformation from litter to soil organic matter (SOM);  $CUE_{max}=0.8$  is the maximum microbial CUE (dimensionless) when growth is limited by C from the organic substrate;  $f_{SA}$ ,  $f_{SS}$  and  $f_{SR}$  are the fractions of decomposed structural litter-C that is transferred to active SOM pool, slow SOM pool and released to atmosphere in forms of  $CO_2$ , respectively. As in the algorithms in CENTURY model (Parton et al., 1988), here  $f_{SA}=CUE_{d\_SA}\times(1-f_{lig})$ ,  $f_{SS}=CUE_{d\_SS}\times f_{lig}$ ,  $f_{SR}=1-(f_{SA}+f_{SS})$ , where  $f_{lig}$  is the lignin fraction (0–1, dimensionless) in the structural litter pool, and  $CUE_{d\_SA}$  and  $CUE_{d\_SS}$  are the CUE of C transformation from structural litter pool to active and slow SOM pool, respectively.” (lines 1428-1445)

**3. As the CUEd was defined as a fraction of it is respired to the atmosphere and the remaining fraction (Line 159-160), it is not correct to use 1-CUEd to simulate CO2 emission in Fig. 1.**

Microbial carbon use efficiency (CUE), defined as the ratio of microbial biomass production to material uptake from substrates (lines 68-69). In our study, the CUE of

decayed litter-C ( $D_{(C-lit)}$ ) is defined as the ratio of C that is transferred into SOC pool ( $CUE \times D_{(C-lit)}$ ) to the total decayed litter-C. Therefore, the remaining fraction ( $(1-CUE) \times D_{(C-lit)}$ ) is respired to the atmosphere as CO<sub>2</sub>. To explain the definition of CUE more explicitly, we have changed the original sentence from "When C is being transferred between pools, a fraction of it is respired to the atmosphere and the remaining fraction ( $CUE_d$  conceptually equal to microbial CUE) enters the acceptor pool."

to

"When litter is being decomposed, a fraction of the decomposed C is respired to the atmosphere and the remaining fraction ( $CUE_d$  conceptually equal to microbial CUE) enters the acceptor SOM pool." (lines 196-199)

**4. Equ (4) is important for this study, which has been used to develop one of model simulations (i.e. M1). However what is the fundamental assumption for adding N effects in the Equ (4)? N mineralization is accompanied with carbon decomposition. So, why use N availability to limit litter decay?**

Biomass of microbes is stoichiometrically constrained. When the supply of N from substrates is lower than the demand of microbes to fulfill their specific stoichiometric C:N ratio, microbes will utilize the mineral N (immobilization). Thus low availability of mineral N can limit microbial activity, and in turn litter decay rate. There is no explicit representation of microbial growth in CENTURY model. But the C:N ratio of SOM pool is assumed to be same to that of the microbial biomass. The mineralized N accompanying with litter decomposition will preferentially enter SOM pool to fulfill the SOM C:N ratio. When the N supply from decomposed litter is lower than the demand of newly formed SOM, soil mineral N will be immobilized. Therefore when soil mineral N concentration is very low and the immobilized N cannot meet the N demand of SOM, then the mineral N becomes a constraint factor of litter decomposition rate.

We have provided a brief introduction on the fundamental assumption for adding the mineral N factor in Eq. 4, and it can be find from: "Microbial biomass is nearly

homeostatic (Cleveland and Liptzin, 2007; Franklin *et al.*, 2011; Allison, 2012).

When the supply of N from substrates is lower than the demand of microbes to fulfill their specific stoichiometric C:N ratio, microbes will utilize mineral N (immobilization) (Manzoni *et al.*, 2012). Thus, low availability of mineral N can limit microbial activity, and in turn litter decay rate (Manzoni and Porporato 2009; Fujita *et al.*, 2014).” (lines 130-135)

and

“The C:N ratio of SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being between the average C:N ratio of soil microbial communities including fungi and bacteria (7.4:1 in Cleveland and Liptzin, 2007) and the C:N ratio of soil fungi (13.4:1 in Zhang and Elser, 2017), which are probably largely responsible for fresh litter decomposition.” (lines 259-264)

#### **5. Line 71: need reference here.**

We have added references for our statement: “During litter decomposition, only a part of the decomposed litter-C is being transferred into SOM, while the remaining C is being released as CO<sub>2</sub> to the atmosphere by microbial respiration (Campbell and Paustian, 2015; Cotrufo *et al.*, 2015).” (lines 73-76)

#### **6. Line 212: typo “The The C:N ratio”**

Sorry for the mistake. We have changed the original sentence from “The The C:N ratio of SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being close to the observed average C:N ratio of soil microbes (7.4:1 in Cleveland and Liptzin, 2007 and 13.4:1 for soil fungi in Zhang *and* Elser, 2017).”

to

“The C:N ratio of SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer biomass, its value being between the average C:N ratio of soil microbial communities including fungi and bacteria (7.4:1 in Cleveland and Liptzin, 2007) and the C:N ratio of soil fungi (13.4:1 in Zhang and Elser, 2017), which are



probably largely responsible for fresh litter decomposition.” (lines 259-264)

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1 **Modeling the effects of litter stoichiometry and soil mineral N**  
2 **availability on soil organic matter formation using CENTURY-CUE**  
3 **(v1.0)**

4  
5 [Haicheng Zhang](#)<sup>1</sup>, [Daniel S. Goll](#)<sup>1</sup>, [Stefano Manzoni](#)<sup>2,3</sup>, [Philippe Ciais](#)<sup>1</sup>, [Bertrand](#)  
6 [Guenet](#)<sup>1</sup>, [Yuanyuan Huang](#)<sup>1</sup>

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16 Type: primary research

17

18 **Abstract**

19 Microbial decomposition of plant litter is a crucial process for the land  
20 carbon (C) cycle, as it directly controls the partitioning of litter-C between CO<sub>2</sub>  
21 released to the atmosphere versus the formation of new soil organic matter (SOM).  
22 Land surface models used to study the C cycle rarely considered flexibility in the  
23 decomposer C use efficiency (CUE<sub>d</sub>) defined by the fraction of decomposed litter-C  
24 that is retained as SOM (as opposed to be respired). In this study, we adapted a  
25 conceptual formulation of CUE<sub>d</sub> based on assumption that litter decomposers  
26 optimally adjust their CUE<sub>d</sub> as a function of litter substrate C to nitrogen (N)  
27 stoichiometry to maximize their growth rates. This formulation was incorporated into  
28 the widely used CENTURY soil biogeochemical model and evaluated based on data  
29 from laboratory litter incubation experiments. Results indicated that the CENTURY  
30 model with new CUE<sub>d</sub> formulation was able to reproduce differences in respiration  
31 rate of litter with contrasting C:N ratios and under different levels of mineral N  
32 availability, whereas the default model with fixed CUE<sub>d</sub> could not. Using the model  
33 with flexible CUE<sub>d</sub>, we also illustrated that litter quality affected the long-term SOM  
34 formation. Litter with a small C:N ratio tended to form a larger SOM pool than litter  
35 with larger C:N ratios, as it could be more efficiently incorporated into SOM by  
36 microorganisms. This study provided a simple but effective formulation to quantify  
37 the effect of varying litter quality (N content) on SOM formation across temporal  
38 scales. Optimality theory appears to be suitable to predict complex processes of litter  
39 decomposition into soil C, and to quantify how plant residues and manure can be  
40 harnessed to improve soil C sequestration for climate mitigation.

41

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

44

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## 48 1 Introduction

49 Plant litter decomposition plays a key role in global carbon (C) cycle, thus  
50 needs to be well represented in land surface models. The decomposition and  
51 transformation processes of plant litter control the formation of soil organic matter  
52 (SOM) (Prescott, 2010; Schmidt *et al.*, 2011; Walela *et al.*, 2014; Cotrufo *et al.*, 2015)  
53 and associate immobilization and mineralization of essential plant nutrients  
54 (Moorhead and Sinsabaugh, 2006; Parton *et al.*, 2007; Manzoni *et al.*, 2008; Manzoni  
55 and Porporato, 2009). Hence, a reliable litter decay model is necessary for estimating  
56 soil C balance and turnover of ecosystem C (Allison, 2012; Bonan *et al.*, 2013;  
57 Wieder *et al.*, 2013; Campbell and Paustian, 2015). In particular, a realistic  
58 representation of litter decomposition in land surface models is helpful to decrease the  
59 uncertainties in predicted effects of climate change and anthropogenic management  
60 on ecosystems (Gholz *et al.*, 2000; Campbell and Paustian, 2015; Luo *et al.*, 2016). As  
61 litter decomposition is a very complex process determined by climate (e.g. temperature  
62 and moisture), litter quality (e.g. nitrogen (N) concentration), soil nutrients and the  
63 physiological characteristics of microorganisms (Lekkerkerk *et al.*, 1990; Prescott,  
64 2010; Manzoni *et al.*, 2012; Frey *et al.*, 2013; Sinsabaugh *et al.*, 2013; Garc ía-Palacios  
65 *et al.*, 2016), there remain large uncertainties in existing litter decay models (Zhang *et*  
66 *al.*, 2008; Bonan *et al.*, 2013; Campbell and Paustian, 2015). Many litter decay  
67 models, especially those incorporated in global land surface models, have ignored  
68 stoichiometric constraints to microbial processes (Bonan *et al.*, 2013; Cotrufo *et al.*,  
69 2013; Wieder *et al.*, 2013; Wieder *et al.*, 2014).

70 Microbial carbon use efficiency (CUE), defined as the ratio of microbial  
71 biomass production to material uptake from substrates (Lekkerkerk *et al.*, 1990;  
72 Manzoni *et al.*, 2012), is an important parameter constraining litter decay, but it has  
73 rarely been represented as a flexible quantity in land surface models. During litter  
74 decomposition, only a part of the decomposed litter-C is being transferred into SOM,  
75 while the remaining C is being released as CO<sub>2</sub> to the atmosphere by microbial  
76 respiration (Campbell and Paustian, 2015; Cotrufo *et al.*, 2015). While CUE is a

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84 physiological property of each decomposer community, it also determines the  
85 ecosystem-level efficiency at which litter C is transferred into SOM a step further from  
86 simple microbial incorporation. We denote this efficiency as carbon use efficiency of  
87 litter decomposition ( $CUE_d$ ). With higher  $CUE_d$ , more plant-produced litter is  
88 transformed biologically into SOM, and soil C storage can reach higher values (Six *et*  
89 *al.*, 2006; Sinsabaugh *et al.*, 2013). In most existing soil biogeochemical models,  
90  $CUE_d$  is assumed to be same as microbial CUE and considered as a fixed parameter.  
91 The Verberne model (Verberne *et al.*, 1990) assumes for instance  $CUE_d \approx 0.25$ . In the  
92 Yasso model (Liski *et al.*, 2005), the  $CUE_d$  is set to 0.2. The CENTURY model sets  
93 the  $CUE_d$  for decomposition of surface and belowground metabolic litter to 0.55 and  
94 0.45, respectively (Parton *et al.*, 1988). In Daisy (Hansen *et al.*, 1991), NCSOIL  
95 (Molina *et al.*, 1983) and ICBM (Kätterer and Andr n, 2001),  $CUE_d = 0.6$  for the labile  
96 litter pools and takes a lower value for recalcitrant substrates. Only a few models  
97 account for variable  $CUE_d$ , letting it vary in response to substrate stoichiometry  
98 (Schimel and Weintraub, 2003) or temperature (Allison *et al.*, 2010).

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99 The increasing evidence for a variable microbial CUE leads to a conceptual  
100 CUE model which can explain trends in CUE of microorganisms along stoichiometric  
101 gradients (Manzoni *et al.*, 2017). The values of  $CUE_d$  used in existing litter decay  
102 models are mostly derived from CUE obtained in laboratory studies, on microbial  
103 physiology or limited observations in certain ecosystems, thus show large variations  
104 without a dynamic link to environmental conditions (Parton *et al.*, 1988; Verberne *et*  
105 *al.*, 1990; Hansen *et al.*, 1991; Liski *et al.*, 2005; Manzoni *et al.*, 2012). Recent studies  
106 (Manzoni *et al.*, 2008, 2012) suggested that the microbial CUE in terrestrial  
107 ecosystems ranges from less than 0.1 for wood decomposers to about 0.5 for  
108 decomposition of N-rich and high-quality litter. To explain those differences, Manzoni  
109 *et al.* (2017) proposed a conceptual model of microbial CUE based on the assumption  
110 that decomposers adapt their metabolism (and hence CUE) to maximize their growth  
111 rate. This model based on optimality theory links CUE to substrate and decomposers  
112 stoichiometry, where the optimal CUE decreases with increasing substrate  
113 C-to-nutrient ratio, and increases with soil nutrient availability. The predictions of this

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124 theoretical model have been verified by empirical evidence from CUE estimates for  
125 different microorganisms in both aquatic and terrestrial ecosystems (Manzoni *et al.*,  
126 2017).

127 Besides variable CUE<sub>d</sub>, many previous studies have also indicated the  
128 necessity for litter decomposition models to consider soil mineral N availability as a  
129 driver of litter decomposition rates, in particular under low N availability (Wieder *et*  
130 *al.*, 2015; Luo *et al.*, 2016; Averill and Waring, 2018). Microbial biomass nearly  
131 homeostatic (Cleveland and Liptzin, 2007; Franklin *et al.*, 2011; Allison, 2012). When  
132 the supply of N from substrates is lower than the demand of microbes to fulfill their  
133 specific stoichiometric C:N ratio, microbes will utilize mineral N (immobilization)  
134 (Manzoni *et al.*, 2012). Thus, low availability of mineral N can limit microbial activity,  
135 and in turn litter decay rate (Manzoni and Porporato 2009; Fujita *et al.*, 2014).

136 Although there are fertilization experiments reporting insignificant or even negative  
137 impacts of added N on litter decay rate (Fog, 1988; Hobbie and Vitousek, 2000; Finn  
138 *et al.*, 2015), many incubation experiments showed a significant decrease of litter  
139 decomposition rate with declining mineral N availability (Recous *et al.*, 1995; Hobbie  
140 and Vitousek, 2000; Guenet *et al.*, 2010). Moreover, recent modeling studies have  
141 indicated that including the limiting effect of low mineral N on decomposition  
142 improved predictions of C and N fluxes (Bonan *et al.*, 2013; Fujita *et al.*, 2014).  
143 Therefore, soil mineral N can alter litter C flux by affecting both the litter decay rate  
144 and the partition of decayed litter-C (via flexible CUE<sub>d</sub>).

145 Some detailed microbial decomposition models actually have included  
146 variable microbial CUE and the limitation of low mineral N availability on litter  
147 decay rate (Ingwersen *et al.*, 2008; Pagel *et al.*, 2013; Campbell *et al.*, 2016; Huang *et*  
148 *al.*, 2018); however, the parameterization and evaluation of these models pose  
149 significant challenges due to their complexity and limited verification data (Wieder *et*  
150 *al.*, 2014; Campbell and Paustian, 2015). There is still scope for implementing the  
151 effects of litter stoichiometry and soil mineral N availability on litter decomposition in  
152 litter decay models with more generalizable structure. In particular, it is important to  
153 test the role of these effects in models that have already been incorporated into land

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171 | surface model for long-term and large-scale applications (e.g. CENTURY, Parton *et*  
172 | *al.*, 1988). In this study, we incorporated flexible CUE<sub>d</sub> based on substrate C:N ratios  
173 | and mineral N limitations into a soil biogeochemical model based on the CENTURY  
174 | equations to simulate the decomposition and transfer processes of litter-C. The study  
175 | was organized as follows. First, the new model was calibrated and tested against data  
176 | from laboratory litter incubation experiments for its ability to capture the effect of  
177 | variable litter quality and soil mineral N on litter respiration rates (short-term  
178 | simulations). Second, the model parameterized assuming flexible CUE<sub>d</sub> and mineral  
179 | N limitations was used to explore the consequences of such stoichiometric constraints  
180 | on the production of soil organic carbon (SOC) (long-term simulations). With these  
181 | two modeling analyses, we aimed at linking stoichiometric constraints acting on  
182 | short-term (months to years) decomposition dynamics to their consequences on SOC  
183 | accumulation occurring at decadal to centennial time scales.

184

## 185 | **2 Materials and methods**

### 186 | 2.1 The CENTURY decomposition model

187 | The basis of the litter decay model used in this study is the CENTURY model  
188 | (Fig. 1), a first-order decay model that describes decomposition as a function of  
189 | substrate availability and quality, clay content, soil moisture and soil temperature  
190 | (Parton *et al.*, 1988). Most land surface models (e.g. Kucharik *et al.*, 2000; Sitch *et*  
191 | *al.*, 2003; Krinner *et al.*, 2005) adopted a similar structure to simulate the litter and  
192 | soil biogeochemical processes. Dead organic matter in CENTURY is separated into  
193 | structural and metabolic litter and three SOM pools (active, slow, passive) with  
194 | different turnover times. There is no explicit representation of microbial biomass in  
195 | CENTURY, instead the biomass of microbes is assumed to be in equilibrium with  
196 | ~~labile~~ SOM and thus implicitly included in the active SOM pool. When ~~litter~~ is being  
197 | ~~decomposed~~, a fraction of ~~the decomposed C~~ is respired to the atmosphere and the  
198 | remaining fraction (CUE<sub>d</sub> conceptually equal to microbial CUE) enters the acceptor  
199 | ~~SOM~~ pool. Three of such fractions are defined to characterize the transfer of C from

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204 litter to SOM:  $CUE_{ma}$  for transfer of the metabolic litter to the active SOM pool, and  
 205  $CUE_{sa}$  and  $CUE_{ss}$  for transfer of structural litter to active and slow SOM pools,  
 206 respectively (Fig. 1). These fractions are set to be time invariant in the original version  
 207 of CENTURY, so that a fixed fraction of decomposed C is retained in the acceptor  
 208 pool regardless of environmental conditions and changes in the quality of the donor  
 209 pool. The N flows in CENTURY follow the C flows and are equal to the product of C  
 210 flow by the N:C ratio of the acceptor SOM pool. N mineralization is defined as the  
 211 difference between N obtained from the donor pools and N stoichiometric demand of  
 212 the acceptor pool (Parton *et al.*, 1988; Metherell *et al.*, 1993). In this way, net N  
 213 mineralization occurs when the donor pool has low C:N ratio, but N is immobilized  
 214 (taken up by microbes) when the donor pool has high C:N ratio.

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## 216 2.2 Optimal CUE

217 To quantify how microbial CUE varies along gradients of nutrient  
 218 availability, it can be hypothesized that microorganisms maximize their growth rate,  
 219 and hence their ecological competitiveness, by adapting resource (C and nutrients) use  
 220 efficiencies. This follows the growth maximization hypothesis (Mooshammer *et al.*,  
 221 2014; Manzoni *et al.*, 2017). Based on this hypothesis, Manzoni *et al.* (2017)  
 222 formulated a theoretical model expressing microbial CUE as a function of the  
 223 stoichiometric difference between decomposers and their substrate. The CUE for  
 224 which growth rate is maximized is the optimal CUE ( $CUE_{opt}$ ) given by:

$$225 \quad CUE_{opt} = CUE_{max} \times \min \left[ 1, \frac{CN_D}{CUE_{max}} \times \left( \frac{1}{CN_S} + \frac{I_N}{U_0} \right) \right] \quad (1)$$

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226 where  $CUE_{max}$  is the maximum microbial CUE (dimensionless) when growth is  
 227 limited by C from the organic substrate.  $CN_D$  and  $CN_S$  are the C:N ratio (in mass,  
 228 dimensionless) of decomposer and their substrate, respectively. Although Manzoni *et al.*  
 229 *et al.* (2017) indicated that mineral phosphorus (P) could also affect optimal CUE we  
 230 only considered N as a limiting nutrient.  $I_N$  (g N kg<sup>-1</sup> soil) is the maximum rate at  
 231 which mineral N can be taken up by microbes, and  $U_0$  (g C kg<sup>-1</sup> soil) is the C-limited  
 232 uptake rate (corresponding to the decomposition rate at optimal mineral N

238 concentration). When litter C:N is low or soil mineral N is in excess, the second term  
 239 in the minimum function (Eq.(1)) is higher than one, and  $CUE_{opt} = CUE_{max}$  (C limited  
 240 conditions, as in nutrient-rich litter). In contrast, when mineral N is scarce,  $CUE_{opt}$   
 241 decreases with increasing substrate C:N ratio (N limited conditions, N-poor litter).  
 242 Lack of N in the organic substrates can be compensated by mineral N being  
 243 immobilized by microorganisms from the soil solution. Immobilization meets the  
 244 nutrient demands as long as it is lower than the maximum supply rate  $I_N$ , at which  
 245 point microbial CUE starts being down regulated. Thus, for any given C:N ratio in the  
 246 substrate,  $CUE_{opt}$  increases with inorganic N concentration in the soil solution until  
 247  $CUE_{max}$  is reached. It should also be noted that Eq. (1) is interpreted at the microbial  
 248 community scale, not for individual organisms.

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### 250 2.3 Adaption of the optimal CUE model in the CENTURY model

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

$$257 \quad CUE_{opt} = CUE_{max} \times \min \left[ 1, \left( \frac{CN_{lit}}{CN_{SOM}} \right)^a \right] \quad (2)$$

258 where  $CN_{lit}$  and  $CN_{SOM}$  are the C:N ratio (dimensionless) of litter (metabolic or  
 259 structural) and SOM pools (active, slow or passive), respectively. The C:N ratio of  
 260 SOM (around 9:1 on a mass basis in CENTURY) is representative of the decomposer  
 261 biomass, its value being between the average C:N ratio of soil microbial communities  
 262 including fungi and bacteria (7.4:1 in Cleveland and Liptzin, 2007) and the C:N ratio  
 263 of soil fungi (13.4:1 in Zhang and Elser, 2017), which are probably largely  
 264 responsible for fresh litter decomposition.  $CUE_{max}$  (dimensionless) is the maximum  
 265  $CUE_d$  achieved when nutrients are not limiting, and it is set to 0.8 based on a  
 266 synthesis of observed CUE of soil microbes (Manzoni *et al.*, 2012). The exponent  $a$  (g

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284 N kg<sup>-1</sup> soil) captures the effect of mineral N uptake by microbes on CUE<sub>d</sub>. Because  
285 CUE<sub>d</sub> is expected to increase with mineral N availability (Eq. (1)), *a* is assumed to be  
286 a linear function of the mineral N concentration (*N*<sub>min</sub>, g N kg<sup>-1</sup> soil):

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$$287 \quad a = m_1 \times (N_{min} - n_1) \quad (3)$$

288 where *m*<sub>1</sub> (kg g<sup>-1</sup> N) and *n*<sub>1</sub> (g N kg<sup>-1</sup> soil) are two coefficients that need to be  
289 calibrated. Eqs. (2) and (3) modulate the decrease in CUE<sub>d</sub> with decreasing litter  
290 quality when mineral N availability changes– the exponent *a* increases with  
291 increasing mineral N availability, causing an increase in CUE<sub>d</sub> at any given litter C:N  
292 ratio. Hence, increasing *a* mimics an increase in *I*<sub>N</sub> in Eq. (1). Fig. 2a illustrates how  
293 CUE<sub>d</sub> from Eq. (2) varies as a function of mineral N concentration, for different  
294 values of litter C:N.

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295 Eqs. (2) and (3) were implemented in CENTURY to modify the originally  
296 fixed CUE<sub>d</sub> (Fig. 1). With this change, the fractions of C from litter that remain in  
297 SOM are mediated by stoichiometric constraints and mineral N availability, at the  
298 expense of additional parameters to fit. The CUE<sub>d</sub> for C transfers between SOC pools  
299 (active, slow and passive) are not modified.

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#### 301 2.4 Constraint of soil nutrient availability on litter decomposition rate

302 CENTURY is a first-order decay model in which decomposition rates of  
303 metabolic and structural litter are modulated by scaling factors of soil temperature  
304 (*f*(*tem*)) and moisture (*f*(*water*)) (Parton *et al.*, 1988). Here, we introduced an  
305 additional mineral N scaling factor (*f*(*N*<sub>min</sub>), 0–1, dimensionless) to account for the  
306 limitation imposed by low mineral N availability on litter decay rate (*D*(*C*<sub>lit</sub>)).

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$$307 \quad D(C_{lit}) = C_{lit} \times k \times f(tem) \times f(water) \times f(N_{min}) \quad (4)$$

308 where *C*<sub>lit</sub> is the C (g C kg<sup>-1</sup> soil) in litter pool (metabolic or structural) and *k* is the  
309 potential maximum turnover rate (day<sup>-1</sup>) at optimal soil temperature, moisture and  
310 nutrient conditions.

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311 In this study, we assumed that the scaling factor of mineral N increases  
312 linearly with increasing soil mineral N concentration (*N*<sub>min</sub>, Eq. (5)) below a threshold  
313 value of *l*/*m*<sub>2</sub> g N kg<sup>-1</sup> soil, where *m*<sub>2</sub> is a positive coefficient which needs to be

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322 calibrated (Fig.2b). The inhibition effect of mineral N only occurs in case of  
 323 immobilization ( $1/CN_{lit} < CUE_{opt}/CN_{SOM}$ ). The specific function  $f(N_{min})$  can be  
 324 expressed as:

$$325 \quad f(N_{min}) = \begin{cases} \min(1, m_2 \times N_{min}), & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} > 0 \\ 1, & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} \leq 0 \end{cases} \quad (5)$$

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326 Existing studies have adopted approaches that differ from our definition to  
 327 explicitly represent the N inhibition effects on microbial processes (Manzoni and  
 328 Porporato, 2009; Bonan et al., 2013; Fujita et al., 2014; Averill and Waring, 2018). In  
 329 these previous studies,  $f(N_{min})$  was assumed equal to the ratio between immobilized  
 330 mineral N and the N deficit for maintaining a stable C:N of decomposer biomass or  
 331 other receiver pools. Using the notation of Section 2, this definition of  $f(N_{min})$  can be  
 332 expressed as:

$$333 \quad f(N_{min}) = \begin{cases} \min\left(1, \frac{m_3 \times N_{min}}{U_0 \times \left(\frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}}\right)}\right), & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} > 0 \\ 1, & \frac{CUE_{opt}}{CN_{SOM}} - \frac{1}{CN_{lit}} \leq 0 \end{cases} \quad (6)$$

334 where  $m_3$  is a coefficient that needs to be optimized.  $U_0$  (g C kg<sup>-1</sup> soil day<sup>-1</sup>) is the C  
 335 uptake rate (equivalent to the litter decomposition rate in absence of leaching) when  
 336 soil mineral N is fully adequate for litter decay (i.e.  $f(N_{min}) = 1$ ), and can be calculated  
 337 from Eq. (7) as:

$$338 \quad U_0 = C_{lit} \times k \times f(tem) \times f(water) \quad (7)$$

339 In this study, we also tested this formulation in the CENTURY-based model, in  
 340 addition to the Eq. (5) (see model M4 in Table A3).

341

## 342 2.5 Model parameterization and validation

343 To determine the respective impacts of including flexible  $CUE_d$  and N  
 344 availability constraining decay rates, we built five conceptual litter decay models  
 345 (Table 1). Model M0 corresponds to the default CENTURY parameterization of a  
 346 fixed  $CUE_d$  and no constraints of N availability on litter decay rates ( $f(N_{min}) = 1$ ).  
 347 Model M1 accounts for flexibility in CUE from Eq. (2) and N constraints on decay

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351 rates by Eq. (5). Model M2 has flexible  $CUE_d$  but no N constraints on decay rates  
352 ( $f(N_{min})=1$ ). Model M3 has N constraints on decay rates but a fixed  $CUE_d$  (Table 1).  
353 All of these four models are run at a daily time step. Finally, model M4 also accounts  
354 for flexibility in CUE and N constraints on decays (Table A3), but it uses Eq. (6) to  
355 represent the N constraints on decays rate rather than Eq. (2). Results from model M4  
356 are presented in the main text, but only shown in the Appendix. This range of models  
357 allows identifying which mechanisms are at play during decomposition – flexible  
358  $CUE_d$  only (M3), mineral N limitation only (M2), both mechanisms (M1, M4), or  
359 none (M0).

360 For calibrating model parameters and evaluation of their results, we collected  
361 data of laboratory litter incubation experiments from Recous *et al.* (1995) (5  
362 experiments) and Guenet *et al.* (2010) (9 experiments, Table A2). The incubation  
363 experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) continued 80 and 124  
364 days, respectively. Recous *et al.* (1995) used corn residues (C:N = 130) and Guenet *et al.*  
365 *et al.* (2010) used wheat straw (C:N = 44) in their incubation experiments. The C:N  
366 ratios of those corn residue and wheat straw span the range of litter C:N ratios among  
367 different ecosystems (Harmon *et al.*, 2009; Brovkin *et al.*, 2012; Manzoni *et al.*, 2010).  
368 In the incubation experiments, plant litter was firstly cut into fine fragments before it  
369 was mixed with mineral soil. Soil temperature and moisture condition were kept  
370 constant during the experiment. Respired C from the incubated litter and SOC, as well  
371 as the soil mineral N concentrations were measured continuously across the  
372 incubation period. To distinguish the litter- and SOC-derived  $CO_2$  flux, Guenet *et al.*  
373 (2010) used straw from wheat grown under  $^{13}C$  labeled  $CO_2$  and they are therefore  
374 able to track the  $CO_2$  coming from litter and the  $CO_2$  coming from soil. In the  
375 experiments by Recous *et al.* (1995), litter-derived  $CO_2$  flux is calculated as the  
376 difference in  $CO_2$  flux between the incubation samples with both soil and litter, and  
377 the control samples without added litter. More detailed information about the  
378 incubation experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) can be found  
379 in Table A2.

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

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397 temperature and moisture condition for decomposition in all of the five versions of the  
398 model (M0-M4) were set based on observations (Table A2). Plant litter was firstly  
399 separated into metabolic and structural litter pools based on its lignin to C ratio ( $LC_{lit}$ ,  
400 dimensionless). The fraction of metabolic litter-C ( $f_m$ , 0-1, dimensionless) is  
401 calculated by:

$$f_m = f_{max} - m_4 \times LC_{lit} \quad (8)$$

402 where  $m_4$  is a coefficient to be calibrated;  $f_{max}=0.85$  is the maximum fraction of  
403 metabolic litter (i.e., the default value in CENTURY; Parton *et al.*, 1988). The  
404 fraction of structural litter-C is thus  $1-f_m$ . The C:N ratios of both metabolic and  
405 structural pools are assumed to be equal to the C:N ratio of litter input.

407 In M1 and M3 models, the observed mineral N concentrations across the  
408 incubation period were used to calculate the daily N inhibition effect (Eq. (5)). The  
409 observed cumulative respired litter-C (g C kg<sup>-1</sup> soil) measured in the incubation  
410 experiments was used to calibrate the model parameter values. Moreover, to quantify  
411 the simulated CO<sub>2</sub> flux derived from the litter, we also performed a set of control  
412 simulations with only SOM (initial litter pools were set to 0 g kg<sup>-1</sup> soil) using the four  
413 model versions. The simulated litter-derived CO<sub>2</sub> flux is calculated as the difference  
414 in CO<sub>2</sub> flux between the simulation with both litter and SOM inputs and the  
415 simulation with only SOM input.

416 Parameter calibration was performed for each model with the shuffled  
417 complex evolution (SCE) algorithm developed by Duan *et al.*, (1993). The SCE  
418 algorithm relies on a synthesis of four concepts that have proved successful for global  
419 optimization: combination of probabilistic and deterministic approaches; clustering;  
420 systematic evolution of a complex of points spanning the space in the direction of  
421 global improvement and competitive evolution (Duan *et al.*, 1993). A more detailed  
422 description of this SCE optimization method can be found in Duan *et al.* (1993, 1994).  
423 In this study, the RMSE (root mean square error, Eq. (9)) between simulated and  
424 measured cumulative respired litter-C (%) on all observation days (Table A2) of each  
425 incubation experiment was used as the objective function, and the parameters  
426 minimizing RMSE between simulated and observed cumulative respired litter-C were

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449 regarded as optimal parameter values.

$$450 \quad RMSE = \sqrt{\left(\frac{\sum_{i=1}^n (Sim_i - Obs_i)^2}{n}\right)} \quad (9)$$

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

453 We used leave-one-out cross-validation (Kearns and Ron, 1997; Tramontana  
454 *et al.*, 2016) to evaluate each of the four models (i.e. M0-M3), a cross validation  
455 method used when data is scarce. The number of cross-validations corresponds to the  
456 number of incubation experiments (14). Each time, one of the 14 incubation  
457 experiments was left out as the validation sample, and the remaining 13 experiments  
458 were used to train model parameters. In addition to RMSE, we also adopted the  
459 Akaike Information Criterion (AIC, Bozdogan, 1987, Eq.(10)) to determine the  
460 relative quality of the four version models on estimating cumulative respired litter-C.

$$461 \quad AIC = n \times \ln\left(\frac{\sum_{i=1}^n (Sim_i - Obs_i)^2}{n}\right) + 2n_p \quad (10)$$

462 where  $n_p$  is the number of model parameters. The evaluation of AIC is important here  
463 because depending on the model version, different numbers of parameters have to be  
464 determined (Table 1), requiring us to weigh both model accuracy and robustness.

465 Note that the turnover times of SOM pools (active, slow and passive) used in  
466 this study are obtained from the ORCHIDEE-MICT (v8.4.1, Guimbertau *et al.*,  
467 2018). The turnover times of litter pools (metabolic and structural), as well as the  
468 coefficient  $m_d$  in Eq. (8) were optimized against the observed cumulative respired  
469 litter-C from all of the 14 incubation experiments using the M0 and M1 models (Table  
470 A3). A previous study has shown that litter decomposability is negatively correlated to  
471 its physical size (for example, Tuomi *et al.*, 2011). Therefore, the turnover times of  
472 the fine litter fragments used in the incubation experiments of Recous *et al.* (1995)  
473 and Guenet *et al.* (2010) are expected to be shorter than the values set in  
474 ORCHIDEE-MICT, which are representative of the turnover times of natural plant  
475 residues. In addition, the mixing of soil and litter particle in the incubation experiment  
476 likely enhances decomposition as spatial disconnection of decomposer and substrate,  
477 which can occur under natural soil conditions (Barnes *et al.*, 2012; Hewins *et al.*,

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2013), is prevented. The calibrated turnover times of the metabolic and structural pools and the value of  $m_d$  in Eq. (8) are 3.5 and 30 days and 0.5, respectively.

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

We used the model M1, with flexible CUE<sub>d</sub> and decomposition rate function of available N to study the impacts of litter stoichiometry (C:N ratio) and soil mineral N availability on the formation and accumulation of SOM. In total, 24 idealized simulation experiments with different values of litter C:N ratios and soil mineral N availabilities were conducted (Table A4). The assumed litter C:N ratios ( $CN_{lit}$ ) of 10, 15, 30, 60, 120 and 200 span the variation among most natural substrates and soil amendments from organic matter input in agriculture (Harmon *et al.*, 2009; Brovkin *et al.*, 2012; Manzoni *et al.*, 2010). The assumed range of mineral N availability ( $N_{min}$ ) of 0.001, 0.005, 0.01 and 0.05 g N kg<sup>-1</sup> soil span the observed concentrations of soil mineral N in major terrestrial ecosystems (Metherall *et al.*, 1993).

In each simulation experiment, model M1 was run for 5000 years to bring the litter and SOM pools in equilibrium with the prescribed litter input flux. The daily input rate of plant litter was set to 0.006 g C kg<sup>-1</sup> soil day<sup>-1</sup>, and the initial C stock of litter and SOM pools were all set to be 0 g C kg<sup>-1</sup> soil. During the simulation, soil temperature and soil water content were assumed to be 25 °C and 60% of water holding capacity, respectively. We emphasized that our goal with this simplified scenario was to single out the effects of stoichiometric constraints, not to simulate the effects of a realistic climatic regime. Parameter values for M1 (with  $m_1 = 0.54$ ,  $n_1 = 0.50$  and  $m_2 = 296.8$ ) used here were optimized based on all of the 14 incubation experiments from Recous *et al.* (1995) and Guenet *et al.* (2010) (see above). More detailed information about the specific settings of our simulation experiments can be found in Table A4.

## 3 Results

### 3.1 Evaluation of different models

删除的内容: Note that the turnover times of SOM pools (active, slow and passive) used in this study are obtained from the ORCHIDEE-MICT (v8.4.1, Guimberteau *et al.*, 2018). The turnover times of litter pools (metabolic and structural), as well as the coefficient  $m_d$  in Eq. (8) were optimized against the observed cumulative respired litter-C from all of the 14 incubation experiments using the M0 and M1 model (Table A3). Previous study has shown that litter decomposability is negatively correlated to its physical size (for example Tuomi *et al.*, 2011). Therefore, the turnover times of the fine litter fragments used in the incubation experiments of Recous *et al.* (1995) and Guenet *et al.* (2010) should be shorter than the values set in ORCHIDEE-MICT, which are corresponding to the turnover times of natural plant residues. In addition the mixing of soil and litter particle in the incubation experiment arguably enhances decomposition as spatial disconnection of decomposer and substrate, which can occur under natural soil conditions (Barnes *et al.*, 2012; Hewins *et al.*, 2013), is prevented. Finally, the calibrated turnover times of metabolic and structural pool and the value of  $m_d$  in ...

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589 Results of leave-one-out cross-validation suggest that model M1 provides  
 590 more accurate prediction of cumulative respired litter-C than other models (Fig. 3).  
 591 The differences between simulated and observed cumulative respired litter-C from  
 592 M1 are mostly less than 6% for over 93% of the data (Fig. A1b). The average RMSE  
 593 of predicted cumulative respired litter-C from M1 (3.0%) is lower than that of model  
 594 M0 (4.1%). Models M2 and M3 have slightly lower RMSE values than M0 (3.7% and  
 595 3.8%, respectively) but perform worse than M1 (Fig.4). However, the average AIC of  
 596 all the models are comparable, suggesting that models with more fitted parameters do  
 597 not over-fit the observations (Fig. 4).

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598 Model M1 captures the differences in respiration rates due to different C:N  
 599 ratios of substrate and varying levels of mineral N availability across the 14  
 600 incubation experiments (Fig.5). While model M3 can reproduce the observed effect of  
 601 soil mineral N availability on litter respiration rates (Fig.5d), it underestimates the  
 602 cumulative respired CO<sub>2</sub> from low quality litter ( $CN_{lit} = 130$ ) at high mineral N  
 603 concentrations ( $> 0.04 \text{ g N kg}^{-1}$  soil). Models M0 and M2 cannot represent the effects  
 604 of soil mineral N on litter respiration rate (Figs. 5a, c), and their predictions are more  
 605 biased from the observed values compared to M1. The Model M4, which uses the  
 606 alternative formulation for N constraints on litter decay (Eq. (6)), reproduces the  
 607 different respiration rates of substrates with contrasting C:N ratios and at different  
 608 levels of mineral N availability (Fig. A2), but with a slightly higher average RMSE of  
 609 cumulative respired litter-C than model M1.

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610 The predicted CUE<sub>d</sub> and the limitation effects of soil mineral N availability  
 611 on litter decay rate ( $f(N_{min})$  function in Eq. (5)) are different among the four tested  
 612 models (Fig. A3). In models M0 and M3, which used a fixed CUE<sub>d</sub>, the fitted values  
 613 of CUE<sub>d</sub> calculated with optimized parameters during the incubation period are about  
 614 0.57 and 0.54, respectively (Figs. A3a, d). In models M1 and M2, the CUE<sub>d</sub> varies  
 615 with the C:N ratios of plant litter, and is only slightly affected by soil mineral N  
 616 concentrations (Figs. A3b, c). For very low quality litter with a C:N ratio of 130, the  
 617 CUE<sub>d</sub> in models M1 and M2 are 0.40 and 0.44, respectively, which are lower than for  
 618 better quality litter with C:N ratio of 44 (approximately 0.55 and 0.56 in M1 and M2,

- 删除的内容: In addition, model M1 can also capture the temporal evolution of cumulative respired litter-C in different incubation experiments (Fig. 5b).
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- 删除的内容: 0.40 and 0.44

640 respectively). Models M0 and M2 do not include the N inhibition effects on litter  
641 decay rate, thus the  $f(N_{min})$  in these two models is always 1 (Figs. A3e, g). In M1 and  
642 M3, the N inhibition effect changes with both the litter C:N ratio and the mineral N  
643 availability (Figs. A3f, h).

644 CUE<sub>d</sub> from Eq. (2) calibrated with the data of the two incubation  
645 experiments, decreases with increasing CN<sub>lit</sub>/CN<sub>SOM</sub> (Fig. 6). The average CUE<sub>d</sub> value  
646 is larger than the average of data compiled for microbial CUE of litter decomposition  
647 in terrestrial ecosystems by Manzoni *et al.* (2017). This is shown by the gray circles in  
648 Fig. 6. Our optimized values of CUE<sub>d</sub> for a given C:N ratio are more comparable with  
649 microbial CUE observed in incubations of soil mixed with litter (Gilmour and  
650 Gilmour, 1985; Devêre and Horváth, 2000; Thiet *et al.*, 2006), shown as black  
651 squares in Fig. 6.

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### 653 3.2 The effect of litter quality vs quantity on equilibrium SOM stocks

654 Model M1 predicts that the size of the SOM pool at equilibrium is mainly  
655 determined by litter stoichiometry, with a minor effect of soil mineral N (Fig. 7). The  
656 lower C:N ratio of litter is, the higher equilibrium SOC stock. For litter with a specific  
657 C:N ratio, high soil mineral N concentration (e.g. above 0.05 g N kg<sup>-1</sup> soil) generally  
658 produces a slightly larger equilibrium SOC stock than a low mineral N concentration  
659 (Fig. 7). Further analysis suggests that the SOC at equilibrium increases with  
660 decreasing litter C:N because the SOC pool is positively related to the CUE<sub>d</sub>; however  
661 the limitation of soil mineral N on litter decomposition rate almost shows no impact  
662 on SOC (Fig. A4).

删除的内容: Models M0 and M2 do not include the N inhibition effects on litter decay rate, thus the  $f(N_{min})$  in these two models is always 1 (Figs. A2e, g). In M1 and M3, the N inhibition effect changes with both the litter C:N ratio and the mineral N availability (Figs. A2f, h).

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## 664 4 Discussion

665 We hypothesized that stoichiometric constraints (flexible CUE<sub>d</sub> or inhibition  
666 of decomposition under N limited conditions) played a role in shaping the trajectory  
667 of litter decomposition, with potential consequences on predicted SOC stocks. Our  
668 results suggest that flexible CUE<sub>d</sub> and inhibition effects of soil mineral N on litter

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681 decay rate improve prediction of litter decomposition when using a modified version  
682 of CENTURY model (denoted as M1). Evaluation of the model M1 using data from  
683 incubation experiments indicate that this modified model captures the effects of both  
684 variable litter quality (stoichiometry) and mineral N availability on respiration rates  
685 (Fig.5), without strongly inflating the complexity of CENTURY (Table 1). As the  
686 stoichiometric constraints are implemented in the generalizable and widely used  
687 structure of CENTURY and require only three parameters to be calibrated, they can  
688 also be easily implemented into land surface models for large spatial scale  
689 applications.

删除的内容: , the model M1 developed from

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690 Accurately representing N control of microbial processes during litter  
691 decomposition has been suggested to be important for modeling the connection  
692 between the litter inputs,  $CUE_d$ , and soil C dynamics (Gerber *et al.*, 2010; Manzoni *et al.*,  
693 2012; Cotrufo *et al.*, 2013; Sinsabaugh *et al.*, 2013). In model M1, soil mineral N  
694 affects the litter-C flux via two mutually different pathways: (1) mineral N availability  
695 affects the litter decay rate and (2) flexible  $CUE_d$  determining the partition of  
696 decomposed C into SOC products and respired  $CO_2$  (Fig. 1). Therefore, an increase in  
697 soil mineral N concentration enhances litter decay rates, which alone will increase the  
698 flux of litter-derived  $CO_2$  (Eq. (5) and Fig. A5). However, as higher N concentration  
699 also results in a higher  $CUE_d$  (Eq. (2)), more C is transferred to SOC and less C is  
700 respired. In this way, SOC is predicted to accumulate with increasing mineral N  
701 availability when using model M1 (Fig. 7). In addition, the model M4, which is  
702 comparable to model M1 but uses an alternative formulation for N effects on the  
703 decomposition rate (Eq. (6)), performed slightly worse than model M1 (Fig. A2).  
704 Arguably, Eq. (6) represents the underlying mechanisms of N inhibition effects  
705 (Manzoni *et al.*, 2009; Bonan *et al.*, 2013; Fujita *et al.*, 2014; Averill and Waring,  
706 2018) better than Eq. (5), and due to the minor differences in RMSE and AIC (Figure  
707 A2b) between these formulations it can serve as an alternative to M1.  
708 Our results indicate that the observed diversity of responses of litter  
709 respiration rate to mineral N additions (Hobbie and Vitousek, 2000; Guenet *et al.*,  
710 2010; Janssens *et al.*, 2010) is likely due to the combined effects of changes in litter

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721 [decay rate and CUE<sub>d</sub> \(Fig. A5\). Thus, N addition effects can differ among fertilization](#)  
722 [experiments if litter quality and background N availability vary. In addition to altering](#)  
723 [litter decay rate and CUE<sub>d</sub>, mineral N addition can induce abiotic formation of](#)  
724 [compounds that resist microbial attack, inhibit oxidative enzymes involved in lignin](#)  
725 [degradation, stimulate microbial biomass production early in decomposition, or lead](#)  
726 [to the accumulation of microbial residues that are resistant to decay \(Fog, 1988;](#)  
727 [Hobbie, 2015\). All these effects might decrease litter respiration rate by inhibiting the](#)  
728 [decomposition process, but have not been considered in our current model.](#)

729 [This study provides insights on processes leading to increased SOM](#)  
730 [sequestration. Enhancing the efficiency at which plant residuals are transformed into](#)  
731 [stable SOM has been suggested as an effective strategy to sequester C in soil \(Prescott,](#)  
732 [2010; Cotrufo \*et al.\*, 2013\). Simulation results from our model suggest a positive](#)  
733 [linear relationship between equilibrium SOC stock and CUE of decomposed litter](#)  
734 [\(Fig. A4\), in line with the earlier findings with a similar model \(for example Frey \*et al.\*](#)  
735 [2013\). In fact, with linear models such as CENTURY it can be shown that the steady](#)  
736 [state SOC scales linearly with CUE, different from nonlinear models predicting that](#)  
737 [higher CUE can trigger SOC loss \(Allison \*et al.\*, 2010\). Our model goes beyond](#)  
738 [earlier attempts \(Bonan \*et al.\*, 2013; Fujita \*et al.\*, 2014; Averill and Waring, 2018\) by](#)  
739 [adapting the optimal metabolic regulation hypothesis of Manzoni \*et al.\* \(2017\) to link](#)  
740 [CUE, litter quality and SOM formation in a process-oriented way.](#)

741 [The importance of litter quality for SOM formation as found here is in](#)  
742 [line with recent experiments \(Bahri \*et al.\*, 2008; Rubino \*et al.\*, 2010; Walela \*et al.\*,](#)  
743 [2014\) and modeling studies \(Grandy and Neff, 2008; Cotrufo \*et al.\*, 2013\). SOM is](#)  
744 [mainly formed through the partial decomposition of plant debris by microorganisms](#)  
745 [\(Paul, 2007; Knicker, 2011; Cotrufo \*et al.\*, 2013\). The conceptual model developed by](#)  
746 [Cotrufo \*et al.\* \(2013\) suggested that although labile litter was decomposed faster than](#)  
747 [recalcitrant litter, a higher fraction of this labile litter-C would be incorporated into](#)  
748 [microbial biomass and subsequently incorporated into SOM pool \(corresponding to a](#)  
749 [higher CUE<sub>d</sub>\). Therefore, labile litter inputs tend to form a larger SOM pool than the](#)  
750 [poor-quality \(high C:N ratio\) litter that is generally used by microbes at lower](#)

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删除的内容: Our results indicate that to explain the observed diversity of responses of litter respiration rate to mineral N in fertilization a better understanding of the N effects on decomposition rate and CUE are needed (Hobbie and Vitousek, 2000; Guenet *et al.*, 2010; Janssens *et al.*, 2010). The net changes in respiration rate depend on the combined effects of changes in litter decay rate and CUE<sub>d</sub> (Fig. A5). Thus N addition effects can differ among fertilization experiments if litter quality and background N availability differs. In addition to altering litter decay rate and CUE<sub>d</sub>, mineral N addition can induce abiotic formation of compounds that resist microbial attack, inhibit oxidative enzymes involved in lignin degradation, stimulate microbial

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删除的内容: This study provides insight on processes leading to increased SOM sequestration. Enhancing the efficiency at which plant residuals are transformed into

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删除的内容: Moreover, describing N limitations on both the decomposition rate and flexible CUE<sub>d</sub> might allow our model to explain the observed diverse responses of litter respiration rate to

删除的内容: . . . . . (9) . We have tested this formulation in the CENTURY-based model, in addition to the other formulations (Table 1). The model with Eq. 8 gave a more biased

896 efficiency. Our simulations of decomposition process of plant litter with different C:N  
897 ratios also suggest that litter of good quality (with low C:N ratio) can induce a larger  
898 SOM pool than the poor-quality litter (Fig. 7).  $CUE_d$  plays a more important role than  
899 the inhibition effect of low mineral N concentration in determining the size of the  
900 stable SOM pool (Fig. A4).

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

912 The  $CUE_d$  formulation from Eq. (2) with parameters calibrated from the two  
913 sets of incubation experiments might underestimate the impacts of litter quality on  
914 microbial  $CUE$  under natural conditions, in particular in case of SOM decomposition.  
915 In both incubation experiments, litter is firstly cut into fine fragments and then fully  
916 mixed with mineral soil (Recous *et al.*, 1995; Guenet *et al.*, 2010). Thus, the nutrient  
917 accessibility, air permeability and some other environmental factors (e.g. pH) of  
918 incubated litter are different from those of decaying litter in more natural,  
919 heterogeneous soil conditions. Those different decomposition conditions might be  
920 responsible for the differences observed in Fig. 6 between our  $CUE$  estimates and  
921 previously reported values. We speculate that more heterogeneous conditions reduce  
922 nutrient availability and thus might cause lower  $CUE$ . Similarly,  $CUE$  of surface litter  
923 decomposers may be lower than we estimated (Fig. 6), because litter not mixed with  
924 soil is probably subject to stronger nutrient limitation.

925 Further validation and development of our model are still necessary to

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删除的内容: This study provides some insights on processes leading to increased SOM sequestration. Soil C sequestration plays a crucial role in food security and land CO<sub>2</sub> emission (Lal, 2004). The international initiative '4 per 1000' has been proposed to increase global SOM stock by 0.4% per year to compensate for anthropogenic CO<sub>2</sub> emissions (Baveye *et al.*, 2018). Transforming more plant litter into stable SOM (e.g. humic substances) has been suggested as an effective strategy to sequester more C in soil (Prescott, 2010). Our model results show a positive linear relationship between equilibrium SOC stock and  $CUE$  of decomposed litter (Fig. A3). This result can also be interpreted by calculating the analytical equilibrium SOC storage of a fully linear model including only one litter pool and one SOC pool. In such a model, SOC receives C from the litter at a rate  $CUE_d \times D$ , where  $D$  is the litter decomposition rate, which equals to litterfall at steady state. SOC is lost via first order decay with a decay constant  $k$ . At steady state, input to and outputs from the SOC pool are equal and thus

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With a mean residence time of C in the SOC between 10 and 20 years and  $D$  approximated by litterfall (Table A3), SOC at equilibrium is predicted to scale linearly with  $CUE_d$ , with a slope approximately between 20 and 40, consistent with results in Fig. A3. Therefore, litter quality needs to be controlled to maximize C sequestration in SOM pool (Eq. (2)). In line with

1031 decrease the model uncertainties. Soil mineral N which affects both litter decay rate  
1032 and CUE of decayed litter is seldom monitored in litter incubation experiments (e.g.  
1033 Walela *et al.*, 2014; Stewart *et al.*, 2015) and field litter decay experiments (e.g. Gholz  
1034 *et al.*, 2000; Harmon *et al.*, 2009), with few exceptions (Recous *et al.*, 1995; Guenet *et*  
1035 *al.*, 2010). An increasing number of land surface models ([Wang \*et al.\*, 2010](#); [Zaehle \*et\*](#)  
1036 [al., 2014](#); [Goll \*et al.\*, 2017](#)) have representations of the terrestrial N cycle. By  
1037 incorporating our [newly developed formulations of CUE<sub>d</sub> and f\(N<sub>min</sub>\)](#) in these land  
1038 surface models that simulate the dynamics of soil mineral N concentration, it will be  
1039 possible to test and validate our developments with more extensive data from  
1040 laboratory and field experiments. Moreover, similar to N, P has also been suggested as  
1041 another important factor for litter decomposition and SOM formation (Güsewell and  
1042 Verhoeven, 2006; Talkner *et al.*, 2009; Manzoni *et al.*, 2010; Prescott, 2010),  
1043 especially in regions with highly weathered soil (Goll *et al.*, 2012, 2017; Yang *et al.*,  
1044 2014). So it might be necessary to include the effects of P on litter decay rate and  
1045 CUE<sub>d</sub> into our model for further decrease the simulation uncertainties.

1046

## 1047 **5Conclusions**

1048 By adapting the hypothesis of optimal microbial CUE proposed by Manzoni  
1049 *et al.* (2017) for use in a CENTURY-based model and also introducing a N scaling  
1050 function to represent the limits of mineral N availability on litter decay rate, we  
1051 developed a simple but effective litter decomposition model that accounts for key  
1052 stoichiometric constraints during decomposition. Validation using observation data  
1053 obtained from laboratory incubation experiments indicated that our model could well  
1054 predict the respiration rates of litter in different qualities at various levels of mineral N  
1055 availability. Idealized simulations using our model revealed that the quality of litter  
1056 inputs plays an important role in determining the soil C stock at equilibrium,  
1057 High-quality litter (i.e. with low C:N ratio) tends to form a larger SOM pool as it can  
1058 be more efficiently utilized by microorganisms than recalcitrant litter (e.g. high C:N  
1059 ratio). Overall, the developed model captures the microbial mechanisms mediating

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Goll *et al.*, 2017

删除的内容: litter decomposition  
formulation

删除的内容: SOM pool

1065 litter stoichiometry and soil mineral N effects on litter decomposition and SOM  
1066 formation. Due to the simple and generalizable structure of our model, it can be  
1067 incorporated into existing land surface models for further long-term and large spatial  
1068 scale applications.  
1069

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1073 **Code and data availability**

1074           The CENTURY-based model used here is programmed in MATLAB  
1075 language. The source code is available online  
1076 ([https://github.com/hchzhang/CENYUTY\\_CUE/tree/v1.0](https://github.com/hchzhang/CENYUTY_CUE/tree/v1.0), DOI:  
1077 10.5281/zenodo.1307384). All the data used in this study can be obtained from  
1078 published literatures. Specific references of these data can be found in section 2.5.  
1079

1080 **Competing interests**

1081 The authors declare that they have no conflict of interest.  
1082

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1087 Formas (grant 2015-468).  
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**Table 1** Optimized parameter values for the five versions of the litter decomposition

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model used in this study.  $cue_{fit}$  is the optimized value of CUE,  $m_1$  and  $n_1$  are the

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coefficients in Eq. (3),  $m_2$  is the coefficients in Eq. (5), and  $m_3$  is the coefficient in Eq.

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(6). Values in brackets following each parameter are the means ( $\pm$  standard deviations)

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of the fitted parameter values based on “leave-one-out” cross-validation (see Section

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2.5 for more details).

following each parameter is the mean

( $\pm$ standard deviation)

<u>Version</u>	<u>CUE</u>	<u><math>f(N_{min})</math></u>	<u>Parameters</u>
<u>M0</u>	<u>Fixed</u>	<u>1</u>	<u><math>cue_{fit}</math> (0.57<math>\pm</math>0.004)</u>
<u>M1</u>	<u>Eqs.(2), (3)</u>	<u>Eq. (5)</u>	<u><math>m_1</math> (0.61<math>\pm</math>0.34), <math>n_1</math> (0.53<math>\pm</math>0.21), <math>m_2</math> (297.4<math>\pm</math>38.0)</u>
<u>M2</u>	<u>Eqs.(2), (3)</u>	<u>1</u>	<u><math>m_1</math> (0.11<math>\pm</math>0.01), <math>n_1</math> (1.96<math>\pm</math>0.13)</u>
<u>M3</u>	<u>Fixed</u>	<u>Eq. (5)</u>	<u><math>cue_{fit}</math> (0.54<math>\pm</math>0.01), <math>m_2</math> (396.9<math>\pm</math>23.6)</u>
<u>M4</u>	<u>Eqs.(2), (3)</u>	<u>Eq. (6)</u>	<u><math>m_1</math> (0.13<math>\pm</math>0.07), <math>n_1</math> (1.91<math>\pm</math>0.37), <math>m_3</math> (0.58<math>\pm</math>0.12)</u>

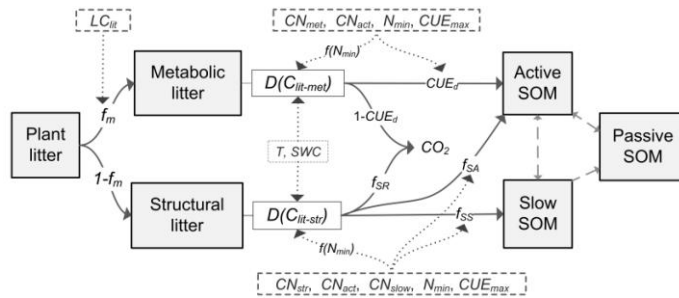
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Model version ...



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1429 **Figure 1** Schematic diagram of the C flows in the litter decay model used in this study.

1430  $f_m$  is the fraction of metabolic compounds in plant litter.  $D(C_{lit-met})$  and  $D(C_{lit-str})$  are  
 1431 the decomposition rates ( $\text{g C kg}^{-1} \text{ day}^{-1}$ ) of metabolic or structural litter, respectively.

1432  $LC_{lit}$  is the lignin:C ratio (on a mass basis) of plant litter;  $CN_{mets}$ ,  $CN_{str}$ ,  $CN_{act}$ , and  
 1433  $CN_{slow}$  are the C:N ratio of metabolic litter pool, structural litter pool, active SOM  
 1434 pool and slow SOM pool, respectively;  $N_{min}$  is the concentration of mineral N in

1435 solution ( $\text{g N kg}^{-1} \text{ soil}$ );  $f(N_{min})$  is a factor reducing litter decay rate when soil mineral  
 1436 N availability is limiting;  $T$  ( $^{\circ}\text{C}$ ) and  $SWC$  (%) are temperature and soil water content,

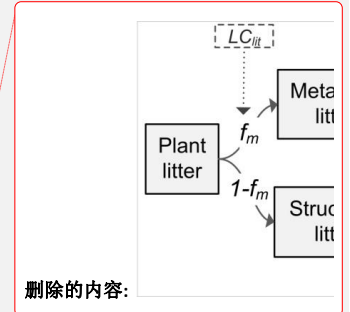
1437 respectively;  $CUE_d$  is C use efficiency of the transformation from litter to soil organic  
 1438 matter (SOM);  $CUE_{max}=0.8$  is the maximum microbial CUE (dimensionless) when

1439 growth is limited by C from the organic substrate;  $f_{SA}$ ,  $f_{SS}$  and  $f_{SR}$  are the fractions of  
 1440 decomposed structural litter-C that is transferred to active SOM pool, slow SOM pool  
 1441 and released to atmosphere in forms of  $\text{CO}_2$ , respectively. As in the algorithms in

1442 CENTURY model (Parton *et al.*, 1988), here  $f_{SA} = CUE_{d\_SA} \times (1 - f_{lig})$ ,  $f_{SS} = CUE_{d\_SS} \times f_{lig}$ ,

1443  $f_{SR} = 1 - (f_{SA} + f_{SS})$ , where  $f_{lig}$  is the lignin fraction (0–1, dimensionless) in the structural  
 1444 litter pool, and  $CUE_{d\_SA}$  and  $CUE_{d\_SS}$  are the CUE of C transformation from structural  
 1445 litter pool to active and slow SOM pool, respectively.

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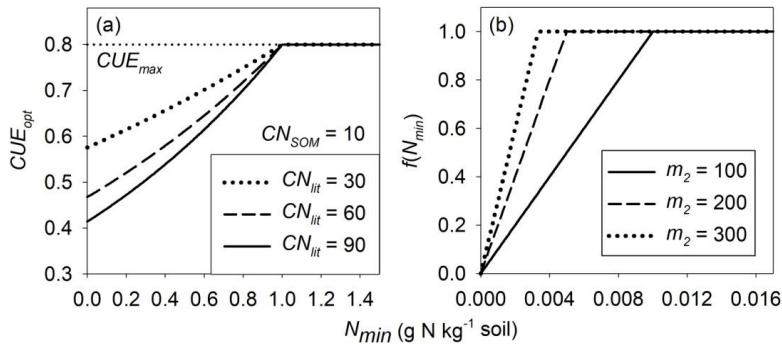
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1457 **Figure 2.** Schematic plot of (a) the optimal carbon use efficiency ( $CUE_{opt}$ ) as a  
 1458 function of soil mineral nitrogen for different litter C:N ratios (from Eq. (2) in the  
 1459 main text with  $m_l = 0.3$ ,  $n_l = 1.0$ ) and (b) the N limitation function  $f(N_{min})$  applied to  
 1460 litter decomposition rates (from Eq. (5) in the main text).  $CN_{lit}$  and  $CN_{SOM}$  are the C:N  
 1461 ratios of the litter and SOM pools, respectively.  $CUE_{max} = 0.8$  is the maximum  $CUE$   
 1462 under optimal nutrient condition (C limitation only).  $m_l$  and  $n_l$  are the parameters of  
 1463 Eq. (3) and  $m_2$  is the parameter of Eq. (5).

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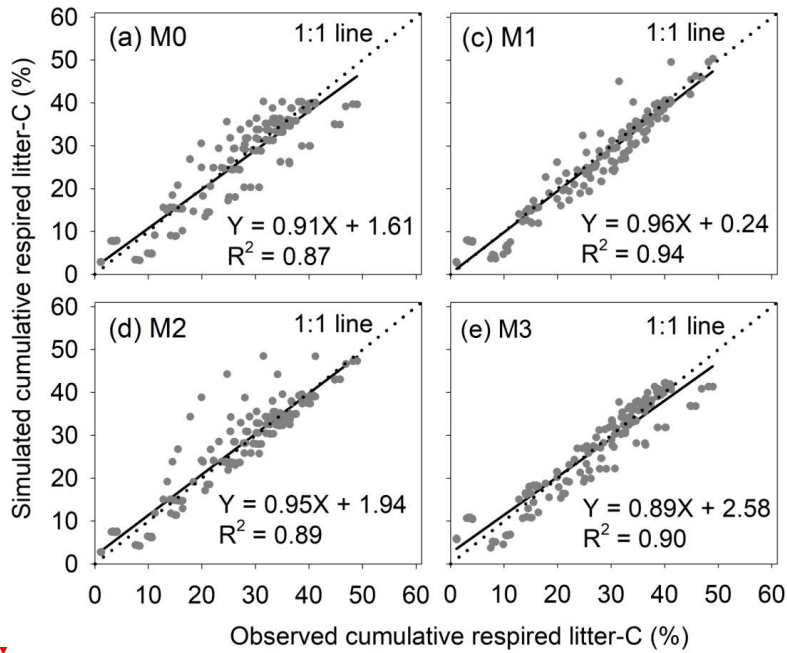
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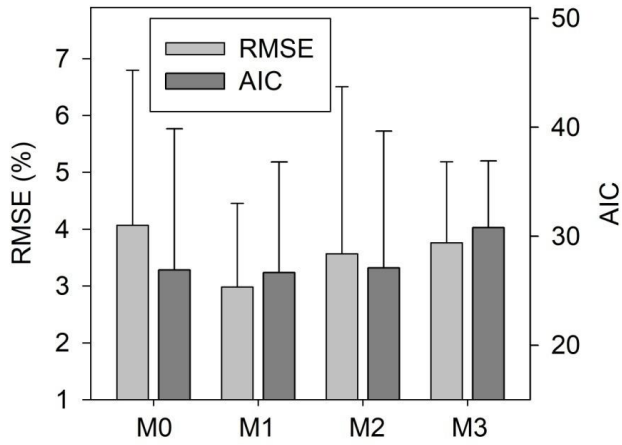
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1469 **Figure 3** Comparison of the predicted cumulative respired litter-C to observed values  
 1470 at different times during litter decomposition process. Each dot denotes an  
 1471 observation of cumulative respired litter-C at a certain day. **In total**, there are 149  
 1472 points. M0-M3 are the four versions of litter decay model tested in this study (Table  
 1473 1).

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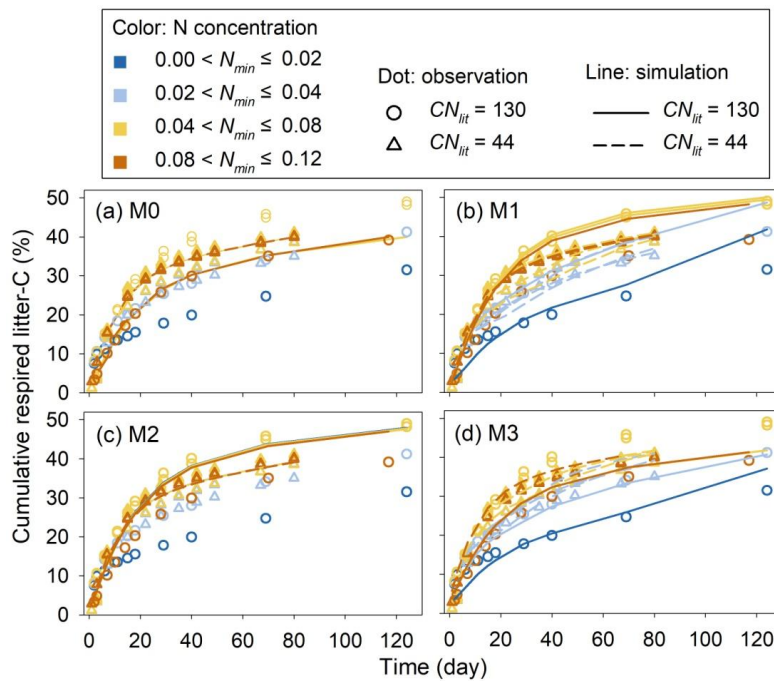
1478 **Figure 4** The RMSE and AIC of the simulated cumulative respired litter-C from the  
 1479 four versions of litter decay model used in this study. Error bars denote the standard  
 1480 deviation of RMSE or AIC for different incubation experiments. M0-M3 denote the  
 1481 four models tested in this study (Table 1).

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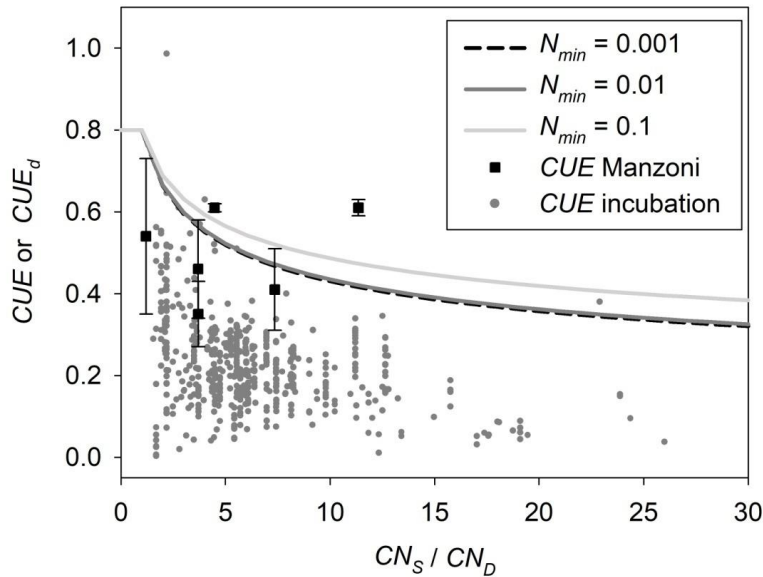


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1486 **Figure 5** Time series of the simulated (lines) and observed (dots) cumulative respired  
 1487 litter-C (% of initial litter-C) at four different levels of soil mineral N availability ( $N_{min}$ ,  
 1488 g N kg<sup>-1</sup> soil).  $CN_{lit}$  is the C:N ratio of plant litter. M0-M3 denote the four models  
 1489 tested in this study (Table 1). Here the simulation results of each model were  
 1490 calculated with parameters optimized based on all of the 14 samples of incubation  
 1491 experiments (Table A2).

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1495 **Figure 6** Comparison of  $CUE_d$  (lines) predicted by Eq. (2) with parameter values ( $m_2$

1496  $= 0.54$ ,  $n_l = 0.50$ ) calibrated based on the incubation experiments (Table A2) of

1497 Recous *et al.* (1995) and Guenet *et al.* (2010) to observed  $CUE$  of terrestrial

1498 microorganisms along a gradient of  $CN_S/CN_D$ . For observed  $CUE$  (dots),  $CN_D$  and

1499  $CN_S$  are the C:N ratio of decomposers and their substrates, respectively. For simulated

1500  $CUE$  (lines),  $CN_S$  and  $CN_D$  correspond to the C:N ratio of donor (litter pool) and

1501 acceptor (the active SOM pool of the CENTURY), respectively. Gray dots are the

1502 estimated microbial  $CUE$  of litter decomposition in natural terrestrial ecosystems

1503 from Manzoni *et al.* (2017). Black squares are the microbial  $CUE$  measured via

1504 laboratory incubation experiments of Gilmour and Gilmour, (1985), Devêre and

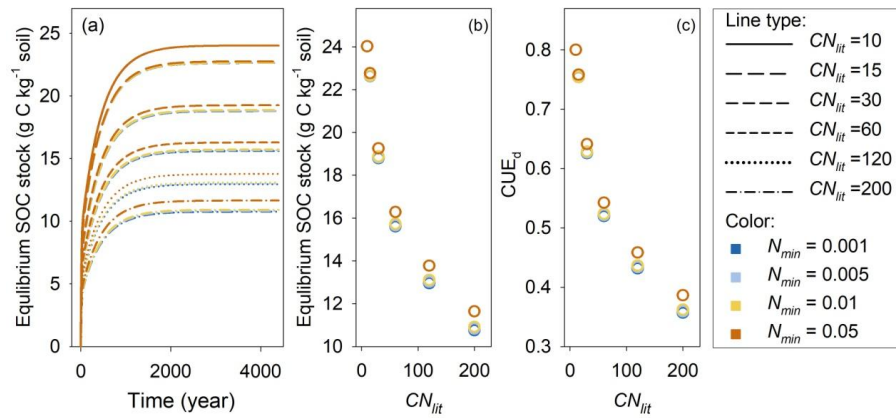
1505 Horváth (2000) and Thiet *et al.* (2006). Error bars represent the standard deviations.

1506  $N_{min}$  ( $\text{g N kg}^{-1}$  soil) is the concentration of soil mineral N.

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删除的内容: , where  $CN_D$  and  $CN_S$  are the C:N ratio of decomposers and their substrates, respectively.





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1512 **Figure 7** (a) Accumulation of soil organic carbon (SOC) for constant substrates input

1513 (plant litter) with different C:N ratios ( $CN_{lit}$ ) at different levels of soil mineral N

1514 concentrations ( $N_{min}$ , g N kg<sup>-1</sup> soil), (b) Change trends of equilibrium SOC stock and

1515 carbon use efficiency of decomposed litter ( $CUE_d$ ) with increasing litter C:N ratio.

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1517 **Appendix:**

1518 **Table A1** List of symbols used in this study: stoichiometric ratios are all expressed on  
 1519 a mass basis.

Symbol	Unit	Description
$a$	$\text{g N kg}^{-1}$ soil	Exponent in Eq. (2)
$AIC$	dimensionless	The Akaike Information Criterion(Eq. (10))
$CN_{act}$	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))
$C_{lit}$	$\text{g C kg}^{-1}$ 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
$D(C_{lit-met})$	$\text{g C kg}^{-1}$ soil $\text{day}^{-1}$	Decomposition rate of metabolic litter
$D(C_{lit-str})$	$\text{g C kg}^{-1}$ soil $\text{day}^{-1}$	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
$I_N$	$\text{g kg}^{-1}$ soil	Maximum mineral N immobilization rate (Eq. (1))
$k$	$\text{day}^{-1}$	potential maximum turnover rate (Eqs. (4) and (7))
$LC_{lit}$	dimensionless	Lignin to C ratio of litter input
$m_1$	$\text{kg g}^{-1}$ N	Coefficients in Eq. (3)
$n_1$	$\text{g N kg}^{-1}$ soil	Coefficients in Eq. (3)
$m_2$	$\text{day}^{-1}$	Coefficients in Eq. (5)

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$m_3$	kg g <sup>-1</sup> N	Coefficients in Eq. (6)
$N_{min}$	g N kg <sup>-1</sup> soil	Soil mineral N concentration (Eq. (5))
$RMSE$	%	Root mean square error (Eq. (9))
$SOC$	g C kg <sup>-1</sup> soil	Soil organic carbon
$SOM$	g C kg <sup>-1</sup> soil	Soil organic matter
$U_0$	g C kg <sup>-1</sup> soil day <sup>-1</sup>	C uptake rate when soil mineral N is fully adequate for litter decay (Eqs. (1) and (8))

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1526 **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  
1527 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).  
1528 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  
1529 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  
1530 and  $N_{min}$  were mostly measured on days 2, 3, 6, 11, 15, 18, 29, 40, 69 and 124.

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Sample	$CN_{lit}$	$LC_{lit}$	$CN_{SOM}$	Initial $N_{min}$ (g N kg <sup>-1</sup> 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)	

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1532 **Table A3** List of parameters calibrated for two versions of the litter decomposition  
 1533 model (M0, M1):  $k_{lim}$  and  $k_{lits}$  are respectively the turnover rates of metabolic and  
 1534 structural litter pools,  $m_4$  is the coefficient in Eq. (8),  $cue_{fit}$  is the optimized value of  
 1535 CUE,  $m_1$  and  $n_1$  are the coefficients in Eq. (3), and  $m_2$  is the coefficients in Eq. (5).

<u>Version</u>	<u>CUE</u>	<u><math>f(N_{min})</math></u>	<u>Parameters</u>
<u>M0</u>	<u>Fixed</u>	<u>1</u>	<u><math>cue_{fit}, k_{lim}, k_{lits}, m_4</math></u>
<u>M1</u>	<u>Eqs. (2), (3)</u>	<u>Eq. (5)</u>	<u><math>m_1, n_1, m_2, k_{lim}, k_{lits}, m_4</math></u>

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删除的内容: Table A3 The two version litter decomposition models used in this study to calibrate the turnover rate of metabolic ( $k_{lim}$ ) and structural ( $k_{lits}$ ) litter pool, as well as the coefficient  $m_4$  in Eq. (6).  $cue_{fit}$  is optimized value of CUE.  $m_1$  and  $n_1$  are the coefficients in Eq. (3), and  $m_2$  is the coefficients in Eq. (5)

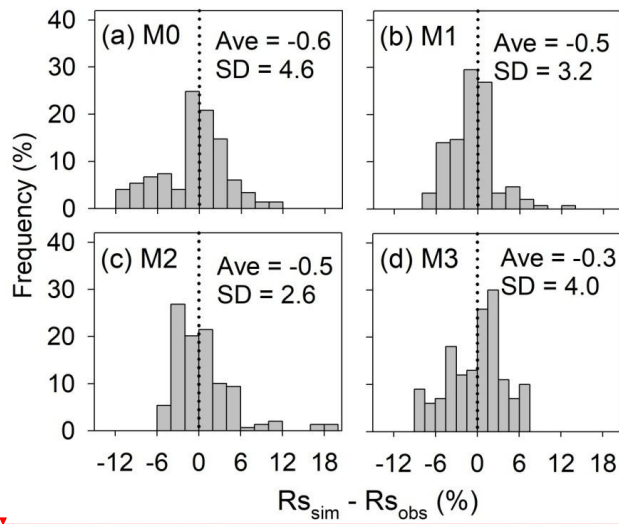
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1547 | **Table A4** Specific setting of litter and SOM properties, and soil conditions in the 16  
1548 idealized simulations for exploring the impacts of litter stoichiometry (i.e. C:N ratio)  
1549 and soil mineral N on SOC accumulation.  $CN_{lit}$  and  $LC_{lit}$  are the C to N ratio and  
1550 lignin to C ratio of plant litter, respectively.  $Lit_{inp}$  ( $\text{g C kg}^{-1} \text{ soil day}^{-1}$ ) is the daily  
1551 input rate of plant litter.  $CN_{SOM}$  is the C to N ratio of SOM pool.  $N_{min}$  ( $\text{g N kg}^{-1} \text{ soil}$ )  
1552 is the concentration of soil mineral N ( $\text{NO}_3^- \text{-N} + \text{NH}_4^+ \text{-N}$ ).  $Tem$  ( $^{\circ}\text{C}$ ) and  $SWC$  (%)  
1553 are the 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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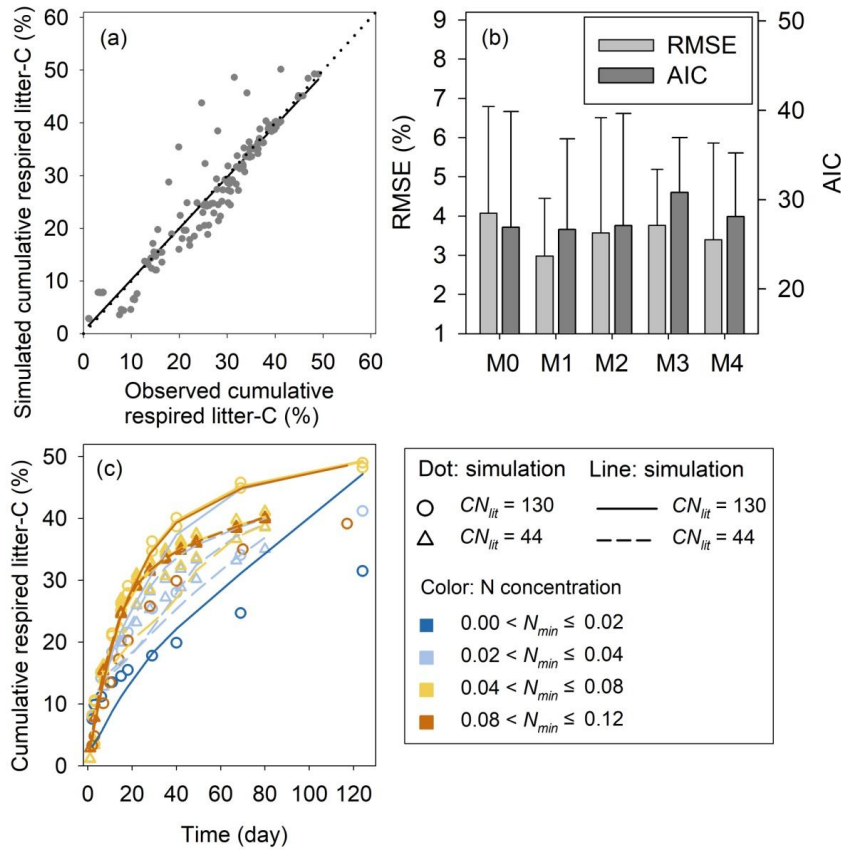


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1557 **Figure A1** Distribution of the difference between the predicted cumulative respired  
 1558 litter-C ( $R_{s_{sim}}$ , %) and the observed values ( $R_{s_{obs}}$ , %) for all experiments and points  
 1559 in time. SD is standard deviation of the biases. M0-M3 denote the four models tested  
 1560 in this study (Table 1).

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**Figure A2** Comparison between simulated cumulative respired litter-C with  $f(N_{min})$

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(inhibition effect of soil mineral N on litter decomposition) calculated by Eq. (6) and

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the observed results from incubation experiments. In figure (c), M0-M4 denote the

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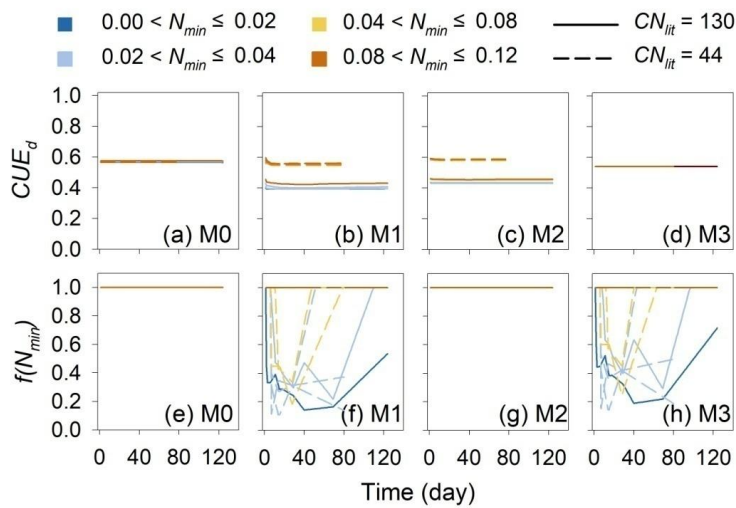
five versions of litter decay model in Table 1. M4 denote the model which used Eq.

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(2) to calculate the dynamic CUE and Eq. (6) to calculate  $f(N_{min})$ .

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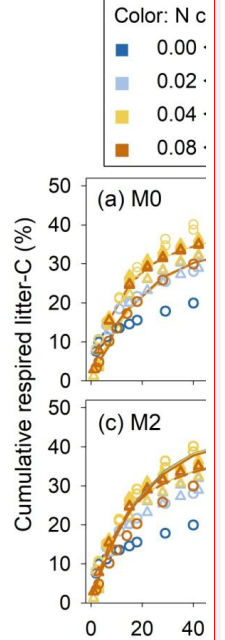




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1572 **Figure A3** Dynamic of the simulated carbon use efficiency ( $CUE$ ) and  $f(N_{min})$  during  
 1573 the incubation experiments (Table A4).  $CN_{lit}$  is the C:N ratio of incubated litter, and  
 1574  $N_{min}$  is the initial soil mineral N concentration ( $\text{g N kg}^{-1}$  soil). M0-M3 are the four  
 1575 models in Table 1. Here the simulation results of each model were calculated with  
 1576 parameters optimized based on all of the 14 samples of incubation experiments  
 1577 (Table A2).

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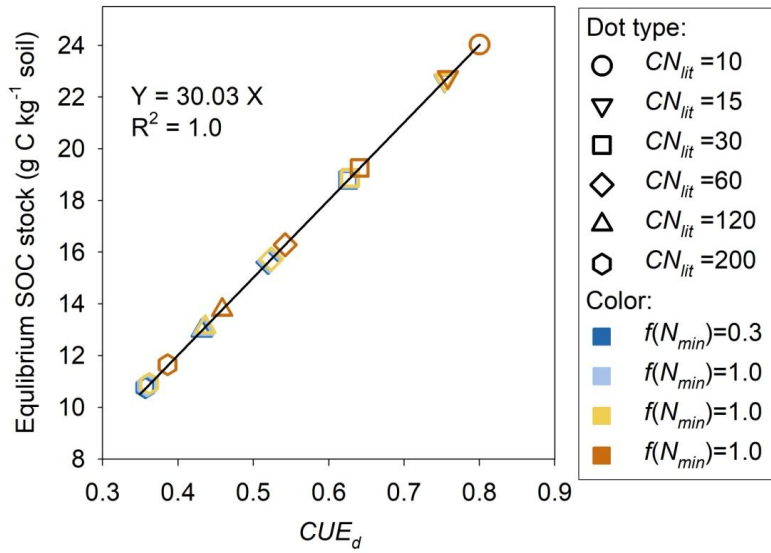
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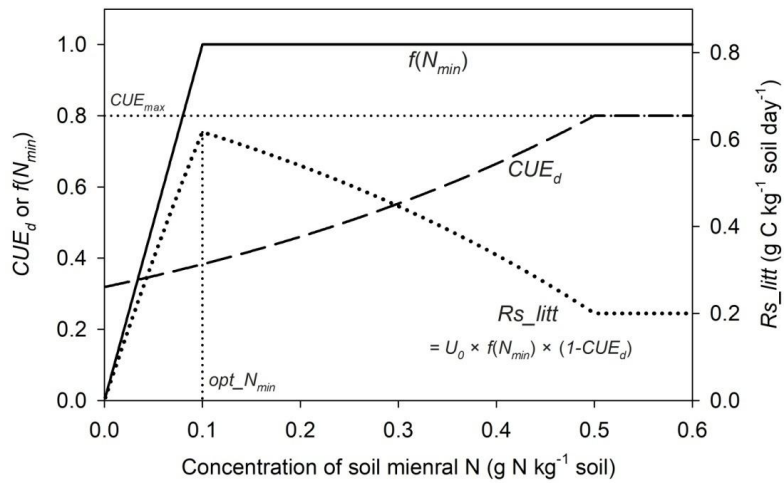


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1585 **Figure A4** Relationship between C stock of the potentially equilibrated SOM pool  
 1586 and the carbon use efficiency of decomposed metabolic litter ( $CUE_d$ ) at the dynamic  
 1587 equilibrium stage.  $f(N_{min})$  denote the inhibition factor (0–1) of soil mineral N on litter  
 1588 decomposition.

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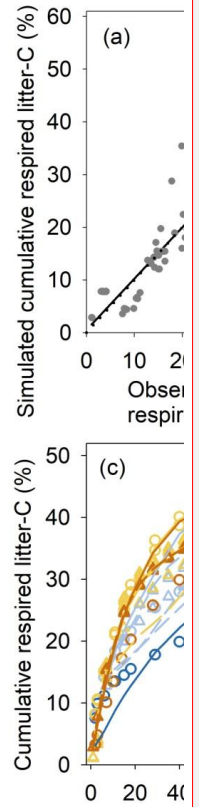
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1592 **Figure A5** Schematic plot for change trends of  $f(N_{min})$  (inhibition effect of mineral N,  
 1593 Eq. (6),  $CUE_d$  (carbon use efficiency of decomposed litter, Eqs. (2), (3)) and  $Rs_{litt}$   
 1594 (litter respiration rate) with increasing concentration of soil mineral N.  $CUE_{max}$  (=   
 1595 0.8) is the maximum CUE set in this study.  $opt\_N_{min}$  denotes the concentration of  
 1596 soil mineral N at which litter respiration is maximized.  $U_0$  is the potential  
 1597 decomposition rate when mineral N is fully adequate for litter decay.

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**Figure A5** Comparison between simulated cumulative respired litter-C with  $f(N_{min})$  (inhibition effect of soil mineral N on litter decomposition) calculated by Eq. 9 and the observed results from incubation experiments. In figure (c), M0-M3 denote the four versions of litter decay model in Table 1. M4 denote the model which used Eq. 2 to calculate the dynamic CUE and used Eq. 6 to calculate  $f(N_{min})$ .

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